



**HAL**  
open science

## Inbreeding impact on litter size and survival in selected canine breeds

Grégoire Leroy, Florence Phocas, Benoit Hedan, Etienne Verrier, Xavier X Rognon

► **To cite this version:**

Grégoire Leroy, Florence Phocas, Benoit Hedan, Etienne Verrier, Xavier X Rognon. Inbreeding impact on litter size and survival in selected canine breeds. *The Internet Journal of Veterinary Medicine*, 2015, 203 (1), pp.74-78. 10.1016/j.tvjl.2014.11.008 . hal-01122782

**HAL Id: hal-01122782**

**<https://univ-rennes.hal.science/hal-01122782>**

Submitted on 4 Mar 2015

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Inbreeding impact on litter size and survival in selected canine breeds**

2

3

4 Grégoire Leroy <sup>a,b,\*</sup>, Florence Phocas <sup>a,b</sup>, Benoit Hedan <sup>c</sup>, Etienne Verrier <sup>a,b</sup>, Xavier Rognon <sup>a,b</sup>

5

6 <sup>a</sup> *AgroParisTech, UMR 1313 Génétique Animale et Biologie Intégrative, F-75231 Paris, France*

7 <sup>b</sup> *INRA, UMR 1313 Génétique Animale et Biologie Intégrative, F-78352 Jouy-en-Josas, France*

8 <sup>c</sup> *CNRS/Université de Rennes, UMR 6061 Institut de Génétique et Développement de Rennes, F-*  
9 *35065 Rennes, France*

10

11

12

13

14 \* Corresponding author. Tel.: +33 144081746.

15 *E-mail address:* [gregoire.leroy@agroparistech.fr](mailto:gregoire.leroy@agroparistech.fr) (G. Leroy).

Accepted Manuscript

16

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.
- 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.

24

Accepted Manuscript

Accepted Manuscript

26 **Abstract**

27 Data obtained from the French Kennel Club and the Fichier National Canin were used to  
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

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

Accepted Manuscript

## 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  
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  
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

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 ~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*

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  
 88 obtained using ASREML software (Gilmour et al., 2008). Analyses were independently  
 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’  
 95 is therefore the dam of the litter):

$$96$$

$$97 \quad Y_{irjmk} = \mu + P_r + By_j + b_1F_i + b_2F_{ir} + b_3F_m + Br_k + Pe_i + A_i + \mathcal{E}_{irjmk}$$

98  
 99 where  $Y_{irjmk}$  is the observed value of the  $r$ th litter bred by sire  $m$  and the dam  $i$ , raised by  
 100 the breeder  $k$ , and  $\mu$  is the overall mean. As environment factors, we included  $P_r$  (the fixed effect  
 101 of the litter rank  $r$ ),  $By_j$  (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  
 103  $k$  of the litter).  $b_1$ ,  $b_2$ ,  $b_3$  are the coefficients of regression of the phenotypic value ( $Y$ ) on the  
 104 coefficients of inbreeding of the dam ( $F_i$ ), its  $r$ th litter ( $F_{ir}$ ) and the sire of the  $r^{\text{th}}$  litter ( $F_m$ ),  
 105 respectively.  $A_i$  is the random genetic effect of dam  $i$ , and  $\mathcal{E}_{irjmk}$  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  $Y_{ijkl}$  was modelled as:

115

$$116 \quad Y_{ijkl} = \mu + Sx_j + Dy_k + b_i F_i + BR_l + A_i + \mathcal{E}_{ijkl}$$

117

118 where  $\mu$  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

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

128

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

129

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

132

## 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  $F \geq 12.5\%$  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 censored 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

234 -0.13 and -0.76 for dam inbreeding, with no notable difference according to breed size. This  
235 result was within the range of values estimated in livestock for the number of offspring weaned  
236 per litter, i.e. -0.69 (standard error 0.15) for litter inbreeding and -0.46 (standard error 0.17), for  
237 dam inbreeding (Leroy 2014). This result is illustrated by the reduction in BMD of 0.8 puppies  
238 between litters with inbreeding coefficients  $< 6.25\%$ , and litters with inbreeding coefficients  $>$   
239  $12.5\%$  (Fig. 2). In EPB and GSD, there was a difference of longevity of  $> 1$  year between dogs  
240 with inbreeding coefficients  $< 6.25\%$  and those with inbreeding coefficients  $> 12.5\%$ .

241  
242         Although it was not possible to identify the causes of death, reduced longevity may be  
243 linked to increased early mortality, early onset of senescence or increased rate of aging (Kraus et  
244 al., 2013). However, given the importance of inherited disorders with a potential impact on dog  
245 survival within dog breeds (Nicholas et al., 2011), it is probable that dogs with high inbreeding  
246 have higher incidences of those disorders, which may significantly reduce their lifespan. As  
247 emphasised by Leroy and Baumung (2010), high individual values of inbreeding coefficients ( $>$   
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

259 close relatives. Given the low value of coancestry, this baseline inbreeding has a limited effect  
260 on longevity. In contrast, at the individual level, Fig. 2 illustrates the deleterious impact of  
261 mating between close-relatives on litter size and longevity. Therefore, measures should be taken  
262 by breed clubs to avoid mating of close relatives (at least between parents-offspring, and half and  
263 full siblings), for example, following the decision taken by the UK Kennel Club in 2009<sup>1</sup>.

264

## 265 **Conclusions**

266 The results presented in this study illustrate that inbreeding affects reproduction  
267 parameters and survival at different stages of life in dogs. Improvement of these traits is  
268 required, since the reduction of survival is generally related to health problems affecting animal  
269 welfare. From a genetic point of view, survival of dogs could be improved by restricting mating  
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  
272 selection on survival traits, given the heritabilities measured here. However there is a need to  
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  
276 manage inbreeding depression phenomenon.

277

## 278 **Conflict of interest statement**

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

281

## 282 **Acknowledgements**

---

<sup>1</sup> See: <http://www.thekennelclub.org.uk>.

283 The authors would like to thank the Société Centrale Canine for the data provided and  
284 Wendy Brand-Williams for linguistic revision.

285

## 286 **References**

- 287 Abadie, J., Hedan, B., Cadieu, E., De Brito, C., Devauchelle, P., Bourgain, C., Parker, H.G.,  
288 Vaysse, A., Margaritte-Jeannin, P., Galibert, F., et al., 2009. Epidemiology, pathology,  
289 and genetics of histiocytic sarcoma in the Bernese mountain dog breed. *Journal of*  
290 *Heredity* 100, S19-27.
- 291
- 292 Bateson, P., Sargan, D.R., 2012. Analysis of the canine genome and canine health: A  
293 commentary. *The Veterinary Journal* 194, 265-269.
- 294
- 295 Boichard, D., Maignel, L., Verrier, E., 1997. Value of using probabilities of gene origin to  
296 measure genetic variability in a population. *Genetics Selection Evolution* 29, 5-23.
- 297
- 298 Boichard, D., 2002. PEDIG: A fortran package for pedigree analysis suited for large populations.  
299 *Proceedings of the 7th World Congress of Genetics Applied to Livestock Production,*  
300 *Montpellier, France, 19-23 August 2002, pp. 525-528.*
- 301
- 302 Bonnett, B.N., Egenvall, A., Hedhammar, A., Olson, P., 2005. Mortality in over 350,000 insured  
303 Swedish dogs from 1995-2000: I. Breed-, gender-, age- and cause-specific rates. *Acta*  
304 *Veterinaria Scandinavica* 46, 105-120.
- 305
- 306 Borge, K.S., Tonnessen, R., Nodtvedt, A., Indrebø, A., 2011. Litter size at birth in purebred dogs  
307 - A retrospective study of 224 breeds. *Theriogenology* 75, 911-919.
- 308
- 309 Dempster, E.R., Lerner, I.M., 1950. Heritability of threshold characters. *Genetics* 35, 212.
- 310
- 311 Egenvall, A., Bonnett, B.N., Olson, P., Hedhammar, A., 2000. Gender, age and breed pattern of  
312 diagnoses for veterinary care in insured dogs in Sweden during 1996. *Veterinary Record*  
313 146, 551-557.
- 314
- 315 Egenvall, A., Bonnett, B.N., Hedhammar, A., Olson, P., 2005. Mortality in over 350,000 insured  
316 Swedish dogs from 1995-2000: II. Breed-specific age and survival patterns and relative  
317 risk for causes of death. *Acta Veterinaria Scandinavica* 46, 121-136.
- 318
- 319 Falconer, D.S., Mackey, F.C. (Eds), 1996. *Introduction to Quantitative Genetics*, 4th Edn. Essex,  
320 UK, 464 pp.
- 321
- 322 Fuerst-Waltl, B., Sørensen, M.K., 2010. Genetic analysis of calf and heifer losses in Danish  
323 Holstein. *Journal of Dairy Science* 93, 5436-5442.
- 324
- 325 Gilmour, A.R., Gogel, B.J., Cullis, B.R., Thompson, R., 2008. *ASReml User Guide Release 3,*  
326 *VSN International, Hemel Hempstead, UK. [www.vsni.co.uk](http://www.vsni.co.uk) (accessed 9 November*  
327 *2014).*
- 328



- 329 Greer, K.A., Canterbury, S.C., Murphy, K.E., 2007. Statistical analysis regarding the effects of  
330 height and weight on life span of the domestic dog. *Research in Veterinary Science* 82,  
331 208-214.  
332
- 333 Guerra, J.L.L., Franke, D.E., Blouin, D.C., 2006. Genetic parameters for calving rate and calf  
334 survival from linear, threshold, and logistic models in a multibreed beef cattle population.  
335 *Journal of Animal Science* 84, 3197-3203.  
336
- 337 Hare, E., Leighton, E.A., 2006. Estimation of heritability of litter size in Labrador retrievers and  
338 German shepherd dogs. *Journal of Veterinary Behavior* 1, 62-66.  
339
- 340 Kraus, C., Parvard, S., Promislow, D.E.L., 2013. The size-life span trade-off decomposed: Why  
341 large dogs die young. *American Naturalist* 181, 492-505.  
342
- 343 Kristensen, T.N., Sorensen, A.C., 2005. Inbreeding - lessons from animal breeding, evolutionary  
344 biology and conservation genetics. *Animal Science* 80, 121-133.  
345
- 346 Leroy, G., Verrier, E., Wisner-Bourgeois, C., Rognon, X., 2007. Breeding goals and breeding  
347 practices of French dog breeders: Results from a large survey. *Revue de Médecine*  
348 *Vétérinaire* 158, 496-503.  
349
- 350 Leroy, G., Verrier, E., Meriaux, J.C., Rognon, X., 2009. Genetic diversity of dog breeds:  
351 Between-breed diversity, breed assignation and conservation approaches. *Animal*  
352 *Genetics* 40, 333-343.  
353
- 354 Leroy, G., Baumung, R., 2011. Mating practices and the dissemination of genetic disorders in  
355 domestic animals, based on the example of dog breeding. *Animal Genetics* 42, 66-74.  
356
- 357 Leroy, G., Rognon, X., 2012. Assessing the impact of breeding strategies on inherited disorders  
358 and genetic diversity in dogs. *The Veterinary Journal* 194, 343-348.  
359
- 360 Leroy, G., 2014. Inbreeding depression in livestock species: Review and meta-analysis. *Animal*  
361 *Genetics* 189, 177-182  
362
- 363 Mäki, K., Groen, A.F., Liinamao, A.E., Ojala, M., 2001. Population structure, inbreeding trend  
364 and their association with hip and elbow dysplasia in dogs. *Animal Science* 73, 217-228.  
365
- 366 Nagy, I., Gorjanc, G., Curik, I., Farkas, J., Kiszlinger, H., Szendro, Z., 2012. The contribution of  
367 dominance and inbreeding depression in estimating variance components for litter size in  
368 Pannon white rabbits. *Journal of Animal Breeding and Genetics*, 1-9.  
369
- 370 Nicholas, F.W., Crook, A., Sargan, D.R., 2011. Internet resources cataloguing inherited disorders  
371 in dogs. *The Veterinary Journal* 189, 132-135.  
372
- 373 Ólafsdóttir, G.Á., Kristjánsson, T., 2008. Correlated pedigree and molecular estimates of  
374 inbreeding and their ability to detect inbreeding depression in the Icelandic sheepdog, a  
375 recently bottlenecked population of domestic dogs. *Conservation Genetics* 9, 1639-1641.  
376
- 377 O'Neill, D.G., Church, D.B., McGreevy, P.D., Thomson, W., Brodbelt, D.C., 2013. Longevity  
378 and mortality of owned dogs in England. *The Veterinary Journal* 198, 638-643.

- 379  
380  
381 Rodríguez, C., García Casco, J.M., Silió, L., 2013. Measuring effects of new and fast inbreeding  
382 on the litter size of Iberian pigs. Proceedings of the 8th International Symposium on the  
383 Mediterranean Pig, Ljubljana, Slovenia, 10-12 October 2013, Acta Agriculturae  
384 Slovenica Supplement 4. 21-23.  
385
- 386 Roehe, R., Shrestha, N.P., Mekkawy, W., Baxter, E.M., Knap, P.W., Smurthwaite, K.M., Jarvis,  
387 S., Lawrence, A.B., Edwards, S.A., 2009. Genetic analyses of piglet survival and  
388 individual birth weight on first generation data of a selection experiment for piglet  
389 survival under outdoor conditions. *Livestock Science* 121, 173-181.  
390
- 391 Ubbink, G.J., Knol, B.W., Bouw, J., 1992. The relationship between homozygosity and the  
392 occurrence of specific diseases in Bouvier Belge des Flandres dogs in The Netherlands.  
393 *Veterinary Quarterly* 14, 137-140.  
394
- 395 Urfer, S.R., 2009. Inbreeding and fertility in Irish Wolfhounds in Sweden: 1976 to 2007. *Acta*  
396 *Veterinaria Scandinavica* 51, 21.  
397
- 398 Van der Beek, S., Nielen, A.L., Schukken, Y.H., Brascamp, E.W., 1999. Evaluation of genetic,  
399 common-litter, and within-litter effects on preweaning mortality in a birth cohort of  
400 puppies. *American Journal of Veterinary Research* 60, 1106-1110.  
401
- 402 Van Wyk, J.B., Fair, M.D., Cloete, S.W.P., 2009. Case study: The effect of inbreeding on the  
403 production and reproduction traits in the Elsenburg Dormer sheep stud. *Livestock*  
404 *Science* 120, 218-224.  
405

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.

411

412

413 Fig. 2. Average litter size and longevities according to inbreeding classes, considering for litter  
414 size the coefficient of inbreeding of the litter (a) or its dam (b), and for longevity the  
415 coefficient of the individual considered (c). BMD, Bernese mountain dog; BSH, Basset  
416 hound; CAI, Cairn terrier; EPB, Epagneul Breton; GSD, German shepherd dog; LEO ,  
417 Leonberger West; WHW, Highland white terrier. <sup>NS</sup> non-significant; \*  $P < 0.05$ ; \*\*  $P <$   
418  $0.01$ ; \*\*\*  $P < 0.001$ .

Accepted Manuscript

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

420

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

421

422 <sup>a</sup> 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 <sup>b</sup> Inbreeding coefficient.

425 **Table 2** Main characteristics of longevity data according to breeds.

426

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

427

428 <sup>a</sup> 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 <sup>b</sup> Inbreeding coefficient.

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

Breed <sup>a</sup>	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 <sup>NS</sup>	0.061	-2.04 <sup>NS</sup>
BSH	0.06	-1.36 <sup>NS</sup>	-0.67 <sup>NS</sup>	0.02 <sup>NS</sup>	0.067	-0.98 <sup>NS</sup>
CAI	0.098	-2.20 ***	-1.18 *	0.14 <sup>NS</sup>	0.064	-1.57 <sup>NS</sup>
EPB	0.1	-2.94 ***	-0.9 <sup>NS</sup>	0.73 *	0.063	-2.70 ***
GSD	0.091	-3.30 ***	-2.19 ***	0.90 <sup>NS</sup>	0.101	-2.80 ***
LEO	0.882	-3.80 *	-3.81 <sup>NS</sup>	1.50 <sup>NS</sup>	-	-
WHW	0.105	-1.32 ***	-1.35 **	1.16 *	0.059	-1.1 <sup>NS</sup>

433

434 <sup>a</sup> 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.

436  $h^2$ , heritability;  $h^2_{01}$ , heritability on the observed scale; <sup>NS</sup> non-significant; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

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. <sup>NS</sup> non-

456 significant; \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

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 <sup>a</sup>	Pedigree file	Trait	Number	Sires	Dams	Breeders	<i>EqG</i>
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

461

462 <sup>a</sup> 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.

464 *EqG*, equivalent number of known generations.



465 **Supplementary Table 2**

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

467

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

Accepted Manuscript

473 **Supplementary Table 3**

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

475

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

476

477  $h^2$ , heritability (additive variance);  $RV_{BR}$ , breeder effect variance ratio;  $RV_E$ , residual variance ratio.478 <sup>a</sup> 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.