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**SELECTION FOR WELFARE AND FEED EFFICIENCY
IN FINNISH BLUE FOX**

DOCTORAL THESIS

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ACADEMIC DISSERTATION

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ABSTRACT

Finland is the world's largest producer of blue fox pelts, and fur animals form the second largest group of production animals in Finland (Profur 2016; SVT 2017). The fur industry has a national breeding value evaluation of blue fox production traits and it is used by one third of fox producers. The primary goals in blue fox breeding are to improve the fertility traits and fur quality of foxes and to produce large pelts, whereas animal health, welfare, conformation traits or feed efficiency are not included in the current breeding value evaluation. The emphasis on production traits has resulted in unfavourable changes in blue fox conformation and health traits. There is an obvious need for revision, if any of the current breeding goals weakens the animals' welfare. In addition to welfare traits, an important new breeding goal would be feed efficiency, given that feeds are a major production cost and their inefficient utilization may lead to poor growth and to nutrients being wasted into the environment.

Improvement of any economically or ethically important trait through animal breeding requires that the trait is heritable and is recorded into a breeding software database. The main objectives of this thesis were to estimate genetic parameters for new conformation, health and production traits for potential introduction into the national blue fox breeding programme, and to determine their correlations to the production traits in the current breeding value evaluation. Phenotypic and genetic evaluation systems for the proposed traits were created in this research project, namely for feed efficiency, body condition score, body length, leg conformation, ability to move about and susceptibility to eye infection.

The study data, consisting of altogether 2076 foxes, are from a two-year experiment carried out during the growth period in 2005 and 2006 at the fur animal research station of MTT Agrifood Research Finland in Kannus (now Kannus Research Farm Luova Ltd). Multiple-trait restricted maximum likelihood (REML) estimation was used, since it enables taking several traits into account at the same time, to calculate the genetic parameters and to determine any antagonistic genetic or phenotypic correlations between conformation, health and production traits.

The heritability estimates for feed efficiency, daily gain and daily intake were moderate (0.23-0.29) (II-IV). The studied conformation and welfare traits were shown to have a genetic background. Moderate heritabilities were found for leg conformation, ability to move about, body condition score (BCS) and susceptibility to eye infection (0.21-0.30) (IV, V). Animal body weight had large genetic variation and moderate to high heritability (0.37-0.50) (II, IV, V). High heritability estimates were obtained for pelt size (0.47-0.50), while the highest estimates were for fox body length (0.51-0.57) (II-V).

Grading size and pelt size, the two size traits in the current breeding value evaluation, had moderately high to high positive genetic correlations with

body weight, daily gain, body length and BCS (fatness) (0.42-0.74) (III). Pelt size and daily gain had moderate to rather high positive genetic correlations with feed efficiency (0.36 and 0.51-0.56, respectively), but all studied size traits had unfavourable positive genetic correlations with feed intake (0.49-0.95) (II-IV). Grading size, October body weight, daily gain and BCS had moderately high unfavourable genetic correlations with leg conformation (-0.40 to -0.53) and high unfavourable genetic correlations with ability to move about (-0.58 to -0.65) (IV). The genetic correlations between the size traits (grading size, BCS, body length and body weight in November) and susceptibility to eye infection did not differ from zero, as the standard errors of these genetic correlations were high (V). However, grading density of fur had an unfavourable genetic correlation with susceptibility to eye infection (-0.49). Body length showed a high positive genetic correlation with grading size and pelt size (0.63-0.87), but its genetic correlations with BCS and susceptibility to eye infection were low and hardly differed from zero (0.04 and -0.18, respectively) (II-V). Genetic correlations between body length and foreleg conformation, and between body length and the animal's ability to move about were negative, although their standard errors were high (-0.38±0.21 and -0.42±0.19) (IV).

While the current, relatively strong emphasis on selection for larger animal and pelt size in blue fox breeding does improve feed efficiency indirectly, it is unlikely to reduce feed intake. Selection for longer pelts tends to favour fast-growing and fat individuals, simultaneously increasing their feed intake and, hence, feeding costs. Fast growth rate and extreme fatness also pose a risk to animal welfare. The results reported in this thesis show that fast growth rate, high body weight, large grading size and BCS (fatness) have unfavourable genetic correlations with leg weakness and impair the ability to move about in the cage in less than six-month-old blue foxes. Although the current emphasis on size traits in the breeding value evaluation does not significantly weaken the foxes' eye health, the focus on thicker fur density can expose them to eye infection due to the antagonistic genetic correlation between the two traits. High BCS (fatness) is also associated with an undesirable reddish fur colour and a lighter pelt colour. The use of animal body length as a selection criterion can open up the possibility to breed well-structured, long, slim foxes instead of fat ones. Selection for longer animal body does not increase the risk of fatness or susceptibility to eye infection nor does it have unfavourable effects on pelt quality traits.

The genetic parameters estimated for conformation, health and feed efficiency traits indicate that these traits are heritable and that genetic improvement through selection has potential to improve the health status and feed efficiency of Finnish blue foxes. The results of this research project can be implemented into the national blue fox breeding scheme taking into account the genetic connections between health and production traits.

Keywords: *Alopex lagopus*, animal breeding, fur animals, heritability

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“More important than to dream is to believe in what you want. It's not worth doing anything you don't believe in. But there is no life without dreams. I reveal my dreams only after they have come true. Then I can say this was yet another fulfilment of my dream.” –Jorma Uotinen

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications:

- I Kempe, R., Koskinen, N., Peura, J., Koivula, M. & Strandén, I. 2009. Body condition scoring method for blue fox (*Alopex lagopus*). *Acta Agriculturae Scandinavica, Section A* 59: 85-92.
- II Kempe, R., Strandén, I., Koivula, M., Rekilä, T., Koskinen, N. & Mäntysaari, E. 2008. Genetic parameters of feed efficiency and its relationships with feed intake, daily gain and animal size traits in Finnish blue fox (*Alopex lagopus*). *Scientifur* 32: 47-52.
- III Kempe, R., Koskinen, N. & Strandén, I. 2013. Genetic parameters of pelt character feed efficiency and size traits in Finnish blue fox (*Vulpes lagopus*). *Journal of Animal Breeding and Genetics* 130: 445-455.
- IV Kempe, R., Koskinen, N., Mäntysaari, E. & Strandén, I. 2010. The genetics of body condition and leg weakness in the blue fox (*Alopex lagopus*). *Acta Agriculturae Scandinavica, Section A* 60: 141-150.
- V Kempe, R. & Strandén, I. 2015. Breeding for better eye health in Finnish blue fox (*Vulpes lagopus*). *Journal of Animal Breeding and Genetics* 133: 51-58.

The publications are referred to in the text by their Roman numerals.

Contribution of the author to papers I to V:

The author participated in preparing the data for statistical analysis, conducted the statistical analysis, participated in interpreting the results and was the main writer of papers I, II, III, IV and V.

ABBREVIATIONS

BCS	body condition score of animal
BLUP	best linear unbiased prediction
BW	body weight
DG	individual daily gain (g/d)
DM	dry matter
DMI	daily dry matter intake
EBV	estimated breeding value
EYE	susceptibility to eye infection
FE	feed efficiency
FENP	fur animal epidemic necrotic pyoderma
gSI	live animal grading size
gGC	grading guard hair coverage
gDE	grading fur density
gCL	grading colour clarity
LEG	foreleg conformation
MOVE	ability to move about
pCL	pelt colour clarity
pDA	pelt colour darkness
pDE	pelt density
pGC	pelt guard hair coverage
pQU	pelt quality
pSI	pelt size

Introduction

1 INTRODUCTION

1.1 BLUE FOX PRODUCTION IN FINLAND

Blue foxes are farmed for their fur, which is used in the fashion and clothing industry. Pelts are sold at fur auctions where their mean prices vary yearly depending on fashion trends, the world economy and weather conditions (Peura 2013). The fur industry is not among those livestock production systems which receive government subsidies (Peura 2013). Making long-term breeding decisions in today's uncertain business environment with fierce competition is challenging and demands flexibility and adaptiveness from fur farms. Efficiency and good planning form the foundation for profitable production, and animal breeding is one of the cornerstones of this foundation. Breeding selection which has emphasized large pelt size and good fur quality has proved quite successful. On the other hand, these traits are also known to have unfavourable genetic and phenotypic correlations with animal fertility, leg conformation and health traits (Rekilä et al. 2000; Keski-Nisula 2006; Koivula et al. 2009). An ideal breeding scheme would, thus, not only be targeted to improve economic productivity, but animal welfare as well.

1.1.1 BREEDING ORGANIZATION

The central organization for genetic improvement and breeding of fur animals in Finland is the auction house Saga Furs Oyj. The majority owner of the auction house is the Finnish Fur Breeders' Association, which has primary responsibility for advising fur producers on breeding issues and the most important breeding goals. Saga Furs provides the technical infrastructure necessary for fur animal breeding and collection of information on the animals' performance and pedigree.

Research and development of breeding programme, and breeding value estimation, is based on farm data, which are collected and stored into the centralized national database of Saga Furs. Each blue fox gets a unique identification number at birth, which links it to the national pedigree through its known parents. All of the animal's measurement data are entered into the national database under its individual identification number. A barcode ticket with the animal's identification number follows it from the farm to the auction house, and is fastened to the skin before being sent to the auction house. The identification number also allows producers to follow the price of the skin at the auction. This individual skin follow-up system is unique to foxes and not used in other fur animals.

Data collection forms one of the biggest challenges in fox breeding, which requires resources from fur producers and the central breeding organization,

as well as good cooperation between fur producers, organization and research. Digitalization and the creation of the fur animal breeding software WebSampo (launched in 2013 by Saga Furs Oyj), together with modern data collection applications (personal digital assistant PDA and WebSampoApp), have opened up new possibilities to collect information on blue foxes and their selection traits in a resource-efficient way.

The most advanced methods, models and innovations of animal breeding research can be put into practice through the WebSampo system. Further, the system produces useful statistics for fur producers, assisting them in mating decisions, and also stores and maintains the collected pedigree information. In 2016, WebSampo was used by one third (211) of Finnish fox farms. Nationwide genetic evaluation will become increasingly efficient as more farms start using the system. Therefore, raising the number of farms taking part in the national breeding programme through WebSampo offers a good opportunity to improve the efficiency of fur animal breeding in Finland.

1.1.2 BREEDING VALUE ESTIMATION

Selection of blue fox breeding animals is based on the estimated breeding value (EBV) of their grading, pelt character and fertility traits (Peura et al. 2004, 2005). EBV indicates the value of the animal with respect to the targeted breeding goals: animals with highest EBV will improve the breeding goal traits, whereas animals with lowest EBV will have an unfavourable effect.

In the early 1990s, the Finnish fur industry established the first BLUP (best linear unbiased prediction) evaluation schemes for animal fertility and fur grading traits (Saarenmaa 1990, Kenttämies & Smeds 1992a, 1992b). The BLUP method is based on a linear mixed effects model and gives the most reliable prediction of an animal's potential to produce offspring that fulfil the requirements of the breeding scheme, including economic and animal welfare aspects. EBVs used to be calculated within-farm using single-trait animal models, without taking into account genetic correlations between different traits. Fur producers selected their breeding animals from a ranking list which was based on EBVs of litter size and grading traits, or litter size and pelt character traits, or simply litter size. The Finnish Fur Breeders' Association gave recommendations on how to weight these traits, but producers could also use their own weighting.

The main limitation of within-farm evaluation was that EBVs were not comparable between farms. Further, the limited computing capacity of individual farms and the smaller amount of generated data compared to national evaluation made it necessary to use single-trait models where genetic correlations could not be considered. Breeding animals with unknown parents represented a common problem. When an animal was moved to another farm it was given a new identification code, which led to its parent information being lost. Thus, the performance information of a

potentially good breeding animal would not be included in the evaluation because its parents were unknown. An advantage of within-farm evaluation was its flexibility: breeding value evaluation could be done at any time of the year.

National evaluation, however, has several advantages. First of all, EBVs are comparable between farms, so it is easier to find the best, healthy breeding individuals at the national level. The requirements for reliable and accurate national breeding value evaluation are a large common database with pedigree and performance information and high computing capacity. This kind of comprehensive pedigree with good genetic links between animals across farms is generated through animal trade; 98% of Finnish fur farms are today connected through this pedigree (Kempe & Strandén 2018). The existing large computing capacity together with a national database will make it possible to improve the statistical models used in breeding value evaluation of Finnish blue foxes. Single-trait models can be replaced by multiple-trait models where genetic correlations and environmental factors are taken into account and several traits are estimated simultaneously. This is especially important because certain production traits may have direct or indirect antagonistic genetic correlations with conformation and health traits or with other production traits. The use of multiple-trait models will also improve the accuracy of EBVs, particularly in the case of traits with low heritability, such as animal fertility and health.

Within-farm breeding value evaluation of Finnish blue foxes was replaced by national evaluation at the beginning of 2015 (Kempe & Strandén 2016; Peura et al. 2016b). National evaluation is expected to reach its full potential within the next few years, depending on how extensively fur producers adopt the new selection system and how quickly the isolated but active farms are connected to the other farms.

1.2 PRODUCTION TRAITS IN THE BREEDING VALUE EVALUATION

There are two parallel fur quality evaluation systems currently in use in Finland (Peura et al. 2005). Live animal grading is performed on the commercial farm by the producer and utilized for indirect selection for pelt character traits (pelt size, colour darkness, colour clarity and overall quality). These pelt traits are evaluated by professional fur graders from dried skins at the auction house. In general, the heritabilities obtained for live animal grading and pelt character traits have varied considerably: from low to high (Table 1). Genetic correlations between grading and pelt traits are high in most cases, and so selection for pelt character traits using grading traits is relatively effective (Peura et al. 2005). The advantage of live animal grading is that these phenotypic records are available at the time breeding animals

Table 1. Estimated heritabilities (h^2) for traits currently included in the Finnish blue fox national breeding value evaluation.

Live animal grading traits	h^2	Pelt character traits	h^2	Fertility traits	h^2
Animal size	0.16-0.27	Pelt size	0.29-0.36	1 st litter size	0.10-0.12
Colour darkness	0.51-0.65	Colour darkness	0.52-0.55	2 nd litter size	0.06-0.18
Colour clarity	0.10-0.23	Colour clarity	0.12-0.16	3 rd litter size	0.17
Overall fur quality	0.11-0.22	Pelt quality	0.22-0.23	Pregnancy rate	0.03-0.05
Fur density	0.15-0.28			Whelping success	0.05
Guard hair coverage	0.19-0.24				

Source: Peura et al. 2004, 2005, 2007; Koivula et al. 2009; Peura 2013; Kempe & Strandén 2016.

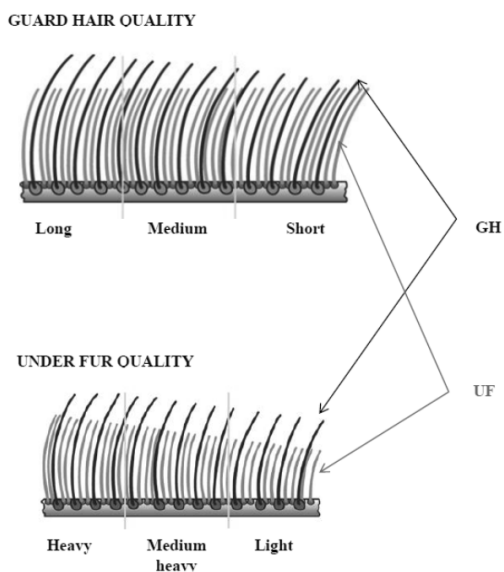


Figure 1. The primary goals of fur quality improvement in blue foxes are high underfur density (UF), thick and strong guard hair (GH) and optimal ratio between underfur and guard hair. Source: Saga Furs Oyj.

are being selected, whereas pelt character records are obtained at a later stage from animals that are no longer alive (Peura et al. 2005).

1.2.1 GRADING TRAITS

The new multiple-trait animal model of grading traits used in national breeding value evaluation of blue foxes comprises six traits: grading size, fur density, colour darkness, guard hair coverage, colour clarity and overall pelt quality. Grading traits are recorded on a scale of 1 to 5. Animal grading size is determined by subjective grading and scored from smallest (1) to largest (5). According to Kenttämies & Smeds (1992b) grading of body size is fairly easy (repeatability is 0.60-0.69) and previous knowledge on the animal increases the reliability of grading assessment. The most important fur quality traits in live animal grading are fur density (gDE) and guard hair coverage (gGC) (V). Fur density is assessed by palpation and graded into five categories according to underfur thickness or density, with 5 as the most desirable score corresponding to thickest fur. Scoring of gGC is based on guard hair length, evenness and coverage. Animals classified into the preferred higher gGC categories also have more guard hair than the lower categories. Individual quality traits are easier to evaluate than overall fur quality (Kenttämies & Smeds 1992b). Fur colour clarity (gCL) is the most difficult trait to evaluate in farm conditions because it is sensitive to various environmental factors, such as cleanness of fur, light conditions and the grader's skill (Kenttämies & Smeds 1992b, Peura et al. 2005). Clarity is graded from reddish (1) to bluish (5), with bluish colour clarity as the most valuable. Colour darkness is relatively easy to evaluate on a scale from whitest (1) to darkest (5) (Kenttämies & Smeds 1992b). The lightest colours are favoured in selection.

1.2.2 PELT TRAITS

Pelt character evaluation, which is done by professional fur graders from dried skins, is more accurate and reliable than grading of live animals (Kenttämies & Smeds 1992a, 1992b). The multiple-trait model of pelt character traits used in national breeding value evaluation includes four traits: pelt size, colour darkness, colour clarity and fur quality (Table 1). Breeding selection has primarily emphasized pelt size because of its major impact on pelt auction prices (Rekilä et al. 2000; Peura et al. 2004).

Pelt length, colour darkness and colour clarity are measured with an automatic grading machine, which sorts the pelts into different categories. Unfortunately, however, these precise grading machine measurements of pelt size (cm) and colour (pixels) are not stored into a database; instead, categorical pelt character traits are used for breeding value estimation (Table 2) (III). In addition to machine measurement, the following pelt quality traits are evaluated subjectively by fur graders: guard hair coverage, underfur density and overall pelt quality. In the study of Kenttämies & Smeds (1992a)

Table 2. Categories of pelt character traits in the Finnish blue fox breeding value evaluation¹ and the Finnish Fur Sales auction house sorting system. (III)

Category ¹	Corresponding classes in the auction house grading system					
	pSI, cm	pDA, pix	pCL, pix	pGC	pDE	pQU
1	<106.1 (0-4) ²	≥412,1 X-pale-white	≤ 7.29 OC- (1-2)	0-2 Samson 3	-	-
2	106.1- 115.0 (20)	376,1-412,0 Pale	7.30-8.29 OC (3-4)	3-5 Woolly 2	0-2	1-2 II
3	115.1- 124.0 (30)	338,1-376,0 Medium	8.30-8.89 R- (5-6)	6-7 Woolly 1	3-5	3-5 IA – IB
4	124.1- 133.0 (40)	298,1-338,0 Dark	8.90-9.99 R (7-8)	8-9 Normal	6-8	6-8 Saga
5	133.1- 142.0 (50) >142.0 (60)	≤298,0 X-dark-black	≥ 10.00 R+ (9-10)	10 Short	9-10	9-10 Saga Royal

pSI=pelt size (cm) and ²corresponding class; pDA=pelt darkness measured in pixels (colour scale from lightest XXXXpale to darkest black); pCL=pelt colour clarity measured in pixels (from OC- off colour or reddish to R+ corresponding to clarity of blue colour); pGC=pelt guard hair coverage (woolly guard hair is shorter than underwool either on part of the skin or almost the whole skin, e.g., Samson); pDE=underfur density; pQU=overall pelt quality (Saga Royal is the best and II the poorest quality).

the repeatability of overall quality assessment was high, 0.74 on average, and the repeatability obtained for grading by various professional fur graders 0.78-0.80. Fur quality improvement is mainly aimed at high underfur density, thick and strong guard hair, and optimal ratio between underfur and guard hair (Figure 1) (V).

1.2.3 FERTILITY TRAITS

Animal fertility is a complex trait which can be measured in various ways (Koivula et al. 2009). Three fertility traits are currently considered in breeding value estimation of Finnish blue foxes: pregnancy rate, whelping success and litter size (Koivula et al. 2009). Two separate indices are used in the national evaluation of fertility traits: FERT₁ and FERT₂. FERT₁ is the litter size index, with five traits: 1st, 2nd and 3rd litter size, and two correlated traits: grading size and quality (Kempe & Strandén 2018). The

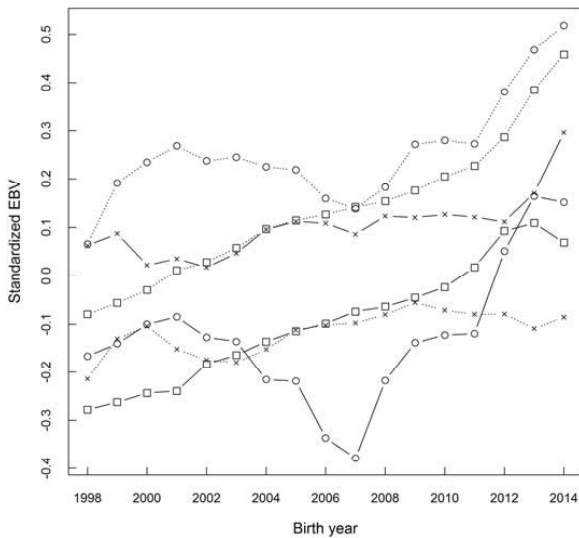


Figure 2. Average standardized estimated breeding value (EBV) by birth year for combined litter size FERT1 (open circles), pregnancy rate and whelping success FERT2 (open squares) and grading size (x symbol) by sex. Breeding females are in dotted lines and breeding males are in solid lines. EBVs were standardized by dividing by the genetic standard deviation (Kempe & Strandén 2018).

heritability estimates for first and subsequent litter sizes (recorded at the age of about 10 to 21 days) are reported to vary from 0.06 to 0.18 (Table 1) (Peura et al. 2004, 2007; Koivula et al. 2009; Kempe & Strandén 2016, 2018). The FERT-2 - index describes the mating and whelping success of young females, and also contains five traits: pregnancy rate, whelping success and three correlated traits: 1st litter size, grading size and quality (Kempe & Strandén 2018). Mating and whelping success are binary (1/0) traits, the value zero representing a situation where the female was barren or aborted or lost all her pups in her first breeding season. The heritability estimates for pregnancy rate and whelping success on the observed binary scale have been between 0.03 and 0.05 (Koivula et al. 2009; Kempe & Strandén 2016, 2018).

Fertility traits are known to be genetically correlated with grading and pelt character traits. Several studies have shown that an animal's large grading size has an unfavourable impact on its fertility traits (Sanson & Ahlstøm 2005; Peura et al. 2004, 2007; Koskinen et al. 2008; Koivula et al. 2009). The fertility traits in Finnish blue foxes weakened significantly during the years 1988-2001 when the focus in selection was almost exclusively on larger animal grading size (Koivula et al. 2009). Figure 2 illustrates the latest genetic trends of standardized breeding value estimates of breeding animals

for FERT1, FERT2 and the grading size in the current national breeding value evaluation of Finnish blue fox (Kempe & Strandén 2018). FERT2 shows improvement from 1998 to 2014, and FERT1 has had a positive genetic trend since 2007, whereas the grading size of breeding animals has remained about the same without change during the study period, reflecting the given breeding recommendations.

1.3 NEW TRAITS FOR THE BREEDING PROGRAMME

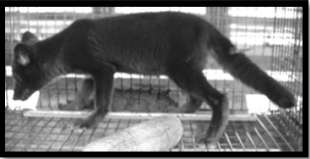




1.3.1 BODY CONDITION SCORE AND FATNESS

Today, most blue foxes are large and fat at pelting time, and there is an increasing risk of the chronic progressive disease of obesity. Obesity is a result of multiple environmental and genetic factors. It is defined as an accumulation of excessive amounts of adipose tissue in the body, either because of excessive dietary intake or low energy utilization, which causes a state of positive energy balance (Zoran 2010). In dogs, several criteria have been established for what constitutes overweight and what constitutes obesity. Obesity can have various detrimental effects on health and longevity. It may cause orthopaedic disease, diabetes mellitus, abnormalities in circulating lipid profiles, cardiorespiratory disease, urinary disorders, reproductive disorders, neoplasia, dermatological diseases and anaesthetic complications in dogs (Zoran 2010). Rekilä et al. (2000) were the first ones who paid attention to blue fox's overweight and obesity, yet the published research on diseases and welfare problems, which relate to fatness, is still sparse in blue fox.

The fact that fur prices continue to be mainly determined by pelt size encourages the breeding of large, extremely fat animals. However, the results of genetic studies and feeding experiments both indicate that large, fat animals are more likely to face fertility problems (Koskinen et al. 2007, 2008; Koivula et al. 2009). Extreme fatness is known to be detrimental especially for young vixens, affecting their pregnancy rate, litter size and early neonatal pup mortality. Fatness also influences the animals' grading size and pelt size, both of which have an antagonistic genetic correlation with fertility traits (Peura et al. 2004, 2007).

Peura et al. (2007) were the first to suggest that fatness should be taken into account in blue fox breeding value evaluation. The authors based their suggestion on two factors: firstly, it was suspected that fat animals were graded higher than average for live animal size, which could lower the accuracy of EBVs, and secondly, fat animals also tended to receive high EBVs for pelt size. Thus, the current breeding goals, particularly selection for larger animal and pelt size, may indirectly increase fatness in foxes and simultaneously raise the feeding costs per pelt.

Table 3. Description of body condition score (BCS) categories for blue foxes using a five-point scale. (I) Photos: Nita Koskinen, MTT Agrifood Research Finland.

Score	Description
<p>1 Very thin</p> 	<p>Animal's general appearance: pinched and bony. Decreased muscle mass. Ribs, shoulder and pelvic bones easily felt. No palpable fat. Abdomen tucked up when viewed from the side.</p>
<p>2 Thin</p> 	<p>Animal's general appearance: slim. Ribs, shoulder and pelvic bones easily felt under a thin fat layer. Abdomen tucked up when viewed from the side.</p>
<p>3 Ideal</p> 	<p>Animal's general appearance: balanced and normal. Ribs, shoulder and pelvic bones felt through a distinctive fat layer. Straight abdominal line.</p>
<p>4 Heavy</p> 	<p>Animal's general appearance: fat. Ribs felt with difficulty. Heavy fat cover in shoulder and pelvic areas. Waist and abdominal area distended because of fat pad.</p>
<p>5 Extremely fat</p> 	<p>Animal's general appearance: extremely fat, massive and round. Massive fat deposits over ribs, shoulders and pelvic area. Noticeable abdominal distension. Fat deposits on face and limbs.</p>

The genetic trend for grading size has at least temporarily levelled down, except for a recent minor increased tendency in males (Figure 2), whereas the animals' phenotypic size has continued to grow (Koivula et al. 2009; Kempe & Strandén 2018). This would suggest that size growth is mainly attributable to increased fatness. Production blue foxes are on unrestricted feeding during the growth period and, as a result of their excessive dietary intake of energy, they tend to be extremely fat or obese at pelting time (Rekilä et al. 2000). Feeding experiments have shown that obese breeding animals need to lose a considerable amount of weight before the mating season, and that the slimming process can lead to problems like weakened fertility, smaller litter size, loose skin and metabolic disorders, such as fatty liver syndrome (Korhonen et al. 2005; Koskinen & Lassen 2006; Koskinen et al. 2007; Koskinen et al. 2008). Therefore, selection of new breeding animals is recommended to be done at weaning, after which the breeding animals are grown on a restricted feeding regime and in lower body condition than production animals (Moisander-Jylhä 2017).

The clinical methods used for fatness evaluation include assigning a body condition score (BCS) to the animals (e.g., Laflamme 1997; Hansen et al. 2009). Body condition scoring is a subjective method by which the thickness of subcutaneous fat is assessed through visual observation and palpation. It gives an estimate for subcutaneous fat thickness and degree of fatness independent of the animal's body weight or size. BCS has been shown to be a reliable measure of the level of fatness in mink, dogs, horses and cattle, and it is incorporated as an animal-based measure into the welfare assessment protocols for mink and dogs, for example (Henneke et al. 1983; Edmonson et al. 1989; Ferguson et al. 1994; Laflamme 1997; Rouvinen-Watt et al. 2005; Hansen et al. 2009; Mononen et al. 2012). Studies in dairy cattle and ewes indicate that BCS is a heritable trait, like fatness in pigs (Koenen et al. 2001; Berry et al. 2003; Banos et al. 2006; Everett-Hincks & Cullen 2009). Pig breeders have a long tradition of selecting against fatness, and pig breeding programmes include several fatness traits (Switonski et al. 2010).

Because there was no consistent basis for the evaluation of blue fox body condition prior to this research, we developed a BCS system for the Finnish blue fox (Table 3) (I). It was also necessary to conduct genetic studies on BCS and its correlation to welfare and production traits, before BCS could be implemented into blue fox breeding and/or welfare programmes.

1.3.2 LEG CONFORMATION AND ABILITY TO MOVE

Leg conformation and ability to move about play an important role in animal wellbeing. Foxes living in wire mesh cages should be able to stand normally, move about actively and be able to jump up and down from the shelf which serves as cage enrichment. The animal's ability to move about may be impaired due to pain, conformation problems or fatness. A fox with severe



Figure 3. Evaluation scale (1=worst, 5=best) of the carpal joint angle as an indicator of foreleg conformation in the blue fox. (IV) Photos: Minna Rintamäki, MTT Agrifood Research Finland.

health problems (injury, paralysis) may be unable to move even if disturbed, and become practically immobile.

Rekilä et al. (2001) and Korhonen et al. (2001) published the first studies on leg weakness, such as carpal laxity, in blue foxes (Figure 3). Similar flexural leg distortions have been reported in dogs, foals and farm animals (e.g., Vaughan 1992; Love et al. 2006; Çetinkaya et al. 2007). Further, it has been suggested that these flexural leg deformities may be hereditary in blue foxes and dogs (Vaughan, 1992; Rekilä et al. 2001; Keski-Nisula 2006). Rekilä et al. (2001) emphasized the need to investigate the genetic background of leg weakness and the possibility to improve leg conformation by means of animal breeding. If the genetic measures of leg weakness were available, they could be used in a BLUP index. However, a BLUP index cannot be constructed without knowledge of the genetic parameters of the trait.

Surgical treatment of chronic leg weakness (bone, tendon and ligament surgery) is not possible in farmed foxes. Preventative action is, therefore, of vital importance and requires identifying any predisposing factors in blue fox management as well as possible antagonistic genetic correlations between leg conformation and breeding goal traits. Heavy body weight is suspected to be among the predisposing factors for foreleg problems, along with a high energy content and high Ca:P ratio in the blue fox diet (Rekilä et al. 2001; Korhonen et al. 2014). Korhonen et al. (2005) and Keski-Nisula (2006) found a fairly high negative phenotypic correlation (-0.58) between body weight and foreleg weakness. Korhonen et al. (2000, 2001) also showed that the housing method affects the animal's leg conformation and its movement activity. The limited space in a wire mesh cage has the overall tendency to decrease the fox's active movement compared to a dirt-floor pen, as a result of which its energy consumption is low and it becomes fat more easily. A dirt-floor pen, on the other hand, has a favourable effect on the fox's leg conformation by increasing the animal's activity and reducing its body weight (Korhonen et al. 2001). Dirt-floor pens generate other kinds of problems, however, such as high incidence of parasitic diseases, higher energy and feed consumption, small and dirty animals, poor fur quality, heavier workload for



Figure 4. Eye infection in blue fox. Photo: Riitta Kempe, Luke.

the producer and unreasonably high production costs, which is why dirt-floor pens are not used in fur animal production.

1.3.3 SUSCEPTIBILITY TO EYE INFECTION

Between 2005 and 2007, fur producers and veterinarians observed an increase in the frequency of eye infections in the Finnish blue fox population (V). This seemed to be a seasonal health problem. Eye infections were most common at pelting time in November-December, when the animals are at their largest, and in January-February, when they are slimmed for breeding (Ahola et al. 2014). Untreatable eye infection can be very painful, which is why sick animals were usually culled. Eye disease causes economic losses to fur producers, because the premature pelts of these culled animals cannot be sold nor will their feeding costs be compensated (Peura et al. 2016a).

The factors contributing to impaired eye health remain unclear, but certain breeding goal traits, such as increased animal size, BCS or fatness, and certain fur quality traits, such as fur density, are suspected risk factors. Animals may also have genetic differences in their susceptibility to infections (Bishop 2011). In 2007, Finnish fur farms were hit by a new type of eye disease where foxes suffered from aggressive conjunctivitis. *Arcanobacterium phocae* was implicated as a potential causative pathogen in this disease (Nordgren et al. 2014). In addition to microbial infections, abnormalities in the animal's eyelid structure may cause eye irritation and expose the eye to bacteria and secondary inflammation (Whitley 2000). Clinical veterinary examinations and necropsies indicate that some foxes have such structural defects of the eyelid (Nordgren, pers. comm.): entropion, ectropion, distichiasis, and a related condition, ectopic cilia, have

all been found in the blue fox (V). These structural eye defects are also common in certain dog breeds that have a massive coat, loose or excess skin, or excessive subcutaneous fatty tissue which may cause folds of skin on the head, as well as in breeds that have diamond-shaped, small or sunken eyes which may contribute to eye disease (Barnett 1988). Similar features have also been found in blue foxes (Moisander-Jylhä 2017). The control of inherited eye disease depends on the ability to diagnose the disease and knowledge of its mode of inheritance (Barnett 1988).

1.3.4 FEED EFFICIENCY

Feed efficiency is an important breeding goal in all fur animals, because feeds represent a substantial production cost and it is expected that feed prices will continue to rise. A decrease in pelt prices would increase the share of feed costs in total production costs even further. Further, larger animal size increases the output of manure and urine, and an inefficient use of feed leads to nutrients being wasted into the environment; indeed, the single biggest factor raising the carbon footprint in blue fox production is nitrous oxide in faecal matter (Rekilä et al. 2000; Silvenius et al. 2012).

Fur animals are seasonal breeders that are grown to a common and fixed time endpoint when the fur is ready for pelting (Peura et al. 2016a). The fur growth period cannot be shortened to achieve savings in feed costs. Thus, the system differs from meat production for instance, where animals are grown to common weight endpoint. If FE is defined as a function of growth and feed intake, then better feed efficiency could be achieved through faster growth, lower feed intake or both (Peura et al. 2016a).

Even though improved FE would be a natural goal in fur animal breeding programmes, the genetic parameters for feed consumption and efficiency are rarely estimated. This is because automatic feeding methods and feed intake recording of individual animals or cage pairs of foxes or minks have only recently been implemented in large-scale genetics research (e.g., Sørensen 2002; Berg & Krogh Hansen 2006; Shirali et al. 2015). An additional challenge is that blue foxes are currently kept in pairs because two animals sharing the same cage have a better growth rate. Feed intake can, therefore, only be registered for pairs of animals, whereas weight or weight gain can be recorded for individual animals.

Possibilities to improve FE by means of animal breeding have been documented in several animal species, such as mink (Berg & Krogh Hansen 2006; Krogh Hansen & Berg 2006; Krogh Hansen et al. 2007), but not in the blue fox. In mink, for example, the heritability for FE (daily gain/feed intake) is estimated to be 0.30 (Sørensen 2002). Another study in mink showed that the heritability estimate for longitudinal residual feed intake in mink increases with age (105-210 days), from 0.18 to 0.49 (Shirali et al. 2015).

2 OBJECTIVES OF THE STUDY

The main objective of the research project reported in this thesis was to contribute to the development of a sustainable, economical and socially approved national breeding scheme for the Finnish blue fox, by planning breeding value evaluation methods for new production, conformation and welfare traits for inclusion into the blue fox breeding goals.

Genetic improvement through selection supports the profitability of the Finnish fur industry, improves animal welfare and yields high-quality fur products for sale in the global market.

The objectives of this research were:

- 1) to develop simple and practical evaluation methods for on-farm measurement of the new traits, including body condition score (I), feed efficiency, daily gain, daily feed intake, body weight, body length (II, III), leg conformation (IV), ability to move (IV) and susceptibility to eye infection (V);
- 2) to establish a comprehensive set of research data and determine statistical models for the estimation of (co)variance components and genetic variation in the new production, size, conformation and health traits (II-V);
- 3) to understand the co-responses (genetic and phenotypic correlations) among the production traits currently included in the breeding value evaluation (grading size and pelt character traits) and the new traits: feed efficiency and size traits, leg conformation, ability to move and susceptibility to eye infection (II-V); and
- 4) to determine the suitability and feasibility of the new traits for the national blue fox breeding programme.

3 MATERIALS AND METHODS

3.1 EXPERIMENTAL DATA

Five separate studies (I-V) were carried out within this research project. We used the same set of experimental data to investigate the selection potential, genetic associations and suitability of the new production and welfare traits for introduction into the breeding scheme.

The experimental part of the studies was carried out during two years, 2005-2006, at the fur animal research station in Kannus, MTT Agrifood Research Finland. The data were obtained by investigating two consecutive generations of animals on the fur farm. The study material comprised 2076 blue foxes representing 48 paternal progeny groups (Table 4). The number of dams was 241. Pedigree information on 1583 animals was obtained from the Finnish Fur Breeders' Association. The body condition scoring (BCS) method (I) used in the subsequent publications (III-V) was developed based on data obtained from the first generation (2005) of animals.

The data structure was designed to be optimal for genetic studies on new traits, and was targeted to capture a large amount of genetic variation in these traits. The maximum degree of relationship between sires was therefore set at 40%, and the maximum inbreeding coefficient of sires and their offspring at 10%. Because the goal was to simulate random mating, no selection of parents was made on the studied traits. In the first breeding year (2005), 19 sires were mated with 138 females, each sire with at least five different females. In the second year (2006), the paternal families were mated crosswise to attain relationships between all animals. Breeding animals were picked evenly from each paternal family, and 35 sires were mated with 167 females. Six males and 64 females from the first breeding year were used for breeding also in the second year. The pedigree structure in the data was monitored using the RelaX2 program (Strandén & Vuori, 2006). Pedigree was found to be good and in line with the study objectives.

Table 4. Structure of study data: number of experimental animals (N) and litters.

	Mean (Range)			
	N	per sire	per dam	per litter
Farms	1			
Sires	48			
Dams	241			
Litters	305	6.5 (1-20)	1.3 (1-2)	
Animals	2076	43 (2-123)	8.6 (4-26)	6.8 (4-16)

The mean inbreeding coefficient among the experimental animals was low (2.02%), and only slightly higher than the mean inbreeding coefficient (1.48%) for the whole stock of animals at the MTT research farm born in 1981-2006.

Dams were preselected based on their litter size, as the aim was to construct at least two full-sib pairs per female. Full-sib pairs were divided into cages as follows: male-male, male-female or female-female pairs (Table 5). At least one pair was required to be a female-male pair, in order to be able to separate the effects of sex and cage. The cages of each sire's offspring were placed evenly into two open-sided two-row sheds and a hall, and full-sib pairs were then randomly allocated to the cages designated to their sires. Forty percent of the traditional wire mesh cages were in the sheds, sixty percent in the hall (Table 5).

Table 5. Fixed effects and number of observations (N) in the study data by categories.

	N	%
Animal pairs per cage:		
Male-male	591	28
Male-female	975	47
Female-female	510	25
Sex:		
Male	1077	52
Female	999	48
Age of dam:		
1 year	1081	52
2 years	948	46
3 years	47	2
Production environment:		
Shed 1	424	20
Shed 2	408	20
Hall	1244	60
Year:		
2005	876	42
2006	1200	58
Time of birth: ¹		
1 (104-129 days)	74	4
2 (130-144 days)	804	39
3 (145-160 days)	974	47
4 (161-180 days)	24	11



Shed



Hall



Full-sib pair

¹ Days from the beginning of the year.

Photos: Riitta Kempe, Luke.

3.2 ASSESSMENT OF TRAITS

Recording of some production traits in foxes involves certain special features compared to other farm animals. Firstly, foxes live outdoors, and the cold weather conditions in winter are not only challenging for the animals but also for fur producers and management systems. All technology used for data collection, such as feeding trucks, scales and PDAs (personal digital assistants), must withstand cold weather conditions. Despite modern technology and digitalization, live animal grading of foxes is heavy and time-consuming work. The most demanding step is removing the fox from its cage. Blue foxes are quite heavy at the time of grading (October-November) and not always tame or easy to handle, which makes the assessment of their grading traits challenging. Moreover, the number of animals to be graded per farm is very high, taking into account that the average size of a Finnish fox farm is around 2000 animals (ProFur 2016). Most of the pelts (66 %) are produced on farms with 1000 to 10 000 animals, the largest farms having over 25 000 animals. Therefore, the assessment of the grading trait should be as easy, quick and low-cost as possible, not to overload the limited resources of family-owned fur farms.

The objective of the study reported in Paper I was to develop a simple and quick method to assess body fat deposits in the blue fox. For this purpose, blue foxes with varying body conditions were examined to identify areas where subcutaneous fat was noticeable. We studied the following methods for live animal grading: subjective visual scoring of the animal's size from small (score 1) to large (score 5); body weight (kg); fat thickness (mm) measured by ultrasound and palpation of the animal's fat stores; and subjective scoring of the animal's body condition (BCS) from very thin (score 1) to extremely fat (score 5) (Tables 3 and 6). After pelting, the carcasses were evaluated as follows: visual assessment of the fat layer on the skinned carcass and skin, which was turned inside out using a five-point scale from thin (score 1) to extremely fat (score 5) and chemical analysis of fat content (%) of the whole carcass including fat separated from the skin (Table 6). The obtained measurements from live foxes, namely BCS, body weight and grading size, were used in the subsequent studies (II-V).

The study reported in Paper II assessed the most appropriate growth phase for the measurement of feed efficiency traits. Animals have different requirements for maintenance energy and nutrients at different stages of their growth (e.g., Dahlman 2003; Huhti 2005; Koskinen et al. 2008). Further, the utilization of feed may change during the growth period like in mink (Krogh Hansen et al. 2007). Therefore, the growth phase in which FE is measured is important. Body weights were recorded six times during the study period and used for the calculation of individual daily gain (g) at five different stages of growth. Average daily feed intake (kg DM) was measured as a cage average of full-sib pairs. Growing full-sibs in the same cage is a typical farming practice and a common pedigree for each fox pair was one

requirement in our statistical analysis. FE for the pairs of foxes was calculated as the ratio of total daily gain (g) to total daily feed intake (kg DM) per cage for the same periods as daily gain. The obtained FE results for August to October were used in the subsequent studies (III, IV).

The live animal grading traits, size and fur quality traits, were assessed subjectively by one evaluator (research technician) on the five-point scale system (1= poorest, 5= best) currently used in Finland (II-IV). Pelt quality was evaluated from the skins of pelted foxes by professional fur graders (Table 2). The data on pelt traits were obtained from the auction house Saga Furs Oyj and, in addition to categorical traits, the data contained the precise grading machine measurements of pelt size (cm) and colour (pix) – unique information that is not routinely stored into the auction house database (Table 6) (III).

Body length, which is one of the new conformation traits, was measured at pelting time by laying the fox down on the table with its hind legs stretched backwards, and measuring its length from the nose to the first tail vertebrae (I-V). The animal's foreleg carpal joint angle and ability to move about in the cage were used as indicators for scoring leg conformation (IV). Forelegs were assessed subjectively by one evaluator on a five-point scale based on the poorer of the forelegs. In the worst case (score 1=very poor), the carpal joint bended to a 90° angle compared to a normal, only slightly angled carpal joint (score 5=excellent) (Figure 3). The animal's ability to move about was evaluated before feeding time. A fox which mainly remained sitting or lying still in the cage, even if shooed off, was given a score of 1 or 2 for its ability to move. If the fox occasionally moved about in the cage and was somehow capable of jumping on the shelf, its ability to move was evaluated at score 3. Finally, if the animal was actively moving about in the cage and could jump on to the shelf easily it received a score of 4 or 5 for its ability to move (5=best score). The foxes' ability to move about, leg conformation and eye health were evaluated on days 7–16 November in 2005 and on days 23–26 October in 2006. Eye health was assessed subjectively by one evaluator based on the animal's phenotype. It was treated as a binary trait: the eyes were recorded as infected if one or both were swollen and excreted a serous fluid (score 0) (Figure 4), and considered healthy if the eyes looked normal without any of the above symptoms (score 1) (V).

Table 6. Total number of observations (N), mean, standard deviation (SD), coefficient of variation (CV), and minimum and maximum values for the traits currently included (*) in the Finnish blue fox breeding value evaluation and for the new traits.

	N	mean	SD	CV	min	max	Paper
Limited data (2005) used in Paper I							
Grading size*	868	3.8	0.87	22.9	1	5	I
Final body weight, kg	868	12.5	1.47	11.74	8.9	17.2	I
BCS of live animal	868	3.9	0.82	21.26	2	5	I
BCS of carcass	618	4.0	0.87	21.70	1	5	I
Body length, cm	619	71	2.72	3.83	64	79	I
Fat thickness, pelvis, mm	138	21	2.43	11.77	14	28	I
Fat thickness, shoulder, mm	138	17	1.92	11.31	12	23	I
<i>Chemical composition of whole carcass</i>							
Dry matter, g/kg	77	62.8	4.01	6.39	51.3	73.5	I
Fat, %	77	44.5	5.43	12.20	30.	56.2	I
Full data (2005-2006) used in Papers II-V							
Grading size*	2 060	3.7	0.90	24.3	1	5	II-V
Guard hair coverage*	2 060	3.8	0.72	19.26	1	5	V
Fur density*	2 060	3.1	0.82	26.3	1	5	V
Colour clarity*	2 060	3.69	0.72	19.54	1	5	V
BCS of live animal	2 056	3.9	0.75	19.0	1	5	III-V
Leg conformation	2 064	2.1	0.96	44.71	1	5	IV
Ability to move about	2 064	3.6	0.86	23.73	1	5	IV
Eye health	2 064	0.6	0.5	-	0	1	V
Body weight _{Aug} , kg	2 076	4.3	1.41	26.6	1.5	7.7	II
Body weight _{Oct} , kg	2 069	10.7	1.56	14.62	5.0	16.3	II, IV
Body weight _{Nov} , kg	2 063	12.6	1.58	13.10	6.2	18.2	V
Final body weight, kg	2 058	13.6	2.01	14.8	7.8	21.7	II-IV
Daily gain _{Aug-Oct} , g/d	2 069	107	16.21	15.21	53	154	II-IV
Dry matter intake _{Aug-Oct} , g/d	1 026	373	40.11	10.76	263	498	II-IV
FE _{Aug-Oct} , g DG/kg DMI	1 026	271	28.6	10.58	192	388	II-IV
Body length, cm	1 805	71	3.01	4.22	60	81	II-V
Pelt size, cm	1 767	123	7.39	6.04	92	146	III
Pelt size*	1 768	3.3	0.85	25.8	1	5	III
Pelt colour clarity, pix	1 765	8.7	0.69	7.95	6.8	11.3	III
Pelt colour clarity*	1 765	3.1	0.90	28.8	1	5	III
Pelt colour darkness, pix	1 774	365	60.0	16.44	173	555	III
Pelt colour darkness*	1 774	2.8	1.33	47.9	1	5	III
Pelt guard hair coverage*	1 773	3.3	0.81	24.7	1	5	III
Pelt density*	1 774	3.5	0.58	16.46	2	5	III
Pelt quality*	1 775	3.5	0.58	16.46	2	5	III

3.3 STATISTICAL ANALYSES

Preliminary statistical analyses were performed using PROC GLM in the SAS system for Windows 9.1.3 through the SAS Enterprise Guide, Release 4.1 (SAS Institute Inc., Cary, NC, USA). Systematic fixed effects and their interactions were studied using GLM by excluding all other random effects than the residual (I-V). The fixed effects used in the analyses were: house-year, sex (two classes: male or female), pair (three classes: male-male, male-female or female-female), time of birth (four classes: 104-129, 130-144, 145-160 or 161-180 days from the beginning of the year) and age of dam (three classes: 1, 2 or ≥ 3 years) (Table 5).

(Co)variance components for the different traits were estimated using the restricted maximum likelihood (REML) method in the DMU program (Madsen & Jensen 2012). Both single- and multiple-trait analyses were carried out. The following linear animal model was used for variance component estimation in Papers II-V:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{W}\mathbf{c} + \mathbf{Z}\mathbf{a} + \mathbf{e} \quad (1)$$

where \mathbf{y} is a vector of observations, \mathbf{b} is a vector of fixed effects, and \mathbf{c} , \mathbf{a} and \mathbf{e} are vectors of random litter, animal/sib group and residual effects, respectively. Matrices \mathbf{X} , \mathbf{W} and \mathbf{Z} are the corresponding incidence matrices.

In the single-trait analyses, the litter (\mathbf{c}), animal (\mathbf{a}) and residual (\mathbf{e}) effects were assumed to be independent, normally distributed random effects with mean zero and $\text{var}(\mathbf{c}) = \mathbf{I}_q \sigma_c^2$, $\text{var}(\mathbf{a}) = \mathbf{A} \sigma_a^2$ and $\text{var}(\mathbf{e}) = \mathbf{I}_n \sigma_e^2$, where \mathbf{I}_n is the identity matrix of size n , n is the number of animals with an observation, \mathbf{I}_q is the identity matrix of size q , q is the number of litter effects, \mathbf{A} is the additive genetic relationship matrix, σ_c^2 is the common litter environment variance, σ_a^2 is the additive genetic variance and σ_e^2 is the residual variance.

Genetic correlations between traits were estimated with the multiple-trait animal model for all the analysed traits (II, IV), three (III) or four (V) traits at a time. Thus, genetic correlations were estimated several times for some of the traits. Genetic correlations and their standard errors were obtained by averaging the results from the multiple estimation runs. In the multiple-trait animal model, the litter, animal, and residual effects were assumed to be independent, normally distributed random effects with zero mean and $\text{var}(\mathbf{c}) = \mathbf{C} \otimes \mathbf{I}_q$, $\text{var}(\mathbf{a}) = \mathbf{G} \otimes \mathbf{A}$ and $\text{var}(\mathbf{e}) = \mathbf{R} \otimes \mathbf{I}_n$, where \otimes is the Kronecker product, \mathbf{C} is the variance-covariance matrix for litter effects among traits, \mathbf{G} is the genetic variance-covariance matrix among traits and \mathbf{R} is the variance-covariance matrix for residual effects among traits.

In analysing the cage averages (for a pair of foxes), we made appropriate changes to the subroutine computing the inverse of the relationship matrix (\mathbf{A}^{-1}) in the DMU program. This was considered necessary because the full-sib mean has reduced genetic variance, which is expected to be three-fourths of the genetic variance of individual measurements, and correspondingly, the

residual variance is also lower, expected to be half of the residual variance of individual measurements (Kovac & Groeneveld 1990).

The heritability (h^2) and proportion of litter variation (c^2) for a trait were calculated as:

$$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2) \quad (2)$$

$$c^2 = \sigma_c^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2) \quad (3)$$

where σ_a^2 , σ_c^2 and σ_e^2 are the additive genetic, litter environment and residual variances for the trait, respectively.

The heritability of susceptibility to eye infection (V), obtained from the linear animal model using binary variable (0 or 1) analysis, was transformed to the underlying continuous scale using the formula (Dempster & Lerner 1950):

$$h^2 = h_{0,1}^2 p(1-p) / z^2 \quad (4)$$

where h^2 is heritability on the underlying continuous scale, $h_{0,1}^2$ is the corresponding heritability estimate from the linear animal model on the binary scale, p is the frequency of eye-infected individuals in the population, and z is the ordinate of the standard normal density function at the threshold value corresponding to incidence p .

4 MAIN RESULTS

4.1 BODY CONDITION SCORING METHOD

The aim of the study presented in Paper I was to develop a body condition scoring system for Finnish blue foxes. The devised method is based on subjective assessment of the animal's subcutaneous fat thickness by visual observation and palpation. BCS was found to have a high positive Pearson correlation coefficient with final body weight (0.70) and a moderate correlation coefficient with grading size and animal length (0.49 and 0.36, respectively) (I). The body weight of foxes rose by about 1.2-1.4 kg per BCS category. The Pearson correlation coefficients for BCS using ultrasonic measurement of subcutaneous fat thickness in the pelvic and shoulder areas were also positive, although quite low (0.22-0.29) (I). A fairly linear increase in subcutaneous fat thickness was observed from August to the beginning of November, with no signs of a slowdown.

The BSC results showed that most (66%) of the animals were scored as heavy or extremely fat (scores 4 and 5). The proportion of extremely fat foxes (score 5) was 25%, while 31% of the foxes were in ideal body condition (score 3). The tendency toward higher fat content was noticeable in the carcasses classified into the higher BCS categories. The average fat content of the 77 carcasses receiving BCS scores 3-5 at pelting time was 45%, ranging from 30% to as high as 56%. In wild Arctic fox, of which the blue fox is a variant, the typical winter fat content of skinned carcasses varies widely, from 3% to 40% (Prestrud 1991; Prestrud & Pond 2003). A recent WelFur study by Ahola et al. (2014) reported an average frequency of 21% of extremely fat animals among the evaluated blue foxes (n=4688).

The mean body weight and length of blue foxes at pelting time were 13.6 kg and 71 cm, with the heaviest fox weighing 21.7 kg and the longest body length being 81 cm (II, III, IV). The size differences between the sexes were rather small at the time of pelting: males were on average 1.2 kg heavier, 3 cm longer and 0.3 BCS points fatter and their grading size was 0.7 points larger than of females (I). This is in line with previous studies (Rekilä et al. 2000; Sirkko 2000). In the mid 1990s, blue foxes generally weighed less than 10 kg at pelting time in November and December (e.g. Korhonen & Niemelä 1994). A decade later, the animals' average pelting weight on commercial fur farms was between 15 to 20 kg, and the increased weight was mainly explained by the increased fatness of the foxes (Rintamäki et al. 2007). In comparison, the average body weight of wild adult Arctic foxes is 3.6 kg and their average body length 57 cm (Jones et al. 2009).

4.2 INCIDENCE OF HEALTH PROBLEMS

Leg weakness was a common problem among blue foxes on the MTT Kannus research farm, with 67% of blue foxes receiving either a very poor (1) or poor (2) score for foreleg conformation (IV). Only 8% of the foxes were given a good (4) or excellent (5) score for leg conformation, the average score being 2.1. Despite the animals' poor foreleg conformation, their ability to move about in the cage was evaluated as fairly good and scored at 3.6 on average. The incidence of leg weakness (scores 1 and 2) in our study was about 15 percentage units higher and the mean 0.3 points lower compared with the results of Keski-Nisula (2006) from the same research farm, indicating that leg conformation among the foxes had weakened quickly within a period of five years.

Almost half the foxes (45%) in the two-year study data were found to suffer from eye infection (V). Contagion of the disease fur animal epidemic necrotic pyoderma (FENP) on the Kannus research farm cannot be completely be ruled out, because there was an epidemic outbreak of FENP in Finland close to the time of data collection (Nordgren et al. 2014). This may partly explain the high frequency of eye infection. A much lower frequency of eye infection, 1.3-3.2% on average among the evaluated blue foxes (n=14840), was reported by Ahola et al. (2014), who assessed eye infections on 88 Finnish fox farms in 2012-2014 following the WelFur animal welfare test protocol (Mononen et al. 2012).

4.3 HERITABILITIES

The estimates for phenotypic variance, heritability and proportion of litter variance for the studied traits (II-V) are presented in Table 7.

The heritabilities for feed efficiency were first estimated for five growth periods of three weeks (II). However, because the estimates were lower than expected (0.08-0.10), the production efficiency traits (FE, daily gain and daily intake) were thereafter re-estimated for a longer, nine-week growth period from August to October (II, IV). The latter estimates were based on a larger amount of information and were higher (0.23-0.29) due to decreased residual, litter and phenotypic variance components.

Body weight showed considerable genetic variation and a moderate to high heritability (0.37-0.50) (II, IV, V). The heritability estimates obtained for pelt size were high (0.47-0.50) and in line with the heritability of fox body length (0.51-0.57) (II-V). The estimates for different pelt character traits varied from low to high, with colour clarity having the lowest (0.20-0.23) and colour darkness the highest heritabilities (0.52-0.54). Pelt density and guard hair coverage were moderately heritable traits (0.34 and 0.36, respectively) (III).

Table 7. Estimated phenotypic variance (σ_p^2), proportion of litter variation (c^2) and heritability (h^2) for the studied traits in the Finnish blue fox.

Proportion of variation				
	σ_p^2	c^2	h^2	Paper
gSI (scores 1-5)	0.55-0.56	0.14-0.15	0.32-0.35	II, IV, V
gGC (scores 1-5)	0.48	0.08	0.11	V
gDE (scores 1-5)	0.55	0.15	0.15	V
gCL (scores 1-5)	0.49	0.08	0.05	V
BCS (scores 1-5)	0.55	0.13-0.18	0.22-0.30	IV, V
LEG	0.72	0.15	0.25	IV
MOVE	0.67	0.11	0.22	IV
EYE (0/1)	0.23	0.05	0.24	V
BW _{Aug} , kg	0.48	0.49	0.35	II
BW _{Oct} , kg	1.50-1.55	0.25	0.37-0.42	II, IV
BW _{Nov} , kg	1.79	0.23	0.37	V
BW _{Fin} , kg	2.86-2.88	0.14	0.49-0.50	II, IV
DG _{Aug-Oct} , g/d	203-217	0.17-0.19	0.28-0.29	II, IV
DMI _{Aug-Oct} , g DM	2 333-2 347	0.14	0.23-0.24	II, IV
FE _{Aug-Oct} , g/kg DM	780-783	0.09	0.26-0.28	II, IV
Body length, cm	6.30-6.36	0.07-	0.51-0.57	II, IV, V
pSI _{cm} , cm	43.53	0.05	0.50	III
pSI (5 classes)	0.60	0.05	0.47	III
pCL _{pix} , pixels	0.28	0.12	0.23	III
pCL (5 classes)	0.48	0.09	0.20	III
pDA _{pix} , pixels	3 652	0.12	0.54	III
pDA (5 classes)	1.82	0.10	0.52	III
pGC (5 classes)	0.62	0.05	0.36	III
pDE (4 classes)	0.31	0.00	0.34	III
pQU (4 classes)	0.31	0.01	0.34	III

gSI=grading size, gGC=guard hair coverage, gDE=fur density, gCL=colour clarity, BCS=body condition score, LEG=leg conformation, MOVE=ability to move, EYE=eye infection, BW=body weight, DG=daily gain, DMI=daily dry matter intake, DM=dry matter, FE=feed efficiency, pSI=pelt size, pCL=pelt colour clarity, pDA=pelt colour darkness, pGC=pelt guard hair coverage, pDE=pelt density and pQU=pelt quality.

The heritability estimates for conformation and health traits (leg conformation, ability to move about, BCS and susceptibility to eye infection) were moderate (0.21-0.30) (IV, V).

4.4 GENETIC CORRELATIONS

The genetic correlations obtained in this research for the studied traits are summarized in Table 8 (II-IV).

Young blue foxes had high feed efficiency and daily gain at the beginning of their growth. The values for these traits started to decrease in October when the animals reached the age of 20 weeks. In the first three studied growth periods, FE was considered to be the same trait because of the high genetic correlations between the said periods (0.71-0.95) (II). The FE measured in this fast growth phase was used in the further studies (III, IV).

4.4.1 FEED EFFICIENCY TRAITS

Feed efficiency was found to have rather high (0.51-0.56) favourable positive genetic correlation with daily gain (II-IV) and a favourable but low negative genetic correlation (-0.14) with daily feed intake (II). When more complicated multiple-trait models were used, the genetic correlation between FE and feed intake had high standard errors and did not differ from zero (III, IV). The corresponding phenotypic correlation was also low (-0.26), but slightly higher than the genetic correlation.

The study reported in Paper II, found low unfavourable correlations between FE and body weight (0.14), grading size (-0.10) and animal length (-0.18), whereas the corresponding genetic correlations in Paper IV did not differ from zero. Genetic correlations for FE with BCS (fatness) or with conformation traits did not differ significantly from zero, and the corresponding phenotypic correlations were either low or close to zero (IV).

FE had a moderate favourable genetic correlation with pelt size (0.36) and a low unfavourable genetic correlation with pelt colour clarity (-0.22) (III). The low genetic correlation observed between FE and colour darkness (0.21) can be either favourable or unfavourable, depending on the prevailing fashion trends. Other genetic correlations between FE and pelt quality traits did not differ from zero.

All animal size traits (body weight, grading size and body length), daily gain, pelt size and BCS (fatness) had high unfavourable positive genetic correlations (0.49-0.95) with feed intake (II-IV). Also, the conformation traits (leg conformation and ability to move) had high negative unfavourable correlations (from -0.41 to -0.55) with feed intake (II-IV).

Table 8. Genetic correlations with absolute values higher than 1.96 xSE between the studied traits in Finnish blue foxes (II-V).

	FE	DG	DMI	BW _{Oct}	BW _{Fin}	Length	gSI	gDE	LEG	MOVE	EYE	pSI _{cm}	pCL _{pix}	PDA _{pix}	pQU
BCS	ns	+++	---	+++	+++	ns	±±	+++	--	--	ns	++	ns	ns	ns
FE _{Aug-Oct}		++	+ / ns	- / ns	ns	- / ns	- / ns		ns	ns		++	--	±±	ns
DG _{Aug-Oct}			---	+++	+++	++	++		--	--		+++	ns	ns	ns
DMI _{Aug-Oct}				---	---	--	---		--	--		--	ns	ns	ns
BW _{Oct}					+++	++	+++		--	--					
BW _{Nov}						++	+++	++			ns				
BW _{Fin}						++	+++		ns	--		+++	ns	ns	ns
Length							+++	ns	ns	--	ns	++	ns	ns	ns
gSI								ns	--	--	ns	+++	ns	ns	ns
gDE									ns	--	ns	+++	ns	ns	ns
LEG											--				
pSI _{cm}										+++			ns	ns	ns

Note: ns, genetic correlation does not differ from zero; "+", favourable correlation; "-", unfavourable correlation; "±" correlation either favourable or unfavourable depending on the situation or perspective.

One symbol: 0.10 < |r_g| < 0.20, two symbols: 0.20 < |r_g| < 0.70, three symbols: |r_g| > 0.70

BCS=body condition score, FE=feed efficiency, DG=daily gain, DMI=daily dry matter intake, DMI=daily dry matter intake, BW=body weight, gSI=grading size, gDE=fur density, LEG=leg conformation, MOVE=ability to move, EYE=susceptibility to eye infection, pSI=pelt size, pCL=pelt colour clarity, pDA=pelt colour darkness, and pQU=pelt quality.

4.4.2 BODY CONDITION SCORE

The results for BCS showed moderate to high positive genetic correlations (0.42-0.86) with animal size traits (body weight and grading size), daily gain, pelt size and grading fur density. Genetic correlations between BCS and FE, body length or pelt quality traits hardly differed from zero (III-V). BCS had moderate to high unfavourable genetic correlations with daily feed intake (0.78), leg conformation (-0.40) and ability to move about (-0.61) (III, IV).

4.4.3 GRADING AND PELT CHARACTER TRAITS

A high favourable genetic correlation (0.72) was found between grading size and pelt size (III). Both had moderate to high favourable genetic correlations (0.42-0.87) with daily gain, final body weight, body length and BCS (II-V). The corresponding phenotypic correlations were mostly moderate (0.36-0.60). In fact, all genetic correlations between the size traits (grading size, body weight and length) and daily gain were positive, ranging from 0.33 to 0.91 (II-V).

The estimates for genetic correlations between animal size traits and pelt quality traits did not differ from zero, as their standard errors were high (III). However, grading density showed a moderate favourable genetic correlation with body weight in November and a high favourable genetic correlation with BCS (0.59 and 0.85, respectively) (V).

4.4.4 LEG CONFORMATION AND ABILITY TO MOVE

Leg conformation had moderate unfavourable negative genetic correlations (-0.40 to -0.53) with grading size, body weight in October, daily gain and BCS. The phenotypic correlations between these traits were also negative, although lower (-0.28 to -0.41). Body weight measured in October had a slightly higher genetic correlation (-0.47 ± 0.17) with leg conformation than body weight measured in August (-0.27 ± 0.19), September (-0.43 ± 0.17) or November (-0.36 ± 0.17 to -0.43 ± 0.17). The results indicated a negative genetic correlation between leg conformation and animal length, even though the standard error was high (-0.38 ± 0.21).

A high positive genetic correlation was observed between the animal's leg conformation and ability to move about (0.94) (IV). Daily gain, body weight in October and grading size showed high unfavourable genetic correlations with ability to move about (-0.65 to -0.66). Also BCS, final body weight, daily feed intake and body length had fairly high unfavourable genetic correlations with ability to move about (0.42 to 0.61). In general, higher genetic correlations with the studied traits were obtained for ability to move than for leg conformation.

4.4.5 SUSCEPTIBILITY TO EYE INFECTION

The genetic correlation for susceptibility to eye infection and grading size or BCS had high standard errors, but all size traits showed a low antagonistic phenotypic correlation with susceptibility to eye infection. A moderate unfavourable genetic correlation was found between susceptibility to eye infection and grading density (thick underfur).

5 DISCUSSION

5.1 QUALITY OF DATA AND METHODS

The design of the two-year experimental study conducted on the Kannus MTT research farm was quite unique. It generated a special set of data, which opened up the possibility to study several new, previously uninvestigated traits in a resource-efficient manner. The pedigree structure of the animals was well suited to our research objectives and also the amount of data for most traits was sufficient to give reliable estimates of genetic parameters, which could be used in further studies. The more controlled environmental conditions typical of a single-farm study were expected to yield slightly higher heritability estimates compared to studies using considerably larger data sets (40000-50000 animals from a large number of farms), as normally used for variance component estimation (Peura et al. 2005; Koivula et al. 2009; Kempe & Strandén 2016). However, larger data sets are likely to contain more genetic variation because they include information on animals from many farms, thus offsetting the effect of higher residual variance.

The analysis of fox pelt character traits would undoubtedly have benefited from a more extensive set of data across several generations and/or with more offspring per sire (III). The skins of breeding animals, which were important links in the pedigree, were of lower quality and not comparable to the winter pelts of production animals. These 'breeder skins' were subjected to the grading process normally used for low-grade pelts, and these results had to be excluded from variance component estimation. Thus, in the absence of pelt results for breeding animals, there was less data on pelts than on the other traits, which made the estimation of variance components, particularly genetic correlations, challenging. While the pelt records of breeding animals could have brought more information into the genetic analysis, such information is not systematically collected at the moment. Investigation of this topic would require collecting data on the 'breeder skins' and making the necessary adjustments in modelling and analysing the data.

The linear animal model used in this research gave sufficiently accurate information on the proportion of genetic variation in the studied traits and the genetic correlations between them (II-V). The linear model was also used to analyse the foxes' susceptibility to eye infection (V), even though theoretically, a threshold model would be more appropriate for analysing binary data (Gianola 1982). To overcome the issue, the heritability estimate for susceptibility to eye infection from the linear animal model was converted from the binary to the underlying continuous scale using the formula by Dempster & Lerner (1950). Heritabilities obtained using the linear model are underestimated compared to those from the liability scale, and the

magnitude of this underestimation depends on the frequency of the symptom.

5.2 SELECTION POTENTIAL FOR THE NEW TRAITS

5.2.1 FEED EFFICIENCY

The definition of feed efficiency in this thesis (II, III) is fairly simple and commonly used in the literature: FE is defined as body weight gain per unit of feed consumed. The genetic parameters for FE traits were estimated for a pair of foxes sharing a cage (II-IV). The results show considerable phenotypic variation in feed intake and feed efficiency between different pairs of foxes: maximum FE was twice as high as the minimum (II-IV). The moderate heritabilities for FE reported in Papers II-IV were within the range found for mink and pigs (Berg & Lohi 1992; Mrode & Kennedy 1993; Von Felde et al. 1996; Sørensen 2002; Cai et al. 2008). Higher heritability estimates than in our study for daily feed intake and daily gain have been reported in mink (Sørensen 2002). Measuring feed intake for a pair of animals instead of individual foxes brought some inaccuracy to our results, and the observed heritabilities may thus be somewhat underestimated compared to a situation where individual feed intake results are available. Further, the value for feed intake does not necessarily reflect the precise feed intake by the fox pair, as each animal will compete for the feed and eat a different amount, and some minor feed spillage from the cage is likely (Risku-Norja et al. 2002), which will also affect the results. The sex differences in feed intake and weight gain are smaller in the blue fox than in mink (Rekilä et al. 2000). In mink, males account for 72% on average of the weight gain and feed intake of a cage and, thus, contribute considerably more to the cage variation of the feed conversion rate than females (Berg & Krogh Hansen 2006; Krogh Hansen & Berg 2006). The feed conversion rate of mink has been studied using a random regression models where the phenotype is obtained from a cage and the individual components are modelled assuming that each cage has a male–female pair (Krogh Hansen & Berg 2007; Shirali et al. 2015).

In our study, genetic parameters were estimated based on the assumption that the fox pairs sharing a cage were full-sibs, which have the same pedigree. However, this is not always the case on commercial farms: animals sharing the same cage may have different parents. Therefore, the methods described by Berg and Krogh Hansen (2006) or Shirali et al. (2015) could be worth studying also in blue foxes. Individual animal records would, of course, give the best estimates for feed intake and FE, but obtaining such records from blue foxes is challenging. While it is possible to measure a fox's weight or daily gain individually on most farms, lifting hundreds of heavy foxes (10-15 kg) on to a scale for weighing and then back into the cage is extremely strenuous and time-consuming work. The benefits gained from this

additional workload should be established before proposing it into practice or it should be connected to pelting phase. An automatic real-time animal (or cage) weight and length recording system would be faster and easier than manual measuring and would also improve feeding management through more accurate, growth-based data on feed intake and FE.

Recording of FE under commercial farm conditions is obviously a challenging task, and the use of effective breeding methods on fur farms is constrained by the farms' inadequate resources for animal performance recording. Due to measurement difficulties, high recording costs and lack of interest or proper control, it may be practical to engage only the most interested farms into the breeding programme in order to achieve genetic progress in FE (Kinghorn 2000). These nucleus breeding farms would perform the recording and genetic evaluation of the new and challenging traits and spread the genetic progress to the commercial farm population by selling animals and/or semen (Kosgey et al. 2006).

5.2.2 NEW PELT CHARACTER TRAITS

The heritability estimate obtained for pelt size in this research is considerably higher than reported earlier by Nikula et al. (2000) and Peura et al. (2005). In general, the heritabilities estimated for continuous measurements of pelt traits (pelt size in centimetres and colour traits in pixels) are slightly higher heritability than for categorical measurements (III), because transition to a categorical scale decreases the measurement accuracy (Falconer & Mackay 1996). This applies especially to the largest pelts, since all skins longer than 142 centimetres are classified into the same category ('60' in the auction house sorting system or class 5 in the breeding value evaluation) (Table 2). The procedure significantly decreases genetic variation in the trait and the prospects of genetic gain, as the breeding value of the trait comes to be underestimated. This loss of information is a distinct weakness in the skin sorting system, which needs to be solved.

Sorting of dried skins at the auction house is highly automated: an automatic grading machine measures pelt length, colour darkness and colour clarity precisely in centimetres and pixels. However, the data generated in this process are currently not fully exploited for the purposes of animal breeding. It would be very important to store these accurate measurements in a database for use in breeding value estimation instead of the categorical pelt traits, as is the practice today.

The study described in Paper III was the first to estimate heritabilities for pelt density and guard hair clarity in the blue fox. The moderate heritabilities obtained for these traits fall within the range found earlier for mink (Berg 1993; Lagerkvist et al. 1994). The estimates for pelt colour traits (darkness, clarity) are in the same order of magnitude as observed in previous blue fox studies, but the heritability estimate for pelt quality is higher than reported by Nikula et al. (2000) and Peura et al. (2005). Our heritability estimates for

pelt traits are somewhat higher than for the corresponding grading traits. This result is similar to Peura et al. (2005), who also found higher heritabilities for pelt traits than for the corresponding grading traits. Evaluation of skins by professional fur graders is considered more accurate than assessment of live animals by fur producers (Kenttämies & Smeds 1992a, 1992b). Also, professional graders may pay attention to slightly different aspects in grading than fur producers (Peura 2013).

5.2.3 BODY LENGTH

Live animal body length is an accurate measurement which shows great potential as a new selection trait (II-V). The body length measurement system was originally developed in Norway. The system is currently use on Norwegian blue fox farms. Body length is measured at the time of grading when breeding animals are being selected and the animals' length growth has ended (Huhti 2005). In this research, the body length of foxes was measured later, at the time of pelting. Body length and weight are objective measures of animal size, which can also be used to monitor animal welfare. In a recent study, Peura et al. (2017) showed that relative weight, calculated as length-based standard weight (Benn 1971), has potential as an objective indicator of fatness in blue foxes. The relative weight-for-length index shows considerable genetic variation and can be used as a tool to assess the fatness of animals for animal management purposes, control by regulatory authorities and breeding selection.

The results for all size traits display large genetic variation and moderate to high heritability. Highest heritabilities were obtained for animal body length (0.51-0.57) and final body weight (0.47-0.50), whereas the estimate for grading size (a categorical trait), which is currently among the most important selection criteria for animal size, is much lower (0.34). Also in mink, the highest heritability estimates (0.20-0.77) have been reported for measurable size traits, such as body weight and body length (Berg 1992; Lagerkvist et al. 1994; Krogh Hansen & Berg 1997; Lohi 2002; Socha 2004).

5.2.4 BODY CONDITION SCORE

The system developed in this research for evaluating the body condition (fatness) of blue foxes is based on visual assessment combined with manual palpation. The BCS method is more convenient and timesaving for distinguishing phenotypic differences between animals than ultrasonic measurement of fat thickness (I). Ultrasonic measurement is challenging in animals with a very thick subcutaneous fat layer. BCS provides important additional information on the size trait by revealing how much of it is due to fatness. Yet, adding one more category above 'extremely fat' (score 5) might help to capture the most serious obesity problems. At the other end of BCS scale, the validity of the lowest BCS score (score 1), i.e. very lean animals, was

considered a bit unclear in the WelFur validation (Mononen et al. 2012). Even if the lean animals were difficult to assess, Mononen et al. (2012) thought that the reliability of BCS scoring is not a problem after proper training of the assessors. Assessment of BCS by palpation in connection with normal grading evaluation can be expected to be more accurate for phenotypic evaluation of fatness and size, and thus for EBV of grading size, than mere grading.

Our results show that BCS has a genetic background, with moderate heritability (IV, V), indicating that fatness could be included as a new trait into the blue fox breeding programme. BCS is known to be heritable also in other animal species, such as sheep, although with somewhat lower estimates (0.16-0.18) than in blue foxes (Everett-Hincks & Cullen 2009), and dairy cattle, where heritability estimates range from moderate to high (0.22-0.51) (Koenen et al. 2001; Berry et al. 2003; Banos et al. 2006).

5.2.5 LEG CONFORMATION AND ABILITY TO MOVE

Leg conformation, ability to move and eye health were assessed visually without touching the animal. Scoring of leg conformation and ability to move are fairly fast evaluation procedures, but in some cases, the fox's long, heavy hair coat or the animal's reluctance to move about may complicate their visual appraisal (IV). Ahola et al. (2012) studied the inter-observer reliability of leg conformation and ability to move about in blue foxes. The assessment of moving difficulties on a four-point scale, instead of five-point scale, had good inter-observer reliability. Its index of concordance (IC value) was 0.86, showing that the results from assessments were consistent (Martin & Bateson 2007; Ahola et al. 2012). The IC value in the assessment of leg conformation was lower, 0.75, indicating that assessors disagreed on the scoring of leg conformation in some cases, especially for mild bending of the foot. Therefore, a three-point scale instead of a five-point scale was implemented in the WelFur protocol. It is clear that consistent evaluation requires proper training in the scoring criteria to ensure that different evaluators assess the animals in a comparable manner. Future studies should consider the possible need to change the scoring scale of leg conformation if the assessment is not consistent for breeding purposes.

Leg conformation and ability to move about were found to have moderate heritability (0.22-0.30) (II, IV, V). The results reported in Paper IV are in line with those obtained in other fast-growing animal species; in pigs, leg conformation traits have mainly shown low or moderate heritability (Jørgensen & Andersen 2000; Serenius et al. 2001) and in broilers, moderate heritability (0.16-0.34) (Le Bihan-Duval et al. 1996, 1997). Conformation traits with moderate heritability could be improved fairly quickly by means of animal breeding, if they were introduced into the blue fox breeding programme.

5.2.6 SUSCEPTIBILITY TO EYE INFECTION

The original subjective grading of eye infection on a five-point scale does not capture phenotypic variation well enough to give unambiguous results, and so we analysed eye health as a binary trait. When eye health was evaluated as a binary trait in the WelFur fox protocol, the inter-observer reliability was excellent (IC value 0.99), indicating that the assessments were the same regardless of the assessor (Ahola et al. 2012). Our results show that the variation in foxes' susceptibility to eye infection is partly genetic. Selection against eye infection is, therefore, possible and should be highly recommended (V). The Finnish Fur Breeders' Association advises to cull all sick animals immediately, which is a fairly easy and effective way to improve eye health in the blue fox population. Recent studies by Ahola et al. (2014) indicate that these guidelines are being followed, as the frequency of eye infections has already decreased since 2005-2006 when our experimental data were collected.

The aetiology of eye infection was not investigated in this research project and requires further study to determine whether it is due to genetic differences in resistance or an eye disease. Diagnosis of eye disease by a veterinarian is necessary, since structural defects and certain microbes may act as predisposing factors for eye infection. Assessment of susceptibility to eye infection should focus on breeding animals and their close relatives in an effort to improve eye health and reduce the harmful effects of eye infection. All collected information on the incidence of eye infection should be stored into the fur animal health care system Fureva and the WebSampo breeding software as soon as it occurs. Other data on welfare and conformation traits, such as leg conformation, ability to move about and BCS, can be recorded at the time of animal grading and/or selection of breeding animals.

5.3 GENETIC AND PHENOTYPIC CORRELATIONS

The focus in breeding is largely on improving the animals' production performance traits. At the same time, however, other traits that are not under selection may unintentionally be impaired due to antagonistic co-responses, which are hard to predict and can only be detected afterwards. It takes a while to realize that an adverse trend in the population is not a coincidence but is related to unfavourable genetic correlations between traits (Oldenbroek & van der Waaij 2015). All animal selection and breeding methods that might cause distress or substantial harm to animal health or welfare are prohibited by Finnish animal protection legislation. Breeding schemes must be carefully designed and monitored in order not to compromise animal wellbeing, and any undesired co-response reversed by selecting in the opposite direction, if necessary (Oldenbroek & van der Waaij 2015). Like Sandøe et al. (1999) wrote in their article: "When we can

reasonably predict the consequences of our actions we must take on the burden of ethical responsibility.”

5.3.1 CORRELATED RESPONSES OF FEED EFFICIENCY

While the current emphasis in selection on larger animal and pelt size does have an indirect positive effect on feed efficiency, selection for larger pelt size tends to favour fast-growing and fat individuals and thereby increases the animals' feed intake (II). Increased feed intake, in turn, is related to higher maintenance energy requirement of large animals (Patience et al. 2012; Sepponen et al. 2014). Indeed, the favourable genetic correlation between FE and feed intake found in this research project was lower than expected (II-IV). If FE is defined as a function of growth and feed intake, then better feed efficiency in blue foxes can only be achieved through faster growth, lower feed intake or both (Peura 2013). Shortening the growth period is not an option to achieve feed savings, because day length has a major effect on fur development and maturation, and consequently, on pelting time (Mäntysalo & Blomstedt 1995).

Selection can be based on FE measured at an early age, especially if the aim is to achieve efficient growth of muscle and bone tissue instead of adipose tissue. The genetic correlation between FE measured in the period of fast growth and FE at the end of the growth period is fairly high, but these are, nonetheless, slightly different traits (II). After the age of 20 weeks, blue foxes appear to become less efficient at converting feed into body weight gain (II), as the focus in growth shifts from bone and lean tissue to fat deposition. This result is consistent with previous studies in blue foxes (Sirkko 2000; Huhti 2005) and in mink (Krogh Hansen et al. 2007). In mink, the feed conversion rate changes during the growth period, and mink use more feed per unit of weight/fat gain towards the end of growth, rather than in the early growth phase, where the focus is on the longitudinal growth (Krogh Hansen et al. 2007). Further, Rekilä et al. (2000) and Peura et al. (2004, 2016a) showed that growing large foxes with a thick fat layer is cost-consuming, which diminishes the economic advantage gained from the larger pelt size of these animals. For example, in pigs, fat deposition requires 16% more energy per unit of gain than lean meat (Patience 2012).

Due to the positive genetic correlation of FE with large animal size, pelt size and BCS (fatness), selection for better FE may indirectly worsen the animals' leg and fertility problems and lead to somewhat shorter body length (II, IV) (Peura et al. 2004, 2007; Koskinen et al. 2008; Koivula et al. 2009). Still, the observed correlation between body length and FE requires additional study, as the results reported in Papers II and IV are not fully consistent, although both suggest a negative correlation. Current breeding selection for pelt quality has only a minor effect on FE, as their genetic correlations are low (III). However, if FE is to be included in the breeding programme, it is necessary to assign an adequate selection weight on pelt

character traits, because selection for better FE may lead to lighter pelt colour and undesirable reddishness. This problem can, of course, be overcome with modern pelt colouring techniques, which reduce the importance of colour for pelt prices.

5.3.2 PROS AND CONS OF FATNESS AND LARGE SIZE

Fatness is a key challenge in blue fox production. As shown in this research, blue foxes have high natural genetic potential for feed intake and for the accumulation of fat reserves for the cold period (I-IV). Unrestricted feeding combined with the high energy and fat content of the feed, exceeding the recommendations (Luke 2016), adds to the animals' fatness. The industry has efficiently utilized the high feed intake capacity of blue foxes in fur production to achieve larger animal and pelt size, better fur quality and, consequently, better economic profitability. Our results show a high positive genetic and phenotypic correlation of grading fur density with BCS and body weight (III). Indeed, fur producers have realized that in addition to larger pelt size, fat animals also have better fur quality, and so they favour high feeding intensity and fat animals in production. Despite the strong favourable correlation of BCS and body weight with grading fur density, their correlations with auction house pelt quality traits are less clear because of large standard errors (III).

The observed increase in fatness among the blue fox population during the past two decades can, at least partly, be explained by genetic selection for larger grading size (Rekilä et al. 2000; Koivula et al. 2009). A positive correlation exists between the animal's subjectively scored grading size and the its BCS (fatness) and also its body weight and length (IV). Selection based on larger grading size would not only result in a larger pelt and animal size, but also increase the average fatness in blue foxes. In fact, most of the size traits (growth rate, body weight, grading size and BCS) have favourable moderate to high genetic and phenotypic correlations with each other as well as with grading fur density and final pelt size (II-V). Selection for these size traits, with the exception of body length, would, consequently, provoke fatness (IV).

However, the aiming toward extreme fatness compromises animal welfare. An important result of this research is the finding that the emphasis on larger grading size in breeding leads to increased incidence of leg weakness in the blue fox population due to the moderate antagonistic genetic correlation between these traits (IV). Fast growth rate, heavy body weight and fatness are other key factors contributing to leg weakness and impaired ability to move about in blue foxes under the age of six months. The critical time period seems to be early October when foxes are growing fastest. Good leg conformation is closely linked both genetically and phenotypically to the animal's ability to move about in the cage. Higher activity strengthens the ligaments, tendons and muscles that support the position of the carpal joint,

and also prevents fatness through increased energy consumption (Korhonen et al. 2001).

No genetic correlation was observed between eye health and size traits or fatness (V). Thus, the current focus on size traits in blue fox selection is not likely to significantly weaken the animals' eye health. The adverse effect of large size and fatness cannot, however, be completely ruled out, if undesirable features, such as a massive coat, loose or superfluous skin on the head or excessive subcutaneous fatty tissue, cause folds of skin on the face and predispose the fox to eye infection (V).

The introduction of live animal body length into the selection criteria would offer the opportunity to breed long, slim blue foxes with good leg conformation and large pelt size. Selection for longer animals would not appear to have any major influence on BCS (fatness), leg weakness, susceptibility to eye infection, FE or pelt character traits, whereas we found a high favourable genetic correlation between length and pelt size (II-V). However, the results show one unfavourable genetic correlation: namely, between body length and the fox's ability to move about (IV). This may partly be explained by the correlated response to selection for size, taking into account that animal size has a favourable genetic correlation with length but an antagonistic correlation with ability to move about. It should also be borne in mind that excessive body length may increase the risk of intervertebral disc abnormalities, as observed in some dog breeds (Packer et al. 2013).

5.4 IMPLICATIONS AND FUTURE DEVELOPMENTS

5.4.1 DATA COLLECTION ON THE NEW TRAITS

Fur producers can register information on the foxes' new health and conformation traits (BCS, leg conformation and eye infection) into centralized data systems, which enable monitoring the state of diseases in the fur animal population and taking preventive action before the health situation grows worse. The centralized database is supported by WebSampo breeding software (Saga Furs Oyj) and the voluntary national health surveillance system Fureva which is provided by the Finnish Fur Breeders' Association. In addition, the WelFur protocol (WelFur 2014) includes evaluation of welfare and conformation traits (leg, eye and BCS), but the data are not collected to selection purposes. WelFur is a science-based animal welfare assessment programme, which was taken into use in European countries in 2017 and was integrated into the certification system of Finnish fur farms. The aim is to create transparency around animal welfare standards and help fur producers to identify areas that need attention and improvement. Further, the BCS evaluation system developed in this research

project has recently been integrated into the updated feeding recommendations for Finnish blue foxes (Luke 2016).

The health survey data on the studied traits collected in the WebSampo software can be utilized for selection purposes. The BLUP-index, which is based on a multiple-trait animal model, enables to simultaneously take into account several health and production traits as well as their antagonistic interactions in national blue fox breeding value estimation. The obtained breeding values can then be used to improve genetic progress in the Finnish blue fox population.

Data collection through the national breeding programme needs to be developed further. The national breeding scheme has great potential if it is expanded to a larger population and larger number of farms. Currently, only a third of Finnish fox farms take part in the national breeding value evaluation of blue foxes, while the majority use their own breeding methods which are not controlled by the central breeding organization. Thus, at the moment it is not possible to utilize their data or to monitor their selective breeding methods, goals and results.

5.4.2 ECONOMIC WEIGHTS OF THE TRAITS

The economic values used for traits in breeding schemes need to be weighted according to the desired gain, if the aim is to achieve genetic improvement in some traits while keeping a certain trait unchanged. The genetic parameters obtained in this research for pelt size (cm), FE and susceptibility to eye infection (II-V) were used by Peura et al. (2016a, 2016b) in further studies to estimate economic values for these traits. The economic value for FE is almost in the same order of magnitude as for pelt quality and higher than for pelt size, but clearly lower than for fertility traits or eye health (Peura et al. 2016a). Although the economic value estimated for FE is lower than expected, it is in the range reported in Danish mink (Meier et al. 2014).

Surprisingly, the economic value calculated by Peura et al. (2016b) for susceptibility to eye infection is so high that it is among the most significant economic traits, right after fertility traits. When eye infection is so severe that the animal has to be culled before pelting, the ensuing economic losses are significant, since most of the production costs invested in the animal have been realized by then (Peura et al. 2016a).

Assessing the economic value for a trait like leg conformation is quite difficult (Peura et al. 2016a, 2016b). Public opinion, consumers and politicians create outside pressure on the fur industry, and the economic value of any animal welfare trait can be very high, if the condition for allowing the fur industry to continue production is good animal welfare. Sustainable breeding schemes should support ethical animal production values and help to raise healthy foxes without major welfare problems. However, recent WelFur results show no improvement in leg conformation among blue foxes (n=4688 on 81 farms), reporting a high frequency of mild

leg weakness and clear bending of legs: 56.5% and 30%, respectively (Mononen et al. 2012; Ahola et al. 2014). The unfavourable genetic correlations observed between size traits and leg weakness (IV), imply that leg conformation is likely to keep on deteriorating if breeding selection continues to emphasize larger animal size, unless some counteractive selection is practised. This was demonstrated in a simulation study on alternative blue fox selection strategies by Peura et al. (2016b). Higher economic gain could be achieved by adding two new selection criteria (FE and leg conformation) to the traits in the BLUP evaluation model than by using only the current selection criteria (animal size, pelt quality and litter size) (Peura et al. 2016b, 2018). Nevertheless, the genetic gain in leg conformation remained negative in the simulation study if its economic value was assumed to be zero. The authors concluded that if leg conformation is to be improved, the trait should be assigned a substantial relative weight in the total merit index (Peura et al. 2016a, 2016b, 2018). This would reduce the total genetic gain by only about 3-4% (Peura et al. 2018). Additional studies and controlled animal trials are currently underway (2016-2019) to increase the understanding of the factors affecting leg weakness (Korhonen et al. 2017). The aim is to develop genetic and nutritional tools to prevent leg problems in blue foxes and to introduce a new advisory service culture through which the results can be effectively implemented into practice.

5.4.3 OTHER NEW TRAITS

Feed efficiency, measured as the ratio of the animal's body length or body mass index to its feed consumption, offers an interesting subject for further research. A more compatible definition for FE needs to be determined which duly takes into account animal welfare and health aspects as well. Selection for FE must not result in increased fatness in foxes. In the ideal situation, selection for longer body length and lower fatness would lead to better FE and large pelts (Peura et al. 2017). Body weight is also an important objective measure, which is needed in the assessment of several other traits, such as body mass index, growth rate and FE. It is therefore important to develop practical methods for weighing foxes for implementation on farms to overcome the difficulties currently faced by fur producers.

Diarrhoea is a health trait that is loosely connected to feed efficiency. A healthy animal is capable of digesting and using its food efficiently for growth, whereas diarrhoea can decrease the animal's FE through an increased maintenance energy requirement and reduced nutrient intake, thus leading to poor growth rate (Patience et al. 2015). Diarrhoea is a serious health problem in blue foxes: Ahola et al. (2014) reported an average frequency as high as 27.4% in blue foxes before pelting. So far, the possible genetic background of susceptibility to intestinal problems has not been studied in blue foxes.

Discussion

It seems that leg weakness is not the only conformation problem in the Finnish blue fox population. Preliminary studies on orthopaedic abnormalities in blue foxes indicate that juvenile individuals may suffer from incipient and mild skeletal problems (Korhonen et al. 2005; Mustonen et al. 2017). The prevalence and severity of these problems needs to be investigated further before conducting genetic studies on the traits.

6 CONCLUSIONS

There is strong social pressure for better welfare of fur animals, making it necessary to broaden current breeding goals and focus selection on diverse traits. The main objective of this research project was to develop breeding value evaluation of new production, conformation and health traits for potential introduction into the blue fox breeding programme. The developed methods proved to be suitable for scoring of the studied health and conformation traits, and they have recently been implemented into the WebSampo breeding software, WelFur protocol and feeding recommendations for Finnish blue foxes. The genetic parameters estimated in this research are the first to be reported for these traits in blue foxes. The results show a reasonable amount of genetic variation in their body condition score, body length, leg conformation, ability to move about and susceptibility to eye infection, with heritability estimates ranging from moderate to high. Thus, there is good potential for genetic improvement of conformation and health traits in the Finnish blue fox population through breeding selection.

From the genetic point of view, selection for feed efficiency also seems possible, although certain practical problems need to be resolved before it can be implemented into the breeding programme. The challenges are related to weighing the animals and measuring their feed intake, as well as to the high cost of these measurements. In addition, FE should be defined in a way that will not lead to larger grading size and fatness, which might increase feed consumption and impair the welfare traits. We found it reasonable to measure FE between weaning and 20 weeks of age, because at that age the emphasis in growth is on lean tissue instead of fat deposition, which accumulates later. Selective breeding for maintenance of adequate muscle mass can be expected to have a beneficial effect on the foxes' body composition and welfare, especially on their ability to move about.

Body length was found to be a promising size trait for selection, as it is not genetically correlated with BCS. Moreover, selection for longer animals does not appear to have any major unfavourable genetic effect on the studied welfare or pelt character traits. A long animal can produce a large pelt without being fattened excessively. Thus, the original idea of this research: to support breeding of well-structured, long and slim blue foxes by broadening the breeding goals, seems feasible. Still, there are several problematic trait combinations in the blue fox breeding scheme which need to be investigated further.

Fatness is a key welfare problem, which has unfavourable side effects on fertility, leg conformation, eye health and general wellbeing. Blue foxes have a high natural genetic ability to store fat. The current breeding goals and feeding recommendations can strengthen this ability because of the favourable influence of animal fatness on economically important production

traits, particularly pelt size and quality. But despite the genetic background of BCS, the fastest way to reduce fatness in blue foxes is to use a restricted feeding regime, since fatness is ultimately related to energy imbalance: too many calories consumed and/or too few calories burned, which causes the accumulation of adipose tissue in the body.

Leg conformation and ability to move about is likely to continue to worsen in the Finnish blue fox population as a result of the current breeding goals, unless these traits are taken into account in the breeding programme. Feeding management also needs to be reconsidered to support better leg conformation and ability to move about. Selection focusing on better grading fur density is linked to large phenotypic size and fatness, and can impair the animals' eye health. Extremely fat foxes typically have a massive coat and skin folds due to subcutaneous fatty tissue, which may change their face conformation and provoke eye infection. Heavy slimming for the breeding season can further aggravate the problem of loose skin on the face and lead to hanging eyelids (ectropion) and increased susceptibility to eye infection. Besides genetic selection, better animal management can also help to improve eye health in blue foxes.

It is recommended that breeding animals should be selected early in life based on their estimated breeding values and then subjected to a restricted feeding regime, because this enables longer-term control of BCS, body weight and growth rate. Genomic selection would reduce the need for fattening and slimming of breeding stock, because the best breeding candidates could be selected already as puppies.

The obtained genetic parameters indicate that the Finnish blue fox breeding programme could be expanded to include traits related to the animals' welfare. Currently the most effective selection method to improve these traits is to use BLUP breeding values estimated by the multiple-trait animal model. The model makes it possible to take simultaneously into account several health and production traits as well as their detected antagonistic genetic correlations in national blue fox breeding value estimation. In addition, it is important to weight the estimated breeding values optimally in the total merit index. The weighting of welfare traits can be based on the economic and/or social relevance of the trait.

REFERENCES

- Ahola, L. K., Huuki, H., Hovland, A. L., Koistinen, T. & Mononen, J. 2012. WelFur – foxes: the inter-observer reliability of the WelFur health measures, and the prevalence of health disorders on fox farms during the growth period. In: Proceedings of the Xth International Scientific Congress in fur animal production (eds. Larsen et al.). *Scientifur* 36 (3/4): 441–447.
- Ahola, L., Huuki, H., Koistinen, T. & Mononen, J. 2014. Eläinten hyvinvointi suomalaisilla kettutiloilla – tuloksia tilakäynneiltä. [Animal welfare on Finnish blue fox farms – results from farm visits]. *Turkistila 2020 -hanke. MTT Raportti* 179. 101 p. [in Finnish]
- Banos, G., Coffey, M. P., Wall, E. & Brotherstone, S. 2006. Genetic relationship between first lactation body energy and later life udder health in dairy cattle. *Journal of Dairy Science*, 89: 2222–2232.
- Barnett, K. C. 1988. Inherited eye disease in the dog and cat. *Journal of Small Animal Practice*, 29: 462–475.
- Benn, R. T. 1971. Some mathematical properties of weight-for-height indices used as measures of adiposity. *British Journal of Preventive and Social Medicine*, 28: 42–50.
- Berg, P. 1993. Present knowledge about heritability of different traits in mink. *NJF Utredning/Rapport*, 90, NJF workshop, Viborg, Denmark. 10 p.
- Berg, P. & Lohi, O. 1992. Feed consumption and efficiency in paternal progeny groups in mink. *Acta Agriculturae Scandinavica*, 42: 27–33.
- Berg, P. & Krogh Hansen, B. K. 2006. Modelling feed conversion efficiency in mink. Proceedings of the NJF seminar no 392, August 22–25, Akureyri, Iceland. 4 p.
- Berry, D. P., Buckley, F., Dillon, P., Evans, R. D., Rath, M. & Veerkamp, R. F. 2003. Genetic parameters for body condition score, body weight, milk yield and fertility estimated using random regression models. *Journal of Dairy Science*, 86: 3704–3717.
- Bishop, S. C. 2011. Breeding for disease resistance in farm animals. 3rd ed. CABI Publishing, 368 p.
- Cai, W., Casey, D. S. & Dekkers, J. C. M. 2008. Selection response and genetic parameters for residual feed intake in Yorkshire swine. *Journal of Animal Science*, 86: 287–298.
- Çetinkaya, M. A., Yardimci, C. & Sağlam, M. 2007. Carpal laxity syndrome in forty-three puppies. *Veterinary and comparative orthopaedics and traumatology*, 20: 126–130.
- Dahlman, T. 2003. Protein and amino acids in the nutrition of the growing-furring blue fox. Academic dissertation, University of Helsinki, Finland. 33 p.
- Dempster, E. R. & Lerner, I. M. 1950. Heritability of threshold characters. *Genetics*, 35: 212–236.
- Edmonson, A. J., Lean, I. J., Weaver, L. D., Farver, T. & Webster, G. 1989. A body condition scoring chart of Holstein dairy cows. *Journal of Dairy Science*, 72: 68–78.
- Everett-Hincks, J. M. & Cullen, N. G. 2009. Genetic parameters for ewe rearing performance. *Journal of Animal Science*, 87: 2753–2758.

References

- Falconer, D.S. & Mackay, T. F. C. 1996. Introduction to quantitative genetics. 4th ed. Longman Group Ltd., London, UK. 464 p.
- Ferguson, J. D., Galligan, D. T. & Thomsen, N. 1994. Principal descriptors of body condition score in Holstein cows. *Journal of Dairy Science*, 77: 2695–2703.
- Gianola, D. 1982. Theory and analysis of threshold characters. *Journal of Animal Science*, 54: 1079–1096.
- Hansen, B. K, Møller, S. H., Berg, P. & Bækgaard, H. 2009. Validation of a method for body condition scoring. Annual report 2008, Danish Fur Breeders Research Center, Holstebro, Danmark. p. 129-135. [In Danish].
- Henneke, D. R., Potter, G. D., Kreider, J. L. & Yeates, B. F. 1983. Relationship between condition score, physical measurements and body fat percentage in mares. *Equine Veterinary Journal*, 15: 371–372.
- Huhti, P. 2005. Siniketun kasvun ja sen koostumuksen mallintaminen. [Modelling of blue fox growth and its composition]. Master's thesis, University of Helsinki, Animal nutrition, Finland. 110 p. [in Finnish]
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., Teacher, A., Bininda-Emonds, O. R. P., Gittleman, J. L., Mace, G. M. & Purvis, A. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90: 2648.
- Jørgensen, B. & Andersen, S. 2000. Genetic parameters for osteochondrosis in Danish Landrace and Yorkshire boars and correlations with leg weakness and production. *Animal Science*, 71: 427–434.
- Kempe, R. & Strandén, I. 2016. New breeding value evaluation of litter size in Finnish blue fox. In: Proceedings of the XIth International Scientific Congress in Fur Animal Production (Eds. Mäki-Tanila, A., Valaja, J., Mononen, J., Sironen, T. & Vapalahti, O.). Helsinki, Finland, 23–26 Aug 2016. *Scientifur*, 40 (3/4): 153–157.
- Kempe, R. M. & Strandén, I. 2018. Joint breeding value evaluation for fertility in Finnish and Norwegian blue foxes. *Journal of Animal Breeding and Genetics*, 00: 1–13. Available at: <https://doi.org/10.1111/jbg.12363>
- Kenttämies, H. & Smeds, K. 1992a. Repeatability of subjective grading in fur animals II: Grading of mink and blue fox pelts. *Agricultural Science in Finland*, 1: 315–322.,
- Kenttämies, H. & Smeds, K. 1992b. Repeatability of subjective grading in fur animals III: Grading of live blue foxes in different environmental conditions. *Agricultural Science in Finland*, 1: 315–322.
- Keski-Nisula, S. 2006. Siniketun tuotanto-ominaisuuksiin vaikuttavien kromosomialueiden kartointi [Survey of chromosome areas affecting production traits in the blue fox]. Master's thesis, University of Helsinki, Kotieläintieteen laitoksen julkaisu 82. 37 p. [in Finnish]
- Kinghorn, B. 2000. Nucleus breeding schemes. In: *Animal Breeding Use of New Technologies*. Post Graduate Foundation in Veterinary Science of the University of Sydney, Australia. p. 152–158.
- Koenen, E. P. C., Veerkamp, R. F., Dobbelaar, P. & De Jong, G. 2001. Genetic analysis of body condition score of lactating Dutch Holstein and Red-and-White heifers. *Journal of Dairy Science*, 84: 1265–1270.
- Koivula, M., Mäntysaari, E. & Strandén, I. 2009. New fertility traits in breeding value evaluation of Finnish blue fox. *Acta Agriculturae Scandinavica*, 59: 131–136.

- Korhonen, H. T., Eskeli, P., Lappi, T., Huuki, H. & Sepponen, J. 2014. Effects of feeding intensity and Ca:P ratio on foot welfare in blue foxes (*Vulpes lagopus*). *Open Journal of Animal Sciences*, 4: 153–164.
- Korhonen, H. T., Happo, M., Rekilä, T., Valaja, J. & Pölonen, I. 2005. Effects of diet calcium:phosphorous ratio and metabolizable energy content on development of osteochondrosis, foot bending and performance in blue foxes. *Animal Science*, 80: 325–331.
- Korhonen, H. T., Jauhiainen, L., Niemelä, P., Harri, M. & Sauna-aho, R. 2001. Physiological and behavioural responses in blue fox (*Alopex lagopus*): comparisons between space quantity and floor material. *Animal Science*, 72: 375–387.
- Korhonen, H. T. & Niemelä, P. 1994. Comparison of production results between blue foxes housed with and without platforms. *Agricultural Science in Finland*, 4: 351–361.
- Korhonen, H. T., Niemelä, P., Jauhiainen, L. & Tupasela, T. 2000. Effects of space allowance and earthen floor on welfare-related physiological and behavioural responses in male blue foxes. *Physiology & Behaviour*, 69: 571–580.
- Korhonen, H. T., Ojala, E., Moisander-Jylhä, A. M., Kempe, R., Sepponen, J., Koistinen, T. & Peura, J. 2017. Effects of plan of feeding on foot condition and animal welfare in blue foxes. *Proceedings of NJF Seminar 498: Annual Autumn Meeting in Fur Animal Research*, 18–20 October 2017, Oslo, Norway. p. 55–56.
- Kosgey, I. S., Baker, R. L., Udo, H. M. J. & Van Arendonk, J. A. M. 2006. Successes and failures of small ruminant breeding programmes in the tropics: a review. *Small Ruminant Research* 61: 13–28.
- Koskinen, N. & Lassen, M. 2006. The occurrence of fatty livers and the influence of feeding, feed composition and quality on fatty liver syndrome on fur animals. *NJF Seminar 392*, Aug 22–25, Akureyri, Iceland. p. 71.
- Koskinen, N., Sepponen, J., Kupsala, K. & Rekilä, T. 2007. Effects of early selection and body conditioning of young blue fox *Alopex lagopus* females on breeding result, a field study. *NJF Seminar 403*, Aug 13–15, Kolding, Denmark. 7 p.
- Koskinen, N., Tauson, A.-H., Sepponen, J. & Rekilä, T. 2008. Feeding history affects cub survival of young breeding blue foxes (*Alopex lagopus*), a field study. *Scientifur*, 32: 16–17.
- Kovac, M. & Groeneveld, E. 1990. Multivariate genetic evaluation in swine combining data from different testing schemes. *Journal of Animal Science*, 68: 3507–3522.
- Krogh Hansen, B. & Berg, P. 1997. Mink kit growth performance in the suckling period. *Acta Agriculturae Scandinavica*, 47: 240–246.
- Krogh Hansen, B. & Berg, P. 2006. Prediction of breeding values for feed conversion rate – Validating models. *NJF Seminar 392*, Aug 22–25, Akureyri, Iceland. 6 p.
- Krogh Hansen, B., Berg, P., Hunnicke Nielsen, V. & Møller, S. H. 2007. Genetics of feed conversion rate in different growth phases of mink. *NJF Seminar 403*, Aug 13–15, Kolding, Denmark. 8 p.
- Laflamme, D. P. 1997. Development and validation of a body condition score system for dogs. *Canine Practise*, 22: 10–15.
- Lagerkvist, G., Johansson, K. & Lundeheim, N. 1994. Selection for litter size, body weight and pelt quality in mink (*Mustela vison*): Correlated responses. *Journal of Animal Science*, 72: 1126–1137.

References

- Le Bihan-Duval, E., Beaumont, C. & Colleau, J. J. 1996. Genetic parameters of the twisted legs syndrome in broiler chickens. *Genetics Selection Evolution*, 28: 177–195.
- Le Bihan-Duval, E., Beaumont, C. & Colleau, J. J. 1997. Estimation of the genetic correlations between twisted legs and growth or conformation traits in broiler chickens. *Journal of Animal Breeding and Genetics*, 114: 239–259.
- Lohi, O. 2002. Genetics of furs and special fibres. Proceedings of the 7th World Congress on Genetics Applied to Livestock Production, Montpellier, France. CD-ROM communication No. 12–07.
- Love, S., Wyse, C. A., Stirk, A. J., Stear, M. J., Calver, P., Voute, L. C. & Mellor, D. J. 2006. Prevalence, heritability and significance of musculoskeletal conformational traits in thoroughbred yearlings. *Equine Veterinary Journal*, 38: 597–603.
- Luke, 2016. Luke Natural Resources Institute Finland, Feed tables. Available at: <https://portal.mtt.fi/portal/page/portal/Rehutaulukot>. Accessed 2 Dec 2016.
- Madsen, P. & Jensen, J. 2012. A user's guide to DMU. A package for analysing multivariate mixed models. Version 6, release 5.1. Danish Institute of Agricultural Sciences, Tjele, Denmark. 22 p.
- Martin, P. & Bateson, P. 2007. Measuring behaviour. An introductory guide. Cambridge University Press, Cambridge, UK. 176 p.
- Meier K., Sørensen A. C., Thirstrup J. P. & Lund M. S. 2014. Genomic selection in mink (*Neovison vison*): A simulation study. In: Proceedings of NJF seminar 482. Denmark, 30 Sep–3 Oct 2014. p. 122–129.
- Moisander-Jylhä A-M 2017. Tuottava siniketun kasvatusta. Osat 1–5: Terveys. [Profitable blue fox production. Part 1–5: Health]. Vuosikiertotiedotteet 7–11. 10 p. Available from <http://www.kpedu.fi/kampanjat/ajantasalla/turkisalan-vuosikiertotiedotteet>. Cited 4th April 2018. [in Finnish]
- Mononen, J., Møller, S. H., Hansen, S. W., Hovland, A. L., Koistinen, T., Lidfors, L., Malmkvist, J., Vinke, C. M. & Ahola, L. 2012. The development of on-farm welfare assessment protocols for foxes and mink: the WelFur project. *Animal Welfare*, 21: 363–371.
- Mrode, R.A. & Kennedy, B. W. 1993. Genetic variation in measures of food efficiency in pigs and their genetic relationships with growth rate and backfat. *Animal Production*, 56: 225–232.
- Mustonen, A.-M., Lawler, D. F., Ahola, L., Koistinen, T., Jalkanen, L., Mononen, J., Lamidi, M.-L. & Nieminen, P. 2017. Skeletal pathology of farm-reared obese juvenile blue foxes (*Vulpes lagopus*). *Journal of Veterinary Anatomy*, 10: 51–74.
- Mäntysalo, E. & Blomstedt, L. 1995. Properties of leathers produced from blue fox pelts taken from animals treated in vivo with melatonin. *Journal of the American Leathers Chemists' Association*, 85: 465–473.
- Nikula, S., Smeds, K., Hietanen, H., Kenttämies, H. & Ojala, M. 2000. Confident behaviour and production traits – results from a field study of foxes. In: B.D. Murphy, O. Lohi (eds), Proceedings of the VIIth Congress on Fur Animal Production. Scientifur, 24: 99–102.
- Nordgren, H., Aaltonen, K., Sironen, T., Kinnunen, P. M., Kivistö, I., Raunio-Saarnisto, M., Moisander-Jylhä, A.-M., Korpela, J., Kokkonen, U.-M., Hetzel, U., Sukura, A. & Vapalahti, O. 2014. Characterization of a new epidemic necrotic pyoderma in fur animals and its association with *Arcanobacterium phocae* infection. *PloS One*, 9(10): e110210.

- Oldenbroek, K. & van der Waaij, L. 2015. Textbook Animal Breeding and Genetics for BSc students. Centre for Genetic Resources The Netherlands and Animal Breeding and Genomics Centre, 2015, 311 p. Available from: Groen Kennisnet: <https://wiki.groenkennisnet.nl/display/TAB/>
- Packer, R. M. A., Hendricks, A., Volk, H. A., Nadia K., Shihab, N. K. & Burn, C. C. 2013. How Long and Low Can You Go? Effect of Conformation on the Risk of Thoracolumbar Intervertebral Disc Extrusion in Domestic Dogs. *PLoS One*, 8(7): e69650.
- Patience, J. F. 2012. Feed efficiency in swine. Wageningen Academic Publishers, The Netherlands. 275 p.
- Patience, J. F., Rossoni-Serão, M. C. & Gutiérrez, N. A. 2015. A review of feed efficiency in swine: biology and application. *Journal of Animal Science and Biotechnology*, 6: 33–41.
- Peura, J. 2013. Optimization of the current breeding scheme for blue fox. Academic dissertation, University of Helsinki. Department of agricultural sciences publications 2013: 19. 46 p.
- Peura, J., Kempe, R., Strandén, I. & Rydhmer, L. 2016a. Risk aversion affects economic values of blue fox breeding scheme. *Journal of Animal Breeding and Genetics*, 133: 485–492.
- Peura, J., Strandén, I. & Mäntysaari, E. A. 2005. Genetic parameters in Finnish blue fox population: Pelt character and live animal grading traits. *Acta Agriculturae Scandinavica*, 55: 137–144.
- Peura, J., Strandén, I. & Mäntysaari, E. 2007. Genetic parameters for Finnish blue fox population: litter size, age at first insemination and pelt size. *Agricultural and food science*, 16: 136–146.
- Peura, J., Strandén, I. & Smeds, K. 2004. Genetics of litter size, age at first insemination and animal size in blue fox (*Alopex lagopus*). *Scientifur*, 28: 206–210.
- Peura, J., Sørensen, A. C. & Rydhmer, L. 2016b. Towards genomic selection – stochastic simulation of alternative blue fox selection strategies. In: Proceedings of the XIth international scientific congress in fur animal production (Eds. Mäki-Tanila, A., Valaja, J., Mononen, J., Sironen, T. & Vapalahti, O.). Helsinki, Finland, 23–26 Aug 2016. *Scientifur*, 40 (3/4): 167–171.
- Peura, J., Sørensen, A. C. & Rydhmer, L. 2018. Strategies for genetic improvement of leg conformation in a Finnish blue fox population. In: Proceedings of World Congress on Genetics Applied to Livestock Production. Auckland, New Zealand, 11–16 Feb. Volume Electronic Poster Session - Genetic Gain - Breeding Strategies 2. 5 p.
- Peura, J., Viksten, S., Kempe, R., Strandén, I. & Mäki-Tanila, A. 2017. Weight-for-length index as a measure of obesity in blue foxes. Proceedings of NJF Seminar 498: Annual Autumn Meeting in Fur Animal Research, 18–20 October 2017, Oslo, Norway. p. 122–127.
- Prestrud, P. 1991. Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter. *Arctic*, 44: 132–138.
- Prestrud, P. & Pond, C. M. K. 2003. Fat indices of Arctic foxes *Alopex lagopus* in Svalbard. *Wildlife Biology*, 9: 193–197.
- ProFur 2016. Tilastot, statistik 2016. [Statistics]. Cited 20 Oct, 2016. Available from: www.profur.fi. 35 p. [in Finnish and Swedish]

References

- Rekilä, T., Korhonen, H., Pölönen, I. & Harri, M. 2000. Relationships between feed intake, body mass and skin length in blue fox. In: Murphy, B.D., Lohi, O. (Eds.), Proceedings of the VIIth International Scientific Congress in Fur Animal Production, Kastoria, Greece, 13–15 Sep 2000. *Scientifur*, 24: 155–158.
- Rekilä, T., Korhonen, H., Siirilä, P., Valaja, J., Pölönen, I. & Sauna-aho, R. 2001. Varhaiskasvunajan rehun energiapitoisuuden ja Ca:P -suhteen vaikutus siniketun etujalkojen kehitykseen [The effect of energy content and Ca:P ratio of growth feed on development of forelegs in the blue fox]. *Rehunvalmistajien luentopäivät*, Nokia, Finland, 30–31 Jan 2001. 4 p. [in Finnish]
- Rintamäki, M., Wiksten, A. & Jauhiainen, L. 2007. Nahkontapaino ja nahan pituus: Saadaanko painavasta eläimestä myös iso ja laadukas nahka? [Pelting weight and pelt length: Do you get large and high quality pelt from a heavy animal?] *Turkistalous*, 8/2007: 20–22. [in Finnish]
- Risku-Norja, H., Mäenpää, I., Vanhala, P., Koikkalainen, K. & Rikkinen P. 2002. Material flows, coefficient and sustainable compatibility of food production. Technical documentation. MTT:n selvityksiä no. 27. 112 p.
- Rouvinen-Watt, K., White, M. B. & Campbell, R. 2005. Mink Feeds and Feeding, Applied Feeding Guide and Mink Feed Ingredient Database. CD-ROM version. Ontario Ministry of Agriculture and Food, through the Agricultural Research Institute of Ontario, and the Nova Scotia Agricultural College.
- Saarenmaa, K. 1990. Skillnader mellan blåävshanarnas indexer. [Differences between blue fox females' indices]. NJF-Utredning/rapport nr. 60. Resultater af de senaeste års nordisk pelsdyrforskning. Foredrag ved NJF seminar nr. 185. [in Norwegian]
- Sandøe, P., Nielsen, B. L., Christensen, L. G. & Sorensen, P. 1999. Staying good while playing god – the ethics of breeding farm animals. *Animal Welfare*, 8: 313–328.
- Sanson, G. & Ahlstrøm, Ø. 2005. Effect of body weight on reproductive success in blue fox. Proceedings of NJF Seminar No. 377, Uppsala, Sweden, 5–7 Oct 2005. p. 9.
- Sepponen, J., Korhonen, H. T., Eskeli, P. & Koskinen, N. 2014. Siniketun energia-aineenvaihdunnan määrittäminen [Determination of energy metabolism in blue fox]. Loppuraportti. Maa- ja elintarviketalouden tutkimuskeskus MTT, Kotieläintuotannon tutkimus. 27 p. Available from: <http://docplayer.fi/5005967-Siniketun-energia-aineenvaihdunnan-maarittaminen.html> [in Finnish]
- Serenius, T., Sevón-Aimonen, M.-L. & Mäntysaari, E. A. 2001. The genetics of leg weakness in Finnish Large White and Landrace populations. *Livestock Production Science*, 69: 101–111.
- Shirali, M., Nielsen, V. H., Møller, S. H. & Jensen, J. 2015. Longitudinal analysis of residual feed intake and BW in mink using random regression with heterogeneous residual variance. *Animal*, 9: 1597–1604.
- Silvenius, F., Koskinen, N., Kurppa, S., Rekilä, T., Sepponen, J. & Hyvärinen, H. 2012. Life cycle assessment of mink and fox pelts produced in Finland. *Scientifur*, 36: 106–111.
- Sirkko, K. 2000. Eri alkuperää olevien sinikettujen kokoerot ja muut ominaisuudet kasvatuskauden eri vaiheissa [Differences in size and other characteristics in blue fox during the growth season]. Master's thesis, University of Helsinki, Finland. 39 p. [in Finnish]

- Socha, S. 2004. Genetic parameters of size and fur quality in a mink population (*Mustela vison* Sch.). *Scientifur*, 28: 251–253.
- Strandén, I. & Vuori, K. 2006. Relax2: pedigree analysis programme. In: Proceedings of the 8th World Congress on Genetics Applied to Livestock Production. Belo Horizonte, Brazil, 13–18 Aug 2006. p. 27–30.
- SVT 2017. Suomen virallinen tilasto. Kotieläinten lukumäärä [Finnish Official Statistics: Number of farm animals]. Helsinki. Luonnonvarakeskus. Cited 27 Nov, 2017. Available from: <http://stat.luke.fi/tilasto/36>. [in Finnish]
- Switonski, M., Stachowiak, M., Cieslak, J., Bartz, M. & Grzes, M. 2010. Genetics of fat tissue accumulation in pigs: a comparative approach. *Journal of Applied Genetics*, 51: 153–168.
- Sørensen, K. 2002. Selection for feed efficiency in mink (*Mustela vison*). Ph.D. thesis. The Royal Veterinary and Agricultural University, Copenhagen. 108 p.
- Vaughan, L. C. 1992. Flexural deformity of the carpus in puppies. *Journal of Small Animal Practice*, 33: 381–384.
- Von Felde, A., Roeche, R., Looft, H. & Kalm, E. 1996. Genetic association between feed intake and feed intake behaviour at different stages of growth of group-housed boars. *Livestock Production Science*, 47: 11–12.
- WelFur 2014. WelFur welfare assessment protocol for foxes. WelFur consortium, Brussels, Belgium. 130 p.
- Whitley, R. D. 2000. Canine and feline primary ocular bacterial infections. *Veterinary Clinics of North America: Small Animal Practice*, 30: 1151–1167.
- Zoran, D. L. 2010. Obesity in Dogs and Cats: A Metabolic and Endocrine Disorder. *Veterinary Clinics of North America: Small Animal Practice*, 40: 221–239.