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Population structure and genetic diversity of worldwide Nova Scotia Duck Tolling Retriever and Lancashire Heeler dog populations

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Keywords

Dog; effective population size; kinship; effective number of founders; effective number of ancestors.

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Summary

The aim of this study was to research the population structure and genetic diversity of the Nova Scotia Duck Tolling Retriever (NS) and the Lancashire Heeler (LH) dog breeds. Data consisted of nearly all the worldwide registration history for both breeds, including 28 668 NS and 4 782 LH individuals. A reference population, including the females born between 1999 and 2008, was defined for genetic analyses for each breed. Average depth of the pedigrees known for the reference population dogs was 12.9 complete generation equivalents in the NS and 6.0 in the LH. Only a small fraction of the born dogs were used later for breeding. Effective number of founders was 9.8 in the NS and 15.2 in the LH. More than 50% of the genetic diversity in the reference population was explained by two ancestors in the NS and five in the LH. Average inbreeding coefficients in the reference populations were 0.26 in the NS and 0.10 in the LH. Average kinships were 0.26 and 0.08 and realised effective population sizes 18 and 28, respectively. Failure to use available genetic resources for sustainable breeding has resulted in depletion of genetic variation in both breeds. To increase genetic variation, a larger proportion of the dogs should be used in reproduction and the contributions of reproducing animals should be equalized. In the LH, it is necessary to use the unregistered farm dogs in breeding. In the NS, crosses with another breed are needed.

Introduction

Recent studies have reported about depletion of genetic variation in many dog breeds, although the consensus number within a breed may be very large (Leroy *et al.* 2006; Calboli *et al.* 2008; Głażewska 2008). Most dog breeds are closed populations with no gene flow from outside, and only a small fraction of the dogs are used for breeding (Ubbink 1998; Mäki *et al.* 2001; Calboli *et al.* 2008). This has spread the gene variants of a small number of dogs to the whole breed. As most dogs carry also detrimental

alleles (McGreevy & Nicholas 1999), a number of genetic problems have accumulated in each breed.

The Nova Scotia Duck Tolling Retriever (NS) is a gun dog originating from Canada. It was developed to lure (toll) ducks and geese within shotgun range and to retrieve them from the water after they have been shot. Nowadays, the NS is used mostly as a pet. The purebred Lancashire Heeler (LH) has been known in its native county at least for one hundred and fifty years (Lancashire Heeler Club 2009), but it was not until 1981 when the United Kingdom Kennel Club (UKKC) recognised the breed and started

official registrations. The LH is originally a working breed, used as a shepherd for cattle and sheep. Many farmers still use dogs of this breed for that purpose, but like the NS, also the LH is nowadays mainly a pet.

According to the Nova Scotia Duck Tolling Retriever breed club in Finland, the largest health problems of the NS are related to immunity. The breed is predisposed to for example immune-mediated rheumatic disease, IMRD (Wilbe *et al.* 2009). In addition, there are dogs with eye diseases and hip dysplasia in the breed (Finnish Kennel Club 2009). In the LH, the frequency of primary lens luxation, a painful condition of the eye, seems to be increasing quickly (Sargan *et al.* 2007). The LH has also other eye diseases, like collie eye anomaly (Lancashire Heeler Club 2009).

Management and selection programs of the NS and LH breeds require information on genetic variability within the breed as well as on gene flow between subpopulations in different countries. The LH is considered as an endangered breed by the UKKC, because of the small number of dogs composing the gene pool and the risk of the breed's known inherited diseases (Lancashire Heeler Club 2009), but no studies regarding genetic structure and diver-

sity have been made so far in this breed or the NS. Thus, the purpose of the study was to assess the population structure and genetic diversity of the worldwide population of these two breeds.

Materials and methods

Materials

The data used in this study consisted of the worldwide registration history of the NS and the LH, which have been collected from the kennel clubs in different countries. The NS dogs in the data originated from 17 different countries and LH dogs from five different countries (Table 1). The data included also non-registered founder dogs from the early years of both the breeds. There were 28 668 NS and 4782 LH individuals in the data. The NS dogs were born between 1931 and 2008, and the LH dogs between 1975 and 2008 (Figures 1 and 2).

The name and the registration number of the dog and its parents, gender, date of birth and country of origin were included in the data. Five per cent of the NS and 57.3% of the LH dogs did not have their registration number included in the data, but instead, every dog had a unique name, which was

Subpopulation	N	F	CGE	% Foreign breeding males
Nova Scotia Duck Tolling Retriever				
Canada	7463	0.27	10.9	7.6
Sweden	5115	0.26	12.6	29.8
Finland	3840	0.27	13.3	39.2
USA	2343	0.26	12.0	46.7
Norway	2285	0.27	13.6	45.7
Denmark	1696	0.27	13.4	61.6
The Netherlands	1334	0.25	13.7	88.3
United Kingdom	950	0.25	12.2	36.0
Belgium	742	0.25	13.2	73.5
Australia	470	0.28	13.2	42.6
Switzerland	316	0.24	13.3	66.1
Germany	234	0.24	13.1	90.2
Czech Republic	234	0.29	14.3	94.0
Poland	80	0.28	14.5	100.0
France	57	0.26	13.6	98.3
Austria	55	0.28	13.6	100.0
New Zealand	13	0.32	13.3	100.0
Lancashire Heeler				
United Kingdom	2956	0.09	5.2	10.4
Sweden	1438	0.06	6.3	6.5
Finland	348	0.07	7.4	54.0
The Netherlands	27	0.10	7.2	100.0
Norway	13	0.04	3.3	92.3

Table 1 Average inbreeding coefficients (F) and complete generation equivalents (CGE) as well as proportion of foreign breeding males in each subpopulation

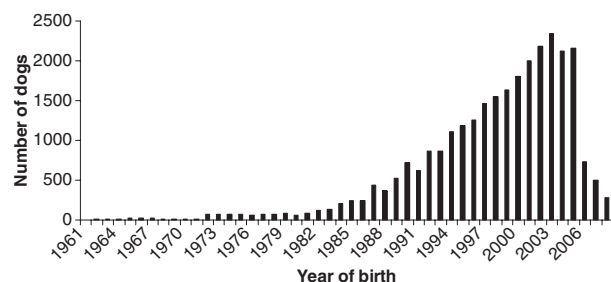


Figure 1 Nova Scotia Duck Tolling Retriever data by year of birth of the dogs.

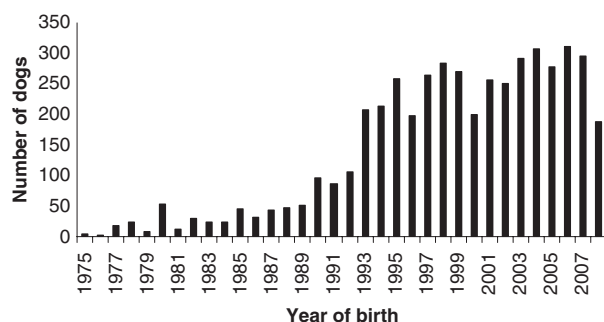


Figure 2 Lancashire Heeler data by year of birth of the dogs.

used as an ID in the study. Dogs with the same name but different registration number and/or parents had either their registration number or a running number written in the end of their name to identify different individuals.

Dogs that were recorded both as a sire and as a dam or as their own parent were eliminated from the analyses. Date of birth was missing for 65 NS and 73 LH dogs. There were 14 058 female and 14 553 male NS dogs. Information on gender was missing for 51 dogs. There were 2461 female and 2313 male LH dogs. Information on gender was missing for five dogs. Information on the country of origin was missing for 1441 NS dogs.

There were altogether 3721 NS and 1184 LH dogs used for breeding, which equals 13.0% and 24.8% of all the dogs in the data, respectively. Of these breeding animals, 77% (the NS) and 93% (the LH) had 1–20 offspring, while 2% of the breeding animals in both breeds had more than 80 offspring (Table 2).

The proportion of the animals used for breeding was lower in males compared to females (Figure 3). On average, 23% of the NS females born in the 1990s had been used for breeding. In males, this proportion was 12%. More recently, proportions of both males and females used for breeding have been

Table 2 Distribution of the number of offspring among breeding dogs

No. of offspring	No. (proportion) of breeding dogs	
	Nova Scotia Duck Tolling Retriever	Lancashire Heeler
0–10	1912 (51%)	903 (76%)
11–20	986 (26%)	202 (17%)
21–30	416 (11%)	51 (4%)
31–40	176 (5%)	12 (1%)
41–60	126 (3%)	9 (1%)
61–80	54 (1%)	5 (0%)
81–100	24 (1%)	1 (0%)
101–150	24 (1%)	1 (0%)
>151	3 (0%)	0 (0%)
Total	3721 (100%)	1184 (100%)

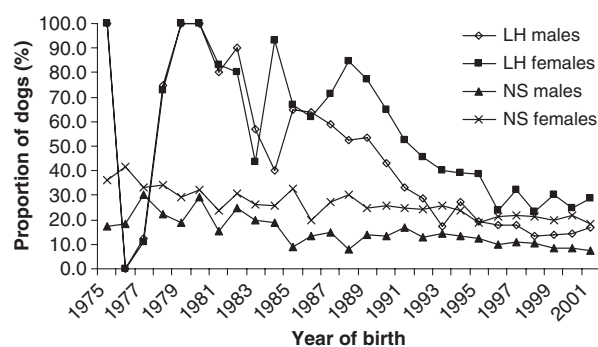


Figure 3 Proportion of dogs by year of birth used for breeding. NS = Nova Scotia Duck Tolling Retriever, LH = Lancashire Heeler.

reducing. Of the NS males and females born in 2000 and 2001, 8.5% and 20.0%, respectively, had been bred.

Because of the late breed recognition and small number of registered dogs, a large proportion of the LH dogs born in the 1980s and early 1990s were used for breeding. Of the males and females born in the 1990s, on average 23.2% and 38.9%, respectively, were used in breeding. Of the males and females born in 2000 and 2001, 16.4% and 26.7%, respectively, had offspring.

Generation intervals were calculated as the average age of parents at the birth of their progeny kept for reproduction (James 1977). The average generation interval was 3.95 years for the NS and 3.99 years for the LH. Paternal generation intervals were above 4 years and maternal generation intervals were below 4 years in both breeds (Table 3).

At generation 10, 97.8% of the ancestors were known for the NS and 23.7% for the LH (Table 4). At maximum, 28 generations were traced for the NS and 15 for the LH. The average depth of the

Table 3 Generation intervals for different paths

Path	Nova Scotia Duck Tolling Retriever			Lancashire Heeler		
	N	Interval	MSE ¹	N	Interval	MSE
Sires to sires	1287	4.20	0.06	270	4.15	0.16
Sires to dams	2412	4.11	0.05	513	4.20	0.12
Dams to sires	1285	3.76	0.05	270	3.72	0.11
Dams to dams	2412	3.88	0.04	496	3.71	0.08
Total	7396	3.99	0.02	1549	3.95	0.06

¹MSE, mean square error.**Table 4** Percentage of known ancestors and results of the genetic analyses

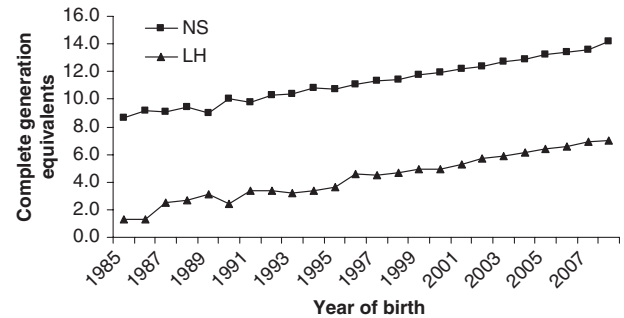
	Nova Scotia Duck Tolling Retriever	Lancashire Heeler
Total no. of animals in the data	28668	4782
No. of animals in the reference population	7707	1291
% Known ancestors at generation 3	99.8	98.4
% Known ancestors at generation 5	99.7	94.4
% Known ancestors at generation 8	98.7	55.0
% Known ancestors at generation 10	97.8	23.7
% Known ancestors at generation 12	88.9	7.5
Total no. of founders (f)	19	72
Effective no. of founders (f_e)	9.8	15.2
Effective no. of ancestors (f_a)	5.2	13.6
Founder genome equivalents (N_g)	2.1	6.4
f_e/f	0.52	0.21
f_a/f_e	0.53	0.89
N_g/f_e	0.21	0.42
Average inbreeding coefficient	0.26	0.10
Average kinship	0.26	0.08

All figures are for dogs born between 1999 and 2008, except for the total no. of animals in the data.

pedigrees known for the dogs born during the last 10 years of the data, i.e. 1999–2008, was 12.9 complete generations for the NS and 6.0 for the LH. This was measured as complete generation equivalents (CGE), which is the sum of the $(1/2)^n$ coefficients over all generations where n is the number of generations separating animals from the known ancestor (Maignel *et al.* 1996). After obtaining CGE for each dog, an average CGE was calculated by birth year for both breeds. Depth of the pedigrees increased steadily during the years (Figure 4).

Methods

Genetic diversity was studied as effective number of founders (Lacy 1989), effective number of ancestors

**Figure 4** Average complete generation equivalents by year of birth. NS = Nova Scotia Duck Tolling Retriever, LH = Lancashire Heeler.

(Boichard *et al.* 1997), founder genome equivalents (Lacy 1989), as well as effective population size and average kinship (Malécot 1948).

Individuals with offspring but no parents in the data were defined as non-inbred and non-related founders in the analyses. The expected genetic contribution of each founder to the reference population is the probability of an allele within the reference population taken at random to originate from a given founder (James 1972). A reference population was defined for both breeds as the females born between 1999 and 2008.

The effective number of founders (f_e) is a measure of the number of equally contributing founders that would be expected to produce the same genetic diversity as in the reference population (Lacy 1989). If the founders have an equal contribution, f_e is the same as the total number of founders (f). Also the effective number of ancestors (f_a) was estimated, as f_e does not account for bottlenecks in a pedigree. f_a measures the minimum number of ancestors, which can be founders or ancestors, needed to explain the genetic diversity in the reference population. If there are no bottlenecks, f_a is the same as f_e . As the most important ancestors can be related to each other, only the marginal contributions of the ancestors were considered (Boichard *et al.* 1997). The marginal contribution of an ancestor is the contribution not yet explained by the other already considered ancestors. The smallest set of contributing ancestors was found with the iterative method by Boichard *et al.* (1997).

Founder genome equivalents (N_g) account for all random losses of alleles during segregations; thus, it is always the smallest when compared with f_a and f_e . N_g measures the probability of founder genomes still being present in a given locus in the population under study (Lacy 1989).

An inbreeding coefficient (F) was calculated for each dog with the method described by Meuwissen & Luo (1992). Average inbreeding coefficients by birth year were computed both using all the data and using only dogs with a minimum of ten (NS10 for the NS) and a minimum of five (LH5 for the LH) CGE in the data. NS10 and LH5 were computed starting from the year of birth with at least 25 dogs in the analysis, i.e. the year 1983 for the NS and the year 1991 for the LH.

The effective population size (N_e) is the number of equally contributing breeding animals that would lead to the increase in inbreeding observed (Wright 1923). N_e was estimated using a regression based approach described by Gutiérrez *et al.* (2003), from the rate of inbreeding (ΔF , Falconer & Mackay 1996):

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

and

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

where F is an average inbreeding coefficient, estimated using all data, and t is the number of generation.

The increase in inbreeding between two generations ($F_t - F_{t-1}$) was calculated as $b * l$, where b is the regression coefficient of the average inbreeding coefficients over the year of birth, including all the years of the data, and l is the average generation interval in a breed. F_{t-1} was computed from the mean inbreeding in the last year studied (F_{ly}) as $F_{ly} - l * b$.

In addition, realised effective population size was estimated following the approach by Gutiérrez *et al.* (2009). This approach is based on the increase in inbreeding for each individual (ΔF_i) in a given population. The values of ΔF_i are averaged and used to estimate the realised effective size.

The average kinship within a breed was estimated both between all females and between all males born between 1999 and 2008. One thousand samples of size 200 each were analysed.

The population structure was investigated from the genetic contributions of the subpopulations by summing up Boichard *et al.*'s (1997) contribution values of the ancestors belonging to each subpopulation. In addition, Wright's (1951) F-statistics were estimated and average pairwise coancestry coefficients (f_{ij}) between individuals of two subpopulations, i and j , computed (Caballero & Toro 2000).

Most parameters were computed using the software package Pedig (Boichard 2002). Percentage of known ancestors and coefficients of inbreeding were computed using Wsys-L (Vilva 1997). Population

structure was studied and realised effective size estimated using the program Endog (v4.6, Gutiérrez & Goyache 2005).

Results

Genetic diversity

There were altogether 22 founders in the NS breed, of which 18 had offspring more remote than the sixth generation. In the LH, altogether 155 founders existed, of which 68 had offspring more remote than the sixth generation (data not shown). Considering only the reference population, i.e. dogs born between 1999 and 2008, the NS had 19 founders and the LH 72 founders (Table 4). These founders had unbalanced genetic contributions in both breeds: the effective number of founder dogs was only 9.8 in the NS and 15.2 in the LH. In addition, comparison of the effective number of founders and the effective number of ancestors revealed genetic bottlenecks in both breeds.

Founder genome equivalents were 2.1 for the NS and 6.4 for the LH. Comparing them with the total number of founders indicated that 11.1% and 8.9% of the genetic diversity among the NS and the LH founders, respectively, have been retained in the population and approximately 90% has been lost in both breeds.

More than 50% of the genetic contributions for the reference population of the NS were explained by only two ancestors (Table 5). Ten ancestors contributed to 97.0% of all genetic variation in the reference population. In the LH, five ancestors were needed to explain 50% of the genetic diversity in the reference population, and 10 ancestors contributed to 62.9%.

The average inbreeding coefficient of the NS increased rapidly from the 1950s and 1960s until the end of the 1980s, when it reached 0.30 (Figure 5). The inbreeding trend from the restricted data (NS10) reached its highest value in 1985, being then 0.33. From the year 1989 onward, NS10 was similar to the trend with all dogs. After the year 1988, the average inbreeding coefficient stabilized at 0.27. The rate of inbreeding during the whole period was 1.87%, resulting in an estimated effective population size of 27. The realised effective population size was 18.

In the LH, increase in the average inbreeding coefficient was quite steady from the year 1988 onward (Figure 5). The trend from the restricted data (LH5) was similar to the trend with all the dogs, although

Breed and ancestor	Gender	Birth year	Contribution (%)
Nova Scotia Duck Tolling Retriever			
Majour of Schubendorf	Male	1957	27.9
Goldie of Schubendorf	Female	1961	27.4
Green Meadows Tawnee Wakon	Female	1961	12.2
Bidewell's Flip (unreg)	Male	Not known	10.2
Bidewell's Lady (unreg)	Female	Not known	8.6
Robie Surf Of Glencoe	Male	1966	7.9
Green Meadows Molly Of Acadia	Female	1962	1.4
Collier's Magnum Load Dory	Female	1986	0.6
Cabottrails Belle Of The Isle	Female	1985	0.5
Hyflyer's Foxy Roxanne	Female	1993	0.3
Total contribution			97.0
Lancashire Heeler			
Pip of Doddslane	Male	1983	19.2
Bowanne Bolshy Bert	Male	1988	10.1
Doddslane Ben	Male	1985	9.4
Basil of Mossbeacon	Male	1982	5.7
Susie of Doddslane	Female	1990	5.3
Teddy Boy of Tushielaw	Male	1982	4.4
Feniscowles Earl Bumble Bee	Male	1985	3.3
Tapatina Little Gem	Female	1982	2.8
Tushielaw Bessie from Haelarbobs	Female	1983	2.7
Acremead Buzz	Female	1988	2.2
Total contribution			62.9

Table 5 Marginal genetic contribution (%) of the ten most influential ancestors of the dogs born between 1999 and 2008

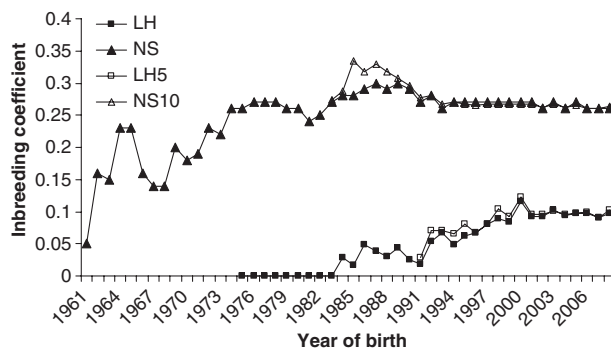


Figure 5 Average inbreeding coefficients by year of birth for all dogs and for the LH with a minimum of five (LH5) and the NS with a minimum of ten (NS10) complete generation equivalents in the data. NS = Nova Scotia Duck Tolling Retriever, LH = Lancashire Heeler.

the inbreeding coefficients were somewhat higher during the 1990s. The average inbreeding coefficient stabilized during recent years also in this breed, being 0.10 for the dogs born in the 2000s. The rate of inbreeding during the whole period was 1.64%. The effective population size was estimated at 30 and the realised effective size at 28. The average kinship within the dogs born between 1999 and 2008 was 0.26 in the NS and 0.08 in the LH (Table 4).

Population structure

The country of origin, i.e. Canada, was the only contributing subpopulation in the NS. Canada had also the numerically largest subpopulation and was the most unfrequent user of foreign breeding males (Table 1). In the LH, the largest genetic contribution (95.8%) came from the country of origin, i.e. the UK, but also the subpopulation in Sweden contributed 4.2% (data not shown). The largest subpopulation was the UK. The proportion of foreign breeding males was smallest in Sweden (6.5%) and largest in The Netherlands, which had not used own males for breeding at all.

No differentiation was found between the populations in different countries in neither of the breeds. The average inbreeding coefficients in the subpopulations varied between 0.24 and 0.32 in the NS and between 0.04 and 0.10 in the LH (Table 1). The proportion of the total inbreeding in the breeds because of differentiation among subpopulations (Wright's F_{ST}) was 0.019 for the NS and 0.009 for the LH. In the NS, the average pairwise coancestry between the subpopulations varied between 0.24 and 0.29 (data not shown), except for the pairs Canada and the UK (0.23), the UK and the USA (0.23), Australia and New Zealand (0.32) and Czech Republic and Poland

(0.32). In the LH, the average pairwise coancestry was lowest between Norway and the UK (0.04) and highest between Finland and the Netherlands (0.08) and the Netherlands and the UK (0.08).

Discussion

The pedigrees of the dogs in the reference population of the NS reached on average 12.9 complete ancestral generations. This is the most complete data set reported in studies on canine population structure and inbreeding (e.g. Mäki *et al.* 2001; Leroy *et al.* 2006, 2009; Calboli *et al.* 2008). The LH data set did not include such deep pedigrees. There are approximately seven generations of registered LH dogs so far.

Official registration of puppies does not require paternity tests or other methods to prove parentage, which may influence the results of this study, as it gives room for errors in the pedigrees. Only if there is reason to doubt the information given by the breeder, the kennel clubs advise the breeder to have the parentage tested. Errors in the pedigrees are expected to be occasional, however.

Founders had unbalanced genetic contributions in both breeds in this study. Leroy *et al.* (2006) reported the effective numbers of founders in French dog breeds to be larger than 20 in all studied breeds, except the very rare breed Barbet. Leroy *et al.* (2009) studied genetic diversity of 61 dog breed populations in France and reported effective numbers of founders between 25 and 656, again except for the Barbet, while this study on NS and LH found the effective numbers of founders to be 9.8 and 15.2, respectively.

Genetic bottlenecks were more severe in the NS, which had a lower f_a/f_e ratio compared to the LH. Also, genetic drift was stronger in the NS compared to the LH, because the ratio N_g/f_e was smaller in the NS. In France, this ratio has been reported to vary between 0.20 (Braque Saint-Germain; Leroy *et al.* 2009) and 0.97 (Barbet; Leroy *et al.* 2006), so the results of this study are between these (Table 4). Given the narrow founder populations of the NS and the LH, as well as the deep pedigrees in the data of this study, the rates estimated here can be considered not as bad as the results of Leroy *et al.* (2006, 2009).

Only two ancestors were needed to explain half of the genetic diversity in the NS, and ten ancestors explained practically all of it. In the LH, five ancestors explained half of the genetic variation, and 10 explained 62.9%. This shows that the situation is somewhat better in the LH compared to the NS.

Leroy *et al.* (2006) reported the number of ancestors explaining half of the genetic diversity in the reference population to be below ten in three breeds and between 10 and 15 in the other six breeds studied.

If the rate of inbreeding is slow enough, i.e. between 0.5% and 1.0% per generation at maximum, natural selection may have enough time to counteract the loss of heterozygosity (Bijma 2000). Both in the NS and in the LH, the rate of inbreeding was larger than 1.0% and N_e clearly smaller than 50, showing that these breeds lose heterozygosity too rapidly to be able to maintain sufficient genetic variation. In the NS, rate of inbreeding has become slower during the recent years, however, indicating that the situation may have been somewhat improved. Breeders are today better informed about the dangers of inbreeding, and most of them avoid mating close relatives. However, with the very high kinship value, it will not be possible to maintain the inbreeding level steady in the long term.

In French dog breeds, N_e between 21 (Barbet) and 152 (Bouledogue Français) have been reported (Leroy *et al.* 2006). Other dog breed populations in France have effective sizes ranging from 46 (Irish Red Setter) to 2136 (West Highland White Terrier; Leroy *et al.* 2009). Calboli *et al.* (2008) reported the N_e ranging from 33 in the Rough Collie to 114 in the Labrador Retriever populations in the UK, and Mäki *et al.* (2001) found the N_e of the Finnish Hound to be 100. Despite a few tens or even hundreds of thousands of dogs registered in the breeds, the genetic basis of most of these breeds is very narrow, especially when estimated from deep pedigrees. Calboli *et al.* (2008) and Leroy *et al.* (2006, 2009) studied subpopulations of the breeds, while the data of this study and the study by Mäki *et al.* (2001) on the Finnish Hound included nearly all the registered individuals worldwide.

Reasons for small N_e of the studied breeds seem to be the imbalance of founder contributions, the small proportion of dogs and genealogical lines used for breeding and the large variation of family size. Also for example Calboli *et al.* (2008), Mäki *et al.* (2001) and Ubbink (1998) have reported that only small fractions of pure-breed dog populations are used as reproductive animals. Of the male NS and LH born in the beginning of the 2000s, more than 90% and 85%, respectively, were not bred.

Many breed clubs in Finland have, in accordance with the Finnish Kennel Club (FKC), decided to set a restriction to the number of offspring of a single dog to equalize the contributions of reproducing animals. For the NS, this limit has been set to 60 from

the beginning of the year 2009, and for the LH, a limit of 20 was adopted from the year 2007 onward (Finnish Kennel Club 2009).

The high average kinship coefficients indicate that the NS dogs are more closely related to each other than full-sibs and the LH dogs more than cousins. This situation makes it very hard to find pairs of potential breeding dogs that are not closely related to each other. Compared to the findings by Leroy *et al.* (2006, 2009), the NS and the LH are among the breeds with the highest average kinship values (0.26 and 0.08, respectively). In fact, the average kinship in the NS is remarkably high. Leroy *et al.* (2006) found the average kinship in the French dog breeds to vary from 0.02 (Basset fauve de Bretagne and Bouledogue Français) to 0.10 (Barbet); and in the study by Leroy *et al.* (2009), kinships were between 0.004 (Poodle) and 0.088 (Braque Saint-Germain). In the LH, the true kinship is probably higher than estimated, given the long history of the breed and the fact that the assumption of non-related founders in the data is probably unrealistic. The history of the breed extends far beyond the time frame of the data, and it is possible that the founders defined here are heavily inbred.

The high average inbreeding and kinship coefficients could result from differentiation between the subpopulations and preferred matings within population because of geographic distances, but this was not the situation in the studied breeds. Instead, the subpopulations formed genetically one large population in both breeds. Wright's F_{ST} and average pairwise coancestry coefficients revealed high rates of gene flow among the countries in both breeds, and proportions of foreign breeding males were large in almost all subpopulations.

According to the results of Leroy *et al.* (2006), the Barbet is critically endangered, and some crosses with other dog breeds have already been made in the Barbet to introduce new genetic variation. The estimates of N_e in this study suggest that the LH is similarly and the NS even more endangered than the Barbet. The NS has also been reported to have narrow diversity of DLA II haplotypes, of which one has been found to be a significant genetic risk factor for IMRD in a homozygous state (Wilbe *et al.* 2009).

Genetic diversity of the studied breeds should be increased by introducing more animals in breeding and equalizing the contributions of the reproducing animals. The situation of the NS requires crossings with another breed. In the LH, most dogs owned by farmers are not registered, so an additional indigenous population, possibly with new gene variants,

exists for this breed. Breeders should use these dogs in breeding.

Mean kinship or average relatedness (Gutiérrez *et al.* 2003) would be useful measures when selecting dogs for breeding. Dogs with low kinship coefficients are valuable breeding dogs, because they may have alleles that other dogs of the breed do not have.

In conclusion, both studied breeds have very low genetic diversity. To increase genetic variation, a larger proportion of the dogs should be used in reproduction and the contributions of reproducing animals should be equalized. In the NS, also breed crosses are essential. In the LH, non-registered dogs can be used in the first place, to supersede breed crosses.

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