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Litter size at birth in purebred dogs—A retrospective study of 224 breeds

Kaja Sverdrup Borge[a,c,*], Ragnhild Tønnessen[a,d], Ane Nødtvedt[a], Astrid Indrebø[a,b]

[a] Department of Companion Animal Clinical Sciences, Norwegian School of Veterinary Science, Oslo, Norway
[b] Norwegian Kennel Club, Oslo, Norway
[c] Department of Basic Sciences and Aquatic Medicine, Norwegian School of Veterinary Science, Oslo, Norway
[d] Department of Food Safety and Infection Biology, Norwegian School of Veterinary Science, Oslo, Norway

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Abstract

Despite the long history of purebred dogs and the large number of existing breeds, few studies of canine litter size based upon a large number of breeds exist. Previous studies are either old or include only one or a few selected breeds. The aim of this large-scale retrospective study was to estimate the mean litter size in a large population of purebred dogs and to describe some factors that might influence the litter size. A total of 10,810 litters of 224 breeds registered in the Norwegian Kennel Club from 2006 to 2007 were included in the study. The overall mean litter size at birth was 5.4 (± 0.025). A generalized linear mixed model with a random intercept for breed revealed that the litter size was significantly influenced by the size of the breed, the method of mating and the age of the bitch. A significant interaction between breed size and age was detected, in that the expected number of puppies born decreased more for older bitches of large breeds. Mean litter size increased with breed size, from 3.5 (± 0.04) puppies in miniature breeds to 7.1 (± 0.13) puppies in giant breeds. No effect on litter size was found for the season of birth or the parity of the bitch. The large number of breeds and the detail of the registered information on the litters in this study are unique. In conclusion, the size of the breed, the age of the bitch and the method of mating were found to influence litter size in purebred dogs when controlling for breed, with the size of the breed as the strongest determinant.

Keywords: Litter size; Breed size; Age; Litter number; Season; Method of mating

1. Introduction

The history of the domestic dog spans over more than 15,000 years, and selective dog breeding performed by humans has resulted in the approximately 400 internationally acknowledged breeds of today. Still, there are very few recent studies on breed specific litter size at birth including a larger number of breeds. Previous studies include only one or a few selected breeds [1–6]. There are some studies of litter size based on data from different kennel clubs, but these are breed specific [5,6] or they only include puppies that were alive at the time of registration [7–9]. Many factors have been suggested to influence on litter size, such as breed, the size of the dog, the age of the bitch, the age of the sire, the season of the year, the number of previous litters born from the bitch, the number of matings, whether the mating occurred naturally or with AI as well as the quality of the semen [2,3,5,7,8,10–15]. However, the results from former studies are inconsistent. Because the vast majority of litters from

* Corresponding author. Tel.: +47 22964537; fax +47 22597310.
E-mail address: KajaSverdrup.Borge@nvh.no (K.S. Borge).

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purebred dogs in Norway are registered in the Norwegian Kennel Club (NKC), a large database of registered litters exists. This database contains information about number of puppies born, including number of live born and dead born puppies, as well as information about the bitch, the sire and the mating. Even though mean litter size at birth varies within a breed, information on the expected mean litter size for a particular breed is useful both for breeders and veterinarians. Moreover, to improve and optimize breeding, increased knowledge regarding factors which might influence litter size is essential. The aim of this cross-sectional study was to estimate the mean litter size at birth in purebred dogs and to determine whether the litter size is influenced by breed, the size of the breed (body weight), the age of the bitch, the total number of litters of the bitch, the method of mating and the time of year the litter was born.

2. Materials and methods

2.1. Study population

This retrospective study is based on the records of data for all purebred dog litters registered by the breeders in the NKC from January 1st 2006 to December 31st 2007. The majority of litters are registered in the NKC when the puppies are five to eight weeks old. The NKC data contains information about the bitch and sire, including breed, registered names, NKC registration numbers, method of mating, birth dates of the bitch, sire and litters and the litter number (= parity) of the bitch. The numbers of live born and dead born puppies, puppies alive seven days after birth and the numbers of registered female and male puppies are included in the database. The study population does not include litters where all puppies died prior to the time of registration. The electronically stored registrations from NKC were controlled for double registrations and extreme values in order to maximize the quality of the data, and litters with incomplete information for our analysis were excluded (n = 181).

2.2. Definitions

2.2.1. Litter size

Litter size was defined as the sum of live born and dead born puppies. The litter size value was described by use of arithmetical mean, SEM and range.

2.2.2. Breed size groups

All breeds were classified into one of five size groups based on the middle value of the body weight interval of the breed (female and male dogs included): Miniature breeds < 5 kg, small breeds 5–10 kg, medium breeds 10–25 kg, large breeds 25–45 kg and giant breeds > 45 kg. The body weight intervals were collected from the Kennel Club, the Fédération Cynologique Internationale (FCI), from breed literature and breed clubs.

2.2.3. Age of the bitch and litter number

The age of the bitch was defined as the age on the day the litter was born. It was calculated, in terms of days, by subtracting the date of birth of the litter from the date of birth of the bitch. The age in years was further defined according to the following for presentation in graphs and figures: < two years of age = less than 729 days, two years = from 730 to (and including) 1094 days, three years = 1094 to (and including) 1459 days and so on. Bitches younger than two years old were grouped together due to few recorded litters, and the same was done for bitches aged seven years or older. In the regression model, age in days was divided by 365.25 to provide age in years. The litter number was defined as the total number of litters born by the bitch, including the present. Because few of the bitches were registered with six or more litters, these were grouped together as “six or more”.

2.2.4. Method of mating

For each litter in the database, the method of mating was given as natural mating, AI, frozen semen or AI, fresh semen. There was no information about the site of the AIs.

2.2.5. Season

To study seasonal variations in the mean litter size, the litters were grouped according to birth month (1 = January, 2 = February, . . . , 12 = December). Furthermore, a categorical variable called “season” was created, where spring = February–April, summer = May–July, autumn = August–October and winter = November–January. The reason for this was that four approximately equally sized groups were desired for the analysis of seasonal effects.

2.3. Statistical analysis and multivariable methods

The software package Stata version 10.0 was used for descriptive statistics and multivariable analysis (Stata Corporation, College Station, Texas, USA). A linear regression model of litter size was fitted using a generalized least squares (GLS) procedure [16]. Initial screening for unconditional associations between litter size and the outcome variables was performed by fitting linear regression models with single predictors and applying a liberal p-value (0.1) for retaining the variables in the analysis. A final model was created through manual elimination, with a cut-off of $P < 0.05$ for keeping variables in the model. Overall significance of groups of variables, e.g. season and litter number, was assessed using likelihood ratio tests. Age in years and its quadratic term (age^2) were entered into the model to reflect the curvilinear effect of age on litter size. Breed was included in the final model as a random effect (using restricted maximum likelihood estimation in the "xtmixed" command), to account for the lack of independence between observations within the same breed. Relevant two-way interactions were tested between variables in the final model. Model diagnostics were performed by examining plots of predicted values and residuals at the two levels of the model (litter and breed). The linear prediction from the fixed part of the model was plotted against age of the bitch for each breed size and is shown in Figure 1. For the purpose of presentation, only litters resulting from natural mating were included in the figure to avoid cluttering of the graph.

3. Results

3.1. Study population

The database consisted of 10,810 litters from 224 breeds. The mean litter size for all the litters in the database was 5.4 puppies (± 0.025). The majority of the bitches, 7502 individuals (82.2%), contributed one litter each in the period from 2006 to 2007, 1564 individuals (17.1%) gave birth to two litters and 60 (0.66%) mothered three litters in this period. Lack of independence between litters born by the same bitch was ignored for the purpose

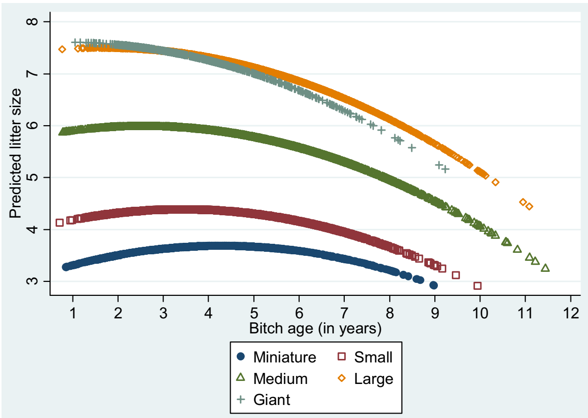

Fig. 1. Predicted litter size by age of the bitch for the five different breed size groups based on a generalized linear mixed model with a random breed intercept (Table 3). Only litters resulting from natural mating are included in the graph (n = 9756).

of this analysis, where the litter was the unit of observation. The mean number of litters born per breed was 45, ranging from 1 to 465 litters.

3.2. Breed and breed size

Mean litter size for the 100 most popular breeds is given in Table 1. Rhodesian Ridgeback was the breed with the largest mean litter size of 8.9 (± 0.6) puppies. Toy Poodle and Pomeranian had the smallest mean litter size, both with 2.4 (± 0.1) puppies. A complete table including the mean litter size for all the 224 breeds in the study is available online (Supplementary file 1).

When looking at all the 10,810 litters in the database, mean litter size increased with the size of the breed. The relationship was statistically significant when tested in a simple linear regression model. The mean litter size was 3.5 (± 0.04) in miniature breeds, 4.2 (± 0.03) in small breeds, 5.7 (± 0.04) in medium breeds, 6.9 (± 0.05) in large breeds and 7.1 (± 0.13) in giant breeds (Table 2).

3.3. Age of the bitch and litter number

According to the initial unconditional analysis, there was no distinct trend within or across the different breed size groups as to how age influenced mean litter size (Table 2). However, the multivariable analysis showed that the relationship between age and litter size was curvilinear and that there was a significant interaction between age and breed size. Therefore, the effect of age was not the same across the different breed size groups. In small dogs both young and old bitches yielded smaller litters than in the ages between. For the larger breeds, low age did not seem to reduce the mean litter size, but the number of puppies in the litter steadily decreased with increasing age (Table 3, Fig. 1). The unconditional association between age of the bitch and litter size within each of the breed size groups was statistically significant at the $P < 0.01$ level. The largest mean litter size was found in bitches recording their first litter (5.7 ± 0.04), and gradually decreased with increasing parities to 4.2 (± 0.24) for the sixth litter (unconditional association, $P < 0.01$). However, this apparent negative effect of parity number on mean litter size was no longer significant when adjusting for age of the bitch through the multivariable statistical analysis.

3.4. Method of mating

Natural mating was by far the most common method of mating in the database (n = 9756), while AI with fresh semen was more frequently performed than AI with frozen semen (n = 376 and 124, respectively). For

Table 1
Mean litter size at birth in the 100 most popular breeds based on reported litters from breeders to the Norwegian Kennel Club during 2006 and 2007.

Breed	n	Mean	SEM	Range	Breed	n	Mean	SEM	Range
Rhodesian Ridgeback	30	8.9	0.6	1–15	Welsh Corgi (Pembroke)	28	5.5	0.4	1–9
Leonberger	46	8.4	0.5	1–15	Dachshund	358	5.4	0.1	1–13
Dalmatian	46	8.4	0.5	1–15	Bulldog	37	5.4	0.4	1–10
German Shorthaired Pointer	64	8.3	0.4	1–15	American Cocker Spaniel	95	5.3	0.2	1–10
Flat Coated Retriever	120	8.3	0.3	1–15	Norwegian Elkhound Black	65	5.2	0.3	1–11
Dogue De Bordeaux	26	8.1	0.8	2–17	Tibetan Terrier	28	5.2	0.3	1–9
Gordon Setter	219	7.6	0.2	1–16	Collie (Rough)	101	5.2	0.2	1–10
Swedish Elkhound	70	7.5	0.3	1–14	Finnish Lapphund	24	5.2	0.3	2–9
Golden Retriever	291	7.5	0.2	1–14	Siberian Husky	88	5.1	0.2	1–14
Rottweiler	214	7.4	0.2	1–14	Border Terrier	27	5.1	0.4	1–9
Norwegian Hound	41	7.4	0.6	1–17	Petit Basset Griffon Vendéen	35	5.1	0.4	1–10
English Springer Spaniel	74	7.3	0.3	1–13	Lhasa Apso	34	4.9	0.3	1–9
German Wirehaired Pointer	53	7.3	0.4	1–14	Norwegian Buhund	36	4.9	0.3	1–8
Pointer	83	7.2	0.3	1–12	Basenji	22	4.8	0.4	1–8
Irish Setter	145	7.1	0.2	1–13	French Bulldog	35	4.7	0.3	1–8
Finnish Hound	74	7.1	0.3	1–13	Miniature Schnauzer	205	4.7	0.1	1–10
Great Dane	29	7.1	0.6	1–13	Manchester Terrier	21	4.7	0.3	2–7
Dobermann	45	7.0	0.4	1–13	Bichon Frise	192	4.6	0.1	1–10
Poodle (Standard)	103	7.0	0.2	2–12	Icelandic Sheepdog	23	4.5	0.3	2–6
Giant Schnauzer	42	7.0	0.5	1–14	Jack Russel Terrier	138	4.4	0.1	1–10
Schnauzer	28	7.0	0.4	2–11	Cairn Terrier	182	4.4	0.1	1–8
Labrador Retriever	223	6.9	0.2	1–13	Dachshund (Miniature)	144	4.4	0.1	1–8
Alaskan Malamute	49	6.9	0.3	2–11	Chow Chow	36	4.4	0.4	1–9
Small Munsterlander	24	6.9	0.5	3–13	Bichon Havanais	73	4.3	0.2	1–9
St. Bernard	45	6.8	0.5	1–18	Chinese Crested	133	4.3	0.2	1–9
Eurasier	22	6.7	0.6	1–13	Miniature Pinscher	76	4.3	0.1	1–7
Basset Hound	21	6.7	0.8	1–11	Danish-Swedish Farmdog	35	4.2	0.3	1–8
Lagotto Romagnolo	26	6.7	0.3	4–12	Pug	120	4.2	0.2	1–8
Boxer	139	6.6	0.2	1–12	Shih Tzu	95	4.2	0.2	1–9
Nova Scotia Duck Tolling Retriever	74	6.6	0.2	2–12	Cavalier King Charles Spaniel	439	4.1	0.1	1–15
Newfoundland	57	6.5	0.4	1–12	Boston Terrier	46	4.1	0.3	1–8
Hamilton Hound	24	6.5	0.5	3–11	Shetland Sheepdog	292	3.9	0.1	1–8
Bernese Mountain Dog	137	6.4	0.3	1–15	Japanese Spitz	91	3.9	0.1	1–7
English Setter	266	6.4	0.1	1–13	Coton de Tulear	27	3.8	0.3	1–7
Brittany	53	6.4	0.3	1–10	Tibetan Spaniel	312	3.8	0.1	1–8
Belgian Shepherd Dog (Groenendael)	29	6.3	0.4	2–11	West Highland White Terrier	37	3.7	0.3	1–8
Belgian Shepherd Dog (Tervueren)	52	6.2	0.4	1–11	Poodle (Medium)	105	3.7	0.2	1–10
Samoyed	41	6.2	0.4	1–12	Finnish Spitz	23	3.7	0.2	2–6
Swedish Dachsbracke	84	6.1	0.3	1–12	Yorkshire Terrier	35	3.5	0.3	1–6
German Shepherd Dog	465	6.1	0.1	1–14	Papillon	166	3.3	0.1	1–7
Whippet	47	6.1	0.3	1–10	Phalène	43	3.3	0.2	1–6
Border Collie	323	6.0	0.1	1–16	Italian Greyhound	34	3.3	0.3	1–6
Irish Soft Coated Wheaten Terrier	57	5.8	0.2	1–10	Shiba Inu	42	3.3	0.3	1–7
Cocker Spaniel	174	5.7	0.2	1–14	Dachshund (Rabbit)	35	3.3	0.2	1–6
Staffordshire Bull Terrier	82	5.6	0.2	1–12	Norwegian Lundehund	46	3.2	0.2	1–5
Greenland Dog	36	5.6	0.4	1–10	Chihuahua	269	3.2	0.1	1–7
Australian Terrier	22	5.5	0.4	1–8	Poodle (Miniature)	151	3.0	0.1	1–8
Bull Terrier	36	5.5	0.4	1–9	Norfolk Terrier	25	2.5	0.2	1–5
Norwegian Elkhound Grey	390	5.5	0.1	1–12	Pomeranian	179	2.4	0.1	1–6
Beagle	113	5.5	0.2	1–10	Poodle (Toy)	100	2.4	0.1	1–4

n: number of litters.

554 litters, the method of mating was not given. In the initial unconditional analysis, the mean litter size was not significantly different for the various methods of mating (natural mating: 5.39 ± 0.02; AI, fresh semen: 5.39 ± 0.14; AI, frozen semen: 5.49 ± 0.24). However, when adjusting for breed, breed size and age in the mixed

Table 2
Mean litter size and number of litters (n) according to the age of the bitch and the different breed size groups for litters registered within the Norwegian Kennel Club in 2006 and 2007 (n = 10,810).

Age of bitch (years)	Miniature breeds (< 5 kg)		Small breeds (5–10 kg)		Medium breeds (10–25 kg)		Large breeds (25–45 kg)		Giant breeds (> 45 kg)		Total	
	Mean litter size	n	Mean litter size	n	Mean litter size	n	Mean litter size	n	Mean litter size	n	Mean litter size	n
<2	3.4	308	4.3	287	5.7	180	7.1	96	7.9	28	4.7	899
2	3.6	462	4.2	732	5.9	536	7.0	551	7.4	170	5.3	2451
3	3.5	347	4.3	551	5.9	579	7.2	614	7.6	183	5.6	2274
4	3.5	245	4.1	402	6.0	482	7.0	510	7.2	126	5.6	1765
5	3.4	182	4.0	274	5.7	430	7.0	469	6.3	83	5.5	1438
6	3.4	84	3.9	185	5.9	341	6.6	351	5.3	44	5.6	1005
7≤	3.1	75	3.8	117	4.9	380	6.0	383	6.0	23	5.1	978
Total	3.5	1703	4.2	2548	5.7	2928	6.9	2974	7.1	657	5.4	10,810

The age of the bitch was defined according to the following: <2 year of age: less than 729 days, two years: from 730 to (and including) 1094 days, three years: 1094 to (and including) 1459 days and so on. Bitches younger than two years old were grouped as <2 years due to few recorded litters and likewise for bitches aged seven years or older.

model, the mean litter size was found to be significantly larger for bitches naturally mated than artificially inseminated. A decrease in mean litter size of 0.4 puppies would be expected for litters conceived by AI with fresh semen and 1.3 puppies for AI with frozen semen, both compared to natural mating ($P < 0.01$).

3.5. Season

Mean litter size varied from 5.1 to 5.6 between the different birth months. The monthly number of litters born also seemed to vary through the year. March was the month with the largest number of litters (n = 1222), while the lowest number of litters was born in November (n = 702). The re-classification of months into four seasons revealed that litters born in the spring appeared to be marginally larger than litters from the other seasons (Table 4). The effect of season was not statistically significant in the linear mixed model.

3.6. Multivariable methods

The factors that were found to be significant predictors of litter size in the linear mixed model were age of the bitch, age^2, method of mating and breed size group (Table 3). Furthermore, there was a significant negative

Table 3
Regression coefficients from a generalized linear mixed model of litter size in registered litters within the Norwegian Kennel Club in 2006 and 2007 (n = 10,211).

Variable	Level	Coefficient[a]	SE	z[b]	P[c]	95% CI	
Age (years)	—	0.354	0.058	6.12	0.000	0.240	0.468
Age (years)^2	—	−0.034	0.006	−6.07	0.000	−0.046	−0.023
Mating method	Natural	—					
	AI, fresh semen	−0.413	0.116	−3.55	0.000	−0.641	−0.185
	AI, frozen semen	−1.288	0.201	−6.40	0.000	−1.683	−0.894
Breed size	Miniature	—					
	Small	0.959	0.252	3.81	0.000	0.465	1.452
	Medium	2.760	0.242	11.42	0.000	2.286	3.233
	Large	4.440	0.274	16.23	0.000	3.904	4.976
	Giant	4.614	0.357	12.94	0.000	3.915	5.313
Age (years)* size	—	−0.060	0.012	−5.11	0.000	−0.083	−0.037
	Constant	2.990	0.227	13.15	0.000	2.544	3.436

Breed (n = 222) was included in the model as a random error term.
599 litters were excluded from the model because method of mating and/or age of the bitch were not given.
Variance components: Breed (intercept): 0.69 (SE 0.10), Litter (residual): 4.59 (SE 0.06).
[a] The coefficient is the change in litter size caused by a one-unit change for a given variable.
[b] The z-value indicates how many standard deviations the observation is above or below the mean.
[c] The P-value is the observed significance level.

Table 4
Mean litter size and total number of litters born per season of the year for litters registered within The Norwegian Kennel Club in 2006 and 2007 (n = 10,810).

Season of birth	n	Litter size	
		Mean	SEM
Spring	3180	5.6	0.047
Summer	2991	5.5	0.049
Autumn	2436	5.3	0.052
Winter	2203	5.2	0.055
Total	10,810	5.4	0.025

Spring: February–April, summer: May–July, autumn: August–October and winter: November–January. n: number of litters.

interaction between age of the bitch and breed size, which yielded an estimated decrease in litter size which was more pronounced for older bitches of larger breeds. The random breed effect was also highly significant. Residual diagnostics were performed and revealed no major short-comings of the model [16]. The interpretation of the model coefficients is that the litter size for the average breed is 3 puppies (constant), and the fixed effects are added to this. For a giant sized bitch aged four years this yields a predicted litter size of (3.0 + 4 years*0.35 − 16*0.03 + 4.6 − (4 years*5)*0.06) = 7.3. For a miniature bitch of the same age the two last parts of the equation do not apply, and the estimated average litter size would be (3.0 + 4*0.35 − 16*0.03) = 3.9. Both examples are based on natural mating, which is the baseline; if AI with frozen semen is performed the litter size would be expected to decrease by approximately 1.3 puppies. Based on the variance components from the random effects model, it was estimated that 87% of the variation in the data existed at the litter-level, or between litters within breeds, while 13% was found between breeds. This corresponds to an intra-class correlation coefficient (ICC or rho) of 0.13. The predicted number of puppies based on the final model is shown in Figure 1, for litters based on natural mating only. Because there is a significant interaction between age and breed size, the shape of the predicted curve varies across the groups.

4. Discussion

4.1. Study population

To the best of our knowledge, no previous publications on litter size at birth have been based on an equally large number of breeds and litters. Accordingly, this study is unique both regarding the size of the study population and number of breeds included. As approximately 90% of Norwegian purebred dogs are registered in the national kennel club database, our results should be highly reliable and representative for the population of purebred dogs in Norway. The results can probably also be extrapolated to similar populations of purebred dogs in other countries with similar dog management systems to Norway. Hence both the internal and external validity of the results in the current study were judged as high.

The mean litter size of 5.4 puppies in this study is similar to the 5.1 reported in purebred dogs in Australia [15]. Except for the Australian study, all former large-scale studies on litter size were performed in the 1960s and 1970s. In a Norwegian study from 1970, the mean litter size was 5.6 puppies [7], while a lower estimate of 4.73 puppies was found by Tedor et al [8]. However, mean litter sizes in these two large-scale studies were estimated from the number of puppies per litter that were registered at the time of weaning or when they were sold at the age of five to eight weeks. Thus, dead born puppies or those that died before the time of registration were not included. It is therefore surprising that the mean litter size found by the previous Norwegian study is somewhat larger than ours. But the proportion of litters from miniature and small breeds, according to the defined classification, was lower (28.1%) [7] compared with the 39.3% found in our study. The increased popularity of smaller dog breeds might have caused the slight decrease in mean litter size observed in our study. Differences in the composition of the dog population within and between countries due to the varying popularity of breeds, together with biological variation, might explain the observed differences in mean litter size between studies. Because litter size was estimated from the sum of live born and dead born puppies, a slight underestimation could result from underreporting of dead born puppies by some breeders. In addition, litters where all puppies die before registration (more likely with small or one-puppy litters) will not be reported and can have affected the results in breeds with few observations.

4.2. Breed and breed size

Rhodesian Ridgeback was the breed with the largest mean litter size (8.9 ± 0.6) among the 100 most popular breeds. In a Norwegian study published by Thomassen et al in 2006, 501 bitches of 99 different breeds which had litters after AI with frozen semen were investigated, and the Rhodesian Ridgeback was found to be the breed with the largest mean litter size (7.9 ± 0.7) [3]. Even so, the estimate was lower compared to our findings, although the difference was not statistically significant as judged by a comparison of the respective means ± the SEM. Two studies have documented a smaller litter size in bitches inseminated with frozen semen compared to fresh semen or natural mating [12,13]. As most of the litters in our study were conceived by natural mating, this could possibly be the reason for the higher estimate. The mean litter size in Rhodesian Ridgeback in another Scandinavian study was 7.5 puppies (n = 320 litters), but this only included puppies who were alive and registered at eight weeks of age [9]. In an Australian study, Rhodesian Ridgeback (n = 10) had the second largest mean litter size among the studied breeds with a mean litter size of 10.6 puppies [15].

Pomeranian and Toy Poodle had the smallest mean litter size in our study, which is in line with the results of previous studies [7–9,15]. A mean litter size of 2.0 puppies in Pomeranian was reported in the Australian study (n = 2) [15]. In studies including only registered puppies, Lyngset et al [7], Tedor [8] and Bergström et al [9] found a mean litter size of 2.04 (n = 108), 2.71 (n = 33,648) and 1.9 (n = 954) puppies in Pomeranian, respectively.

The mean litter size increased significantly with the size of the breed. This is consistent with the findings in previous studies [3,15,17]. A large dog can give birth to a greater number of puppies. The relative size of the foetus compared to the bitch is larger in bitches of smaller breeds than in bitches of larger breeds. But at some point, the linear correlation between litter size and breed size must level out due to biological factors, such as limited space in the uterus and a limited number of teats. This is not explicit from our results, although the increase in mean litter size is not as substantial between large and giant breeds as between the other size groups. The grouping of breeds is based on body weight only, and breeds with different body conformation can sometimes end up in the same body weight class. For example medium sized, broadly and compactly built breeds might weigh the same as large, slim breeds. Previous studies on larger dog breeds report a mean litter size of 6.9 [18] and 7.6 [4], which is similar to the results found for the large and giant dog breed groups. Unfortunately, the database contained no information about the body weight of the individual bitch. Thus, we could not analyse the effect of individual dog size on mean litter size independently of breed.

The main part of the variation in mean litter size (87%) was due to between-litter factors. The fairly low ICC of 0.13 indicates that in a model which includes breed size there is only modest correlation between two litters from the same breed; hence a small litter might very well occur in a given breed even though other litters from the same breed tend to be large. However, it should be noted that the presented ICC is based upon a model where size of the breed is taken into account and is a strong predictor of litter size. A separate model was built ignoring breed size (data not shown), and this yielded an ICC of 0.33 which indicates a stronger within-breed correlation in this scenario. Because the size information was based upon estimates at the breed level rather than individual weight measurements, the size versus breed effects can not be fully separated in this analysis. However, the data were submitted by breeders and retrieving accurate individual weights was not considered feasible. Therefore the general size variable was deemed useful, and proved to be the most significant determinant of litter size in this material.

4.3. *Age of the bitch and litter number*

There was a significant association between the age of the bitch and litter size in our study, which is in line with other studies [5,10,11,15,19]. However, reports from other studies still vary somewhat from our results. Gill reported peak fertility in the bitch to occur at the age of two years, with a tendency of decreasing mean litter size thereafter [15]. Andersen [11] and Sierts-Roth [19] found a higher mean litter size in young bitches and a reduced reproductive performance after three years of age, in the Beagle and the Hungarian Shepherd, respectively. Mean litter size in the Drever decreased after five years of age [5]. In Beagles, the number of puppies per bitch and per year was in the optimum range up to five years of age and declined thereafter [10]. Both the Drever and the Beagle are medium-sized breeds according to our classification. In our study, the litter size of medium breeds started decreasing earlier than five years of age (Fig. 1). The whelping rate and litter size in a study of larger breeds tended to be smaller in bitches older than six years [3]. The decrease in litter size occurred at an earlier age in our large and giant breed groups. Immature reproduction organs might be the reason for smaller litter size in young age groups, while age-related changes in the uterus have been suggested as a cause for the smaller mean litter sizes in older bitches [3]. The significant age-size interaction found in our analysis supports the observation that the effect of increasing age on litter size varies across the groups formed by breed size.

Miniature and small breeds were overrepresented among the youngest bitches in this study population.

The same tendency was seen in an Australian study [15]. This might be because small breeds are expected to be fully grown and gain sexual maturity earlier than large breeds [20]. The fact that the mean litter size was smaller for the youngest bitches of smaller breeds in our study might indicate that they are not as early mature as previously believed. Further, it would be likely to assume that smaller breeds would also be overrepresented in litters from bitches over seven years of age due to a shorter expected life span in larger than smaller breeds [20–22]. However, this is not the case in our study. But the decrease in litter size at older age is more pronounced in large breeds than small breeds in our study. The NKC has strongly advised against breeding a bitch at her first heat or after the age of eight years [23]. The low numbers of very young and very old bitches in our database indicate that most Norwegian breeders follow these guidelines.

When evaluating whether litter size was influenced by the number of previous litters of the bitch (or parity), the confounding factor between litter number and the age of the bitch must be considered. Initial analysis of unconditional associations showed a decreasing litter size with increasing litter number. However, multivariable analysis revealed that this tendency was mainly due to increased age of the bitch, and the effect of litter number was insignificant when tested in the mixed model. Neither Pearson et al [24] nor Rowlands et al [2] found a significant effect of parity on litter size. In the Drever breed, the number of registered pups increased from the first to the second parity in the Swedish Kennel Club (SKC) data, and then decreased [5]. The results of Gill [15] suggested that mean litter size decreased with increasing litter number, but the relationship between age and litter number was not analysed.

4.4. Method of mating

Compared to natural mating, the number of litters conceived by AI was low. This imbalance should be kept in mind when considering the results. However, the significant decrease in mean litter size for AI with fresh semen compared to natural mating is in line with the findings of Linde-Forsberg et al [12]. As we have no information about the site of the insemination in our study, it is not possible to determine the effect of site of semen depositon on litter size. However, as for the study of Linde-Forsberg et al, most AIs with frozen semen in Norway are intrauterine. This is the method used by the Norwegian School of Veterinary Science (NSVS) [3], which is one of the few places in Norway performing AIs with frozen semen. The mean litter size in a study of AI with frozen semen performed at the NSVS (5.7 $\pm$ 0.1) was not significantly different from ours. Mickelsen et al [14] found a mean litter size of 5.6 in a study of AI with fresh semen (SEM not given). This is slightly larger than ours, but Mickelsen et al mainly studied large breeds. It could be speculated that lower semen quality might be the reason for the lower mean litter size from AIs compared to natural mating. However, Thomassen et al and Mickelsen et al found no decrease in litter size due to bad quality semen, only reduced conception rate [3,14].

4.5. Season

The seasonal variation in litter size was significant in the initial unconditional analysis. Both litter size and the total number of litters were largest in the spring and smallest in the winter. Season was, however, not included in the final model due to a lack of effect on litter size when controlling for breed, age and size. However, a two-year period might not be enough for studying the effect of season on litter size due to long-term fluctuations in climatic factors. Other studies found the mean litter size to be largest in the spring [5], or that the monthly variations in mean litter size was almost negligible [8], or they did not find significant effects of season on litter size at all [2,10]. A possible explanation for more litters being born in the spring is that more bitches tend to come into estrus during the winter and spring than during autumn, which is in accordance with the reproductive period of the wolf [5]. Seasonal variations in the number of litters born might also be due to management factors such as mating procedures, housing, exercise, feeding and what is the convenient time of birth for the puppy to reach an optimal age at hunting and competition debuts [5,8,23].

5. Conclusion

Based on the linear regression model with a breed random effect, the size of the breed appears to be the strongest determinant for litter size in purebred dogs in Norway. The age of the bitch and the method of mating were also significant predictors of litter size. The significant interaction between age and size indicates that the effect of age varies with the size of the breed. The large scale of this study is unique, both regarding the number of breeds and registered information about the litters. Thus, the results should be reliable and representative for purebred dogs in Norway, and possibly also for similar populations of purebred dogs in other countries.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.theriogenology.2010.10.034.

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