

Population Analysis for the Drentsche Partridge Dog

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August - 2023



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**Vereniging
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<https://docs.dogsglobal.com/2023/PopulatieAnalyseDrentschePatrijshond.pdf>

Summary

The Drentsche Partridge Dog, an esteemed hunting breed from the Netherlands, has regrettably experienced a considerable decline in genetic diversity. With the first recorded birth in 1928, multiple factors contribute to this reduction. Causes include the matador effect and an overlook of animals with unique genes, along with a heavy selection against diseases. The risk to the breed's future health due to this decline of genetic diversity is considerable.

A comprehensive genetic analysis is vital for assessing the state of the breed and forming effective preservation strategies. Key metrics in this analysis include Inbreeding, Kinship, FGE, OFE, and FGS. While some of these metrics might require familiarisation, they are vital for understanding the breed's past, present, and potential future. The most important metric FGE was 2.15, which basically means that the current genetic diversity is the same as if the population was started with little more than two unrelated animals.

Upon assessing the breed's current situation using these metrics, several alarming issues come to light. The risk of further decrease of genetic diversity is high due to the presence of unique genes predominantly in old individuals who are no longer used in breeding. Over the past 30 years, unique genes introduced by founders have halved, and the population size has reduced from 500 puppies annually to around 250 nowadays, potentially leading to a further drop in genetic diversity. A seemingly counterintuitive aspect is that avoiding inbreeding does not necessarily improve the breed's health. However, a diverse genetic base is essential for the breed's long-term survival.

Addressing this decrease of genetic diversity likely requires a multi-faceted approach. Efforts to promote the breed could be helpful alongside a careful selection of dogs (especially males) for maximise genetic diversity. The number of breeding animals should be high as well and for this to happen it is important to realise that seemingly harmless regulations, such as requiring participation in dog shows, can inadvertently lead to elimination of unique genes. Breeders can identify dogs with unique genes by using Mean Kinship which is a more general and blunter tool, while highly unique dogs could be



targeted with precision **by Optimal Contributions. Since “hidden diversity” has been decreasing over time and almost disappeared completely within the last 5 years, outcross litters can play a crucial role in increasing “hidden diversity”.**

The breed's potential predisposition to diseases such as epilepsy but also the question if hip/elbow dysplasia is actually a serious health issue necessitates further research and incorporation into breeding selection criteria. Together, these strategies could help counteract the decrease of and even increase the genetic diversity and ensure the longevity of the Drentsche Partridge Dog breed.

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1. Introduction

The Drentsche Partridge Dog is a versatile hunting breed serving as all-purpose hunting dog, including pointing and retrieving. Its roots date back to the 16th century in the Netherlands. Tragically, it, along with many other dog breeds, has experienced a considerable decline in genetic diversity. This loss of diversity, while somewhat inevitable, has proven more drastic than necessary, and is widely considered a leading cause of the breed-specific diseases that many breeds endure (Leroy, 2014; Neradilová Silvie AND Connell, 2019; Oliehoek et al., 2009; Ubbink et al., 1998; Voges & Distl, 2009). Despite an abundance of research on these breed-specific diseases, studies focusing on genetic diversity – the underlying cause of diseases - are less frequent.



To conduct these indispensable analyses, a complete studbook that includes all ancestors, including the founders who initiated the breed, is essential. Dogs Global provides such a database as well as thorough checks on data-integrity. Furthermore, Dogs Global is specialised in comprehensive genetic analysis, which is critical for breeding decisions and developing breeding strategies.

Several factors contribute to genetic erosion or the loss of genetic diversity in dog breeds. For the Drentsche Partridge Dog, these factors include: matador-breeding, selection against diseases, and selection of animals that are already overrepresented in the population overlooking animals with unique genes, but also rules that appear innocent. As an extreme example about the latter: a simple requirement for dogs to have participated in dog shows may eliminate 95% of a population if only 5% of that population has been shown, meaning 19 out of 20 dogs are lost.



Photo 1: 'The' Nimrod; born in 1940. He stood at the base of the breed standard of the Drentsche Partridge Dog. In the current population still 38,9% of all genes descend from this dog, an important cause of the inbreeding nowadays. He is the most dominant ancestor.

To characterise the past and current situation of the breed several diversity metrics are presented. These metrics have two basic scales. The first is the basic and very common scale of percentages, used for the metrics: Inbreeding and Kinship. The second scale is the equivalent number of unrelated founder animal used for the metrics: the Founder Genome Equivalents (FGE: Lacy, 1995), Optimal Founder Equivalents (OFE: Oliehoek et al., 2009), Founder Genome Surviving (FGS: Lacy, 1989), number of original founders, and simply the actual size of the current breeding population. Especially the second scale is important to understand consequences of breeding practices. If you are not familiar with it, the metrics **might get some time 'getting used to'**. While describing the metrics for the Drentsche Partridge Dog, examples are given to provide a better idea what the metrics actually represent. You can also find all metrics in the Glossary at the end of this document.

The most important metric is Founder Genome Equivalents which is a common representation of genetic diversity within conservation genetics that intuitively links to the breed's founders. First the report presents the metrics of the current breeding population



and thereafter throughout history, after which the report describes the implications of these metrics and possible recommendations for the Drentsche Partridge Dog. These insights could serve for potential breeding strategies to counteract the genetic erosion and if possible, reverse the loss of genetic diversity within this esteemed breed.

2. Current breeding population (genetics)

Before delving into the breed's history, let us first examine its current standing. The current breeding population was estimated based on all animals up to 2022 that are capable of reproducing, including all males up to 14 years old and females up to 9 years old. However, it should be noted that this estimate may not accurately reflect the actual population size, as the ability to produce offspring is crucial in breeding. Dogs that are castrated are excluded for example. For the current breeding population, the following metrics were calculated:

	2022	2016
Current breeding population size (global estimate)	4000	
Founders contributing to current breeding population	44 (of 75)	
Founder Genome Survival (FGS)	5.45	5.88
Optimal Founder Equivalents (OFE)	2.19	2.35
Founder Genome Equivalents (FGE)	2.15	2.25
Average Mean Kinship (AMK)	23.3%	
Average Inbreeding	23.5%	

Table 1: metrics of current breeding population of 2022 as well as some for 2016

2.1 The metrics and their meaning

The original founder stock consisted of about 75 animals (depending somewhat on how you determine founders), but some of the genes of only 44 different animals survived until today. Founder Genome Survival (FGS) of 5.45 means that from the original founder stock, less than six partial founders are still present in the current population. These are not five **to six founders you can identify, but it's more like 'pieces' of each of the 40 founders that** together sum up to 5.45 genomes. Some founders will have contributed more than others. These pieces or parts of genomes are connected to unique genes (unique alleles) the founders carried with them.

By losing these founders the unique genes are also lost, which means this diversity is lost without the ability to restore.



Though FGS says something about if unique genes survived, it does not tell anything about how diverse these genes are, in other words if they are rare or overrepresented within the population. Therefore, we also need to look at genetic diversity, which is expressed in Founder Genome Equivalents (FGE). Having a FGE of 2.15 means that if you could start all over, you can build a population with only 2.15 founder, having the same genetic diversity as in the current population.

Even though the genetic diversity of the Drentsche Partridge Dog breed is low: 2.15, this metric still outpaces many other breeds, including several Dutch ones. When you consider that many other analyzed breeds (Dogs Global - , like the Frysian Stabyhoun, Wetterhoun, and Broholmer, have lower genetic diversity, with their Founder Genome Equivalent (FGE) values being 1.43, 1.53, and 1.35, respectively. So, while the Drentsche Partridge Dog may face challenges in increasing its diversity, it could have been worse.

Now, how is it possible to have a total of 5.45 founder left in the population (FGS) and still have a genetic diversity (FGE) of only 2.15? Many dogs, even those having unique genes, will also have genes that are overrepresented in the whole population. Their contribution to the diversity is diminished by these genes that many other dogs have as well. Therefore, by calculating the genetic diversity, you should also take into account the degree of having genes equally divided within the population. If all genes would be equally divided within the population, the FGE would be as high as the FGS. Unfortunately, due to an overrepresentation of some founders and other ancestors, within the Drentsche Partridge Dog the FGE is more than twice as lower than the FGS. This correlation between FGS and FGE will be further explained in the history section of this document.



Photo 2: Norbert, a dominant ancestor born in 1938. His genes still contribute for 22,5% to all genes in the current breed. He's the father of 'the' Nimrod (photo 1).



The “Average Mean Kinship (AMK) is: 23.3%. The numbers 23,3% AMK and 2.15 FGE are basically the same metric just expressed on another scale: percentage instead of effective founder genomes. The formula used is: $AMK = 1/(2 * FGE)$. In this report we also use the scale of effective founder genomes because a **‘number of animals’ instead of percentages, is intuitively easier to comprehend**. Furthermore, it becomes easier to compare FGE to the FGS.

Let’s make this clear with another example. If 1000 litters would be bred out of one male and one female, all animals would be brother and sister. The kinship between siblings is 25%. Thus, an FGE of 2 corresponds with an average kinship of 25%; and indeed $1 / (2 * 2) = 0.25$ or 25%. Because the FGE of the current breeding population is a little higher than 2: 2.15, the AMK is a little lower: 23.3% instead of 25%.

On average, the inbreeding of the current breeding population is 23.5%, which is somewhat higher than the average kinship of 23.3% AMK. The inbreeding is close to the AMK, which is expected. This means that there are very likely no strong divisions within the population.

Example:	FGS,	OFE,	FGE
Consider these terms: Founder Genome Survival (FGS), Founder Genome Equivalents (FGE), and Optimal Founder Genome Equivalents (OFE). Imagine a dog breed that comes from many different original dogs or 'founders', meaning the FGS is high. But if most dogs are 80% related to one main founder, and only 20% related to all the other original dogs, the overall genetic diversity or 'mix' (FGE) will be very low, even if FGS is high. If we change our breeding plan to use more dogs not related to that main founder, we can slightly improve the diversity or mix (OFE), which is the same as reducing average mean kinship. The 'hidden diversity' is the difference between the current diversity (FGE) and the best possible diversity (OFE).			

Until now, we haven't discussed an important concept: Optimal Founder Equivalents. This term refers to the maximum genetic diversity that can be achieved in a population through ideal breeding methods. Now, the Optimal Founder Equivalent is a value that reveals the breed's "hidden diversity." It's always somewhere between the FGE (Founder Genome Equivalent) and the FGS (Founder Genome Size) of a breed. To illustrate, let's dive into the Drentsche Partridge Dogs metrics. The current genetic diversity (FGE) is currently 2.15. So how much can this be increased? In the Drentsche Partridge Dog, the OFE is 2.19, which is very close to the current FGE value of 2.15, but significantly lower than 5.45 which is the Founder Genome Size (FGS). Though the FGE is higher than other Dutch breeds, even with the best breeding practices, the genetic diversity, can only be increased up to 2.19. Unfortunately, this means that there isn't much "hidden diversity" that could be used to further improve the 2.15 FGE; it can hardly be increased. This limitation is due to "linkage disequilibrium," a process where certain genetic variants (alleles) become associated more



often than would be expected by chance. When rare and common alleles mix, increasing the frequency of rare ones also boosts the frequency of common ones.

Comparing to five years ago, this number was relatively higher at 2.35, with the FGE back then being 2.25. This indicates that much of the 'hidden diversity' has been lost over the last five years. A process that is probably still going on.

2.2 Mean Kinship & Preference lists

Dogs that carry unique alleles are most important in breeding. By using those, it is possible to keep or even increase the genetic diversity which in turn keeps the inbreeding the same or even lower. At the same time, it is necessary to prevent dogs from breeding too much.

Dogs Global adopts a colour-coded system for a more lucid interpretation of breeding choices towards genetic diversity. Every dog within the current breeding population is assigned a colour, in order of their preference: green, yellow, orange, or red, using the following steps:

1. Calculate the Mean Kinship value for each animal.
2. Divide the population into three groups based on Mean Kinship (MK): green (lowest), yellow (middle), and orange (highest). Note that MK-values are not static, **they depend on the population. That's why dogs can change colour.**
3. Determine if an animal has reproduced. If an animal has produced more than 10 puppies, it will move down one category: from green to yellow, from yellow to orange, or from orange to red.

Table 2 shown below, illustrates the distribution of dogs by colour and age-group, aiming to clarify the relationship between genetic diversity and the age of each dog:

Age	Green	Yellow	Orange	Red
13	153	28	20	4
12	112	49	56	6
11	92	60	51	3
10	64	61	49	7
9	152	121	86	8
8	152	108	150	15
7	122	119	93	8



6	89	116	127	6
5	67	126	156	6
4	68	145	112	2
3	83	131	140	1
2	34	86	110	
1	49	135	122	

Table 2: Mean Kinship list thresholds per 1 January 2023.

Green	MK values < 22.57
Yellow	MK values 22.57 - 23.76
Orange	MK values > 23.76

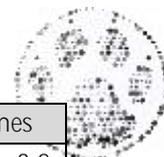
Note: the values of these thresholds are arbitrary and chosen only to divide the current breeding population in three. The red list only contains animals that have reproduced themselves (more than recommended).

Table 2 provides a valuable insight into the future of the population. It reveals that the older age groups have a higher proportion of green animals, indicating a greater diversity. On the other hand, the younger age groups are mostly categorized as yellow or orange, suggesting a lower diversity. It is worth noting that the majority of dogs tend to give birth around 5 years old, which puts them in the age categories of 1-6 years. As these age groups have a higher percentage of yellow and orange animals, the risk of decreasing diversity is significant, especially if breeders do not consider Mean Kinship or Optimal Contributions (see paragraph 7.2). It is highly likely that the FGE will continue to decrease and thus the AMK will continue to increase.

Let's break down the current situation in bullet points:

- The original founder stock of the breed consisted of around 75 animals, but only 44 have survived until now, partially.
- Founder Genome Survival (FGS) of 5.45 means that less than six partial founders are left from the original founder stock. These are not distinct founders, but rather pieces of each of the original founders that add up to 5.45 genomes. Some founders have contributed more than others, resulting in a loss of diversity.
- The actual genetic diversity (FGE) of the Drentsche Partridge Dog is less than half the FGS: 2.15, due to the fact that many genes are not equally spread within the breed.
- An FGE of 2 corresponds to an average kinship of 25%, but the current breeding population's diversity: the FGE is slightly higher than 2 (2.15), resulting in an average kinship of 23.3%.
- the OFE is 2.19 maximum FGE possible, is very close to the current FGE of 2.15, but **significantly lower than 5.45, which means there is hardly any "hidden diversity"** left.
- The spread of Mean Kinship suggests that the risk of decreasing diversity is significant, since large part of the unique genes are found in (very) old individuals, which are likely not used in breeding anymore.





Registration no.	Founder: Name	Gender	Born	Puppies	RPs	%	Genomes
NL224/1928/009	Freija	F	1928	1	1	0.1	3.2
NL224/1929/049	Botha	M	1929	3	3	8.5	340.8
NL224/1930/025	Max v. Westerbork	M	1930	5	1	0.2	6.4
NL224/1932/076	Frida	F	1933	3	3	11.1	443.9
NL224/1933/070	Nimrod	M	1933	6	2	6.0	240.3
NL224/1932/075	Banko	M	1935	1	1	5.6	225.1
NL224/1937/055	Sonja Be	F	1938	5	3	6.7	266.8
NL224/1936/011	Frija	F	1939	1	1	19.5	777.4
NHSB RS35544	Wodan	M	1939	3	3	3.2	129.8
NL224/1937/061	Nellie	F	1940	1	1	2.5	100.2
NHSB RS35482	Dini	F	1940	1	1	1.4	56.3
NL224/1941/031	Diana	F	1942	2	2	4.1	162.1
NHSB VR 10009	Gerda	F	1942	5	1	0.1	5.3
NHSB RS40704	Leanda	F	1943	1	1	2.7	108.5
NL224/1943/112	Cora	F	1943	2	1	0.1	5.3
NHSB RS35543	Willi	F	1943	1	1	0.1	3.0
NL224/1940/113	Flora	F	1943	1	1	0.1	2.8
NHSB VR 10047	Leda	F	1944	4	2	6.2	247.1
NL224/1941/013	Flora	F	1944	1	1	3.9	155.0
NHSB RS35531	Miep	F	1944	1	1	2.4	96.9
NHSB OS35482	Dini	F	1944	1	1	0.7	28.2
NL224/1942/114	Flora	F	1945	1	1	0.4	14.6
NL224/1942/020	Rita	F	1945	1	1	0.0	1.1
NL224/1945/098	Asta	F	1946	2	1	0.2	6.8
NL224/1943/001	Mother of Sonja	F	1946	1	1	0.1	3.0
NHSB G° 140746	Carla	F	1946	3	1	0.1	2.2
NHSB RS76371	Arthur	M	1947	1	1	0.3	11.3
NL224/1945/058	Sindra	F	1948	1	1	0.3	12.1
NL224/1945/010	Cunera	F	1948	2	1	0.3	10.5
NHSB VR 10161	Tref	M	1948	1	1	0.1	5.6
NL224/1948/017	Boy	M	1951	2	2	0.3	13.5
NL224/1948/099	Asta	F	1951	1	1	0.2	6.8
NHSB RS47564	Conra	M	1951	1	1	0.0	0.4
NL224/1949/032	Bennie	M	1952	1	1	1.1	45.2
NHSB G° 243014	Mina	F	1953	13	3	6.3	250.9
NL224/1951/108	Manuschka	F	1954	1	1	0.3	11.4
NL224/1954/106	Meta	F	1957	2	2	1.3	53.6
NL224/1962/018	Leta	F	1957	1	1	0.4	14.4
NL224/1955/001	Mother of Max and Trix	F	1959	2	1	0.1	3.0
NL224/1958/044	Bonzo	M	1959	3	1	0.1	3.0
NHSB RS16280	Prachy	M	1960	2	1	0.9	34.8
NL224/1957/107	Mother of Nelson and Jolly	F	1960	2	1	0.9	34.8
NHSB G° 459551	Astor	M	1962	62	3	1.0	39.2
NL224/1960/067	Nimmy	F	1963	1	1	0.4	17.4

Table 3: overview of all founders that are still present in the current breeding population, however small their contribution.



3. Genetic History of the breed

3.1. Population Size

The history of the Drentsche Partridge Dog goes back a long way, predating the Second World War, but the number of litters was limited during this period. Around the 70s the breed saw a significant increase in numbers. However, from 1984 onwards, the number of litters born per year began to decrease.

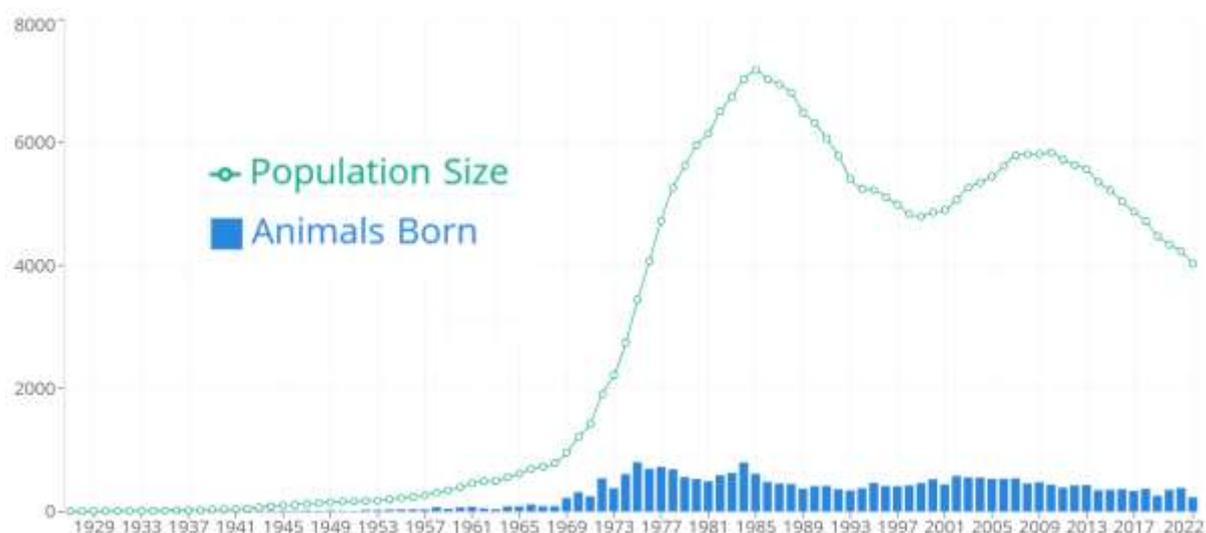


Figure 1: history in number of animals: Population Size: estimated number of animals able to breed and Animals born

3.2. Founders

Another word for founders would be “original **forefathers**”. With the database having complete data it is possible to identify which animals were actual founders. On most cases **the parents of ‘founders’ are unknown**. However, this is not necessarily the case: after all, every animal has parents. The most important characteristic of a founder animal is that they are unrelated to every other founder (or to be very precise: **‘equally related’**). In total, 44 founders have been identified with some influence on the current breeding population, which means their genes are still present. These founders are presented in *Table 3* (previous page).

In *Table 3* “Puppies” represent: **the number of puppies this founder produced**. “RPs” is the number of puppies of this founder that reproduced themselves, which reproduced themselves, which reproduced themselves, etc. all the way down to the current breeding population. “RPs” **stands for** Reproductive Puppies. Unlike most breeds, there are not one or two founders that contribute the most to the current breeding population, which might explain the relatively lower loss of genetic diversity in the Drentsche Partridge Dog compared to some other (Dutch) breeds. “%” is the **percentage in which a founder**



contributed to the current breeding population. Since founders have been introduced into the population a long time ago, these contributions are unlikely to change dramatically.

Finally, “Genomes” means the number ‘genomes/animals’ a founder contributed to the current breeding population. Since each and every gene of the current breeding population is inherited from one of the founders, the sum of all founders is equal to the size of the current breeding population: 4000.

An example of a founder is **Botha**, who was born in 1929 and has had a relatively large impact on the Drentsche Partridge Dog today with around 340 genomes, or 8.5% of the current breeding population. In contrast, **Freija**, estimated to be born in 1928, has only a negligible impact of 0.1% on the breeding population.

Founders were frequently introduced into the population till 1963. Only one founder: “Ximfor v. Adomarkin”, born around 1969, was introduced after. Though he had a lot of offspring, none is alive today and for this reason he is not present in *Table 3*.

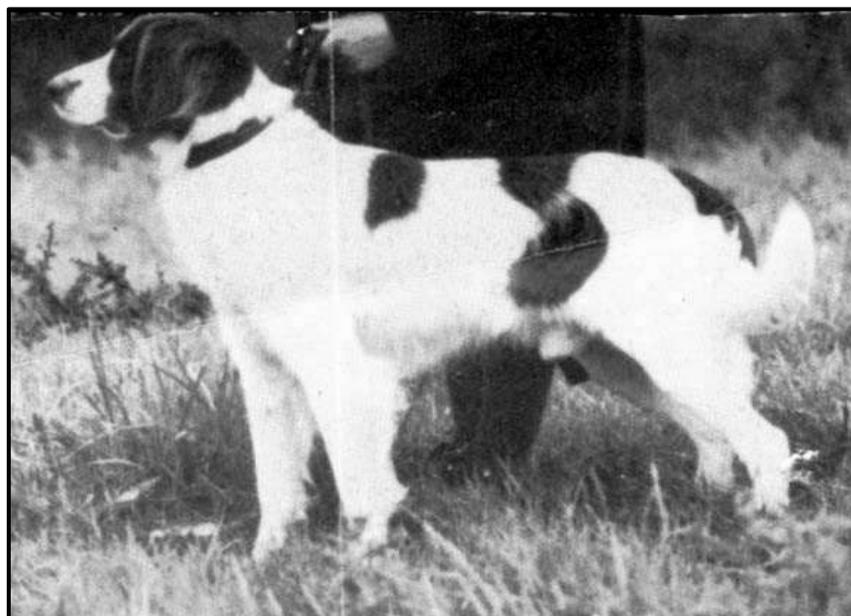


Photo 3: Astor, born in 1962, was one of the final founders contributing to the breed, despite having unknown parentage. Astor's contribution to the current breed's gene pool is 1%. There also exist founders contributing as little as 0.1%.

3.3. Dominant Ancestors

Founders are the first ancestors of a breed, but there are also other ancestors that have made a significant contribution to the current breeding population, known as dominant ancestors. It's important to recognize, when two animals have a high contribution from the same ancestor, they are likely closely related. Mating between closely related animals can result in inbreeding. Dominant ancestors may have a high contribution even if they did not produce a lot of puppies themselves, but through frequent use of their descendants. *Table 4* of dominant ancestors includes the same data as the table of founders: puppies, reproductive puppies (RPs), percentage, and genomes. The table is sorted by their impact.



While parents of founders are often not known, most non-founder dominant ancestors have known parents as are shown in the table as well. Some points of interest. First of all, if we would sum all contributions, we will by far exceed 100%. So, where founders sum up to 100, dominant ancestors do not.

This is because dominant ancestors are related to each other. Unlike founders, which are unrelated, contribution of an ancestor also increases the contribution of their parents for example.

Let's take the example of Frija, who is the mother of Nimrod (1940). She only has a large contribution because of being the mother of Nimrod who contributes 39% (35-43%) towards the current breeding population. This is understandable given the small number of dogs in the breed's early stages, which allowed for a single dog to have a significant impact. However, it is more surprising to see the high contribution of Nimko (1955) of about 30%. These two animals are responsible for the breeding population being family.

The impact of dominant ancestors can accumulate over generations, and those with low RP values can have a high contribution through an accumulative effect of their progeny over time. Contribution of dominant ancestors is increased by the contribution of their progeny. It is also because of this principle that ancestors with a huge impact did not necessarily produce many puppies (matador-breeding). In fact, the opposite can be seen in many breeds: often the impact of dominant ancestors, also the males, is not by having a large number of puppies themselves but much more often through large number of puppies by several of their progeny. Thus, the impact of ancestors might accumulate over generations through highly productive descendants. **Hence, the table of 'Dominant Ancestors'** indirectly elucidates an accumulation effect: the only way dominant ancestors with low RPs still have a high contribution, is through an accumulative effect of their progeny over time. This phenomenon makes the decrease of genetic diversity by having many puppies partly invisible.

This way dominant ancestors have a negative impact on genetic diversity, as all progeny descending from them will be carrying the same genes, making them more related to each other. This will also influence the average mean kinship, followed by inbreeding, as the genes of dominant ancestors will dominate the gene pool, "pushing out" the other genes. This is what it means that genetic diversity is decreased. This also means that the genetic diseases which ancestors like Nimrod and Nimko were carrying also spread throughout the population. The more significant an individual's contribution to the gene pool, the greater the likelihood of their specific genetic issues (diseases or more benign dispositions) manifesting. This would be true for all ancestors, as there isn't a dog that lacks a genetic predisposition.





Registration no.	Dominant ancestors		Born	Puppies	RPs	Father	Mother	%	Genomes
NHSB G° 135286	Nimrod	M	1940	36	19	Norbert	Frija	38.9	1554.9
NHSB G° 456966	Nimko	M	1955	178	24	Booy	Alba	31.0	1240.0
NHSB 35536	Norbert	M	1938	8	4	Nimrod	Flora	22.5	900.3
NL224/1936/011	Frija	F	1939	1	1			19.4	777.4
NHSB G° 158089	Alba	F	1948	6	1	Nimrod	Astrid	15.5	620.0
NHSB10271	Booy	M	1953	6	1	Jimmy	Sientje	15.5	620.0
NHSB 1077727	Boaïke Astha v. Bircmede	M	1979	140	19	Arno	Astha	14.4	577.1
NHSB 479350	Ascon v.d. Jachtpassie	M	1969	203	14	Eros v. Biljoen	Tarda	12.6	505.3
NHSB G° 550483	Maras	M	1971	244	13	Ascon v.d. Jachtpassie	Marjolein	12.2	489.2
NHSB G° 226025	Eros v. Biljoen	M	1959	11	5	Martijn v. Biljoen	Ditha v. Biljoen	11.3	452.8
NL224/1936/014	Flora	F	1936	3	1	Botha	Frida	11.3	450.2
NL224/1936/066	Nimrod	M	1936	3	1	Banko	Flora	11.3	450.2
NL224/1932/076	Frida	F	1933	3	3			11.1	443.9
NHSB10268	Sientje	F	1947	11	4	Nimrod	Darling	10.9	434.1
NHSB G° 453650	Frya	F	1965	20	7	Riko	Meta	10.7	426.1
NHSB G° 147128	Leda v. Dubbeldam	F	1948	10	5	Marinus	Petra	10.6	425.0
NHSB 134820	Sax' Tom	M	1947	10	5	Clovis	Florina	10.6	425.0
NHSB G° 172881	Martijn v. Biljoen	M	1955	46	8	Martijn v.'t Hooyvelt	Leda v. Biljoen	10.1	405.0
NHSB G° 453647	Riko	M	1964	81	9	Nimko	Letha	10.1	403.5
NHSB G° 496376	Neass	M	1961	59	10	Nimko	Ada	10.0	401.1
NHSB G° 148141	Martijn v.'t Hooyvelt	M	1951	26	6	Spot	Donata	9.7	387.6
NHSB10090	Jimmy	M	1946	8	2	Nimrod	Bea v.d. Oude Velddijk	8.7	349.5
NL224/1929/049	Botha	M	1929	3	3			8.5	340.8
NHSB10477	Meta	F	1960	5	2	Nimko	Wandaa	8.4	337.0
NHSB 952026	Arno	M	1977	194	7	Dax of the Sunny Dogs	Sändy	8.4	336.3
NHSB G° 467876	Vanka	M	1969	387	22	Mina's Lodewijk the Pooh	Natasha	8.4	334.1
NHSB G° 268442	Mina's Lodewijk the Pooh	M	1961	151	10	Ditlev	Mina	8.3	330.6
NHSB 236730	Siep	F	1960	25	5	Pittah	Ladylike	8.1	324.9
NHSB G° 638630	Nimrod v. Bircmede	M	1973	41	7	Patrick	Frya	8.0	321.7
NHSB G° 941106	Sil	M	1977	154	6	Sloeber	Lobke	7.8	313.4
NHSB G° 135145	Astrid	F	1945	3	1	Nimrod	Flora	7.7	310.0
NHSB G° 865884	Astha	F	1976	5	2	Jurre v. Bircmede	Birka v. Bircmede	7.7	307.5
NHSB 1765028	Basco v.'t Boterdiep	M	1991	63	12	Marco v.h. Iemenholt	Sarah	7.5	300.6
NHSB G° 155051	Ditha v. Biljoen	F	1952	15	3	Sax' Tom	Leda v. Dubbeldam	7.2	286.2
NHSB G° 137843	Tref v.d. Vogelwereld	M	1946	19	5	Nimrod	Leda	7.0	281.6
NL224/1937/055	Sonja Be	F	1938	5	3			6.7	266.8
NHSB 398690	Tarda	F	1966	15	2	Nimrodimo	Siep	6.7	266.3
NHSB G° 1007159	Maaïke	F	1978	16	5	Pasja	Laska	6.3	251.1
NHSB G° 243014	Mina	F	1953	13	3	Turk	Cora	6.3	250.9
NHSB10095	Clovis	M	1942	10	6	Nimrod	Sonja Be	6.3	250.7
NHSB G° 168463	Ditlev	M	1954	38	3	Tref v.d. Vogelwereld	Brune v. Biljoen	6.2	249.6
NHSB 1110324	Anjo v. Groevenbeek	F	1980	29	9	Sil	Cindij v.'t Drente Horst	6.2	248.3
NHSB G° 497623	Nimrodo	M	1965	36	6	Riko	Meta	6.2	247.9
NHSB10047	Leda	F	1944	4	2			6.2	247.1
NHSB G° 155048	Brune v. Biljoen	F	1952	11	3	Sax' Tom	Leda v. Dubbeldam	6.2	246.6
NHSB G° 531654	Marjolein	F	1968	7	1	Jokko the Pooh	Dianada	6.1	244.6
NHSB G° 1323590	Bentho v.'t Oale Hemelriek	M	1984	101	11	Nimrod v. Bircmede	Maaïke	6.1	244.5
NHSB 1487533	Kathinka Anjo v. Groevenbeek	F	1986	27	5	Boaïke Astha v. Bircmede	Anjo v. Groevenbeek	6.1	244.3
NHSB 351362	Nimrodimo	M	1964	43	3	Eros v. Biljoen	Siep	6.1	242.8
NHSB 2367758	Monty's Hanna fan 't Suydevelt	F	2001	34	10	Mosehøjs Monty	Famke fan 't Suydevelt	6.1	242.7

Table 4: overview of ancestors having a large impact on current breeding population



3.4. Average Inbreeding and Kinship (AMK) during the years

The following graph, *Graph 2*, shows the average Inbreeding and the Average Mean Kinship (AVK) in percentages between 0 and 100%. Though inbreeding receives most attention, kinship is actually the metric that is most important to manage. Higher levels of kinship among parents causes offspring to be inbred. Thus, if all animals have a high kinship among each other (are related/family), inbreeding becomes inevitable in every mating. Hence, inbreeding eventually always follows (average mean) kinship of a population.

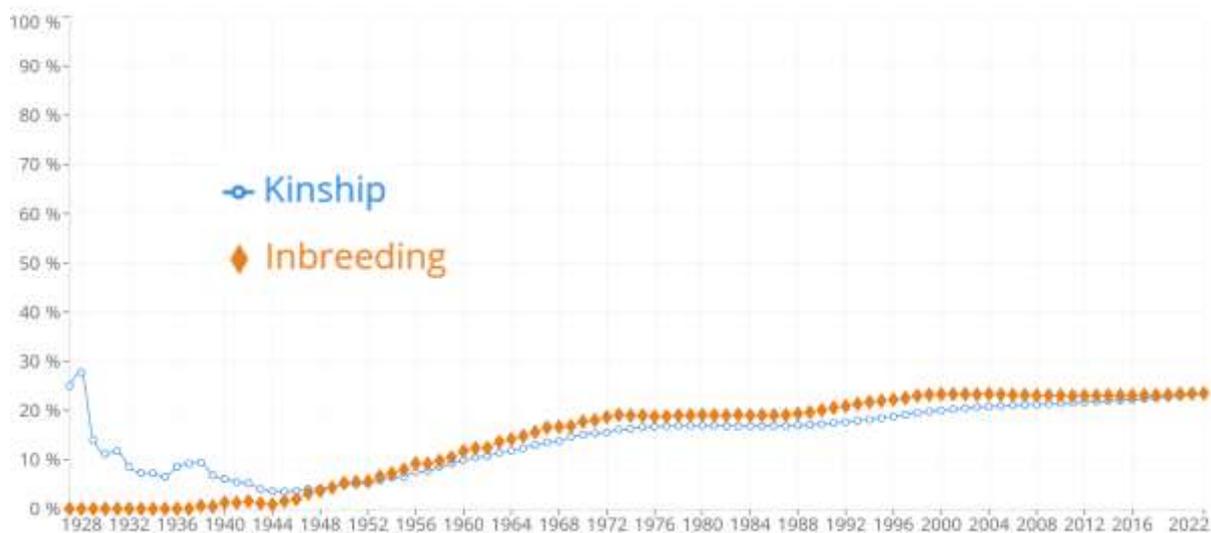


Figure 2: history in percentages of average Inbreeding and Average Mean Kinship (AMK)

In the beginning years, prior to World War II, the average mean kinship was high while inbreeding was close to 0%. This is typical for small populations with a limited number of individuals who are not yet related. Due to the small population, the impact of each animal is significant, and litters often consist of mating between founders, resulting inbreeding of 0%.

From 1950 onwards, inbreeding became slightly higher than the average mean kinship, possibly due to some breeders focusing more on their own families and less on others, a practice sometimes referred to as "line-breeding". However, this term is not scientifically precise and can lead to confusion. From *Graph 1*, we can conclude that population size was still low in those days as well. During the 1976 till 1987, the average mean kinship remained stable: 2.97 (also see *Table 9*). This means that the AMK did not profit from the founder introductions from the years before. How to profit from founders is further explained while describing *Graph 3*.

From the 90s onward, the Average Mean Kinship increased while inbreeding did not. However, the decrease in genetic diversity or in other words: the increase in kinship is of greater concern. Although inbreeding may not be immediately apparent, it will eventually increase as genetic diversity declines.



3.5. Scale of Effective Founders (number of animals)

Graph 3 presented below depicts three levels of diversity and their connection with the founders who were responsible for all the diversity. The scale used in Graph 3 is based on the number of animals, rather than percentages used for inbreeding and kinship in Graph 2. The Founder Genome Equivalents (FGE) is another way to represent the Average Mean Kinship (AMK), which never exceeded 15 animals and is currently only 2.15. If breeding had been carefully managed from the beginning throughout history, the breed could have maintained *at least seven times* more diversity than it is today. However, the breed faced a dramatic loss of genetic diversity.

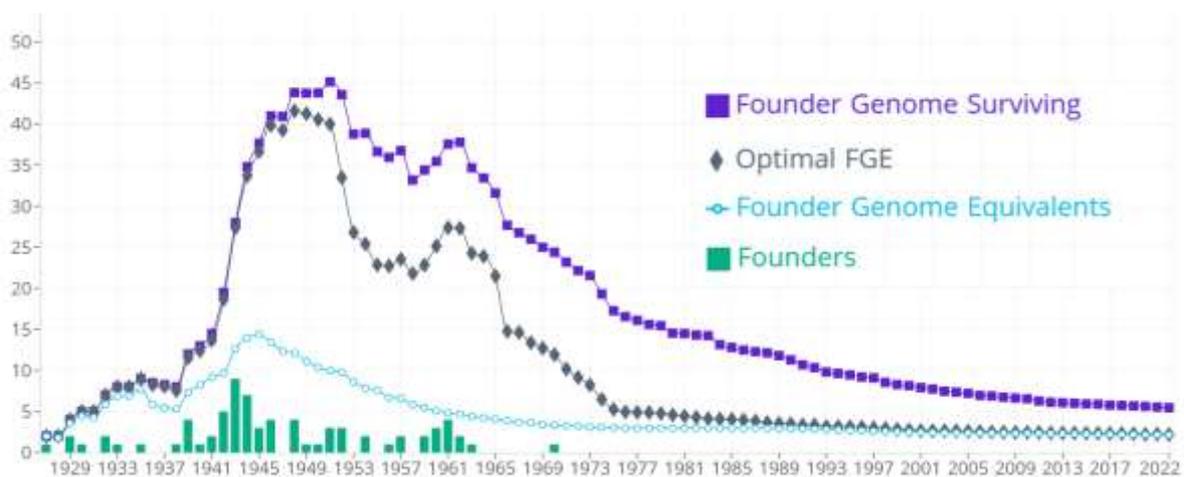


Figure 3: history in effective founder genomes for genetic diversity (Founder Genome Equivalents), maximum genetic diversity (Optimal Founder Equivalents), alleles (Founder Genome Survival), and Founders themselves.

Graph 3 displays the Founder Genome Surviving (FGS), which represents the number of unique genes (alleles) in the population that come from each of the founders. When a new animal with a unique founder genome is added to the gene pool, the FGS value increases since each founder contributes a distinct set of genes to the population.

Kinship means being family by having common ancestors scaled as a percentage. These percentages are calculated between entities. In this report we have three different levels. (1) Between **two animals** the kinship is the percentage in which these two animals are family. Between a brother and a sister, assuming their parents are completely unrelated, the kinship is 25%. This is also the percentage of inbreeding when this brother and sister are crossed. An inbreeding coefficient of 25% means chance for each locus of that the progeny being homozygous is 25%, having the same gene from the same grandparent through both the father and the mother in this case. (2) Kinship can also be calculated between an **animal and its breeding population**. This is called Mean Kinship: the mean of that animal with the entire population. (3) Last but not least we write about Average Mean Kinship, which is basically the average throughout the **entire breeding population**: the average of all Mean Kinship of all animals that can breed.



As briefly explained before, FGE is seldom equal to FGS as diversity is not only about the presence of unique genes but also their spread. This is also clearly visible in the graph. In the 50s, founders increased FGS but hardly increased FGE since the population already had over 150 animals. Thus, the unique genes of one founder had limited influence on the overall population. Unfortunately, FGS itself has decreased continuously from the 50s until now, demonstrating in the disappearance of unique alleles. To prevent this loss, animals that carry unique genes should have been used. In conclusion, to keep FGS high, it is important to select males and/or bitches carrying unique alleles. The FGE could be increased to a maximum. This Optimal FGE is called the Optimal Founder Equivalents (OFE) is the line in between FGS and FGE. If this metric is much higher than FGE, it indicates hidden genetic diversity. However, the optimum has been decreasing much faster than FGS since the 50s, and currently, it is hardly higher than the current FGE (2.19 vs. 2.15). This implies that careful breeding can only increase genetic diversity to a small extent. How come that we cannot increase FGE to the FGS? It is near impossible to increase the FGE to the same level as the FGS due to the mixing of unique genes with common or "overrepresented genes" from dominant ancestors. When founders or their descendants were only bred with dominant ancestors and then became infertile or died, their unique genes became irreversibly coupled with the overrepresented genes. Therefore, increasing unique genes would automatically increase overrepresented genes, making it challenging to increase the FGE.

At the start, when mixing did not yet occur, the OFE was the same as FGS before and during the Second World War. **The "hidden diversity" could be utilised to increase FGE. But since WW2 it has decreased towards the FGE; in other words: the "hidden diversity" is lost.**

Especially during the 60s and the 70s the OFE drops much faster than the FGS. This means that there **is a lot of mixing of "overrepresented" and unique alleles.** In the Appendix in *Table 9* we included several metrics per 5-year periods throughout history. From this table two metric is very interesting for that same period, especially: 1965-1975. During this period the average number of progeny of Fathers and Grand-fathers was particularly high (31.13 & 103.55, respectively). Note that those are averages, meaning for each animal having lower number of puppies, another male will have more. These very high average of number of puppies is very likely the cause of the steep drop of OFE.

Finally, *Graph 3* illustrates founder introductions alongside the Founder Genome Surviving (FGS) metric and reveals a distinct pattern. With each introduction, there is an observable increase in the FGS, signifying the addition of one effective founder to the gene pool, a logical outcome. Concurrently, the Original Founder Equivalent (OFE) also incrementally rises with each founder introduction. The genes of a recently introduced founder still remain unmixed with overrepresented genes. Optimise the contribution of a new founder would maximise the Founder Gene Equivalent (FGE), thereby minimising the Average Mean Kinship. In practise this might mean that a founder needs to produce many



offspring It's noteworthy that similar effects are seen with outcross litters. Every initial introduction of a different breed adds one to the FGS.

Also OFE increases with each new founder, which means that 'hidden diversity' increases. Only by using this new founder whether it is an outcross (other breed) or not, only when significant number of progeny is bred, the FGE will benefit as well.



4. Litter size and Inbreeding

A multitude of parameters may affect litter size, and these parameters could potentially vary across different breeds. To gain insights into these factors, correlations between numerous parameters and litter size were examined. Data from 4400 Drentsche Partridge Dog litters were considered credible and used for the statistical analysis. In this breed, no significant effects on litter size were found for the following parameters: the sire's inbreeding coefficient, the order of the litter (first, second, third, etc.), and the season or month of birth. However, three parameters exhibited a negative impact: with a baseline starting value (read: the average, even though it's not exactly the same) of 7.83 puppies, the dam's age reduced this by -0.24 per year ($p < 0.001$), litter inbreeding decreased it by 0.033 ($p < 0.001$), and dam inbreeding lowered it by 0.008 ($p = 0.0707$). Although none of these parameters had a potent effect and in practice it will not be noticeable, on average the dam's age had the most significant impact. The impact of inbreeding depression on litter size is relatively small: a 10% increase in inbreeding reduces the litter size by 0.33 puppies, and a 10% increase in dam inbreeding reduces it by just 0.08.

While the Drentsche Partridge Dog shows relatively low sensitivity to inbreeding depression on litter size, it does not imply that the breed is largely unaffected by inbreeding depression. Inbreeding effects can vary considerably among individual dogs and also between breeds. For example, while not showing vulnerability to inbreeding depression regarding litter size, it could have an impact on male fertility, evident in lower semen quality, for example. Presently, such inbreeding depression effects remain uncertain, however, their possibility cannot be conclusively negated.



5. Conclusion

This report studies the current genetic situation of the Drentsche Partridge Dog population on all possible levels. And on all levels the trend is negative, except on the level that is least predictive: the average level of inbreeding. If breeding practices do not change also inbreeding will increase together with risk of breed specific diseases. First, the population size is decreasing. **if we take the ‘corona-years’ effect into account, this** trend is rather dramatic: from around 500 puppies born each year about 10 years ago to about 250 in 2022. However, on all three levels of diversity we see a dramatic decrease. Secondly, the unique alleles introduced by founders is now half (5.45) of what it was 30 years ago (10.68 see *Table 9*). Note that this loss is irreversible, unless new founders are introduced. Third and maybe most importantly: the genetic diversity decreased and very likely continues to decrease. In this study we use FGE (Founder Genome Equivalents) to express genetic diversity and the FGE of 2.15 and used to be 2.19 only few years ago. An FGE of 2.15 means that the genetic diversity could be recreated by breeding 2.15 animal. FGE and AMK (Average Mean Kinship) is basically the same number but opposite in behaviour. An FGE of 2.15 is transposed to a AMK of 23.3%.

In *Graph 2* the decrease is visible in the continues increase of the AMK. Fourth, in the average inbreeding (\bar{F}) we can see only little increase for the past 20 years, in fact in 2022 ($\bar{F}_{2022} = 25.5$) it was not much higher than in 2002 ($\bar{F}_{2002} = 25.3$; also see *Table 9* in the appendix). Looking only at inbreeding however would be very misleading (see next chapter: General Interpretations). On all other levels, the genetic metrics - the ones that truly matter - show serious decrease. Moreover, inbreeding is often only the result of increased kinship among parents which is directly related to loss of genetic diversity. With the current trend in AMK and likely further increase based on *Table 4*, we can predict that the average inbreeding (\bar{F}) will also rise in the coming decennium if breeding practices are not changed. At last, **we also evaluated the “hidden diversity”** and can conclude that there is hardly any **“hidden diversity” left. A lot of “hidden diversity” has been lost even during the recent** years, probably because this diversity was largely present in older individuals. Thus, the current breeding population represents little more than two unrelated dogs and are very likely to continue in the direction of an inbreeding level of brother and sister.

Let's break down the conclusions in bullet points:

- The Drentsche Partridge Dog's population is shrinking drastically, from 500 puppies annually a decade ago to around 250 now, causing a severe drop in genetic diversity.
- Unique genes brought in by founders have halved from 10.68 to 5.45 over the past 30 years. This loss is permanent unless new original dogs are added.
- Genetic diversity, expressed in FGE, has decreased to 2.15 and is likely to continue decreasing. The current genetic diversity is akin to breeding from 2.15 animals.



- Also, other genetic metrics show a serious decline. If breeding practices don't change, inbreeding is predicted to increase due to higher kinship among parents.
- There's little "hidden diversity" left. Much of it, present in older dogs, has been lost recently.

6. General interpretation

Genetic diversity begins with the original forefathers, or founders. The unique genes they carry get passed to their offspring and all genes in the populations come from these founders. However, just adding a new founder, or doing an outcross mating, doesn't always boost the genetic diversity (FGE). This is because the new genes need to spread to really make a difference.

This trend can be seen in *Graph 3* and *Table 9*. Even as more founders were added up to 1961, the FGE barely increased. But the FGS and OFE will normally go up by 1 with each new founder. If you notice the FGS and OFE didn't increase in 1938; this is because while a new founder was added, other founders' genes were lost, possibly due to their or their descendants' death.

Many dog breeds are losing genetic diversity. This drop in diversity will always lead to inbreeding, increasing the risk of breed-specific diseases, allergies, cancer, and fertility issues, hurting their health and welfare. Despite knowing the problems inbreeding can cause, simply avoiding inbred pairings doesn't solve the underlying issue. It's important to focus not (only) on reducing inbreeding but especially on increasing genetic diversity in our breeds for their long-term health. This is further discussed below. Compared to most breeds, the Drentsche Partridge Dog is not extremely high inbred. Despite the genetic diversity is not as low as most other breeds that have been thoroughly analysed, it still is a very low amount compared to many other populations, like endangered species that are bred in captivity in zoos.



Photo 4: Frequently, champions, are chosen for breeding becoming dominant ancestors. One such example is Boaike Astha v. Bircmede. Born in 1979, this international champion currently accounts for a significant 14.4% of all genes in the existing population.

As already discussed, an increase in inbreeding can lead to health problems in dog breeds. At first glance, the solution appears straightforward: Avoid inbreeding. It's not quite so simple, however. Avoiding inbreeding has no effect whatsoever on the health of the population. An explanation for this seeming paradox follows shortly. Nevertheless, avoidance of inbreeding has its merits. By making sure the inbreeding of the future litter is not much higher than the average of the population, breeders can mitigate unnecessary risks. Thus, avoiding inbreeding, if calculated accurately (meaning calculated using all generations), remains an important aspect of responsible breeding practices.

Yet, it's a misapprehension to think that avoiding inbreeding safeguards a population, a fallacy sometimes even held by experts, including professors in population genetics. The surprising truth is, avoidance of mating of siblings or (grand-)parent-offspring as well as the opposite strategy: to find the least related dogs: it doesn't do anything to lower inbreeding in the long run.

This is because avoiding inbreeding does not prevent a small population from becoming more related which will be followed by inbred over time. All actions that intend to lower inbreeding do not contribute to the population's health. Also, the commonly suggested strategy of mating a bitch to an unrelated male does not serve the breed's long-term interests. If a female dog possesses numerous unique genes, this approach could, in fact, even erode the breed's **“hidden diversity”**. The unique genes will be mixed with overrepresented genes.



Conservation geneticists, who specialise in preserving rare breeds and endangered species, comprehend this complex situation. Their strategies are centred on maintaining or increasing genetic diversity within breeds. Case in point: the Drentsche Partridge Dog. Globally, however, there are not many experts in this field. The vast majority of (population) geneticists are not experts in the area of preventing inbreeding and maintaining diversity. A general population geneticist might find no cause for alarm when examining the breed's average inbreeding over the past two decades. A conservation geneticist reviewing the data could raise a concern, recognising an ongoing decrease in genetic diversity. The following chapter will explore potential strategies for safeguarding or even increasing genetic diversity.

In conclusion, this does not negate the breeder's responsibility to consider the inbreeding of a future litter. Since it seems highly counterintuitive that what benefits a litter does not necessarily benefit the breed, the following statement cannot be overstated: selecting dogs that carry unique alleles and thus favour genetic diversity, is a critical aspect for the keeping inbreeding low and overall preservation of the breed in the long run.



7. Ways to preserve the Drentsche Partridge Dog

The key step in preservation of the breed is to (1) keep; (2) spread; and at times: (3) add unique genes within the gene pool. Each Tools to accomplish this are: (1) maximise number of males and bitches in breeding, (2) calculate Mean Kinship and Optimal Contributions and (3) find new founders or perform outcross. Each tool serves a different purpose, which will be discussed below. Besides diversity, selection is desirable for breed specific traits and at times necessary for improvement of health. All these goals need to be in balance.

7.1 Stopping decrease of genetic diversity: keeping unique alleles

The importance of using an adequate number of breeding males and females to maintain genetic diversity cannot be overstated. Breeding population size is dependent on both the number of litters per male and female, and the overall population size. Reverting to the issue of a shrinking population size and its consequences, advocating for the Drentsche Partridge Dog will very likely be advantageous. However, strategies that increase genetic diversity could exert a larger protective effect on the breed. As an illustration, maintaining current diversity levels and managing the average inbreeding rate is wholly possible, even with a 50% reduction in the yearly puppy births. Bear in mind, with a minimal quota of 25 litters or 150 puppies per annum, it's feasible to conserve the genes of 5.45 genomes (FGS) and uphold a genetic diversity comparable to 2.15 effective founder genomes (FGE), *if* you select different individuals carrying unique alleles.

This is, of course, assuming careful selection of the 'right' male and female for each litter. Thus, the main message is: promote the breed, however, even amidst a shrinking population size, small targeted steps can make significant difference in preserving the health of the Drentsche Partridge Dog. One step might be to explore ways to increase the number of breeding animals. Suppose only one breeding male and female were used, the overall population size becomes irrelevant, as it results in only two individuals' multiplication, leading to the loss of all other genetic diversity.

Thus, utilising enough breeding males and bitches is crucial for retaining unique genes in the gene pool. Historical data illustrates this was not always the case. Born in 1969, Vanka sired 387 puppies, preventing more than 60 other males from imparting their unique genes to the gene pool. Two methods can optimise breeding candidates. In canine breeding, the most common rule is to limit the number of litters per dog. While extremes of 387 puppies no longer occur, restricting the number of litters as much as possible, particularly for males, could give space to utilise other males. Another beneficial approach involves encouraging one-time-litters, where both the bitch and the male are utilised for the first time. Breeders often rely on their females, and these are already committed. Thus, strategies targeting the increased use of males in breeding could have a more profound impact. From a genetic



perspective, there is no rationale for allowing more litters per male than for bitches. This remains a common practice in many breeding regulations, however.

7.2 Increasing genetic diversity: finding unique alleles

The key step in preservation of the breed is to keep by maximise number of males and bitches in breeding and increase unique genes within the gene pool. Tools to accomplish the latter are: Mean Kinship and Optimal Contributions. Mean Kinship can help find dogs unrelated to the population (Ballou & Lacy, 1995). Mean Kinship was introduced in dog breeds for the first time in 2001 in the Icelandic Sheepdog (Oliehoek et al., 2009). Dogs with low Mean Kinship are likely to have unique genes, making them unrelated in the first place. To be effective for preservation, it's vital that Mean Kinship is calculated based on the entire current breeding population and that coefficients are calculated up to the founders within the breed.

Calculation of kinship or inbreeding while limiting the number of generations is not accurate enough to find dogs with unique genes. It might even reduce genetic diversity by creating a false sense of low inbreeding or Mean Kinship when that's not the case.

Country	Green	Yellow	Orange	Red
Austria		35		
Belgium	224	50	24	
Denmark	43	82	41	1
France			2	
Nederland	981	1035	1219	66
Sweden	32	88	12	
US	42	33		

Table 5: Contribution to diversity per list per country

A glance at *Table 5* presents diversity across countries. The Netherlands is home to a majority of Drentsche Partridge Dogs, with Belgium also hosting a significant population of dogs exhibiting low Mean Kinship values. The optimal strategy for breeding dogs with unique genes appears to lie within the country itself for the Netherlands, Belgium, and potentially the United States. Conversely, Sweden could enhance the breed's genetic diversity by considering imports from Belgium and the Netherlands, especially dogs with low Mean Kinship values, if the breed's population is set to increase. The report's insights underline the importance of individual dogs to the breed, assessed by Mean Kinship and the number of offspring.

The trend is that dogs with low Mean Kinship are often older, which may result in them not being used in breeding enough. If these older dogs, carrying unique genes, aren't used for breeding, their special genetic contributions could be lost. This loss might also push out the already limited "hidden diversity" in the breed. Once this diversity is lost, it can't be regained without introducing new genes through outcross with another breed. Thus, older



animals having low Mean Kinship need priority in breeding to keep (potential) genetic diversity, since they are about to become infertile. Though low fertility is indeed a problem with older animals, there is another advantage of using older animals. **They have 'proven'** to be able to reach old age in good health.

The application of Optimal Contributions is the most potent strategy to identify unique genes (Kettunen et al., 2022; Meuwissen, 1997). This technique can accurately target those animals that should contribute the most offspring. The drawback however: application of Optimal Contributions would require full control over the population and all dogs would have to be available. The tool's value becomes particularly apparent when only minor actions can be undertaken, given that it doesn't need to be employed across the entire population. For instance, Optimal Contributions could be applied to select animals for a sperm bank, thereby securing their unique genes for future generations. In this way, the 'hidden diversity' within a breed, although minimal in the case of the Drentsche Partridge Dog, is safeguarded and could potentially augment diversity to 2.19 in the future. As described previously, in the case of the Drentsche Partridge Dog, genetic diversity could be increased only a little without the use of outcross. To keep at least the potential to increase the genetic diversity in the future, Optimal Contributions is the most effective way to do so.



Photo 5: Vanka, a dominant ancestor, born in 1969. He had 387 children. Genetic traces of 22 of his direct offspring are still to be found in the current population.

7.3 Outcross: introducing unique alleles

Outcross, here defined as crossing with other breeds, is used for two main reasons (1) to enlarge to potential to increase genetic diversity by adding unique alleles, and (2) to introduce new properties to improve breed type or health of the breed. An example that combines both reasons is the outcross project to improve the health of the Norwegian



Lundehund. The genetic diversity of the Lundehund is the lowest recorded in dog breeds – probably three times lower than the Drentsche Partridge Dog. Outcross was necessary to overcome intestinal lymphangiectasia. Due to the low genetic diversity, there was simply **no ‘genetic answer’ against the disease within the population.** The outcross program seems successful, since more and more dogs are born looking and behaving like a Lundehund, but **without the “Lundehund syndrome”** (Melis et al., 2023).

In previous paragraphs we discussed stopping loss of alleles and spreading unique alleles. But what if the number of unique alleles is low? Within the Drentsche Partridge Dog the unique genes that can be utilised, expressed in an OFE of 2.19, have declined recently. This is only marginal distinct from the actual genetic diversity of 2.15 FGE. Hence, there is a mere 0.05 effective founder to exploit for spreading unique genes, whereas one founder introduction could contribute an entire 1.0 effective founder. Given the lack of new founders, outcrossing is the sole method for the introduction of new unique alleles that can be utilised to increase genetic diversity. Therefore, if a decision is made to increase genetic diversity beyond 2.19, outcrossing becomes a necessary strategy.

The success of an outcross project should be determined by the increase in OFE and FGE. Inbreeding is not a suitable metric for the assessment of outcross success, as it could give a falsely positive impression, considering outcross litters have zero inbreeding. However, within the population, inbreeding reverts rapidly.

For a notable increase in genetic diversity, genes from other breeds must significantly merge with the population. This is probably the reason why outcrosses to increase genetic diversity not always have been successful (**Głazewska & Prusak, 2012**). Outcrossing is not an instant remedy, and one outcross nest does not uplift a breed (Windig & Doekes, 2018). The Drentsche Partridge Dog's entire gene pool needs considerable dilution. The success of outcross in actual genetic diversity increase depends on three aspects:

1. The number of unrelated breeds introduced.
2. The degree of backcrossing to the original breed.
3. The number of offspring engaged in breeding, both from F1 and all subsequent litters.

Using numerous different breeds offers an advantage. Firstly, no single breed leaves a pronounced impact, assisting in maintaining the Drentsche Partridge Dog's integrity. Additionally, since these breeds are unrelated to each other, they don't increase mutual kinship, contributing additionally to genetic diversity and thus, reducing the risk of introducing new genetic problems and as a bonus: enhanced possibilities to select for desired traits. In practise, a such strategy would require a long-term program.



To sum up, while outcrossing introduces new unique genes into the current breeding population, to increase genetic diversity, a significant portion of genes from outcross breeds need to infiltrate the current gene pool. This requires actions like breeding with outcross litters' offspring. Therefore, outcrossing should be part of a comprehensive approach, alongside measures like one-time litters and selection of animals with low Mean Kinship, which descendants from outcross litter will show.

Now, is outcross really necessary? The answer to that question depends on the goal.

- While not having sufficient data: if there are many health-issues in the breed, outcross can help diminishing the problems more efficient.
- If the goal is only to preserve current genetic diversity a breeding program that keeps and increase the spread of unique genes is essential. For example, use animals having low Mean Kinship and ensure sufficient unused males. It's not inherently essential to undertake an outcross program.
- If the goal is to dramatically increase genetic diversity resulting in decreased future inbreeding, an outcross program is the only way, due to the limited amount of unmixed utilisable unique genes in the breed. Nonetheless, the impact of such an outcross program may be constrained or even negated if not paired with a low MK-centric strategy and sufficient male candidates. Undertaking both remains essential.

7.4 Breeding for properties: breed improvement

Breeders are primarily driven by two key goals: a) breed preservation and b) breed improvement. Specific focuses, however, can vary amongst breeders, core objectives tend to revolve around utility (hunting skills), shows (appearance), and companionship. Nearly all desired traits are polygenic, making their selection a complex science, beyond the scope of this report. Still, a few general guidelines can be suggested. Firstly, polygenic traits are frequently subject to strong environmental influences, which significantly impacts the predictability of inheritance. Essentially, a dog's observable traits may not always reflect its breeding potential. The stronger the environmental influence on a trait, the longer it takes for improvements to manifest across a breed, known as the a slow 'selection-response'.

Take hunting abilities for instance. An untrained dog exhibiting natural hunting skills could genetically be a superior hunter compared to a highly trained dog, despite the latter performing slightly better. Behaviour, particularly, is profoundly influenced by the



environment. Therefore, the selection-response is typically slower, requiring several generations before any improvement become apparent.

However, this doesn't imply that traits are not genetic, but rather that selection becomes more challenging. For instance, each breed tends to exhibit a distinct hunting profile, undeniably attributable to breed-specific genes. In the case of outcrossing, this understanding can be utilised - the selected breed will likely demonstrate a different hunting profile compared to the Drentsche Partridge Dog. Therefore, choosing breeds that offer complementary traits to the Drentsche Partridge Dog offer a quicker route to the improvement of hunting abilities.

7.5 Breeding for properties: health

For this report no data was offered on disease prevalence. However, it might be reasonable to assume a higher-than-average incidence of epilepsy in the Drentsche Partridge Dog population, based on input from many different sources. If the incidence exceeds the typical average of 0.8% in the general dog population (Zimmermann et al., 2009), it suggests multiple genes are involved. One such gene, linked to the *CCDC85A* gene was found (Beckers et al., 2023). While in the future this information could aid in development of tests, for now, combatting the disease relies on quantitative genetic selection methods.

Epilepsy, a typical polygenetic disease, implies an unpredictable nature in terms of inheritance and selection. Non-affected dogs may still sire affected offspring, and non-genetic factors might trigger epileptic signs in an animal. The management of polygenic diseases, notably in breeds prone to epilepsy, presents a significant obstacle for effective selection against the condition. Simply eliminating epileptic animals and their immediate parents from breeding may yield slow improvements. However, extending this exclusion of three generations in all directions might place undue strain on sufficient number of breeding candidates. This dilemma between safeguarding genetic diversity and necessity of selection will be discussed in the next chapter. Regardless of these complexities, it's crucial to refrain from breeding with animals displaying epilepsy symptoms. In absence of reliable risk assessment, like Estimated Breeding Values, risk should probably be avoided by refrain from closest kin as well.

A pragmatic approach forward includes:

1. Document affected animals
2. Document animals that have aged without displaying signs of epilepsy
3. Computing Estimated Breeding Values (EBVs)
4. Incorporating these EBVs into the breeding selection criteria



For situations where health and fertility are significant concerns, outcross may be an option worth considering. However, success in this context relies heavily on diligent documentation of diseases and fertility issues.

An area of significant concern is the lack of information regarding clinical hip dysplasia and elbow dysplasia. Although X-ray examinations are prevalent, the interpretation can vary substantially among different breeds. Some breeds continue to lead active lives despite D-classified hip scores, while others face discomfort with B-scores. Unfortunately, there is limited scientific research in this domain. In the case of the Drentsche Partridge Dog, close to 1000 X-ray examinations have been conducted for hip dysplasia and over 250 for elbow dysplasia. Yet, due to the lack of information about how this breed is affected by reduced hip quality, based on X-ray examinations, a complete overview is absent. A clinical evaluation is crucial for assessing the gravity of the condition. It is thus recommended to classify the number of animals that reach old age without any observable movement issues or indications of pain, especially animals that have been X-rayed.

In the realm of canine breeding, it's crucial to understand that selection for health extends beyond individual or litter health; it also impacts the health of the entire breed in the long run. The objective is to reduce animal suffering while maintaining or enhancing welfare. As previously noted, however, preserving population health is more complex than merely selecting against diseases: the conservation of genetic diversity is vital for the breed's long-term health. This potential conundrum is discussed in the subsequent chapter.



In photos 6, 7, and 8, observe the champion lineage. On the left is Eros v. Biljoen, a champion born in 1959, contributing 11.3% to the current gene pool. Centred is his son, Ascon v. Jachtpassie, another champion, born in 1969, with a 12.6% genetic contribution. Finally, on the right is Maras, Ascon's son and a champion himself, born in 1971, contributing 12.2%. Nonetheless, these percentages cannot be cumulatively added as they partially share genetic material, given their familial ties as grandfather, father, and son.

7.6 Selection pressure and genetic diversity

In the world of canine breeding, a delicate balance exists between robust selection and the need to maintain genetic diversity. High selection pressure comes with consequences. The policy direction isn't always clear-cut and depends on the breeding objectives. For example,



strong selection against (clinical) hip dysplasia in the Bernese Mountain Dog is very likely the cause of high incidence of cancer in the breed. This text presents guidelines for the Drentsche Partridge Dog, but might be applicable to other breeds.

Selection in breeding is typically directed towards a goal, either health, or specific desirable traits. This goal can be pursued with low, moderate or strong selection. Low selection is unavoidable, given that not every dog from a litter will reproduce unless the breed population expands rapidly. Conversely, strong selection is seldom beneficial, as it often hampers progress towards other goals and isn't always more effective than moderate selection. This is due to the differences between genotypes and phenotypes in dogs. The

In the Netherlands, it is a common belief that an X-ray exam is mandated by law. While legislation obliges breeders to actively guard against genetic diseases, to date, no document has been discovered, issued by any governmental institution, specifically requiring hip or elbow examinations in populations where mobility is not adversely affecting welfare. If a document to this effect *does* exist, individuals are urged to share the source with the author.

observable characteristics of a dog don't necessarily mirror its breeding capabilities. Therefore, moderate selection is often the preferred approach.

For the Drentsche Partridge Dog, genetic diversity preservation needs priority in breeding, given the steady decrease and forecasted future decline in genetic diversity. But how can this align with breeding requirements such as X-ray certification, dog show results, and clean epilepsy history? Two primary strategies may help.

Firstly, collecting and sharing health data more intensively can enhance selection and prediction of selection response by identifying hereditary of traits. Secondly, ensuring sufficient breeding males and females meet all criteria, particularly their genetic importance for genetic diversity, is crucial. Within the Drentsche Partridge Dog, especially for the males: make sure that at least half of the male list are animals that were not used in breeding yet, preferably having low Mean Kinship. Though there's no exact science to quantify, it's highly probable that the continued use of a select few male candidates in breeding will persistently diminish genetic diversity.

So how to implement moderate selection? There is not one straightforward answer. However, may the following example be an inspiration. Most dog breeds mandate an X-ray exam to detect hip dysplasia, but not all breeds show signs of discomfort or mobility problems, such as the Drentsche Partridge Dog. The X-ray policy aims to preclude future breed issues. However, when an animal is used only once for breeding, it won't drastically degrade hip quality across the population. Thus, a potential strategy for increasing genetic diversity might be to exempt the first litter from this requirement. Next, when for any subsequent litters, the X-ray requirement is reinstated, it still prevents the undetected spread of potential health issues as the animal begins to influence the breed's genetic pool. A similar approach could be adopted for dog show attendance rules. But, if the list of unused males is long enough, this first-litter-lenience may not be required.





8. How Dogs Global can help

The age-old tradition of dog breeding has led to the preservation and cultivation of more than 400 distinct, authentic breeds. This rich heritage offers future owners the chance to find their ideal canine companion. Despite this, media often presents dog breeding in a negative light. They focus solely on traits that have been exaggerated as being to the detriment of animal welfare. Such portrayals have led governments, organisations, and certain breeders to amplify measures promoting health-based selection criteria. Admittedly, dog breeding can result in unwanted genetic dispositions, the majority of these dispositions are not due to exaggerated traits.

Instead, they arise from the loss of genetic diversity, which instigates inbreeding and consequentially breed-specific diseases that are undesirable to all. This situation is set to deteriorate if selection intensity increases, even when the selection is health-focused.

Media narratives sometimes suggest that closed populations in breeds lead to their suffering. While it's true that many breeds decline in health, the discourse around dog breeding has been unjustly polarised. It is often presented as a choice between: one must **either favour breeds... or health, as it seems impossible to breed healthy dogs with a pedigree**. This is a misconception. In fact, with dedication and perseverance, and thorough scientific guidance it's entirely feasible to cultivate breeds that will gain a reputation for their robust health and longevity. Imagine breeds that radiate vitality, breeds that are a testimony to the rewards of tradition and diligent work, balancing integrity and health.

Achieving this balance requires acknowledging and adapting to the considerable differences among breeds. This should go together with a fusion of conservation genetics, quantitative genetics, precise high-quality data, and devoted breeders who deeply care for their breed.

Achieving balance calls for an appreciation of each breed's distinct characteristics. It requires a synthesis of conservation genetics and quantitative genetics, supported by high-precision, top-quality data. Essential to this process are dedicated breeders, passionately caring for their unique breeds.

Dogs Global provides precisely this balance. Offering a platform for breeders across the entire spectrum of breeds, Dogs Global archives, processes and supplies essential information for breed health and diversity improvement while enabling breeders to meet their personal breeding goals. Underpinned by unmatched data accuracy from top-tier technology, expert guidance from state-of-the-art quantitative and conservation genetics, and a deep-seated affection for dog breeds. Dogs Global delivers tailor made advice per breed that resonates with breeders' needs.



8.1 Test Litters

Dogs Global promotes breeding freedom while also aiding in the maintenance or improvement of genetic diversity and health. A vital instrument in our toolkit, the test-litters, empowers breeders to make informed decisions, understanding the ramifications of their choices on the possible litter, population genetic diversity and health.

Upon the selection of a female and male candidate, Dogs Global provides an insightful analysis of three pivotal aspects:

1. The influence on the breed's genetic diversity
2. The level of inbreeding within the potential litter
3. Where ample data is accessible, a health assessment

Each aspect is visually represented with a colours: green; yellow; orange; or red, offering an instant, intuitive understanding of the results.

The screenshot shows a user interface for selecting a mother and father dog to create a test litter. It displays the names and IDs of the selected dogs, their breed and color, and their genetic diversity and inbreeding scores. Below this, the results are summarized in three colored boxes: green for diversity, yellow for inbreeding, and orange for health. The diversity result is 'Increase', inbreeding is 'Acceptable', and health is 'High risk of epilepsy'. The interface also shows a 'Test mating' button and a 'Mean Kinship List'.

1. Choose mother:	2. Choose father:
NHSB 3053455 Imke v. Old-Diek	NHSB 3275047 V.d. Dongensehoeve Lars
Imke v. Old-Diek NHSB 3053455 Gold brindle 21.478	V.d. Dongensehoeve Lars NHSB 3275047 Gold brindle 22.161
Colour	Colour
Inbreeding	Inbreeding
Litters	Litters
Puppies	Puppies
Mean Kinship	Mean Kinship

Results

Diversity:	Inbreeding:	Health:
Increase	Acceptable	High risk of epilepsy
This combination contributes to diversity	Inbreeding coefficient: 24.054%	Based on current information available: the risk of epilepsy is high.
Mean Kinship: 21.75%		
Mean Kinship List:		

1. Genetic diversity

Determining the value towards genetic diversity for each dog, is the starting point for healthy breeding. Recognising that each breed is unique, Dogs Global weekly performs a



population analysis. This analysis is the input to balance the following three critical criteria:

- A. Mean Kinship and
- B. Number of direct offspring per animal.
- C. Optimal Contributions (a second conservation-tool),

The first criterion, Mean Kinship, measures the percentage to which an animal is genetically related to the entire current breeding population, including itself. The criterion 'Optimal Contributions' is highly sensitive, determining the breeding aim and each individual's contribution towards achieving the optimal genetic diversity possible. Optimal Contributions is leveraged to counterbalance the challenges posed by the Mean Kinship method. These criteria, while having varying impacts, jointly manage the population effectively.

Their application is tailor-made per breed. Given the Drentsche Partridge Dog has a low amount of "hidden diversity", the number of puppies born have a stronger impact for this breed. Currently, the threshold is set at 10 puppies. The combination of these three criteria safeguards the genetic diversity and thus the survival of the breed. With more progeny, the colour might change colour to yellow, orange or red.

2. Inbreeding

As discussed previously, inbreeding and contribution towards genetic diversity of the breed are two entirely distinct goals and are therefore indicated separately. Inbreeding does *not* genetic diversity, but the opposite is true: the diversity determines to what extent inbreeding can be avoided. Inbreeding is meticulously calculated, always based on all generations. At Dogs Global, we use two distinct algorithms to calculate the Coefficient Of Inbreeding (COI). This dual approach ensures the accuracy of our results, as both methods, despite their different processes, consistently produce the same outcome.

3. Health:

The health check is the third pillar in our test-litter evaluation. For a robust health assessment, extensive data is needed. Harnessing the power of quantitative breeding science, Dogs Global quantifies health factors. Selection efficiency for health significantly hinges on the volume and quality of data. For instance, we currently lack data on epilepsy. However, as soon as we collate reliable information, an epilepsy-estimator will instantly flag with red any breeding combinations presenting high risks based on proximity to affected relatives, or show increased risk in orange or moderate risk in yellow. Combinations deemed safe carry the reassuring sign of a green marker.

Test litters are tailor made per breed. As litter numbers decline, the traffic light system may be modified for the Drentsche Partridge Dog. While male selection is flexible, bitches are often preselected. Conservation genetics favour breeding, even with less significant bitches. From a conservation genetics perspective, breeding - even with less significant bitches - is



favourable over non-breeding. Specifically for the Partridge Dog, more tolerance will be exercised towards the bitches, considering their contribution to genetic diversity. And every extra bitch used for breeding, can be crossed with an extra male dog with low MK, which gives even bitches with high MK an important role.

8.2 Outcross Dashboard

Maintaining a neutral stance on outcrossing, Dogs Global ensures that no action, or inaction compromise the wellness of breeds, whilst diligently safeguarding their integrity. Dogs Global includes an innovative outcross dashboard, offering breeders access to a suite of tools designed to oversee their population. These evolving tools already brings essential information on the impact of outcross animals, contributing to successful management of outcross projects. In future, Dogs Global plans to facilitate the determination of the proportion of other breeds per dog, another milestone in assisting breeders in realising their personal breeding goals.

8.3 Updates

Recognising the dynamic nature of our field, we are continuously working on advancements. Instead of outlining future plans here, we recommend subscribing to our newsletter: www.dogsglobal.com/newsletter/ This ensures that you stay informed and engaged with our ongoing enhancements. Rest assured, numerous improvements are on the horizon, each promising to bring about positive change in dog breeding.

Passionate about the health and diversity of dog breeds, Dogs Global appreciates the value of shared wisdom. Each piece of feedback, advice, comment, or critique we receive is viewed as an integral part of our quest to reshape the future of reliable dog breeding. This ongoing dialogue accelerates the constant refinement of our future services manifested in a platform for dog breeds.

A final warning

Should this report be accessed by individuals not directly connected with Dogs Global, it's important they understand that the following conclusions *cannot* be accurately made based on the given data:

1. The breed is at risk due to insufficient genetic diversity or excessive inbreeding.



2. There is no problem since the inbreeding has not declined notably over the last 20 years. As highlighted earlier, it is not scientifically credible to categorise levels of inbreeding or genetic diversity as excessively high or low. The sole valid indicators of undue inbreeding are: (1) a high incidence of breed-specific illnesses or (2) statistically substantiated proof of inbreeding depression. The latter pertains to clear associations between increased inbreeding and health or fertility complications.

Similarly, this report should not be employed to disregard any concerns regarding the Drentsche Partridge Dog. Firstly, the report doesn't encompass analysis of health issues, or fertility concerns other than litter sizes. Secondly, whilst the decrease in diversity may be relatively minor, it is nonetheless discernible. Given that the existing diversity equates to roughly 2.5 founding individuals, any further decrease could amplify risk factors.

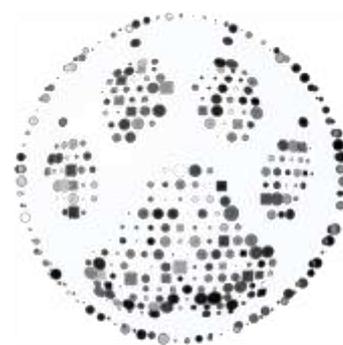
If you're a third-party reader of this document, please take heed of this cautionary note: the provided plan neither endorses the idea that inbreeding in the Drentsche Partridge Dog is too high, nor does it present any data (as of June 2022) to substantiate such a claim. This was, however, the premise of a statement made by a Dutch organisation purporting to seek welfare improvements. It's evident that the organisation didn't reference any scientific data in its claim, making it a largely speculative statement, and from a scientific perspective, inaccurate.

The author

Since the age of 11, dr. ir. P.A. (Pieter) Oliehoek has been actively involved in dog breeding. During his biology studies in Wageningen, he delved into canine genetics through DNA and pedigree analysis. In 1999, he examined the global population of the Icelandic Dog, introducing Mean Kinship to dog breeds —a testament to his pioneering approach.

After completing his studies, he expanded his skill set into software development. His passion for breed preservation led him back to scientific research. In 2009, he earned his PhD in Wageningen, specializing in the genetic management of endangered species and rare domestic breeds.

As a post-PhD, he worked on breeding programmes for zoos and continued his in professional website development. In 2018, he founded Dogs Global, merging his expertise in genetics, experience in software development, and love for dogs. This versatility sets him apart as an expert in his field.



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Glossary

Founders are the forefathers or primogenitors of the population. By definition they are (genetically) unrelated to each other. A founder can be added later in time as well, for example if another unrelated animal is found in a remote area. Also, an outcross-parent from another breed is unrelated to all founders and is therefore theoretically a founder as well. Founders are often animals from which their own parents are unknown, however this is not necessarily true. Their only real property is that they are unrelated to each other.

Foundlings animals having unknown parents, however they are related to other animals in the population. They direct or indirect descendent from founders. This relation is not known however due to the missing registration of one or both parents. If foundlings are not addressed, an analysis would regard them as founders, making foundlings unrelated where in fact they are not. The effect can be so dramatic that genetic diversity is even lost when this issue is not corrected.

Founder Retention is the part of alleles (genes) per founder that survived till the current population. The value is between 0 and 100%. This is not about the frequency of alleles (how often they are present), but if they are present at all and is an individual value per founder, not a population metric.

Effective founder genomes is the number of founder-genomes with equally contributing founders without any loss of unique founder alleles, that would give the exact same value as the population under study. This is a scale in number of animals (founder genomes) instead of percentages (%). This scale can be derived from percentage by the formula: $F_e = 1 / (2 * X)$, where X is the same metric on the scale of percentage.

Founder Genome Equivalent (FGE) represents the genetic diversity of the population. This diversity metric is expressed on the scale of the number of founders. The official definition: the number of founder-genomes with equally contributing founders without any loss of unique founder alleles, that would give the exact same genetic diversity and average mean kinship as the current breeding population. A higher number means a more genetically divers population having a lower average mean kinship. FGE is the same metric as AMK expressed on the scale of effective founder genomes.

Optimal Founder Equivalent (OFE) is the number of equally contributing founders that would be expected to produce the maximum genetic diversity possible within the population under study in most cases the reproductive (breeding) population.

Founder Genome Surviving (FGS) represents the number of unique alleles (genes) in the population, scaled to a number of animals. Since founders have unique alleles, each contributes 1 FGS. Only if all founders are alive, FGS equals the total founder count. For example, a lost founder having only one progeny contributes 0.5 FGS, as only half its



genome is passed on. Higher FGS indicates more original alleles remain. It's not about allele frequency, but presence.

Genetic Diversity Several definitions are applied. They all express in some way, the variation of genes within a population; whether this is only presence of unique alleles (see also FGS) or the frequency of alleles or in other words: how often genes are present or how they are spread. Dogs Global uses FGE to evaluate the genetic diversity of a breed.

Inbreeding Even within science there are three different definitions on inbreeding. Within Dogs Global we utilise the following definition: inbreeding is the chance of homozygosity – having the same gene on one locus - due to common ancestors until the founders. Or in other words: inbreeding of one individual dog is the chance of having the same gene inherited from the father side as well as from the mother side because the father and mother share common ancestors. Inbreeding is expressed in the coefficient of inbreeding (COI).

Coefficient of Inbreeding (COI) The percentage of inbreeding of an individual dog.

Average inbreeding (\bar{F}) is the average of the sum of all COI of all individuals in the population. For the biologist among us: within this study we could regard \bar{F} as observed homozygosity under the assumption that all founder alleles were unique.

Kinship (f) is the percentage in which an animal is genetically related to another animal (or group of animals). One could say: in what percentage animals are family to each other. Yet another description is the percentage of genes two animals share due to common ancestry.

Relatedness (r) **Besides kinship there is another definition: “relatedness”** which has a different scientific meaning. It is a metric of genetic similarity between animals; or in other words how much one animal will have the same genetic properties as another animal. Though kinship and *relatedness* are connected, they have (slightly) different values, especially when inbreeding is low. *Relatedness* is often used within breeding for properties, especially for production and is part of breeding value estimation. *Relatedness* is not (yet) used as a genetic term within Dogs Global documents. It is addressed to avoid confusion when other documents or scientific literature is consulted.

Average Mean Kinship (AMK or \bar{f}) is quantified as a percentage, ranging from 0 to 100%. An elevated AMK percentage bears an inverse correlation with a diminished percentage of genetic diversity, and contrarily. To elaborate, the exact representation of genetic diversity as a percentage is 100% less the average MK. When AMK or genetic diversity percentages are re-scaled to the domain of founder genomes, this produces the Founder Genome Equivalents (FGE).

For those with a background in biology, another term for genetic diversity is expected heterozygosity, based on the presumption that all founder alleles were distinct. In parallel, under the same assumption, average MK equates to expected homozygosity.



Mean Kinship Is basically the kinship of an individual with the entire current breeding population, including itself. A low mean kinship means the individual is relatively unrelated to the population and is therefore genetically important. It has a high chance of carrying genes that are unique or underrepresented within the population. Mean kinship is a tool developed for zoos to preserve genetic diversity of endangered species. Mean kinship gives only an indication if an animal is likely to be beneficial for the population; or not: in case Mean Kinship is high.

Optimal Contributions is a breeding tool for genetic population management, which determines the actual contribution each individual should have to maximise the breeding goal. One application is to minimise the average mean kinship and thus maximise the genetic diversity. Optimal contributions can determine which animals are genetically most important for genetic diversity of the breed.

References

- Ballou, J. D., & Lacy, R. C. (1995). Identifying Genetically Important Individuals for Management of Genetic Variation in Pedigreed Populations. In *Population Management for Survival and Recovery, Analytical Methods and Strategies in Small Population Management* (pp. 76–111). Columbia University Press.
- Beckers, E., Bhatti, S. F. M., Van Poucke, M., Polis, I., Farnir, F., Van Nieuwerburgh, F., Mandigers, P., Van Ham, L., Peelman, L., & Broeckx, B. J. G. (2023). Identification of a Novel Idiopathic Epilepsy Risk Locus and a Variant in the CCDC85A Gene in the Dutch Partridge Dog. *Animals*, 13(5). <https://doi.org/10.3390/ani13050810>
- Głazewska, I., & Prusak, B. (2012). Evaluation of the effectiveness of introducing new alleles into the gene pool of a rare dog breed: Polish Hound as the example. *Czech Journal of Animal Science*, 57, 248–254. <https://doi.org/10.17221/5923-CJAS>**
- Kettunen, A., Kallsoy Joensen, S., & Berg, P. (2022). Optimum contribution selection (OCS) analyses prompted successful conservation actions for Faroese Horse population. *Genetic Resources*, 3(5), 59–67. <https://doi.org/10.46265/genresj.KKXV5870>
- Lacy, R. C. (1989). Analysis of founder representation in pedigrees: Founder equivalents and founder genome equivalents. *Zoo Biology*, 8(2), 111–123. <https://doi.org/https://doi.org/10.1002/zoo.1430080203>
- Lacy, R. C. (1995). Clarification of genetic terms and their use in the management of captive populations. *Zoo Biology*, 14(6), 565–577. <https://doi.org/https://doi.org/10.1002/zoo.1430140609>
- Leroy, G. (2014). Inbreeding depression in livestock species: review and meta-analysis. *Animal Genetics*, 45(5), 618–628. <https://doi.org/https://doi.org/10.1111/age.12178>



- Melis, C., Billing, A. M., Wold, P.-A., & Ludington, W. B. (2023). Gut microbiome dysbiosis is associated with host genetics in the Norwegian Lundehund. *Frontiers in Microbiology*, *14*. <https://doi.org/10.3389/fmicb.2023.1209158>
- Meuwissen, T. H. E. (1997). Maximizing the response of selection with a predefined rate of inbreeding. *Journal of Animal Science*, *75*(4), 934–940. <https://doi.org/10.2527/1997.754934x>
- Neradilová Silvie AND Connell, L. A. N. D. H. P. A. N. D. Č. B. B. (2019). Tracing genetic resurrection of pointing dog breeds: Cesky Fousek as both survivor and rescuer. *PLOS ONE*, *14*(8), 1–12. <https://doi.org/10.1371/journal.pone.0221418>**
- Oliehoek, P. A., Bijma, P., & van der Meijden, A. (2009). History and structure of the closed pedigreed population of Icelandic Sheepdogs. *Genetics Selection Evolution*, *41*(1), 39. <https://doi.org/10.1186/1297-9686-41-39>
- Ubbink, G. J., van de Broek, J., Hazewinkel, H. A. W., & Rothuizen, J. (1998). Risk estimates for dichotomous genetic disease traits based on a cohort study of relatedness in purebred dog populations. *Veterinary Record*, *142*(13), 328–331. <https://doi.org/https://doi.org/10.1136/vr.142.13.328>
- Voges, S., & Distl, O. (2009). Inbreeding trends and pedigree analysis of Bavarian mountain hounds, Hanoverian hounds and Tyrolean hounds. *Journal of Animal Breeding and Genetics*, *126*(5), 357–365. <https://doi.org/https://doi.org/10.1111/j.1439-0388.2009.00800.x>
- Windig, J. J., & Doekes, H. P. (2018). Limits to genetic rescue by outcross in pedigree dogs. *Journal of Animal Breeding and Genetics*, *135*(3), 238–248. <https://doi.org/https://doi.org/10.1111/jbg.12330>
- Zimmermann, R., Hülsmeier, V. I., Sauter-Louis, C., & Fischer, A. (2009). Status epilepticus and epileptic seizures in dogs. *Journal of Veterinary Internal Medicine*, *23*(5), 970–976. <https://doi.org/10.1111/j.1939-1676.2009.0368.x>



Appendix

Within conservation genetics there is a long history of pinpointing factors that increase inbreeding. Especially because even many population geneticists are not aware, it is important to point out: implicitly all those factors first reduce genetic diversity, and hereafter inbreeding becomes unavoidable. So many factors measure decrease of diversity and NOT increase of inbreeding. In wild populations, there is no pedigree available, nor any other method that would actually calculate the true genetic diversity, (average mean) kinship and inbreeding. Hence, methods have been developed to estimate the effect of specific population dynamics causing loss of genetic diversity, among which sex ratio, fluctuating population size and variation in 'family size' (number of puppies per ancestor) for endangered species. These methods were expressed as the "effective population size". When we have no means to estimate the actual loss of diversity and actual level of kinship of a population, at least population geneticist could look at the rate of increase/decrease. And that is what the effective population size does: it enables to have a rough indication if a population is viable or not.

With dog breeds we actually have pedigrees. Moreover, nowadays we have the power of computing the actual level of genetic diversity, kinship and inbreeding of a population. Basically, there is no need for an effective population size estimate anymore. Moreover, the actual loss of genetic diversity and increase of inbreeding is much higher than the effective population size estimates would have predicted. At least this is found in every research done so far on dog breeds. However, to give full input for (future) policy making, the effective population size and similar interesting metrics have been included within this analysis. Calculation and interpretation of these metrics can be found in general scientific literature, since they are quite standard in the science of conservation genetics.

Period	Born	Inbreeding	AMK	Inbreeding Effective Population Size	Kinship Effective Population Size	Sex ratio Effective Population Size
1930-1934	8	0.00	9.2	100000.0	-3.0	6
1935-1939	18	0.69	8.1	72.5	-41.3	16
1940-1944	64	0.93	4.85	206.9	-14.1	54
1945-1949	83	7.38	3.98	7.7	-54.7	85
1950-1954	102	8.06	5.43	68.1	33.1	65
1955-1959	215	12.22	7.89	11.1	19.2	104
1960-1964	318	16.38	10.84	10.6	15.6	154
1965-1969	585	17.56	13.45	35.4	17.1	248
1970-1974	2087	19.40	15.66	22.4	19.6	689
1975-1979	3465	18.89	16.79	-79.0	37.3	1145
1980-1984	3029	18.77	16.85	-338.0	693.4	985
1985-1989	2358	21.07	16.92	17.7	593.9	794
1990-1994	1891	24.11	17.68	13.0	54.7	642
1995-1999	2152	23.00	19.11	-34.2	28.8	726
2000-2004	2628	23.33	20.44	116.7	30.4	878
2005-2009	2486	22.76	21.14	-67.3	56.8	825
2010-2014	2019	23.18	21.69	92.0	71.7	686



2015-2019	1627	23.53	22.39	109.7	55.9	554
2020-2022	720	24.29	23.05	50.3	58.8	237

Table 6. Metrics over 5-year time periods, especially effective population sizes (N_e)

The definition for the inbreeding effective population size is: the number of individuals in an ideal population that would give rise to the same rate of inbreeding as in the actual population. According to Falconer and Mackay (1996) the (inbreeding) effective population size would be obtained from the calculated rate of inbreeding (changes in heterozygosity), ΔF , as

$$N_e = \frac{1}{\Delta F}$$

The effect of sex ratio on N_e can be expressed in the following equation, originally published by Wright (1938):

$$N_e = \frac{4N_m N_f}{N_m + N_f}$$

where N_m and N_f are the numbers of males and females, respectively. If the number of males is equal to the number of females, the N_e is equal to the actual population size.

Generation Interval

The generation interval has effect on loss of diversity. The generation interval is calculated by the difference of the date of birth between the litter and the father and/or mother. In other words: the average age of parents at the time of birth of a litter. As an example, why this might be relevant: suppose we select older males (on average 2 years), we could increase the generation interval, making the decrease of genetic diversity go slower (by one year).

Period	Born	Generation Interval Fathers	Generation Interval Mothers	Generation Interval
1930-1934	8			
1935-1939	18	6.22	3.29	4.76
1940-1944	64	3.98	3.55	3.76
1945-1949	83	4.64	3.43	4.04
1950-1954	102	5.89	6.08	5.99
1955-1959	215	4.66	4.20	4.43
1960-1964	318	5.11	4.22	4.67
1965-1969	585	5.34	4.77	5.06
1970-1974	2087	4.90	3.95	4.42
1975-1979	3465	4.30	3.94	4.12
1980-1984	3029	5.47	4.42	4.95
1985-1989	2358	5.48	4.45	4.96
1990-1994	1891	5.26	4.58	4.92
1995-1999	2152	4.99	4.58	4.78
2000-2004	2628	4.89	4.61	4.75
2005-2009	2486	5.21	4.58	4.90
2010-2014	2019	5.27	4.82	5.05



2015-2019	1627	5.47	4.68	5.07
2020-2022	720	5.77	4.74	5.25

Table 7: Generation interval in years over 5-year time period

Number of offspring & matador-breeding

In dog world we are used to a show-winning stud dog being used for many litters. Moreover, there is often a run on its progeny as well. This creates the matador-breeding effect and decreases genetic diversity. But what is favourable if you want to save genetic diversity? **What would be ‘the best practice’?** The best is that the number of puppies per animal would be: 2!. Simulations carried out by Sonesson & Meuwissen (2000) indicate that restricting the number of offspring used in breeding is highly effective as a genetic conservation tool. This theoretic practice would mean that each animal will have 2 offspring and 4 grandchildren, 8 greatgrandchildren etc. Of course, in practice a litter is already 6 on average in case of the Drentsche Partridge Dog. There will be a factor 3 more progeny in every generation even if each animal would only have one litter of which only 2 animals would be selected for breeding themselves. So, in this scenario where the population size is steady, animals bred, will have 6 animals of which 4 *will not* have progeny themselves by

In this report we described the accumulative effect over generations, increasing the contribution of dominant ancestors through their (distant) progeny. This effect already starts in the second generation as grandfathers (or less often grandmothers). One way to elucidate this effect in the second generation was developed by the late Per Erik Sundgren from the Swedish University of Agricultural Sciences, who introduced: grandfather curves and implemented this in “Lathunden” Swedish software for Genetic management of dog breeds. In the report we put the spotlight on this effect through time-periods by the Average Progeny Grandfathers and Grandmothers in *Table 9*

definition. Next, the minimum number of grandchildren is 12. Keep those two numbers in mind (6 and 12) when you study the *Table 9* on the next page.

Not only the number of offspring, but also the number of grandchildren is relevant. As presented previously in this report, the contribution of dominant ancestors is often not achieved by having a high number of direct offspring, but through progeny over many generations. The contribution of ancestors might accumulate (but also can be lost completely) over time. The number of grandchildren is second accumulative step, so to say, and therefore it is another indicator if some ancestors will become dominant while others will in turn diminish or vanish from the population. Hence a high number of grandchildren



per grandparent underline the accumulative effect of contribution of matadors over time. Note that the standard deviation of grandchildren of grandfathers is very high in between 1965 and 1975 as is the average number of grandchildren by grandfathers: about 90.97 and 103.55. Note that the optimal would be about 12 grandchildren on average. So genetic diversity in this period is lost about 8 times faster than necessary.

Year	Born	Size	Founders	FGS	OFE	FGE	AMK	F
2022	229	4029		5.45	2.19	2.15	23.28	23.48
2021	380	4228		5.52	2.25	2.16	23.11	23.41
2020	353	4343		5.61	2.23	2.18	22.89	23.33
2019	257	4476		5.68	2.29	2.20	22.68	23.19
2018	370	4721		5.74	2.31	2.22	22.53	23.12
2017	336	4873		5.78	2.33	2.23	22.39	23.14
2016	362	5041		5.88	2.35	2.25	22.19	23.05
2015	352	5226		5.93	2.38	2.27	22.05	23.03
2014	345	5355		6.00	2.38	2.28	21.93	23.05
2013	429	5566		6.06	2.38	2.29	21.80	23.01
2012	424	5633		6.13	2.40	2.31	21.66	22.99
2011	387	5720		6.26	2.44	2.32	21.53	22.97
2010	435	5836		6.54	2.45	2.33	21.45	23.04
2009	475	5812		6.63	2.45	2.34	21.36	23.05
2008	456	5809		6.74	2.48	2.35	21.23	23.06
2007	539	5789		6.88	2.51	2.36	21.14	23.13
2006	532	5617		6.96	2.55	2.38	21.02	23.14
2005	529	5451		7.22	2.60	2.39	20.92	23.20
2004	552	5351		7.35	2.64	2.40	20.79	23.33
2003	554	5265		7.47	2.65	2.42	20.63	23.23
2002	578	5073		7.75	2.66	2.44	20.47	23.31
2001	438	4900		7.90	2.67	2.47	20.27	23.30
2000	523	4866		8.14	2.75	2.50	20.01	23.29
1999	461	4800		8.29	2.82	2.53	19.75	23.21
1998	423	4838		8.53	2.93	2.57	19.46	22.99
1997	409	4992		9.09	3.00	2.62	19.12	22.53
1996	413	5113		9.20	3.09	2.66	18.77	22.22
1995	466	5229		9.45	3.12	2.71	18.45	21.97
1994	379	5248		9.63	3.16	2.75	18.15	21.73
1993	342	5413		9.80	3.16	2.79	17.91	21.32
1992	359	5783		10.34	3.36	2.84	17.63	20.87
1991	416	6068		10.68	3.35	2.87	17.45	20.55
1990	412	6318		11.29	3.48	2.90	17.26	20.06
1989	371	6487		11.80	3.54	2.92	17.10	19.63
1988	447	6811		12.14	3.64	2.94	16.99	19.34
1987	453	6943		12.29	3.82	2.97	16.85	19.06
1986	481	7035		12.48	3.95	2.97	16.86	19.01
1985	613	7176		12.79	4.03	2.98	16.79	19.03



Year	Born	Size	Founders	FGS	OFE	FGE	AMK	F
1984	797	7028		13.14	4.08	2.98	16.80	18.96
1983	628	6748		14.23	4.13	2.97	16.81	19.12
1982	588	6508		14.31	4.29	2.97	16.83	18.97
1981	490	6150		14.49	4.44	2.96	16.91	19.01
1980	526	5960		14.52	4.57	2.96	16.91	19.05
1979	561	5621		15.45	4.77	2.96	16.90	19.01
1978	685	5262		15.58	4.87	2.96	16.90	19.01
1977	724	4732		16.11	4.89	2.97	16.83	18.77
1976	693	4069		16.56	4.95	2.99	16.74	18.75
1975	802	3446		17.27	5.26	3.01	16.58	18.96
1974	608	2744		19.31	6.47	3.08	16.24	18.95
1973	379	2220		21.55	8.22	3.10	16.13	19.09
1972	538	1908		22.15	9.14	3.22	15.54	18.66
1971	247	1426		23.19	10.17	3.26	15.34	18.02
1970	314	1218	1	24.38	11.92	3.32	15.06	17.74
1969	219	955		25.00	12.70	3.41	14.65	16.81
1968	85	784		25.97	13.38	3.64	13.74	16.66
1967	115	691		26.76	14.61	3.69	13.54	16.51
1966	115	691		27.67	14.76	3.86	12.95	15.58
1965	83	612		31.59	21.48	4.05	12.35	14.80
1964	82	556		33.44	23.90	4.24	11.80	14.15
1963	35	496	1	34.67	24.26	4.40	11.38	13.61
1962	49	492	2	37.79	27.31	4.67	10.71	12.38
1961	76	457	4	37.56	27.39	4.80	10.41	12.31
1960	66	396	3	35.45	25.14	5.05	9.89	11.73
1959	42	343	2	34.40	22.83	5.47	9.15	10.47
1958	70	310		33.18	21.79	5.81	8.60	9.78
1957	32	258	2	36.78	23.54	6.57	7.61	9.14
1956	33	236	1	35.93	22.72	6.66	7.50	9.21
1955	33	218		36.64	22.85	7.62	6.56	7.98
1954	30	195	2	38.89	25.39	7.83	6.39	7.20
1953	22	176		38.79	26.81	8.62	5.80	6.62
1952	23	171	3	43.59	33.48	9.74	5.13	5.58
1951	7	164	3	45.16	40.00	9.97	5.02	5.49
1950	11	161	1	43.79	40.54	10.37	4.82	5.26
1949	19	153	1	43.75	41.27	11.09	4.51	4.31
1948	10	136	4	43.82	41.61	12.10	4.13	3.62
1947	18	125		40.91	39.25	12.34	4.05	3.13
1946	15	110	4	40.99	39.85	13.40	3.73	1.94
1945	9	94	3	37.66	36.64	14.38	3.48	1.56
1944	15	85	7	34.80	33.71	13.96	3.58	0.85
1943	11	65	9	27.99	27.37	12.62	3.96	1.11
1942	8	47	5	19.49	18.65	9.65	5.18	1.53
1941	1	34	2	14.49	13.67	9.18	5.45	1.19
1940	5	32	1	12.99	12.39	8.23	6.08	1.27
1939	3	27	4	12.00	11.52	7.34	6.81	0.46
1938	2	20	1	8.00	7.53	5.29	9.45	0.63
1937	1	19		8.25	8.07	5.46	9.16	0.00
1936	6	19		8.50	8.26	5.85	8.55	0.00
1935		14	1	9.00	9.00	7.69	6.51	0.00
1934	1	13		8.00	8.00	6.90	7.25	0.00
1933	1	12	1	8.00	8.00	6.86	7.29	0.00
1932		10	2	7.00	7.00	5.88	8.50	0.00
1931	1	8		5.00	5.00	4.27	11.72	0.00
1930	1	7	1	5.00	5.00	4.45	11.22	0.00



Year	Born	Size	Founders	FGS	OFE	FGE	AMK	F
1929		5	2	4.00	4.00	3.57	14.00	0.00
1928	1	3		2.00	2.00	1.80	27.78	0.00
1927		2	1	2.00	2.00	2.00	25.00	0.00

Table 8: All number for Graphs 1, 2 & 3



Period	Born	Fathers	Mothers	Litter size	Average Offspring Fathers	Average Offspring Mothers	Average Progeny Grand-fathers	Average Progeny Grand-mothers	Standard Deviation Offspring Fathers	Standard Deviation Offspring Mothers	Standard Deviation Progeny Grand-fathers	Standard Deviation Progeny Grand-Mothers
1930-1934	8	3	4	1.00	1.33	1.00	6.33	4.75	0.58	0.00	1.53	1.89
1935-1939	18	5	8	1.50	2.40	2.00	4.40	3.67	1.95	2.00	2.97	3.61
1940-1944	64	11	27	1.48	3.64	1.74	10.36	4.96	4.30	1.39	14.40	8.24
1945-1949	83	22	44	1.61	3.23	1.97	10.73	6.56	4.52	1.54	23.15	8.20
1950-1954	102	20	34	2.74	4.65	3.58	15.05	11.58	5.05	3.48	18.65	15.49
1955-1959	215	17	53	3.96	12.35	5.25	33.35	14.18	15.62	4.20	44.84	29.56
1960-1964	318	33	77	3.99	9.30	5.29	44.39	25.26	17.59	4.08	88.91	40.39
1965-1969	585	35	124	4.72	16.71	7.41	90.97	40.30	25.76	5.79	188.02	67.81
1970-1974	2087	67	346	6.03	31.13	9.57	103.55	31.83	48.45	7.07	175.92	54.53
1975-1979	3465	129	577	6.01	26.86	10.50	49.45	19.33	40.36	7.43	94.13	43.41
1980-1984	3029	111	495	6.12	27.28	10.66	44.62	17.44	36.10	8.45	70.12	35.09
1985-1989	2358	115	398	5.92	20.50	9.83	33.12	15.87	25.75	6.78	70.61	26.49
1990-1994	1891	99	322	5.87	19.10	9.50	40.86	20.33	17.00	7.11	60.79	36.27
1995-1999	2152	106	365	5.90	20.30	9.87	50.13	24.38	19.02	6.79	71.00	46.45
2000-2004	2628	118	440	5.97	22.27	9.81	43.37	19.10	21.76	6.30	64.43	30.42
2005-2009	2486	142	414	6.00	17.51	9.17	29.45	15.43	17.76	5.95	52.12	32.33
2010-2014	2019	119	345	5.85	16.96	8.97	27.68	14.64	16.60	5.45	47.91	22.86
2015-2019	1627	109	278	5.85	14.93	9.24	13.14	8.14	11.50	5.88	22.59	13.65
2020-2022	720	62	120	6.00	11.61	7.27	0.11	0.07	9.18	4.22	0.89	0.70

Table 9: Number of descendants (direct offspring & grand-children), litter-size and standard deviations over 5-year periods