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Historical Litter Size Development in the Nederlandse Kooikerhondje

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ABSTRACT A study of the Kooikerhondje reproductive traits based on data collected in the online ZooEasy database finds that average litter size has increased from 2.5 pups/litter in the period 1955–1965 to 5.2 in the period 2015–2020. The correlation factor between coefficient of Inbreeding (6 generations) and average litter size was -0.85. Average litter size heritability was found to be 8% for the dam, 6% for the sire.

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1 INTRODUCTION

All purebred dogs are essentially inbred, only select individuals are used for breeding, therefore offspring becomes increasingly more related. Mating closely related individuals produces homozygous offspring which on average are less healthy i.e. “less fit” [14].

Litter size is associated with population fitness [4, 17] and is therefore an interesting first parameter to study for the Kooikerhondje. This study was performed on Kooikerhondje dogs born between 1955 and 2020 to provide an overview of the breed’s development during this period.

2 MATERIALS & METHODS

HISTORY OF THE BREED

The Netherlands Kooikerhondje is believed to be an old breed, or collection of breeds, referred to as “Spaniels,” often depicted by the Old Masters from the seventeenth century. By the end of the nineteenth century, catching ducks by means of an eendenkooi was no longer commercially feasible, and the little dogs used during its practice were no longer needed. Baronesse (duchess) van Hardenbroek van Ammerstol, well known for her ability to bring back other old Dutch breeds[1], began to resurrect the Kooikerhondje in the late nineteen thirties. After several years, an effective founder stock of 5 males and 10 females was formed. As far as we know, the background of these dogs has not been described or was not know at the time. The duchess’ focus was to bring back the dog in the paintings and its ability to work in the eendenkooi (pond for trapping ducks).

The breed’s registry, maintained by the Dutch breed club “Vereniging Het Nederlandse Kooikerhondje” (VHNK), shows the recorded breeding choices that were made, the challenges as well as successes. The initial focus on phenotype and general proportions has given way to a focus on health and hereditary diseases in later years.

THE POPULATION

The Kooikerhondje population grew to approximately 5000 individuals by 1990, when a first study of reproductive traits was conducted by Mandigers[1]. Although by that time, some dogs had left the Netherlands and became the foundation stock in other (European) countries, the vast majority of the population was based in the Netherlands. During the subsequent 30 years, the population grew to over 32,000 dogs towards the end of 2020, with substantial clusters in Denmark, Finland, Sweden, and Germany.

Litters born before 1955 were excluded from this study as the population was quite small and many litter descriptions are incomplete. A total of 6518 litters were part of this study, representing 32,769 pups with dates of birth from 1955/1/1 until 2021/1/1. The details were obtained from the online ZooEasy database, stillborn dogs were not included. 1342 sires and 2731 dams were identified as the parents for the litters. Some sires were used only once, others many times (e.g. Carlo vh Beloken Land, responsible for 265 pups). Many dams gave birth to 2 or 3 litters but the registry shows a number of dams with 10 litters even one with 14 litters.

PROPERTIES OF THE DATA

The following data were available for this study:

1. Date of Birth (DoB) of sire, dam, and litter.

1) The Duchess was involved in the Friese Staby, Patrish Dog, Markiesje, Kooikerhondje, Pieter de Hoogh hondje (now extinct), de keeshond and possibly others.

2. Litter size and number of male vs female puppies.
3. Litter Coefficient of Inbreeding (CoI) as computed by ZooEasy.
4. Location of residence.

From the litter DoB, sire DoB, and dam DoB we can compute the ages of the sire and dam when the litter was born. A table of litters by dam and date allowed computation of litter parity. This also allowed for the computation of time in between litters (litter interval) by dam.

Location (country) is recorded at the time of birth/registration and is generally updated when the dog changes ownership. Update of the country of residence depends on the owner and may not always be done. The breeder (code and/or name) is also recorded in the registry though with large gaps (unreported) and is therefore not reviewed in this study.

No detailed data was available on feeding before or during pregnancy, time of mating, natural or artificial insemination, or vaccination status. Data was obtained from the online ZooEasy database, any inconsistencies or errors were resolved consulting the VHNK Club Register (CR). For the remainder of the study these two sources may be regarded as synonymous.

TOOLS & METHODS

All pedigree data was stored in a SQLite SQL database and custom python code was created for data extraction and manipulation. Statistical computations were made through the pandas library as well as Orange Data mining and some correlations were computed in Apple Numbers. Figures were created with DataGraph.

3 RESULTS

Table 1 below provides a general overview of the population distribution across the world in the study period showing total population by country and its sires and dams (showing countries with population larger than 500 only)

Country	Population	Sires	Dams
Denmark	1961	166	195
Finland	1636	249	295
Germany	2849	243	297
Japan	1597	74	157
Netherlands	18171	702	1510
Norway	779	71	73
Sweden	2067	256	300
Swiss	956	136	115
UK	558	57	74
USA	726	111	140

Table 1

Figure 1 depicts a general overview of litter sizes collected in the Club Registry. The figure shows litters with sizes up to 12 pups. As can be seen, the number of litters steadily increased over the years as did the litter size. Litter size after 2004 remains relatively stable.

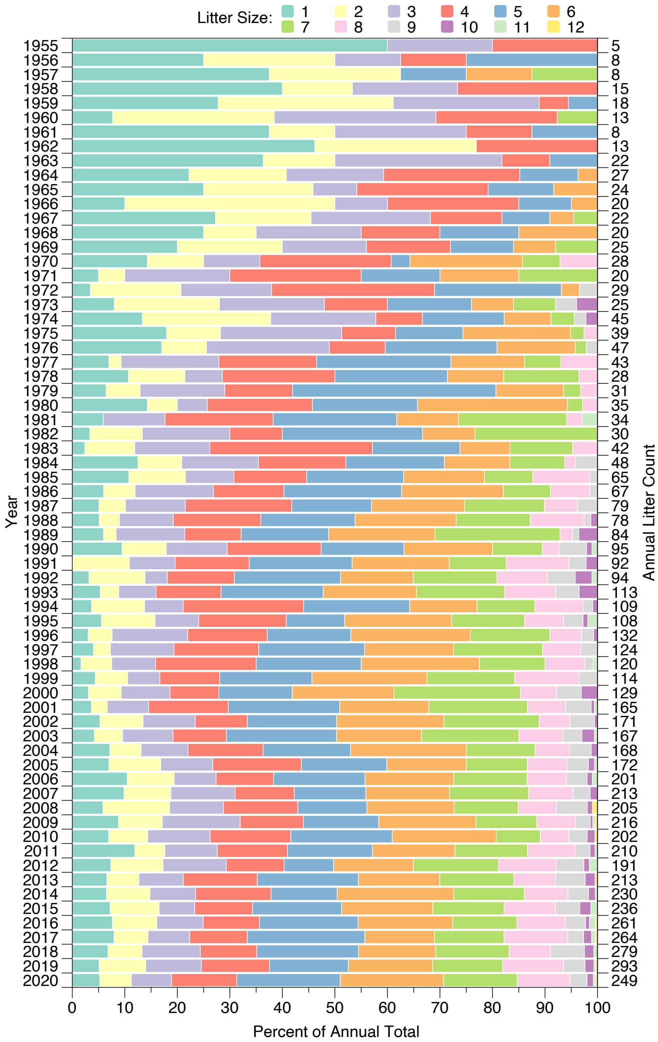


FIG 1: Relative litter size by year. Litter sizes are shown by count as a percentage of all litters per year. For example 1955 shows a total of 5 litters, 60% of these had a single pup (green), 20% had 3 pups (purple) and the remaining 20% had 4 pups (red). The left Y-axis shows the year, the right Y-axis the total number of litters.

A simplified view of the litter data is provided in figure 2 whereby the average litter size is computed for each decade since 1955. Notice that the last bar covers only 5 years (2015-2020)

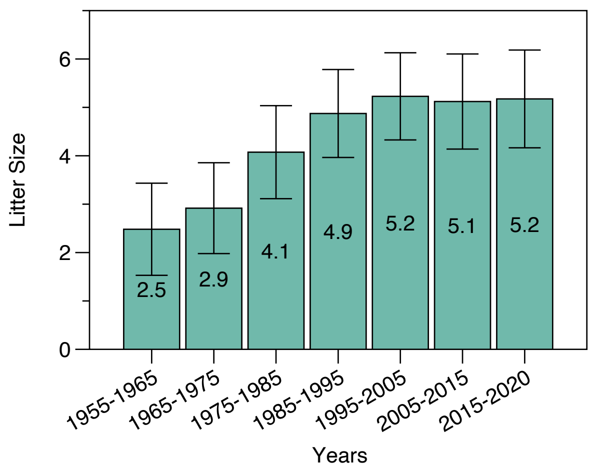


FIG 2: Average Litter Size by Decade. Error bars indicate +/- 1 standard deviation. Litter size is not a Gaussian distribution but skewed towards 1 (pup). Notice the relative stability over the last 20 years.

COEFFICIENT OF INBREEDING VS LITTER SIZE

Coefficient of Inbreeding[2] (CoI) for litters was computed for 6 generations (Figure 3, green curve) as well as all generations (red curve). As expected, the 6G curve drops as dogs in the immediate location of pedigree are increasingly less related. However, as the total CoI computation shows, the actual relatedness continues to increase. Litter size and CoI-6G correlate −0.85 whereas litter size and CoI-all correlate 0.87.

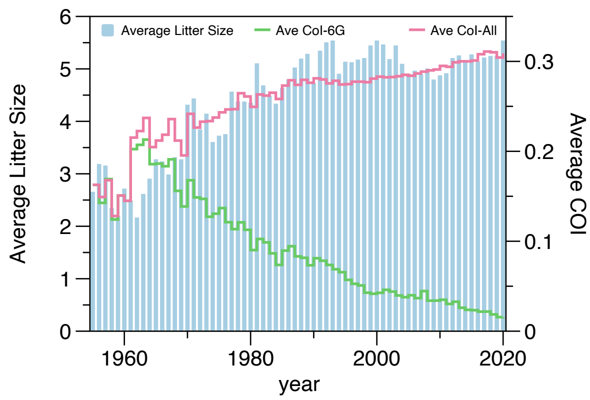


FIG 3: Average Litter Size and COI trend

LITTER SIZE BY PARITY

Parity is the number of litters a dam has carried, parity 1 being the first litter. Relating litter size to parity shows that the 4th litter is the most prolific <u>on average</u> albeit by a small margin. Beyond the 4th litter, litter size drops off at a steady rate as shown in figure 4 below.

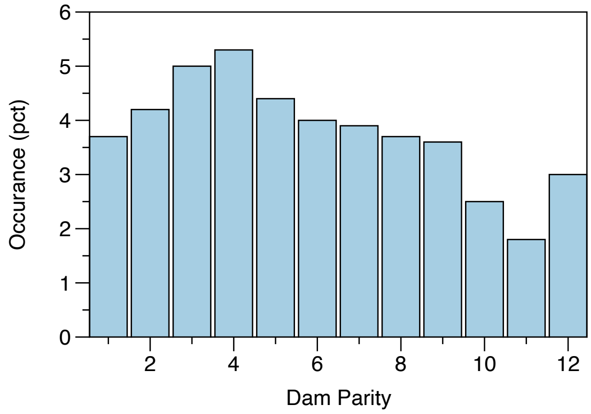


FIG 4: Average Litter Size by Month

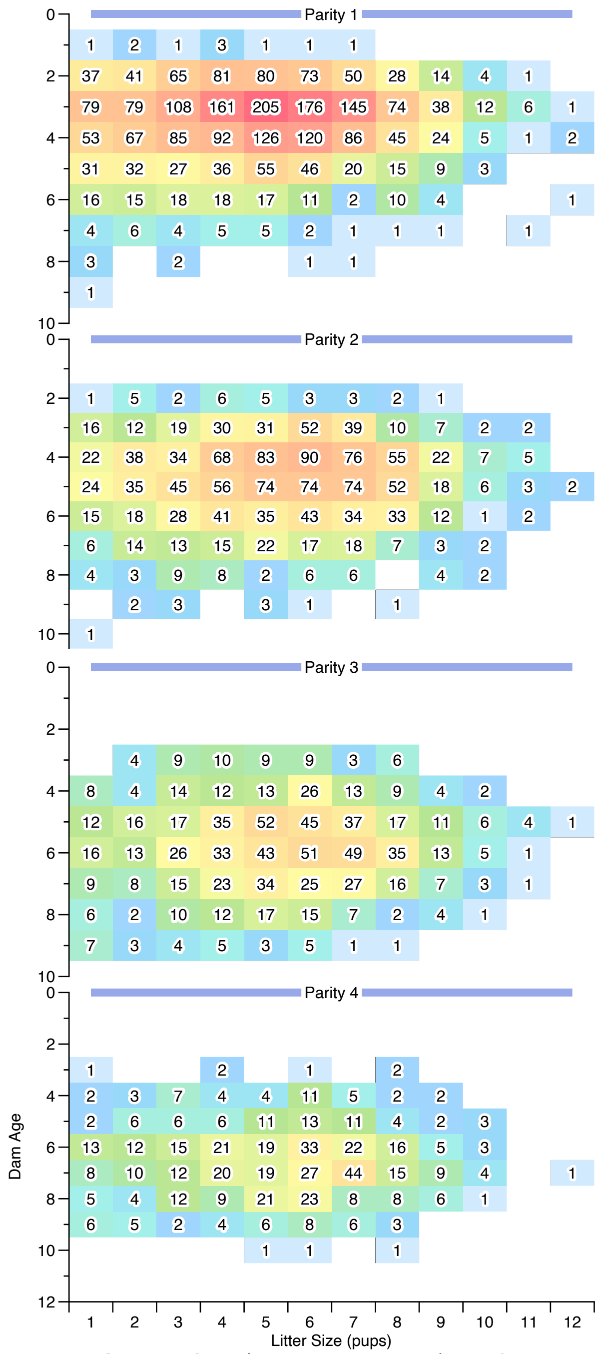


FIG 5: Litter Count by Parity, Dam Age and Litter Size

A second view on the aspect of parity is shown in figure 5 where the first 4 parity sequences and litter counts are provided as a heat-map. This shows the relation between parity, dam age and litter size quite well. The numbers in each cell is the litter count.

Cells in the heat-map with a red background color indicate a higher overall count. For example, for parity 1, 205 litters with a litter size of 5 pups whereby the dam was 3 years old were counted. Naturally, the most litters are counted under parity = 1. Subsequent parities show fewer litters simply because fewer dams are bred more than once, twice etc. Each parity forms a small "hill" indicated by the colors with a peak at high litter rates. Observe that the peak of each "hill" (red, orange and yellow) is shifting slightly to the right by each parity, corroborating higher parities having a relative higher litter count as shown in figure 4.

2) The CoI = Σ [½ n (1+FA)] – the sum of all ancestral paths, FA is the CoI of the ancestor common to both sire and dam. The ZooEasy database reports CoI computed over the last 5 generations.

LITTER SIZE VS DAM, SIRE AGE

Parity and dam-age correlate naturally as a dam cannot have a high parity at young age. With sires such correlation is not as relevant. Figure 6 shows both sire and dam ages as they relate to litter size. The pink trend line tracks the dam age, the blue the sires.

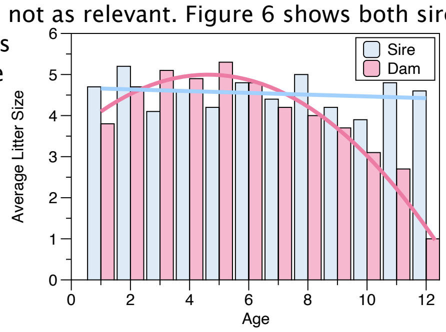


FIG 6: Average Litter Size by Sire & Dam Age

BIRTH FREQUENCY SEASONALITY

To determine if births occur more often in a specific season, litters were sorted and summed by month across all measured years. The result is shown as three groups of roughly similar size;

1955 – 1998, 43 years, 2221 litters
1999 – 2010, 11 years, 2209 litters
2011 – 2020, 10 years, 2494 litters

Figure 7a shows average litter sizes by month in each period. A notable increase between February and March is observed. All months fall within the 95% confidence index, with exception to June in the 2011..2020 period.

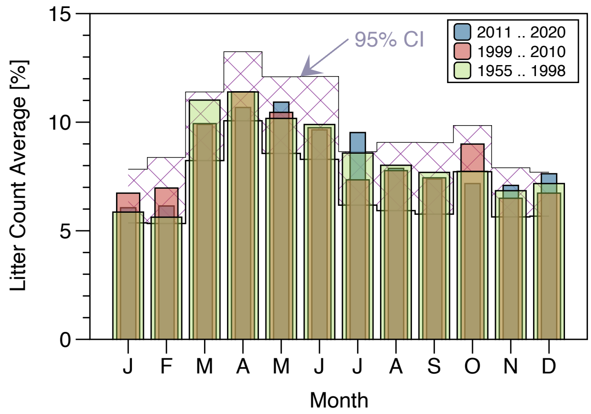


FIG 7a: Litter Frequency by Month and Periods. Plotted periods are roughly equal in size. Each month displays the average number of litters within the measured period as a percentage of the period's total. For comparison, monthly averages of each period are shown on top of each other with a 95% confidence interval (CI) as the background. CI is computed across the entire population. Only June of the > 2010 period is outside the CI. There is a marked seasonal effect with a 4-5% increase from February to March.

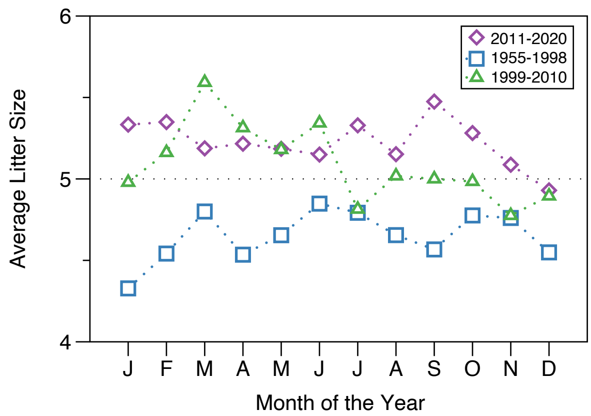


FIG 7b: Average Litter Size by Month and Period. Table XX below provides detailed statistics.

LITTER SIZE HERITABILITY

Though Tommie (stammoeder, founder) is the most well known founder dam, she was not the only one. Koala and Sita[3] are some other notable founders. Most founder dams do not have a registered date of birth, Tommie's is believed to be born in the late thirties. Her first registered litter is in 1942, whereas Koala's (only) registered litter was much later, in 1956. Therefore we must remain open to the possibility that Koala (as well as other dams) may be related to dams already in Tommie's lineage and thus some of the values of early litters may not be independent. For the heritability study, only Tommie's, Koala's and Polly's genetic lines were considered in this study.

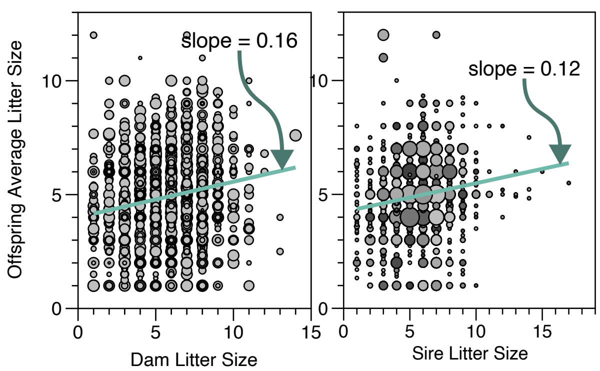
The dataset registers each pup with its sire and dam, allowing a complete lineage to the founder dogs to be computed. This makes two observations of heritability computable:

a. Litter-size heritability.
b. Ancestral line productivity.

To compute Litter Size heritability, it is modeled as a genetic trait of the dam and sire separately [4, 5, 25]. Heritability is generally computed as the averaged parent factor (mid-parent) to averaged child factor relationship. Note computing a mid-parent result is not possible for litter size. This because the sire and dam are not permanently paired so a common average result cannot be computed.

The heritability computation performed here does not consider environmental factors, gene-gene interactions, nor dominant/recessive genes etc. It assumes heritability as a proportion of trait variance due to additive genetic factors. This is commonly referred to as the "narrow sense heritability" (h^2). Sire litter size heritability reflects embryonic survival and semen quality.

The h^2 estimate was computed by forming parent-pup pairs for both dam-pup and sire-pup combinations of their respective litter sizes. For example, Tommie (stammoeder,founder) has had a 4 pup litter, which included "Margrietje v Walhalla" (1942-03-01). Margrietje in turn has had 2 litters: the first with 1 pup, the second with 3 and therefore an average litter size of 2. This forms the combination (4,2). These parent-pup pairs are plotted as the scatter plots shown in figures 8a (dam heritability) and 8b (sire heritability). The bubble size in the figures reflects the number of samples with the same or similar combination i.e. sample data density.



Heritability Scatter Scatter Plots on the left Fig8a: Dams, on the right Fig8b: Sires. Regression lines are computed by minimum mean square error straight fit.

The regression lines depict an estimated heritability factor of 0.16 for the dams and 0.12 for the sires. Note that each scatter plot is computed for a single parent, not the (average) mid-parent. This means the computed heritability is between 1 parent and the average of direct offspring. Thus the computed slopes must be divided by two and the actual heritability factors are 8% and 6% respectively for dam and sire litter size heritability. The computation was performed for the population as a whole; all maternal and paternal

3) Koala – origin unknown, dam of litter 1956-05-18. Sita – origin unknown, dam of litters 1968-05-14, and 1969-03-17

lines are averaged together.

Ancestral line productivity can be computed by accumulating all produced pups from founder till last descendant. Naturally, many lines share initial pup counts (as they have common ancestors). Secondly, some branches stop producing earlier than others. Therefore, accumulated line results are compared by their average, not absolute value.

To illustrate this method, consider the following partial result:

position	registration	pups in L1
1	Tommie stammoeder	4
1.2	Margrietje, 1942-03-01	1
1.2.2	Carlieneke, 1943-12-01	2
1.2.2.1	Buzzer, 1952-05-30	3
1.2.2.1.1	Bea, 1953-07-29	2
1.2.2.1.1.1	Cathrijntje, 1954-07-06	4
1.2.2.1.1.1.6	Noortje, 1959-11-30	1

Table 2

This yields a total of 17 pups across 7 generations. The line ending with Noortje is therefore labelled with a 2.43 pup Line Litter Size Average (LLSA). All lines were thus computed and labelled with their LLSA of their first litter production. Tommie's maternal lineage is by

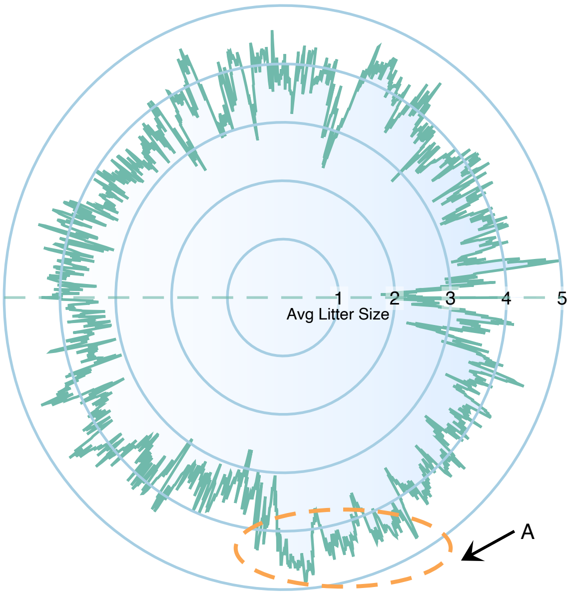


FIG 9: Tommie's Line Litter Size Averages for each descendant. Lines are sorted by DoB and shown clockwise, starting with Tommie at the horizontal at 3 o'clock position. Therefore, the close points on the curve are litter production of related blood lines i.e., distant points on the curve are distant blood lines. The area indicated by "A" appears to show grouping of some ancestral lines with a higher than average production. Histogram statistics show that these values are within expectations.

far the largest and includes 2376 litters; Koala is second with 199 litters and Polly with 32 litters.

Figure 9 depicts the result of this LLSA computation as a radar plot (for founder Tommie) with the first average litter result on the positive X-axis and the following generations going clockwise in succession. With the generations sorted so that close relatives are close data points, the radar plot reveals where some branches ("families") may be more productive. One such area is indicated on the plot as "A" where sustained higher LLSA levels are recorded.

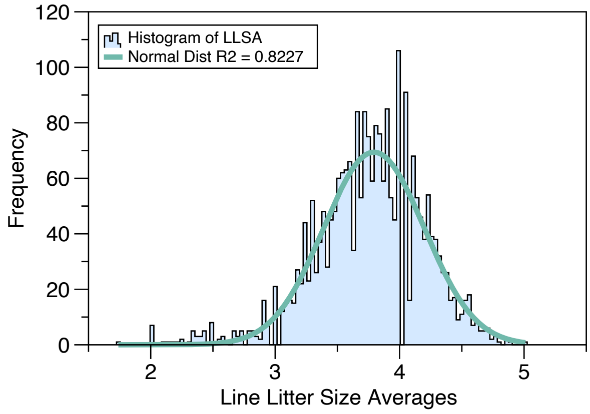


FIG 10: Line Litter Size Averages Distribution by Frequency

The probability density function for all LLSA is given by the normal distribution shown in figure 10 below with (μ, σ) = (3.7, 0.40). Notice that for the LLSA computation, only first litter production were used to produce these results, higher parities were not included.

4 DISCUSSION

The years since 1994, when Paul Mandigers published a first study on litter size and other reproductive traits [1], show that the initial trends found by his study have continued. Average litter size has increased to 5.32 in 2000 and since appears to have plateaued at this level. Gierdziewicz [14] reports mean litter sizes of Beagles and German Shephards between 5.53 and 5.36 pups/litter - inline with the Kooikerhondje average litter size found by this study.

Table 1 shows a general overview of the Kooikerhondje population by country and their sires and dams. Besides informing how geographically dispersed the breed is, we can observe that the use of the producing dogs vs entire population is fairly small which may have consequences for the genetic variety available for later generations. This should be studied at a future date.

Coefficient of Inbreeding correlates to litter size as has been shown in previous studies [17, 18]. The CoI 6 generation trend correlation to litter size is a computed factor of -0.85; quite a strong confirmation of the relationship. Notice that this is a pedigree based computation and a genetically based analysis of inbreeding and kinship will provide a more accurate finding.

Parity is known to affect litter size in dogs [1,2,12] and have been described in non-canid mammalian species such as foxes [5]. The pedigree analysis shows that the 4^{th} litter of the dam is on average the most prolific. Sires may go on to produce active semen at advanced ages with no relation to their productive level and litter parity. Older, less viable semen may relate to the chance of having a litter at all but the size of the litter is not determined by it. Artificial Insemination (AI) may be related to a smaller litter production as semen quality may be affected but this was not studied here.

Moreover, AI is not used in most countries and in particular the Netherlands and has therefore at best a very small effect.

Seasonality affects reproduction in many species. Temperature extremes, nutrition, amount of daylight and other environmental factors are known modulators. The litter count results shown in figure 7a shows a significant step change from February to March. We must keep in mind that litter counts by season are not purely driven by the canine but of course influenced by the breeder who makes breeding decisions. Though not shown in this article, the under lying data shows that the step change is mostly due to the litters born in the Netherlands. A VHNK club member remarked that aiming for a "spring litter" was preferred amongst the breeders. This could explain the observed step change. Therefore, we cannot conclude that there is a reproductive advantage for a particular season in the Kooikerhondje. The average litter size by month, depicted in figure 7b, also shows no correlation to season. This finding corresponds with findings by other studies [13, 16, 28], though [2] found a seasonal difference of litter size in the Drever breed (similar in size and weight to Kooikerhondje) located in Sweden.

The litter size heritability for dogs (h^2) is reportedly less than 15% [23, 25]. A study in large white pigs [24] found litter size to be a < 10% heritable trait, and a study on American Minks [22] showed less than 7% probability. The computed heritabilities of 8% (dams) and 6% (sires) are in line with these earlier findings. The low heritability factors mean that breeding for litter size has little or no effect. A portion of the litters may have come from artificially inseminated dams – this information was not available (AI litters are not reported as such and rare during the measurement period). A study which traces heritability factors for natural vs artificial insemination is of interest for a future project, though would require the acquisition and categorization of such data.

The Line Litter Size Average (LLSA) study shows some grouping around a common ancestral line/branch. Several areas (families) that produce more than the average number of pups are highlighted in figure 9 by the area "A" indicator. The higher values in these groups are approaching and sometimes exceeding 4.5 pups per litter. Though this may at first seem that some genetic lines are more productive, the probability density function given in figure 10 shows that this is mostly anticipated and falls within the expected values. This means that no specific genetic line has an advantage as it relates to litter size which is corroborated by the low heritability factors also presented above.

5 CONCLUSIONS

The development of the Kooikerhondje from just a few founders to over 32,000 dogs in 70 years should be regarded as a success of its breeders. Average litter size has increased and appears to be stable over the last 2 decades, a sign of a "fit" breed. Though it should be pointed out that a possible factor of influence contributing to this increasing litter size, may be the use of progesterone test kits. Progesterone test kits became available in the early 2000 and result in a better judgement of the dam's ovulation timing and thereby higher chance of a successful breeding and larger litter size [2]. The early smaller litter sizes may be associated with "bad timing" to some degree.

Low sire as well as dam usage ratios and in particular the use of a very select group of sires is concerning. How this influences litter size specifically and overall health of the breed may be subject of a future study.

This study found no single or combinatory factor other than COI that can be correlated to litter size in the Kooikerhondje. A negative correlation between COI and litter size agrees with existing studies [1,4] for COI computed over a shallow generation depth. Litter size heritability factor for the Kooiker dog is lower than found for other breeds [25]. With a dam heritability factor of 8%, breeding for litter size is not practical.

One of the first components of fitness affected by inbreeding is fertility, such as litter size, viability and number of litters [11]. This study considered only litter size in the Kooikerhondje and concludes that though a high COI is found (approximately 30% in the last decade), average litter size shows no negative trend.

All observations made here apply to the entire Kooikerhondje population as a whole. A future study specific to individual countries may reveal differences related to the club's breeding policies and genetic base in each country. Secondly, a study to better understand the use of the sires may help guide the future development of the Kooikerhondje.

It is important to note that this study presents correlations and averages. Correlation measures the strength of a relationship between two different variables (in this study, inbreeding and litter size). Correlation is used to describe relationships in data. It does not always mean that one variable is the cause of the other. Specifically, it may be tempting to take the negative correlation between CoI and litter size as a guiding principle for breeding practice. This would be a mistake. The CoI – Litter Size correlation must be understood as a statistical property of the Kooikerhondje population, not a specific direction for the next litter.

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