

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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| 17 | Highlig | hts |
| 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 | 1 | relatives. |
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| 27 | Data obtained from the French Kennel Club and the Fichier National Canin were used to |
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| 28 | estimate the effect of inbreeding on average litter size and survival in seven French breeds of |
| 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

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| 38 | Inbreeding is a phenomenon that is difficult to avoid in domestic species because breeds |
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| 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

inbreeding depression. 61

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| 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. |
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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 |
| 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 |
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| 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). |
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| 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 |
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| 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). |

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| 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 |
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| 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 |
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| 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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| 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 | |
| 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 ± | 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 | |
| | | 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 *** | $-0.9^{\rm \ NS}$ | 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

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| 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. $^{\rm NS}$ 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 | $RV_{BR} \pm \text{standard deviation}$ | $RV_{Pe} \pm \text{standard deviation}$ | $RV_E \pm \text{standard deviation}$ |
|---------|------------------------------|---|---|--------------------------------------|
| 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.