Inbreeding impact on litter size and survival in selected canine breeds

Grégoire Leroy [a,b,]*, Florence Phocas [a,b], Benoit Hedan [c], Etienne Verrier [a,b], Xavier Rognon [a,b]

[a] *AgroParisTech, UMR 1313 Génétique Animale et Biologie Intégrative, F-75231 Paris, France*
[b] *INRA, UMR 1313 Génétique Animale et Biologie Intégrative, F-78352 Jouy-en-Josas, France*
[c] *CNRS/Université de Rennes, UMR 6061Institut de Génétique et Développement de Rennes, F-35065 Rennes, France*

* Corresponding author. Tel.: +33 144081746.
E-mail address: gregoire.leroy@agroparistech.fr (G. Leroy).

Highlights

- In dogs, litter size and 2 year survival are traits with relatively low heritability level.
- A large part of within-breed inbreeding is related to assortative mating practice.
- Litter size is negatively affected by both litter and dam inbreeding.
- 2 year survival and longevity are negatively affected by inbreeding.
- Measures should therefore be taken by canine breed clubs to avoid mating of close relatives.

Abstract

Data obtained from the French Kennel Club and the Fichier National Canin were used to estimate the effect of inbreeding on average litter size and survival in seven French breeds of dog. Depending on the breed, litter sizes were 3.5-6.3 puppies and longevities were 7.7-12.2 years. Estimated heritabilities were 6.0-10.9% for litter size and 6.1-10.1% for survival at 2 years of age. Regression coefficients indicated a negative effect of inbreeding on both individual survival and litter size. Although the impact of baseline inbreeding within breeds appears to be limited, the improper mating of close relatives will reduce biological fitness through significant reduction of litter size and longevity.

Keywords: Canine; Inbreeding depression; Survival; Longevity; Litter size

Introduction

Inbreeding is a phenomenon that is difficult to avoid in domestic species because breeds constitute selected populations with limited sizes (Kristensen and Sorensen, 2005). In pet animals, mating between close relatives (e.g. between half- or full siblings) is still a common breeding practice (Leroy and Baumung, 2011). As an example, 24% of French dog breeders have declared having practised such matings (Leroy et al., 2007) with the main purpose being to 'fix the qualities of a given reproducer'. Given the deleterious consequences of inbreeding on health through inbreeding depression and diffusion of inherited diseases within the breed (Bateson and Sargan, 2012), management of inbreeding should be a major concern for dog breeders.

Inbreeding depression is defined as the reduction of the mean phenotypic value shown by a given trait in relation to inbreeding (Falconer and Mackey, 1996). The phenomenon is well documented for several traits in livestock species (Leroy, 2014). In dogs, consequences of inbreeding on traits related to reproduction or occurrence of some specific diseases have been reported previously (Ubbink et al., 1992; van der Beek et al., 1999; Maki et al., 2001; Ólafsdóttir and Kristjánsson, 2008; Urfer, 2009).

Litter size and longevity constitute two interesting life history indicators because they are tightly linked to prenatal and postnatal survival. In dogs, there is strong variability of these two traits in relation to the large morphological differences existing amongst breeds. Longevity relating to body size or occurrence of various disorders has been studied in dogs (Egenvall et al., 2005; Greer et al., 2007; Kraus et al., 2013), but there is a lack of genetic characterisation of this trait. Similarly, litter size, which is genetically linked to female reproductive capacities and survival of the litter, also constitutes an interesting trait for the investigation of the impact of inbreeding depression.

Based on the hypothesis that individual inbreeding may have a significant impact on dog survival, the aim of this study was to provide a phenotypic and genetic characterisation of litter size and longevity in seven breeds of dogs in France. We investigated inheritance and the impact of inbreeding so as to provide practical recommendations for breeders.

Materials and methods

Source of population data

The French Kennel Club (Société Centrale Canine, SCC) has curated phenotypic and genealogical information on dogs in France since 1975, using a database comprising all purebred puppies registered at the age of 2 months. Dog owners are also supposed to indicate when their dog dies (without giving the cause of death) to a national identification file (Fichier National Canin, FNC). In practice, this information has been transmitted to and recorded in the FNC for only ~10% of dogs since 2005. To study litter size, we considered litters born from 1990 to 2012 with at least three equivalent generations of known ancestors (Boichard et al., 1997). To assess longevity, we considered individuals whose death had been registered in the years 2007 to 2012, with at least three equivalent generations of known ancestors.

We chose seven breeds to cover a large range of morphology, use and demography, namely the Bernese mountain dog (BMD), Basset hound (BSH), Cairn terrier (CAI), Epagneul Breton (EPB), German shepherd dog (GSD), Leonberger (LEO) and West Highland white terrier (WHW).

Statistical analysis

An equivalent number of known generations (*EqG*) and inbreeding coefficients (*F*) were computed with PEDIG software (Boichard, 2002), while estimates of variance components were obtained using ASREML software (Gilmour et al., 2008). Analyses were independently performed for each breed.

Litter size was defined as the number of puppies alive at registration, i.e. at the age of 2 months. Data were based on records ranging from 3468 (BSH) to 39,080 (GSD) litters born from 1543 (BSH) to 15,869 (GSD) bitches (Table 1; see Appendix: Supplementary Table 1). The trait was analysed using a repeatability animal model and litter size as a trait of the dam (the 'animal' is therefore the dam of the litter):

$$Y_{irjmk} = \mu + P_r + By_j + b_1F_i + b_2F_{ir} + b_3F_m + Br_{k} + Pe_i + A_i + \varepsilon_{irjlmk}$$

where Y_{irjmk} is the observed value of the *r*th litter bred by sire *m* and the dam *i*, raised by the breeder k, and μ is the overall mean. As environment factors, we included P_r (the fixed effect of the litter rank *r*), By_j (the fixed effect of birth year *j* of the litter), Pe_i (the random permanent environmental effect of the dam *i* across all her litters) and Br_k (the random effect of the breeder *k* of the litter). b_1, b_2, b_3 are the coefficients of regression of the phenotypic value (*Y*) on the coefficients of inbreeding of the dam (F_i), its *r*th litter (F_{ir}) and the sire of the rth litter (F_m), respectively. A_i is the random genetic effect of dam *i*, and ε_{irjmk} the random residual.

Longevity analyses were based on 1113 (BSH) to 15,059 (GSD) dogs whose death was registered (Table 2). Models based on the trait itself did not lead to convergence during estimation (considering either linear mixed animal model or survival analysis). Given the bimodal distribution of longevity (Fig. 1), with a first mortality peak before 2 years in each breed, the trait was transformed into a binary variable describing juvenile survival; the value was equal to 0 if the longevity was < 2 years, and 1 otherwise. A linear model was written after a probit transformation of the observed survival trait. The underlying normal dependent variable Y_{ijkl} was modelled as:

$$Y_{ijkl} = \mu + Sx_j + Dy_k + b_iF_i + BR_l + A_i + \varepsilon_{ijkl}$$

where μ is the mean, Sx_j is the fixed effect of sex j of animal i, Dy_k is the fixed effect of death year k, b_i is the regression coefficient for inbreeding of the individual i, F_i is the inbreeding coefficient of individual i, Br_l is the random effect of breeder l, A_i is the random genetic effect for animal i and ε_{ijkl} is the random residual.

Heritabilities (h^2) and other variance ratios were computed by dividing genetic variance and variance components of all the other random effects by phenotypic variances for each statistical model. To assess juvenile survival, heritability on the observed scale (h^2_{01}) was obtained by transforming heritability estimated on the underlying normal scale using the following equation (Dempster and Lerner, 1950):

$$h^2{}_{01} = h^2 \text{ x } z^2/p\,(1-p)$$

where p is the proportion of the population showing the trait (survival at 2 years) and z is the ordinate on the standard normal density function corresponding to the threshold p.

Results

Demographic parameters

Individual breeds had different population sizes, with the number of observations ranging from 1775 (longevity for LEO breed) to 39080 (litter size for GSD breed) (Table 1). Among the breeds studied, BMD showed an increase in the number of litters produced over the 1990-2012 period (see Appendix: Supplementary Fig. 1). Since there are many hobby breeders, there was only a small number of observations per female, per male or per breeder (see Appendix: Supplementary Table 1); as an example, the average number of litters produced per male over the 1990-2012 period ranged from 3.8 (LEO) to 9.9 (WHW). In each data set, the pedigree knowledge was relatively good, with average *EqG* ranging from 5.02 (longevity for BMD and GSD) to 8.77 (litter size for EPB).

Characterisation of traits

The seven breeds showed large variations in the studied traits; average litter size ranged from 3.5 (WHW) to 6.3 (LEO) puppies, with variations between years (Table 1; see Appendix: Supplementary Fig. 1) and according to litter rank (Table 1; see Appendix: Supplementary Fig. 2). There was an increase in litter size until the second (BSH, EPB, GSD, LEO) or the third litter (BMD, CAI, WHW), and then a decrease in subsequent ranks.

Mean longevity ranged from 7.7 (BMD) to 12.2 (CAI) years (Table 2), with three breeds (CAI, EPB, WHW) showing a regular increase in longevity over the 6 year period of the study (see Appendix: Supplementary Fig. 3). Male longevity was significantly lower (P<0.001) than female longevity for BMD and GSD, but higher for CAI and WHW (see Appendix: Supplementary Fig. 4).

Inbreeding depression

The coefficients of inbreeding were relatively low, ranging from 1.60 to 5.02%, with some contrasts across individuals; for example, the proportion of observations with inbreeding coefficient $F \geq 12.5\%$ ranged from 2.4 (litter size for GSD) to 7.9% (litter size for CAI) (Tables 1 and 2). The negative impact of inbreeding classes on litter size and longevity is illustrated in Fig. 2. In all breeds, litter size was significantly reduced ($P < 0.05$) for classes with more litter inbreeding. Litter size also decreased significantly ($P < 0.05$) for litters produced by dams of the BMD, CAI, GSD, LEO and WHW breeds with larger inbreeding coefficients. There were significant ($P < 0.05$) differences in longevity according to individual inbreeding levels for BMD, EPB, GSD, and LEO breeds (Fig. 2).

The regression coefficients for inbreeding were negative in all breeds for both litter size (litter and dam inbreeding effect) and 2 year survival (individual inbreeding effect). On average over all breeds, litter sizes were reduced by 0.026 per % of litter inbreeding and by 0.02 per % of dam inbreeding. In other words, we would expect, for litters with an inbreeding coefficient of 25% (equivalent to a mating between full siblings), a reduction of 0.65 puppies per litter on average in comparison with non-inbred litters. Females with this inbreeding coefficient could be expected to produce 0.5 puppies fewer per litter in comparison with non-inbred females. The coefficient of inbreeding for the sire had a significant effect on litter size only for EPB ($r = 0.73$; $P = 0.04$) and WHW ($r = 1.16$; $P = 0.007$).

Variance components and quantitative genetic parameters

Estimated heritabilities for litter size were 6.0 (BSH) to 10.9% (BMD) (Table 3). Breeder and environment ratios (i.e. permanent environment variance divided by phenotypic variance) for litter size ranged from 2.4 (BSH) to 8.1% (EPB), and 0 (BSH) to 9.81% (BMD), respectively (see Appendix: Supplementary Table 2).

No convergence was obtained for the estimation of variance components for survival for LEO. Estimated values of heritability for survival for the different breeds (excluding LEO) were 22.4 (BSH) to 34.5% (GSD) on the underlying normal scale (see Appendix: Supplementary Table 3). Corresponding heritability values on the 0-1 bimodal scale were 5.9 (WHW) to 10.1% (GSD) (Table 3).

Discussion

The larger litter sizes and lower longevities for breeds of large size (BMD and LEO) were in agreement with the results of previous studies (Borge et al., 2011; Kraus et al., 2013). Distribution of mortality was similar to those found by Egenvall et al. (2005) and O'Neill et al. (2013). The particularly low life expectancy of BMD (mean 7.7 years) may be a consequence of the high prevalence of histiocytic sarcoma within this breed (Abadie et al., 2009).

The significantly lower life expectancy for male BMD and GSD are consistent with previously published data (Bonnett et al., 2005; O'Neill et al., 2013). The significantly higher male longevity in the two terrier breeds is unexpected. However, mortality risks related to sex differ when considering different disorders; for example, Bonnett et al. (2005) showed that, in general, females had up to two times greater risk of dying from tumours than males. Dog breeds have large variations in disease prevalence and, therefore, variation between breeds in risk related to sex is to be expected.

There were many (statistical) cells with few data because of low numbers of performances per reproducer or per breeder (see Appendix A: Supplementary Table 1), which led to difficulties in adjusting genetic models. It was possible to assess heritabilities for litter sizes with low to moderate heritabilities (6.0-10.9%), of the same order to those estimated in sheep, rabbits or pigs (Van Wyk et al., 2009; Nagy et al., 2012; Rodriguez et al., 2013). However, a study on German shepherd and Labrador retriever guide dogs revealed much larger heritabilities for litter size at 49 days (31 and 26%, respectively) (Hare and Leighton, 2006), which may result from better monitoring of those populations and a larger number of litters per reproducer.

The structure of the data set did not allow identification of censured data (animals still alive at the end of the study) and so it was not possible to perform direct survival analysis on longevity data. Heritabilities estimated for 2 year survival were found in the same range (5.9-10.1% according to breeds) as those reported for piglet and calf survival (4.2-19%) (Gerra et al., 2006; Rohe et al., 2009; Fuerst-Waltl and Sørensen, 2010).

Since litter size was measured at 2 months of age, i.e. after weaning, it was related to female prolificacy, and embryo and early puppy survival. Therefore, it was not surprising to find a negative impact of both litter and dam inbreeding on the trait. This result is in contrast with a study on the Irish Wolfhound (Urfer, 2009), which found a limited impact of dam inbreeding on litter size, although the data set was relatively small (822 litters). Inbreeding depression appeared to be larger for breeds of larger body size, which could be linked to the larger litter size estimated for those breeds. Supposing a similar impact of inbreeding on embryo and puppy survival, the consequence of inbreeding on litter size could be expected to be higher for more prolific breeds.

The scaled estimation of inbreeding depression (dividing the regression coefficient by the mean of the phenotypic trait computed for the breed) was -0.27 to -0.65 for litter inbreeding and

-0.13 and -0.76 for dam inbreeding, with no notable difference according to breed size. This result was within the range of values estimated in livestock for the number of offspring weaned per litter, i.e. -0.69 (standard error 0.15) for litter inbreeding and -0.46 (standard error 0.17), for dam inbreeding (Leroy 2014). This result is illustrated by the reduction in BMD of 0.8 puppies between litters with inbreeding coefficients < 6.25%, and litters with inbreeding coefficients > 12.5% (Fig. 2). In EPB and GSD, there was a difference of longevity of > 1 year between dogs with inbreeding coefficients < 6.25% and those with inbreeding coefficients > 12.5%.

Although it was not possible to identify the causes of death, reduced longevity may be linked to increased early mortality, early onset of senescence or increased rate of aging (Kraus et al., 2013). However, given the importance of inherited disorders with a potential impact on dog survival within dog breeds (Nicholas et al., 2011), it is probable that dogs with high inbreeding have higher incidences of those disorders, which may significantly reduce their lifespan. As emphasised by Leroy and Baumung (2010), high individual values of inbreeding coefficients (> 6.25%, 12.5 or even 25%) are most of the time caused by recent inbreeding, i.e. mating between close relatives (cousins, half or full siblings, parent-offspring matings).

We consider that a large part of within-breed inbreeding is related to this breeding practice. In 60 dog breeds studied, average coancestry at the breed scale was lower (2.1% on average) than inbreeding (3.5% on average) (Leroy et al., 2013). The coefficient of coancestry estimates the genetic similarity between two individuals and is equal to the coefficient of inbreeding of a potential offspring of these two individuals. At the population scale, average coancestry corresponds to baseline inbreeding, i.e. inbreeding because of the reduction of genetic variability at the population scale. Therefore, within a breed under random mating conditions, those two estimators should be similar, the difference here being explained by mating between close relatives. Given the low value of coancestry, this baseline inbreeding has a limited effect on longevity. In contrast, at the individual level, Fig. 2 illustrates the deleterious impact of mating between close-relatives on litter size and longevity. Therefore, measures should be taken by breed clubs to avoid mating of close relatives (at least between parents-offspring, and half and full siblings), for example, following the decision taken by the UK Kennel Club in 2009[1].

Conclusions

The results presented in this study illustrate that inbreeding affects reproduction parameters and survival at different stages of life in dogs. Improvement of these traits is required, since the reduction of survival is generally related to health problems affecting animal welfare. From a genetic point of view, survival of dogs could be improved by restricting mating between close relatives, as well as through the implementation of efficient selection programmes against widely spread inherited disorders. A third approach could be to consider a direct selection on survival traits, given the heritabilities measured here. However there is a need to improve the recording of phenotypes, in number and quality, before such a selection approach could be implemented. Also, the development of molecular tools, allowing, among others, genome-wide estimates of inbreeding, should improve our capacity to better understand and manage inbreeding depression phenomenon.

Conflict of interest statement

None of the authors of this paper has a financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

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[1] See: http://www.thekennelclub.org.uk.

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Figure legends

Fig. 1. Distribution of mortality over years according to breed. BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier.

Fig. 2. Average litter size and longevities according to inbreeding classes, considering for litter size the coefficient of inbreeding of the litter (a) or its dam (b), and for longevity the coefficient of the individual considered (c). BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier. ^{NS} non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 1 Main characteristics of litter size data according to breeds.

Breed [a]	Number of litters	Litter size (mean ± standard deviation)	Litter rank (mean ± standard deviation)	Litter inbreeding			
				Mean F [b] (%)	< 6.25 (%)	6.25-12.5 (%)	≥ 12.5 (%)
BMD	7566	5.51 ± 2.78	2.5 ± 1.72	2.08	88.8	7.1	4.1
BSH	3468	5.14 ± 2.66	2.21 ± 1.42	3.92	76.6	16.8	6.5
CAI	8846	3.89 ± 1.77	3.04 ± 2.04	3.25	82.6	9.5	7.9
EPB	23,005	5.32 ± 2.25	2.53 ± 1.96	5.02	75.7	16.9	7.3
GSD	39,080	5.1 ± 2.44	2.87 ± 1.98	2.42	88	8.3	3.6
LEO	3246	6.33 ± 3.08	1.92 ± 1.17	3.21	85.9	10.5	3.7
WHW	16,163	3.47 ± 1.69	2.87 ± 1.92	2.35	87.2	7.1	5.7

[a] BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier.

[b] Inbreeding coefficient.

Table 2 Main characteristics of longevity data according to breeds.

Breed [a]	Number of litters	Longevity (mean ± standard deviation)	Longevity (median)	2 year survivability (%)	Inbreeding			
					Mean F [b] (%)	< 6.25 (%)	6.25-12.5 (%)	≥ 12.5 (%)
BMD	2831	7.74 ± 3.03	8.15	93.7	1.59	91.7	5.1	3.2
BSH	1113	9.33 ± 3.67	10.3	92	3.51	80.4	13.4	6.2
CAI	2111	12.23 ± 4.18	13.42	95.4	3.2	82.3	10.2	7.4
EPB	6286	11.34 ± 4.28	12.58	94.1	4.57	78.2	15.6	6.1
GSD	15,056	9.16 ± 3.72	10.08	92.3	1.9	91	6.6	2.4
LEO	1775	8.18 ± 3.1	8.75	94.5	3.26	84.6	11.5	3.9
WHW	3559	11.89 ± 3.92	12.93	95.6	2.08	88.3	6.8	4.9

[a] BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier.

[b] Inbreeding coefficient.

Table 3 Heritabilities and estimates of inbreeding depression on litter size and 2 year survival.

Breed [a]	Litter size				2 year survival	
	h^2	Inbreeding regression coefficient			h^2_{01}	Inbreeding regression coefficient
		Litter	Dam	Sire		
BMD	0.109	-3.06 **	-4.18 **	-1.89 [NS]	0.061	-2.04 [NS]
BSH	0.06	-1.36 [NS]	-0.67 [NS]	0.02 [NS]	0.067	-0.98 [NS]
CAI	0.098	-2.20 ***	-1.18 *	0.14 [NS]	0.064	-1.57 [NS]
EPB	0.1	-2.94 ***	-0.9 [NS]	0.73 *	0.063	-2.70 ***
GSD	0.091	-3.30 ***	-2.19 ***	0.90 [NS]	0.101	-2.80 ***
LEO	0.882	-3.80 *	-3.81 [NS]	1.50 [NS]	-	-
WHW	0.105	-1.32 ***	-1.35 **	1.16 *	0.059	-1.1 [NS]

[a] BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier.

h^2, heritability; h^2_{01}, heritability on the observed scale; [NS] non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Appendix

Supplementary Fig. 1. Changes in number of litters registered and average litter size over years according to breed BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier.

Supplementary Fig. 2. Changes in average litter size according to litter rank. BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier.

Supplementary Fig. 3. Changes in longevity over years according to breed BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier.

Supplementary Fig. 4. Average longevity according to the sex and breeds of individuals BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier. ^{NS} non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Supplementary Table 1

Characteristics of data set analysed, considering litters born from 1990 to 2012 for litter size and individuals whose death has been registered from 2007 to 2012 for longevity.

Breed [a]	Pedigree file	Trait	Number	Sires	Dams	Breeders	*EqG*
BMD	55,434	Litter size	7565	1399	3138	917	5.59
		Longevity	2831	626	1171	608	5.02
BSH	25,890	Litter size	3468	608	1543	606	6.34
		Longevity	1113	290	602	239	5.88
CAI	43,399	Litter size	8846	1178	2855	1053	6.46
		Longevity	2111	547	1055	423	6.27
EPB	190,395	Litter size	23,005	5402	10,711	5863	8.77
		Longevity	6286	2065	3476	1880	8.28
GSD	419,447	Litter size	39,080	6966	15,869	5818	5.39
		Longevity	15,059	3447	6907	2524	5.02
LEO	30,843	Litter size	3246	848	1730	846	6.68
		Longevity	1775	422	767	394	6.58
WHW	70,464	Litter size	16,163	1629	5429	2205	5.81
		Longevity	3559	848	1927	845	5.50

[a] BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier.

EqG, equivalent number of known generations.

Supplementary Table 2

Estimated variance ratios for models estimating litter size according to breeds.

Breed [a]	h^2 ± standard deviation	RV_{BR} ± standard deviation	RV_{Pe} ± standard deviation	RV_E ± standard deviation
BMD	0.109 ± 0.203	0.049 ± 0.01	0.098 ± 0.019	0.744 ± 0.015
BSH	0.06 ± 0.014	0.024 ± 0.009	0.0 ± 0.0	0.916 ± 0.014
CAI	0.098 ± 0.018	0.069 ± 0.011	0.085 ± 0.016	0.748 ± 0.014
EPB	0.1 ± 0.01	0.081 ± 0.007	0.059 ± 0.01	0.76 ± 0.009
GSD	0.091 ± 0.008	0.057 ± 0.005	0.088 ± 0.008	0.765 ± 0.007
LEO	0.088 ± 0.027	0.075 ± 0.018	0.092 ± 0.029	0.745 ± 0.025
WHW	0.105 ± 0.013	0.044 ± 0.007	0.059 ± 0.011	0.792 ± 0.01

h^2, heritability ; RV_{BR}, breeder effect variance ratio ; RV_{Pe}, permanent environmental variance ratio ; RV_E, residual variance ratio.

[a] BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO , Leonberger West; WHW, Highland white terrier.

473 **Supplementary Table 3**

474 Estimated variance ratios for models estimating 2 year survival according to breeds.

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Breed [a]	h^2 ± standard deviation	RV_{BR} ± standard deviation	RV_E ± standard deviation
BMD	0.236 ± 0.05	0.124 ± 0.046	0.641 ± 0.037
BSH	0.224 ± 0.074	0.208 ± 0.078	0.568 ± 0.051
CAI	0.298 ± 0.065	0.054 ± 0.057	0.648 ± 0.046
EPB	0.253 ± 0.031	0.122 ± 0.029	0.625 ± 0.024
GSD	0.345 ± 0.018	0.056 ± 0.015	0.599 ± 0.014
LEO	-	-	-
WHW	0.289 ± 0.048	0.076 ± 0.042	0.635 ± 0.035

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477 h^2, heritability (additive variance); RV_{BR}, breeder effect variance ratio; RV_E, residual variance ratio.

478 [a] BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German

479 shepherd dog; LEO , Leonberger West; WHW, Highland white terrier.