# Pedigree analysis of Irish greyhounds

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## Introduction

Analyses of the pedigree of the Irish greyhound population are dated (McCarthy and Blennerhasset, 1973) with no recent published analysis available. Based on a relatively small sample population of Irish racing greyhounds, McCarthy and Blennerhasset (1973) documented an accumulation of inbreeding of <1% per generation or less than 0.22% per year. A paucity of information also exists globally of the pedigree structure and inbreeding levels in dogs. In an analysis of the genetic variability among nine French breeds of dogs, Leroy et al. (2006) reported a mean inbreeding coefficient (of dogs with at least both parents known born between the years 1997 and 2001) per breed of between 3.3% (Bouledogue Francais) and 12.4% (Basset fauve de Bretagne). Nielen et al. (2001) reported breed average inbreeding coefficients of Dutch dogs born in 1994 of 5.6%, 4.6%, 6.1%, 1.8% and 7.0% for Bernese Mountain, Bouvier des Flanders, Boxer, Golden Retriever, and Kooiker Dogs breeds, respectively. Voges and Distl (2009) documented breed average inbreeding levels of 4.5%, 6.8% and 9.5% in three scent-hound breeds (i.e., Bavarian mountain hound, Hanoverian hound and Tyrolean hound) born between the years 1992 and 2004.

Inbreeding may be defined as the probability that two alleles at any locus are identical by descent (Malécot, 1948). Inbreeding occurs when related individuals are mated to each other. The practice of inbreeding generally results in inbreeding depression, which may be described as the decline in performance in inbred animals (Falconer and MacKay, 1996). The expected decline in performance associated with the accumulation in inbreeding is due to an increase in homozygosity at the genomic level. The greater level of homozygosity increases the likelihood of lethal recessive mutations existing in the homozygous state but greater homozygosity also affects performance through loci that exhibit an advantage at the heterozygote state. Increased inbreeding however may not always have deleterious repercussions for animal performance, especially if inbreeding accumulates slowly concurrent with selection (McParland et al., 2009).

The objective of this study was to quantify the genetic diversity and related population parameters of the modern Irish greyhound population. The results could be useful to benchmark the Irish population against other populations as well as benchmark against international guidelines on the ideal genetic diversity. Such information could also be useful for informing future studbook management.

**Materials and methods**

*Data*

Pedigree information was available on 626,275 greyhounds with a recorded year of birth between 1900 and 2013, inclusive; 85 dogs had an unknown date of birth. The frequency distribution of records by year of birth is in Figure 1.

*Pedigree Analysis*

Pedigree analyses were undertaken using the Pedig (Boichard, 2002) software suite. The depth of pedigree known per individual was measured in complete generation equivalents (CGE) and computed as $\sum_{i=1}^{n_j} \frac{1}{2^{g_{ij}}}$ , where $n_j$ = number of ancestors of greyhound j, and $g_{ij}$ is the number of generations between individual j and its ancestor i (Sorensen et al., 2005). The inbreeding coefficient (F) per greyhound was calculated using the Meuwissen and Luo (1992) algorithm. Following the calculation of the inbreeding coefficients for all greyhounds, the annual mean inbreeding of all greyhounds was calculated. The annual rate of inbreeding over a given time period was calculated using simple linear regression through a given time period. Mean annual generation intervals were calculated for each of the four selection pathways: sire to male offspring, sire to female offspring, dam to male offspring, and dam to female offspring. The effective population size ($N_e$) may be defined as the number of breeding greyhounds that would lead to the observed increase in inbreeding if they contributed equally to the next generation (Wright, 1923). The effective population size was calculated as: $N_e = \frac{1}{2\Delta F_y * L}$ , where $\Delta F_y$ is the annual rate of inbreeding in the population (from the regression analysis) and L is the generation interval (Hill, 1972).

The marginal contribution of the top 100 ancestors to the population of greyhounds born between the years 2010 and 2013, inclusive was calculated. The expected genetic contribution of an individual to the reference population may be defined as the probability than an allele selected at random from the reference population originated from that ancestor (James, 1972). The marginal contribution of an individual was also calculated which quantifies its contribution to this reference population, which has not previously been explained by greater contributing individuals (Boichard et al., 1997). Founder greyhounds were defined for the purpose of this study as dogs with unknown parents. The effective number of founders (Lacy, 1989) is the number of equally contributing founders that would be expected to produce identical genetic diversity to that observed in a given population; in the present study the reference population was dogs born between the years 2010

and 2013, inclusive. The effective number of founders equals the actual number of founders if all founders contribute equally to the reference population; otherwise the former is smaller, but increases as the contribution among founders is more balanced. Nonetheless, the effective number of founders does not account for bottlenecks in a pedigree. For this reason the effective number of ancestors (Boichard et al., 1997), which is the minimum number of ancestors (including founders and non-founders) required to explain the genetic diversity of the reference population, was also calculated. Finally, the effective number of founder genomes (MacCluer et al., 1986; Lacy, 1989), which is the number of equally contributing founders with no random loss of founder alleles in the offspring that would be expected to produce a level of genetic diversity identical to that observed in the reference population, was calculated.
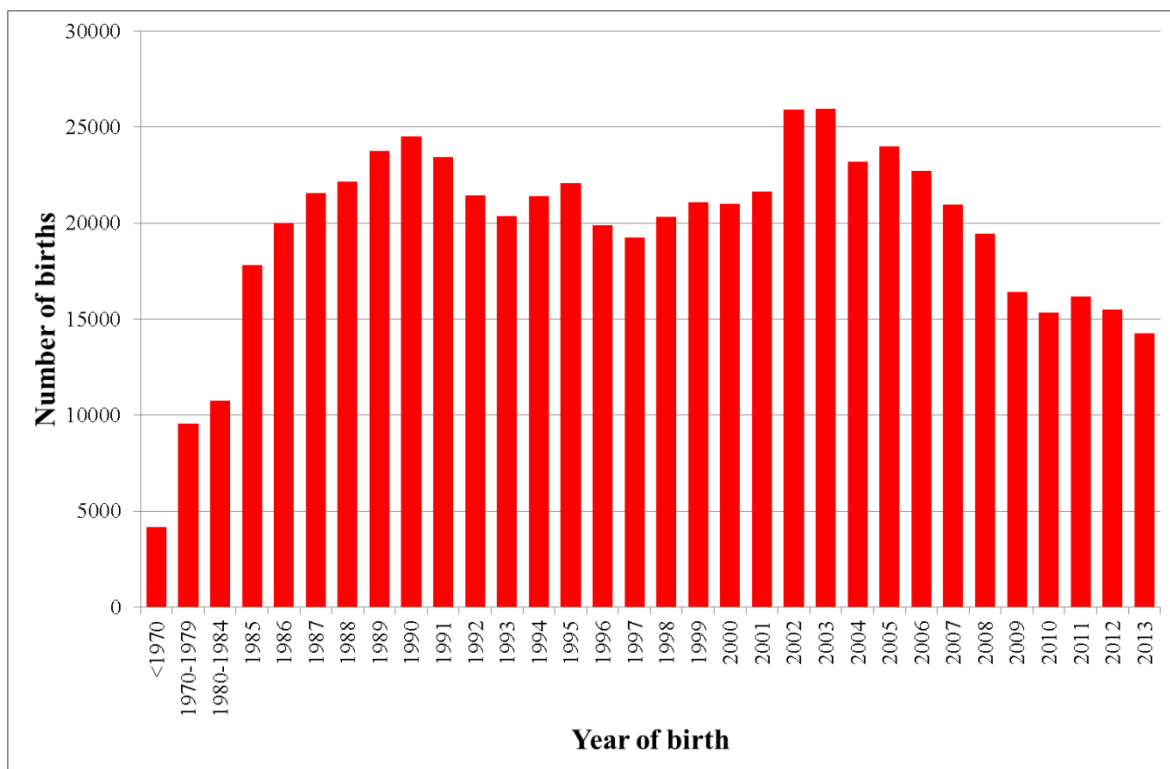


**Figure 1.** *Number of records included in the pedigree by year of birth.*

**Results and Discussion**

Depth of pedigree has a large influence on calculated inbreeding coefficients. In the extreme case, a greyhound with only parents known must have a calculated inbreeding coefficient of zero. Figure 2 summarises the mean number of complete generation equivalents for male and female greyhounds by year of birth. Clearly the depth of pedigree is increasing with time. Greyhounds born in recent years have, on average, the equivalent of 6 complete generations of pedigree information

recorded. The extent of pedigree completeness in the Irish population is slightly less than reported by Leroy et al. (2006) for most of the 9 French dog breeds between the years 1997 and 2001 which were included in their study. The extent of pedigree completeness in the Irish greyhound population is nonetheless similar to what exists for most of the Irish dairy and beef cattle breeds (McParland et al., 2007).
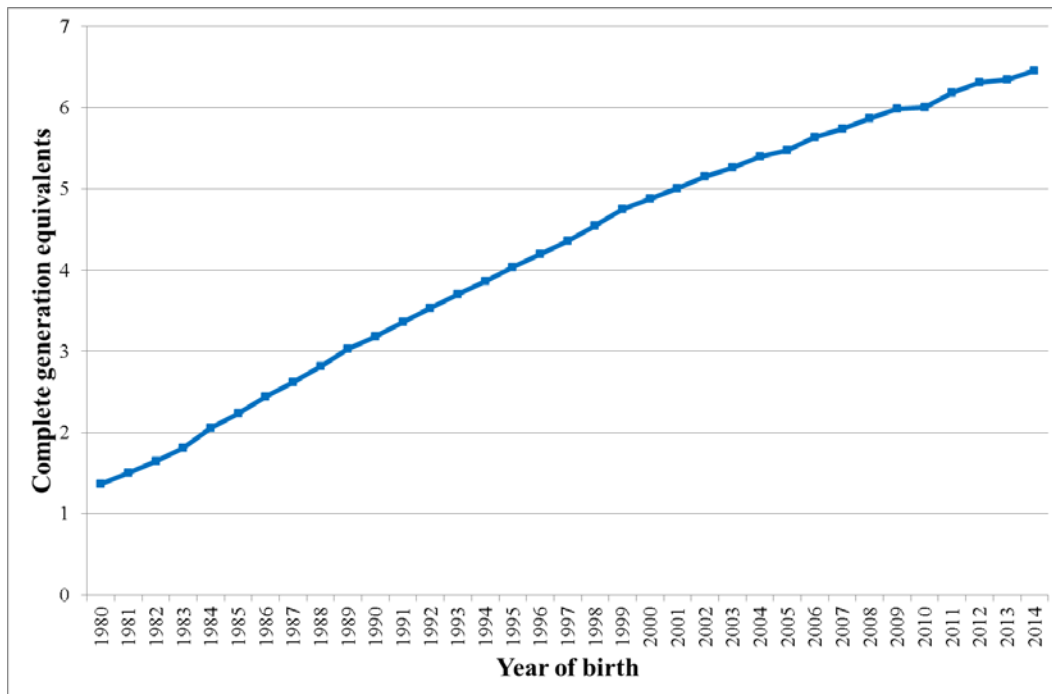


**Figure 2.** *Population average number of complete generation equivalents by year of birth.*

The average age of sires of males, sires of females, dams of males, and dams of females for each year of birth of the offspring is in Figure 3; the average age of sires of males, sires of females, dams of males and dams of females that subsequently become parents themselves (i.e., the generation interval) for each year of birth is in Figure 4. The average age of sires has increased almost consistently since 1999 by, on average, 0.1 years annually. The trend in average age of dams is less obvious but is remaining relatively stable at approximately 5 years of age. The existence of a longer generation interval in sires suggests that males are, on average, older than females when their progeny are born. This could be due to the males being either older when they first produce progeny, or the males are used as sires for a longer period than females. In fact, based on the population of greyhounds born between 2010 and 2013, the sires were, on average, 0.45 years older than the dams when their first progeny were born; the average difference in years between the earliest and latest born greyhound offspring for sires and dams of the reference years (i.e., 2010 to 2013) was 2.7 and 1.9 years, respectively. The generation intervals in the Irish greyhound population for dams of offspring, who in turn become parents, was similar to reported by Leroy et al. (2006) in 9 different French dog breeds but the generation interval of sires to produce progeny was

approximately one year greater than documented in the 9 French dog breeds (Leroy et al., 2006). Nonetheless, corroborating the results of the present study, Leroy et al. (2006) also documented a longer generation interval of the sire-to-offspring pathway compared to the dam-to-offspring pathway.

*Inbreeding*

The median inbreeding level of Irish greyhounds by year of birth is in Figure 5; also included is the median annual inbreeding level of the population when confined to only include dogs with at least 3 full generations of pedigree information. It is generally not the inbreeding level *per se* which is informative but the rate of accumulation of inbreeding. This is because inbreeding itself is a function of depth of pedigree known, although the pedigree information available in the present study was very deep. Nonetheless, the mean inbreeding in the recent population of Irish greyhounds was considerably less than the breed average reported by Nielen et al. (2001) in Ducth Bernese Mountain (5.6%), Bouvier des Flanders (4.6%), Boxer (6.1), and Kooiker Dogs (7.0%) born in the year 1994, but similar to the inbreeding level of 1.8% reported in Dutch Golden Retrievers (Nielen et al., 2001). The inbreeding levels in the modern Irish greyhound were also considerably lower than reported across 9 French dog breeds in the period 1997 to 2001 (3.3% to 12.4%) documented by Leroy et al. (2006) as well as the breed average inbreeding levels of between 4.5% and 9.5% in German populations of Bavarian Mountain hounds, Hanoverian hounds and Tyrolean hounds born between the years 1992 and 2004 which were the years investigated (Voges and Distl, 2009). The mean genetic relationship between the sires and dams of Irish greyhounds born between 2010 and 2013 was 2.4% suggesting that, if mating was random, a mean inbreeding coefficient of 1.2% would be expected in this population; the fact that the actual calculated mean inbreeding of this population of offspring was double this (i.e., 2.4%) suggests assortative mating favouring the mating of related animals.

Inbreeding accumulated in the Irish greyhound population from the year 1994 to 1999 after which it declined until the year 2004 and has been accumulating almost consistently thereafter. It is not clear why the level of inbreeding declined in the early 2000's. The registered population of greyhounds did increase substantially in this period (Figure 1) but the decline in inbreeding level was not attributable to a reduction in pedigree recording (Figure 2). Figure 6 shows the number of sires and number of dams of greyhounds born in each year. A noticeable increase in the number of sires and dams existed in 2002 and 2003; this increase in genepool is a likely contributor to the temporary reduction in population wide inbreeding levels.The rate of increase in median inbreeding levels between the years 2009 and 2013, inclusive, estimated using simple least squares linear regression,

was 0.15% per year. Using the weighted mean generation interval across all four selection pathways of greyhounds that subsequently go on to reproduce (i.e., 6.10 years), this equates to an accumulation of inbreeding per generation of 0.89% per generation. This rate of inbreeding per generation is just below the recommended maximum of 1% per generation (FAO, 1998). The rate of accumulation of inbreeding per generation in the Irish greyhound population is between that documented by Voges and Distl (2009) for German Bavarian Mountain hounds (0.69%) and Hanoverian hounds (0.98%) but more than half the rate reported in Tyrolean hounds (1.88%; Voges and Distl, 2009).
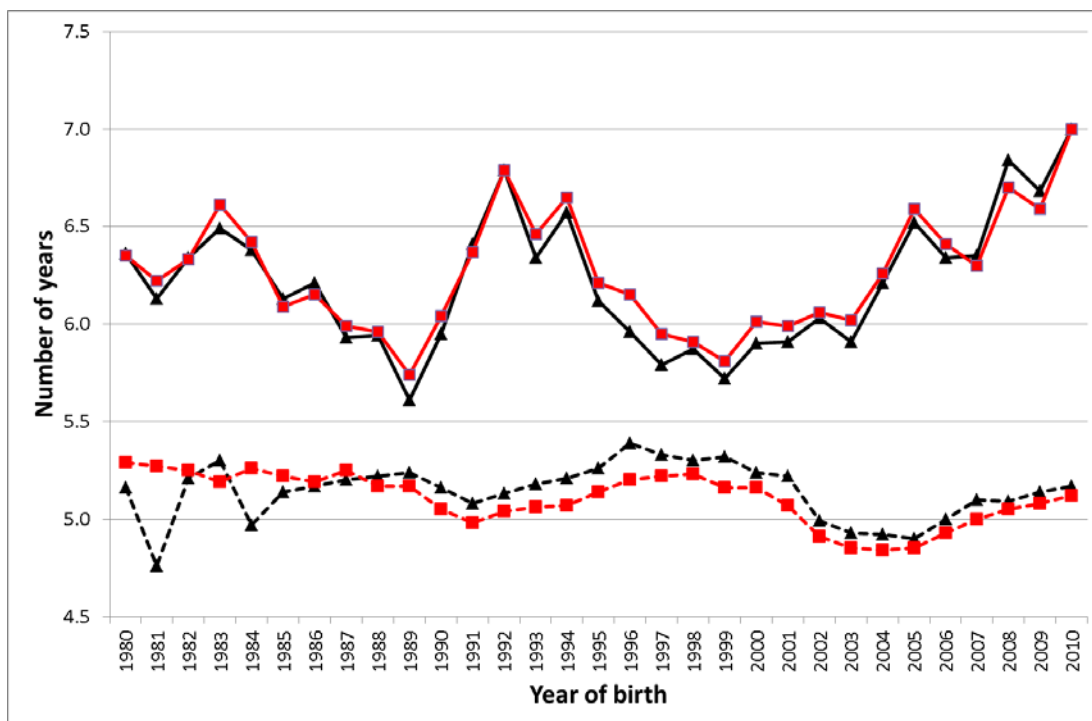


**Figure 3.** *Average age of sires of males (black triangle; continuous line), sires of females (red square; continuous line), dams of males (black triangle; broken line) and dams of females (red square; broken line) by year of birth.*

The rate of accumulation of inbreeding in the Irish greyhound population in past 5 years equates to an effective population size of 56 greyhounds. This effective population size is less than the average (median) effective population size of 68 (70) reported across 9 French dog breeds (Leroy et al., 2006). The effective population size in the Irish greyhound is close to the 50.9 documented by Voges and Distl (2009) for German Hanoverian hounds born between 1992 and 2004 but less than the respective statistics for the Bavarian mountain hounds (72.7), but greater than documented for the Tyrolean hounds (26.5; Voges and Distl, 2009). Nonetheless the annual rate of increase in inbreeding in the Irish greyhound population (0.15% per year) between the years 2009 and 2013 is less than the average of 0.21% reported across 9 French dog breeds (Leroy et al., 2006) between the years of 1997 and 2001 which were investigated in their study.

The maximum inbreeding per individual in the population by year of birth is also depicted in Figure 5. Although the annual trend was erratic, the maximum inbreeding in recent years was generally between 15% and 30%.
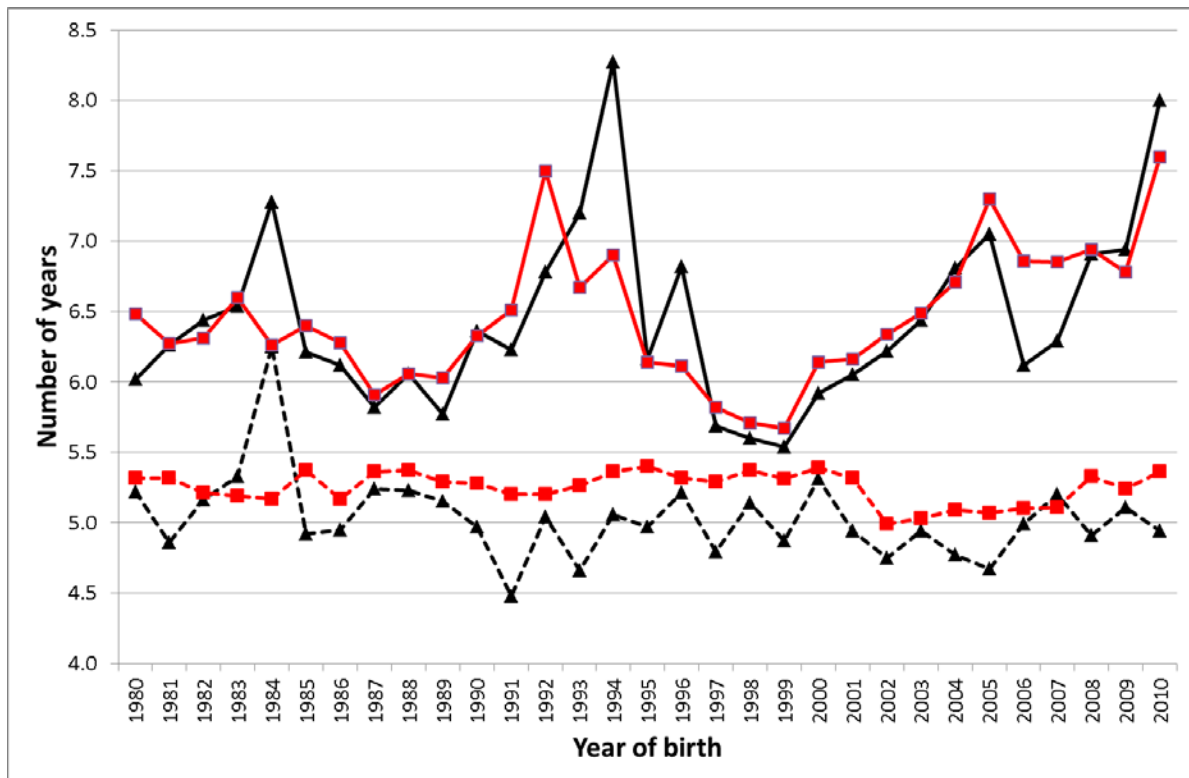


**Figure 4.** *Generation interval of sires of sires (black triangle; continuous line), sires of dams (red square; continuous line), dams of sires (black triangle; broken line) and dams of dams (red square; broken line) by year of birth.*

Figure 7 summarises the proportion of the Irish greyhound population that are inbred categorised into different degrees of inbreeding. Ninety-five percent of greyhounds born in 2013 were inbred to some extent. This should not be viewed as an alarming statistic as some degree of detected inbreeding is almost inevitable, especially in populations where deep pedigree information exists. The number of ancestors a non-inbred greyhound has is $2^n$ where n is the number of generations. Therefore a greyhound with 10 generations of recorded pedigree has a potential 1,024 (i.e., $2^{10}$) ancestors; a greyhound with 20 recorded generations has >1 million (i.e., $2^{20}$) potential ancestors. Hence, the likelihood of common ancestors existing somewhere in the pedigree is highly likely and difficult to avoid. Of the 94% of inbred greyhounds born in 2013, 54% were <0.5% inbred. Nonetheless the proportion of greyhounds between 2.5% and 10.0% inbred is increasing in recent years and should be monitored.

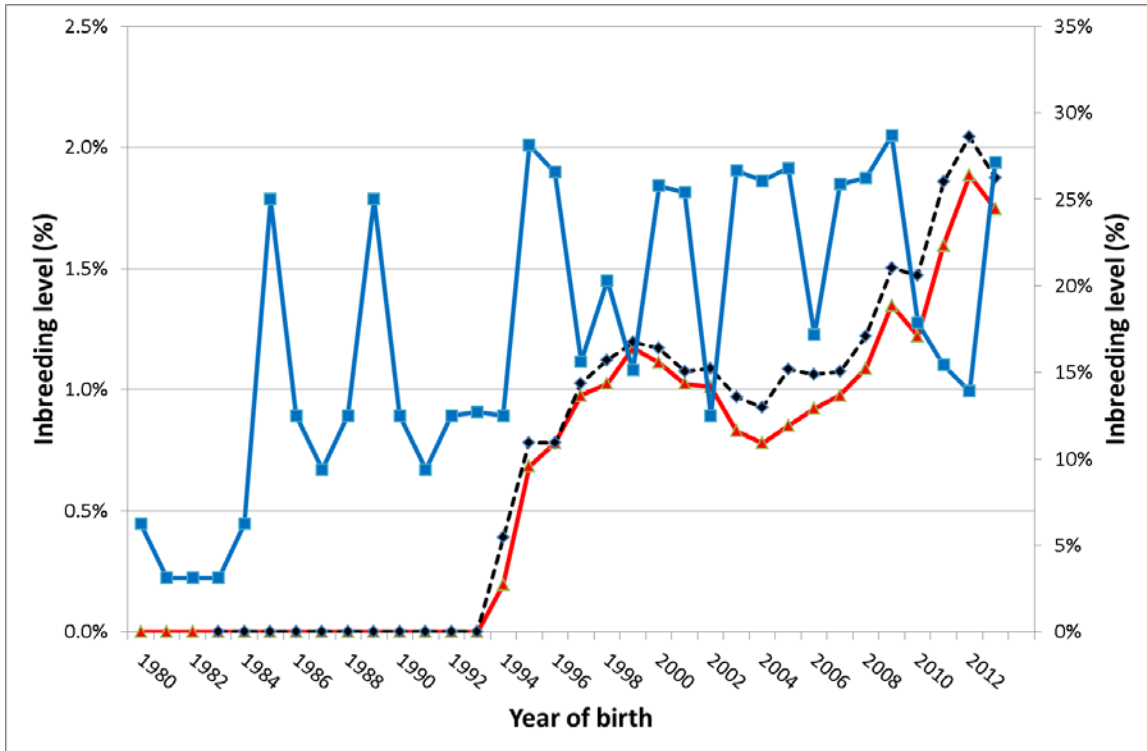**Figure 5.** *Median inbreeding level per year for the entire Irish greyhound population (red triangle) or greyhounds with at least 3 full generations of pedigree information (black diamond); also included is the individual greyhound maximum inbreeding level by year of birth (blue).*
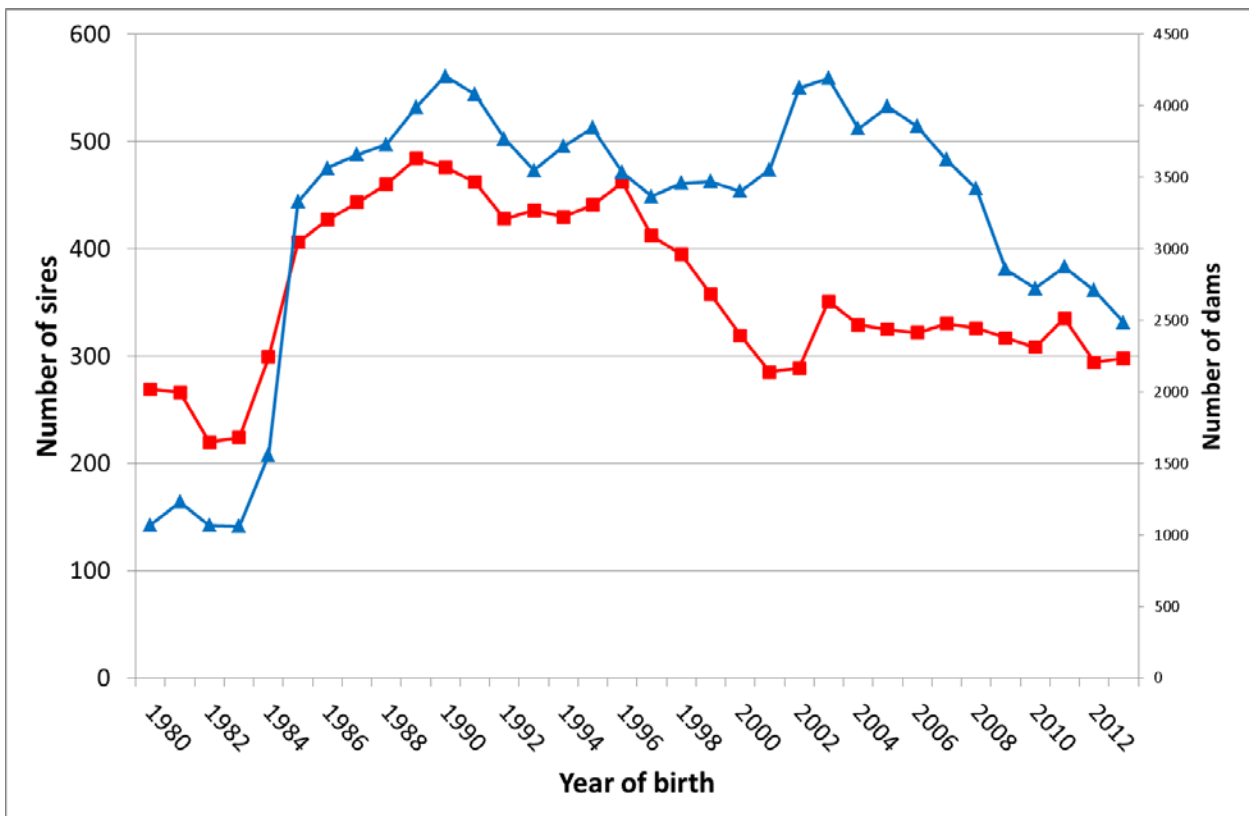


**Figure 6.** *Number of sires (red squares) and number of dams (blue triangles) by year of birth of the progeny*
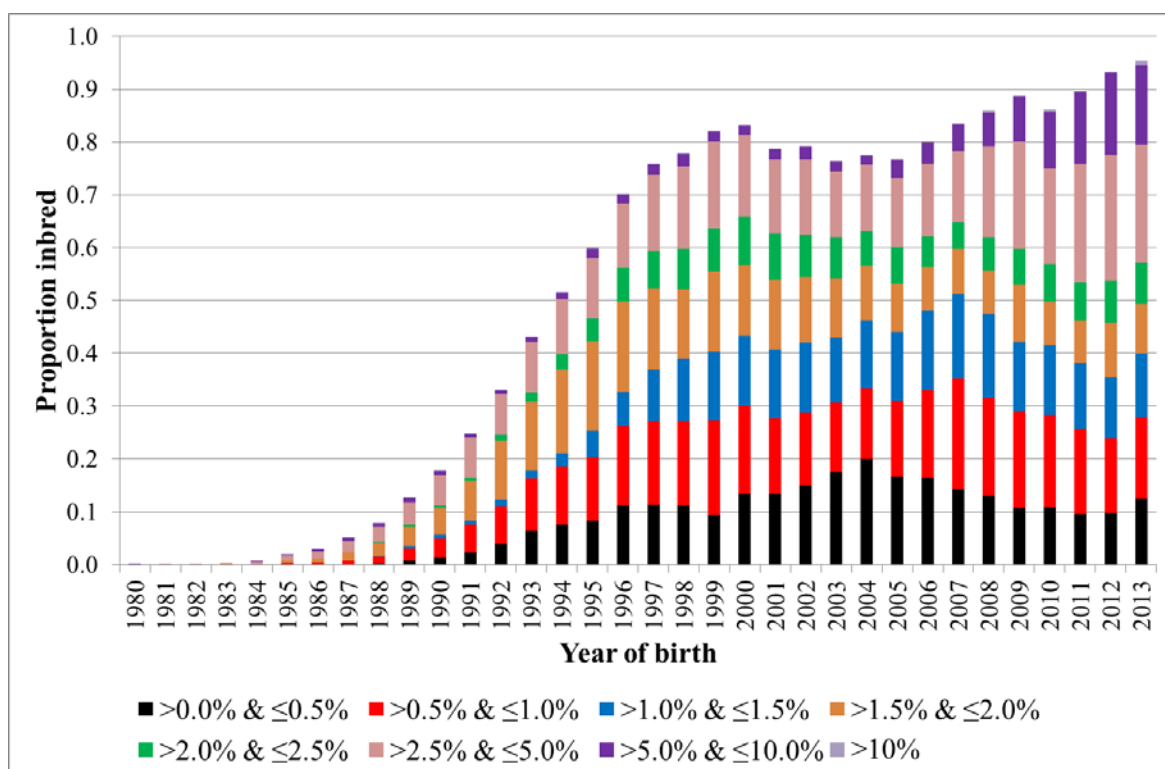
**Figure 7.** *Proportion of greyhounds inbred by category of inbreeding for each birth year.*

Information was available on whether the dog was used for track or coursing for the years of birth of 2010 to 2013, inclusive. The mean inbreeding level of course dogs was approximately 4 times greater for coursing dogs than for track dogs (Figure 8).

### Probability of gene origins

The expected cumulative contribution of individual greyhounds to the genome of males and females born between the years 2010 and 2013 is in Figure 9; the list of top 10 contributors to both the male or female population is in Table 1. One hundred ancestors are expected to, on average, contribute 94% of the genome of Irish males and females born between the years 2010 and 2013; 10 ancestors contributed 44% of the genome. The dog Head Honcho, born in 1990, is expected to, on average, have contributed 7% to the genome of both males and females born between 2010 and 2013, inclusive (Table 1). One female, Rainbow High, was in the top ten contributors to dogs born between 2010 and 2013 (Table 1). Thirteen greyhounds are expected to have contributed 50% of the genome of the Irish greyhounds born between 2010 and 2013; this is within the range (3 to 14) reported by Leroy et al. (2006) from an analysis of 9 different French dog breeds but is also similar to documented by McParland et al., (2007) in Irish Angus and Simmental cattle. Similar to observed in

the present study, 54.4%, 65.2% and 77.9% of the genome of Bavarian mountain hounds, Hanoverian hounds and Tyrolean hounds born between the years 1992 and 2004 could be traced back to just 10 animals (Voges and Distl, 2009). The list of top 10 contributors to both the male or female track and coursing dog population is in Table 2 and 3, respectively.
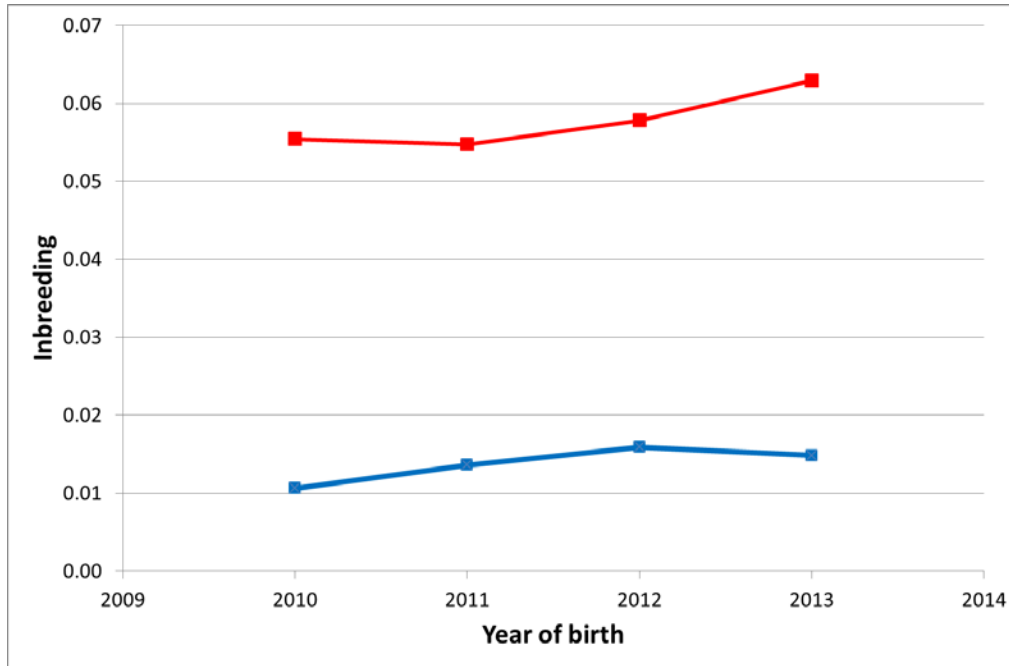


**Figure 8.** *Mean annual inbreeding level for coursing (red squares) and track (blue squares) born between 2010 and 2013.*
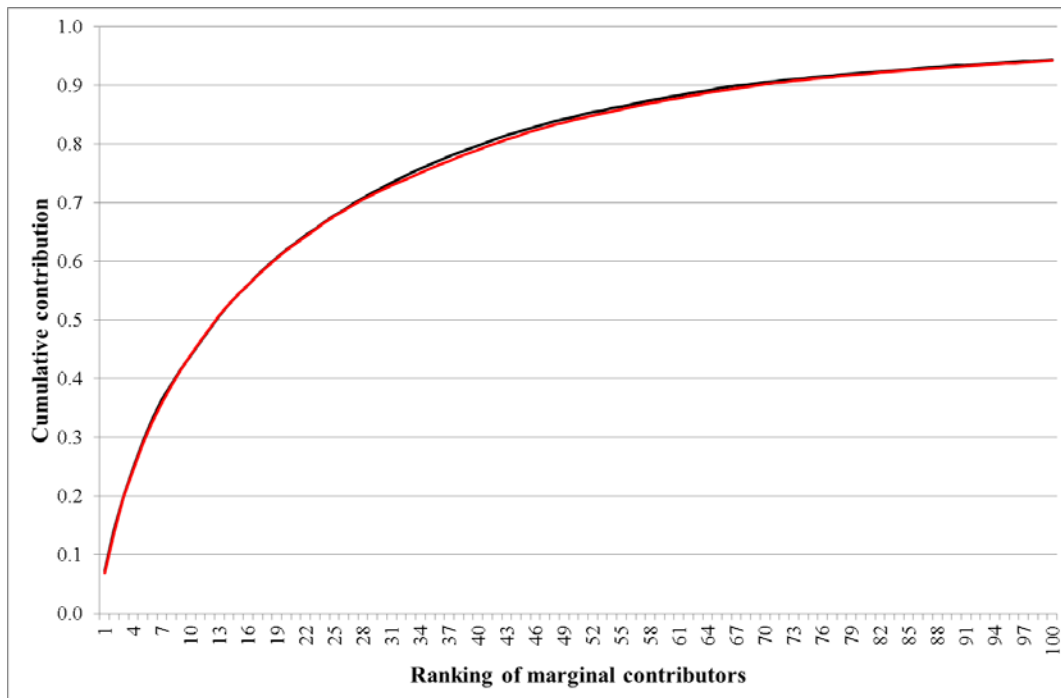


**Figure 9.** *Cumulative contribution of ancestors to the pedigree of male (black) and female (red) dogs born in the period 2010 to 2013, inclusive.*

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The effective number of founders may be defined as the number of equally contributing founders expected to produce the same genetic diversity as the reference population being studied (Lacy 1989). The effective number of founder greyhounds to the population of males born between the year 2010 and 2013 was 88.0; the corresponding statistic for females was 88.8. The effective number of genomes contributing to the male population born between the years 2010 and 2013 was 19.25; the corresponding statistic for females was 19.5. The effective number of founders in the Irish greyhound is slightly greater than reported by Leroy et al. (2006) for 9 different French dog breeds (range of 6.9 to 75.9) with the exception of 91.3 for the Basset fauve de Bretagne breed. The effective number of founder genomes in the Irish greyhound population is also larger than reported by Voges and Distl (2009) in three scent-hound breeds in Germany (4.32 to 10.85).

The effective number of ancestors contributing to the reference population of males and females was 35.9 and 36.4, respectively which is greater than reported in three scent-hound breeds in Germany (Voges and Distl, 2009). The ratio of effective founders to effective ancestors in the Irish greyhound population investigate is 2.4. Ratio values documented by Voges and Distl (2009) in three scent-hound breeds in Germany varied from 1.3 to 2.1.

**Table 1.** *List of the top 10 contributing ancestors, and their contributions, to the male and females born between the years 2010 and 2013, inclusive.*

| Ancestor | Date of birth | Gender | Male | | | | Female | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Rank | Total contribution | Marginal contribution | Cumulative contribution | Rank | Total contribution | Marginal contribution | Cumulative contribution |
| HEAD HONCHO | 01/07/1990 | Male | 1 | 0.0728 | 0.0728 | 0.0728 | 1 | 0.0692 | 0.0692 | 0.0692 |
| LARKHILL JO | 04/09/1995 | Male | 2 | 0.0685 | 0.0685 | 0.1413 | 2 | 0.0661 | 0.0661 | 0.1353 |
| BRETT LEE | 17/01/1999 | Male | 3 | 0.0591 | 0.0591 | 0.2004 | 3 | 0.0631 | 0.0631 | 0.1984 |
| SAND MAN | 01/08/1973 | Male | 4 | 0.0565 | 0.0479 | 0.2483 | 4 | 0.0554 | 0.0472 | 0.2456 |
| IM SLIPPY | 01/05/1981 | Male | 5 | 0.0459 | 0.0459 | 0.2942 | 5 | 0.0448 | 0.0448 | 0.2904 |
| SPIRAL NIKITA | 08/11/1994 | Male | 6 | 0.0424 | 0.0371 | 0.3313 | 6 | 0.0411 | 0.0359 | 0.3263 |
| RAINBOW HIGH | 01/01/1990 | Female | 7 | 0.0341 | 0.0341 | 0.3655 | 7 | 0.0336 | 0.0336 | 0.3599 |
| KINLOCH BRAE | 03/08/2005 | Male | 8 | 0.0307 | 0.0259 | 0.3914 | 8 | 0.035 | 0.0295 | 0.3894 |
| STAPLERS JO | 12/06/1993 | Male | 9 | 0.0592 | 0.025 | 0.4163 | 10 | 0.0583 | 0.0252 | 0.4405 |
| WESTMEAD HAWK | 02/05/2003 | Male | 10 | 0.0263 | 0.0232 | 0.4395 | 11 | 0.0266 | 0.0235 | 0.464 |
| HONDO BLACK | 22/07/1999 | Male | 11 | 0.0228 | 0.0228 | 0.4623 | 9 | 0.0258 | 0.0258 | 0.4153 |

**Table 2.** *List of the top 10 contributing ancestors, and their contributions, to the male and females track dogs born between the years 2010 and 2013, inclusive.*

| Ancestor | Date of birth | Gender | Male | | | | Female | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Rank | Total contribution | Marginal contribution | Cumulative contribution | Rank | Total contribution | Marginal contribution | Cumulative contribution |
| HEAD HONCHO | 01/07/1990 | Male | 1 | 0.0816 | 0.0816 | 0.0816 | 1 | 0.0786 | 0.0786 | 0.0786 |
| LARKHILL JO | 04/09/1995 | Male | 2 | 0.0770 | 0.0770 | 0.1586 | 2 | 0.0745 | 0.0745 | 0.1531 |
| BRETT LEE | 17/01/1999 | Male | 3 | 0.0669 | 0.0669 | 0.2255 | 3 | 0.0719 | 0.0719 | 0.2250 |
| IM SLIPPY | 01/05/1981 | Male | 4 | 0.0517 | 0.0517 | 0.2771 | 4 | 0.0508 | 0.0508 | 0.2758 |
| SAND MAN | 01/08/1973 | Male | 5 | 0.0605 | 0.0509 | 0.3280 | 5 | 0.0596 | 0.0503 | 0.3261 |
| SPIRAL NIKITA | 08/11/1994 | Male | 6 | 0.0474 | 0.0415 | 0.3695 | 6 | 0.0465 | 0.0407 | 0.3668 |
| RAINBOW HIGH | 01/01/1990 | Female | 7 | 0.0385 | 0.0385 | 0.4081 | 7 | 0.0383 | 0.0383 | 0.4050 |
| KINLOCH BRAE | 03/08/2005 | Male | 8 | 0.0347 | 0.0293 | 0.4374 | 8 | 0.0399 | 0.0337 | 0.4387 |
| STAPLERS JO | 12/06/1993 | Male | 9 | 0.0666 | 0.0281 | 0.4655 | 10 | 0.0660 | 0.0287 | 0.4964 |
| WESTMEAD HAWK | 02/05/2003 | Male | 10 | 0.0306 | 0.0270 | 0.4925 | 11 | 0.0309 | 0.0273 | 0.5237 |
| HONDO BLACK | 22/07/1999 | Male | 11 | 0.0257 | 0.0257 | 0.5182 | 9 | 0.0290 | 0.0290 | 0.4677 |

**Table 3.** *List of the top 10 contributing ancestors, and their contributions, to the male and females course dogs born between the years 2010 and 2013, inclusive.*

|  | Name | Date of birth | Rank | Total contribution | Marginal contribution | Cumulative contribution |
|---|---|---|---|---|---|---|
| Males | NEWRY HILL | 11/02/1990 | 1 | 0.1586 | 0.1586 | 0.1586 |
|  | BEXHILL EOIN | 02/04/2004 | 2 | 0.1449 | 0.1087 | 0.2673 |
|  | CRAFTY THRILLER | 07/06/1983 | 3 | 0.1068 | 0.0932 | 0.3605 |
|  | TULLAMORE | 23/04/1994 | 4 | 0.0805 | 0.0805 | 0.441 |
|  | SHAUNS DILEMMA | 13/04/1992 | 5 | 0.0873 | 0.0655 | 0.5065 |
|  | BEST MAN | 01/04/1975 | 6 | 0.0747 | 0.0548 | 0.5613 |
|  | TIVOLI SMUT | 01/03/1985 | 7 | 0.0744 | 0.0452 | 0.6065 |
|  | CILLOWEN BLONDE | 12/05/1993 | 8 | 0.043 | 0.0416 | 0.6482 |
|  | ASHMORE VIEW | 01/02/2001 | 9 | 0.0484 | 0.0363 | 0.6845 |
|  | MATT HYLAND | 15/03/1999 | 10 | 0.0617 | 0.026 | 0.7105 |
|  |  |  |  |  |  |  |
| Females | NEWRY HILL | 11/02/1990 | 1 | 0.1599 | 0.1599 | 0.1599 |
|  | BEXHILL EOIN | 02/04/2004 | 2 | 0.1487 | 0.1115 | 0.2714 |
|  | CRAFTY THRILLER | 07/06/1983 | 3 | 0.1057 | 0.0917 | 0.3632 |
|  | TULLAMORE | 23/04/1994 | 4 | 0.0795 | 0.0795 | 0.4427 |
|  | BROOKVIEW MASTE | 27/06/1987 | 5 | 0.066 | 0.066 | 0.5087 |
|  | BEST MAN | 01/04/1975 | 6 | 0.0747 | 0.0572 | 0.5659 |
|  | TIVOLI SMUT | 01/03/1985 | 7 | 0.075 | 0.0458 | 0.6117 |
|  | CILLOWEN BLONDE | 12/05/1993 | 8 | 0.042 | 0.0407 | 0.6524 |
|  | SAFETY LEADER | 19/06/1985 | 9 | 0.0448 | 0.0392 | 0.6916 |
|  | NEEDHAM HOUSE | 03/03/1986 | 10 | 0.0286 | 0.025 | 0.7167 |

**Conclusions**

Excellent pedigree information exists for the Irish greyhound population which is crucial for the quantification of inbreeding levels at an individual animal and population level. The rate of accumulation of inbreeding in recent years is 0.15% per year which translates to a rate of 0.89% per generation. This accumulation of inbreeding is of concern but it nonetheless lower than the maximum recommended threshold of 1% per generation set out by the World Food and Agriculture Organisation (FAO, 1998). The level of inbreeding in the coursing population is considerably greater than in the track population. Several next steps are possible: 1) use of molecular information to more accurately quantify the level of inbreeding within the modern greyhound population and 2) quantification of inbreeding depression on performance traits. The former would require the genotyping of several hundred animals and calculate inbreeding at a genomic level; results from the Irish cattle population (Purfield et al., 2012) clearly show that pedigree-based inbreeding coefficients under-estimate the true level of inbreeding. Quantification of inbreeding depression would require

performance records on individual greyhounds differing in inbreeding levels; such analyses have been undertaken in Irish cattle (McParland et al., 2007, 2008).

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