ORIGINAL ARTICLE

Recent breeding history of dog breeds in Sweden: modest rates of inbreeding, extensive loss of genetic diversity and lack of correlation between inbreeding and health

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Summary

One problem in modern dogs is a high occurrence of physical diseases, defects and disorders. Many breeds exhibit physical problems that affect individual dogs throughout life. A potential cause of these problems is inbreeding that is known to reduce the viability of individuals. We investigated the possible correlation between recent inbreeding and health problems in dogs and used studbook data from 26 breeds provided by the Swedish Kennel Club for this purpose. The pedigrees date back to the mid-20th century and comprise 5–10 generations and 1 000–50 000 individuals per pedigree over our study period of 1980–2010. We compared levels of inbreeding and loss of genetic variation measured in relation to the number of founding animals during this period in the investigated dog breeds that we classified as 'healthy' (11 breeds) or 'unhealthy' (15) based on statistics on the extent of veterinary care obtained from Sweden's four largest insurance companies for pets. We found extensive loss of genetic variation and moderate levels of recent inbreeding in all breeds examined, but no strong indication of a difference in these parameters between healthy versus unhealthy breeds over this period. Thus, recent breeding history with respect to rate of inbreeding does not appear to be a main cause of poor health in the investigated dog breeds in Sweden. We identified both strengths and weaknesses of the dog pedigree data important to consider in future work of monitoring and conserving genetic diversity of dog breeds.

Introduction

Selective breeding for one or a few particular traits typically results in loss of overall genetic variation (Johansson & Rendle 1968). During recent years, increasing conservation genetic focus has been devoted to domestic animal populations because rapid reduction in genetic variation can result in various types of problems including reduced potential for future breeding needs. The attention includes both scientific efforts (Baumung *et al.* 2004) and international policy work within, for example the United Nations Convention on Biological Diversity (CBD; www.cbd.int), and is particularly directed towards food-producing domestic animals (FAO 2007). Relatively little attention has been paid to conservation genetics of other domestic animals including dogs.

The dog has many important roles in modern society and its use includes: for therapy, herding, hunting, sports activities, medical and genomics research, in police, customs, military, rescue and security work, for identifying biological material, and for company (Lindblad-Toh *et al.* 2005; Browne *et al.* 2006; Wells 2007; Horvath *et al.* 2008; Pastore *et al.* 2011; Turcsán *et al.* 2011). To serve all these purposes, an increasing number of different dog breeds have been created through strong selective breeding (Wayne & Ostrander 2007). During the past 100 years, dog shows

have also emerged as increasingly popular, and current selective breeding typically focuses on physical appearance (Lindblad-Toh *et al.* 2005). Recent breeding has been shown to be coupled with rapid loss of genetic variation in several dog breeds in Europe (Leroy *et al.* 2006; Calboli *et al.* 2008; Voges & Distl 2009).

A high occurrence of physical diseases, defects and disorders (Hedhammar *et al.* 2011) is an increasing problem of many dog breeds, resulting in physical problems that affect individual dogs already at young ages (Fleming *et al.* 2011), and veterinary treatments are frequently needed throughout life (Olsson *et al.* 2011). A potential cause of these problems is loss of genetic variation and inbreeding that is known to reduce the viability of individuals. Inbreeding is often associated with increased occurrence of hereditary disorders governed by autosomal recessive alleles (Wright 1977), and inbreeding depression has been documented both in various dog breeds (Hall & Wallace 1996; Ubbink *et al.* 1998; Ólafsdóttir & Kristjánsson 2008) and in the wild ancestor of dogs – the wolf (Laikre & Ryman 1991; Liberg *et al.* 2005).

In this study, we report recent breeding history in a sample of dog populations in Sweden that were selected to represent breeds with a high occurrence of health problems ('unhealthy' breeds) as well as breeds that were classified as 'healthy'. We quantified rates of recent inbreeding and loss of genetic variation measured in terms of founder alleles using pedigree data from the Swedish Kennel Club comprising the past few decades and analysed whether the two groups of breeds differ in these quantities.

Materials and methods

We used pedigree data from a total of 26 dog populations (breeds) in Sweden obtained in 2011 from the Swedish Kennel Club (SKC; a kennel club is a nationwide organization which works and cares for purebred dogs in a country). SKC was founded in 1889 and their computerized studbook database was created in 1975–1976 (Th. Wink, personal communication, 2011) and comprises pedigrees of almost all dog breeds kept in Sweden; approximately 90 per cent of pedigree dogs in Sweden are included in these records (H. Rosenberg, personal communication, 2011). Most of our 26 breed pedigrees date back to the mid-1900s. This means that individuals of that time are regarded as 'founders' with no information back in time with respect to ancestry.

We selected breeds for analysis by first identifying healthy and unhealthy dog breeds based on informa-

tion from insurance companies. Statistics reflecting the extent of veterinary care per dog breed were obtained from Sweden's four largest insurance companies for pets (*Agria*: www.agria.se, *Folksam*: www.folksam.se, *If*: www.if.se, and *Sveland*: www.sveland.se).

The insurance companies classify dog breeds with respect to the amount of insurance money disbursed for each breed compared with the total insurance premium income for the breed. These classifications are updated annually, and we used the health classifications as of December 2009. The companies *Agria*, *Folksam*, and *Sveland* used six categories (six being the highest cost for veterinary care per dog, and one being the lowest). The *If* insurance company used eight categories (where eight represents the highest costs for veterinary care per dog, and one the lowest). We ranked dog breeds based on the classifications from the four companies and defined 'unhealthy' breeds as those classified as most expensive with respect to veterinary care by at least three of the four companies. The opposite was carried out to identify 'healthy' breeds (breeds classified in the category of lowest veterinary care expenses by at least three of the four companies).

Our study is based on 11 'healthy' and 15 'unhealthy' breeds comprising a total of over 330 000 individuals (Table 1). The breeds in the unhealthy group were typically of molossoid type (a category of large solidly built dogs mostly used as guard dogs or livestock guardian dogs), while the breeds in the healthy group typically were of hunting type.

To address the issue of possible temporal trends, we analysed levels of inbreeding and loss of founder genetic variation at three points in time including dogs alive on December 31 of 1980, 1995 and 2010 (Table 1). The pedigrees of December 31, 2010, represent the full pedigree of each breed. The number of individuals per full pedigree varied from 994 (Norwegian elkhound, black; Table 1) to 51 574 (Norwegian elkhound, grey).

To determine the number of live dogs at the three points in time, we had to make assumptions about the longevity of dogs. This is because the SKC studbooks do not include information on date of death of separate individuals. We assumed that each dog lives for twelve years after its date of birth. For example, a dog born on January 1, 1999, was assigned a date of death on January 1, 2011. Thus, our analyses of dogs alive in, for example, December 31, 1995, include animals born between January 1, 1984, and December 31, 1995. The number of living individuals as of December 31, 2010, varied from 204 (Neapolitan

Table 1 Information on the pedigrees of the 26 dog populations in Sweden included in this study. The breeds have been classified with respect to their health status as either 'healthy' or 'unhealthy' (see text for details). Type of breed refers to the nomenclature of the international kennel organization Fédération Cynologique Internationale (FCI; http://www.fci.be/nomenclatur.aspx). Individual dog pedigrees have been assessed at three different points in time, and for each year and breed, the number of living individuals in the Swedish populations, the total number of individuals in the pedigree of that breed and the number of founders are listed.

Classification	Breed	Type of breed (FCI Breeds nomenclature)	December 31, 1980			December 31, 1995			December 31, 2010		
			No. living	No. in ped.	No. founders	No. living	No. in ped.	No. founders	No. living	No. in ped.	No. founders
Healthy	Coton de tuléar	Companion and toy dog	0	0	0	95	423	64	2217	3564	235
Healthy	Finnish lapphund	Spitz type	0	52	0	481	999	115	4400	6465	340
Healthy	Finnish spitz	Spitz type	1491	2392	190	6386	10503	344	3509	15449	439
Healthy	Hamilton hound	Scenthound	13076	14320	532	NA	37870	NA	6066	46573	271
Healthy	Norrbottenspitz	Spitz type	1900	2001	76	2803	6111	58	1549	8178	99
Healthy	Norwegian buhund	Spitz type	611	760	45	1569	2896	78	742	4123	136
Healthy	Norwegian elkhound (black)	Spitz type	122	251	20	128	577	37	220	994	81
Healthy	Norwegian elkhound (grey)	Spitz type	9552	10995	312	NA	37484	NA	9971	51574	605
Healthy	Schiller hound	Scenthound	4768	5211	183	4345	11377	118	1777	13660	102
Healthy	Siberian husky	Spitz type	593	1341	119	4522	7567	299	5324	15641	889
Healthy	Småland hound	Scenthound	2133	2426	143	2434	5705	120	1055	7118	108
Total			34246	39749	1620	22763	121512	1233	36830	173339	3305
Unhealthy	Bernese mountain dog	Mountain dog	1441	1788	111	6092	9811	237	6884	20095	561
Unhealthy	Bulldog	Molossoid breed	235	455	95	1053	2266	232	1484	5830	903
Unhealthy	Bullmastiff	Molossoid breed	78	257	38	525	1397	142	1216	3750	421
Unhealthy	Bull terrier	Bulltype terrier	280	546	75	1168	2481	212	1394	4881	443
Unhealthy	Deerhound	Sighthound	157	301	39	185	884	98	259	1557	199
Unhealthy	Dobermann	Pinscher	1774	2527	220	6164	11315	431	3699	18128	775
Unhealthy	Dogo Argentino	Molossoid breed	0	0	0	8	202	47	534	1295	224
Unhealthy	French bulldog	Small molossian type	834	1076	124	927	2794	181	3301	8941	1075
Unhealthy	German boxer	Molossoid breed	8556	9850	602	7592	21134	677	6690	30998	1057
Unhealthy	Great Dane	Molossoid breed	2269	2941	285	2809	7953	566	4757	15197	1134
Unhealthy	Irish wolfhound	Sighthound	790	1209	117	2237	4528	240	1731	7504	430
Unhealthy	Mastiff	Molossoid breed	20	155	34	240	726	137	482	1678	268
Unhealthy	Neapolitan mastiff	Molossoid breed	4	52	12	145	505	103	204	1217	234
Unhealthy	Rottweiler	Molossoid breed	2473	3113	165	9270	15580	482	14921	36072	1131
Unhealthy	Shar pei	Molossoid breed	0	0	0	12	395	53	1092	2478	498
Total			18911	24270	1917	38427	81971	3838	48648	159621	9353

NA, not available, and refers to pedigrees that were too large to assess due to computer limitations. See Supporting Information Table S1 for more per breed data.

mastiff) to 14 921 (Rottweiler, Table 1). We have only considered dogs with a Swedish registration number as being alive. Dogs with foreign registration numbers but which should be alive according to the maximum age of 12 years criterion have been marked as dead.

Approximately 14 per cent (approximately 45000 individuals of c. 330 000) of the dogs in the pedigrees, we investigated lacked or had obvious incorrect date of birth. A complete date of birth is required for the applied pedigree software (see below), and we therefore assigned suitable date of birth to individuals lacking these data based on existing information (i.e. birth dates of parents and/or offspring in the studbook). We used our own software mPed to modify date of birth and death (Jansson *et al.* 2013).

Statistical analysis and software

We computed the inbreeding coefficient (F; Wright 1977) and mean kinship (MK; Lacy 1995) for individual dogs alive at the three separate points in time (December 31, 1980, 1995 and 2010, respectively). The mean kinship of an individual is its average coefficient of kinship (coancestry; Wright 1977) computed from its kinship to all other individuals alive in the population including individuals of the same sex and the individual itself (Lacy 1995).

To address the issue of maintenance of genetic variation in separate breeds we computed the number of founder genome equivalents (*fge*; Lacy 1995), and compared *fge* to the number of founders. A population founder is defined as an individual that is unrelated to all other individuals in the pedigree except for its descendants. In our case, founders are dogs for which information on potential parents and other ancestors is not available. Such dogs are typically located in the earliest records in the separate studbooks or are ancestors of dogs that have been imported from other countries where the same breed is kept, but where possible, studbook data are not linked to the SKC studbooks. Founder genome equivalents (*fge*) are defined as the number of equally contributing founders with no random loss of alleles in descendants that would be expected to produce the same genetic diversity as in the population under study (Lacy 1995). We used the quantity *fge*/founder as a measure of the proportion of the genetic variation contributed by the founders that remains in the population at a particular time.

We used the software Population Management x (PMx) 2011.05.18 V65 (Ballou *et al.* 2011) for F, MK and *fge* computations. PMx also converts the rate of inbreeding of the pedigree into the effective population size (N_e) by relating inbreeding increase to the number of generations of the pedigree. We used information on the number of generations to check for differences in pedigree depth between breeds and differences in N_e as a complementary measure of inbreeding rate. To create input files in correct format for PMx from the SKC studbook data in text format, we used the converter software mPed (Jansson *et al.* 2013). mPed was also used to 'strip' pedigrees to sizes possible to handle by PMx, which can only deal with pedigrees comprising around 20 000 individuals depending on the complexity of the pedigree. 'Stripping' implies removing individuals from the pedigree which do not contribute to information on individuals alive, that is, dead individuals that do not have any living descendants. For two breeds, the Norwegian elkhound, grey and the Hamilton hound, the studbooks of 1995 were too large and/or complex for PMx analyses even after stripping and were therefore excluded (Table 1).

To evaluate potential differences between the two groups of healthy and unhealthy breeds, we used standard parametric tests (t-tests), median tests and nonparametric tests (Kruskal–Wallis one-way analysis of variance and randomization tests) using the means of the inbreeding and mean kinship coefficients, respectively, so that numerically larger breeds do not have a larger impact on the results than smaller ones. We also performed analyses of variance tests (ANOVAS) to search for differences in F among and within groups of breeds performed with MS Excel and R 2.15.1 (R Development Core Team 2011). R 2.15.1 was also used for Kruskal–Wallis tests. T-tests, randomizations and median tests were carried out using MS Excel; for the randomization, we used the MS Excel add-in Pop-tools.

Results

The size of pedigrees for separate breeds varies greatly, both among breeds and over time within breeds (Table 1). The numerically smallest breed is the Neapolitan mastiff with the 204 individuals regarded as alive in 2010. The largest pedigree is that of the Rottweiler that comprised almost 15 000 living individuals in 2010.

The number of founders of the separate populations varies from 12 founders that were genetically represented in the four Neapolitan mastiffs alive in Sweden in 1980 to the 1134 founders that are genetically represented in almost 5000 Great Danes regarded as alive in 2010 (Table 1).

The pedigree depths are consistent over breeds; the number of generations that have passed over the studied time periods are very similar at the three dates of assessment (Supporting information Table S1). In 1980, an average of 4 generations have passed in both the healthy and the unhealthy group, and a t-test yields p = 0.36 when comparing the two groups of breeds with respect to number of generations. In 1995, 5.6 generations have passed in the unhealthy group and 5.4 in the healthy group (t-test gives p = 0.64), and in 2010, there is a small difference between groups with on average 6.4 generations in the unhealthy group versus 7.5 in the healthy group although not fully statistically significant (t-test gives p = 0.06).

Average inbreeding coefficients (F) for separate breeds are relatively modest. Average F per breed vary from 0.011 to 0.075, and the means and medians of both the healthy and unhealthy group increase somewhat during 1980–1995, means from 0.039 to 0.048 in healthy breeds and from 0.035 to 0.044 in the unhealthy ones (Figure 1; Table 2; Supporting Information Table S1). We find no statistically significant differences between the two groups healthy versus unhealthy at those two points in time. In contrast, inbreeding decreases over the period 1995–2010 and is reduced by almost 50
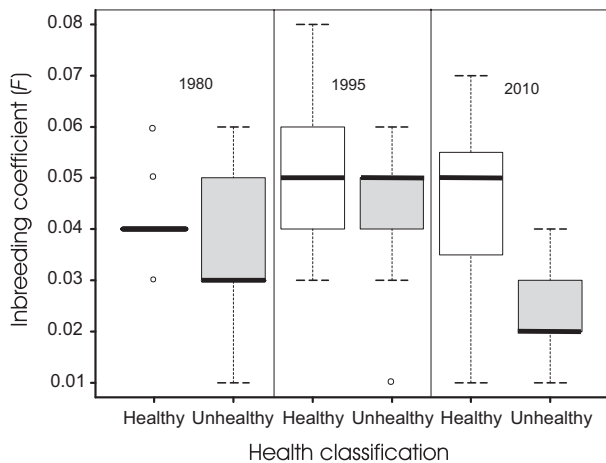

Figure 1 Inbreeding levels (F) over time of the two groups of dog breeds classified as healthy and unhealthy. The following observations are shown per group and point in time: the median (solid, thick black line), the lower and upper quartile (lower and upper box limits, respectively), and the smallest and largest observations (thick dashed lines). Values regarded as outliers are indicated by open circles. For the healthy group of 1980, there is not enough variation among the nine breeds to provide quartiles; smallest and largest values coincide with outliers and are indicated by circles (cf. Supporting Information Table S1).

Table 2 Mean and median values, including range of means (in parenthesis), of inbreeding and mean kinship coefficients for breeds classified as healthy and unhealthy, and retention of genetic variation measured as number of founder genome equivalents (fge; Lacy 1995) and fge/founder. Results from tests for equal means of these coefficients among healthy and unhealthy groups of dog breeds are also given: t-test (P), Kruskal–Wallis (KW), randomization test (R) and median test (M).

		1980 Healthy	1980 Unhealthy	1980 P, KW, R, M	1995 Healthy	1995 Unhealthy	1995 P, KW, R, M	2010 Healthy	2010 Unhealthy	2010 P	2010 KW	2010 R	2010 M
Inbreeding (F)	Mean	0.040	0.035	ns	0.048	0.044	ns	0.045	0.025	**	**	***	**
	(range)	(0.029–0.057)	(0.011–0.057)		(0.025–0.075)	(0.010–0.059)		(0.013–0.069)	(0.013–0.045)				
	Median	0.039	0.034		0.048	0.048		0.047	0.023				
Mean kinship (MK)	Mean	0.047	0.069	ns	0.057	0.049	ns	0.048	0.027	**	*	**	ns
	(range)	(0.028–0.111)	(0.016–0.194)		(0.033–0.107)	(0.018–0.077)		(0.020–0.079)	(0.011–0.041)				
	Median	0.041	0.049		0.055	0.050		0.050	0.029				
fge	Mean	12.6	11.8	ns	9.9	12.0	ns	12.7	22.4	**	*	***	ns
	(range)	(4.5–18.0)	(2.6–30.7)		(4.7–15.1)	(6.5–28.0)		(6.3–25.7)	(12.3–45.3)				
	Median	12.1	10.3		9.1	10.0		10.0	17.0				
fge/founder	Mean	0.11	0.11	ns	0.10	0.06	ns	0.06	0.04	ns	ns	*	ns
	(range)	(0.03–0.23)	(0.05–0.21)		(0.04–0.18)	(0.03–0.14)		(0.02–0.12)	(0.02–0.07)				
	Median	0.11	0.10		0.08	0.05		0.06	0.04				

*p < 0.05, **p < 0.01, ***p < 0.001, ns, non–significant.

per cent in the group of unhealthy breeds, from 0.044 to 0.025, whereas mean inbreeding decreases only slightly in the healthy group, from 0.048 to 0.045. When comparing the healthy and unhealthy groups in 2010, there is a significant difference in mean and median inbreeding values with unhealthy breeds having approximately half the values of healthy breeds, and the trend is similar when comparing mean and median mean kinship coefficients (Table 2). The significant difference in MK between the groups observed among dogs alive in 2010 indicates that the current difference in inbreeding level between the two groups will persist into the next generation.

Measuring inbreeding rate as effective population size gives consistent results; mean per generation N_e over the first approximately four generations in 1980 is 57 in the healthy group and 51 in the unhealthy one (Supporting Information Table S1) with no statistical difference between groups (t-test gives p = 0.67). N_e over the on average 5(healty breeds) respective 6(unhealthy) generations that had passed in 1995 is 58 in the healthy group and 73 in the unhealthy group with non-significance (p = 0.3), but in 2010, after 6(unhealthy) respecitve 8(healthy) generation, there is a significant difference in N_e in the healthy group (mean = 94) versus the unhealthy group (N_e = 149; p = 0.03).

Differences in inbreeding among breeds

Inbreeding levels differ among the breeds of our study. The ANOVA analyses indicate significant differences in inbreeding levels among breeds at all three points in time within the healthy group (1980: $F_{8,34237} = 59.9$; 1995: $F_{8,22754} = 240.4$; 2010: $F_{10,36819} = 849.4$; all p $\ll$ 0.001), in the unhealthy group (1980: $F_{12,18898} = 31.6$; 1995: $F_{14,38412} = 103.7$; 2010: $F_{14,48633} = 278.6$; all p $\ll$ 0.001), as well as among breeds in the total material (1980: $F_{21,53135} = 50.6$; 1995: $F_{23,61166} = 140.6$; 2010: $F_{25,85452} = 699.8$, all p $\ll$ 0.001). In all cases, Kruskal–Wallis tests agree with the ANOVA results. Tukey's Honestly Significant Difference (HSD) *post hoc* test of multiple comparisons of means show that many of the breeds differ significantly from each other with respect to inbreeding levels. For the three points in time, Tukey's HSD gives 113 significant pairwise comparisons out of 231 in 1980 involving 22 breeds, 130 of 276 in 1995 involving 24 breeds, and 272 of 325 in 2010 involving 26 breeds.

Comparing the two groups healthy versus unhealthy but not separating the material into breeds within these two groups results in significant differ-ences in inbreeding levels in 1980 with healthy dogs being more inbred than unhealthy ones ($F_{1,53155} = 172.9$, p $\ll$ 0.001) and in 2010 ($F_{1,85476} = 4071.0$, p $\ll$ 0.001) but not in 1995 ($F_{1,61188} = 0.285$, p = 0.59). The Kruskal–Wallis tests for the same material provide significance for all three points in time. These results do not hold, however, when the variation among breeds within the two groups is accounted for by means of nested ANOVAs. Rather, nested ANOVAs agree with the t-tests in showing no dif-ference between the healthy and unhealthy groups in the living populations of 1980 ($F_{1,20} = 3.97$, p = 0.06) or in 1995 ($F_{1,22} = 0.002$, p = 0.96), but giving a significant difference in 2010 ($F_{1,24} = 8.77$, p = 0.007) when inbreeding of particularly the unhealthy group has decreased. Thus, we conclude that difference in inbreeding levels is primarily a result of differences between separate breeds and not caused by different inbreeding levels of healthy versus unhealthy breeds.

Increase in number of founders over time in the unhealthy group

The number of founders increases over the study period for the majority of breeds (Table 1). This trend is statistically significant for the total material (combining healthy and unhealthy breeds) over the study period (1980–2010; $F_{2,69} = 12.3$, p < 0.0001, and Tukey's HSD gives p < 0.0001 between 1980 and 2010, and p < 0.001 for 1995–2010). The trend of an increasing number of founders over time is also observed for the unhealthy group separately ($F_{2,40} = 13.9$, p < 0.0001, and Tukey's HSD gives p < 0.0001 for 1980–2010 and p < 0.01 for 1995–2010), but not for the healthy group. The increase in founders is most likely due to imports of dogs from countries with separate studbooks. For three breeds of Swedish origin – the Hamilton, Schiller and Småland hounds – the number of founders con-tributing to the live population decreased over time as is expected when a population is closed, and no additional founders are contributing genes over time.

Number of founders and inbreeding levels

We find no significant correlation (r) between the number of founders of separate breeds and the aver-age inbreeding levels at the three points in time. Over all breeds, $r = 0.02$, 0.1 and 0.32 in 1980, 1995 and 2010, respectively. In no case, there is statistical significance.

Loss of genetic variation

Both healthy and unhealthy breeds are characterized by a pronounced loss of genetic variation quantified as founder genome equivalents (*fge*) in relation to the number of founders (*fge*/founder; Table 2). In 1980, only just above ten percent of the genetic variation that the founders represented remains in the healthy and unhealthy groups. This retention is ten per cent or lower in 1995, and only around five per cent in 2010 indicating a consistent loss of 90–95 per cent of the genetic variation represented by the founders. For the two groups, combined *fge*/founder decreases over the full study period (1980–2010; $F_{2,69} = 13.2$, $p < 0.0001$), as well as during the two separate time periods (1980–1995 and 1995–2010; Tukey's HSD test yields $p < 0.05$ for both periods). This trend of decreasing *fge*/founder ratios over time is observed both within the healthy group ($F_{2,26} = 3.4$, $p < 0.05$, but Tukey's HSD only provides significance for the period 1980–2010) and the unhealthy one ($F_{2,40} = 14.0$, $p < 0.0001$, with Tukey's HSD giving $p < 0.001$ for the period 1980–1995, and $p < 0.0001$ for 1980–2010, but no significant difference between 1995 and 2010). There was no significant difference in *fge*/founder between the healthy and unhealthy groups in the 1980 and 1995, but a weak tendency for a higher ratio in the healthy group as of 2010 (Table 2).

Discussion

We find no strong correlation between recent inbreeding and health in dog breeds in Sweden over the study period of 1980–2010. Significant difference between the two groups is observed for the populations alive in 2010 when the unhealthy group is significantly less inbred than the healthy group. This finding suggests that inbreeding during this period does not explain the differences in health problems among the breeds we studied. Inbreeding levels generally increased over the first period (1980–1995) as expected when populations are closed. In contrast, inbreeding decreased over the period 1995–2010 in both healthy and unhealthy breeds, and this trend is most pronounced for the unhealthy group; we observe significantly lower inbreeding levels in unhealthy breeds in the 2010 populations as compared to the healthy ones. Overall, inbreeding levels are modest, with measures of central tendency (mean and median) for separate breeds generally falling below that generated by first cousin mating ($F = 0.0625$). Such modest levels of recent inbreeding appear typical of dog breeds as reported from pedigree studies of populations in other countries (Leroy 2011; Leroy & Rognon 2012) although a temporal trend of increasing inbreeding over the last few decades was observed in a majority of studied breeds in Australia (Shariflou et al. 2011).

The breeds of our study differ with respect to rate of recent inbreeding, but when comparing the two groups of healthy versus unhealthy breeds, we find no strong indications of difference with respect to recent breeding history. Generation shifts are consistent with an average of 7 generations passing over approximately five decades studied, and rates of inbreeding do not differ between groups until in 2010. This pattern is true both when comparing average inbreeding levels among dogs alive at the three points in time, as well as when measuring inbreeding rate in terms of effective population size.

Our analysis of maintenance of genetic variation measured in terms of *fge*/founder indicates that the loss of genetic variation is extensive in all the 26 breeds. Around 90–95 per cent of the potential founder genetic variation is lost over just a few generations. The loss increases substantially over time indicating no tendency for breeding strategies that aim at slowing down the rate of reduction in genetic variation. Our observation is consistent with that of other workers who have also documented approximately 90 per cent loss of genetic variation during the last few decades in nine dog breeds in France (Leroy et al. 2006), three scent hound breeds in central Europe (Voges & Distl 2009) and ten dog populations bred in the United Kingdom (Calboli et al. 2008).

The temporal trend of reduced inbreeding levels and increasing number of founders and *fge* indicates that these Swedish dog populations are not closed but that dogs from other pedigrees of the same breeds in other countries are added to the majority of the populations. We found out from the Swedish Kennel Club (SKC) that when a dog is imported from another country, up to three generations of its pedigree (parents, grandparents and great grandparents) are typically included in the SKC database (Th. Wink, personal communication, 2011). An imported dog will obtain a Swedish registration number, but its ancestors will keep their foreign identification numbers, and therefore, foreign dogs are included in the studbooks. We have regarded all such animals as being dead in our analyses but there are still several ways in which imported dogs and their ancestors can affect the parameters we investigate here. First, inbreeding and mean kinship coefficients might be underestimated in cases where imported dogs have ancestors in the Swedish population further back than

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three generations. Such a situation will occur if a Swedish dog is exported to another country reproduces in that country, and its descendants are imported back to Sweden. The imported dogs will be regarded as unrelated to the Swedish population while, in fact, they are not.

Second, founder statistics can be affected by how the information on imported dogs is registered. If an imported dog does not have Swedish ancestors in its pedigree, then three generations, that is, up to eight new founders, will be added by the SKC into their database. The exact number depends on relationships among the dogs in the three generations back of the imported dog. If any one dog occurs in several places in this pedigree, then the number of added founders will be less than eight.

The number of fge will also be affected because one imported dog can represent up to eight founders that are only represented in this one dog. For instance, when one imported dog represents eight founders in the great grandparent generation then the number of founders = 8, fge = 1 and fge/founder = 0.125. Thus, adding the three generation pedigree will automatically result in a very low fge/founder-ratio even if the imported dog contributes to the gene pool by producing offspring. In contrast, if the imported dog is regarded as a founder in itself, then loss of variation from this dog and its contribution to the fge/founder-ratio of the breed depends only on how this dog is used in reproduction. At the same time, the information on three generations back is important for as accurate as possible relatedness among imported dogs.

The proportion of dogs with a foreign registration number in the full pedigrees as of 2010 varies from 0.005 in the Småland hound to 0.539 in the deerhound (Supporting Information Table S1) and is significantly lower in the healthy group (mean of 0.14) as compared to the unhealthy group (mean = 0.36, p < 0.01). There is a significant negative association between the proportion of foreign registered dogs in the full pedigree and average inbreeding among live animals in 2010 (linear regression gives $b = -0.06$, p < 0.001). Thus, dog imports clearly affect level of inbreeding of separate dog pedigrees and such imports are less likely to occur for the native Swedish breeds of which several are among the healthy dog breeds (Småland, Schiller and Hamilton hounds).

A number of additional factors can further affect the estimates of inbreeding in the breeds we studied. The Swedish Kennel Club's (SKC) databases originate from around 1975, and most of the pedigrees do not go much further back in history. This implies that it is only possible to follow the relative change of inbreed-

ing coefficients over the past 40 years. Pedigrees that go further back in time will result in larger inbreeding coefficients. As an example, we compared the SKC pedigree for the Swedish population of Australian kelpie dating back to 1976 with that of the national breeding club of this breed that has access to additional pedigree data from Norway, Denmark, Finland and Australia as well as pedigrees from the late 19th century (MacLeod 1985). Using the information from the SKC's registers resulted in a mean inbreeding level of 0.032 among dogs alive in 2010, whereas the average for the same dogs, but with the added historical pedigree data, is 0.087.

Similarly, most breeds were probably created through strong inbreeding, and potential historical inbreeding is not reflected in our analyses. Ancestral inbreeding only to a minor extent affected inbreeding depression in 25 mammalian zoo populations (Ballou 1997), but this might not be the case for domestic populations that typically have a more pronounced history of inbreeding. Here, we traced back to founders using the available pedigree data, but these founding animals are, in fact, more or less closely related. Thus, it is possible that the inbreeding coefficients we computed do not reflect true degrees of identical homozygosity very well (Ubbink et al. 1998; Vilá et al. 1999). Potentially, molecular data reflecting levels of genomic homozygosity could help addressing this issue (cf. Ruiz-López et al. 2009).

If true inbreeding is not sufficiently reflected in our data, this can explain the lack of correlation between health and inbreeding level. Also, it is possible that our ranking of health does not optimally reflect health, as our ranking rests on the assumption that there is an association between costs for veterinary care and health.

Finally, lack of association between recent inbreeding and health in dogs may be due to a long history of inbreeding resulting in the major part of the genetic load having accumulated before the start of our pedigrees. Clearly, the unhealthy morphology and physiology of many breeds are results of selective breeding and accumulation of alleles resulting in these phenotypes. Present-day inbreeding might not add enough depression to result in health problems possible to detect by our approach.

Monitoring genetic variation and inbreeding in dog breeds

Increased focus on how dog populations are bred from a conservation genetics perspective and monitoring of parameters quantifying inbreeding, mean kinship,

and loss of genetic variation are necessary to meet international agreements with respect to domestic animals (FAO 2007). The experience from this study shows that the Swedish Kennel Club has generated a wealth of data that can be used for this purpose. We recommend that this and similar data of Kennel Clubs of other countries are increasingly used for genetic monitoring purposes.

We have identified several limitations with respect to the studbook databases of the Swedish Kennel Club, however, which affect pedigree analysis for conservation genetic evaluation. Such limitations include (i) lack of records of date of death, (ii) a considerable amount of fully or partly missing birthdates or obviously erroneous birthdates (parents born before offspring) and (iii) insufficient information on dogs imported from other countries. We recommend that these problems are considered in future record keeping, and we also propose that international collaboration is expanded so that international studbooks of separate breeds can be established. Such studbooks would allow monitoring and evaluating the extent to which present-day dog breeding is carried out in line with the political aims of retaining the genetic resources of domestic breeds.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Summary statistics of the 26 analysed dog breeds including inbreeding and mean kinship coefficients, number of generations, and census and effective population sizes.