

Inbreeding impact on litter size and survival in selected canine breeds

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2	indreeding impact on litter size and survival in selected canine dreeds
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16		
17	Highlig	ghts
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.
21	•	2 year survival and longevity are negatively affected by inbreeding.
22	•	Measures should therefore be taken by canine breed clubs to avoid mating of close
23		relatives.
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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

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inbreeding depression.

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	
47	Inbreeding depression is defined as the reduction of the mean phenotypic value shown by
48	a given trait in relation to inbreeding (Falconer and Mackey, 1996). The phenomenon is well
49	documented for several traits in livestock species (Leroy, 2014). In dogs, consequences of
50	inbreeding on traits related to reproduction or occurrence of some specific diseases have been
51	reported previously (Ubbink et al., 1992; van der Beek et al., 1999; Maki et al., 2001; Ólafsdóttir
52	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

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

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62	
63	Based on the hypothesis that individual inbreeding may have a significant impact on dog
64	survival, the aim of this study was to provide a phenotypic and genetic characterisation of litter
65	size and longevity in seven breeds of dogs in France. We investigated inheritance and the impact
66	of inbreeding so as to provide practical recommendations for breeders.
67	
68	Materials and methods
69	Source of population data
70	The French Kennel Club (Société Centrale Canine, SCC) has curated phenotypic and
71	genealogical information on dogs in France since 1975, using a database comprising all purebred
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
75	only \sim 10% of dogs since 2005. To study litter size, we considered litters born from 1990 to 2012
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	
80	We chose seven breeds to cover a large range of morphology, use and demography,
81	namely the Bernese mountain dog (BMD), Basset hound (BSH), Cairn terrier (CAI), Epagneul
82	Breton (EPB), German shepherd dog (GSD), Leonberger (LEO) and West Highland white terrier
83	(WHW).
84	
85	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.

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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):

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$$Y_{irjmk} = \mu + P_r + By_j + b_1 F_i + b_2 F_{ir} + b_3 F_m + Br_{k+} Pe_i + A_i + \mathcal{E}_{irjlmk}$$
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where Y_{irjmk} is the observed value of the rth 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_i (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 rth litter (F_{ir}) and the sire of the rth litter (F_m) , respectively. A_i is the random genetic effect of dam i, and \mathcal{E}_{irimk} the random residual.

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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:

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$$Y_{ijkl} = \mu + Sx_j + Dy_k + b_i F_i + BR_l + A_i + \mathcal{E}_{ijkl}$$

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 \mathcal{E}_{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):

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

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.

133 Results

134 Demographic parameters

135	Individual breeds had different population sizes, with the number of observations ranging
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
146	The seven breeds showed large variations in the studied traits; average litter size ranged
147	from 3.5 (WHW) to 6.3 (LEO) puppies, with variations between years (Table 1; see Appendix:
148	Supplementary Fig. 1) and according to litter rank (Table 1; see Appendix: Supplementary Fig.
149	2). There was an increase in litter size until the second (BSH, EPB, GSD, LEO) or the third litter
150	(BMD, CAI, WHW), and then a decrease in subsequent ranks.
151	
152	Mean longevity ranged from 7.7 (BMD) to 12.2 (CAI) years (Table 2), with three breeds
153	(CAI, EPB, WHW) showing a regular increase in longevity over the 6 year period of the study
154	(see Appendix: Supplementary Fig. 3). Male longevity was significantly lower (P <0.001) than
155	female longevity for BMD and GSD, but higher for CAI and WHW (see Appendix:
156	Supplementary Fig. 4).
157	
158	Inbreeding depression

159	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
162	1 and 2). The negative impact of inbreeding classes on litter size and longevity is illustrated in
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
165	BMD, CAI, GSD, LEO and WHW breeds with larger inbreeding coefficients. There were
166	significant ($P < 0.05$) differences in longevity according to individual inbreeding levels for
167	BMD, EPB, GSD, and LEO breeds (Fig. 2).
168	
169	The regression coefficients for inbreeding were negative in all breeds for both litter size
170	(litter and dam inbreeding effect) and 2 year survival (individual inbreeding effect). On average
171	over all breeds, litter sizes were reduced by 0.026 per % of litter inbreeding and by 0.02 per % of
172	dam inbreeding. In other words, we would expect, for litters with an inbreeding coefficient of
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
175	expected to produce 0.5 puppies fewer per litter in comparison with non-inbred females. The
176	coefficient of inbreeding for the sire had a significant effect on litter size only for EPB ($r = 0.73$;
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	
185	No convergence was obtained for the estimation of variance components for survival for
186	LEO. Estimated values of heritability for survival for the different breeds (excluding LEO) were
187	22.4 (BSH) to 34.5% (GSD) on the underlying normal scale (see Appendix: Supplementary
188	Table 3). Corresponding heritability values on the 0-1 bimodal scale were 5.9 (WHW) to 10.1%
189	(GSD) (Table 3).
190	
191	Discussion
192	The larger litter sizes and lower longevities for breeds of large size (BMD and LEO)
193	were in agreement with the results of previous studies (Borge et al., 2011; Kraus et al., 2013).
194	Distribution of mortality was similar to those found by Egenvall et al. (2005) and O'Neill et al.
195	(2013). The particularly low life expectancy of BMD (mean 7.7 years) may be a consequence of
196	the high prevalence of histiocytic sarcoma within this breed (Abadie et al., 2009).
197	
198	The significantly lower life expectancy for male BMD and GSD are consistent with
199	previously published data (Bonnett et al., 2005; O'Neill et al., 2013). The significantly higher
200	male longevity in the two terrier breeds is unexpected. However, mortality risks related to sex
201	differ when considering different disorders; for example, Bonnett et al. (2005) showed that, in
202	general, females had up to two times greater risk of dying from tumours than males. Dog breeds
203	have large variations in disease prevalence and, therefore, variation between breeds in risk
204	related to sex is to be expected.
205	
206	There were many (statistical) cells with few data because of low numbers of
207	performances per reproducer or per breeder (see Appendix A: Supplementary Table 1), which
208	led to difficulties in adjusting genetic models. It was possible to assess heritabilities for litter

209	sizes with low to moderate heritabilities (6.0-10.9%), of the same order to those estimated in
210	sheep, rabbits or pigs (Van Wyk et al., 2009; Nagy et al., 2012; Rodriguez et al., 2013).
211	However, a study on German shepherd and Labrador retriever guide dogs revealed much larger
212	heritabilities for litter size at 49 days (31 and 26%, respectively) (Hare and Leighton, 2006),
213	which may result from better monitoring of those populations and a larger number of litters per
214	reproducer.
215	
216	The structure of the data set did not allow identification of censured data (animals still
217	alive at the end of the study) and so it was not possible to perform direct survival analysis on
218	longevity data. Heritabilities estimated for 2 year survival were found in the same range (5.9-
219	10.1% according to breeds) as those reported for piglet and calf survival (4.2-19%) (Gerra et al.,
220	2006; Rohe et al., 2009; Fuerst-Waltl and Sørensen, 2010).
221	
222	Since litter size was measured at 2 months of age, i.e. after weaning, it was related to
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
228	estimated for those breeds. Supposing a similar impact of inbreeding on embryo and puppy
229	survival, the consequence of inbreeding on litter size could be expected to be higher for more
230	prolific breeds.
231	
232	The scaled estimation of inbreeding depression (dividing the regression coefficient by the
233	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.e0.69 (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 2009¹.

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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285	
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402	

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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413 414 415 416 417 418	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.

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

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	a	Litter size (mean ±	tter size (mean ± Litter rank (mean ±		Litter inbreeding				
Breed ^a		standard deviation)	standard deviation)	Mean F ^b	< 6.25	6.25-12.5	≥ 12.5		
			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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[,] Cain ...and white to 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.

Table 2 Main characteristics of longevity data according to breeds.

	Number	er Longevity (mean ±	Longevity	2 year	Inbreeding			
Breed ^a	of litters	standard deviation)	(median)	survivability	Mean F ^b	< 6.25	6.25-12.5	≥ 12.5
	or mucrs	standard deviation)	(inediaii)	(%)	(%)	(%)	(%)	(%)
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

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a, Cairn aland white ter 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.

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

		I	Litter size	2 year survival			
Breed a	h^2	Inbreed	ling regression coe	efficient	<i>l</i> ₂ I	nhroading ragrassion acafficient	
	n- <u>-</u>	Litter	Dam	Sire	_ h^2_{0l} I	Inbreeding 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^{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}	$1.50^{\rm NS}$	- 6	-	
WHW	0.105	-1.32 ***	-1.35 **	1.16 *	0.059	-1.1 ^{NS}	

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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.

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

437	
438	Appendix
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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. $^{\rm NS}$ non-
456	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.

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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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464 *EqG*, equivalent number of known generations.

^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.

465 Supplementary Table 2

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

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

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

470 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.

Supplementary Table 3

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

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

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