Inbreeding impact on litter size and survival in selected canine breeds

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ARTICLE INFO

ABSTRACT

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

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Introduction

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

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

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

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

Materials and methods

Source of population data

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

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

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

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

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

[b] Inbreeding coefficient.

Statistical analysis

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

Litter size was defined as the number of puppies alive at registration, i.e. at the age of 2 months. Data were based on records ranging from 3468 (BSH) to 39,080 (GSD) litters born from 1543 (BSH) to 15,869 (GSD) bitches (Table 1; see Appendix: Supplementary Table S1). The trait was analysed using a repeatability animal model and litter size as a trait of the dam (the 'animal' is therefore the dam of the litter):

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

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

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

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

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

Heritabilities (h^2) and other variance ratios were computed by dividing genetic variance and variance components of all the other random effects by phenotypic variances for each statistical model. To assess juvenile survival, heritability on the observed scale (h_{01}^2) 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*.

Results

Demographic parameters

Individual breeds had different population sizes, with the number of observations ranging from 1775 (longevity for LEO breed) to 39,080 (litter size for GSD breed) (Table 1). Among the breeds studied, BMD showed an increase in the number of litters produced over the 1990–2012 period (see Appendix: Supplementary Fig. S1). Since there are many hobby breeders, there was only a small number of observations per female, per male or per breeder (see Appendix: Supplementary Table S1); as an example, the average number of litters produced per male over the 1990–2012 period ranged from 3.8 (LEO) to 9.9 (WHW). In each data set, the pedigree knowledge was relatively good, with average *EqG* ranging from 5.02 (longevity for BMD and GSD) to 8.77 (litter size for EPB).

Characterisation of traits

The seven breeds showed large variations in the studied traits; average litter size ranged from 3.5 (WHW) to 6.3 (LEO) puppies, with variations between years (Table 1; see Appendix: Supplementary Fig. S1) and according to litter rank (Table 1; see Appendix: Supplementary Fig. S2). There was an increase in litter size until the second (BSH, EPB, GSD, LEO) or the third litter (BMD, CAI, WHW), and then a decrease in subsequent ranks.

Mean longevity ranged from 7.7 (BMD) to 12.2 (CAI) years (Table 2), with three breeds (CAI, EPB, WHW) showing a regular increase in

Table 2
Main characteristics of longevity data according to breeds.

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

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

[b] Inbreeding coefficient.