Population Analysis

Spaniel (Irish Water)

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To effectively safeguard and manage the genetic diversity of breed populations, breeders need to make breeding decisions with knowledge of the unique characteristics of their breed. Following the previous population analysis carried out in 2015, this new analysis builds on what we know about each individual breed population, so that we can determine key factors that may be limiting genetic diversity within a breed, and from these develop actions within the Breed Health and Conservation Plan to help support the breed into the future.

The population analysis used complete electronic pedigree records for 222 breeds recognised by The Kennel Club to explore registration trends, as well as genetic diversity through measures such as the rates of inbreeding and effective population size. In addition, we have also added several new parameters describing the breed populations in more detail, which we hope will aid us in determining points that need to be addressed to protect the future of the breed. For example, we have explored litter size statistics, and their relationship to the coefficient of inbreeding (COI).

The data used for the analyses was extracted in August 2022, with the data for 2022 being incomplete. As such, unless otherwise stated, statistical analyses which considered year of birth focused on dogs born between period 1990 – 2021.
The results summarise the data as it is within The Kennel Club database, and as such, there are some nuances in their interpretation that will require input from the breed communities. As such, the population analysis reports will form the basis for further discussions with those communities to develop actions within the Breed Health and Conservation Plans which breeds will be provided support in developing with The Kennel Club health team.

Contents

GENETIC DIVERSITY – DEFINITIONS

Genetic diversity is crucially important for the long-term survival of any population. There are several interlinked factors that affect the rate of loss of a population's genetic diversity:

- The size of the population – numerically small breeds tend to lose genetic diversity faster
- Migration – breeding from imported dogs can restore some genetic diversity
- Mating systems – certain practices, such as the use of popular sires, drastically reduce genetic diversity
- Selection reduces genetic diversity, as dogs that possess the desired characteristics are typically more genetically similar to each other
- Inbreeding – see below

Inbreeding is the breeding of related individuals, and a **coefficient of inbreeding (COI)** calculates the probability that two copies of a dog's gene variants are identical by descent – i.e. they have been inherited from an ancestor common to both the mother and the father. A COI ranges from 0% (all known ancestors are unrelated) to 100% for a completely inbred individual (the two copies of all genes are identical by descent). In dogs, it is unlikely to find an individual with a COI equal to 100%, as high inbreeding levels usually result in fatal defects. The COI accounts for both the number of common relatives found on the sire and dam sides of the pedigree, as well as how closely related they are. The more common ancestors between parents, and the closer the relation of those common ancestors to the parents, the higher the COI will be in the offspring.

Inbreeding is not inherited – two highly inbred individuals can produce non-inbred offspring, if there are no common relatives between the dam and the sire (e.g. breeding a highly inbred Labrador and Poodle).

Inbreeding depression

Elevated levels of inbreeding result in **inbreeding depression** – a widespread reduction in fertility (e.g. smaller litter sizes), health and overall survival, caused by an accumulation of harmful recessive mutations. If not counteracted, inbreeding depression can lead to the complete extinction of a population.

Rate of inbreeding

The average COI of a breed population depends on a number of factors. Populations can arrive at the same average COI through different routes. For example,
one population could have an average COI of 10% accrued over many generations of very gradual inbreeding on distant breed founders only, whereas another breed could have the same average COI of 10% resulting from a few generations of strong inbreeding through the mating of closely related individuals. Even though the average COI of those two populations is the same, the inbreeding depression risks are considerably higher in the latter population. Sustainable management of genetic diversity is thus related to the **rate of inbreeding**, i.e. how quickly inbreeding is accumulating over the generations. A population is deemed as sustainable if the rate of inbreeding per generation does not exceed 1%.

Effective population size

The rate of inbreeding is sometimes presented as the **effective population size (*Ne*)**. *Ne* describes the size of a theoretical population, which under completely random mating would lose genetic diversity at the same rate as the population in question. Without any selection, and under random mating, loss of diversity is directly related to the population size (the smaller the population, the more rapid the loss of genetic diversity). Such theoretical populations have been modelled to need at least 50 individuals for the inbreeding rate not to exceed 1%. Therefore, populations with Ne below 50 are at critical risk of suffering from inbreeding depression. Populations with Ne between 50 and 100 are thought to be endangered (some inbreeding depression signs may be present but the population could survive). Populations with Ne larger than 100 (inbreeding rate below 0.5%) are thought to have sustainable levels of genetic diversity.

Limitations of the effective population size calculation

The calculation used to derive the Ne assumes that the pedigree information provided is complete. Therefore, where pedigree information is limited (e.g. for imported dogs), the last known ancestors of those dogs are treated as genetically distinct, similarly to breed founders. If the proportion of such dogs used in breeding has increased over the recent years, the rate of inbreeding for the population may appear to be negative. Due to mathematical constraints, it is impossible to calculate Ne in such situations.

Considerations for imported dogs

Introducing imported dogs to a national population is generally thought to increase diversity. This is because populations that are separated geographically tend to diverge genetically. However, the pedigree information available for imported dogs is of limited depth. As such, relationships between imported dogs and the national population may be underestimated, if common ancestors appear in generations which are not represented in the limited-depth import pedigree. For example, based on a 3-generation imported pedigree a dog may appear completely unrelated to the national population, but if his ancestor in the 4th generation (not included in the import pedigree) was a UK-born popular sire, then the relationship of this dog to the UK dogs may be severely underestimated.

<u>Average genetic relationships (AGR)</u>

Minimising inbreeding for a single mating reduces the risks of inbreeding depression in a specific litter, but it doesn't necessarily help safeguard the genetic diversity in the breed. Using COI does not provide the breeder with an assessment of the relationship of the dog to the rest of the population. For example, if an unrelated sire is introduced into a breeding pool, the COI of his offspring will be 0%. However, if he is used extensively, his half-sibling offspring will form a considerable proportion of the next generation and so it soon becomes difficult to find mates that are not a descendant of his. An average genetic relationship (AGR) estimates how valuable a dog is to a population in the context of genetic diversity. Dogs that have a low average relationship to the breed are the most valuable, representing unique genetic make-up. When using AGR in making breeding decisions, breeders should choose dogs with lower AGR. Over time, as dogs are used in breeding, the AGR of individual dogs will change to reflect the changes in the population.

To put AGR figures into perspective, a dog with an AGR equal to 12.5% is on average as related to a randomly selected dog from the breed as a first cousin, whereas the relationship between a dog with an AGR equal to 1.5%, and a random dog in the breed, can be compared to a relationship between 4th cousins.

Popular sires

Popular sires contribute disproportionally to the next generation and are the main cause of the loss of genetic diversity in pedigree dog breeds. Presence of popular sires is dangerous for several reasons. First, the larger the number of offspring any dog produces, the higher the chances that he will pass on harmful mutations that are unique to him to his offspring, and the wider the spread of those mutations in the breed population. Further, the more offspring the sire produces, the fewer generations it will take before this dog will appear in the pedigree of all dogs in the breed, and so it will be impossible to avoid inbreeding with the sire as a common ancestor.

While certain dogs may be very attractive breeding candidates from the point of view of known health conditions, having passed all recommended health testing with good results, it is important to remember that every dog carries novel and unknown mutations. Given the proven and dangerous consequences of using popular sires, breeding from any dog extensively should be avoided. Further, replacing a popular sire with his son is of limited value, as the son will have inherited 50% of his genes from the sire. It is worth noting that whatever the size of the breed, the use of popular sires will have a drastic impact on the genetic diversity of that breed, and all breeds should be aware of this.

Comparison to genomic estimates of inbreeding

The results of the population analyses are based on pedigree records only and are likely to differ from estimates based on DNA analysis available for individual dogs. This is because pedigree- and DNA-based estimates of inbreeding are derived using different methods and have different meaning. In pedigree-based estimation, we use pedigree to define a so-called "base population" and we assume that all gene copies among base individuals are unique. In contrast, genomic methods compare the biochemical properties of gene copies, irrespective of their origin. For example, using DNA-based methods, all Weimaraner dogs will be commonly treated as inbred for at least two genes which determine their characteristic colour. In contrast, pedigree-based methods would prioritise more recent inbreeding events, ignoring genetic variants which were common to all breed founders. As such, pedigree-based and DNA-based estimates of inbreeding and diversity are interpreted differently.

KEY FINDINGS FOR THE SPANIEL (IRISH WATER)

- Around three quarters of the breed pedigree held in the KC's database consisted of dogs born in the UK and registered under the Litter Registration
- The breed population suffered a significant decline in size between 1990 and 2021
- The percentage of dogs used in breeding was very low, which poses a considerable risk to genetic diversity
- The number of imported dogs has been variable over the years, but the percentage of litters produced from imported parents increased
- Large percentage of litters were produced by at least one parent with a stud book number
- Average litter size was 6, with a significant but modest increase over time
- Average COI for dogs born in 2021 was 7.9%
- Based on the rate of inbreeding calculated for dogs born between 1990 and 2021, the effective population size was estimated at 360 which is thought to be sustainable
- The average relationship among dogs assumed to be alive is 15.0% - i.e. average Irish Water Spaniel in the current population is more related to any other dog in the same cohort than first cousins, but not as closely as half-siblings
- Across time, there was some evidence of popular sire use
- Sires with stud book numbers and imported sires had significantly higher numbers of litters

GENERAL PEDIGREE STATISTICS

As of September 2022, the Irish Water Spaniel pedigree included 7,344 dogs, of which 5,767 were born and first registered in the United Kingdom (Breed Register, Litter Registrations). Table 1 shows the number of dogs with particular registration types.

Table 1 Number and frequency of dogs by registration type[1]

Registration Type	No. of dogs	Frequency
Litter Registration	5,767	78.5%
Activity Registration	3	0.0%
Importations	88	1.2%
Authority To Compete (ATC)	50	0.7%
Other	1,436	19.6%

IMPORTS

In total, there were 88 (28 male and 60 female) Irish Water Spaniels imported from 12 countries. The largest number of dogs (49.4% of all imported dogs of the breed) were imported from Ireland. Table 2 shows the number of imports per country. Of the imported dogs, 71.4% males and 41.7% females were used in breeding. There is no significant trend in the number of imports over year of birth calculated over the period 1993 - 2021, as shown in Figure 1. This is likely due to the relatively small number of imports per year and an initial increase in the numbers up to 7 imported dogs born in 2001, which was followed by a steep decline.

Table 2 Number and frequency of imported dogs by country. 9 import records were missing country of origin

Country	No. of dogs	Frequency
Ireland	39	49.4%
USA	15	19.0%
Netherlands	5	6.3%
Finland	5	6.3%
Republic of Ireland	4	5.1%
Other countries	11	13.9%

[1] Registration types were determined as follows: Litter Registrations were calculated as a sum of Litter and Litter Single Dog Registrations within Breed Register. Activity Registration was calculated as a sum of all registrations within Activity Register (e.g. Activity Registration and Importations). Importations were counted as number of dogs with registration type Importation, within the Breed Register (i.e. did not include Activity Register Importations). Authority to Compete numbers were counted as number of dogs with this title, and outside of Breed Register. Other group included primarily ancestors of imported dogs.

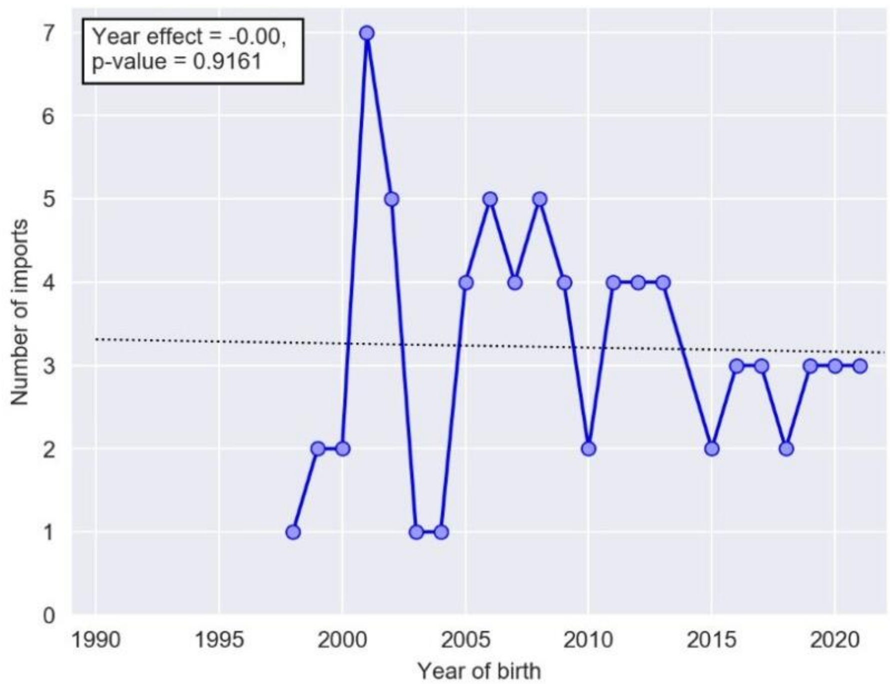

Figure 1 Trends in the number of imports by year of birth

CHAMPIONS[2]

The number of Irish Water Spaniels with a stud book number across all registration types is 948 (12.9% of total), of which 193 (2.6% of total dogs of the breed) have champion titles, all being Show/Conformation champions.

DEMOGRAPHICS[3]

The number of Irish Water Spaniels born in the UK and registered in Breed Registry by year of birth between January 1990 and December 2021 are shown in Figure 2. The trend of registrations over year of birth (1990 - 2021) was -1.5 per year (with a 95% confidence interval[4] of -2.3 to -0.6), reflecting the statistically significant decrease in registration numbers during this time, from 150 Irish Water Spaniels registered with The Kennel Club in 1990 to 97 registered in 2021. This breed is currently on The Kennel Club's vulnerable native breeds list (breeds with fewer than 300 registrations a year).

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[2] There are several types of awards that dogs can achieve in a number of activities, such as conformation shows or field trials. The most commonly known awards are champion titles and stud book numbers. To win a champion title, a dog needs to win three Challenge Certificates (CC) at championship shows where CCs are on offer, and under three different judges. A stud book number is achieved when either a dog wins a stud book qualifying award at a championship show, or obtains a Junior Warrant. Thus, there are more dogs with stud book numbers than champion dogs. Statistics pertaining to champion dogs, and dogs with stud book number, indicate the proportion of dogs actively engaged in activities governed by The Kennel Club.

[3] The trends in the data are represented in form of regression coefficients calculated via simple linear regression. In some instances, other types of regression and/or transformations of the data would provide a better statistical fit. The trends provided are meant to be used as broad guidelines only.

[4] 95% confidence intervals (C.I.s) indicate that we are 95% confident that the true estimate of a parameter lies between the lower and upper number stated.

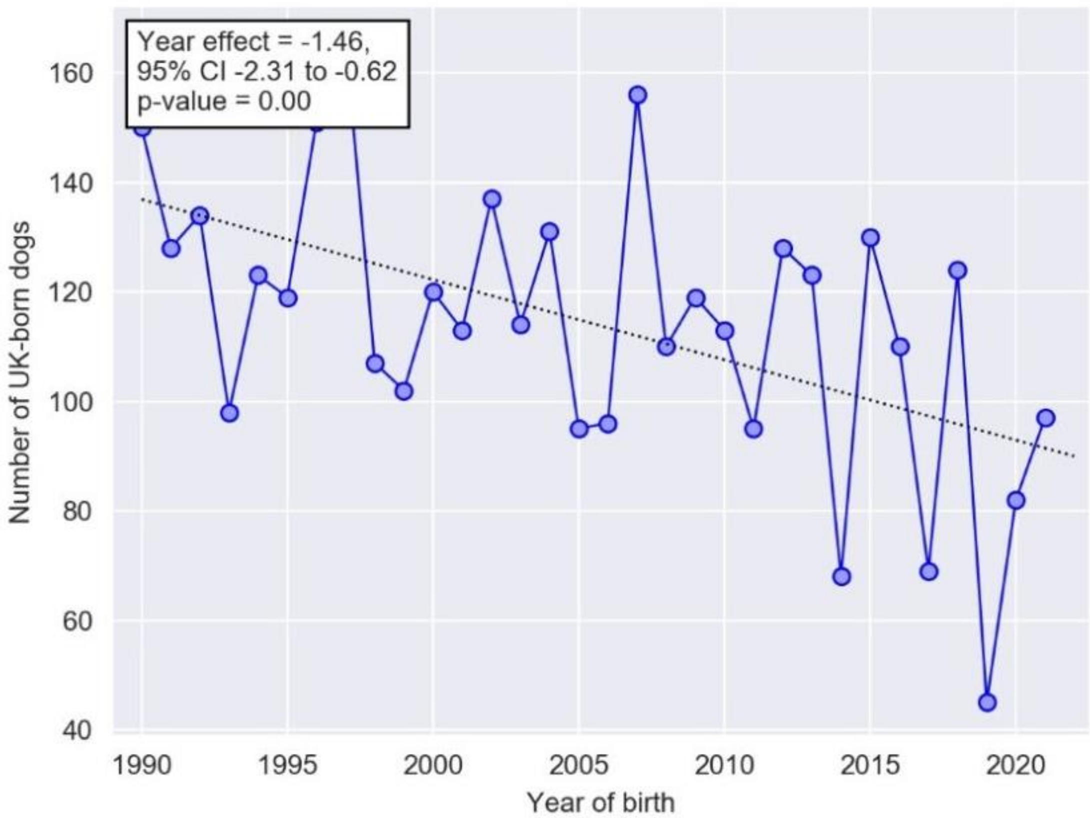

Figure 2 Trends in the number of registrations per year of birth

Overall, 12.3% of all national dogs born between 2005 and 2015 (inclusive) have been used in breeding, and about 11.1% of national male dogs born in 2015 have been used in breeding to date. This indicates moderate selection intensity – and consequentially, a reduction in the genetic diversity. It should be noted that this percentage may be affected by the trends in breed popularity – where registration numbers drop, then a lower percentage of dogs born in the preceding years will be used in breeding.

The proportion of litters[5] where at least one parent has a stud book number (referred to henceforth as “Purpose-bred”) has fluctuated over time, as shown in Figure 3. In 2021, 33.3% of litters had at least one parent with a stud book number. On the other hand, litters where at least one parent is an imported dog (referred to henceforth as “ImportBred”) are on the increase, as shown in Figure 3, from 3.8% in 1990 to 20.0% in 2021.

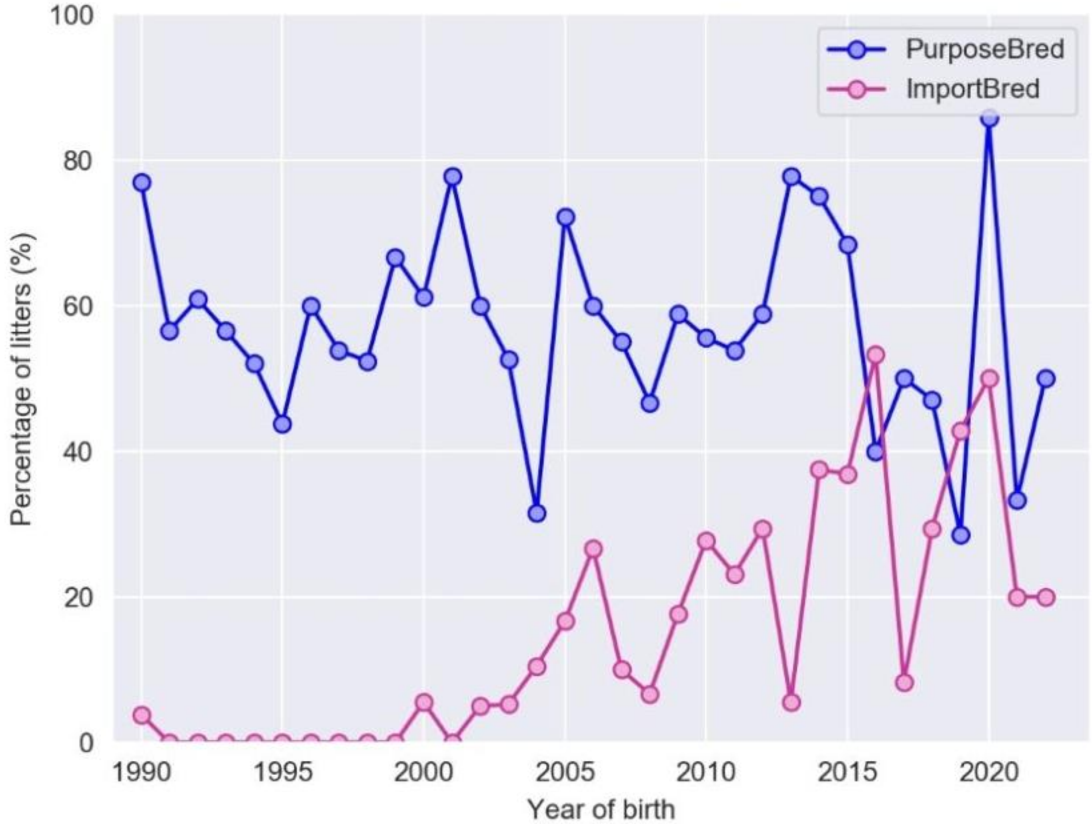

Figure 3 Percentage of litters where at least one parent had a stud book number ("PurposeBred") or was an import ("ImportBred")

LITTER SIZE[6]

On average, Irish Water Spaniels produce 6 puppies in each litter (range from 1 to 14, median 7, standard deviation 2.9), and the yearly average litter size has significantly increased over time, from 5.8 in 1990 to 6.5 in 2021, as shown in Figure 4. The distribution of litter sizes is shown in Figure 5.

[5] Litter identifiers have been assigned to dogs in Breed Register, with registration type “Litter Registration”, (i.e. dogs born and first registered in the UK) and where both parents and date of birth are known.

[6] The statistics for litter size were calculated from available data – it should be noted that these data could be biased if not all puppies born in a litter are registered with The Kennel Club by the breeder. Further, litter size statistics do not account for early mortality (stillborn and puppies which die soon after birth will not be registered).

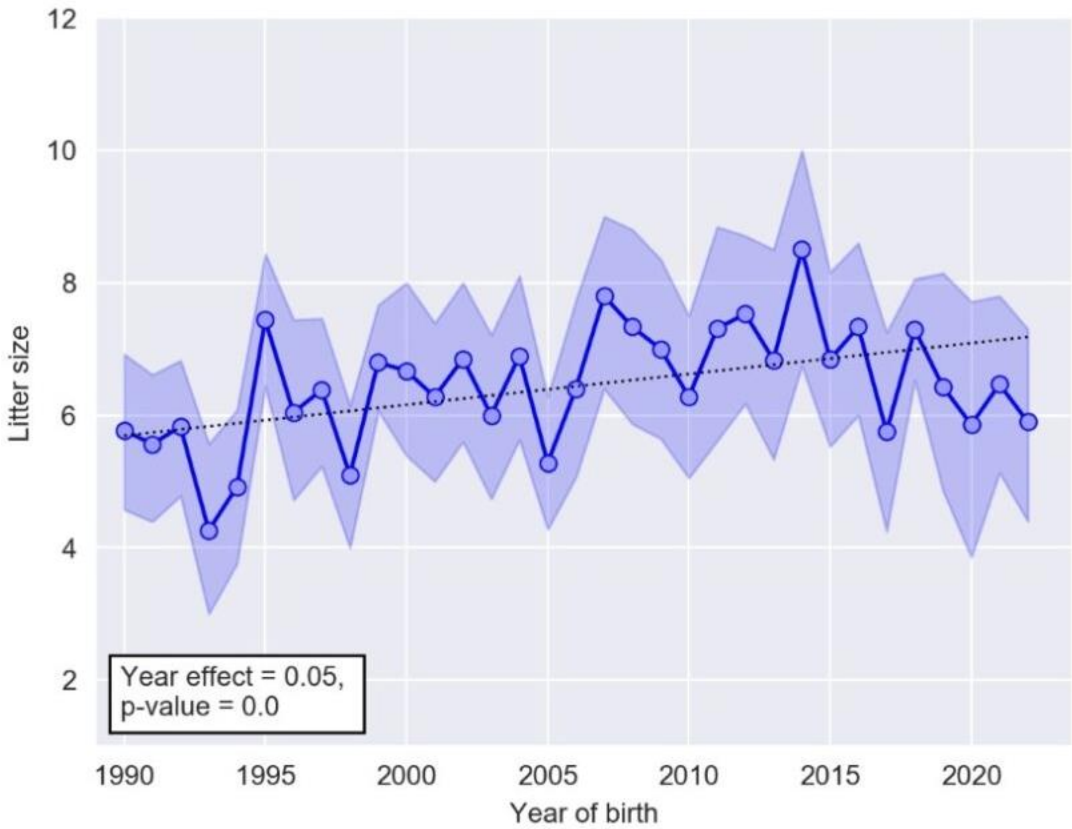

Figure 4 Trend in litter size over year of birth

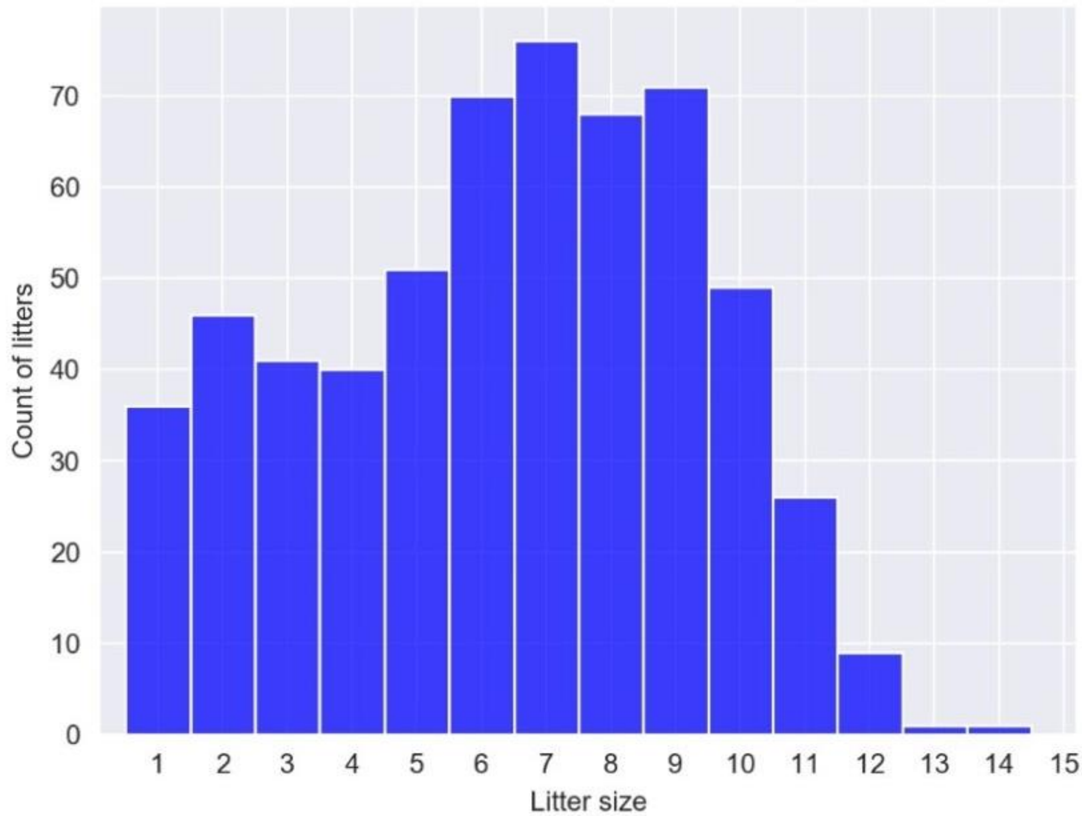

Figure 5 Distribution of litter size

GENETIC DIVERSITY IN IRISH WATER SPANIELS

The rate of inbreeding observed in the complete electronic pedigree of Irish Water Spaniels born between 1990 and 2021 increased between 1990 and 2005, but has decreased since (although with considerable fluctuation). The resulting effective population size is estimated at 360.1, which is within the level thought to be sustainable. This means that given the electronically held pedigree data, there appears to be a suitable balance between selective breeding and inbreeding in the UK population of Irish Water Spaniels (Food & Agriculture Organisation of the United Nations, "Breeding strategies for sustainable management of animal genetic resources", 2010).

The current annual breed average inbreeding coefficient (COI), i.e. the average inbreeding coefficient for dogs in the Breed Register, Litter Registrations born in 2021, is 7.9%.

The annual mean observed COI, mean observed COI after removing dogs with COI=0% (i.e. removing dogs with limited pedigree depth, primarily imported dogs) and mean expected COI (calculated as a result of random mating of dogs born 4 years earlier) over the period 1990-2021 are shown in Figure 6.

Departure between the observed and expected mean COI would indicate presence of selection. If the observed COI was higher than the expected COI this would indicate a preference for mating of genetically more similar dogs, through selection for particular traits which are more common among these dogs, or through breeding within some subpopulations (e.g. kennel preferences, geographic separation, within working/show lines).

A reduction in the rates of inbreeding can be attained primarily in two ways – through the use of imported dogs which introduce new genetic diversity, or through change of breeding practices, particularly breeding animals which are less related to each other. In Irish Water Spaniel, it appears that the reduction in the rates of inbreeding observed since 2005 is mostly attributable to the change in breeding practices, as the difference between observed inbreeding with and without dogs with COI=0% (i.e. without imported dogs and their close descendants) is small. If the reduction in the rate of inbreeding was caused by the extensive use of imported dogs, we would expect the observed inbreeding without dogs with COI=0% to be considerably higher than the overall observed inbreeding.

It should be further noted that both popular sires and geographic bottlenecks can decrease the genetic diversity in a breed, without necessarily having a detectable effect on the mean COI across the complete pedigree.

For full interpretation see Lewis et al, 2015
https://cgejournal.biomedcentral.com/articles/10.1186/s40575- 015-0027-4.

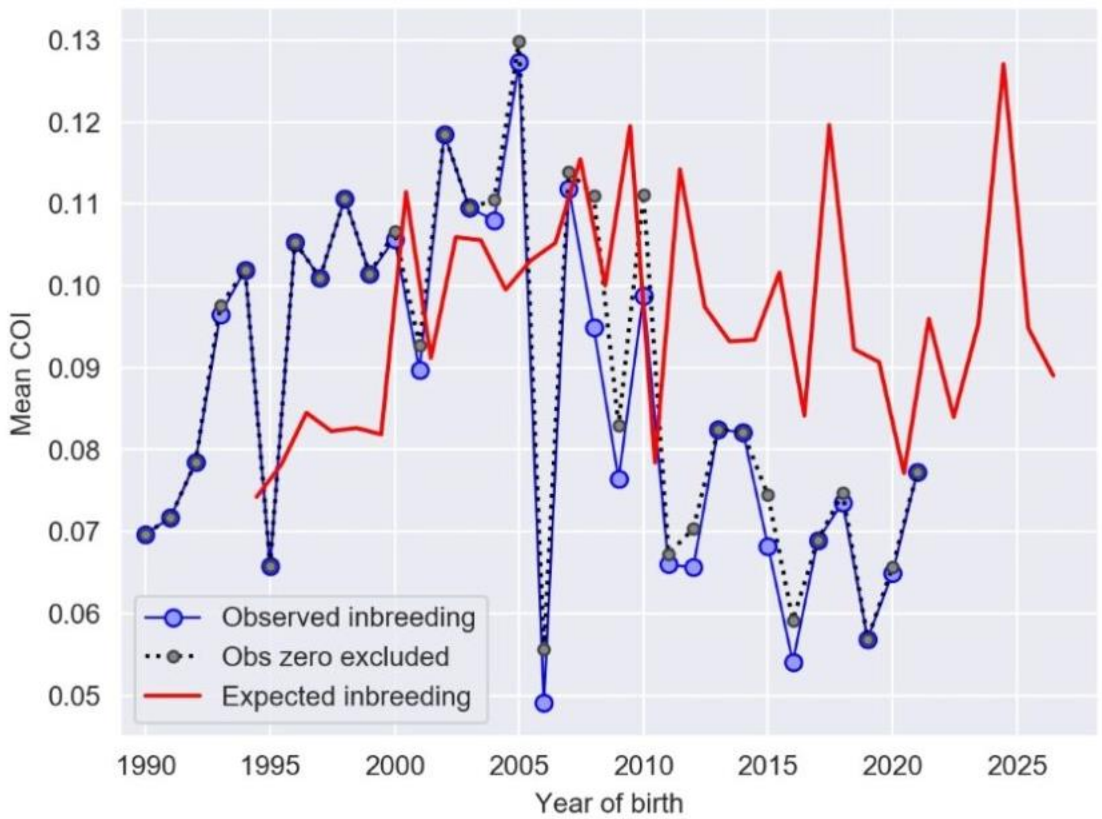

Figure 6 Annual mean observed and expected inbreeding coefficients

COI AND LITTER SIZE

Based on the available data, no significant association between litter size and coefficient of inbreeding (COI) was found. Figure 7 illustrates the relationship between litter size and COI in form of a boxplot[7] with litters divided into COI categories of 0 – 5%, 6 – 15%, 16 – 25%, 26 – 35% and >35%. Litters where the COI exceeds 25% likely have been produced through rapid and close inbreeding.

While singleton litters were found in all categories, large litters (larger than 12 puppies, with 12 calculated as mean litter size + 2*standard deviation) were produced primarily in the 6 – 15% COI category.

[7] A boxplot displays the distribution of the data within certain categories. The box marks the interquartile range (25th to 75th percentile), midline indicates median, stars indicate mean, whiskers indicate minimum and maximum calculated in reference to interquartile range, and diamonds indicate outliers – real values which reach beyond the expected minimum or maximum values.

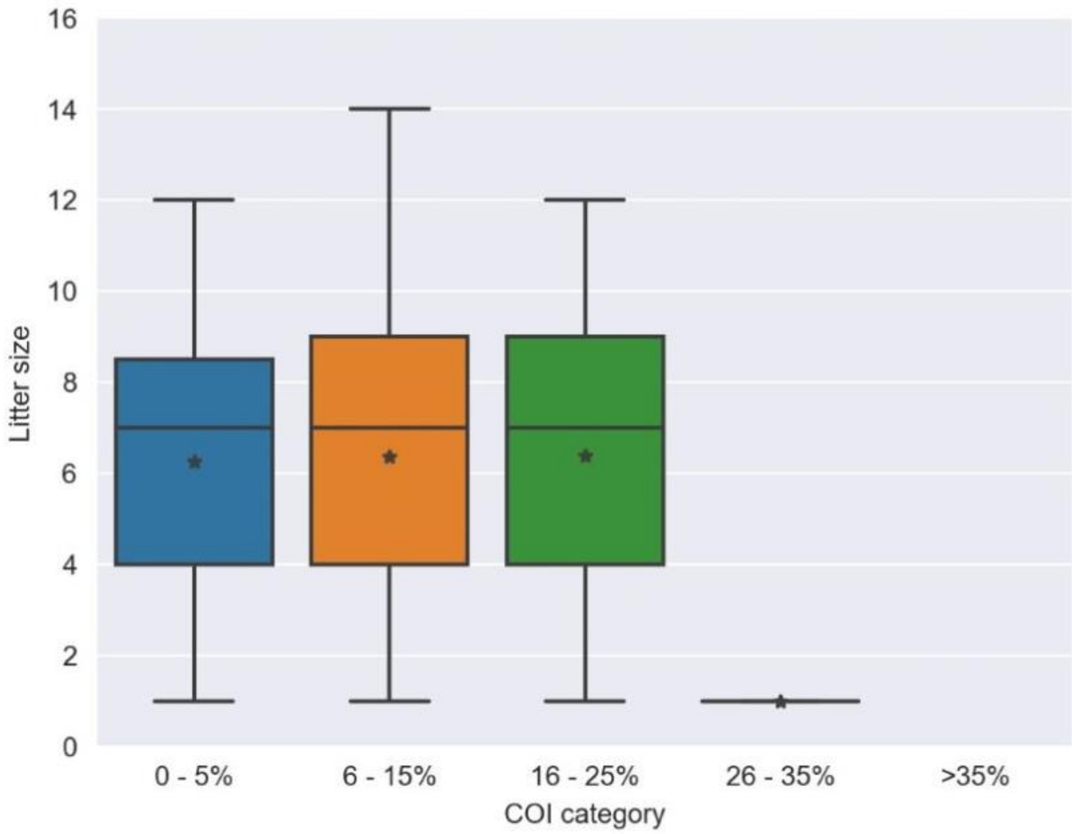

Figure 7 Boxplot of litter size distribution by category of COI. The number of litters in the particular categories were: 0-5% = 147, 6-15% = 358, 16-25% = 79, 26-35% = 1, >35% = 0

COI IN PURPOSE-BRED AND PET LITTERS

The coefficient of inbreeding is generally higher in Purpose-bred litters (i.e. litters where at least one parent has a stud book number) than in Pet[8] litters (i.e. litters where neither parent has a stud book number), as shown in Figure 8. It should be noted that there is a large variability in both Purpose-bred and Pet litters, therefore the differences are not likely to be statistically significant.

[8] Pet litters in this context are used only to distinguish litters where neither parent has been proven to partake in activities such as e.g. showing.

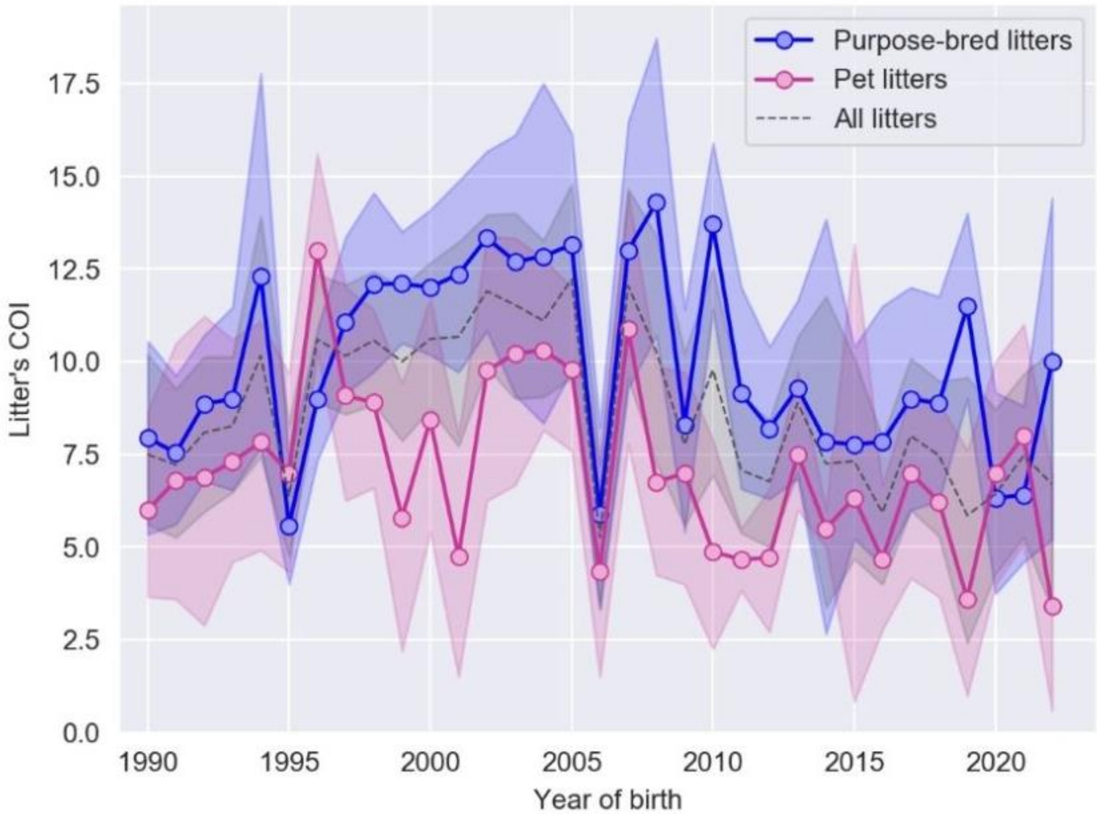

Figure 8 Annual mean inbreeding coefficients in Purpose-bred litters (where at least one parent has a stud book number), and Pet litters (where neither parent has a stud book number)

RELATIONSHIPS BETWEEN DOGS AVAILABLE FOR BREEDING

Mean relationship estimates are calculated for dogs thought to represent a current breeding population, i.e. bitches in Breed Register and born in the last 8 years (i.e. born since 2014) and dogs in Breed Register and born in the last 10 years (i.e. born since 2012), including imported dogs. The mean relationship is calculated from the average relationship of each dog to the rest of the breeding population. These estimates can be compared to relationship estimates between relatives. For example, the relationship between parent and offspring, or between full siblings is 50%, the relationship between half-siblings is 25% and the relationship between first cousins is 12.5%. The mean relationship estimate for the current breeding population in Irish Water Spaniels is 15.0% (maximum 23.6%, median 15.8%, standard deviation 4.9%). This means that an average Irish Water Spaniel in the current population is more related to any other dog in the same cohort than first cousins, but not as closely as half-siblings.

Figure 9 shows the distribution of the average relationship coefficients between dogs in the current breeding population.

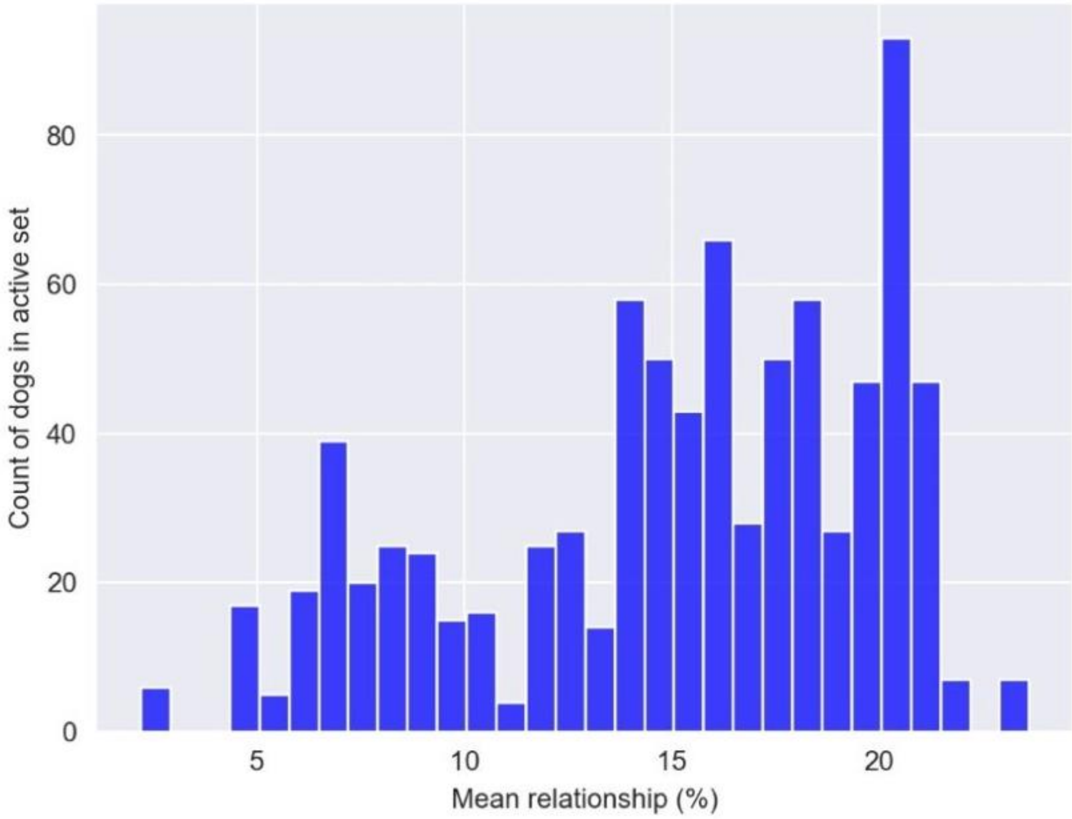

Figure 9 Histogram of the average relationships between dogs in the current breeding population (bitches born in last 8 years and dogs born in last 10 years, total of 837 dogs)

SIRE AND DAM USAGE

Below is a histogram ('tally' distribution) of the proportion of progeny per sire and dam over 5-year blocks (Figure 10).

A longer 'tail' on the distribution of progeny per sire is indicative of 'popular sires' (few sires with a very large number of offspring), known to be a major contributor to a high rate of inbreeding. It appears that the extensive use of popular dogs as sires has eased over time since 1990's (the 'tail' of the blue distribution shortening). The highest producing sire in the 2015 – 2019 block produced about 7.4% of the puppies born in that period.

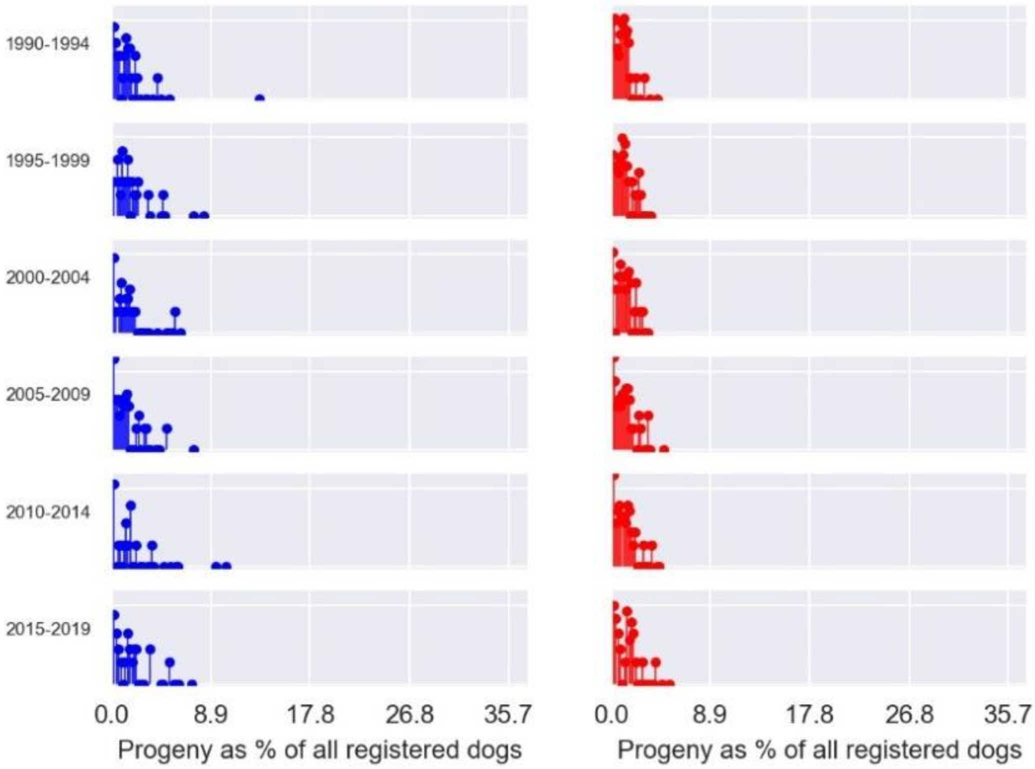

Figure 10 Distribution of progeny per sire (blue) and per dam (red) over 5-year blocks. Vertical axis is a logarithmic scale

Across litters in Litter Registration, a majority of sires produced between 1 and 5 litters (90.8% of the total of 228 sires). However, there were 21 (9.2%) sires which produced more than 5 litters, as shown in Figure 11. There was one (0.4%) sire which produced more than 15 litters.

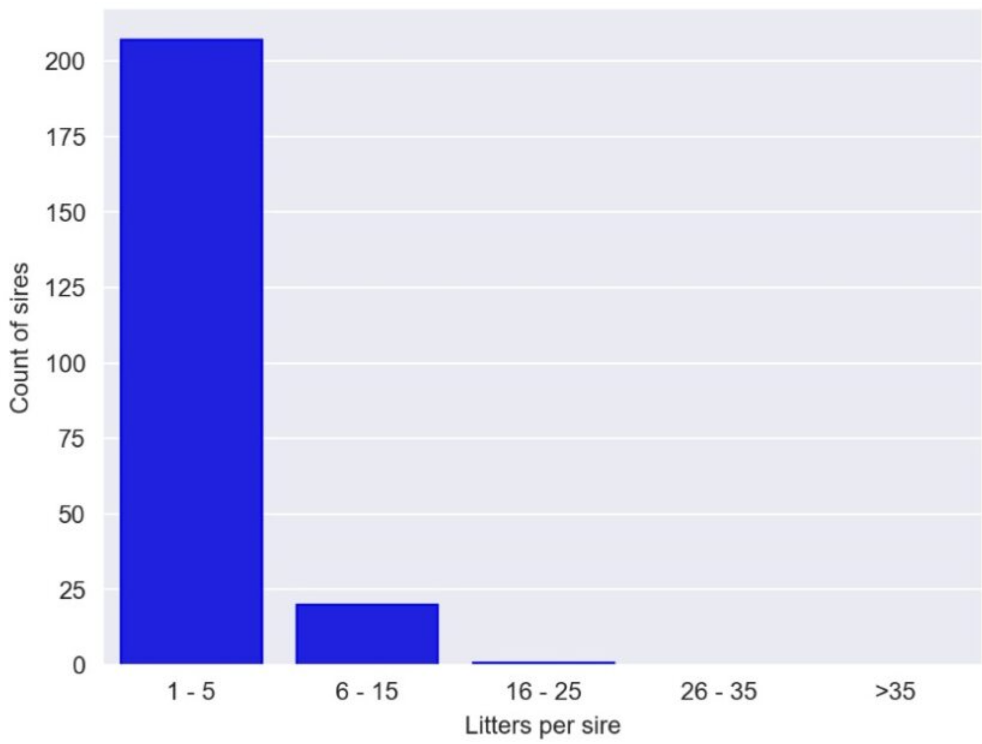

Figure 11 Histogram of sires in categories of number of litters produced

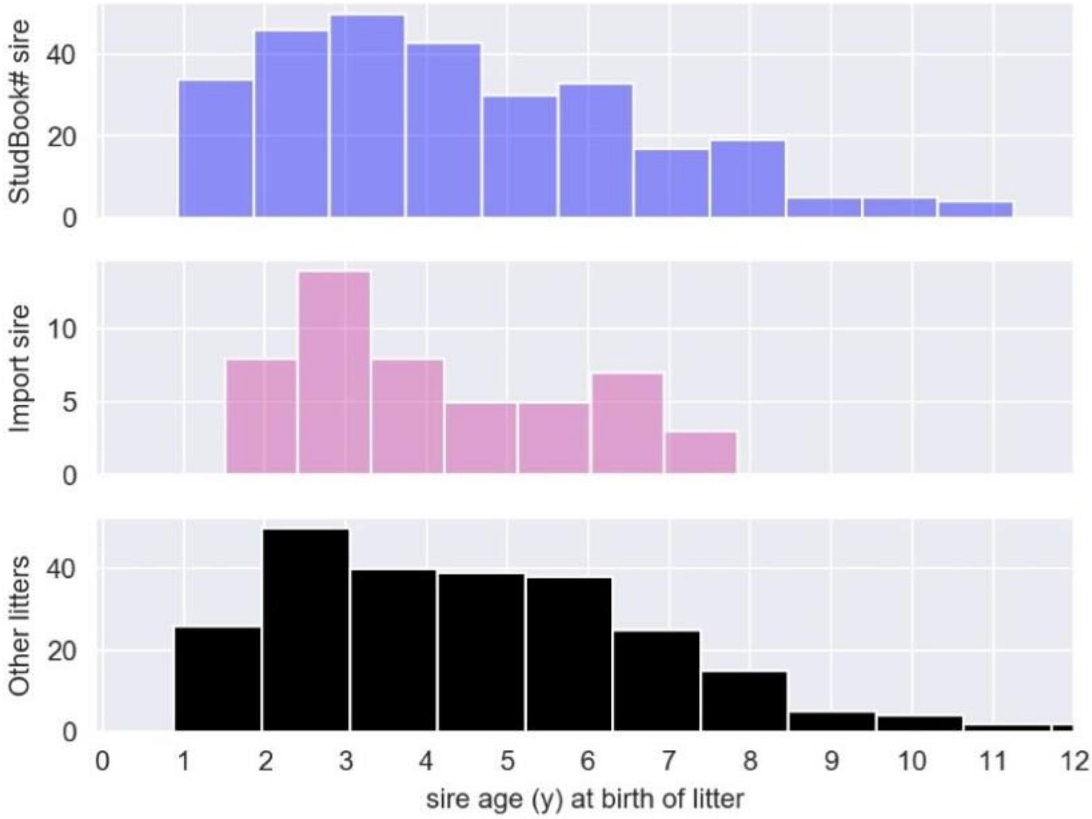

Figure 12 Age of sires at the birth of litter, divided into sires with stud book numbers (top plot in blue), imported sires (middle plot in pink) and remaining sires (bottom plot in black)

The statistics for sire's age at birth of litter were calculated for 557 litters, after removing 28 litters where the sire's age was younger than 6 months or older than 15 years, and the dam's age was younger than 8 months or older than 12 years. Following the peaks of productivity at 2-3 years for sires with stud book numbers, 2-3 years for imported sires, and 1-3 years for national sires without stud book numbers, the number of litters produced by sires generally decreases in older ages, as shown in Figure 12. However, both groups of sires with stud book numbers and national sires without stud book numbers include litters produced by sires older than 10 years and younger than 14 months of age.

Comparison of the number of litters produced by sires in the three categories shows that:

a) There is a significant difference (p=0.000) between dogs with and without stud book numbers. Sires with stud book numbers produced on average 3 litters, compared to 2 litters for sires without stud book numbers.

b) There is no significant difference (p>0.05) between imported and national sires, with the average number of litters being 3 and 2 respectively.

c) There is no significant difference (p>0.05) between imported sires with and without stud book numbers, with the average number of litters being 6 and 2 respectively.

d) There is no significant difference ($p>0.05$) between imported and national dogs with stud book numbers, with the average number of litters being 6 and 3 respectively.

Table 3 presents the summary statistics for the number of litters produced by sires in particular categories.

Table 3 Summary statistics for numbers of litters produced by sires in different categories

Sire category	No. of sires	Mean no. of litters per sire	Standard deviation	Max no. of litters
All sires	228	2.4	2.3	18
Sires with stud book no.	89	3.2	3.0	18
Sires without stud book no.	139	1.9	1.6	12
Imported sires	15	3.3	2.9	10
National sires	213	2.4	2.3	18
National sires with stud book no.	85	3.1	2.9	18
Imported sires with stud book no.	4	6.3	3.9	10
Imported sires without stud book no.	11	2.3	1.6	5