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Breeding Against Hip and Elbow Dysplasia in Dogs

Katariina Mäki

Academic dissertation

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Cover:

Molla (Birch Bark's Amore) and **Wilma** (Eliitin Ebony Eugenie), my Cavalier King Charles Spaniels, who have given me a personal touch with hereditary problems in dogs. Molla has hip dysplasia, elbow dysplasia, spondylosis deformans, and some structural problems of the muzzle and throat. She is now ten years old. Wilma had to be put down when she was seven, because of a severe chronic valvular disease, typical for Cavaliers. She had also epilepsy.

Abstract

The objective of this study was to develop breeding strategies to reduce the incidence of canine hip and elbow dysplasia. For this purpose, investigations were conducted on the mode of inheritance as well as genetic parameters, genetic trends and selection differentials for the traits. Population structure and inbreeding were also examined, and finally, various selection schemes were compared by a simulation study to find out potential genetic responses and possibilities for a comprehensive breeding program.

Screening information for hip and elbow dysplasia, collected within the health program of the Finnish Kennel Club, was used. A total of 42 421 records on hip dysplasia and 13 543 on elbow dysplasia were available on seven breeds, the German Shepherd, the Golden Retriever, the Labrador Retriever, the Rottweiler, the Bernese Mountain Dog, the Finnish Hound and the Rough Collie.

Based on the results of this thesis, both hip and elbow dysplasia seemed to be quantitative traits. Neither of the traits fitted to a mitochondrial or sex-linked inheritance. According to segregation analysis, a major gene could be segregating in hip dysplasia in four studied breeds.

Estimates of heritabilities in the studied breeds indicated that there is sufficient genetic variation for successful selection of breeding dogs according to their dysplasia status. The positive, although mainly low, estimates of genetic correlations between hip and elbow dysplasia allow for simultaneous selection for both traits. In spite of this, the genetic level of hip dysplasia had improved over the study period only in the Rottweiler, while the genetic levels were getting worse in the other three studied breeds. For elbow dysplasia, a slight improvement was noticed in all studied breeds. However, the phenotypic selection differentials for both hip and elbow dysplasia were quite small in all studied breeds.

Despite of the weak selection practised against hip and elbow dysplasia, the populations studied in this thesis were observed to be otherwise under stringent selection, since only a small proportion of annually born animals were used later for breeding. In addition to the small proportion of breeding animals, a few sires had been excessively favoured in breeding. Besides passive inbreeding due to the resulting small effective population sizes, inbreeding had also been used actively in the studied breeds. The inbreeding coefficient of a dog had a significant detrimental effect for hip dysplasia in the German Shepherd and the Labrador Retriever. No inbreeding depression for elbow dysplasia was observed. However, the amount of pedigree information used in this thesis was not necessarily sufficient to properly study inbreeding depression.

Potential genetic responses for hip and elbow dysplasia were studied by simulation. When simultaneously selecting for hip and elbow dysplasia, as well as behaviour and appearance, a very small relative index weight for appearance was enough to maintain the trait without negative genetic gain. The only way to reach the breeding goal set for hip and elbow dysplasia was to clearly favour the traits in the selection. Behaviour traits should receive also much more emphasis than has been given to them so far.

The most effective selection against hip and elbow dysplasia would be based on BLUP breeding values. However, the accuracy of the breeding values could be improved if a larger proportion of the dogs were screened for hip and elbow dysplasia. Further, if major genes affecting hip and elbow dysplasia exist, considerable genetic progress could be achieved by selection for them, since the possibly existing unfavourable alleles were found to have relatively high frequencies.

Systematic breeding programs, including preservation of genetic variation, should be developed and followed to maintain or improve the desired behaviour and working traits, as well as the health of the dogs in the current populations.

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1 Original articles

This thesis is based on the following original papers, which are referred to in the text by their Roman numerals:

I Mäki, K., Liinamo, A.-E. and Ojala, M. 2000. Estimates of genetic parameters for hip and elbow dysplasia in Finnish Rottweilers. Journal of Animal Science 78: 1141-1148.

II Mäki, K., Groen, A.F., Liinamo, A.-E. and Ojala, M. 2001. Population structure, inbreeding trend and their association with hip and elbow dysplasia in dogs. Animal Science 73: 217-228.

III Mäki, K., Groen, A.F., Liinamo, A.-E. and Ojala M. 2002. Genetic variances, trends and mode of inheritance for hip and elbow dysplasia in Finnish dog populations. Animal Science 75: 197-207.

IV Mäki, K., Janss, L.L.G., Groen, A.F., Liinamo, A.-E. and Ojala M. 2004. An indication of major genes affecting hip and elbow dysplasia in four Finnish dog populations. Heredity, in press.

V Mäki, K., Liinamo, A.-E., Groen, A.F., Bijma, P. and Ojala M. 200X. Genetic responses for hip and elbow dysplasia, behaviour traits and appearance from alternative breeding schemes in a dog population. Manuscript, submitted.

Contribution of the author to the papers:

The author participated in the planning of the study, conducted the statistical analyses and simulations, interpreted the results and was the main writer of the papers.

2 Introduction

2.1 General breeding objectives of dogs

Most dog breed associations in Finland state their breeding objective to be "a healthy dog with a good character". In breeds where the majority of dogs are used for working, such as hunting, this objective is also put into practice: the performance of the dogs is used as the main criterion when selecting animals for breeding (e.g., Karjalainen *et al*. 1996; Liinamo *et al*. 1997). The selection on performance indirectly accounts also for health and conformation of the dog, since only a healthy dog with a functional conformation is able to perform well in trials and the field.

However, in numerous other breeds the stated breeding objectives are in reality not effectively carried out. Only a few breed associations have established some centralised control for breeding practices, such as health or behavioural criteria for selection of breeding animals, or restrictions for the maximum number of offspring for a single stud dog. According to McGreevy and Nicholas (1999), peripheral traits have become important when breeding purebred dogs. The trend in dog breeding is to concentrate on exterior or appearance traits, without systematic selection for other traits (Lemonick 1994). Appearance is often more important than functionality, and requirements of breed standards may actually contradict welfare and health of the dogs (Lemonick 1994; McGreevy and Nicholas 1999; Fischer 2003). Breeding decisions are mainly based on appearance evaluations by judges at dog shows, as well as on information on the obligatory screening for some disorders, such as hip and elbow dysplasia.

It has become increasingly difficult for authorities, such as police, customs and guide dog organisations, to find healthy and functional dogs for their duties. In most dog populations, information on behaviour or working traits is not gathered routinely, and there is no systematic screening for or selection against genetic disorders either. For example, the Rottweiler is the most numerously tested breed in the behaviour tests of the Finnish Kennel Club (FKC), but only 20 percent of the dogs born yearly are tested annually either in this test or other working trials. In Sweden, the proportion of Golden Retriever breeding dogs tested with a hunting test during 1991 to 2000 was 20 percent, while the corresponding proportion of dogs participating in dog shows was 80 percent (Bucksch and Lindberg 2002). Breeding practices for the Golden Retriever in Finland have been similar to Sweden: only 12 percent of the Golden Retrievers born in 2002 have both parents undergone a hunting test. There is simply not enough information on behaviour and working traits in most breeds to take these traits systematically into consideration when selecting breeding dogs.

Breeding mainly for general appearance as judged in dog shows has other drawbacks as well. Unphysical, exaggerated appearance traits are often rewarded in the shows (McGreevy and Nicholas 1999; Fischer 2003), which makes the breeders actively strive for them. In 1995, the European Council made a pronouncement concerning certain dog breeds with dubious conformation traits (European Council 1995). It was recommended to pay great attention to reducing problems related to extreme appearance traits in these breeds. The European Union directives as well as national legislation in many European countries such as Finland also state that it is forbidden to breed animals with detrimental characteristics. The problems have also been discussed in the popular press both in Finland and abroad (e.g., Lemonick 1994; Mäki 1998, Davis 2003).

Recently, the FKC has started to instruct the show judges in order to limit the rewarding of exaggerated characteristics. Furthermore, the Fédération Cynologique Internationale (FCI) has published a leaflet appealing to show judges for interpreting any breed standard in such a way that a dog must be “functionally healthy” (Fischer 2003). According to this leaflet, also aggressive dogs should be penalised by disqualification.

2.2 Hip and elbow dysplasia in dogs

To date, over 450 disorders with a suspected genetic background have been reported in dogs (OMIA 2004). About one hundred of these disorders have been certified as single gene traits. A large proportion of the disorders are breed-specific, and many have a high within breed prevalence (Ubbink 1998; McGreevy and Nicholas 1999).

2.2.1 Etiology

Hip and elbow dysplasia are the most common hereditary disorders in dog breeds worldwide. They have a genetic basis, with environment having an effect on the severity of the phenotypic disorder. Both types of dysplasia are congenital orthopaedic defects that manifest as growth disorders of the bone and subsequent osteoarthrosis. Osteoarthrosis is common also in the shoulder and stifle joints of dogs, and often two or more joints of a dog are affected (Farquhar *et al.* 1997; Kealy *et al.* 2000). Hip and elbow dysplasia develop during the period of rapid growth, i.e., during three and eight months of age (Lust 1973a; Kasström 1975), especially in dogs with a large mature weight (Guthrie and Pidduck 1990; Distl *et al.* 1991).

Hip dysplasia was reported first by Schnelle (1935), and studies concerning malformations of the elbow joint date back to the 1950s. Hip dysplasia is characterised by the development of a loose, ill-fitting hip joint (Brass 1989). In a normal joint, the soft tissue links between the pelvis and the femur, the synovial fluid, and the joint capsule stabilise the joint with a vacuum-like effect (Brass 1989). A dysplastic joint has insufficient stability, and the femoral head is able to move out of the acetabular cup to a varying degree during weight bearing, which results in abnormal wearing of the joint surfaces and a degenerative joint disease. The worst alteration is a permanent luxation of the hip joint (Brass 1989).

Elbow dysplasia is a common name for osteoarthrosis of the elbow joint, which results from a failure during the process of endochondral ossification (Bedford 1994). Besides elbow incongruence, three different lesions leading to arthrosis of the elbow joint have been found. Stiern (1956) reported ununited anconeal process in 1956, although using different term for the condition. Olsson (1974) further described fragmented coronoid process and osteochondrosis dissecans in the medial part of the humeral condyle.

The most important environmental factor causing hip dysplasia has been suggested to be energy overfeeding, which causes rapid growth and weight gain (Kasström and Olsson 1973; Kasström 1975; Lust and Farrell 1977; Kealy *et al.* 2000). Kaman and Gossling (1967) reported that slowly growing pups had less hip dysplasia than those growing rapidly. Feeding affects also the development of elbow osteoarthrosis. In a study by Kealy *et al.* (2000), 48 Labrador Retrievers were randomly assigned to a control-fed group and a limit-fed group given 25 percent less food than the control-fed group. Dogs were monitored from the age of eight weeks until they were eight years old. Osteoarthrosis in the hip, shoulder, elbow and stifle joints was significantly more common and more severe in the control-fed group than in the limit-fed group. Contrary to the findings by Kealy *et al.* (2000), Lust (1973a) did not find restricted dietary intake to affect development of hip dysplasia. He did observe that pups growing at a strongly reduced rate had a low incidence of the defect. However, dietary restriction alone was not able to prevent development of hip dysplasia in progeny when parents had moderate to severe hip dysplasia (Lust *et al.* 1978). Exercise during the puppyhood is another factor commonly considered as affecting development of joints, but Lust (1973a) did not find it to influence the hip joints.

Hip and elbow dysplasia are not the most detrimental defects found in dogs, compared to for example disorders affecting the circulatory system or internal organs, but they cause clear clinical symptoms and have often an adverse effect on the working performance of the dog (Townsend 1973). In severe cases, both types of dysplasia cause lameness for the dog. Also, even without arthrosis hip dysplasia can be highly disabling when the joint is severely deformed.

Compared to hip dysplasia, elbow dysplasia often causes faster development of severe arthrosis. Majority of the weight of a dog is carried on its front legs. A dog can cope with imperfect hip joints if its musculature in the pelvis area is strong, but the heavy load on the elbow joints makes the animal often respond to even mild elbow dysplasia by lameness.

Prevalence of hip dysplasia among the 6 556 dogs screened in Finland in 2002 from various breeds was on average 36 percent (Eerola 2003). The corresponding proportion for elbow dysplasia in the 3 835 screened dogs was 22 percent. However, the prevalence of dysplastic dogs varies greatly between breeds (Table 1).

2.2.2 Diagnosis

Diagnosis of hip and elbow dysplasia is based on a clinical and a radiographic examination. Official hip dysplasia screening in Finland is performed according to the worldwide standard of the FCI (Brass and Paatsama 1983). Animals have to be identified either by a microchip or by a tattoo. The minimum screening age is one year, and for very large breeds, such as Great Dane and Saint Bernhard, one and a half years. Both hip and elbow radiographs are being evaluated by an authorised veterinarian in the FKC. Screening results are registered by the FKC, and they are made available as public information.

Dog is positioned in the hip radiograph with its hip joints fully extended and knees internally rotated. Radiographs should show the whole pelvis and the femurs up to the stifle joints (Brass 1989). In the evaluation of hip radiographs, the form of the femoral head and the acetabulum, the joint space, and the acetabular angle, i.e., Norberg angle, are judged (I; Figure 1; Brass and Paatsama 1983).

Table 1. Numbers of observations used in the different papers of the study, and the proportion of dysplastic dogs (dogs with mild, moderate or severe dysplasia) per breed.

Breed*						
GS	GR	LR	CO	RO	BM	FH
Hip dysplasia						
II: 12 302; III, IV: 13 006	II: 7 872; III, IV: 8 440	II: 7 130; III, IV: 7 826	II: 3 964; III: 4 337	I: 2 764; II: 3 985; III, IV: 4 397	III: 2 271	II: 1 671; III: 2 144
37%	32%	25%	12%	32%	46%	22%
Elbow dysplasia						
II: 2 566; III, IV: 3 121	II: 2 119; III, IV: 2 640	II: 1 985; III, IV: 2 627	-	I: 2 278; II: 2 972; III, IV: 3 386	III: 1 769	-
19%	21%	14%	na	44%	38%	na

*GS = German Shepherd, GR = Golden Retriever, LR = Labrador Retriever, CO = Rough Collie, RO = Rottweiler, BM = Bernese Mountain Dog, FH = Finnish Hound

A significant risk of moderate to severe arthrosis has been found in dogs diagnosed as dysplastic by the radiographs, compared to dogs diagnosed as normal (Banfield *et al.* 1996). Joint laxity is considered as the most important predictor of degenerative joint disease, i.e., arthrosis in hip joints (Smith *et al.* 1995), and new methods, which are better able to measure it than the currently used FCI method, have been suggested (Smith 1997, Flückiger *et al.* 1999).

The protocol of the International Elbow Working Group (IEWG) is used in Finland for official elbow dysplasia diagnosis. Evaluated sites in the joint are the dorsal edge of the anconeal process, the dorsal proximal edge of the radius, the dorsal edge of the coronoid process, the lateral palmar part of the humeral trochlea, and the area caudal to the distal end of the ulnar trochlear notch and the proximal radius (I; Figure 2). In Finland, a single 45° flexed, lateral radiograph of the elbow is taken. However, many authors have reported that osteochondrosis dissecans and lesions of the coronoid process are difficult to interpret by this routine radiography (e.g., Olsson 1977; Grøndalen 1981; Bedford 1994), and that at least two or three radiographic projections should be taken (Hazewinkel *et al.* 1995; Lang *et al.* 1998). Also the new IEWG protocol recommends at least two projections (Flückiger 1997). The exact nature and extent of the lesions can only be defined by arthrotomy. Actual degenerative changes in the joint, i.e. secondary osteoarthrosis, confirm the diagnosis (Bedford 1994), and these are visible in the routine radiography. However, they do not occur as early as the primary lesions.

2.2.3 Genetics

Numerous studies have aimed to reveal the mode of inheritance of hip dysplasia. Both a simple autosomal recessive gene (e.g., Grounds *et al.* 1955) and a dominant mode of inheritance (Schalles 1956) have been suggested. Henricson and Olsson (1959) suggested the mode of inheritance of hip dysplasia to be associated with the sex of the dog. Furthermore, Börnfors *et al.* (1964) and Burns and Fraser (1966) postulated dominance with an incomplete penetrance. According to Hutt (1967), the term "incomplete penetrance" is often used to describe a mode of inheritance that does not fit a monogenic hypothesis.

Current knowledge on the mode of inheritance for hip dysplasia indicates it to be a quantitative trait with genes and environment having a joint effect on the expression of the trait (e.g., Hutt 1967; Leighton *et al.* 1977, Swenson *et al.* 1997b). Differences between the sexes in the frequency of hip dysplasia have been reported by Hedhammar *et al.* (1979) and Swenson *et al.* (1997b), while sexes were found equally affected by Keller and Corley (1989) and also by Swenson *et al.* (1997b) in four of the seven breeds in their study.

The different conditions causing elbow arthrosis may have divergent modes of inheritance and may be regulated by different genes. In the Bernese Mountain Dog, fragmented coronoid process and elbow incongruence have been reported to be genetically different traits (Ubbink 1998). Also fragmented coronoid process and osteochondrosis dissecans have been suggested to be inherited independently (Padgett *et al.* 1995). In a few studies, fragmented coronoid process has been suggested to be controlled by a major gene (Everts 2000), or sex-linked or imprinted genes (Janss and Brascamp 1998). A maternal effect has been suggested as an explanation for dams contributing significantly more than sires to the progeny incidence of osteoarthrosis (Studdert *et al.* 1991). Everts (2000) found penetrances of fragmented coronoid process to be different in males and females, which could imply a mode of inheritance that is associated with sex. Likewise, many studies have reported males to be more frequently and more severely affected than females (Grøndalen 1976; Guthrie and Pidduck 1990; Grøndalen and Lingaas 1991; Studdert *et al.* 1991; Lang *et al.* 1998). The possible causes have been speculated to be the faster growth rate of males, their different hormonal status from females, and X-linked minor genes (Guthrie and Pidduck 1990).

Heritabilities for hip and elbow dysplasia have been estimated in several dog populations with various methods. A wide range of estimates has been reported both for hip dysplasia (0.10

to 0.60; e.g., Leighton *et al.* 1977, Swenson *et al.* 1997b, Leppänen *et al.* 2000, Ohlerth *et al.* 2001) and elbow dysplasia (0.10 to 0.77; e.g., Guthrie and Pidduck 1990, Grøndalen and Lingaas 1991, Studdert *et al.* 1991). On the average, the estimates have however been moderate of their magnitude. This indicates that even phenotypic selection, if done systematically, could result in genetic improvement in these traits.

2.2.4 Breeding against hip and elbow dysplasia

Efforts to reduce the incidence of canine hip dysplasia in Finland have been going on for 40 years. The first screening program was started for the German Shepherd in the 1960s. Compulsory hip dysplasia screening of breeding dogs, which formed the beginnings of the so-called PEVISA health program of the FKC, was established in 1984 for the retriever breeds, 1986 for the German Shepherd, 1987 for the Rough Collie, 1991 for the Bernese Mountain Dog, and in 1994 for the Rottweiler (Table 2). The PEVISA program was later expanded by official screening for elbow dysplasia that started in 1994 for the Rottweiler and the Bernese Mountain Dog, and became mandatory in 2001 for the German Shepherd and the retriever breeds. The decision on joining the health program is up to the individual breed associations. However, voluntary screening for both hip and elbow dysplasia has been practised to some extent in other breeds such as the Finnish Hound as well.

In the German Shepherd, only dogs with at maximum mildly dysplastic hips have been approved for breeding since the year 1989 (Table 2). A threshold of moderate hip dysplasia was established for the Golden Retriever and the Labrador Retriever in 1991. This threshold was, however, totally removed from the Labrador Retriever in 1999, while the threshold for the Golden Retriever was made more strict in 2002, i.e., up to mild dysplasia. No selection thresholds for breeding dogs exist in the PEVISA program for elbow dysplasia grade in the breeds studied in this thesis, nor is there a threshold for hip dysplasia grade in the Rottweiler and the Rough Collie.

Besides hip and elbow dysplasia, the PEVISA program for some of the studied breeds includes also screening for various inherited eye disorders, like hereditary cataract (HC), progressive retinal atrophy (PRA) and retinal dysplasia (RD). In addition, a restriction for the maximum total number of offspring allowed for a single male, 80, was established for the Rottweiler in 2000. Among the studied breeds, selection thresholds regarding eye disorders exist only in the Golden and the Labrador Retrievers. In both breeds, no HC, PRA or RD was allowed for a breeding dog during 1991 to 1999. Starting from the year 2000, grade I of these three disorders has been allowed in the Golden Retriever, whereas all thresholds in the Labrador Retriever have been removed.

Further to the restrictions imposed in the breed specific PEVISA programs, all male dogs used in breeding should have two properly descended testicles, i.e. cryptorchidism is not allowed.

In most breeds, no phenotypic gain can be observed in hip dysplasia despite of the many years of applying the PEVISA program in the Finnish breed populations (Leppänen and Saloniemi 1999). The situation is probably the same for elbow dysplasia. A few possible reasons for the poor progress in hip dysplasia have been reported for the German Shepherd: an increase in the use of parents whose hip status is the worst allowed, i.e., mild dysplasia, and an increase in the use of imported sires, which showed clear negative effects on hip dysplasia (Leppänen *et al.* 2000). Breeding restrictions for imported animals are not as strict as for animals born in Finland. Another reason for the negligible gain could be that breeding dogs have not been genetically better than the breed average.

Abroad, genetic improvement of hip and/or elbow dysplasia status has been achieved mostly in closed breeding populations with systematic breeding programs (Hedhammar *et al.* 1979, Lingaas and Klemetsdal 1990; Leighton 1997, Ohlerth *et al.* 2001). However, some studies have reported reasonable progress in hip and elbow dysplasia also in general breed populations (e.g., Brass 1989; Swenson *et al.* 1997a, 1997b; Beuing *et al.* 2000).

Table 2. Date of entering in the health program of the Finnish Kennel Club (FKC) and possible thresholds for breeding dogs for official FKC offspring registration in the studied breeds.

Breed	Hip dysplasia	Elbow dysplasia
German Shepherd	screening 1986; threshold 1989: mild	screening 2001; no threshold
Golden Retriever	screening 1984; threshold 1991: moderate 2000: mild	screening 2001; no threshold
Labrador Retriever	screening 1984; threshold 1991: moderate 2000: no threshold	screening 2001; no threshold
Rough Collie	screening 1987; no threshold	no obligatory screening
Rottweiler	screening 1994; no threshold	screening 1994; no threshold
Bernese Mountain Dog	screening 1991; threshold 1994: moderate	screening 1994; threshold 2000: moderate
Finnish Hound	no obligatory screening	no obligatory screening

2.5 Inbreeding and hereditary defects

Accumulation of breed-specific disorders within the purebred dog breeds has been suggested to be caused by high selection intensities in genetically closed dog populations (Ubbink *et al.* 1992; Ubbink 1998). Another likely reason for the high frequency of disorders is founder effect. Most dog breeds have been established from only a few founder animals, and a uniform appearance of dogs within breeds was achieved by intense inbreeding. Since establishing the uniform breed type, inbreeding has continued to be used by many dog breeders (e.g., Karjalainen and Ojala 1997; Nielen *et al.* 2001).

Inbreeding leads to a relative loss in the heterozygous loci, allowing expression of harmful, recessive genes as well as declined performance and fitness of the inbred animals, i.e., inbreeding depression (e.g., Falconer and Mackay 1996). The traits most typically affected by inbreeding depression have a low heritability and are hypothesised to be regulated by gene pairs with dominance effects. However, also polygenic, quantitatively inherited traits have been reported to show inbreeding depression (Ubbink *et al.* 1992).

Small, closed populations make inbreeding to some extent inevitable, but the common practice of excessively favouring only a few sires and lines in breeding causes effective population sizes of many dog breeds to be further smaller (Nielen *et al.* 2001). The "popular sire syndrome" has raised the average relationship between the animals within several breeds. Together, the founder effect, the high selection intensities, and the extensive use of popular sires have possibly made the within-breed allele diversity limited, and thus influenced the accumulation of genetic defects in the modern purebred dog breeds.

2.6 Objectives of the study

The overall objective of this study was to develop breeding strategies to reduce the incidence of hip and elbow dysplasia in dogs. Developing a functional breeding program for hip and elbow dysplasia can also help clear the way for applications with regard of other important traits, like other health traits and behaviour traits such as working ability. Hip and elbow dysplasia are good pioneer traits: large databases of screening information have been gathered of them, and dog breeders and owners generally have a positive attitude for taking hip and elbow dysplasia into account in breeding.

In this study, data sets available in Finland were analysed. The main studied subjects were:

- Mode of inheritance and genetic parameters for hip and elbow dysplasia, to investigate if genetic improvement in these traits is possible and how selection of the breeding dogs could be done effectively.

- Genetic trends and selection differentials in hip and elbow dysplasia, in order to study the efficiency and success of selection practised in these traits so far.

- Population structure and inbreeding, to study mating systems used by the breeders, and to estimate effective population sizes and intensity of selection practised.

- Potential genetic responses from various selection strategies when simultaneously selecting for health and behaviour traits, while maintaining exterior appearance constant, to study possibilities for a comprehensive breeding program.

3 Materials and methods

3.1 Materials

3.1.1 Hip and elbow dysplasia screening data

Screening information for hip and elbow dysplasia collected within the Finnish PEVISA program was used in papers I, II, III and IV, together with pedigree information of the breeds. Computerised information on hip and elbow dysplasia was available from 1988 onward. The breeds with the largest number of dogs screened for both hip and elbow dysplasia were selected for the study.

For paper I, screening data for the Finnish Rottweiler population during the years 1988 to 1996 was used (Table 1). In paper II, information on six breeds screened during 1988 to 1999 was studied: the German Shepherd, the Golden Retriever, the Labrador Retriever, the Rough Collie, the Rottweiler and the Finnish Hound. Data used in paper III included the same breeds as the data in the paper II, and in addition, the Bernese Mountain Dog. Screening years 1988 to 2000 were included. The same data were used for paper IV, but including only four breeds, i.e., the German Shepherd, the Golden Retriever, the Labrador Retriever and the Rottweiler. Data for the paper I were obtained from the breed club of the Rottweiler, while data for the rest of the papers were provided by the FKC.

All dogs in the screening data had a record for hip dysplasia, but not all dogs were screened for elbow dysplasia, especially not during the earlier years. The screening data contained the identification number of the dog, the date of screening, the identification numbers of both the X-raying and the screening veterinarian (radiologist), and a grade for both left and right hip and/or elbow joint.

Hip dysplasia grading had been performed using three different systems over the period the data covered (II). All three systems were based on the shape of the parts of the joint, as well as the existence of osteoarthrotic changes. For use in the analysis, the grading systems were combined in this thesis to form one numerical system (I-II). Elbow joints were graded in the data according to the International Elbow Working Group protocol, with numbers from 0 to 3. This grading is based solely on the existence and degree of arthrosis in the elbow joint, without separating the four possible lesions (I-II).

For both hip and elbow dysplasia, the measures used in the statistical analyses were the means of the left and the right joint of each dog. Information on both sides has been reported to be more informative for instance when estimating breeding values (Ohlerth *et al.* 2001). Taking the mean made the original skewed distributions complicated with regard to the analyses in paper IV (IV; Figure 1). As a result, altogether 11 to 15 possible values existed in hip dysplasia, and likewise seven possible values in elbow dysplasia grades. This resulted from the possibility of the left and the right joint having different grades of dysplasia. The distributions were multimodal for hip dysplasia in all breeds, and skewed for elbow dysplasia in all breeds except the Rottweiler that had a bimodal distribution.

3.1.2 Pedigree information

Pedigree information used in the analyses included all dogs registered in the studied breeds in Finland from the year 1978 onward, as well as some registered dogs born before 1978 (II; Figure 1). Information available included the identification numbers of the dog and its parents, a sex code, the breed, the breeder of the dog and the date of birth.

The information in the data sets was further expanded by calculating for all dogs a litter identification number, their litter size, the screening age of the dog and the age of the dam at the time the puppies were born.

3.2 Methods

3.2.1 Statistical analyses

3.2.1.1 Estimating variance components and genetic parameters

In paper I, the models used for estimating the genetic parameters differed between hip and elbow dysplasia. The model for hip dysplasia included the fixed effects of age class, class for the experience of the veterinarian doing the X-ray, and birth year*season subclass. The random effects in the model were litter, additive genetic effect of an animal, and residual. The model for elbow dysplasia included the same random effects as the model for hip dysplasia, and the fixed effects of the age class, the sex, the year of birth, and the panellist grading the x-rays.

A general model for both traits based on the data of all the seven studied breeds was developed in paper III. This general model included all fixed and random effects of the models used in the paper I for hip and elbow dysplasia, except for the birth year*season subclass. In addition, it included a random effect of breeder.

Testing the statistical significance of fixed effects for the models was done using the F-test, with the contrast option of the package PEST (Groeneveld 1990). Variance components in all animal models in this thesis were estimated by the REML method, using VCE4.0 software (Neumaier and Groeneveld 1998).

3.2.1.2 Investigating the mode of inheritance

Frequency distributions and heritabilities of the traits as well as regressions of offspring phenotypes on parental breeding values were estimated separately in males and females to assess the existence of possible mitochondrial and sex-linked inheritance as well as incomplete penetrance (III). The regression approach was similar to the study of Janss and Brascamp (1998). Animals born until 1995 were included in the parental breeding value estimation, and phenotypes of the offspring born after 1995 were used. That way the records on offspring did not affect the breeding values of their parents. Two models were used: one for estimating the breeding values, and the other for analysing the regression. The breeding value model was the general model for both hip and elbow dysplasia that was applied in the paper III, omitting the effect of veterinarian doing the X-ray. The regression model did not include animal or random effects, but otherwise it was the same as the general model.

To assess the possible existence of major genes affecting the studied traits, offspring frequency distributions of the traits were studied (III) and a segregation analysis was performed (IV) on the data. Frequency distributions were studied in the males having the largest number of dysplasia-screened progeny. With a major gene having an effect on the expression of a trait with complete dominance, the phenotypic distribution would be bimodal within a heterozygote sire, while within a homozygote sire only one mode would be observed.

For the segregation analysis, Monte Carlo Markov Chain algorithm, based on Gibbs sampling, with MaGGic software (Janss 1998), was used. Several procedures were followed to exclude possible false detection of major genes based on non-normality of data: permuted datasets were analysed, residuals were judged on normality, and data-transformation was applied when needed. Permutation was made with data shuffling, where each trait value and the corresponding model effects were reassigned to a new individual, while the individual's genetic links were retained (Churchill and Doerge 1994). If a major gene would be detected from that kind of re-arranged data, it would be caused by other factors than the actual existence of a major gene.

3.2.1.3 Estimating genetic trends and selection differentials

Genetic trends were studied by comparing the estimated average breeding values of the dogs born in different years (III). Breeding value estimation was performed based on Best Linear Unbiased Prediction (BLUP) as applied in the PEST software package (Groeneveld 1990). Differences in phenotypic hip and elbow dysplasia status between selected animals and all animals born in certain years were compared in order to assess the realised selection differentials.

3.2.1.4 Analysing population structure and inbreeding

Population structure was studied first by calculating inbreeding trends and the proportion of animals used for breeding (II). Inbreeding trends were calculated with the formula of Falconer and Mackay (1996):

$$\Delta F = (F_t - F_{t-1}) / (1 - F_{t-1}).$$

For the only closed population in the study, the Finnish Hound, the effective population size (N_e) was estimated from the rate of inbreeding:

$$N_e = 1 / (2\Delta F).$$

Secondly, intentional use or avoidance of inbreeding was assessed using computer simulations. The actually used sires and dams of three separate offspring generations were randomly mated within a generation, and the resulting average (expected) inbreeding coefficients of the generations were compared with the realised coefficients from the data. Matings were simulated as either completely random, or as excluding the parent-offspring and the full-sib matings.

Thirdly, inbreeding depression on hip and elbow dysplasia was analysed in four breeds applying the models in paper I, and including individual inbreeding coefficients in the model. For the hip dysplasia model, birth year*season subclass was replaced by the year of birth. Effect of the inbreeding coefficient was studied both as a class and as a regression effect. Two restricted data sets were used: the first included only dogs with at least two complete ancestral generations in the data, and the second included the dogs with at least five complete ancestral generations.

3.2.2 Comparing selection strategies

Potential genetic responses with simultaneous selection for four traits were studied using a deterministic simulation program SelAction (V; Rutten *et al.* 2002) and its option for overlapping generations and truncation selection. The population structure parameters for the Rottweiler breed in Finland were used to simulate a population for the study. Traits considered were hip and elbow dysplasia, a behaviour trait, and the exterior appearance as judged in dog shows.

The simulations were started by defining the current population structure, and searching the current relative selection index weights of the traits by iteration, based on the population structure reported in paper II and the realised genetic gains for hip and elbow dysplasia in paper III. After this, alternative systematic selection strategies were studied by varying the index weights of the traits, the number of selection candidates, the number of selected animals, and the number of information sources for the selection candidates. The breeding goal for the next ten years was defined as 0.5 to 1.0 genetic standard deviations (SD) for behaviour and 1.0 genetic SD for both hip and elbow dysplasia. The appearance of the dogs was constrained to remain unchanged. Thus, the changes for the other three traits were 0.05, 0.10 and 0.10 genetic SD per year, respectively.

4 Results

4.1 Genetic parameters and mode of inheritance

The estimates of heritabilities in the studied breeds were moderate to high for hip dysplasia (III; Table 1) and low to moderate for elbow dysplasia (III; Table 2). Estimates of the genetic correlation between hip and elbow dysplasia were quite low, although positive in all breeds except the Golden Retriever.

The mode of inheritance for both hip and elbow dysplasia seemed to be polygenic (quantitative) and autosomal with equal parental contributions. Neither of the traits fitted a mitochondrial or a sex-linked inheritance. Males and females were equally affected for both types of dysplasia. The regression coefficients of the offspring phenotypes on the estimated parental breeding values were close to their expected values assuming equal parental contribution (0.5), especially for hip dysplasia. The estimates of heritability differed between males and females for hip dysplasia in the Rough Collie and for elbow dysplasia in the German Shepherd and the Golden Retriever, but the differences were within the range of the standard errors of the estimates.

The segregation analysis suggested that a major gene could be segregating for hip dysplasia in the four breeds included in the study. In the Rottweiler, the existence of a major gene seemed likely also for elbow dysplasia. For both hip and elbow dysplasia, a statistically significant major gene variance was detected in each breed. The allele effects at the suggestive major gene locus revealed close to complete dominance and a recessive, unfavourable allele in both traits. However, the major gene detection for elbow dysplasia in the German Shepherd, the Labrador Retriever and the Golden Retriever was most likely caused by the skewed data distribution.

4.2 Genetic trends and selection differentials

During the years 1983 to 1998, the genetic level of hip dysplasia improved only in the Rottweiler, while the levels were getting worse in the other three studied breeds (Table 3 and III; Figure 1). In the Rottweiler, a genetic improvement of nearly one genetic SD was observed both for hip and elbow dysplasia during the years 1988 to 1995 (I; Figure 3). However, when analysed for a longer time period and with a lower estimate of heritability, the estimated gain in the Rottweiler was smaller (III; Figure 1). For elbow dysplasia, a slight improvement was noticed in all breeds, starting from the year 1992.

The phenotypic selection differentials for both traits were quite small: for hip dysplasia 0.3 to 0.5, and for elbow dysplasia 0.2 to 0.7 phenotypic standard deviations, varying between the breeds and between males and females (Table 3).

4.3 Population structure and inbreeding

The proportions of animals used for breeding were small in all studied populations: the proportion of stud males varied from approximately 4% in the Golden Retriever to approximately 12% in the Finnish Hound, and that of females from approximately 13% in the Golden Retriever to approximately 31% in the Rottweiler (II; Figures 2 and 3). Furthermore, the distributions of the number of offspring per sire were unequal within all studied breeds (II; Figure 4).

The effective population size (N_e) based on an observed inbreeding trend could be calculated in the Finnish Hound only, because it was the only closed population and, hence, the only breed with a steadily rising average inbreeding coefficient. All other breeds had imported dogs introduced in the data regularly, which made the inbreeding trends irregular. The estimate of N_e in the Finnish Hound was 100, relating to an increase of the inbreeding coefficient of 0.5% per generation.

In each breed, the expected mean inbreeding coefficients were lower than those observed (II; Table 5). The difference varied from 0.39 percent units in the Labrador Retriever to 2.32 units in the Rough Collie. These figures were obtained when no restrictions were made on the simulated matings. When excluding full sib and parent-offspring matings, the differences between the expected and the observed inbreeding coefficients were somewhat larger.

The inbreeding coefficient of a dog had a significant detrimental effect for hip dysplasia in the German Shepherd and the Labrador Retriever (II; Table 6). Inbreeding depression was not detected for hip dysplasia in the Golden Retriever and the Rottweiler or for elbow dysplasia in all four studied breeds. In the Labrador Retriever, the effect of inbreeding on hip dysplasia was larger when the inbreeding coefficients were calculated from more complete pedigrees, i.e., minimum of five ancestral generations, as when compared to shorter pedigrees, i.e., minimum of two ancestral generations. The inbreeding depression was, however, statistically significant only among the dogs with at least five ancestral generations in the analyses.

Table 3. Genetic gains for hip and elbow dysplasia as proportions of genetic standard deviations, and corresponding phenotypic selection differentials for the traits, as proportions of phenotypic standard deviations, for four studied breeds.

	German Shepherd	Golden Retriever	Labrador Retriever	Rottweiler
		Hip dysplasia		
Gain 1983-1998	-0.06	-0.26	-0.20	0.38
Selection differential	♂* 0.28 ♀ 0.34	♂ 0.36 ♀ 0.41	♂ 0.47 ♀ 0.42	♂ 0.37 ♀ 0.32
		Elbow dysplasia		
Gain 1992-1998	0.25	0.29	0.24	0.29
Selection differential	♂ 0.65 ♀ 0.38	♂ 0.42 ♀ 0.26	♂ 0.50 ♀ 0.28	♂ 0.26 ♀ 0.23

*♂ = males; ♀ = females

4.4 Simultaneous selection for behaviour, soundness of hip and elbow joints, and appearance

Increase in the number of relatives screened for hip and elbow dysplasia and behaviour traits for each selection candidate did not result in an increased genetic gain in these three traits, when keeping the relative breeding goal emphasis of the traits at the current level (V; Table 3, scheme 2a). Likewise, increasing the number of selection candidates alone resulted in only a small additional genetic gain (V; Table 3, schemes 3a to 3b).

The only way to reach the breeding goal set for the hip and elbow dysplasia was to change the relative selection index weights to dramatically favour these traits (V; Table 3, schemes 4a to 4c). As long as the index weights clearly favoured hip and elbow dysplasia (and behaviour), an increase in the number of selection candidates resulted in additional genetic gains (V; Table 3, scheme 5a). For behaviour, changing the index weights alone was not enough to reach the goal, but the number of selection candidates had to be increased as well. A very small relative index weight for appearance was enough to maintain the trait without negative genetic gain.

5 Discussion

5.1 Mode of inheritance for hip and elbow dysplasia

A quantitative inheritance with equal contribution from both parents seemed to be the most likely option for both hip and elbow dysplasia, based on the results of this thesis, although some evidence was observed in a few breeds suggesting otherwise, such as the differences in the estimates of heritability between the males and the females. This evidence was, however, not considered significant, because it could be explained by the large standard errors of the estimates. Splitting the data by sex made the estimates also less accurate, since analysing for example litter effect was not possible from such data sets. Further, the results supporting equal parental contribution were similar over most breeds. The findings for hip dysplasia are supported by Reed *et al.* (2000) and Ohlerth *et al.* (2001).

For elbow dysplasia, Janss and Brascamp (1998) proposed a mitochondrial or sex-linked inheritance for fragmented coronoid process in Labrador Retrievers. Incomplete penetrance has also been suggested for the condition (Everts 2000). These two studies had data only on the fragmented coronoid process, while in the data used in this thesis all four growth disorders of the elbow joint were included jointly, since the grading of the joints in the data was based on secondary osteoarthrosis.

The segregation analysis in four breeds gave some evidence of a major gene segregating for hip dysplasia, and also for elbow dysplasia in one breed. Further study on this subject is needed for both traits. Consistently with the results of this thesis, Leighton (1997) reported a possibility of a major gene for hip dysplasia in the German Shepherd and the Labrador Retriever. Also Todhunter *et al.* (1999) reported the existence of major genes for hip dysplasia. A major gene model has been suggested also for fragmented coronoid process (Everts 2000).

Contrary to many other studies on elbow dysplasia (Grøndalen 1976; Guthrie and Pidduck 1990; Grøndalen and Lingaas 1991; Studdert *et al.* 1991; Lang *et al.* 1998), males and females were equally affected in the data used in this study. Unequal expression between the sexes detected in other studies is not necessarily caused by different modes of inheritance; it may also be due to other factors affecting endochondral ossification, such as differences in growth rate. Moreover, Lang *et al.* (1998) reported that elbow radiography based solely on the presence of osteoarthrosis in dogs between 12 to 24 months of age underestimates the number of affected dogs and also the severity of the disease, particularly in female dogs. This might be another reason for males seeming to be more frequently affected than females.

5.2 Efficiency of selection practised against hip and elbow dysplasia

The results from this study (III, V) demonstrated that selection conducted thus far against hip and elbow dysplasia in the Finnish dog populations has been weak. The estimated genetic trends showed genetic improvement in hip dysplasia only in one breed. Interestingly, the breed making improvement, the Rottweiler, joined the PEVISA health program only ten years ago, while the other breeds for which the genetic trends were estimated have been involved in it for twenty years (Table 2). However, a large number of Rottweilers have been involved in voluntary health screening already before officially joining the program. The relatively large heritability estimate for hip dysplasia might be another reason for achieving genetic gain in the Rottweiler, while no gain can be observed in the other studied breeds. The selection differentials being of the same magnitude in all breeds support this view (Table 3). For elbow dysplasia, some genetic improvement was noticed in all studied breeds, starting a few years before the official screening started. However, the gain was very small on a practical level.

Despite of the weak selection practised against hip and elbow dysplasia, the populations studied in this thesis were observed to be otherwise under stringent selection, with only a small proportion of born animals used later for breeding. Based on the small selection differentials in hip and elbow dysplasia and the very small proportion of dogs that were screened for behaviour or utility traits in the studied populations, it may be assumed that the main selection of breeding animals has been made according to other factors and traits, such as the appearance judged in dog shows. This observation is supported by Hutt (1967), Bedford (1994), McGreevy and Nicholas (1999) and Fischer (2003).

Hutt (1967) postulated that elimination of hip dysplasia is only one of the breeders' objectives, while other traits, such as conformation and behaviour, may often be considered more important. Bedford (1994) speculated that the high prevalence of inherited diseases is due to a lack of knowledge concerning the diseases and the appropriate control measures, selection for traits that inadvertently select for the defect as well, and the unwise breeding of known affecteds or carriers of the defects. Like Bedford (1994), Lust and Farrell (1977) stated that breeders may inadvertently favour hip dysplasia when selecting for other traits, since it is not known how selection for certain traits affects hip joints. This could be the reason for the worsened hip status of the breeds in this study. Moreover, Kasström and Olsson (1973) have reported a narrow and slanting pelvis to be a risk factor for hip dysplasia. On the other hand, Kaman and Gossling (1967) found a correlation between dysplasia-free hip joints and steepness of the pelvis, but reported a high degree of hindlimb angulation to be associated with hip dysplasia. The German Shepherds rewarded in the shows typically have extremely slanting pelvis and highly angulated hind legs.

5.3 Improving selection efficiency against hip and elbow dysplasia

The magnitudes of the heritability estimates obtained in this study are in agreement with other studies, e.g., Leighton *et al.* (1977), Distl *et al.* (1991), Grøndalen and Lingaas (1991) and Beuing *et al.* (2000). Considering the mainly moderate estimates of heritability in most studied breeds, much genetic variation exists in both hip and elbow dysplasia. This available genetic variation should thus allow for achieving genetic progress by systematically selecting breeding dogs according to their dysplasia status.

The most effective selection against hip and elbow dysplasia could be conducted using BLUP breeding values. The heritability estimates for hip dysplasia in the Rottweiler, the Bernese Mountain Dog and the Finnish Hound, as well as for elbow dysplasia in the Rottweiler, were even high enough to make efficient selection based on phenotype information (mass selection) only. The FKC has started breeding value estimation with the BLUP method for hip and elbow dysplasia in 2002, based on the genetic parameters estimated and the models defined in this study. However, the accuracy of the breeding values could be improved if more dogs were screened for hip and elbow dysplasia (V). Further, if major genes affecting hip and elbow dysplasia exist, considerable genetic progress could be achieved by selection for them, since the possibly existing unfavourable alleles were found to have relatively high frequencies (IV). The major genes could be modelled for example by calculating carrier probabilities for breeding candidates. In the future, it may be also possible to use gene markers. Information on candidate genes or gene regions found in other species, such as human and mouse, can aid in this work.

The heritability estimates for elbow dysplasia were smaller than for hip dysplasia. This could be associated with the fact that the animals in the most severe cases suffer from elbow dysplasia already before the official minimum screening age of one year and thus do not enter the database of the FKC. This problem of incomplete data has been recognised also by Lang *et al.* (1998) as well as the International Elbow Working Group (IEWG), which addresses that the databases should contain also the preliminary evaluations between 6 and 12 months of age, so that young lame dogs would get registered (Grøndalen 1999). Moreover, false negative diagnoses of elbow dysplasia have been reported to be as frequent as 12 percent of all diagnoses (Lang *et al.* 1998), when using only one lateral flexed projection at radiography. This can happen for example when there are lesions in the elbow joint that have not yet caused osteoarthrosis by the age of examination. Thus elbow dysplasia cannot necessarily be excluded based on only one projection. Including the young, lame dogs in the database, and taking two or three radiographic projections of the elbow joints would give important additional information for genetic analyses and breeding value estimation, resulting perhaps in higher estimates of heritability.

Like elbow dysplasia, a diagnosis of hip dysplasia may be false negative as well. In a study of Lust (1973b), 25 percent of dogs that were normal in the standard hip joint radiography had degenerative hip joint lesions at necropsy. Joint laxity has also been reported to be difficult to diagnose with the standard view, and new methods have been suggested for detecting it (e.g., Smith 1997, Flückiger *et al.* 1999).

Another problem with both hip and elbow dysplasia is that some radiographs showing dysplastic joints are not being sent to the FKC for official evaluation. The owner of the dog has to sign an agreement on the publicity of the screening results, and sometimes he/she is not willing to publish the records of a dysplastic dog. This may introduce bias to the data.

The positive, although mainly low, estimates of genetic correlations between hip and elbow dysplasia allow simultaneous selection for both traits. Positive correlations between traits that are both related to growth of the bones were a likely finding, even though one might have expected the estimates to be larger. On the other hand, the disorders are not similar, due to the different structures of the joints involved, although both types of dysplasia are inherited skeletal growth disorders. For a hip joint, dysplasia causes malformation, whereas loose fragments within the joint are common for elbow dysplasia.

5.4 Inbreeding and effective population size

Comparing average inbreeding levels over different breeds was not possible in this thesis, since the amount of ancestral information included in the calculation of the inbreeding coefficients varied greatly between breeds. Imported dogs were observed to lower the average inbreeding level in all breeds, either as a result of being non-related to the Finnish population, or by having too limited pedigree information in the data. This was noticed as several decreases in the average annual inbreeding coefficients in all breeds except the Finnish Hound. In the Finnish Hound, the inbreeding level rose slowly but steadily, which is a common feature of a closed population. This made it possible to estimate the realised effective population size (N_e) of the Finnish Hound.

Of all born animals, only a very small proportion was used for breeding, thus resulting in small N_e. In the Netherlands, an even smaller proportion of dogs than reported in this thesis, i.e., three to five percent, have been contributing to the population gene pools over the past 30 years (Ubbink 1998). Small N_e makes the average relationship and thus the average inbreeding coefficient within a breed rise quickly. On the other hand, all the studied breeds except for the Finnish Hound introduce imported dogs to their populations regularly. Continuous importations do not necessarily make the N_e larger, however, since foreign breeding lines within a breed become genetically related to the ones in Finland.

According to the distributions of the numbers of offspring per sire estimated in this thesis, some popular sires have been favoured extensively in breeding while most others have either not been used at all or have only been used to sire a few litters. This practice further reduces the N_e. A small N_e affects the loss of alleles in these breeds: an abundant use of only a few popular sires can be considered as a genetic bottleneck of the population, enlarging the random dispersion of which alleles are being transmitted to the next generation. However, severe bottlenecks were not detected in the recent past in a study by Koskinen and Bredbacka (2000). Koskinen and

Bredbacka (2000) studied microsatellite variation in five Finnish dog breed populations, including the Golden Retriever and the German Shepherd. However, the current testing methods can detect only bottlenecks in the very recent past, and not the ones that occurred earlier. Instead of genetic bottlenecks, deviations from the Hardy-Weinberg equilibrium, due to deficiencies of heterozygotes, were detected.

Because of random drift and selection, some alleles might have been fixed in the dog populations while some others may have disappeared. Harmful, recessive alleles may be present at a high frequency (Ubbink *et al.* 1992), resulting in a situation where practically all matings produce affected puppies. This view is supported by many studies reporting better health and longevity of mixed-breed dogs compared to most purebreds (e.g., Studdert *et al.* 1991; Bonnet *et al.* 1997; Egenvall *et al.* 2000). On the other hand, inbreeding does not bring any problems in a situation where the founder population does not have any hazardous alleles. Most dog breeds are not clean from harmful alleles, however. For some breeds, the only way to improve them would be to introduce new alleles into the population, by crossing with another breed. Crosses have recently been seriously considered or even carried out in a few dog breeds in Finland, like the introgression of the Schnauzer into the German Pinscher, which has been approved by the FKC for a few breeders. Crossing does not, however, eradicate the deleterious alleles, although it lowers their frequencies.

Inbreeding in the German Shepherd and the Labrador Retriever had a clear detrimental effect on hip dysplasia: in both breeds hip dysplasia got worse when the inbreeding coefficient reached 18.75 percent or larger. The studies of Laben *et al.* (1955) and Ercanbrack and Knight (1991) support this finding by noting animals to have been more affected by inbreeding depression when the inbreeding coefficient reached 20 percent or more. However, the amount of pedigree information used in this thesis was not necessarily sufficient to study inbreeding depression. Only in the Rottweiler over 50% of the dogs had at least five complete ancestral generations in the data. Because of the generally short pedigrees, only a few dogs with a large inbreeding coefficient existed in the data.

In the Labrador Retriever, the effect of inbreeding depression was clearly larger and statistically significant among dogs that had more information available for the calculation of inbreeding coefficients, i.e., a minimum of five ancestral generations, as compared to dogs having a minimum of two ancestral generations in the data. With more complete pedigree information it might have been possible to detect inbreeding depression also in elbow dysplasia. Moreover, it was not possible to study the effect of long-term inbreeding with these data.

Besides unintentional (passive) inbreeding due to the small effective population sizes, inbreeding has also been used on purpose (actively) in the studied breeds. The comparison of the observed and the expected inbreeding coefficients showed that inbreeding has been used intentionally by some breeders in each breed. This observation is supported by Karjalainen and Ojala (1997) in the Finnish Spitz and by Nielen *et al.* (2001) in Dutch populations of the Bernese Mountain Dog, the Bouvier des Flandres, the Boxer and the Golden Retriever. According to Hutt (1969), breeders use inbreeding as an assortative mating system to try to fix desirable traits of an illustrious champion. Uniform dogs are being bred for the dog shows (Kaman and Gossling 1967). Show judges compare the presented dogs with a breed standard that strictly defines the desired conformation and appearance of that breed, and the dog that is most similar to the ideal standard wins. Consequently, the breeders aim to breed uniform dogs that closely resemble the standard.

In the future, excessive inbreeding should be avoided in the studied breeds by keeping progeny group sizes as uniform as possible between the animals, and by using a larger proportion of the animals, especially males, for breeding. A useful tool for this end is to establish a limit for the number of offspring allowed for a single male. This practice has already been adopted by a few breed clubs, including the Rottweiler. A possible drawback of this practice may be the rush of breeders to fulfil the quota of some sires before they have any 'proof' of the sires' breeding values for various traits. Mating systems managing inbreeding trends in small populations under selection, or maintaining genetic diversity, could also be applied (Sonesson and Meuwissen 2000).

Intentional inbreeding should also be avoided in the future. This view is supported by e.g., Kaman and Gossling (1967), Hutt (1969) and Goddard and Mason (1982). Healthy and feasible breeding and mating systems ought to be used in order to achieve the breeding goals. In a study of Nielen *et al.* (2001), it was shown in the Kooiker Dog that successful selection of breeding stock for health or show characteristics was possible also when a larger proportion of sires was used than what had traditionally been done.

5.5 Social values in dog breeding

5.5.1 Beauty

Show characteristics have apparently a high "social value" in the dog world. The main emphasis in many dog breeds is currently on appearance traits (Lemonick 1994; McGreevy and Nicholas 1999; Bucksch and Lindberg 2002). In Finland, like in many other countries, dog breeding is different from livestock breeding in that it is mainly a hobby for the breeders. The breeders' aim is to have their kennel's name recognised, and often this can be achieved easiest in dog shows as it requires much more work to make a dog win for example in working trials. Dogs have to meet rigorous standards regulating their external characteristics in order to be approved for breeding. Willis (1989) stated that even cosmetic surgeries are undertaken on dogs, in order to make the dogs approved for breeding.

Dogs winning in the shows often represent extreme types and may even exhibit traits which are unhealthy and bring discomfort to the dog itself (McGreevy and Nicholas 1999; Fischer 2003). Yet, aiming at the extremes still continues, despite the pronouncement made by the Council of Europe (1995) with the premise that if voluntary restrictions are not put into action the Council of Europe may totally ban breeding the worst affected dog breeds. One might ask: when is appearance at the desired level? Was it there at the beginning when the dog was able to hunt and do its other work well? Or is it there now, when the dogs are being rewarded for their "beauty"? "Ideal" dogs from many breeds looked quite different hundred years ago when the breed standards were created, compared to the current "ideal" dogs.

According to the results of this study, a very small relative index weight for appearance was enough to maintain the trait without negative genetic gain (V), presuming that the assumed genetic parameters used in the simulations in this study were not very far from the real ones. Thus there would be no need to continue putting a strong emphasis on the trait in breeding.

5.5.2 Health and disorders

Many breeders are today concerned for their dogs' health. According to two survey studies by Leppänen *et al.* (1999a; 1999b), Finnish breeders and dog owners find skeletal and eye disorders to be the most important traits affecting a dog's well being. Most breeders are very positive with the PEVISA health program. Screening a potential breeding dog for hip and elbow dysplasia is considered as "health promotion", allowing a breeder to have a good conscience when having carried out the important checks before breeding. It is also advantageous for his/her reputation. If the breeder thinks positively about health screening, he/she may have a significant effect in motivating the dog buyers also to participate in the PEVISA program (Leppänen *et al.* 1999a).

Most other canine genetic defects have a less favourable position in recording than hip and elbow dysplasia. Many disorders are relatively widespread in different populations, but their full extent is usually not realised or admitted. For example, based on Swedish insurance data, veterinary care events related to stifle joint were about three times as common as events related to elbows (Hedhammar *et al.* 1999). The full extent of hip and elbow dysplasia problem may be unknown as well, because of the pre-selection made by breeders and owners of the dogs when making the screening results public. This view is supported by Hamann *et al.* (2003), who found that German Shepherd litters with a small proportion of examined dogs appeared to be more prone to hip dysplasia than litters with a larger proportion of dogs examined. Besides hip and elbow dysplasia, and a few ocular diseases, other serious defects should also be routinely reported to the breed clubs and the FKC. Open discussion is needed, followed by careful listing of the various problems and their frequencies.

5.5.3 Behaviour

The behaviour and working traits of the different dog breeds have been highly developed during the past centuries of dog breeding. Maintaining these traits at a sufficient level probably still requires selection pressure on them. When there is no such selection pressure, the traits most probably decline because of random drift and natural selection, until they reach the level of an "average dog".

Selecting breeding dogs according to their working ability has been suggested to be the reason for the good hip joint status of the working breeds (Goddard and Mason 1982). Kaman and Gossling (1967) found a higher incidence of hip dysplasia in show-ring German Shepherd Dogs as compared to sheep-herding lines. This may imply that a favourable correlation between hip dysplasia and working traits exists. A favourable correlation between hip dysplasia and temperament has been estimated in the studies of Hedhammar (1976) and MacKenzie *et al.* (1985).

At present, selection for behaviour traits is difficult in most breeds because no sufficient data are gathered on them. Behaviour screening of potential breeding dogs should be done routinely. A dog with a genetically poor behaviour is of no use for anyone, and does not bring joy to its owner even when being perfectly healthy. On the other hand, a mentally well-balanced dog with various skills can be an enormous help for its owner or handler.

6 Conclusions

The most likely mode of inheritance for hip and elbow dysplasia was quantitative, with equal contribution from both parents. Although it would be theoretically very interesting to further study the mode of inheritance of these traits, the current understanding of quantitative traits is sufficient for practical purposes to start systematic selection.

The estimates of heritability for hip and elbow dysplasia were mainly moderate in the studied breeds. This indicates that a reasonable amount of genetic variation exists for the traits, thus making it possible to achieve genetic progress by selection. The positive, although mainly low, estimates of genetic correlations between hip and elbow dysplasia allow for simultaneous selection of both traits. The most effective selection against these traits could be conducted using BLUP breeding values. However, the accuracy of the breeding values could be improved if the number of dogs screened for hip and elbow dysplasia was higher, and if the unofficial diagnoses of young, lame dogs were also included in the database. Furthermore, in elbow dysplasia, taking at least two radiographic projections would decrease the number of false negative cases and increase the accuracy of the breeding value estimation.

Selection conducted thus far against hip and elbow dysplasia has been very weak. The estimated genetic trends showed genetic improvement in hip dysplasia only in one breed and only a small genetic gain in all breeds for elbow dysplasia. Despite of the weak selection practised against hip and elbow dysplasia, the populations studied in this thesis were observed to otherwise be under stringent selection, with only a small proportion of the born animals used later for breeding. Some other traits, such as show characteristics, have obviously been considered more important than hip and elbow dysplasia when making breeding decisions. Selection for other traits may also inadvertently have favoured hip and elbow dysplasia, since it is not known how selection for certain traits affects the joints.

In the future, excessive inbreeding should be avoided in the studied breeds by using a larger proportion of the animals, especially males, for breeding, and by keeping progeny group sizes as uniform as possible between the animals. Intentional inbreeding should be avoided in the future as well. Mating systems managing inbreeding trends in small populations under selection, or maintaining genetic variation, could also be applied.

Most puppy buyers want to have a sound dog with a good character. Dog breeding does not, however, correspond with this demand at the present. To provide puppy buyers better what they are looking for, behaviour and health traits should be clearly favoured in the selection. To achieve these aims in practice, dog breeders should be sufficiently educated in the fields of genetics and breeding, and puppy buyers should be informed about what to look for when buying a puppy. Some control is also needed from the authorities in the field. Systematic breeding programs, including preservation of genetic variation, should be developed and followed to maintain or improve the desired behaviour and working traits as well as health of the dogs in the current populations.

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