

Population Analysis

Collie (Rough)



Royal Kennel Club

To safeguard and manage genetic diversity of each breed, breeders need to make informed decisions based on the specific characteristics of their breed. Since the previous population analysis in 2015, we have expanded our understanding of each breed. This updated analysis summarised in this document builds on our knowledge of the breed populations, so that we can determine key factors that may be limiting genetic diversity within breeds. Alongside the parameters such as effective population size, or proportion of progeny per sire, we have also introduced several new parameters that describe breed populations in more depth. These additions are intended to highlight areas that may require attention to help protect the long-term health of each breed. For example, we have included an exploration of litter size patterns and how they related to coefficients of inbreeding.

The data for these analyses was extracted in August 2022, and the 2022 records were not yet complete at that time. Therefore, unless otherwise stated, analyses based on year of birth focus on dogs born between 1990 and 2021.

Dr Joanna J. Ilska



Royal Kennel Club Geneticist

London

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Important Note

This report is based only on dogs registered with the Royal Kennel Club (RKC). It does not include unregistered dogs. If many breeding dogs are imported from outside the UK or if there is a larger, unregistered population, the genetic results shown here may not fully reflect the true situation in the breed. For help understanding what these findings mean for your breed, please speak to your Breed Health Co-ordinator.

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GENETIC DIVERSITY DEFINITIONS

Genetic diversity is essential for the long-term health and survival of any breed. A population with a broad range of genetic variation is better able to stay healthy, avoid inherited diseases, and adapt to future challenges. Several factors influence how quickly a breed may lose genetic diversity:

- **Population size:** small populations lose diversity more quickly.
- **Migration:** bringing in imported dogs can add new genetic variation.
- **Breeding practices:** using certain mating strategies, such as repeatedly using the same sire (popular sire effect), may drastically reduce genetic diversity.
- **Selection:** Strong selection for particular traits narrows the gene pool, because dogs with similar traits are often genetically similar.
- **Inbreeding:** Explained below.

Inbreeding

Inbreeding means mating dogs that are related. The **coefficient of inbreeding (COI)** estimates the chance that a dog has inherited the same copy of a gene from both parents because they share common ancestors. A COI ranges from **0%** (no shared ancestors found in the pedigree), to **100%** (the dog inherited identical copies of every gene from both parents - something not seen in dogs because such high inbreeding is usually fatal). The COI depends on how many ancestors the parents share, and how closely related those ancestors are. More shared or closer ancestors lead to a higher COI in the puppies.

Important: Inbreeding itself is *not* inherited. Two inbred dogs can produce a non-inbred puppy if they share no common ancestors.

Inbreeding Depression

With high levels of inbreeding dogs are more likely to inherit the same harmful variant from both parents, allowing it to have an effect. This can lead to inbreeding depression - a reduction in fertility, health, and overall survival. If left unmanaged, inbreeding depression can threaten the long-term future of the breed.

Rate of Inbreeding

Two breeds can have the same average COI but reach it in very different ways. For example:

- One breed may reach a COI of 10% very slowly, over many generations, because breeders avoid mating dogs with close relatives.
- Another breed may reach the same 10% COI much more quickly, within only a few generations, if close matings are used.



Although the average COI appears the same, the risks are much higher when inbreeding increases rapidly.

A breed is considered to have sustainable diversity if its inbreeding increases by no more than 1% per generation.

Effective Population Size (N_e)

The effective population size (N_e) describes how quickly a breed is losing genetic diversity. It represents the size of a “theoretical ideal population,” breeding at random, that would lose diversity at the same rate as the real breed population.

N_e is usually smaller than the actual number of dogs because not all individuals contribute equally. N_e is influenced by:

- How many dogs are used for breeding, and how closely they are
- How many breeding puppies each dog produces
- How evenly different dogs contribute to future generations
- Skewed sex ratios (e.g. many more breeding females than males)
- Past bottlenecks - even one small generation can have a lasting impact
- Selection - strong selection for specific traits reduces N_e because genetically similar dogs are repeatedly chosen for breeding

As a guide:

- $N_e < 50$: critical risk of inbreeding depression
- $N_e 50-100$: endangered and requires careful management
- $N_e > 100$: more sustainable, with slower loss of diversity

Limitations of N_e Calculations

N_e calculations rely on complete pedigree information. Imported dogs often have short pedigrees, meaning their relationships to the UK population may be underestimated. If a breed population includes many imported dogs, the breed may appear to have decreasing or even negative inbreeding rates. In these cases, N_e cannot be estimated reliably.

Imported Dogs

Imported dogs can increase genetic diversity, but this depends on how long the overseas population has been separated from the UK population. If the two populations have been breeding independently for a substantial period, they are more likely to have accumulated different genetic variants. However, if they have shared ancestors more recently, the added diversity may be limited.

Short pedigrees of imported dogs can also hide shared ancestry. A dog with a 3-generation pedigree may appear unrelated to UK lines, but a shared ancestor in the



4th or 5th generation would not be visible. This can lead to underestimates of how closely the imported dog is actually related to the UK population.

Average Genetic Relationship (AGR)

While COI looks at the parents of a specific litter, AGR measures how closely a dog is related to the entire breed. Dogs with a low AGR carry rarer genetic material and are especially valuable for maintaining diversity.

AGR can be interpreted like family relationships:

- AGR ~12.5%: similar to a first-cousin relationship
- AGR ~1.5%: similar to distant fourth cousins

AGR changes over time as breeding patterns shift.

Popular Sires

A popular sire is generally understood to be a male dog used far more often than others. Over-use of a single sire is one of the greatest threats to a breed's genetic diversity, because it allows his genes, along with any harmful recessive variants he carries, to spread rapidly throughout the population. Within only a few generations, such a sire may appear in the pedigree of nearly every dog in the breed, making inbreeding increasingly difficult to avoid. Replacing an over-used sire with his son does not solve the problem, as the son inherits half of the sire's genes.

Despite its importance, there is no simple, universal definition of a "popular sire." Different measures can be used to assess how influential a sire is, but each has limitations. Ranking sires by the number of puppies may give different results from ranking by number of litters, and thresholds based on puppy counts can unintentionally favour sires that have smaller litters. Measures such as the average genetic relationship (AGR) may offer a deeper understanding of long-term impact, but shallow pedigrees, especially common in imported dogs, can underestimate true relatedness. In this report, we take a practical approach. We identify potential popular sires by looking for a longer 'tail' in the distribution of progeny per sire. Specifically, we examine histograms showing the proportion of offspring produced by each sire (and each dam), calculated over rolling 5-year blocks. A pronounced tail, where a small number of sires contribute a disproportionately large share of puppies, indicates a risk of popular sire effects.

Regardless of the metric used, the principle remains the same: to protect long-term genetic diversity, no individual dog should dominate the gene pool, and breeding should be spread across as many dogs as possible.

Comparing Pedigree and DNA Estimates of Inbreeding

The analyses in this report use pedigree data, which differ from genomic (DNA-based) estimates:



- Pedigree-based methods track ancestry and assume all founders (dogs with unknown parents) were unrelated.
- DNA methods measure actual genetic variants, regardless of pedigree.

For example, using DNA-based methods, all Weimaraners 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.

Because they measure different things, pedigree-based and DNA-based estimates are not expected to match and should be interpreted separately.



KEY FINDINGS FOR COLLIE (ROUGH)

- The majority 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 males used in breeding was low, which poses a risk to genetic diversity
- The number of imported dogs significantly increased over time, with concurrent increase in the percentage of litters produced from imported parents over time
- Average litter size was 5, with a significant but modest increase over time
- Average COI for dogs born in 2021 was 11.3%
- Due to apparently negative rate of inbreeding, it was impossible to calculate effective population size for the breed
- There was a significant and negative association between COI and litter size – litters with higher COI tend to be smaller
- The average relationship among dogs assumed to be alive is 16% - i.e. average Rough Collie 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 strong evidence of popular sire use
- Sires with stud book numbers had significantly higher numbers of litters

GENERAL PEDIGREE STATISTICS

As of October 2022, the Rough Collie pedigree included 120,866 dogs, of which 111,201 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 type¹

Registration Type	No. of dogs	Frequency
Litter Registration	111,201	92.0%
Activity Registration	82	0.1%
Importations	632	0.5%
Authority To Compete (ATC)	396	0.3%
Other	8,555	7.1%

IMPORTS

In total, there were 632 (235 male and 397 female) Rough Collies imported from 35 countries. The largest number of dogs (24.7% of all imported dogs of the breed) were imported from Ireland. Table 2 shows the number of imports per country. Of the imported dogs, 48.1% males and 49.8% females were used in breeding. There is a significant and increasing trend in the number of imports over year of birth calculated over the period 1990 - 2021, with the number of imported dogs increasing by 1.4 each year, as shown in Figure 1. However, the number of imports has declined since the peak of nearly 50 dogs born in 2016.

Table 2 Number and frequency of imported dogs by country. 21 import records were missing country of origin

Country	No. of dogs	Frequency
Ireland	151	24.7%
France	95	15.5%
Russian Federation	73	11.9%
Romania	57	9.3%
Italy	32	5.2%
Other countries	203	33.2%

¹ Registration types were classified in the following way. Litter Registrations included all dogs registered through the Breed Register (both whole litters and single-dog registrations). Activity Registrations included all dogs registered for activities other than conformation shows, such as agility or obedience, and this category also counted any dogs imported specifically into the Activity Register. Importations referred only to dogs imported into the Breed Register (and did not include imports recorded in the Activity Register). Authority to Compete registrations counted dogs that were approved to take part in competitions but were not part of the Breed Register. The Other category consisted of ancestors of imported dogs.

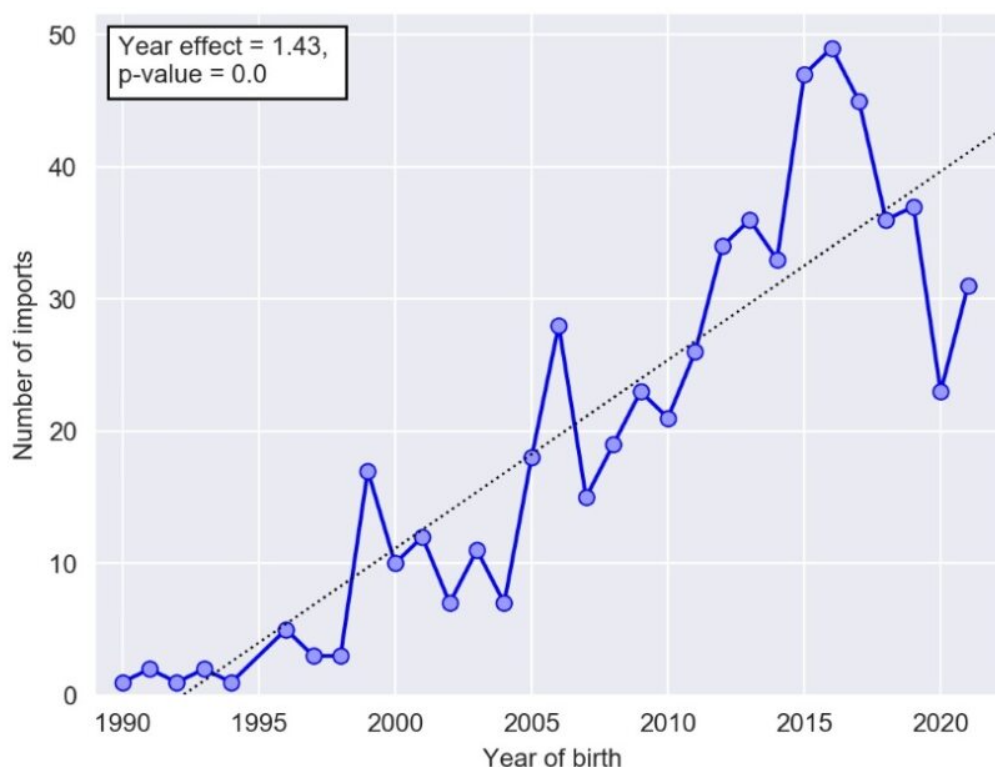


Figure 1 Trends in the number of imports by year of birth

CHAMPIONS²

The number of Rough Collies with a stud book number across all registration types is 6,496 (5.4% of total). There are 878 (0.7% of total dogs of the breed) with champion titles, all being Show/Conformation champions.

DEMOGRAPHICS³

The number of Rough Collies 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 -109.9 per year (with a

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 a dog 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.

95% confidence interval⁴ of -126.1 to -93.7), reflecting a statistically significant decrease in registration numbers during this time, from 4,380 Rough Collies registered with The Kennel Club in 1990 to 578 registered in 2021. This breed is currently on The Kennel Club's vulnerable native breeds 'at watch' list (breeds with between 300 and 450 registrations a year).

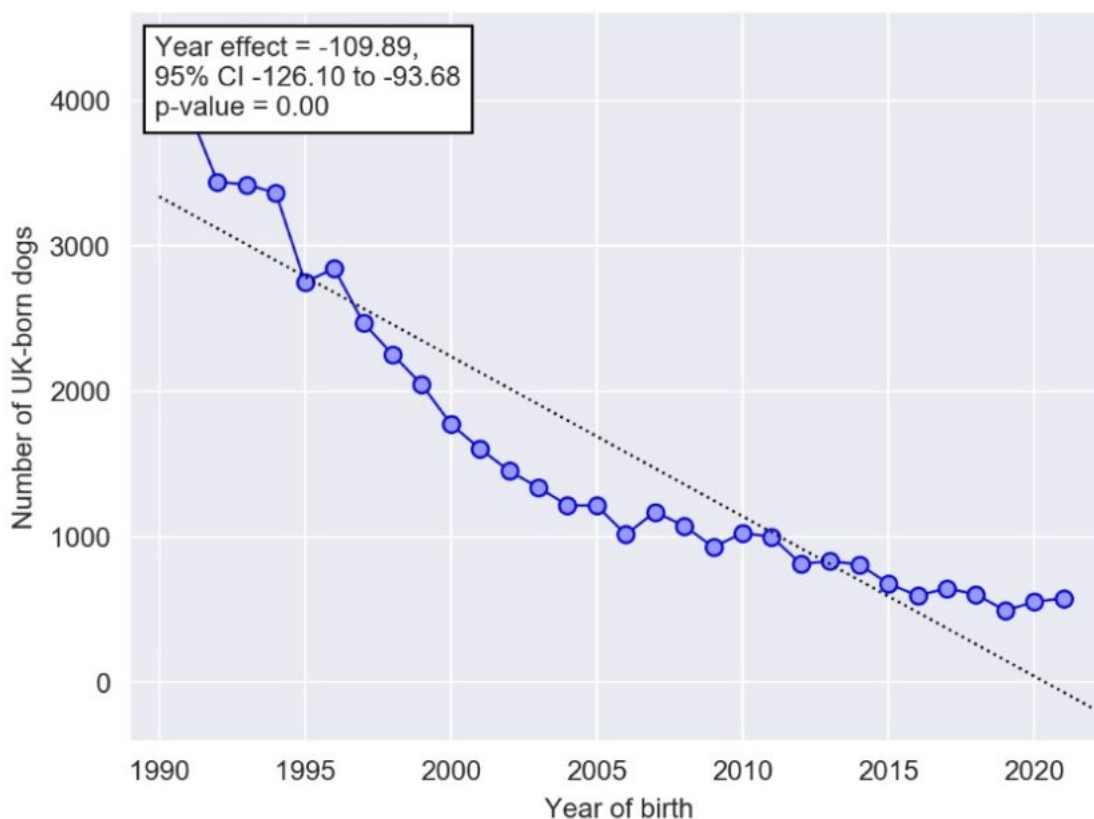


Figure 2 Trends in the number of registrations per year of birth

Overall, 13.3% of all national dogs born between 2005 and 2015 (inclusive) have been used in breeding, and only about 6.8% of national male dogs born in 2015 have been used in breeding to date. This indicates high selection intensity – and consequentially, a considerable 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.

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.

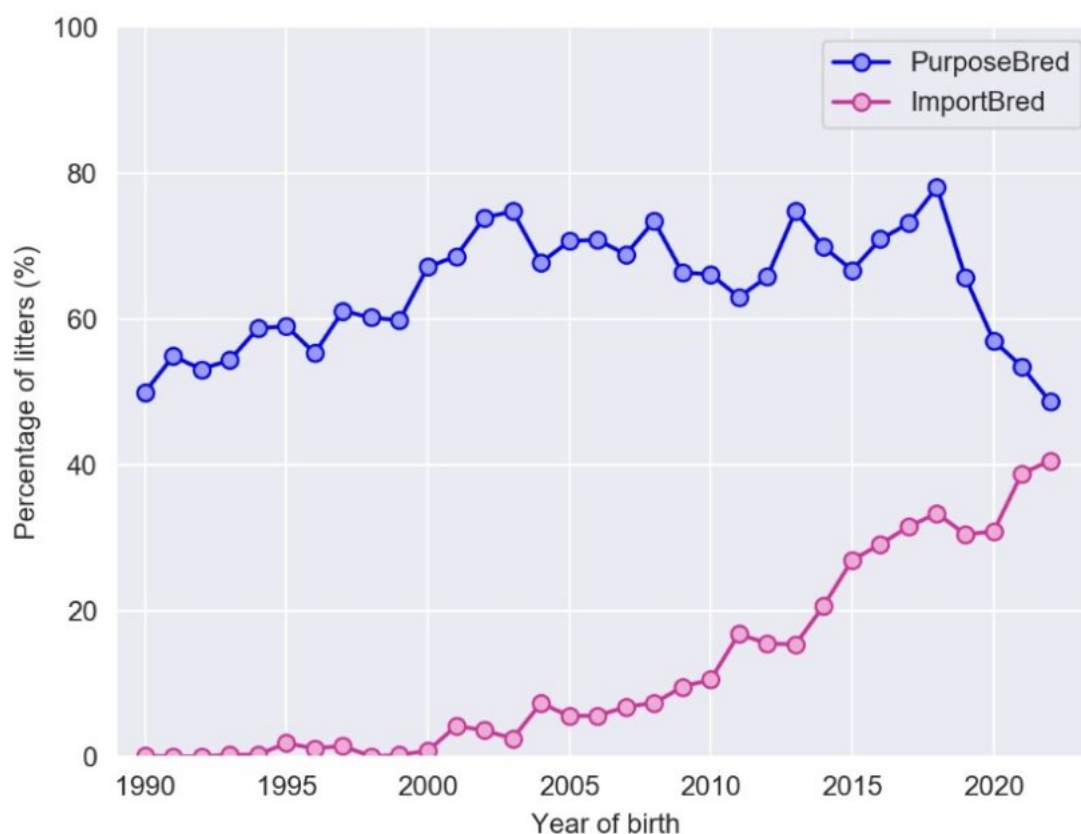


Figure 3 Percentage of litters where at least one parent had a stud book number ("PurposeBred") or was an import ("ImportBred")

The proportion of litters⁵ where at least one parent has a stud book number (referred to henceforth as "Purpose-bred") increased until 2018 but has decreased again since, as shown in Figure 3. In 2021, 53.4% of litters had at least one parent with a stud book number. On the other hand, the proportion of litters where at least one parent is an imported dog (referred to henceforth as "ImportBred") has continued to increase, as shown in Figure 3, from 0.1% in 1990 to 38.8% in 2021.

LITTER SIZE

Litter size statistics were calculated using the information available in The Kennel Club's registration records. It is important to keep in mind that these figures may not reflect the full number of puppies actually born. Some breeders do not register every puppy from a litter, and The Kennel Club registration system does not include puppies that are stillborn or that die shortly after birth. In addition, although uncommon, some breeders may incorrectly record litters, for example, by combining puppies from two litters into one registration.

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.

On average, Rough Collies produce 5 puppies in each litter (range from 1 to 12, median 5, standard deviation 2.1). The average litter size calculated for litters born each year has significantly increased over time, however the increase was modest, from 4.5 in 1990 to 5.1 in 2021, as shown in Figure 4. The distribution of litter sizes is shown in Figure 5.

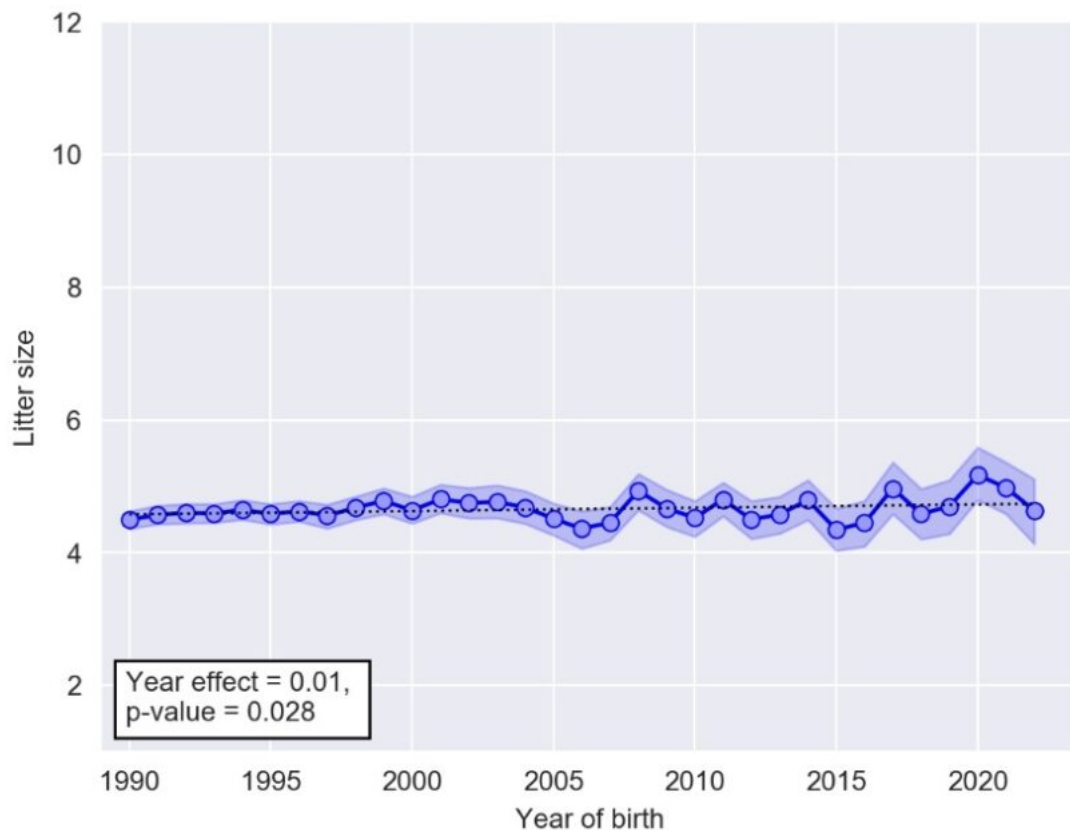


Figure 4 Trend in litter size over year of birth

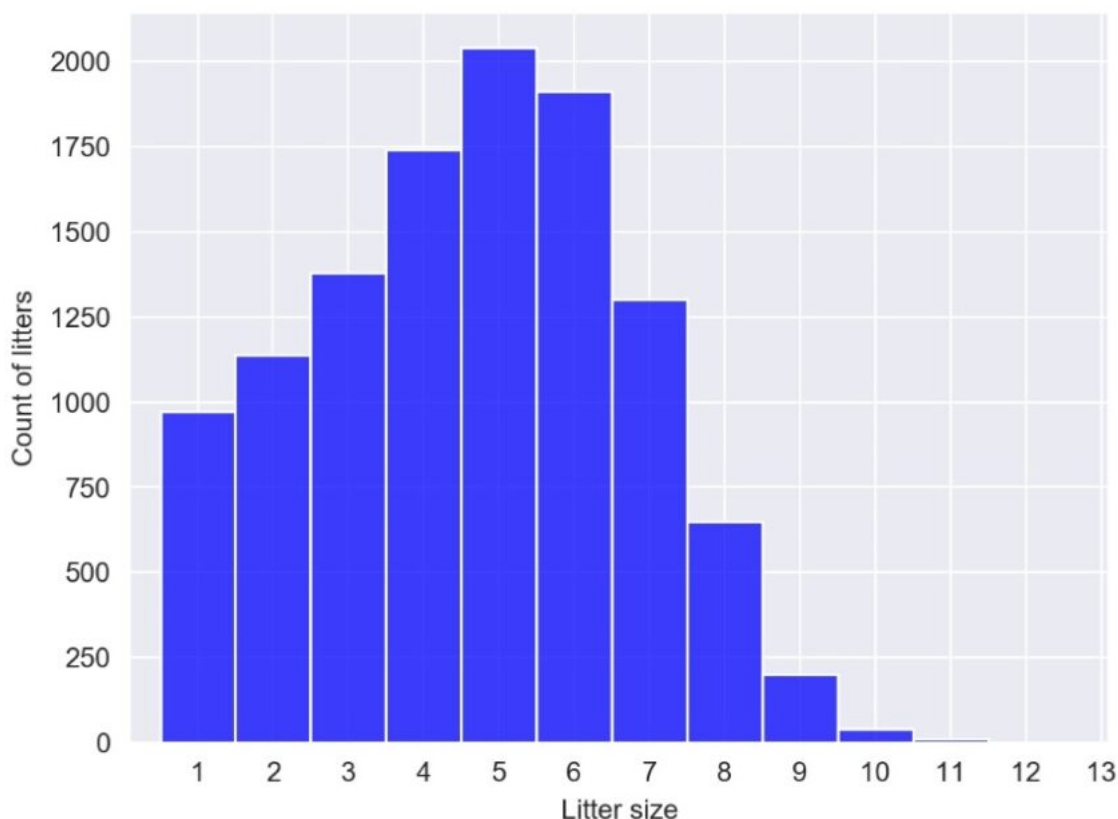


Figure 5 Distribution of litter size

GENETIC DIVERSITY IN ROUGH COLLIES

The rate of inbreeding observed in the complete electronic pedigree of Rough Collies born between 1990 and 2021 increased between 1990 and 2002, but has decreased since. At the moment, the rate of inbreeding in the breed appears to be negative. In simple terms, this would suggest that genetic diversity in the population is increasing. However, this is not biologically possible in a fully closed, UK-bred population where all dogs come from the same national gene pool. Because of this, it is not currently possible to produce a reliable estimate of the breed's effective population size.

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 11.3%.

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.

Comparing the overall observed and expected mean COIs indicates presence of selection, as there is a considerable departure between the observed and expected

COI. The higher observed COI indicates 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 Rough Collies, it appears that the reduction in the rates of inbreeding observed since 2002 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>.

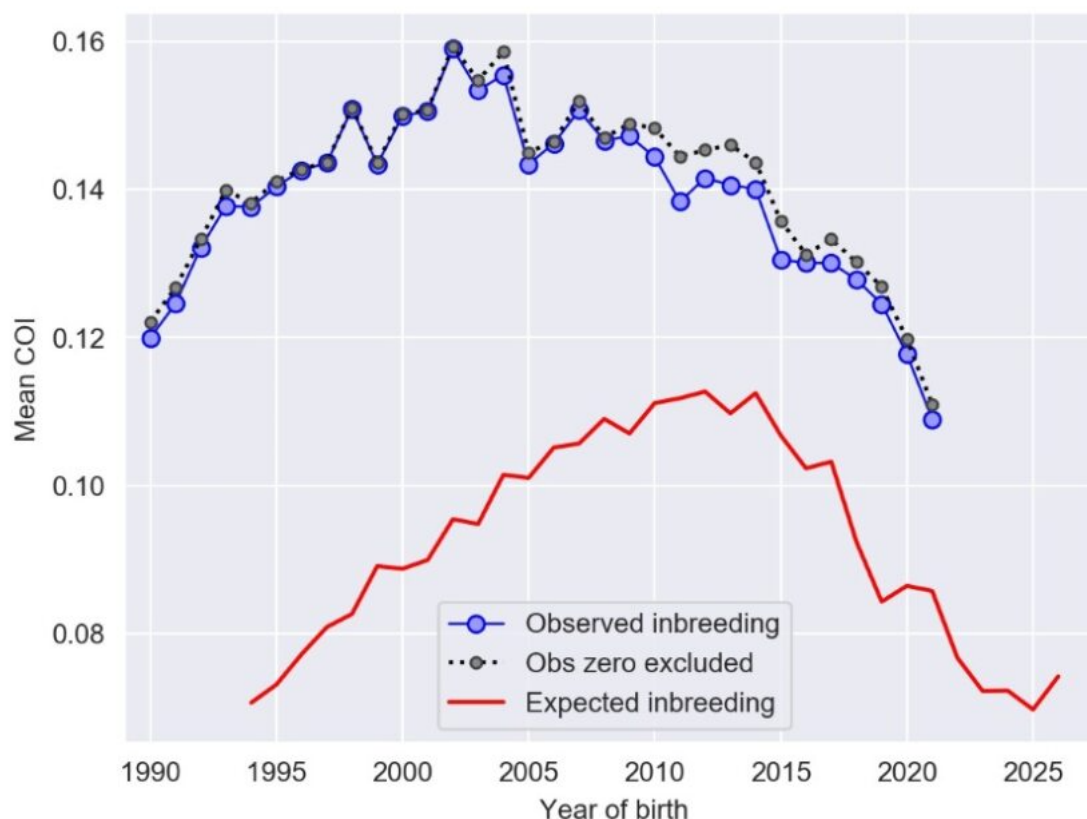


Figure 6 Annual mean observed and expected inbreeding coefficients

COI AND LITTER SIZE

There is a significant and negative association between litter size and coefficient of inbreeding (COI), i.e. litters with a higher COI are smaller. A 10% change in litter's COI reduces the litter size by -0.1 puppies. Figure 7 illustrates the relationship between litter size and COI in form of a boxplot⁶ 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 9 puppies, with 9 calculated as mean litter size + 2*standard deviation) were produced primarily in the lowest four COI categories (below 36%). There is a clear declining trend in the litter size with the increasing COI.

It is important to note that COI is only one of many factors that influence litter size in dogs. Other contributors include genetics, health, age and nutrition of the parents, and management practices around breeding - such as timing the mating using progesterone testing.

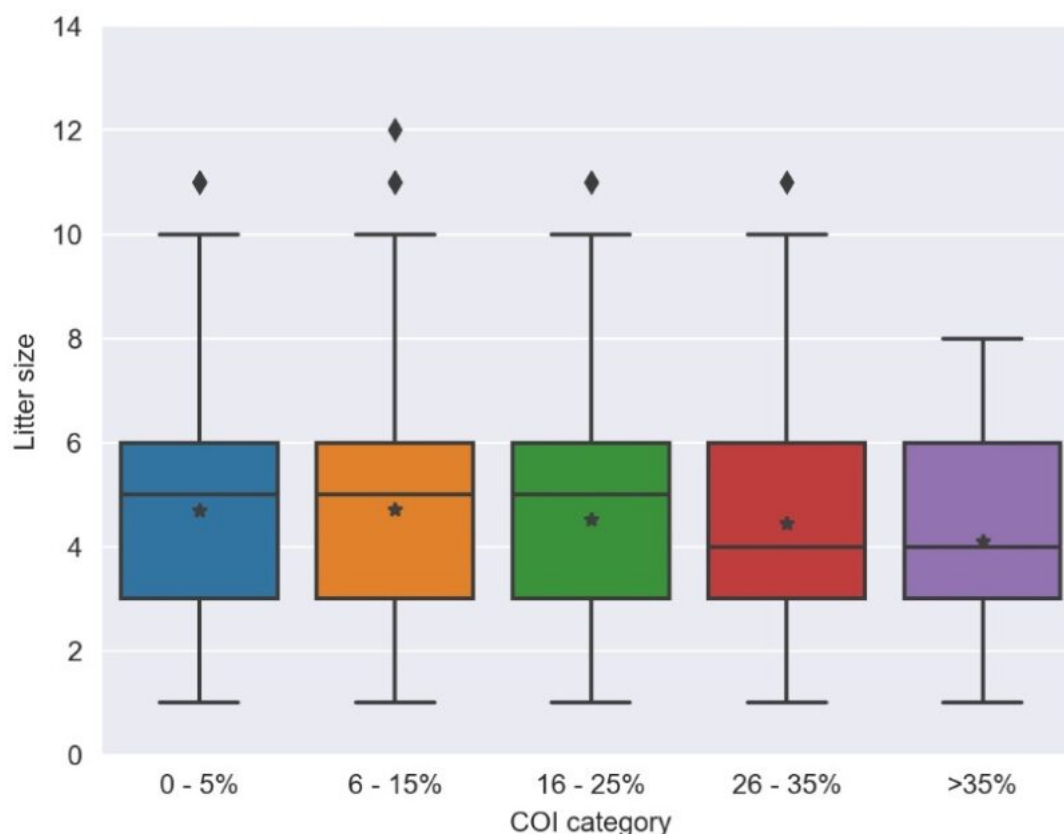


Figure 7 Boxplot of litter size distribution by category of COI. The number of litters in the particular categories were: 0-5% = 1,263, 6-15% = 5,390, 16-25% = 3,669, 26-35% = 957, >35% = 109

⁶ 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.

COI IN PURPOSE-BRED AND PET LITTERS

The coefficient of inbreeding is higher in Purpose-bred litters (i.e. litters where at least one parent has a stud book number), than in Pet⁷ litters (i.e. litters where neither parent has a stud book number) as shown in Figure 8.

While there is a difference between the average COI in Purpose-bred and Pet litters, the trends in COI in the two groups are similar. The mean COI increased from 1990 until 2007 in Pet litters and until 2013 in Purpose-bred litters, but has decreased since. This indicates that the importance of genetic diversity and the awareness of the dangers of inbreeding may have increased in both groups of breeders, however the levels of inbreeding remain higher in Purpose-bred litters.

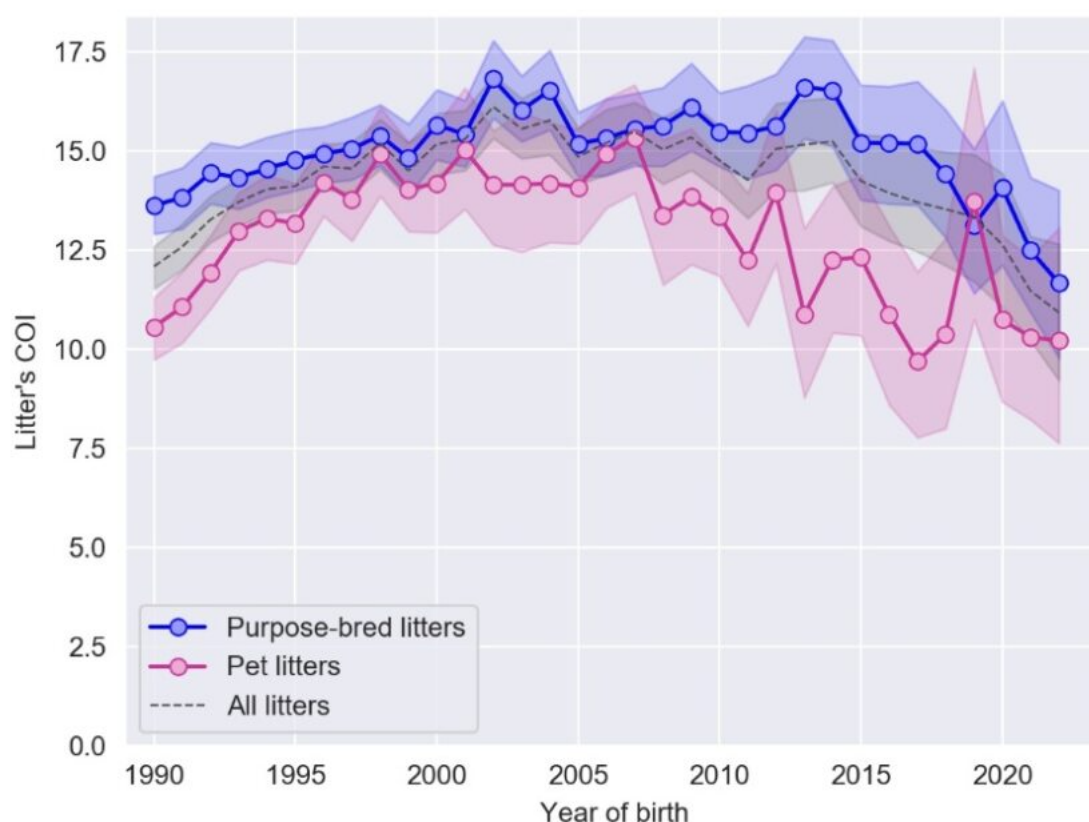


Figure 8 Annual mean inbreeding coefficients in Purpose-bred litters (where at least one parent has a stud book number), and Pet litters (where neither parent has a stud book number)

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

⁷ 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.

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 Rough Collies is 16.0% (maximum 24.2%, median 16.8%, standard deviation 5.0%). This means that an average Rough Collie 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.

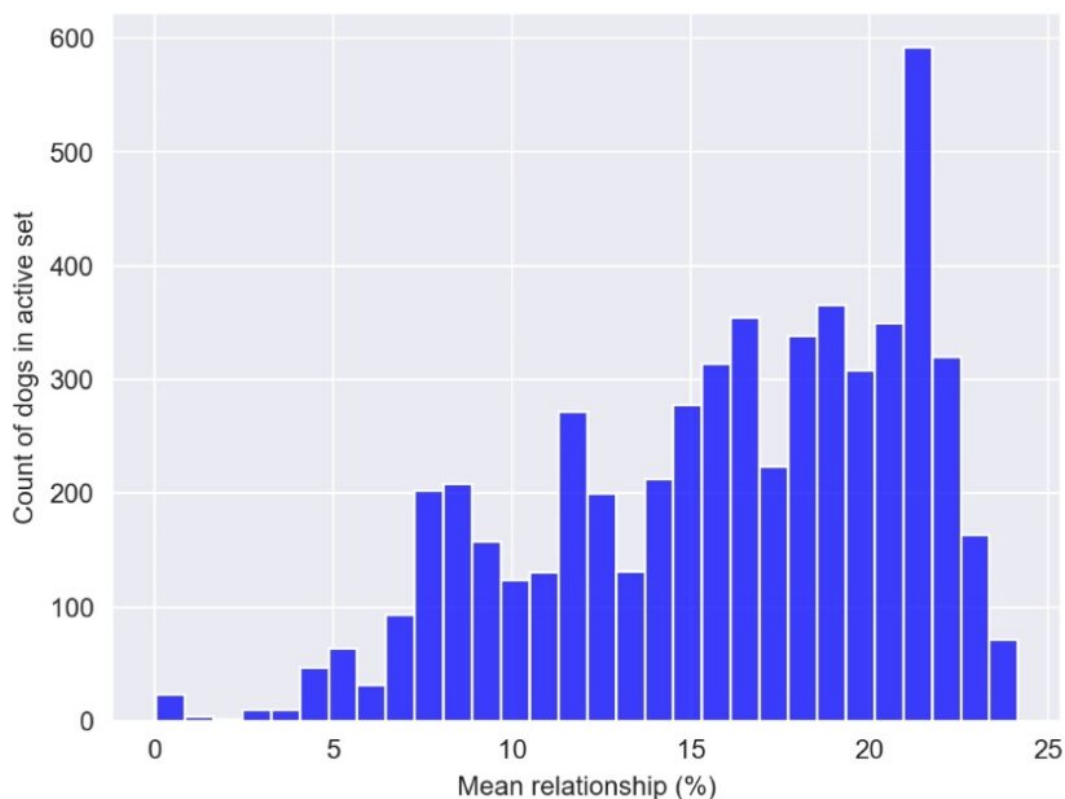


Figure 9 Histogram of the average relationships between dogs in the current breeding population (bitches born in last 8 years and dogs born in last 10 years, total of 5,611 dogs)

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 increased over time since 1990's (the 'tail' of the blue distribution becoming longer). The highest producing sire in the 2015 – 2019 block produced about 3.6% of the puppies born in that period.

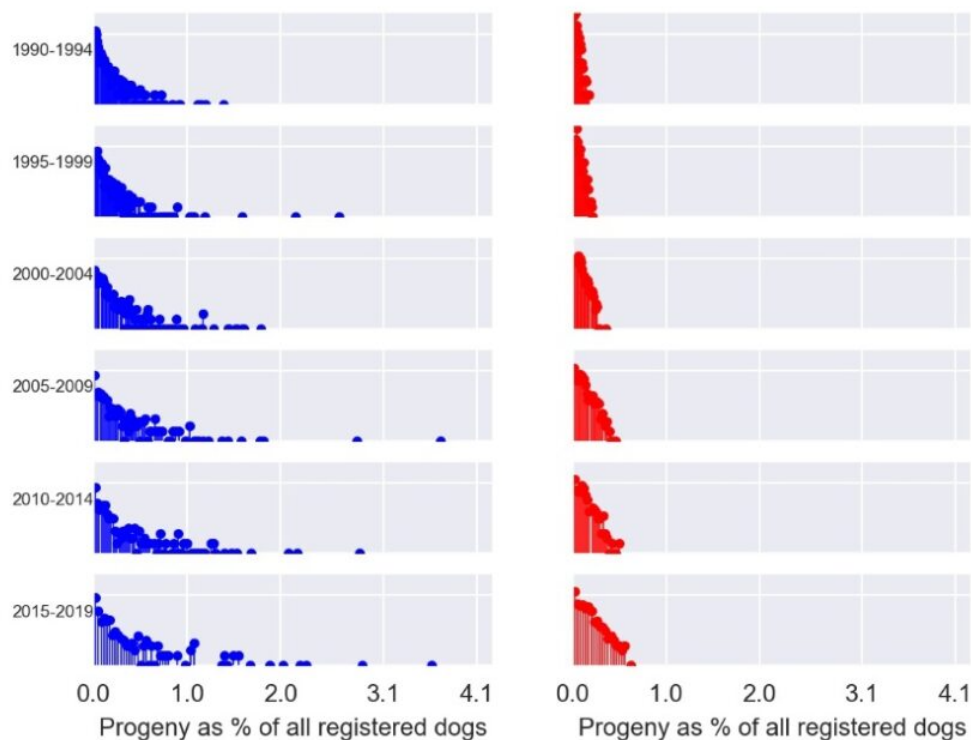


Figure 10 Distribution of progeny per sire (blue) and per dam (red) over 5-year blocks. Vertical axis is a logarithmic scale

Across litters in Litter Registration, a majority of sires produced between 1 and 5 litters (76.5% of the total of 2,399 sires). However, there were 19 (0.8%) sires which produced more than 35 litters, as shown in Figure 11. There was also 1 (0.0%) sire which produced more than 100 litters.

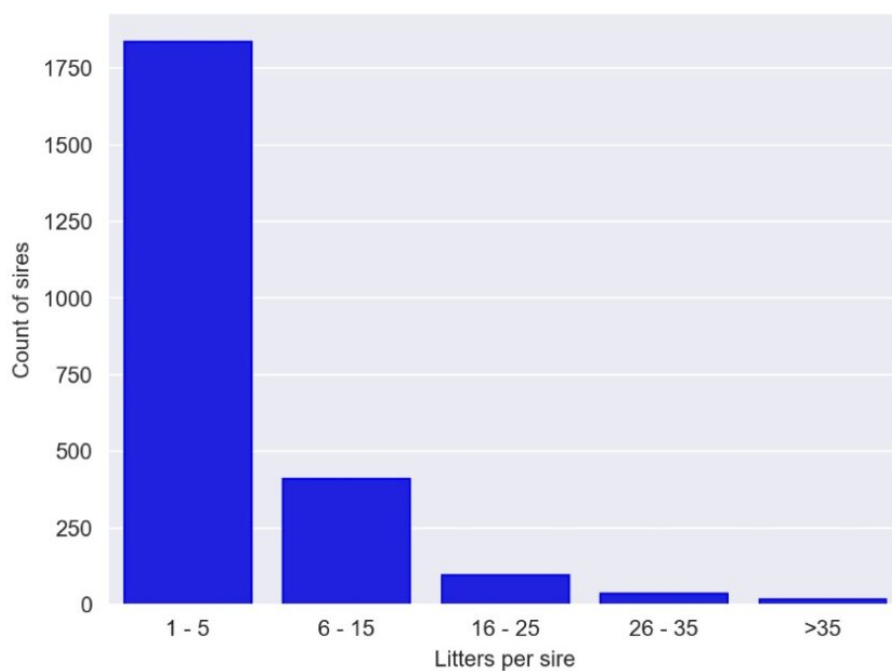


Figure 11 Histogram of sires in categories of number of litters produced

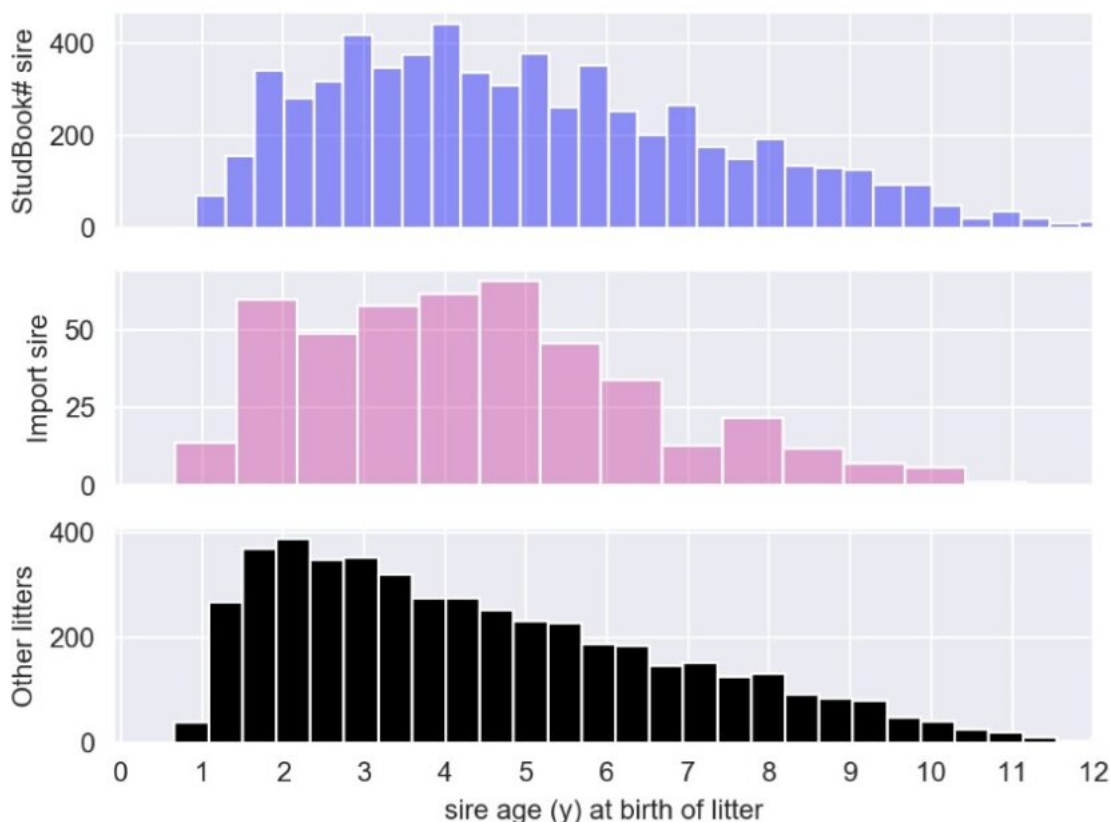


Figure 12 Age of sires at the birth of litter, divided into sires with stud book numbers (top plot in blue), imported sires (middle plot in pink) and remaining sires (bottom plot in black)

The statistics for sire's age at birth of litter were calculated for 11,260 litters, after removing 128 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. These litters were likely recording errors as, with exception of artificial insemination, reproduction at such ages is biologically unlikely. Following the peaks of productivity at 3-4 years for sires with stud book numbers, 4-5 years for imported sires, and 1-2 years for national sires without stud book numbers, the number of litters produced by sires decreases in older ages, as shown in Figure 12. However, all three groups 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:

- There is a significant difference ($p=0.000$) between dogs with and without stud book numbers. Sires with stud book numbers produced on average 7 litters, compared to 3 litters for sires without stud book numbers.
- There is no significant difference ($p>0.05$) between imported and national sires, with the average number of litters being 5 for both groups.

- c) There is a significant difference ($p=0.019$) between imported sires with and without stud book numbers. Imported dogs with stud book numbers produced on average 6 litters, whereas imported sires without stud book numbers produced on average 4 litters.
- 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 8 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	2,399	4.7	7.1	106
Sires with stud book no.	859	7.4	9.5	106
Sires without stud book no.	1,540	3.2	4.7	55
Imported sires	93	4.8	5.1	28
National sires	2,306	4.7	7.2	106
National sires with stud book no.	819	7.5	9.6	106
Imported sires with stud book no.	40	6.3	5.6	28
Imported sires without stud book no.	53	3.7	4.5	22