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1 2 2	Inbreeding impact on litter size and survival in selected canine breeds
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17 Highlights

- 18 In dogs, litter size and 2 year survival are traits with relatively low heritability level. •
- 19 A large part of within-breed inbreeding is related to assortative mating practice. •
- 20 Litter size is negatively affected by both litter and dam inbreeding. •
- 2 year survival and longevity are negatively affected by inbreeding. 21 •
- Measures should therefore be taken by canine breed clubs to avoid mating of close 22 • 23 relatives.
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26 Abstract

27 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 28 29 dog. Depending on the breed, litter sizes were 3.5-6.3 puppies and longevities were 7.7-12.2 30 years. Estimated heritabilities were 6.0-10.9% for litter size and 6.1-10.1% for survival at 2 years 31 of age. Regression coefficients indicated a negative effect of inbreeding on both individual 32 survival and litter size. Although the impact of baseline inbreeding within breeds appears to be 33 limited, the improper mating of close relatives will reduce biological fitness through significant 34 reduction of litter size and longevity.

- 35
- Keywords: Canine; Inbreeding depression; Survival; Longevity; Litter size 36

Larviv

37 Introduction

38 Inbreeding is a phenomenon that is difficult to avoid in domestic species because breeds 39 constitute selected populations with limited sizes (Kristensen and Sorensen, 2005). In pet 40 animals, mating between close relatives (e.g. between half- or full siblings) is still a common 41 breeding practice (Leroy and Baumung, 2011). As an example, 24% of French dog breeders have 42 declared having practised such matings (Leroy et al., 2007) with the main purpose being to 'fix 43 the qualities of a given reproducer'. Given the deleterious consequences of inbreeding on health 44 through inbreeding depression and diffusion of inherited diseases within the breed (Bateson and 45 Sargan, 2012), management of inbreeding should be a major concern for dog breeders.

46

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).

53

54 Litter size and longevity constitute two interesting life history indicators because they are 55 tightly linked to prenatal and postnatal survival. In dogs, there is strong variability of these two 56 traits in relation to the large morphological differences existing amongst breeds. Longevity 57 relating to body size or occurrence of various disorders has been studied in dogs (Egenvall et al., 58 2005; Greer et al., 2007; Kraus et al., 2013), but there is a lack of genetic characterisation of this 59 trait. Similarly, litter size, which is genetically linked to female reproductive capacities and 60 survival of the litter, also constitutes an interesting trait for the investigation of the impact of 61 inbreeding depression.

62

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.

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68 Materials and methods

69 Source of population data

70 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 71 72 puppies registered at the age of 2 months. Dog owners are also supposed to indicate when their 73 dog dies (without giving the cause of death) to a national identification file (Fichier National 74 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 75 76 with at least three equivalent generations of known ancestors (Boichard et al., 1997). To assess 77 longevity, we considered individuals whose death had been registered in the years 2007 to 2012, 78 with at least three equivalent generations of known ancestors.

79

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).

84

85 Statistical analysis

86 An equivalent number of known generations (EqG) and inbreeding coefficients (F) were 87 computed with PEDIG software (Boichard, 2002), while estimates of variance components were obtained using ASREML software (Gilmour et al., 2008). Analyses were independently 88 89 performed for each breed. 90 91 Litter size was defined as the number of puppies alive at registration, i.e. at the age of 2 92 months. Data were based on records ranging from 3468 (BSH) to 39,080 (GSD) litters born from 93 1543 (BSH) to 15,869 (GSD) bitches (Table 1; see Appendix: Supplementary Table 1). The trait 94 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): 95 96 $Y_{irjmk} = \mu + P_r + By_j + b_1 F_i + b_2 F_{ir} + b_3 F_m + Br_{k+} Pe_i + A_i + \mathcal{E}_{irjlmk}$ 97 98 99 where Y_{irimk} is the observed value of the *r*th litter bred by sire *m* and the dam *i*, raised by 100 the breeder k, and μ is the overall mean. As environment factors, we included P_r (the fixed effect 101 of the litter rank r), By_i (the fixed effect of birth year j of the litter), Pe_i (the random permanent 102 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 103 coefficients of inbreeding of the dam (F_i) , its *r*th litter (F_{ir}) and the sire of the rth litter (F_m) , 104 105 respectively. A_i is the random genetic effect of dam *i*, and $\boldsymbol{\mathcal{E}}_{irjmk}$ the random residual. 106 107 Longevity analyses were based on 1113 (BSH) to 15,059 (GSD) dogs whose death was 108 registered (Table 2). Models based on the trait itself did not lead to convergence during 109 estimation (considering either linear mixed animal model or survival analysis). Given the 110 bimodal distribution of longevity (Fig. 1), with a first mortality peak before 2 years in each

111	breed, the trait was transformed into a binary variable describing juvenile survival; the value was
112	equal to 0 if the longevity was < 2 years, and 1 otherwise. A linear model was written after a
113	probit transformation of the observed survival trait. The underlying normal dependent variable
114	Y_{iikl} was modelled as:

115

116
$$Y_{ijkl} = \mu + Sx_j + Dy_k + b_iF_i + BR_l + A_i + \boldsymbol{\mathcal{E}}_{ijkl}$$

117

118 where μ is the mean, Sx_j is the fixed effect of sex *j* of animal *i*, Dy_k is the fixed effect of 119 death year *k*, b_i is the regression coefficient for inbreeding of the individual *i*, F_i is the inbreeding 120 coefficient of individual *i*, Br_l is the random effect of breeder *l*, A_i is the random genetic effect 121 for animal *i* and \mathcal{E}_{ijkl} is the random residual.

122

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):

128

 $h_{01}^2 = h^2 \ge z^2/p (1-p)$

129

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*.

132

133 Results

134 Demographic parameters

Individual breeds had different population sizes, with the number of observations ranging

135

136 from 1775 (longevity for LEO breed) to 39080 (litter size for GSD breed) (Table 1). Among the

137 breeds studied, BMD showed an increase in the number of litters produced over the 1990-2012

138 period (see Appendix: Supplementary Fig. 1). Since there are many hobby breeders, there was

139 only a small number of observations per female, per male or per breeder (see Appendix:

140 Supplementary Table 1); as an example, the average number of litters produced per male over

141 the 1990-2012 period ranged from 3.8 (LEO) to 9.9 (WHW). In each data set, the pedigree

142 knowledge was relatively good, with average EqG ranging from 5.02 (longevity for BMD and

143 GSD) to 8.77 (litter size for EPB).

144

145 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.

151

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).

157

158 Inbreeding depression

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The coefficients of inbreeding were relatively low, ranging from 1.60 to 5.02%, with 160 some contrasts across individuals; for example, the proportion of observations with inbreeding 161 coefficient $F \ge 12.5\%$ 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 162 163 Fig. 2. In all breeds, litter size was significantly reduced (P < 0.05) for classes with more litter 164 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 165 significant (P < 0.05) differences in longevity according to individual inbreeding levels for 166 BMD, EPB, GSD, and LEO breeds (Fig. 2). 167

168

The regression coefficients for inbreeding were negative in all breeds for both litter size 169 (litter and dam inbreeding effect) and 2 year survival (individual inbreeding effect). On average 170 171 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 172 173 25% (equivalent to a mating between full siblings), a reduction of 0.65 puppies per litter on 174 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 175 coefficient of inbreeding for the sire had a significant effect on litter size only for EPB (r = 0.73; 176 177 P = 0.04) and WHW (r = 1.16; P = 0.007).

178

179 *Variance components and quantitative genetic parameters*

180 Estimated heritabilities for litter size were 6.0 (BSH) to 10.9% (BMD) (Table 3). Breeder 181 and environment ratios (i.e. permanent environment variance divided by phenotypic variance) 182 for litter size ranged from 2.4 (BSH) to 8.1% (EPB), and 0 (BSH) to 9.81% (BMD), respectively 183 (see Appendix: Supplementary Table 2).

184

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).

190

191 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).

197

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.

205

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.

215

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).

221

Since litter size was measured at 2 months of age, i.e. after weaning, it was related to 222 223 female prolificacy, and embryo and early puppy survival. Therefore, it was not surprising to find 224 a negative impact of both litter and dam inbreeding on the trait. This result is in contrast with a 225 study on the Irish Wolfhound (Urfer, 2009), which found a limited impact of dam inbreeding on 226 litter size, although the data set was relatively small (822 litters). Inbreeding depression appeared 227 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 228 229 survival, the consequence of inbreeding on litter size could be expected to be higher for more prolific breeds. 230

231

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%.

241

Although it was not possible to identify the causes of death, reduced longevity may be 242 linked to increased early mortality, early onset of senescence or increased rate of aging (Kraus et 243 al., 2013). However, given the importance of inherited disorders with a potential impact on dog 244 survival within dog breeds (Nicholas et al., 2011), it is probable that dogs with high inbreeding 245 246 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 (> 247 248 6.25%, 12.5 or even 25%) are most of the time caused by recent inbreeding, i.e. mating between 249 close relatives (cousins, half or full siblings, parent-offspring matings).

250

251 We consider that a large part of within-breed inbreeding is related to this breeding 252 practice. In 60 dog breeds studied, average coancestry at the breed scale was lower (2.1% on 253 average) than inbreeding (3.5% on average) (Leroy et al., 2013). The coefficient of coancestry 254 estimates the genetic similarity between two individuals and is equal to the coefficient of 255 inbreeding of a potential offspring of these two individuals. At the population scale, average 256 coancestry corresponds to baseline inbreeding, i.e. inbreeding because of the reduction of genetic 257 variability at the population scale. Therefore, within a breed under random mating conditions, 258 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 2009¹.

264

265 Conclusions

266 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 267 required, since the reduction of survival is generally related to health problems affecting animal 268 welfare. From a genetic point of view, survival of dogs could be improved by restricting mating 269 270 between close relatives, as well as through the implementation of efficient selection programmes 271 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 272 273 improve the recording of phenotypes, in number and quality, before such a selection approach 274 could be implemented. Also, the development of molecular tools, allowing, among others, 275 genome-wide estimates of inbreeding, should improve our capacity to better understand and manage inbreeding depression phenomenon. 276

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278 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: <u>http://www.thekennelclub.org.uk</u>.

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- 285

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406 Figure legends

407

408 Fig. 1. Distribution of mortality over years according to breed. BMD, Bernese mountain dog;

409 BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog;

410 LEO, Leonberger West; WHW, Highland white terrier.

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- 412

413Fig. 2. Average litter size and longevities according to inbreeding classes, considering for litter414size the coefficient of inbreeding of the litter (a) or its dam (b), and for longevity the415coefficient of the individual considered (c). BMD, Bernese mountain dog; BSH, Basset416hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO ,417Leonberger West; WHW, Highland white terrier.4180.01; *** P < 0.001.

	419	Table 1	Main characteristics	of litter size	e data according to breeds.
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	Number	Litter size (mean +	Litter renk (meen +	Litter inbreeding			
Breed ^a	of litters	standard deviation)	standard deviation)	Mean F^{b}	< 6.25	6.25-12.5	≥ 12.5
	of fitters	standard deviation)	standard deviation)	(%)	(%)	(%)	(%)
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

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422 ^a BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German

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

424 ^b Inbreeding coefficient.

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 Table 2 Main characteristics of longevity data according to breeds.
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	Number	Longevity (mean +	Longovity	2 year		Inbre	eeding	
Breed ^a	oflittora	atondord deviation)	(madian)	survivability	Mean F^{b}	< 6.25	6.25-12.5	≥ 12.5
	of inters	standard deviation)	(median)	(%)	(%)	(%)	(%)	(%)
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

427

428 ^a BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German

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

430 ^b Inbreeding coefficient.

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Table 3 Heritabilities and estimates of inbreeding depression on litter size and 2 year survival. 431 432

		Ι	Litter size			2 year survival			
Breed ^a	h^2	Inbreed	ling regression coe	efficient	h^2	Inbraading regression coefficient			
	n² _	Litter	Dam	Sire	<i>n</i>	indreeding regression coefficient			
BMD	0.109	-3.06 **	-4.18 **	-1.89 ^{NS}	0.061	-2.04 ^{NS}			
BSH	0.06	-1.36 ^{NS}	-0.67 ^{NS}	$0.02^{ m NS}$	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 ***	$0.90^{\rm NS}$	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}			

433

434 ^a BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German

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

 h^2 , heritability; h^2_{0l} , heritability on the observed scale; ^{NS} non-significant; * P < 0.05; ** P < 0.01; *** P < 0.001. 436

, nan , scale; ^{NS}.

437	
438	Appendix
439	
440	Supplementary Fig. 1. Changes in number of litters registered and average litter size over years
441	according to breed BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB,
442	Epagneul Breton; GSD, German shepherd dog; LEO, Leonberger West; WHW, Highland white
443	terrier.
444	
445	Supplementary Fig. 2. Changes in average litter size according to litter rank. BMD, Bernese
446	mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German
447	shepherd dog; LEO, Leonberger West; WHW, Highland white terrier.
448	
449	Supplementary Fig. 3. Changes in longevity over years according to breed BMD, Bernese
450	mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German
451	shepherd dog; LEO, Leonberger West; WHW, Highland white terrier.
452	
453	Supplementary Fig. 4. Average longevity according to the sex and breeds of individuals BMD,
454	Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD,
455	German shepherd dog; LEO, Leonberger West; WHW, Highland white terrier. ^{NS} non-
456	significant; * <i>P</i> < 0.05; ** <i>P</i> < 0.01; *** <i>P</i> < 0.001.

457 Supplementary Table 1

- 458 Characteristics of data set analysed, considering litters born from 1990 to 2012 for litter size and
- 459 individuals whose death has been registered from 2007 to 2012 for longevity.
- 460

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

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462 ^a BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German

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

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464 *EqG*, equivalent number of known generations.

Supplementary Table 2 465

Estimated variance ratios for models estimating litter size according to breeds. 466

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Breed ^a	$h^2 \pm$ standard deviation	$RV_{BR} \pm$ standard deviation	$RV_{Pe} \pm$ standard deviation	$RV_E \pm$ 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

468

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

470 variance ratio.

471 ^a BMD, Bernese mountain dog; BSH, Basset hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German

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

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Supplementary Table 3 473

- 474 Estimated variance ratios for models estimating 2 year survival according to breeds.
- 475

Breed ^a	$h^2 \pm$ standard deviation	$RV_{BR} \pm$ standard deviation	$RV_E \pm$ 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

476

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.