

The effect of breeding schemes on the genetic response of canine hip dysplasia, elbow dysplasia, behaviour traits and appearance

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Abstract

Current dog breeding programmes must be changed if genetic improvement in health and behaviour traits is to be achieved. A computer simulation programme was used to assess the possible genetic improvement in hip dysplasia (HD), elbow dysplasia (ED) and behaviour (BE) traits in a dog population whilst simultaneously selecting for appearance (AP). The structure of the Finnish Rottweiler population was used in the simulation. Over a ten-year period (1989–1998), the realised genetic response to selection in the Finnish Rottweiler population was 0.03 genetic standard deviations (SD) for both HD and ED. The relative selection index weights were iterated in the simulation, accordingly, as 0.4 for both traits. In the current breeding strategies, AP dominates other traits. Present index weights for BE and AP were therefore assumed to be 0.5 and 2.0, respectively. With these assumed current index weights, using best linear unbiased prediction (BLUP) breeding values, neither an increase in the number of breeding candidates nor an increase in the number of screened relatives of the candidates resulted in further genetic response for HD, ED or BE. The desired genetic responses for HD, ED and BE over a period of 10 years could only be attained by changing the relative selection index weights dramatically in favour of these traits. As long as the index weights clearly favoured HD, ED and BE, the increase in the number of breeding candidates, ie in the number of screened dogs, resulted in a further response in these traits. To preserve desired behaviour and to improve health in dog breeds, systematic breeding programmes favouring these traits should be developed, and a greater number of dogs should be screened for health and behaviour. Breeders should stop breeding exhaustively for appearance and place more emphasis on health and behaviour traits.

Keywords: animal welfare, appearance, behaviour traits, breeding, dog, genetic defects

Introduction

Domestication has resulted in the dog (*Canis familiaris*) being employed for a number of different purposes. The most skilled and useful dogs were favoured in breeding, which led to the emergence of breeds with specific abilities, such as hunting and guarding (McGreevy & Nicholas 1999). During the last one hundred years, the principal trend in dog breeding has been the selection for appearance and other traits outlined in the standards of the breed societies, eg the Kennel Club, without systematic breeding for other traits (Lemonick 1994; McGreevy & Nicholas 1999). A few exceptions exist, such as breeding for improved hunting traits in some breeds of hunting dog (Karjalainen *et al* 1996; Liinamo *et al* 1997). The dogs that most closely meet the rigorous standards regulating their external characteristics, as demonstrated by their success at breed shows, are most in demand for use in breeding. Even unhealthy, exaggerated conformations are desired in the standards of some breeds (McGreevy & Nicholas 1999; Fischer 2003). Together with the use of inbreeding as a common mating system, this has led to a growing number of breed-specific hereditary problems (Ubbink *et al* 1992). It has also become increasingly

difficult for those different authorities that use dogs, such as the police, the customs, and guide dog organisations, to find healthy dogs with sufficient working abilities for their different duties.

In Finland, as in many other countries, dog breeding differs from production animal breeding because it is mainly a hobby activity. Central controls for breeding practices exist for only a few dog populations and include restrictions on the maximum number of matings by a single stud dog or on the minimum criteria for selection of breeding animals. The breeders aim to have their kennel's name recognised, and often this can be achieved most readily in dog shows; it requires much more work to make a dog win in working trials. Potential puppy buyers commonly go to see the dogs in the shows and become interested in purchasing puppies of the winning dogs and those that are highly acclaimed by the kennel and breed clubs. This makes show characteristics, ie appearance, the most important trait when selecting a breeding dog. However, winning dogs in such shows often represent extreme types and may even exhibit traits that are unhealthy and bring discomfort to the dog (McGreevy & Nicholas 1999; Fischer 2003).

Table 1 Information sources for the candidates.

Candidate age categories (years)	Number of candidates in age class	Own record	Number of offspring records ¹			Number of full-sib records			Number of paternal half-sib records			Number of females producing these half-sibs		
			HD,ED	BE	AP	HD,ED	BE	AP	HD,ED	BE	AP	HD,ED	BE	AP
Males														
2	8	HD,ED,AP	0	0	0	1	0	2	2	1	6	1	1	2
3	19	HD,ED,BE,AP	0	0	0	1	0	2	2	2	6	1	2	2
4	31	"	0	0	0	2	0	2	4	2	6	2	2	2
5	24	"	2	0	4	2	0	2	4	2	6	2	2	2
6	20	"	4	2	6	2	1	2	4	3	8	2	3	3
7	18	"	6	4	8	2	1	2	6	3	8	3	3	3
8	8	"	8	4	10	2	1	2	6	3	8	3	3	3
9	5	"	8	4	12	2	1	2	6	3	8	3	3	3
Females														
2	15	HD,ED,AP	0	0	0	1	0	2	2	1	6	1	1	2
3	36	"	0	0	0	1	1	2	2	2	6	1	2	2
4	35	"	0	0	0	2	1	2	4	2	6	2	2	2
5	24	"	2	0	2	2	1	2	4	2	6	2	2	2
6	14	"	2	1	2	2	1	2	4	3	8	2	3	3
7	9	"	4	1	4	2	1	2	6	3	8	3	3	3
8	1.2	"	4	2	6	2	1	2	6	3	8	3	3	3

¹HD = hip dysplasia, ED = elbow dysplasia, BE = behaviour trait(s), AP = appearance

In 1984, the Finnish Kennel Club (FKC) started a health programme for hip dysplasia in the Golden Retriever and the Labrador Retriever. This programme includes obligatory screening of dogs used in breeding. More breeds and genetic defects have been subsequently introduced into the programme. Specific guidelines about acceptable traits may also exist for individual breeds. For example, in the German Shepherd, only dogs with no worse than mild dysplasia can be used for breeding. The Rottweiler was introduced into the programme in 1994, but, as yet, no specific guidelines exist for this breed.

The two most important inherited defects included in the current programme are hip and elbow dysplasia, which are growth disorders of the bone, prevalent in large, fast-growing and heavy dogs. The disorders are screened by X-raying the hip and elbow joints. In spite of the breeding programme, the selection pressure against hip and elbow dysplasia, and consequently the realised genetic response to selection, in these breeds has been very small (Mäki *et al* 2002). In other countries and other dog breeds, genetic improvement has been achieved in hip and elbow dysplasia using systematic breeding programmes (eg Leighton 1997; Swenson *et al* 1997a,b; Beuing *et al* 2000; Ohlerth *et al* 2001). Genetic improvement occurs when there is a generation-by-generation increase in the proportion of animals carrying beneficial/desirable genes that have a positive effect on a specific trait.

Besides health, the behavioural traits of dogs are also important, especially in modern society. More and more cases are being reported of problems or even injuries being caused by 'badly behaved' dogs. Breed-specific behaviour is one of the major factors that make a dog a good representative of its breed. This behaviour should be maintained in the breeds.

The aim of this study was to use a computer simulation programme to assess the possible genetic improvement in hip dysplasia, elbow dysplasia and behaviour traits in a dog population whilst simultaneously selecting for appearance. The purpose was to identify what changes to current breeding practices are required if genetic improvement in health and behaviour traits is to occur.

Methods

Traits studied

Four traits were considered simultaneously: hip dysplasia (HD), elbow dysplasia (ED), a specific behaviour or working trait (BE), and appearance whilst at dog shows (AP). A behaviour trait was based on a result in the FKC test or in a working trial. The FKC behavioural test includes several components in which the dogs are confronted by different situations. Each situation is scored on the basis of the dogs' reactions. Appearance was based on a result given by judges in a breed show or by inspectors during a specific

Table 2 Phenotypic variances (σ^2_p), ratios of litter variance (c^2) relative to phenotypic variance, heritability (**bold**), genetic and phenotypic correlations used in the simulations. Genetic and phenotypic correlations were assumed to be equal.

Trait ¹	HD	ED	BE	AP
σ^2_p	1.10	0.69	1.10	1.10
c^2	0.04	0.04	0.10	0.04
Heritability and correlations				
HD	0.38	0.30	0.31	0.00
ED		0.37	0.31	0.00
BE			0.20	0.00
AP				0.40

¹HD = hip dysplasia, ED = elbow dysplasia, BE = behaviour trait(s), AP = appearance

breeding examination. To simplify the simulations, both behaviour and appearance were considered as a single trait.

Breeding goal

During a period of ten years (1989–1998), the realised genetic change in the Finnish Rottweiler population was 0.20 trait units for HD and 0.14 for ED, which corresponds to 0.03 genetic standard deviations (SD) per year for both traits (Mäki *et al* 2002). The breeding goal for the study was to achieve improvement from 0.5 to 1.0 genetic SD for BE and 1.0 genetic SD for both HD and ED, ie 0.05, 0.10 and 0.10 genetic SD per year, respectively, during a ten-year period. Therefore, the desired genetic response in trait units per year was 0.025–0.050 for BE, 0.070 for HD and 0.040 for ED. To reach this goal, systematic selection for these important traits is required. For AP, the goal was to keep the trait constant, ie no unfavourable change.

Population structure and information sources

Mäki *et al* (2001) reported on the population structure of the Finnish Rottweiler. This structure was used in the study, and also some additional parameters were calculated. The number of dogs born per year varied between 600 and 700; however, only offspring of the dogs with an official record of HD and ED screening can be registered, according to the registration regulations of the health programme for the Rottweiler. Approximately 40% of dogs born per year were screened for HD and ED. Of these, 28% of males and 63% of females were selected. The effective population size (N_e) was estimated to be 100 using the formula of Falconer and Mackay (1996):

$$N_e = \frac{4 N_m N_f}{(N_m + N_f)}$$

where N_m = number of breeding males,
 N_f = number of breeding females.

This makes the rate of inbreeding 0.5% per generation, because rate of inbreeding is defined as $1/(2N_e)$.

In the population, the average number of registered offspring was 11 per female and 26 per male. The mean litter size was six, which means that on average females had two litters and males had four litters. In practice, much more variation exists in the number of litters among males,

making the effective population size smaller than assumed in these simulations. Furthermore, it was assumed that males were mated to the same female only once.

Eight age classes existed in the population for the breeding males, 2–9 years, and seven for breeding females, 2–8 years. Most breeding dogs were 3–6 years of age. Information sources for the prediction of breeding values varied among the traits, between the sexes, and also between the age classes (Table 1). Approximately two to three dogs per litter were screened for HD and ED. Besides the result of the candidates themselves, information was also known regarding one or two of their littermates. In addition, for candidates of ≥ 5 years of age, information on HD and ED was known for their offspring. Only one dog per litter was screened for BE; this is equivalent to the 20% of dogs per litter that are routinely tested. Approximately three dogs per litter enter shows and are scored for AP. The generation interval, ie the average age of the parents at the time their offspring are born, in the Finnish Rottweiler is approximately 4 years (Mäki *et al* 2001).

Genetic parameters of the traits studied

The genetic parameters for HD and ED in the Finnish Rottweiler population were obtained from Mäki *et al* (2002). An average figure from the literature of 0.20 (Ruefenacht *et al* 2002) was used as an estimate of heritability (h^2) for BE (Table 2). Heritability is used to describe the size of genetic variance as a proportion of total phenotypic (genetic plus environmental) variance (for details, see eg Bourdon 1997). Heritability varies between 0 and 1: values <0.20 are considered low; 0.20–0.40 is moderate; and >0.40 high. With a high heritability, differences seen between the dogs are mainly genetic. For AP h^2 was assumed to be 0.40, according to established knowledge on conformation traits in production animals, and also, for example, on body weight in dogs (Reuterwall & Ryman 1973; Hedhammar *et al* 1979).

The reported estimates of genetic correlation of 0.30 between HD and ED (Mäki *et al* 2002), and 0.31 between BE and HD (Mackenzie *et al* 1985) were used. The genetic correlation indicates either that the genes affecting both traits are closely linked together or that there are genes that affect both traits (pleiotropy). If two phenotypic traits have

a negative genetic correlation, an increase in the genetic level of one trait is associated with a decrease in the genetic level of the second trait. However, if two phenotypic traits have a positive genetic correlation, selection changes the genetic levels of the two traits in the same direction.

Phenotypic correlation is a measure of the association between two traits caused by both genetic and environmental factors. In this study, the phenotypic correlations were assumed to be equivalent to the genetic correlations. No estimates for genetic or phenotypic correlations between ED and BE, or between AP and the other three traits, were found in the literature. Consequently, both correlations between ED and BE were assumed to be 0.30, ie the same size as the correlations between HD and BE. This was considered a reasonable assumption because both HD and ED are traits related to the growth of bones. Genetic and phenotypic correlations between AP and the other three traits were assumed to be zero. The current FKC breeding programme was also simulated assuming a negative correlation of -0.30 between BE and AP (termed the 'realised Golden Retriever'). This assumption was made in order to investigate the genetic change in BE when the main breeding emphasis is on a trait (AP) assumed to have a negative correlation with BE. In Sweden, over the past ten years, the Golden Retriever has been bred mainly for AP (Bucksch & Lindberg 2002) and there has been a deterioration in BE. This deterioration in BE may result either from insufficient selection for BE or because BE and AP have a negative correlation. Breeding practices for the Golden Retriever in Finland have been similar to those in Sweden.

The common environmental correlation, ie the association between two traits caused by environmental factors common to full siblings, was assumed to be zero between all the traits except HD and ED, between which the correlation had been estimated to be -0.58 with a standard error of 0.24 (Mäki *et al* unpublished data). Here, a value of -0.50 was used.

Computer simulations

This study used the deterministic simulation principle in the SelAction software (Rutten *et al* 2002), with its option of overlapping generations and truncation selection, to assess the expected genetic responses to simultaneous selection for the traits. No scores for the traits were required for the simulation programme. Best linear unbiased prediction (BLUP) breeding values (Henderson 1984) had not been used for HD and ED in the real-life population, and the population structure — as well as the genetic and phenotypic parameters — was as described above. In using the BLUP procedure, breeding values of the animals are predicted by simultaneously accounting for the fixed environmental effects and making use of genetic relationships among the animals (for details see eg Bourdon 1997).

Using the population parameters described above, different selection index weights (ie the relative emphasis of the traits during breeding) were tested in the simulation until the realised genetic responses in HD and ED in the Finnish

Rottweiler population were met, as reported by Mäki *et al* (2002). No selection index has previously been calculated, but index weights that have been implicit in the selection decisions of the breeders were back-calculated from the current genetic responses. When the realised relative weights were found, alternative selection strategies were studied by varying the index weights of the traits, the number of candidates, the number of selected animals, and the number of information sources for the candidates. These realised selection index weights were determined as 0.4 for both traits. Furthermore, the weightings for BE and AP were assumed to be 0.5 and 2.0 respectively, based on discussions with representatives of the Finnish Rottweiler association as well as the authors' own experience of dog breeding practices in Finland. All of the weights were expressed per genetic SD. These relative weights in the realised breeding programme indicate only weak selection on behaviour and health traits in the Finnish Rottweiler.

Selection strategies

Once the realised selection index weights had been determined for the current programme, we gradually moved toward a predictive breeding programme that would give the desired genetic improvement in HD, ED and BE (Table 3). When a near optimal scheme was found (5a), the sensitivity of the results based on the unknown genetic and phenotypic correlations between AP and the other three traits was investigated by running the simulation using three different assumptions: the correlations to be zero; moderate and positive; or moderate and negative (schemes 6a–6e). Moderate correlations between the traits were considered as most likely.

The simulation programme, SelAction, assumes that the data have been pre-corrected for fixed effects, ie that fixed effects are known. Estimation of fixed effects is not included in the programme because there is no general pattern for their distribution. In reality, fixed effects and breeding values have to be simultaneously estimated using the BLUP procedure. Because fixed effects are not known without error, the selection response in reality may be slightly lower than values presented in this study. Therefore, in this study, the comparison of the schemes with and without BLUP gives an indication of the extra response that may be obtained by using BLUP, which originates primarily from the inclusion of full pedigree. Apart from stochastic simulation, there are at present no methods to quantify how the fixed effects affect selection response when not using BLUP. Furthermore, the results would be very dependent on the specific structure of the fixed effects, which obviously vary between different data sets. Hence, it would be impossible to provide generally valid results accounting for the different structures of fixed effects.

Results and discussion

Changing the breeding structure

A doubling in the number of relatives of the candidates screened for HD, ED and BE did not result in further

Table 3 The schemes simulated in the study.

Scheme	Relative weights ¹ HD,ED,BE,AP ²	Screened relatives HD,ED,BE ³	BLUP	Candidates ⁴	Genetic and phenotypic correlations
Realised	0.4;0.4;0.5;2.0	Current	–	40%	As in Table 2
Realised Golden Retriever (GR)	"	"	–	"	BE-AP –0.3
1	"	"	HD,ED,BE	"	As in Table 2
2a	"	Double current	–	"	"
2a2	"	"	HD,ED,BE	"	"
2b	"	Half current	–	"	"
3a	"	Current	–	60%	"
3a2	"	"	HD,ED,BE	"	"
3b	"	"	–	80%	"
3b2	"	"	HD,ED,BE	"	"
4a	10;10;20;1	"	–	40%	"
4a2	"	"	HD,ED,BE	"	"
4b	20;20;40;1	"	–	"	"
4b2	"	"	HD,ED,BE	"	"
4c	30;20;40;1	"	–	"	"
4c2	"	"	HD,ED,BE	"	"
5a	5;5;10;1	"	–	60%	"
5a2	"	"	HD,ED,BE	"	"
6a	"	"	–	"	BE-ED 0.3
6b	"	"	–	"	AP-HD; AP-ED 0.3
6c	"	"	–	"	AP-HD; AP-ED –0.3
6d	"	"	–	"	BE-AP 0.3
6e	"	"	–	"	BE-AP –0.3

¹Relative weights = how the traits are emphasised among other traits during breeding

²Relative selection index weights for hip dysplasia (HD), elbow dysplasia (ED), behaviour (BE) and appearance (AP)

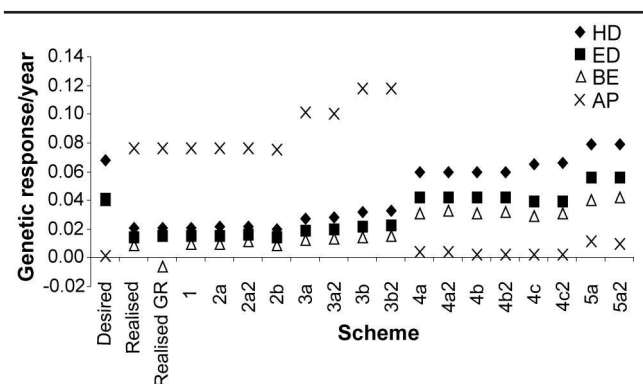
³Amount of information from relatives of the candidates for HD, ED and BE

⁴Proportion of candidates (dogs screened for HD and ED) out of all the dogs born yearly

genetic response in the three traits when the relative emphasis of the traits was kept at the current level (Figure 1; Table 3, scheme 2a). Reduction in the number of relatives also did not affect the already negligible response. This demonstrates that selection for HD, ED and BE has been practically nonexistent, and AP has dominated the breeding strategy. This finding is similar to that of Bucksch and Lindberg (2002). When the genetic and phenotypic correlations between AP and BE were assumed to be –0.3 ('realised Golden Retriever'), the genetic trend for BE became negative. Therefore, selecting for only AP caused deterioration in BE when the correlations between the traits were negative. Deterioration in behaviour and working traits can also occur if there is no selection for maintaining these traits and the genetic correlations between them and the traits selected for are zero. An increase in the number of candidates resulted in only small additional genetic responses, and the total responses were not close to the desired responses for the traits (schemes 3a–3b). This gave further evidence of the current breeding programme's failure to improve HD and ED.

Changing the relative weights of the traits

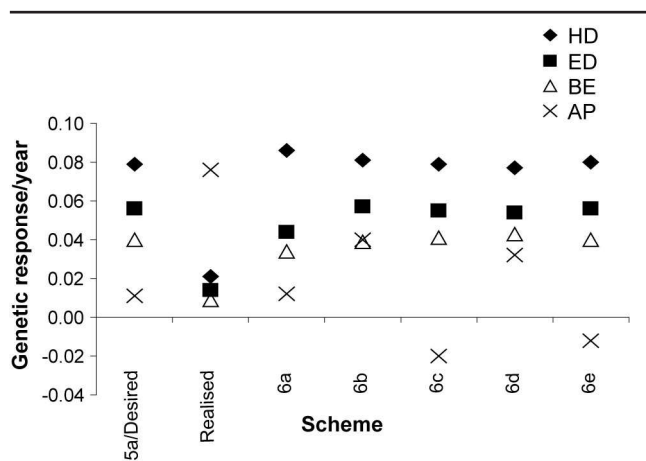
The only way to attain the desired genetic responses for HD and ED was to change the relative selection index weights strongly toward favouring these traits (Figure 1, schemes 4a–4c). Furthermore, increasing the number of candidates

Figure 1

Genetic responses in trait units for hip (HD) and elbow (ED) dysplasia, a behaviour trait (BE) and appearance (AP) from selection schemes simulated in the Finnish Rottweiler — see alternatives in Table 3.

resulted in additional responses for HD and ED, as long as the index weights clearly favoured them (schemes 5a–5a2). For BE, changing the index weights alone was not sufficient to attain the desired improvement, and the number of candidates also had to be increased. This was to be expected because the heritability for BE is small, making it difficult to select effectively among a small group of animals, especially when all selection candidates did not have a screening result on BE themselves. A very small relative index weight for AP was

Figure 2



Genetic response in trait units for hip (HD) and elbow (ED) dysplasia, a behaviour trait (BE) and appearance (AP) from selection schemes simulated in the Finnish Rottweiler with different phenotypic and genetic correlations assumed between the traits — see alternatives in Table 3.

sufficient to maintain the trait without negative genetic change. Assuming that the genetic parameters used in this study were near the 'real' values, the results show that strongly favouring AP reduces the genetic improvement in other traits, whereas achieving genetic progress in AP does not require as much emphasis on it as has been given traditionally. AP has a high heritability and it is easier to evaluate than, for instance, behaviour traits, which makes genetic improvement for AP more easily achievable.

Increasing the number of candidates from 40% to 60%, while defining the relative weights of the traits as 5.0, 5.0, 10.0 and 0.5 for HD, ED, BE and AP, respectively (scheme 5a), resulted in the desired responses in all the traits. In fact, the responses for HD and ED were even larger than desired in this scheme. Consequently, the relative weights of HD and ED can be kept at a smaller level if more dogs are screened and tested as potential candidates. Increasing the number of candidates from 60% to 80% increased the response further in all traits. However, the scheme with 80% of the dogs as candidates is not very feasible for the majority of the breeds in Finland, as it would require that 80% of all the dogs born would have to be screened for HD and ED.

Use of BLUP indices

The use of BLUP indices as extra sources of information for HD, ED and BE resulted in only a small further genetic response in the simulated schemes (Figure 1). One reason for this is that heritability of selected traits was high in this study. With a high heritability, phenotypic selection, ie selection based on an animal's own result only, is effective enough to lead to noteworthy genetic improvement, and the extra information from relatives brought by BLUP procedure is only marginal. Furthermore, only a low number of direct relatives for candidates were screened for HD and ED and tested for BE. These are the possible reasons for phenotypic selection being as effective as BLUP selection in this study.

With a lot of information from relatives, BLUP becomes more accurate than selection using the phenotypic records. In reality, the advantage of using BLUP is not only the use of a full pedigree, but also the estimation of fixed effects, which is difficult when using a sib index.

Use of BLUP indices can have also negative effects on the population. If the best animals are used in breeding without limiting the number of offspring allowed for them, inbreeding in the population will increase. With BLUP, the genetically superior animals will be identified more accurately than with phenotypic selection. These animals are likely to be related to each other and use of only a few families in breeding may result in a decrease in the genetic diversity of the population.

Changing the assumed correlations

Only the response in AP changed markedly when correlation coefficients were varied in the optimal breeding structure (Figure 2; Table 3, schemes 6a–6e). Responses of the other three traits stayed approximately at the same level in the five schemes despite the differing genetic and phenotypic correlations between the traits. Changing the correlations between AP and the other traits to be negative resulted in a slightly negative response in AP, because of the strong emphasis given to the other three traits in the optimal breeding strategy. Correlations between AP and HD could well be negative in some dog breeds, for instance in breeds such as the German Shepherd where an exaggerated sloping conformation to the hind quarters of the dog is being rewarded in the dog shows (Kaman & Gosling 1967). This conformation can make the posture of the hip joint suboptimal resulting in an increased risk of degenerative joint disease.

Putting the optimal breeding plans into practice

Although this study suggested that the current breeding programme in the Finnish Rottweiler is not working as effectively as it could, the results still have to be considered as optimistic when applied to many other breeds in Finland. The Rottweiler breed has one of the largest proportions of dogs screened for HD and ED and is also the breed most frequently tested with a behaviour test by the FKC. Additionally, it is quite common for Rottweiler owners to train their dogs in working trials and other activities. This automatically puts a selection pressure on the behaviour and working traits of the dogs.

In many dog breeds, appearance and even exaggerated, unhealthy traits are dominating the breeding goal. This practice continues, despite a pronouncement by the Council of Europe concerning certain dog breeds with undesirable or extreme conformations (Council of Europe 1995). The pronouncement recommends that careful attention is paid to reducing problems related to extreme conformation traits in these breeds, with the premise that if voluntary restrictions are not put into action the Council of Europe may totally ban breeding the most severely affected dog 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.

To improve the situation, dog breeders should be sufficiently educated in the field of genetics and breeding, and puppy buyers should be better informed about what to look for when buying a puppy. Some control is also needed from the authorities in the field. Kennel clubs and breed clubs, as well as the judges evaluating the dogs in the shows, have a key role in changing the direction of dog breeding toward healthier principles. Grøndalen (1979) states that a lighter and more functional dog would be bred if the standard measures of dogs presented at dog shows were decreased. Recently, the FKC has started to instruct the show judges in order to end the rewarding of exaggerated breed characteristics, and The Fédération Cynologique Internationale has published a leaflet appealing to show judges to interpret any breed standard in such a way that a dog must be 'functionally healthy'. Judges are also advised to penalise aggressive dogs by disqualification (Fischer 2003). McGreevy and Nicholas (1999) suggest that breed standards should be reviewed, by removing aspects contributing to animal welfare problems. In the shows, dogs should be rewarded for sound, healthy and functional conformation, without arranging them in any order, least according to the current 'beauty' ideals often defined only to please the human eye. Working and hunting trials, as well as other activities carried out by people with their dogs, should also receive more attention from the kennel clubs. This would automatically favour dogs with a more suitable character and functional conformation. Many options are available for improving the health and well-being of dogs. Most puppy buyers just want to have a healthy dog with a good character. At present, breeding does not correspond with this demand.

To conclude, changes are required in the current dog breeding programmes in order to achieve genetic improvement in both health and behaviour traits. The results of this simulation study show that the emphasis on hip dysplasia, elbow dysplasia, and behaviour traits needs to be increased in the breeding strategy, and, if the breeding strategy is to be achieved, this emphasis has to be at the expense of appearance. Furthermore, the number of dogs that are screened for health, and especially for behaviour, should be higher. This would increase both the number of candidates and the amount of information from relatives of the candidates, which would allow efficient selection. BLUP breeding values would also become more accurate if information on a larger proportion of the population existed.

Animal welfare implications

To preserve or improve the desired behaviour and working traits, as well as the health of the dogs in the current populations, systematic breeding programmes should be developed and followed. The relative weights of these important traits should be raised drastically at the expense of appearance, ie show characteristics.

Acknowledgements

Funding for this study was provided by the Emil Aaltonen Foundation and the Alfred Kordelin Foundation. Nora Salonen from the breed club for the Finnish Rottweiler is

acknowledged for providing the information on the proportion of dogs tested for behaviour traits and on the proportion of dogs evaluated in the dog shows.

References

- Beuing R, Mues Ch, Tellhelm B and Erhardt G** 2000 Prevalence and inheritance of canine elbow dysplasia in German Rottweiler. *Journal of Animal Breeding and Genetics* 117: 375-383
- Bourdon RM** 1997 *Understanding Animal Breeding*. Prentice-Hall: New Jersey, USA
- Bucksch A and Lindberg S** 2002 *Retrieveravel i Sverige*. MSc Thesis, Swedish Agricultural University, Uppsala, Sweden [Title translation: Retriever breeding in Sweden.]
- Council of Europe** 1995 European convention for the protection of pet animals. Resolution on the breeding of pet animals. Available at: <http://www.felinewelfare.co.uk/coemcp.htm#resolution>
- Falconer DS and Mackay TFC** 1996 *Introduction to Quantitative Genetics, 4th Edition*. Longman: Harlow, UK
- Fischer U** 2003 We are responsible. *Fédération Cynologique Internationale Magazine* 2: 5-7
- Grøndalen J** 1979 Arthrosis with special reference to the elbow joint of young, rapidly growing dogs. II. Occurrence, clinical and radiographical findings. *Nordisk Veterinær Medicin* 31: 69-75
- Hedhammar Å, Olsson S-E, Andersson S-A, Persson L, Pettersson L, Olausson A and Sundgren P-E** 1979 Canine hip dysplasia: a study of heritability in 401 litters of German Shepherd Dogs. *Journal of the American Veterinary Medical Association* 174: 1012-1016
- Henderson CR** 1984 Best linear unbiased estimation. In: *Applications of Linear Models in Animal Breeding* pp 17-27. University of Guelph Press: Guelph, Canada
- Kaman CH and Gossling HR** 1967 A breeding program to reduce hip dysplasia in German Shepherd dogs. *Journal of American Veterinary Medical Association* 151: 562-571
- Karjalainen L, Ojala M and Vilva V** 1996 Environmental effects and genetic parameters for measurements of hunting performance in the Finnish Spitz. *Journal of Animal Breeding and Genetics* 113: 525-534
- Leighton EA** 1997 Genetics of canine hip dysplasia. *Journal of the American Veterinary Medical Association* 210: 1474-1479
- Lemonick MD** 1994 A Terrible Beauty. Available at http://www.time.com/time/archive/preview/from_redirect/0,10987,1101941212-163404,00.html
- Liinamo A-E, Karjalainen L, Ojala M and Vilva V** 1997 Estimates of genetic parameters and environmental effects for measures of hunting performance in Finnish Hounds. *Journal of Animal Science* 75: 622-629
- Mackenzie SA, Oltenacu EAB and Leighton E** 1985 Heritability estimate for temperament scores in German Shepherd dogs and its genetic correlation with hip dysplasia. *Behavior Genetics* 15: 475-482
- Mäki K, Groen AF, 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
- Mäki K, Groen AF, 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
- McGreevy PD and Nicholas FW** 1999 Some practical solutions to welfare problems in dog breeding. *Animal Welfare* 8: 329-341
- Ohlerth S, Lang J, Busato A and Gaillard G** 2001 Estimation of genetic population variables for six radiographic criteria of hip dysplasia in a colony of Labrador Retrievers. *American Journal of Veterinary Research* 62: 846-852

- Reuterwall C and Ryman N** 1973 An estimate of the magnitude of additive genetic variation of some mental characters in Alsatian dogs. *Hereditas* 73: 277-284
- Ruefenacht S, Gebhart-Henrich S, Miyake T and Gaillard C** 2002 A behaviour test on German Shepherd dogs: heritability of seven different traits. *Applied Animal Behaviour Science* 79: 113-132
- Rutten MJM, Bijma P, Woolliams JA and van Arendonk JAM** 2002 SelAction: Software to predict selection response and rate of inbreeding in livestock breeding programs. *Journal of Heredity* 93: 456-458
- Swenson L, Audell L and Hedhammar Å** 1997a Prevalence and inheritance of and selection for hip dysplasia in seven breeds of dogs in Sweden and benefit:cost analysis of a screening and control program. *Journal of the American Veterinary Medical Association* 210: 207-214
- Swenson L, Audell L and Hedhammar Å** 1997b Prevalence and inheritance of and selection for elbow arthrosis in Bernese mountain dogs and Rottweilers in Sweden and benefit:cost analysis of a screening and control program. *Journal of the American Veterinary Medical Association* 210: 215-221
- Ubbink GJ, Knol BW and Bouw J** 1992 The relationship between homozygosity and the occurrence of specific diseases in Bouvier Belge des Flandres dogs in the Netherlands. *Veterinary Quarterly* 14: 137-140