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Modern pedigree dogs in the United Kingdom Kennel Club: a journey through shifting population landscapes and demography

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Abstract

Background The limited genetic diversity in pedigree dog populations and the associated increased burden of inherited disease have led to calls for the development and implementation of effective population management strategies. Such strategies must be rooted in a thorough understanding of the genetic reserves and demographics of each population to be managed. Although numerous studies have examined the genetic diversity within various dog breeds, information on the structure of breeding populations and the characteristics of the dogs used for breeding is scarce. Furthermore, the few existing estimates typically represent the most common breeds, which may not be directly relevant for many of the numerically smaller breeds. We examined the demographic parameters of all 222 pedigree breeds recognised by The Kennel Club (KC) in the UK between 1990 and 2021. A meta-analysis was used to test whether all breeds can be represented by a single pedigree dog population, establish reference values for that population and determine the presence of significant variability between breeds.

Results Overall, the KC-registered pedigree dog population is declining in size, and the percentage of dogs used in breeding is low. Dogs which have been successful in activities such as conformation shows and field trials have been popular in breeding. However, their use in breeding is in decline, partly in favour of imported dogs. The number of imported dogs, and their use in breeding have increased over time, particularly following amendments to the Pet Travel Scheme (PETS) in 2012. Across analyses, the within-breed estimates varied significantly, with the proportion of variation attributed to true variability between breeds exceeding 90% for the majority of estimates.

Conclusion The results of this study provide reference values which can be used to describe the demographics of the KC-registered pedigree dog population and its changes over the last three decades. However, the significantly high variability observed between breeds does not support the hypothesis of a single pedigree dog population and underlines that population management strategies must be tailored to the unique circumstances of each breed.

Keywords Pedigree, Breed, Dog, Demographic, Trends, Popular sire

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Plain English Summary

The limited genetic diversity of pedigree dog populations has led to calls for the development and implementation of effective population management strategies, which must be rooted in a thorough understanding of the population to be managed. In this study, we used a meta-analysis to combine the results of population analyses across all 222 breeds recognised by The Kennel Club (KC) in the UK between 1990 and 2021. The objective was to test whether all breeds can be represented by a single pedigree dog population, establish reference values for that population and determine the presence of significant variability between breeds.

We found that the overall population of KC-registered pedigree dogs in the UK declined in size between 1990 and 2021, particularly since 2010. Dogs that have been successful in activities such as conformation shows and field trials have been popular in breeding. However, their use in breeding is in decline, partly in favour of imported dogs. The number of imported dogs and their use in breeding have increased over time, particularly following amendments to the Pet Travel Scheme (PETS) in 2012.

We detected significant differences between breeds for all demographic parameters studied here. As such, efficient management strategies for pedigree dog populations need to be tailored to the unique circumstances of each breed.

Background

The domestic dog is the most phenotypically diverse species in the world, with over 400 breeds characterised by vastly different appearance and behaviour. Each breed has a unique history, ranging from the slow evolution of traditional landraces developed for the needs of inhabitants of specific regions over hundreds of years, to the purposeful creation of a new breed over just a few decades through deliberate crossing between existing breeds. Most breeds have experienced reduction in genetic diversity from genetic bottlenecks, genetic isolation, selection for performance and/or appearance, and breeding practices such as the use of popular sires or linebreeding [1–4]. Although genetic uniformity benefits the high predictability of breeding outcomes [5], it also carries the risk of unfavourable outcomes through inbreeding depression driven by an accumulation of deleterious recessive alleles [6]. Over the last few decades, the increasing understanding of the genetic basis of inbreeding depression, as well as quickly accumulating evidence on the inherited diseases associated with specific breeds [7–9] and with reduced genetic diversity [1, 3, 10, 11], has resulted in calls for improved management of pedigree dog populations [2, 9, 12–16].

Effective management of pedigree populations is challenging, partly due to the structure of the dog breeding industry. Across breeds, the fraction of the population that is under the control of any single breeder is insignificant, with the majority of breeders owning only a few breeding bitches and producing a few litters per year [17]. This can create a disparity between the interests of individual breeders and the interests of the breed as a population. In the absence of a single decision maker for each population, the responsibility for the management of pedigree dog populations is frequently placed on national kennel clubs.

The regulations employed by national kennel clubs across the globe are highly variable, both in terms of their scope and severity [18]. For example, the breed registries are closed in most kennel clubs, such that only dogs born to parents documented to be of the same breed by a recognised kennel club can be registered. However, in France, the registries are open for many breeds [19], and in the UK, dogs of unknown origin may be registered in the breed registry under regulation B2c [20]. Furthermore, in 2010, the Federation Cynologique Internationale (FCI) issued a recommendation that no sire should produce more than 5% of puppies born in the breed population during a five-year period. Although the FCI has 98 member countries and is partnered with kennel clubs in Canada, the United States and the UK, enforcement of this recommendation is not common, and evidence to support how effectively this recommendation has been integrated within breeding practices is not available.

In the absence of standardised population management strategies, several possible solutions have been offered to improve population management, including the use of relatedness estimates in selecting breeding dogs, limits on the contributions of sires to the population, increased migration of dogs from genetically divergent populations, or outcrossing to other breeds or breed varieties [2, 19, 21–25]. However, for these solutions to be effective in sustainable management of genetic diversity, they must be rooted in a thorough understanding of the population to be managed.

There is a scarcity of published evidence on the structure of dog populations, particularly with respect to how it changes over time. Most demographic studies have examined national populations of dogs, with no clear distinction between pedigree and presumed purebred dogs of unknown origin, and often include cross-bred and mixed-breed dogs [26, 27]. Studies focusing on pedigree dog populations are primarily based on retrospective analyses of genetic diversity [2, 21, 24, 28, 29]. However, there is little evidence on how dogs are selected for breeding, with few available studies based on surveys carried out among French [17] and Australian [30, 31] dog breeders. Published evidence for pedigree dog populations typically utilise data on variable subsets of breeds [23, 24, 32–34], often representing only the most common breeds [21]. For many breeds, particularly those that are numerically small and thus arguably more at risk of suffering from inbreeding depression, there are no reports available.

In the UK, The Kennel Club (KC) is the largest organisation that registers pedigree dogs and is commonly identified as the main body representing UK pedigree dogs [12, 13]. Hereafter, UK pedigree dogs will strictly reflect those dogs also registered by KC, unless stated otherwise. At the time of writing, rules and regulations pertaining to the management of genetic diversity and inbreeding issued by KC were limited to a ban on the registrations of puppies produced through mating between full siblings, or between parent and offspring. Breeders are advised to choose matings that would result in a coefficient of inbreeding (COI) below the breed average and to consider the previous mating output of a sire they are planning to use with their breeding bitch. To help breeders meet the recommendations to reduce COI, in 2011, KC introduced a 'COI Calculator' (originally 'MateSelect') as a tool for breeders to test the COI values for prospective matings [35]. In 2015, Lewis et al. [29] published a population analysis describing the genetic diversity of 215 breeds recognised by KC, utilising complete electronic records in KC's database and showing declining inbreeding rates. However, the results were highly variable between breeds, indicating the need for further support to breed communities. Furthermore, this study did not address the demographic characteristics of the breeding population, such as the impact of the limited pedigree depth of imported dogs on the estimates of genetic diversity. Such information, alongside estimates of genetic diversity, would improve the efficacy of population management strategies.

The objective of this study was to examine demographic characteristics of KC-registered pedigree dog populations in the UK over the three decades between 1990 and 2021 and across 222 breeds recognised by The Kennel Club, with a particular focus on the structure of the breeding populations. The study employed a meta-analysis to test whether all breeds can be represented by a single pedigree dog population and determine the presence of significant variability between breeds.

More specifically, we aimed to identify universal trends common to all breeds and find evidence of significant variability in these trends between breeds. KC's complete database of pedigree records was used, comprising a total of 11 million dogs. The metrics examined were trends in population sizes, percentages of the pedigree populations used in breeding, characteristics of the dogs used in breeding, and specifically, the characteristics of male dogs with the highest reproductive output (popular sires). The results of this study provide comprehensive reference values for describing the KC-registered pedigree dog population in the UK and will be used to shape the management strategies of individual breeds.

Materials and methods

Data description

Founded in 1873, The Kennel Club is the oldest dog registering body in the world. Initial records of KC-registered dogs were kept in paper format, with some historical records still available in KC's library. Registrations in electronic format began in 1985, with only some of the earlier, primarily breeding dogs, migrated to the electronic database prior to this date.

Data for dogs of 222 breeds were extracted from KC's electronic database in late 2022. The data for each dog included breed, parentage (sire and dam identification), register and registration type, country of origin, titles (champion and Studbook number), date of birth and sex. Dogs of each breed were classified into three groups based on register and registration type:

- Litter Registrations (LReg)—dogs in the breed register, registered in the UK through litter registration and born since 1990.
- Breed Register (BReg) – dogs in LReg as well as imported dogs, and dogs with Authority To Compete (temporary registration allowing the dog to partake in KC activities), born since 1990.
- Whole Pedigree (WP) – all available dogs, including ancestors of imported dogs, dogs in the Activity Register, and dogs born before 1990 or with an unknown date of birth.

Thus, LReg is a subset of Breg, which is a subset of WP. Analyses of trends in LReg and BReg were limited to dogs born since 1990, unless stated otherwise, to represent three decades of pedigree dog breeding.

The total number of records in WP across all breeds was 11,159,418; of which 8,192,201 (73.4% of WP) were in BReg and 8,100,503 (72.6% of WP) were in LReg. The mean breed size in WP was 50,268 with standard deviation of 135,389, ranging from 56 in American Water Spaniel to 1,408,204 in Labrador Retriever (Supplement 1).

To obtain parameters related to breeding, the data for unique dogs in LReg were converted to litter data. Each sire, dam and date of birth combination was assigned a unique number. Each litter where data were incomplete was treated as unique. Litters were filtered against the parent age at whelping. Litters were removed if the sire was younger than 6 months or older than 15 years or if the dam was younger than 8 months or older than 12 years. Notably, KC does not currently register litters born to a dam younger than 1 year at the time of the mating or older than 8 years at whelping, or litters born to a bitch that already produced 4 litters. However, these rules were not always in place, so the thresholds were chosen on the basis of the expected age at sexual maturity and longevity. Due to age limits, it is possible that some litters produced through artificial insemination were not accounted for, but the number of such litters is expected to be low. Across 221 breeds, 1,583,217 unique litters were used in the analyses described below, ranging from 1 litter in Pyrenean Mastiff to 173,855 litters in Labrador Retriever. There were no LReg dogs recorded for American Water Spaniels; hence, no litters were identified in that breed.

Statistical analyses

The parameters described below were first estimated within each breed separately via custom python scripts (https://github.com/joannailska/population_analysis) and then combined across breeds in subsequent meta-analyses. The within-breed estimates were also documented in reports for dissemination to relevant breed communities.

The objective of the meta-analyses was to test whether all breeds can be represented by a single pedigree dog population, estimate parameters and trends describing that population and determine the presence of significant variability between breeds. A meta-analysis approach was used to ensure all breeds, including the numerically small, sufficiently contributed to the universal estimates. All meta-analyses were performed using the R package "meta" [36], with a random effects model option producing a pooled estimate of the mean of the distribution of true within-breed parameters along with 95% confidence intervals (CIs), calculated with Knapp-Hartung adjustment [37]. The random effects option accounts for variability arising from sampling error in addition to true variability between breeds, as estimated via residual maximum likelihood, unless otherwise stated. The significance of the estimated variability between breeds was determined via a log-likelihood ratio test or Q profile, depending on the function used and as reported by the "meta" package. The proportion of estimated variability between breeds attributed to true variability is reported as I^2[38], with the remaining proportion attributed to sampling error.

The meta-analyses involved all breeds with sufficient data (as described for each analysis) or the top 10 breeds, as identified from the number of dogs born in 2021 (Table 1). The top 10 breeds represent 44.0% of WP records across all breeds and thus illustrate the most commonly found pedigree dogs in the UK. Within-breed estimates for the top 10 breeds only are provided in Supplement 7.

Trends in pedigree dog population size

Trends in the popularity of a breed were calculated by fitting a linear regression to the number of dogs in BReg by year of birth across two periods: between 1990 and 2021 and between 2010 and 2021. Specifically, we aimed to detect global linear trends across the entire period

Table 1 Size of pedigrees, and LReg registration statistics for 2021 in the top 10 breeds

Breed	WP	Breg as % of WP	LReg as % of WP	# LReg dogs in 2021	# LReg litters in 2021
Labrador Retriever	1,408,204	85.8%	85.6%	58,359	8165
French Bulldog	314,356	95.2%	94.1%	51,925	10,192
Cocker Spaniel	730,593	85.4%	85.1%	36,943	6844
Bulldog	180,788	86.5%	85.4%	14,641	2929
Dachshund Miniature Smooth-Haired	129,037	84.4%	83.8%	14,533	3358
English Springer Spaniel	493,956	80.6%	80.4%	14,027	2235
Golden Retriever	481,898	73.2%	72.6%	11,484	1604
Staffordshire Bull Terrier	326,199	79.2%	78.5%	7393	1355
Pug	145,597	88.8%	88.0%	5628	1299
German Shepherd Dog	673,955	65.4%	65.0%	2818	1179

LReg dogs born in the UK since 1990 and registered through the Litter Registration in the Breed Register, BReg dogs born since 1990 in LReg as well as dogs in the Activity Register and imported dogs, WP all dogs registered in the breed of study, while the period between 2010 and 2021 was chosen to identify more recent linear trends, covering approximately the last three generations of dog breeding [29].

The regression for each breed and period was given by:

$$\log(n_i + 1) = a_i + b_i \cdot year$$

where n_i is the number of BReg dogs in breed i, a_i is the intercept, *year* is the year of birth and b_i is the slope of the regression, which provides an estimate of the trend in popularity of breed i. A log transformation was applied to allow for calculation of proportional change in the population size, which could be meaningfully compared between breeds of different census sizes. A constant of 1 was added to allow for response values of 0.

The estimates of b_i and their standard errors were pooled across breeds in a meta-analysis using the 'metagen' function. This produced a pooled estimate of the slope, b, along with an estimate of variability between breeds, I^2. Only breeds with at least 10 dogs in LReg in the first year of the studied period were included, with 159 breeds for 1990–2021 and 184 breeds for 2010–2021. The filter was applied to remove breeds imported to the UK at later stages, and thus not represented across the entire period studied. The estimates of b_i and b were converted to an estimate of the proportional growth or decline of a population, for example as:

$$Percentage\ change = 100 \cdot \left[\exp\left(\hat{b}\right) - 1\right]$$

with 95% CIs for the estimates also calculated in this manner.

Percentage of dogs used in breeding

To reflect recent breeding practices, the percentage of dogs used in breeding was calculated for dogs in LReg born between 2005 and 2015, with 210 breeds containing at least 10 dogs registered in this period. The period was limited to 2015 in order to avoid including dogs presumed to be alive at the time of analysis and which may still be used in breeding for the first time. Breeds with fewer than 10 dogs were removed from the analysis to prevent potential extreme values. A random logistic regression was fitted with a logit link to the raw counts of dogs born and bred from each breed using the 'metaprop' function, with the variability between breeds estimated via maximum likelihood and 95% CIs within breeds calculated via the Clopper–Pearson method [36]. As the impact of males on genetic diversity is more pronounced than that of females, the analysis was repeated for two subsets of males born in 2015: 177 breeds in which at least 10 males were born in 2015 and the top 10 breeds only. The analyses were limited to males born in 2015 only to reflect the most recent breeding population that could be expected to have been bred from by the time of the analysis.

Purpose-bred dogs and their use in breeding over time

The popularity of dogs bred for a specific purpose and its change over time were investigated in terms of the number of dogs that achieved a Studbook number (SBN) by winning a qualifying award at one of KC-managed activities (e.g., conformation showing, field trials, agility, obedience and working trials). We assumed dogs which achieved an SBN had been bred from stock selected for the traits required for a given activity. Champion titles assigned to the most successful dogs were not considered in the analyses, as the number of dogs with champion titles was only 0.55% of the WP across all breeds and recording of national and international champion titles was inconsistent.

First, the overall proportion of dogs with an SBN in a WP was calculated. This was achieved by fitting the 'metaprop' function, as described above, to the number of dogs with SBNs and the total number of dogs in a WP. A pooled estimate of the overall proportion was obtained for 173 breeds where at least one SBN was awarded as well as for the top 10 breeds only.

The use of dogs with SBNs in breeding was then examined by calculating the proportion of litters where at least one parent had an SBN (henceforth referred to as Purpose-bred litters) for each year of birth. The proportions were pooled across 143 breeds with at least one Purpose-bred litter and at least three litters born every year between 1990 and 2021, and across the top 10 breeds. The pooling of the overall proportion was performed via the 'metaprop' function using the raw number of litters born and the number of Purpose-bred litters.

The trends in the use of dogs with SBNs in breeding were calculated by fitting a beta regression with a logit link to the proportion of Purpose-bred litters by year of birth. The proportions used in the beta regression were rescaled as:

$$p_{ij}{'} = \left[p_{ij} \cdot (n_{ij} - 1) + 0.5\right] \Big/ n_{ij}$$

where p_{ij} is the raw proportion of Purpose-bred litters calculated for breed i in year j and n_{ij} is the associated number of litters born [39]. The rescaling was applied to accommodate proportions equal to 0 and 1. All regressions were fitted using the 'betareg' package in R [40] and resulted in within-breed estimates of b_i and their standard errors, which were then pooled across breeds using the 'metagen' function [36]. The estimates of b_i and the pooled estimate, b, were converted to estimates of percentage change, as described above, for proportional growth of the population. The analysis was repeated for the top 10 breeds.

Imported dogs and their use in breeding over time

Imported dogs were characterised in terms of their exporting country, trends in the growth of the imported population and use of imported dogs in breeding.

The top export countries were identified based on the percentage of overall imported dogs from the given country, as well as countries appearing within the top 3 export countries across the largest number of breeds.

The within-breed trends in the number of imported dogs were calculated with a linear regression of the natural logarithm of the number of imported dogs on year of birth between 1990 and 2021. This was done for 159 breeds with at least 10 dogs in BReg born in 1990. A constant of 1 was added to allow for response values of 0. The estimates of the slope of the regression for individual breeds were pooled in the meta-analysis using the 'metagen' function, as described above. The estimates for the within-breed and pooled analysis were converted to proportional growth of the imported population, also as described above.

The use of imported dogs in breeding was examined via the analysis of litter data, where litters with at least one imported parent were labelled Import-bred. The proportion of litters that were Import-bred was calculated for 149 and 171 breeds with at least one Import-bred litter and at least three litters in each year between 1990–2012 and 2013–2021, respectively. The within-breed estimates were then pooled using the 'metaprop' function. The analysis of trends in the proportion of Import-bred litters followed the steps described above for Purpose-bred litters. The trends were calculated by fitting a beta regression to the rescaled proportions, and the resulting within-breed estimates were pooled using the 'metagen' function. Notably, owing to the large impact of the legislative changes related to the import of dogs in 2012, trends in the use of imported dogs in breeding were calculated separately for the periods 1990–2012 and 2013–2021.

Sires and their characteristics

Sires of litters in LReg were categorised as national or imported, and with or without an SBN. A series of pairwise comparisons was carried out to obtain the mean difference in the number of litters produced by the sires in particular categories, with the pooled mean difference was calculated using the 'metacont' function [36]. The meta-analyses were carried out for all breeds with at least 5 sires in each of the compared categories and for the top 10 breeds.

The mean number of litters in LReg and the mean age (in months) at the first LReg litter of the 10 highest producing sires were compared against the median of sires in their breed. The highest producing sires were selected based on the number of offspring in LReg, and the within-breed raw mean differences were pooled using the 'metamean' function [36]. The analysis included 175 breeds with at least 50 sires born between 1990 and 2021.

The number of highest producing sires born between 1990 and 2021 that were imported and/or had an SBN was summed across breeds and compared to the number of highest producing sires that were imported and/or had an SBN and were presumed to be alive at the time of analysis (i.e., born since 2015). For SBN comparison, only breeds where at least one SBN has been awarded were considered (173 breeds out of 175 breeds with at least 50 sires born between 1990 and 2021).

Results

Trends in pedigree dog population size

Overall, The Kennel Club registered pedigree dog population is declining in size. The pooled estimate of proportional change in population size across 159 breeds with at least 10 dogs in LReg born in 1990 was -0.89% (CI: -1.55 to -0.22%), with significant variability between breeds ($p < 0.0001$); almost exclusively explained by true variability *($I^2 = 99.0\%$, CI: 99.0 to 99.1%).* The within-breed estimates were significantly different from 0 in 123 breeds, with 84 (68.3%) experiencing a significant decline and 39 (31.7%) experiencing a significant growth (Supplement 2). Of these, only one breed declined by more than 10% each year while seven breeds grew by more than 10%. The largest decline over the period 1990 – 2021 was found in Yorkshire Terrier with -10.6% (CI: -11.3 to -9.9%), while the largest growth was found in French Bulldog with 22.1% (CI: 18.5 to 25.7%). Note, however, the proportional changes were relatively modest in most breeds, with 83 breeds declining by less than 10% each year and 32 growing by less than 10%.

The decline in KC-registered pedigree dog population sizes was more pronounced between 2010 and 2021. The pooled estimate of proportional change across 184 breeds with at least 10 dogs in LReg born in 2010 was -1.29% (CI: -2.31 to -0.26%), with significant variability between breeds ($p < 0.0001$); almost exclusively explained by true variability, although there was more uniformity than when the whole period was considered, with non-overlapping confidence intervals ($I^2 = 97.0\%$, CI: 96.8 to 97.2%). Within this period, 103 breeds experienced significant change in population size, of which 72 breeds (69.9%) experienced significant decline (Supplement 2). There were 12 breeds that declined by more than 10% each year, with the largest decline found in

Pyrenean Sheepdog (Long Haired) at -16.9% (CI: -24.5 to -8.5%). Among the 31 breeds that experienced significant growth, 15 increased by more than 10% each year. The largest growth was found in French Bulldog with 34.9% (CI: 29.4 to 40.7%).

Among the top 10 breeds (Supplement 7), five breeds (Labrador Retriever, Cocker Spaniel, English Springer Spaniel, Staffordshire Bull Terrier and Pug) showed no significant change in KC-registered population size between 2010 and 2021, and four increased significantly: French Bulldog, 34.9% (CI: 29.4 to 40.7%); Dachshund Miniature (Smooth-Haired), 17.4% (CI: 14.1 to 20.8%); Bulldog, 11.7% (CI: 10.3 to 13%); and Golden Retriever, 2.8% (CI: 0.9 to 4.8%). The German Shepherd Dog was the only top 10 breed which declined in KC-registered population size, with -2.5% each year (CI: -3.8 to -1.2%). The pooled estimate across the top 10 breeds revealed a 5.8% increase each year; however, this was not significantly different from 0 (CI: -1.7 to 14.0%).

Percentage of dogs used in breeding and its relation to breed size

The percentage of KC-registered dogs of either sex which are used in breeding of other KC-registered dogs is low (Supplement 3). The pooled estimate across 210 breeds with at least 10 dogs in LReg born between 2005 and 2015 revealed that only 13.7% (CI: 13.0 to 14.4%) of the KC-registered dogs were bred from, with significant variability between breeds ($p<0.0001$); almost exclusively explained by true variability ($I^2=99.6\%$). The highest percentage was found in Jack Russell Terrier with 46% of the 50 LReg dogs bred from (CI: 31.8 to 60.7%), while the lowest percentage was found in Small Munsterlander with 0% of the 13 LReg dogs bred from (CI: 0 to 25%), followed by Belgian Shepherd Dog (Laekenois) with 2.7% of the 37 LReg dogs bred from (CI: 0.7 to 14.6%).

The percentage of KC-registered males used in breeding was lower, with a pooled estimate across 177 breeds with at least 10 males in LReg born in 2015 of 6.3% (CI: 5.8 to 6.9%), with significant variability between breeds ($p<0.0001$); predominately explained by true variability ($I^2=86.1\%$, CI: 84.2 to 87.7%). The highest percentage was found in German Pinscher with 35.7% of the 14 KC-registered males bred from (CI: 12.8 to 64.9%), while the lowest percentage was found in 9 breeds (Bouvier Des Flandres, Belgian Shepherd Dog (Groenendael), Catalan Sheepdog, Hungarian Puli, Kooikerhondje, Polish Lowland Sheepdog, Portuguese Podengo, Swedish Vallhund and Xoloitzcuintle Standard) with none of the LReg males born in 2015 bred from. The lowest non-zero percentage was found in Samoyed with 1.7% of the 115 LReg males born in 2015 bred from (CI: 0.2 to 6.1%) (Supplement 3).

The percentage of KC-registered males bred from in the top 10 breeds was 6.6% (CI: 5.0 to 8.8%), with significant variability between breeds ($p<0.0001$) almost exclusively explained by true variability ($I^2=98.3\%$, CI: 97.7 to 98.7%) (Supplement 10). The highest percentage was found in French Bulldog with 11.5% of the 7312 KC-registered males bred from (CI: 10.8 to 12.3%), while the lowest percentage was found in Golden Retriever with 3.1% of the 3596 KC-registered males bred from (CI: 2.6 to 3.8%) (Fig. 1).

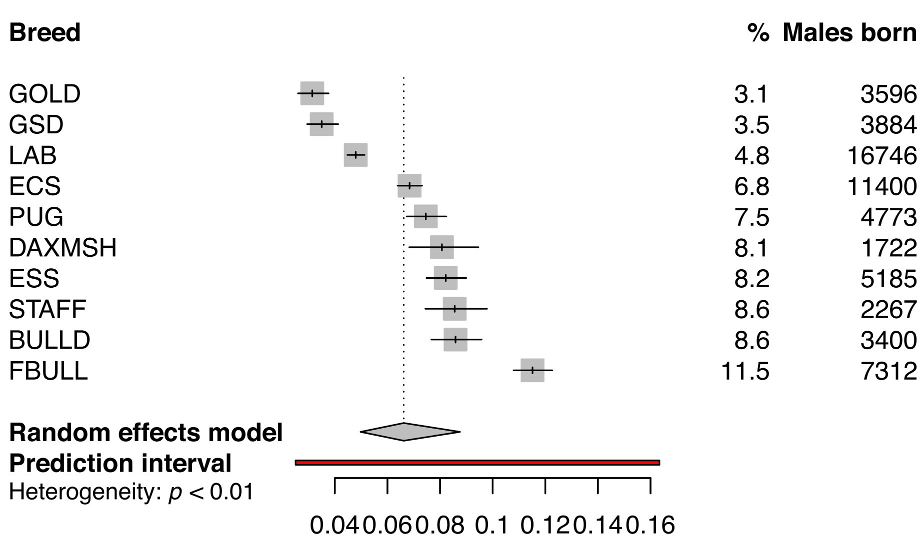

Fig. 1 Forest plot for the meta-analysis across the top 10 breeds for the percentage of males born in 2015 that were bred from. Breeds include: Bulldog (BULLD), Dachshund Miniature (Smooth-Haired) (DAXMSH), Cocker Spaniel (ECS), English Springer Spaniel (ESS), French Bulldog (FBULL), Golden Retriever (GOLD), German Shepherd Dog (GSD), Labrador Retriever (LAB), Pug, Staffordshire Bull Terrier (STAFF)

The percentage of KC-registered males used in breeding is only partly explained by the overall number of males registered, as shown in Fig. 2. The percentage was most variable in breeds with a low number of males; however, considerable variation existed between breeds of comparable size. For example, the number of KC-registered males in Japanese Chin and Nova Scotia Duck Tolling Retriever was nearly identical at 96 and 97, respectively, but the percentage bred from was considerably different, with 18.7% in Japanese Chin (CI: 11.5 to 28%) and 3.1% in Nova Scotia Duck Tolling Retriever (CI: 0.6 to 8.8%).

Purpose-bred dogs and their use in breeding over time

The percentage of dogs with an SBN is low across KC-registered pedigree dogs (Supplement 4). The pooled estimate across 173 breeds with at least one SBN awarded revealed that 5.1% of the dogs in WP were awarded an SBN (CI: 4.3 to 5.9%), with significant variability between breeds ($p < 0.0001$); almost exclusively explained by true variability ($I^2 = 99.9\%$). The highest percentage was found in Sealyham Terrier with 30.1% of the 7747 dogs in WP awarded an SBN (CI: 29.0 to 31.1%), while the lowest percentage was found in Lagotto Romagnolo with only one dog awarded an SBN of in WP (0.03%, CI: 0.0 to 0.1%). The variability in percentages was greatest among breeds with WP sizes between 1000 and 10,000 (Fig. 3). For example, Sealyham Terrier and Belgian Shepherd Dog (Malinois), with similar WP sizes of 6934 and 7747, had significantly different percentages at 30.1% and 2.0% (CI: 1.7 to 2.3%), respectively, and non-overlapping confidence intervals.

The percentage of dogs with an SBN was significantly lower and consistent in the largest breeds (Supplement 7), with a pooled estimate across the top 10 breeds of 1.6% (CI: 1.2 to 2.0%) and significant variability between breeds ($p < 0.0001$); almost exclusively explained by true variability ($I^2 = 99.9\%$). The highest estimates in the top 10 breeds was found in English Springer Spaniel with 2.8% (95% CI: 2.7 to 2.8%) and Pug with 2.3% (CI: 2.2 to 2.3%), while the lowest estimate was found in French Bulldog with 0.7% (CI: 0.7 to 0.7%).

Despite the low percentage of dogs with an SBN, their use in KC-registered breeding is high, with a total of 439,501 litters out of all 1,560,113 litters (28.2%) across 143 breeds having at least one parent with an SBN (Supplement 4). The pooled percentage was 48.0% (CI: 44.0 to 52.9%), with significant variability between breeds ($p < 0.0001$); almost exclusively explained by true variability ($I^2 = 99.9\%$). The highest percentage of

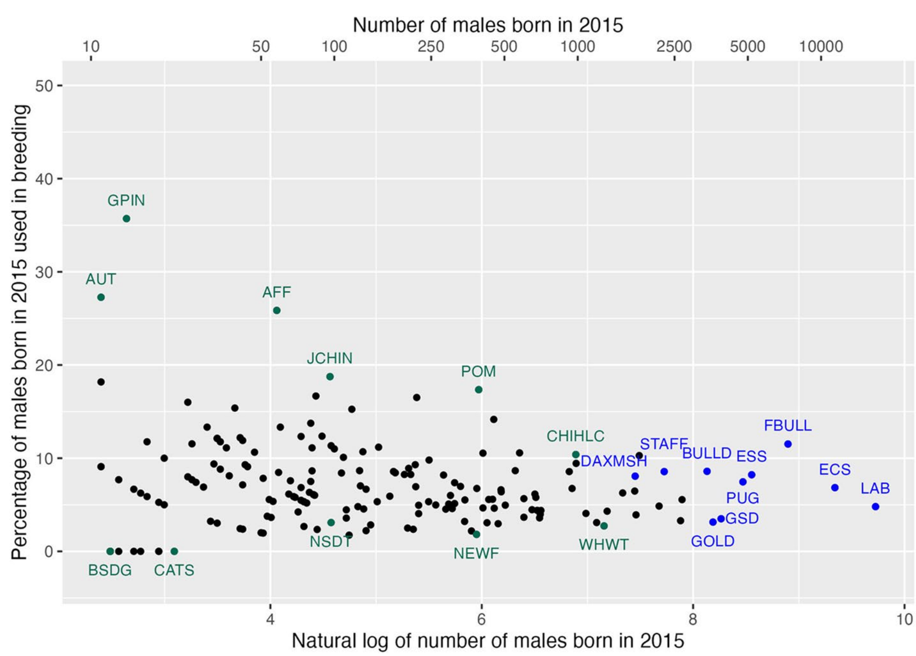

Fig. 2 Relationship between the number of LReg males born in 2015 and the percentage of males used in breeding. Breeds marked in green indicate some of the extreme values at a given census size and include: Affenpinscher (AFF), Australian Terrier (AUT), Belgian Shepherd Dog (Groenendael) (BSDG), Catalan Sheepdog (CATS), Chihuahua Long Coat (CHIHLC), German Pinscher (GPIN), Japanese Chin (JCHIN), Newfoundland (NEWF), Nova Scotia Duck Tolling Retriever (NSDT), Pomeranian (POM), and West Highland White Terrier (WHWT). The top 10 breeds are marked in blue, i.e., Bulldog (BULLD), Dachshund Miniature (Smooth-Haired) (DAXMSH), Cocker Spaniel (ECS), English Springer Spaniel (ESS), French Bulldog (FBULL), Golden Retriever (GOLD), German Shepherd Dog (GSD), Labrador Retriever (LAB), Pug, Staffordshire Bull Terrier (STAFF)

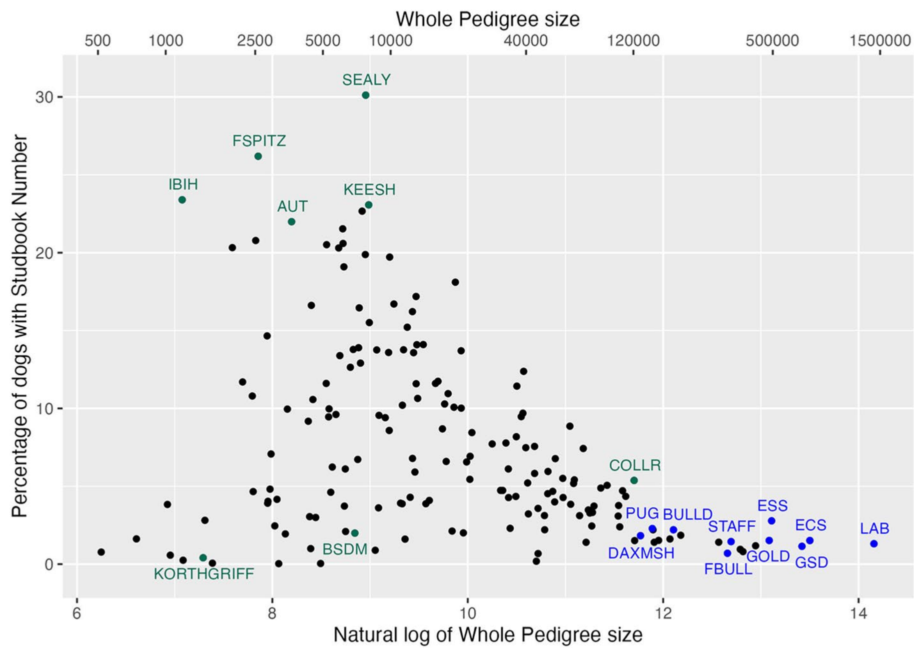

Fig. 3 Relationship between Whole Pedigree size and the percentage of dogs with Studbook numbers. Breeds marked in green indicate some of the extreme values at a given census size and include: Australian Terrier (AUT), Belgian Shepherd Dog (Malinois) (BSDM), Collie (Rough) (COLLR), Finnish Spitz (FSPITZ), Ibizan Hound (IBIH), Keeshond (KEES), Korthals Griffon (KORTHGRIFF) and Sealyham Terrier (SEALY). The top 10 breeds are marked in blue, i.e., Bulldog (BULLD), Dachshund Miniature (Smooth-Haired) (DAXMSH), Cocker Spaniel (ECS), English Springer Spaniel (ESS), French Bulldog (FBULL), Golden Retriever (GOLD), German Shepherd Dog (GSD), Labrador Retriever (LAB), Pug, Staffordshire Bull Terrier (STAFF)

Purpose-bred litters was found in Basenji with 87.1% (CI: 83.6 to 90.2%), while the lowest percentage was found in French Bulldog with 4.3% (CI: 4.1 to 4.5%).

The pooled estimate across the top 10 breeds (Supplement 7) was lower than across all breeds at 20.4% (CI: 13.5% to 29.7%), with significant variability between breeds ($p < 0.0001$); completely explained by true variability ($I^2 = 100\%$). The percentage in French Bulldog at 4.3% (CI: 4.1 to 4.5%) was lower than in any other top 10 breed (Fig. 4). The highest percentage of Purpose-bred litters among the top 10 breeds was found in Golden Retriever with 36.7% (CI: 36.3 to 37.1%).

Across breeds, there has been a decline in the use of dogs with SBNs in KC-registered breeding (Supplement 4). The pooled estimate across 143 breeds revealed that the percentage of Purpose-bred KC-registered litters has declined by 1.6% each year (CI: -2.4 to -0.8%), with the decline more pronounced in the top 10 breeds at -4.8% (CI: -7.7 to -1.9%). In both cases, there was significant variability between breeds ($p < 0.0001$); almost exclusively explained by true variability ($I^2 = 97.4\%$, CI: 97.2 to 97.6% in 143 breeds, and $I^2 = 98.8\%$, CI: 98.4 to 99.1% in the top 10 breeds). The largest decline was found in Italian Greyhound with a -13.8% decline each year (CI: -15.5 to -12.1%), while the largest increase was found in Chesapeake Bay Retriever with a 17.6% increase each year (CI: 13.8 to 21.6%). Nine of the top 10 breeds (Supplement 7) produced a negative trend in the percentage of Purpose-bred litters, with the largest decline found in French Bulldog at -12.4% (CI: -14.5% to -10.2%). Golden Retriever was the only top 10 breed where the trend was not negative, with 0.5% (CI: -0.4 to 1.4%), although this was not significantly different from 0 (Fig. 5).

Figure 6 illustrates the global negative relationship between KC-registered population growth and the changes in the percentage of Purpose-bred litters, although there are some notable outliers, such as Chesapeake Bay Retriever, Australian Shepherd, Glen of Imaal Terrier and Alaskan Malamute.

Imported dogs and their use in breeding over time

Across all Whole Pedigrees (all breeds, all time), there were 55,130 KC-registered dogs (0.005%) imported into the UK from 102 countries. More than 50% were imported from just six countries (Fig. 7), with the highest number originating from Ireland (21.0%), the Russian Federation (8.0%) and Poland (7.1%). While some countries are primary exporters of a specific breed (e.g., Italy contributed only 3.4% of imports across all breeds, but in Maremma Sheepdog, all 73 imported dogs originated from Italy), there are countries that are common exporters of many breeds. Ireland appears in the top

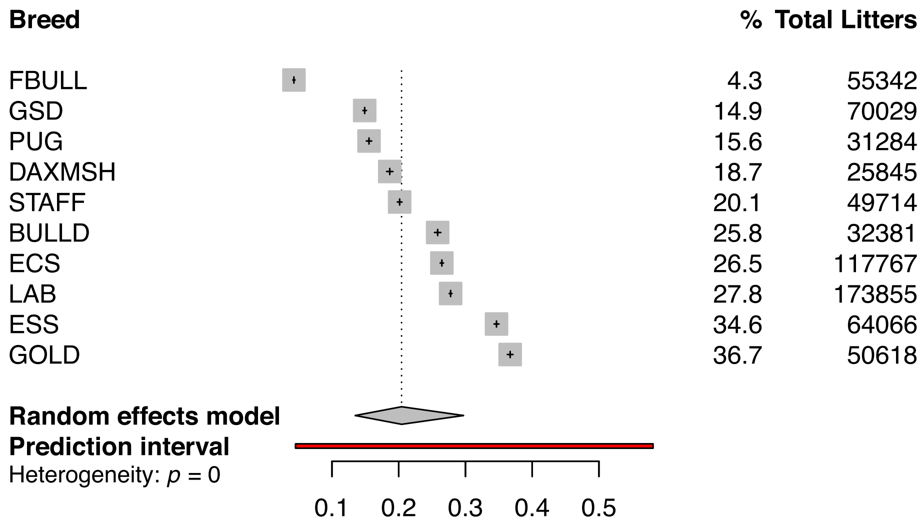

Fig. 4 Forest plot for the meta-analysis across the top 10 breeds for the percentage of Purpose-bred litters where at least one parent holds a Studbook number. Breeds include: Bulldog (BULLD), Dachshund Miniature (Smooth-Haired) (DAXMSH), Cocker Spaniel (ECS), English Springer Spaniel (ESS), French Bulldog (FBULL), Golden Retriever (GOLD), German Shepherd Dog (GSD), Labrador Retriever (LAB), Pug, Staffordshire Bull Terrier (STAFF)

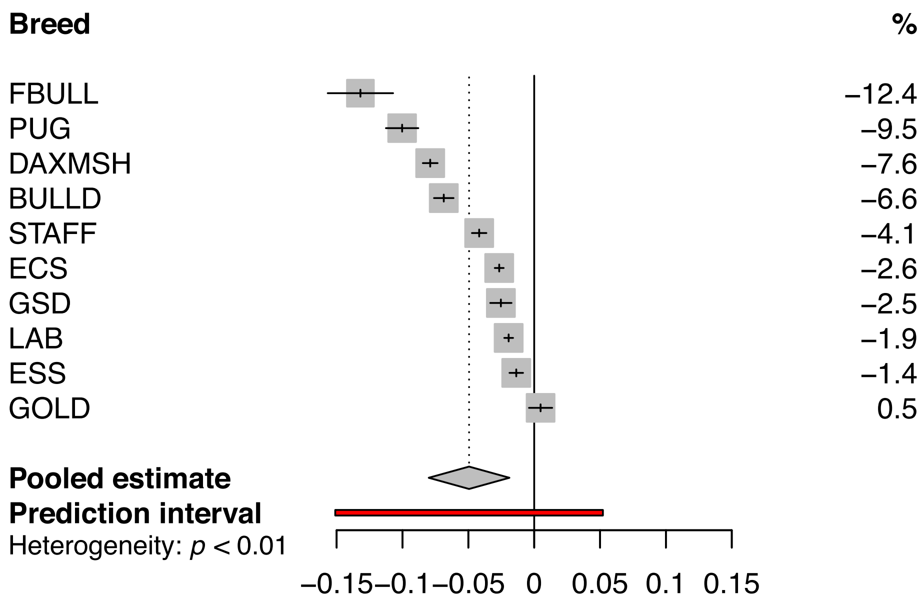

Fig. 5 Forest plot for the meta-analysis across the top 10 breeds for trends in the use of dogs with Studbook numbers in breeding. Breeds include: Bulldog (BULLD), Dachshund Miniature (Smooth-Haired) (DAXMSH), Cocker Spaniel (ECS), English Springer Spaniel (ESS), French Bulldog (FBULL), Golden Retriever (GOLD), German Shepherd Dog (GSD), Labrador Retriever (LAB), Pug, Staffordshire Bull Terrier (STAFF)

three countries for the largest number of breeds (114), followed by France (61) and Poland (60). The Russian Federation is within the top three export countries for 46 breeds, with the highest contributions to KC-registered Pomeranian, Dachshund Miniature (Long-Haired) and Xoloitzcuintle Standard at 44.5, 44.1 and 38.6% of imported dogs, respectively.

The number of KC-registered imports across all breeds has increased significantly since 1990 (Supplement 5). Across the 159 breeds considered, the pooled estimate revealed a 6.5% (CI: 5.9 to 7.1%) increase in the KC-registered imported population each year, with significant variability between breeds ($p < 0.0001$); predominately explained by true variability ($I^2 = 91.2\%$, CI:

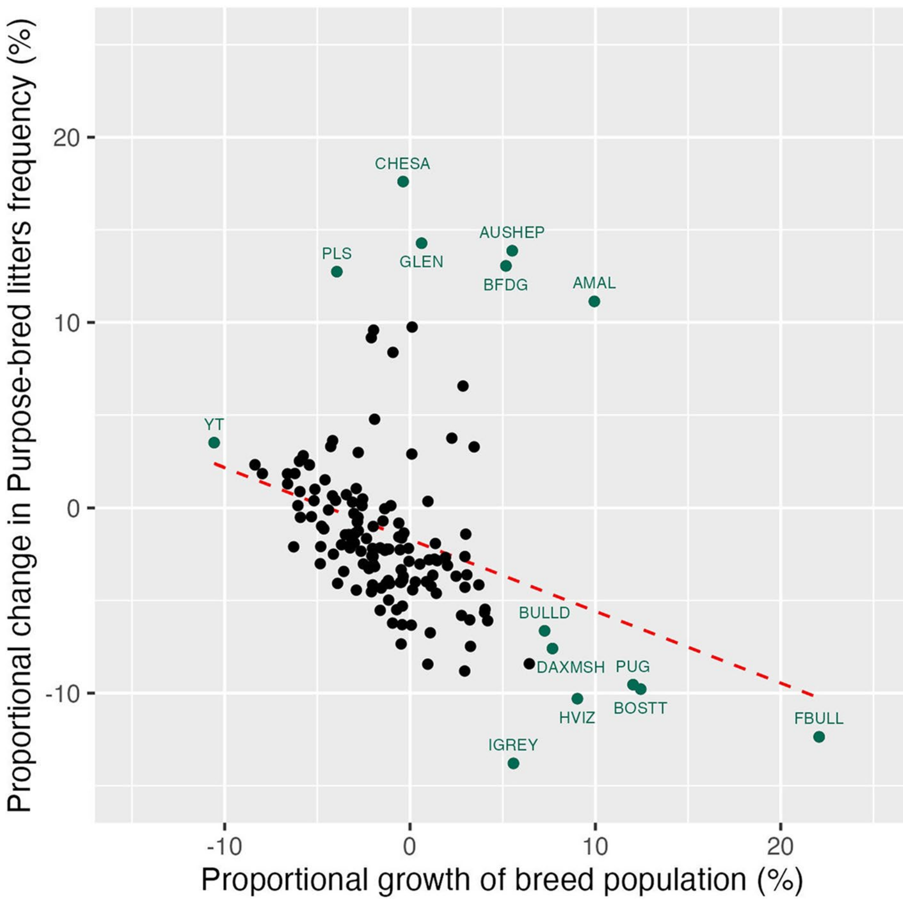

Fig. 6 Relationship between proportional change in population size and the percentage of Purpose-bred litters, with extreme values marked for Alaskan Malamute (AMAL), Australian Shepherd (AUS), Basset Fauve de Bretagne (BFDG), Boston Terrier (BOSTT), Bulldog (BULLD), Chesapeake Bay Retriever (CHESA), Dachshund Miniature (Smooth-Haired) (DAXMSH), French Bulldog (FBULL), Glen of Imaal Terrier (GLEN), Hungarian Vizsla (HVIZ), Italian Greyhound (IGREY), Polish Lowland Sheepdog (PLS), Pug and Yorkshire Terrier (YT)

90.2 to 92.2%). Among 139 breeds in which the trend was significantly different from zero, all have experienced an increase in KC-registered imported population size, from 2.2% in Tibetan Terrier (CI: 0.3 to 4.1%) to 23.6% in French Bulldog (CI: 18.9 to 28.6%). The increase in overall KC-registered import numbers was not linear, with spikes in the number of dogs born in 1999 and 2012 (Fig. 8), which coincided with the changes in legislation related to the importation of animals into the UK.

Given the relatively low number of KC-registered imports, their use in KC-registered breeding is high (Supplement 5). The pooled estimate across 171 breeds revealed that 24.9% of litters in LReg born between 2013 and 2021 had at least one imported parent (CI: 22.0 to 28.0%), with significant variability between breeds ($p < 0.0001$); almost exclusively explained by true variability ($I^2 = 99.5\%$). The estimates ranged from 2.7% in Border Terrier (CI: 2.4 to 3.0%) to 87.2% in Xoloitzcuintle Miniature (CI: 74.2 to 95.2%). The percentage was considerably lower in KC-registered litters born between 1990 and 2012, with a pooled estimate across 149 breeds of 5.9% (CI: 4.9 to 7.0%), with significant variability between breeds ($p < 0.0001$); almost exclusively explained by true variability ($I^2 = 99.6\%$).

Among the top 10 breeds (Supplement 7), the percentage of KC-registered litters born between 2013 and 2021 and with at least one imported parent was lower at 8.9% (CI: 5.6 to 13.8%), with significant variability between breeds ($p < 0.0001$); almost exclusively explained by true variability ($I^2 = 99.9\%$). The within-breed estimates ranged from 3.5% in Cocker Spaniel (CI: 3.3% to 3.7%) to 26.2% in German Shepherd Dog (CI: 25.4 to 27.1%). The corresponding estimate for KC-registered litters born between 1990 and 2012 was 2.3% (CI: 14.3 to 16.8%), with significant variability between breeds ($p < 0.0001$); almost exclusively explained by true variability ($I^2 = 99.9\%$).

The use of imports in KC-registered breeding has increased since 2012 (Supplement 5), with a pooled

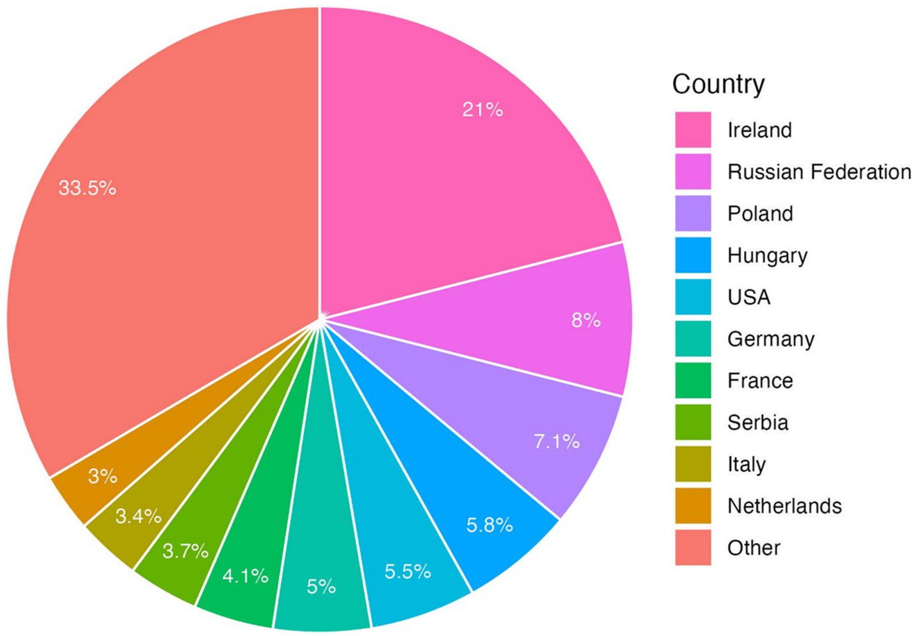

Fig. 7 Pie chart representing the percentage contribution of exporting countries to the overall number of imported dogs across all Whole Pedigrees

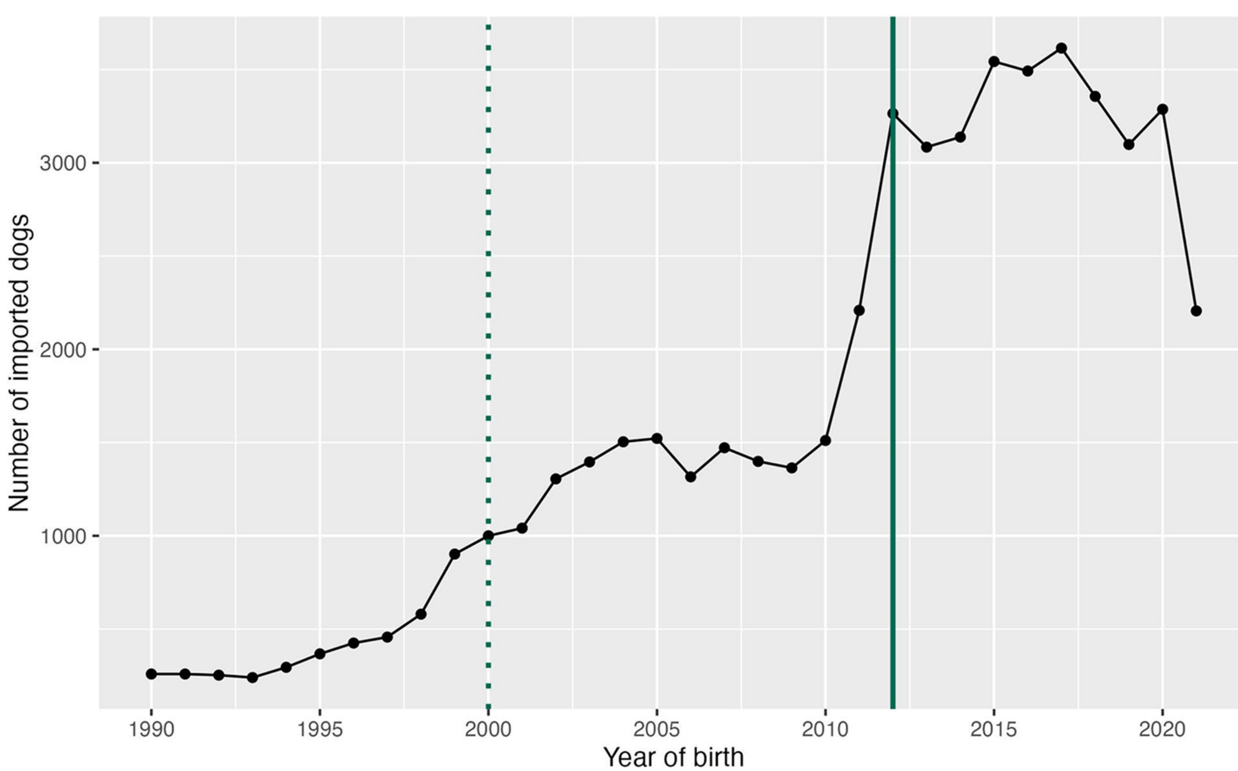

Fig. 8 Overall import numbers by year of birth across all breeds. The vertical lines indicate changes to legislation related to the import of animals into the UK

estimate of 8.4% increase each year (CI: 6.4 to 10.4%) and significant variability between breeds ($p<0.0001$); almost exclusively explained by true variability ($I^2=91.0\%$, CI: 89.9 to 91.9%). The highest increase was found in Jack Russell Terrier with 55.5% (CI: 27.5 to 89.6%), while the largest decrease was found in French Bulldog with -31.3% (CI: -35.9 to -26.5%). The pooled estimate of the trends in the proportion of import-bred litters in the top 10 breeds was not significantly different from 0 at 5.2% (CI: -7.1 to 19.2%), with significant variability between breeds ranging from the -31.3% decline in French Bulldog mentioned above to a 37.0% increase in Staffordshire Bull Terrier (CI: 24.4 to 50.8%).

The trends in the use of imported dogs in the breeding of KC-registered litters born between 1990 and 2012 were similar, with a pooled estimate across 149 breeds of 8.2% (CI: 7.1% to 9.2%) and a pooled estimate for the top 10 breeds of 13.0% (CI: 9.7% to 16.3%), with both showing significant variability between breeds almost exclusively explained by true variability ($I^2=91.9\%$, CI: 90.9 to 92.7% for 149 breeds, and $I^2=90.0\%$, CI: 83.7 to 93.8% for the top 10 breeds).

Sires and their characteristics

The number of KC-registered litters produced by a sire was greater for imported dogs and for dogs that were awarded an SBN. Table 2 presents the results of the meta-analyses for the pairwise comparisons for KC-registered dogs with an SBN and without an SBN, imported and national dogs, imported dogs with an SBN and without an SBN, and imported and national dogs with an SBN. The individual breed results are provided in Supplement 6. In all comparisons, there was a significant difference between the categories of sires; however, significant variability between breeds existed, with a large proportion of variability explained by true variability.

The pooled mean differences were largest when dogs with an SBN were compared with those without an SBN at 2.9 (CI: 2.5 to 3.3) and smallest when imported and national dogs with an SBN were compared at -0.9 (CI: -1.3 to -0.4). Similarly, the within-breed differences were significantly different from zero in the largest number of breeds for the first comparison (84.8%) and lowest for the latter (19.7%).

The differences between sires were more pronounced in the top 10 breeds (Supplement 7), with the exception of the comparison between imports and national dogs, where the pooled mean difference in the top 10 breeds was not significantly different from 0, although a significant difference was found in Bulldog at 5.5 (CI: 2.6 to 8.4), Staffordshire Bull Terrier at 3.9 (CI: 1.9 to 6.0) and German Shepherd Dog at -10.4 (CI: -15.1 to -5.6).

The confidence intervals of I^2 overlapped between pooled estimates calculated for a given sire category comparison based on all breeds, and the top 10 breeds only. However, they did not overlap between the category comparisons. The highest proportion of variability between breeds explained by true differences was found when sires with and without an SBN were compared at $I^2=95.5\%$ (CI: 95.1 to 95.0%), while the lowest proportion was found for imports with or without an SBN at $I^2=61.8\%$ (CI: 54.3 to 68.1%).

The highest producing KC-registered sire across all breeds was an English Springer Spaniel with 381

Table 2 Results of the comparison of the number of litters produced by sires categorised by their origin (imported versus national) and success in activities (sires with or without Studbook numbers). 95% confidence intervals are provided in parentheses

Comparison	Pooled mean difference	I^2	Fraction of breeds with significant difference	Breed with minimum mean difference	Breed with maximum mean difference	Pooled mean difference in top 10 breeds	I^2 In top 10 breeds
Dogs with SBN and without	2.9 (2.5 to 3.3)	95.5% (95.1 to 95.0%)	140/165	Nova Scotia Duck Tolling Retriever -1.8 (-3.3 to -0.4)	Boxer 13.9 (12.0 to 15.7)	7.9 (5.8 to 10.1)	96.4% (94.9 to 97.5%)
Imports and national dogs	1.4 (1.2 to 1.6)	79.2% (76.3 to 81.7%)	83/198	Shetland Sheepdog -2.7 (-4.4 to -1.0)	Hungarian Vizsla 10.6 (6.7 to 14.5)	4.0 (2.8 to 5.3)	78.5% (60.8 to 88.2%)
Imports with SBN and without	2.0 (1.6 to 2.5)	61.8% (54.3 to 68.1%)	41/143	Nova Scotia Duck Tolling Retriever -5.0 (-9.1 to -0.9)	West Highland White Terrier 22.8 (9.4 to 36.2)	5.1 (1.0 to 9.2)	79.2% (62.4 to 88.5%)
Imports and national dogs with SBN	-0.9 (-1.3 to -0.4)	71.0% (65.8 to 75.4%)	29/147	German Shepherd Dog -10.4 (-15.1 to -5.6)	Dachshund Miniature (Long-Haired) 6.1 (3.5 to 8.7)	*Not significant ($p=0.5$)*	*81.1% (66.3 to 89.4%)*

SBN Studbook number

KC-registered litters since 1990 (2286 puppies), compared to the breed median of 1 litter (inter-quartile range IQR = 2). The next highest producing KC-registered sire was a Cocker Spaniel with 299 litters (1591 puppies), compared to the breed median of 2 litters (IQR = 5). The smallest difference between the highest producing sire and the breed median was found in Bloodhound and Australian Silky Terrier, where the highest producing KC-registered sires produced 8 and 9 litters, respectively, compared to the breed medians of 2 litters (IQR = 2 in both breeds).

The pooled mean difference in the number of litters between the 10 highest producing KC-registered sires and the breed median across 175 breeds was 35.2 (CI: 29.3 to 41.0), with significant variability between breeds ($p < 0.001$); almost exclusively explained by true variability ($I^2 = 98.8\%$, CI: 98.7 to 98.9%). The mean difference ranged between 2.4 in Estrela Mountain Dog (CI: 1.7 to 3.1) and 219 in English Springer Spaniel (CI: 167.2 to 270.8) (Supplement 6).

The highest producing KC-registered sires started breeding at a younger age than the breed median at first litter. The pooled mean difference was -6.8 months (CI: -7.6 to -5.9), with significant variability between breeds ($p < 0.001$); predominately explained by true variability ($I^2 = 76.0\%$, CI: 72.3 to 79.2%). The age differences ranged between -23 months in Flat Coated Retriever (CI: -25.2 to -20.8) and 10.3 months in Anatolian Shepherd (CI: -6.2 to 26.7) (Supplement 6).

Less than 1 in 4 (22.3%) of KC-registered highest producing sires born between 1990 and 2021 were imported, although this proportion increased by 33.5% to 29.8% for the currently alive highest producing sires (Fig. 9A). The number of breeds in which none of the 10 highest producing sires were imported dropped from 55 to 17, out of the 175 breeds considered (Supplement 6).

More than half (55.1%) of the KC-registered highest producing sires born between 1990 and 2021 were awarded an SBN, and in 18 (of 173) breeds all the highest producing sires had an SBN. This proportion declined by 43.0% to 31.6% for sires presumed to be currently alive (i.e., born since 2015), with no breed having all the current highest producing sires with an SBN (Fig. 9B).

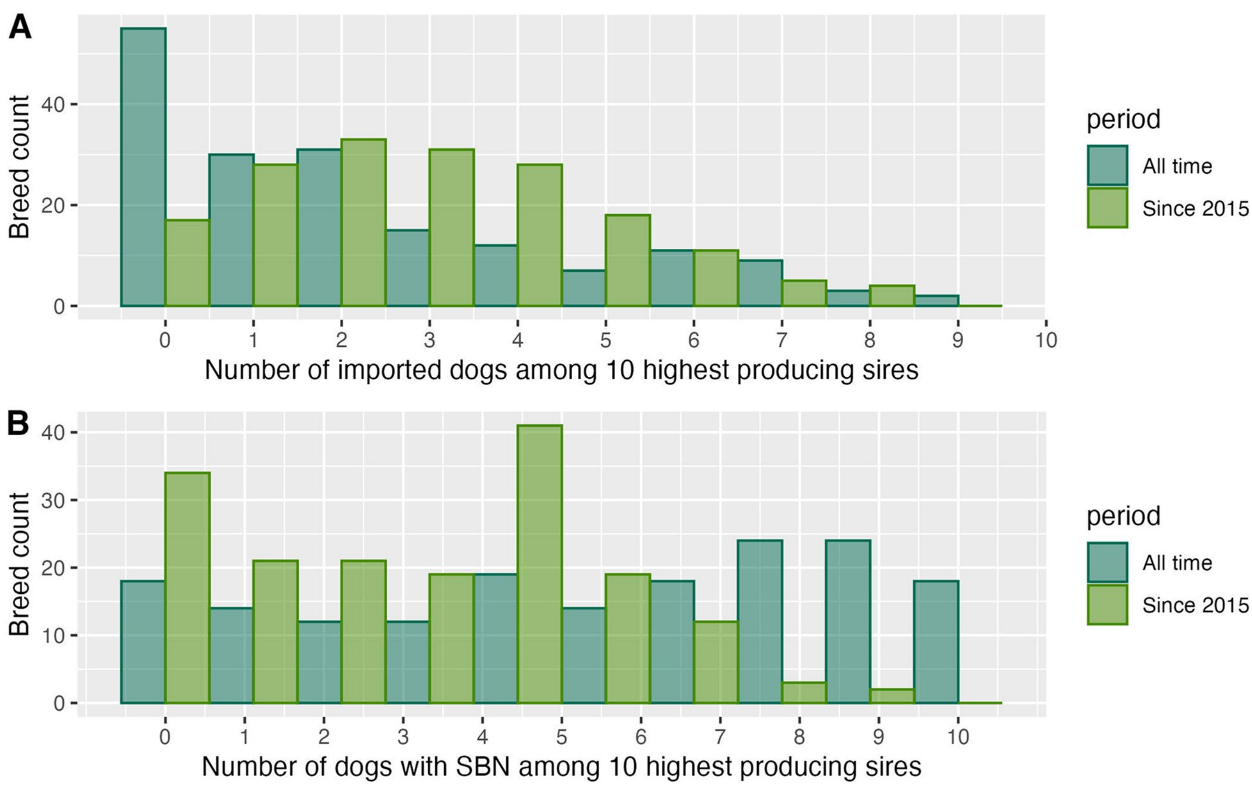

Fig. 9 Number of imported dogs (**A**) and dogs with an SBN (**B**) among the ten highest producing sires across 175 (A) and 173 (B) breeds with at least 50 sires born between 1990 and 2021. In dark green are the numbers calculated based on data from 1990 to 2021, while in light green are the numbers calculated based on the highest producing sires born since 2015

Discussion

Using comprehensive datasets for all 222 pedigree dog breeds recognised by The Kennel Club in the UK between 1990 and 2021, we tested whether all breeds can be represented by a single pedigree dog population and derived a number of demographic reference values describing this single pedigree dog population. However, we identified significant variability in the demographic values that were almost always explained by true differences between breeds, as opposed to sampling error in the within-breed estimates.

We have shown that the sustainability of the KC-registered pedigree dog population is at risk from declining population sizes, small percentages of dogs used in breeding, and the use of popular sires. However, the increasing numbers of imported dogs and their increasing use in breeding may have a restorative effect on genetic diversity. These results provide a framework for the development of new strategies for the management of the genetic diversity of KC-registered pedigree dog populations in the UK. However, individual breed plans must be tailored to unique circumstances in each breed, as a consequence of the significant and consistently high variability found between breeds.

Our analysis of the decline in KC-registered pedigree dog populations are expected to have produced more accurate estimates than those reported previously, e.g., [7, 8, 41], which were typically based on overall registration statistics or on a subset of the most common breeds. As a result, previous estimates suffer from bias caused by the power-law distribution of registration statistics, where few numerically large breeds dominate many smaller breeds [42]. We have shown that the KC-registered pedigree dog population, as represented by estimates derived from all breeds, is declining in size, despite the lack of a significant trend in the top 10 breeds. The decline observed in our data is modest; however, it is likely underestimated due to the so-called "pandemic puppy-boom" of 2020–2021 [43], where the number of puppies bred temporarily increased.

As the general population of pet dogs in the UK has increased over time, from 7.6 M in 2011–2012 to 12 M in 2021 [44], the observed decline in KC-registered pedigree dog population size indicates a declining popularity of pedigree dogs, despite the increasing popularity of pet dog ownership. There are two potential explanations for the results of our study. Firstly, the estimate may reflect the declining popularity of KC-registered pedigree dogs only, whereas the population of unregistered purebred dogs may be experiencing different trends. Several breeds, such as Greyhound [21, 45] and Jack Russell Terrier [27], retain a large, traditionally working dog population, with few dogs registered with KC. However, there are no reports available comparing the trends in the popularity of registered and unregistered purebred dogs in the UK over the last three decades; therefore, this explanation cannot be verified. Secondly, the estimate could reflect a true decline in the popularity of all pedigree dogs, in favour of mixed and crossbred dogs. This explanation is supported by recent analyses of pet dog populations in the UK, which revealed an increasing popularity of so-called designer crossbreeds, such as 'Cockapoos'—a cross between the Cocker Spaniel and Poodle, due to the perception of their improved health compared with that of purebred dogs, and hypoallergenicity [27, 43, 46].

The changes in KC-registered pedigree population size could be expected to have an impact on the proportion of dogs used in breeding, and this has been observed in some cases, e.g., in French Bulldog, where 1 in 3 KC-registered dogs born between 2005 and 2015 were used in breeding, which coincided with the exponential growth in the popularity of the breed in the same period. However, this relationship was not consistent between breeds, with both a low percentage of breeding dogs in breeds apparently increasing in size (e.g., Belgian Shepherd Dog (Malinois) and Nova Scotia Duck Tolling Retriever) and a relatively high percentage in breeds declining in popularity (e.g., Japanese Chin). The overall estimate of 13.7% of the population used in breeding is considerably lower than the 20.0% reported previously for 10 breeds using KC data [21]. The difference could be due to a true decline in the proportion of KC-registered dogs used in breeding, either due to different breeding practices or a general decline in KC-registered population sizes, the choice of breeds used in the previous study, or different treatment of pedigree data. Our estimate pertains to KC-registered dogs born in the UK and since 1990 only, whereas the estimate in [21] used Whole Pedigrees and was thus inflated by ancestors of imported dogs, as well as historical dogs (i.e., those born before 1985), which were typically entered into KC's electronic database only if they were bred from. Our estimate is close to the estimates of 13–14% reported previously for KC-registered population of Labrador Retriever and Cavalier King Charles Spaniel born between 1989 and 2000 [47].

Both the decline in the overall KC-registered pedigree population and the low percentage of KC-registered dogs used in breeding may be linked to generally negative attitudes towards dog breeding [48–50]. The adoption of dogs from shelters is seen as a more ethical choice than the purchase of a dog from a breeder [48, 49], and ownership, let alone breeding, of a pedigree dog has been stigmatised [51]. This is driven by the perception of pedigree dog breeding contributing to overpopulation of pet dogs in shelters and rescue organisations [48], despite the percentage of purebred dogs in shelters being low [52].

Furthermore, routine neutering has been widely treated as a gold-standard and mark of responsible dog ownership [53] with a recent estimate showing that approximately 44% of dogs in the UK are neutered [27]. The blanket recommendations for neutering have recently been called into question, both in the context of the impact on the genetic diversity of populations [53] and the health impact on individual dogs [53–56]. Maintaining large populations, with small breeding inputs from a large number of individuals, is key for the maintenance of genetic diversity and prevention of the accumulation of deleterious recessive alleles [3, 32]. As such, the decline in KC-registered pedigree population size and low percentage of KC-registered dogs used in breeding reported in this study emphasise that a change in attitudes toward pedigree dog breeding is necessary to ensure their sustainability.

In addition to the small size of the breeding population, the use of popular sires is frequently reported to be a main cause of reductions in genetic diversity and dissemination of recessive disorders [22, 33, 57, 58]. Different publications use various approaches to identify popular sires, such as sires exceeding a given number of progeny [21], unequal contributions of sires and dams [29], or the percentage of puppies produced by a sire over a given period [59]. Here, we present evidence of popular sires in the form of a pooled estimate of the difference of 35 litters produced between the 10 highest producing KC-registered sires and the median for the breed.

Despite the risks associated with the use of popular sires in both closed and open populations of pedigree dogs, there are currently few management strategies in place to combat it. In 2010, the Federation Cynologique Internationale issued a recommendation that no sire should produce more than 5% of puppies born in a 5-year period, which has been adopted by few countries. However, this recommendation proves challenging for both rare and common breeds. In our data, there were 33 breeds with < 20 litters born between 2017 and 2021; thus, even if each litter had a unique sire, all would violate the 5% recommendation. The same recommendation would also not capture any of the highest producing sires in the top 10 breeds, including the highest producing KC-registered sire of all time, who, at the height of his productivity, produced 2.5% of puppies born between 1990 and 1994. An alternative solution would be to tailor the threshold limit given the size of the breed population; however, such limits would pose a challenge with sometimes volatile changes in registration numbers between years. Furthermore, it would not account for the relatedness between sires and their replacements.

The limits placed on the number of litters per sire are designed to promote the contributions of other sires. However, the benefits of such methods shown in simulations typically assume that the replacement sires are selected at random from the population [25, 34]. This is unlikely in pedigree dog breeding, where the replacements are more likely to be drawn from the relatives, e.g., sons, of a sire that has reached the allowed limit. In our data, the highest producing sires often showed close relationships with each other; e.g., two of the 10 highest producing sires in Labrador Retriever born since 2015 were sons and a third dog was a grandson, of one of the 10 highest producing sires of all time in this breed, born in 2008. Where a sire's replacement is selected from his close relatives, the effect of the imposed limits may be contrary to intended, with a reduced generation interval and an increase in inbreeding rates [25]. It could be argued that differential limits be applied to genetically unique sires as opposed to high producers from a lineage of high producers across multiple generations. As such, management strategies based on relatedness estimates of the sire to the rest of the population have been suggested as the most efficient [25, 60, 61].

In parallel, attention must be given to the motivation behind breeders' choices to overuse particular sires. The ability to identify dogs that are likely to become popular sires before they produce large numbers of offspring offers a unique opportunity to open a pre-emptive dialogue with owners and breeders on the risks associated with this breeding practice. We have shown that across the entire period considered, KC-registered dogs that were successful in activities such as conformation shows or field trials were popular in breeding, as evidenced by high percentages of litters where at least one parent had an SBN, significant differences in the number of litters produced by sires with and without an SBN, and high numbers of dogs with an SBN among the 10 highest producing sires in each breed. However, the attractiveness of such dogs has declined considerably in recent years, particularly in breeds that are increasing in popularity. The inverse relationship between trends in popularity and the use of SBN dogs in breeding shown here confirms the anecdotal belief that breeds that increase in popularity do so primarily in the so-called "pet" population, i.e., the population not bred for a specific purpose other than being a family pet, whereas breeds declining in popularity tend to remain in the hands of breeders who, at least partially, select breeding dogs on the basis of their success in specific activities.

We have not formally differentiated between conformation shows, field trials, working trials, agility and obedience; however, it is clear that the preferred activities differ between breeds. Interestingly, in breeds where both conformation shows and field trials are common, such as in Cocker Spaniel, English Springer Spaniel and Labrador

Retriever, the field trial champions are over-represented among the highest producing sires (Table 3).

Recently, selection for performance and conformation has been shown to be a driver of genetic differentiation within a sample of 608 Labrador Retrievers, with dogs reported by owners to be "Show/Companion" having lower genetic diversity than dogs selected for performance [57]. Considering that the sample contained dogs from multiple countries and had undisclosed pedigree status, it is difficult to assess whether these findings would be replicated in the UK Labrador Retriever population. If they were, however, it would indicate that practices other than the use of popular sires contribute to the reduced diversity in the population partaking in conformation shows, and conversely, some genetic rescue events counter-act the presence of popular sires in the subpopulation of field trials dogs. These results indicate the need for further exploration of possible population stratification within breeds and the likely differences in breeding cultures within subpopulations.

The comparison of KC-registered all-time and recent highest producing sires indicates that, at least in some breeds, the stud dog preferences are shifting from dogs with SBNs to imported dogs. However, a growing number of national highest producing sires that do not participate in KC-governed activities or at least have not gained SBN or champion titles, indicates that new criteria determine the attractiveness of stud dogs. The investigation of the additional characteristics of the highest producing sires in each breed is beyond the scope of this paper; however, examination of only the two most popular breeds indicates that the criteria are likely to be breed specific. The current highest producing KC-registered sire in Labrador Retriever, which at the time of writing of this paper has produced 2084 puppies and nearly 4000 descendants across 4 generations at less than 7 years of age, has neither conformation nor activity titles; however, he is advertised as clear from over 200 monogenic conditions, the majority of which have no relevance for the breed. Interestingly, all 10 of the current highest producing KC-registered sires in Labrador Retriever originate from field trials lines (with field champions within 2 generations of pedigree), and all have been tested for at least some of the recommended health tests for the breed, with generally good results. The widespread use of these extensively health-tested sires illustrates an imbalance between selection for testable health conditions and understanding the risks associated with the use of popular sires. In contrast, in French Bulldog, all 10 highest producing KC-registered sires, with 600–1200 puppies each, are either of colour not accepted within the breed standard or are carriers of such colours. French Bulldog, and a few other breeds that have recently risen in popularity, have seen a concurrent increase in fashion for so-called designer colours, not accepted by the breed standard, and which would therefore disqualify a dog from the conformation show ring. In 2021, 69.5% of French Bulldog and 53.3% of Bulldog registered with KC were of non-breed standard colour.

These two examples show the departure from the traditions of selecting dogs successful in conformation or field trials, in favour of dogs excelling in novel categories, while retaining the disproportionate use of individual dogs. While selection on the basis of health test results in Labrador Retriever is ethically more understandable than selection on the basis of coat colour in French Bulldog, in both cases, the individual dogs carrying the desired characteristics have been disproportionately used in breeding and will have a negative impact on the genetic diversity of their respective breeds.

In contrast, the increased use of imported dogs in KC-registered breeding reported here, and elsewhere for a small subset of breeds [19], is likely to have a beneficial effect on the genetic diversity of UK populations. Geographic isolation has been shown to drive genetic divergence between subpopulations of some breeds; thus, imported dogs are expected to introduce novel genetic variants to UK populations. Historically, some breed communities have been reluctant to import dogs due to perceived risks of introducing undesirable genetic variants [62]; however, these risks can now be managed with judicious use of genetic health testing, which appears to have shifted the perception of breeders in favour of using such dogs in breeding, as shown in our data.

Table 3 Number of Field and Conformation Champions among the 10 highest producing sires and across the Whole Pedigree (WP) in 3 popular breeds

Breed	# Within the 10 highest producing sires		Total # of champions in WP (% of all champions)	
	Field Champions	**Conformation Champions**	**Field Champions**	**Conformation Champions**
Cocker Spaniel	7	1	415 (38.2%)	658 (60.6%)
English Springer Spaniel	9	0	866 (57.4%)	644 (42.6%)
Labrador Retriever	6	0	803 (51.0%)	753 (47.8%)

It should be noted that our estimates of the imported population of pedigree dogs is likely an underestimate of the UK-wide population of imported dogs. Dogs imported by puppy buyers for purposes other than breeding or performance in KC-governed activities are less likely to be registered with KC, as their origins will be already documented by the exporting kennel club.

The extent of the genetic rescue that migrant animals offer will depend on the degree of divergence between the UK and exporting countries' populations of a specific breed, which will in turn depend on the history of the breed and the rate of gene flow [19, 63]. Consistent gene flow between small subpopulations of a breed in different countries will likely result in low levels of differentiation, as has been shown for the Nordic Spitz [33], Leonberger [64] and Bernese Mountain Dog [65]. Where the degree of divergence between geographically isolated populations is low, the increased use of imported animals is unlikely to influence genetic diversity. Moreover, it will likely lead to an underestimation of pedigree-based coefficients of inbreeding and an overestimation of the overall genetic diversity within breeds [32] due to the limited depth of the export pedigrees provided by exporting kennel clubs. One solution to this problem is to maximise pedigree completeness by forming global pedigree databases, with tracking of the pedigrees ideally extending to true breed founders [19]. This has been done in a few breeds, e.g., in the Irish Wolfhound [66], Icelandic Sheepdog [63] and Leonberger [64], thanks to considerable efforts of the breed enthusiasts. However, this task may prove considerably more difficult, or in some cases unrealistic even, in numerically large breeds. Another solution would be to change the commonly used methods of calculating inbreeding and kinship estimates, for example, by utilising approaches that differentiate recent dogs with unknown ancestors from true breed founders by using the concept of metafounders [67]. Finally, pedigree-based estimates of inbreeding could be enhanced by genomic estimates, which are free from bias associated with pedigree depth [68].

Although we have shown that the migration of dogs to the UK has increased over the last few decades, the continuation of this trend heavily depends on geopolitical and legal circumstances. The importation of dogs has become far more attractive to the UK's breeders with the amendments to the PETS introduced in 2012. The amendment reduced the age at which dogs originating from European Union and listed countries could be brought to the country to a minimum of 15 weeks of age, as compared to the previous 6 months of age, with the latter age now being re-considered under the Animal Welfare (Import of Dogs, Cats and Ferrets) Bill [69]. The increase in the popularity of imported animals owing to the PETS regulations of 2012 has been connected to an increase in the illegal puppy trade [70], as well as an increase in the number of veterinary patients presenting with exotic conditions [71]. In contrast to imported dogs purchased online [72], which often belong to designer crossbreeds [73], imported dogs registered with KC represent a highly traceable group of animals, with the details of owners and breeders recorded by both KC and the exporting country's kennel club. Although the proposed Bill aims to target the illegal smuggling of puppies younger than 15 weeks, it is highly likely that it will also influence the numbers of legally imported, and traceable, dogs.

The future numbers of KC-registered imported dogs are also in question in view of the current geopolitical situation. As of the 1st of March 2022, KC no longer accepts registrations of dogs imported from the Russian Federation and Belarus in response to the invasion of Ukraine [73]. It is unclear at this time whether this ban will result in a decrease in the number of KC-registered imports or whether breeders will find alternative export sources to replace the high numbers of dogs previously imported from the Russian Federation.

This study presented several estimates that could be used to describe the overall KC-registered pedigree dog population in the UK over the last three decades. However, the significant variability in these estimates between breeds calls for caution in their use for the construction of management strategies for individual breeds. Previously, the breed's original purpose was shown to have an impact on breeding practices, such as the number of litters produced [17] or the prioritisation of certain aspects when breeding animals are selected [31]. Although we have not formally differentiated breeds by their original function, we have seen variability even between breeds of the same group – e.g., Skye Terrier and Glen of Imaal Terrier, two vulnerable terrier breeds of British and Irish origin, which have a considerably different percentage of dogs with an SBN at 19.0% in Skye Terrier and 4.0% in Glen of Imaal Terrier. We have shown that the breeds' census size has impact on some of the parameters, with the largest KC-registered breeds having generally more uniform estimates. However, considerable and sometimes extreme variation exists between KC-registered breeds of small and medium population sizes. The variability between breeds for the demographic estimates investigated in this paper complements the variability detected in genetic diversity estimates reported previously [17, 29, 32, 64] and further strengthens the need for the development of breed-specific management strategies.

This study has several limitations, and more information could be gleaned from a more granular approach. For example, breeds could be divided into functional groups, such as herding or toy breeds, by characteristics such as physical size, skull shape, or even coat colour. Furthermore, individual dogs' reproductive outputs could be compared against other characteristics, e.g., their health testing status. Although a more detailed approach could provide further explanation of breed cultures, in many cases, it would be difficult to apply them uniformly across all breeds. Our objective was to identify global trends common to all KC-registered pedigree dogs over the studied period, which could thus be used in the management of all KC-registered breed populations.

Furthermore, we used SBNs to identify dogs successfully competing in activities governed by KC as a proxy for dogs bred for specific purposes and as opposed to dogs bred solely to be a family companion. We are aware that the SBN records do not represent all dogs participating in activities, regardless of whether those activities are governed by KC or not. However, there are currently no other means of identifying such dogs other than through owner-reported surveys, and those methods are highly unlikely to yield the depth of data necessary to provide reliable estimates across all breeds.

Conclusions

In this study, we used a meta-analysis of comprehensive datasets to explore the demographic characteristics of the KC-registered pedigree dog population, with a particular focus on the characteristics of dogs used in breeding. This approach enabled us to establish reference values for a single pedigree dog population representing all breeds considered here, without the estimates being biased toward those derived from the few, most prolific breeds. Our results show that management strategies for pedigree dog populations need to account for the declining sizes of KC-registered populations and should focus on the reproductive outputs of individuals, both through increasing the number of dogs used in breeding and limiting outputs from the most prolific sires. Furthermore, management strategies must account for the increasing number of imported dogs used in breeding, which will impact the accuracy of the estimates of inbreeding and genetic diversity. We have shown that some characteristics of sires can be used to highlight individuals more likely to produce larger numbers of offspring; however, we have also shown that those preferred characteristics are changing. Most importantly, the high variability between breeds demonstrates that all strategies must be tailored to the unique circumstances of each breed, accounting not only for their different genetic diversity reserves but also for their highly variable demographic parameters and differing breeding cultures.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40575-025-00142-1.

Supplementary Material 1. List of 222 breeds and their abbreviations, and the corresponding sizes of Whole Pedigrees, Breed Register and Litter Registrations.

Supplementary Material 2. Within-breed estimates of proportional change (1990–2021 and 2010–2021).

Supplementary Material 3. Within-breed percentage of dogs bred from for both sexes born between 2005 and 2015, and just males born in 2015.

Supplementary Material 4. Within-breed count of dogs with Studbook numbers, also expressed as percentage of Whole Pedigree. Number and percentage of Purpose-bred litters, and the percent change in the proportion of Purpose-bred litters over time.

Supplementary Material 5. Within-breed proportional growth of imported dog population. Number and percentage of Import-bred litters, as well as percent change in the proportion of Import-bred litters over time.

Supplementary Material 6. Within-breed mean differences in the number of litters produced by sires in different categories. Within-breed mean difference in age at first litter, and in the number of litters produced by 10 highest producing sires and breed median. The number of imported sires, and sires with studbook numbers among the 10 highest producing dogs in each breed.

Supplementary Material 7. Within-breed estimates for the top 10 breeds.

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Authors' contributions

JI conceived and developed the methodology, curated the data, conducted the analyses and wrote the manuscript. PR transferred within-breed estimates into breed reports and provided comments on the concept of the analyses. DT provided input on the statistical methods and helped draft the manuscript. All authors have read and approved the final manuscript.

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Data availability

The within-breed estimates used as input in the meta-analyses are available in Supplementary materials. The pedigree records of individual dogs registered with The Kennel Club, and which were used in to derive the within-breed estimates, are available for research purposes in anonymised format.

Declarations

Ethics approval and consent to participate

Authors declare that ethics approval was not needed for this study. By registering their dog with The Kennel Club, owners give their permission for the dog data to be used for the purposes of research according to the Kennel Club's Privacy policy:
https://www.thekennelclub.org.uk/policies/privacy-policy/. There was no research on live animals, humans, or inclusion of identifiable human data.

Consent for publication

Not applicable.

Competing interests
JI and PR are employed by The Kennel Club.

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