

Genetic Diversity Testing for the Whippet

Overview

The Veterinary Genetics Laboratory (VGL), in collaboration with Dr. Niels C. Pedersen, has developed a panel of short tandem repeat (STR) markers that will determine genetic heterogeneity and diversity across the genome and in the Dog Leukocyte Antigen (DLA) class I and II regions for specified dog populations. This test panel will be useful to dog breeders who wish to use DNA-based testing to track and increase genetic diversity as a supplement to in-depth pedigrees. DNA based information on genetic heterogeneity and diversity, along with genetic testing results for desired phenotypes and health traits, can aid in informing breeding decisions.

Genetic diversity testing in the Whippet has been established, and almost all existing alleles at the 33 STR loci and 7 DLA class I and II regions have potentially been identified. As of November of 2023, 110 Whippets from the USA (n=100), Canada (n=4), Italy (n=4), and Australia (n=2) were tested to assess genetic diversity in the breed. We will continue to add new alleles and haplotypes if they are found in the breed, and their respective frequencies will be updated if necessary.

Results reported as:

Short tandem repeat (STR) loci: A total of 33 STR loci from carefully selected regions of the genome were used to assess genetic heterogeneity and existing genetic diversity within an individual as well as across the breed. The alleles inherited from each parent are displayed graphically to highlight heterozygosity and genetic diversity in individuals and breed wide.

DLA haplotypes: Seven STR loci linked to the DLA class I and II genes were used to identify genetic differences in a region that regulates immune responses and self/non-self-recognition. Problems with self/non-self-recognition, along with non-genetic factors in the environment, are responsible for autoimmune disease, allergies, and susceptibility to infectious agents.

Internal Relatedness: The IR value is a measure of the genetic relatedness of an individual's parents. The value takes into consideration both heterozygosity of alleles at each STR loci and their relative frequency in the population. Therefore, IR values heterozygosity over homozygosity and uncommon alleles over common alleles. IR values are unique to each dog; two individuals from different sources may have identical IR values, but a quite different genetic makeup.

I. Introduction

A. History [1-5]

The Whippet is a sighthound breed that originated in England, where they descended from Greyhounds brought by the Romans. The name is derived from an early 17th-century word meaning "to move briskly". There has been a continuum of Greyhound-type breeds from the time of ancient Egypt through the Middle Ages, ranging from large (Greyhound), to medium (Whippet), to small (Italian Greyhound). A small Greyhound breed became popular as a ratting dog in medieval England, and the first written use of the name Whippet for a dog happened in 1610. Paintings from the 17th and 18th centuries also show dogs of Whippet type. The Whippet was held in especially high regard in the northern and more rural parts of England and Wales, where it was described as "the poor man's racehorse". They are the fastest dog of their weight, capable of achieving speeds of up to 35 miles per hour (56 km/h).

There were originally two varieties of Whippets. A smooth coat was more popular in Lancashire, Yorkshire, and the Midlands of England; this type evolved into the modern Whippet. A second type had a rough coat from crossbreeding with Bedlington Terriers, and was more popular in Durham and Northumberland. The breed achieved worldwide recognition in the late 19th century, as did many other English breeds. The modern type Whippet was officially recognized in 1891 by The Kennel Club, making it eligible for competition in dog shows and recording of pedigrees. The Whippet was recognized in 1888 by the American Kennel Club. Currently, the Whippet ranks 54 out of 201 in the AKC Breed Popularity ranking.

Whippet racing appeared in the mid-nineteenth century as a form of coursing known as 'ragging'. Several dogs would be lined up and released from their collars by handlers at the same time, racing towards their owners standing at the opposite end of the track waving towels. This type of racing was a popular Sunday event in the north and Midlands of England, and became a common weekend sport in countries such as Australia. Racing to a cloth evolved to dogs usually chasing after a live or mechanical hare. A dichotomy ultimately developed because of those who did not consider pure breeding as important as winning races. The British Whippet Racing Association was established in 1967 to establish race rules and procedures involving non-purebred Whippets. This was viewed as a threat to pure breeders and a Whippet Club Racing Association was established exclusively for purebred animals. Whippets also participate in dog sports such as lure coursing, agility, and flyball.

B. Appearance [2, 4, 6]

Whippets are a medium-sized sighthound dog. The AKC breed standard calls for heights at the lowest point of the withers of 19 to 22 inches for males, and 18 to 21 inches for females. A height over a one-half inch above or below these ranges constitutes a disqualification. The length from the forechest to the buttocks should be equal to or slightly greater than height at the withers. Coat color is considered immaterial in judging of Whippets, and they come in a wide variety of marking patterns. They can range from solid black to solid white, with red, fawn, brindle, blue, or cream. The coat is short, smooth and close. Any other coat type constitutes a disqualification. Blue eyes and eyes not of the same color also disqualify.

C. Temperament [1-4]

Whippets are quiet but require regular exercise. They are friendly and not prone to anxiety and barking. When not running, they prefer the furniture or the owner's lap. These attributes make the Whippet an excellent housedog. They are not aggressive to other dogs, but due to their sighthound nature they have been known to chase small pets or animals when the opportunity arises.

II. Genetic diversity of the contemporary Whippet

A. Population genetics based on 33 STR loci on 25 canine chromosomes

STR markers are highly polymorphic and have great power to determine genetic differences among individuals and breeds. The routine test panel contains 33 STRs consisting of those that are recommended for universal parentage determination for domestic dogs by the International Society of Animal Genetics (ISAG) and additional markers developed by the VGL for forensic purposes. Each of these STR loci is known to contain from 7 to 29 different alleles (avg. 15.4 alleles/locus) when tested across many breeds of dogs. Each breed, having evolved from a small number of founders and having been exposed to artificial genetic bottlenecks will end up with only a portion of the total available diversity. Artificial genetic bottlenecks include such things as popular sire effects, geographic isolation, catastrophes, outbreaks of disease, and ups and downs in popularity and resulting increases and decreases in population size. The alleles identified at each of the 33 STR loci and their relative frequencies were determined for the 110 Whippets and are listed in **Table 1**.

Table 1: 33 Alleles and their frequencies for 33 STR markers in Whippet (n=110). The allele that occurs at the highest frequency at each locus is bolded.

AHT121	AHT137	AHTH130	AHTH171-A	AHTH260	AHTk211
94 (0.072)	131 (0.284)	119 (0.023)	219 (0.014)	238 (0.014)	87 (0.644)
96 (0.149)	133 (0.032)	121 (0.191)	225 (0.005)	240 (0.117)	89 (0.153)
98 (0.369)	137 (0.495)	127 (0.282)	227 (0.270)	242 (0.018)	91 (0.126)
100 (0.185)	141 (0.032)	131 (0.436)	229 (0.685)	244 (0.464)	95 (0.077)
104 (0.081)	147 (0.126)	133 (0.064)	237 (0.027)	246 (0.225)	
106 (0.113)	149 (0.009)	135 (0.005)		248 (0.023)	
110 (0.032)	151 (0.023)			250 (0.072)	
				252 (0.054)	
				254 (0.014)	
AHTk253	C22.279	FH2001	FH2054	FH2848	INRA21
286 (0.032)	116 (0.324)	132 (0.095)	148 (0.077)	228 (0.018)	95 (0.523)
288 (0.275)	118 (0.423)	136 (0.027)	152 (0.158)	230 (0.203)	97 (0.005)
290 (0.450)	120 (0.050)	140 (0.027)	156 (0.428)	232 (0.005)	99 (0.225)
292 (0.243)	124 (0.131)	144 (0.599)	160 (0.059)	236 (0.050)	101 (0.248)
	126 (0.045)	148 (0.252)	164 (0.189)	238 (0.122)	
	130 (0.027)		168 (0.086)	240 (0.293)	
			172 (0.005)	242 (0.198)	
				244 (0.113)	

INU005	INU030	INU055	LEI004	REN105L03	REN162C04
110 (0.014)	144 (0.113)	208 (0.018)	95 (0.626)	229 (0.218)	202 (0.288)
124 (0.541)	148 (0.090)	210 (0.748)	97 (0.005)	233 (0.500)	206 (0.712)
126 (0.288)	150 (0.784)	214 (0.167)	105 (0.050)	235 (0.145)	
130 (0.005)	152 (0.014)	218 (0.068)	107 (0.315)	237 (0.027)	
132 (0.153)			109 (0.005)	239 (0.009)	
				241 (0.014)	
				243 (0.055)	
				245 (0.032)	
REN169D01	REN169O18	REN247M23	REN54P11	REN64E19	VGL0760
202 (0.077)	162 (0.209)	268 (0.555)	222 (0.495)	139 (0.473)	18.2 (0.063)
210 (0.032)	164 (0.136)	270 (0.173)	226 (0.005)	143 (0.005)	19.2 (0.005)
212 (0.632)	166 (0.382)	272 (0.214)	228 (0.054)	145 (0.324)	20.2 (0.270)
214 (0.045)	168 (0.018)	278 (0.059)	232 (0.045)	147 (0.189)	21.2 (0.059)
216 (0.191)	170 (0.255)		234 (0.041)	149 (0.009)	22.2 (0.194)
218 (0.023)			236 (0.279)		23.2 (0.401)
			238 (0.081)		24.2 (0.009)
VGL0910	VGL1063	VGL1165	VGL1828	VGL2009	VGL2409
13 (0.185)	8 (0.356)	18 (0.176)	15 (0.099)	9 (0.180)	13 (0.108)
14 (0.005)	9 (0.050)	19 (0.036)	16 (0.207)	12 (0.009)	15 (0.306)
15 (0.045)	11 (0.369)	20 (0.090)	17 (0.108)	13 (0.378)	16 (0.014)
16.1 (0.009)	12 (0.036)	21 (0.009)	18 (0.032)	14 (0.158)	17 (0.437)
17.1 (0.347)	13 (0.018)	22 (0.063)	19 (0.257)	15 (0.275)	18 (0.131)
18.1 (0.032)	14 (0.099)	25 (0.234)	20 (0.207)		19 (0.005)
19.1 (0.378)	15 (0.054)	26 (0.113)	21 (0.054)		
	16 (0.014)	27 (0.023)	22 (0.036)		
	18 (0.005)	28 (0.014)			
		29 (0.041)			
		30 (0.140)			
		31 (0.045)			
		32 (0.018)			
VGL2918	VGL3008	VGL3235			
12 (0.054)	14 (0.005)	13 (0.054)			
13 (0.104)	15 (0.095)	14 (0.568)			
13.3 (0.005)	16 (0.014)	15 (0.018)			
14 (0.149)	17 (0.315)	19 (0.041)			
15 (0.045)	18 (0.509)	20 (0.059)			
16 (0.005)	19 (0.059)	21 (0.243)			
17.3 (0.140)	20 (0.005)	22 (0.014)			
18.3 (0.014)		23 (0.005)			
19.3 (0.162)					
20.3 (0.230)					
21.3 (0.014)					

22.3 (0.077)

23.3 (0.005)

The number of alleles identified in the 33 STR loci included in this study ranged from two (REN162C04) to thirteen (VGL1165, VGL2918). These numbers are relatively high when compared to other breeds analyzed at the VGL to date. Similar to other pure dog breeds, a single allele predominated at most loci (bolded in **Table 1**), while the other alleles were identified at lower frequencies. However, one allele predominated at an especially high frequency (greater than 70%) in three STR loci (INU030, INU055, and REN162C04). This might indicate that the genomic regions harboring these STR loci have been under strong positive selection since the formation of the breed and can be associated with highly valued traits. It is possible that additional alleles will be identified as more dogs are tested by the VGL, albeit at a low frequency.

B. Assessment of population diversity using standard genetic parameters

Allele and allele frequencies at each of the 33 STR loci listed in **Table 1** can be used to determine basic genetic parameters (**Table 2**) such as the number of alleles found at each STR locus (N_a); the number of effective alleles (N_e) per locus (i.e., the number of alleles that contribute to heterozygosity in the population); the observed or actual heterozygosity (H_o) that was found in the population; and the heterozygosity that would be expected (H_e) if the existing population was being randomly bred. The value F is a coefficient of inbreeding derived from the H_o and H_e values. A value of +1.0 would occur only if every individual were genetically indistinguishable at each of the 33 STR loci, while a value of -1.0 would be seen if all the dogs were completely different at each of the 33 loci. An F value of zero happens if the selection of sires and dams is entirely random within the existing gene pool.

Using the panel of 33 STR markers, the 110 Whippets had an average of 6.36 alleles/locus (N_a) (**Table 2**). This is higher than for the Berger Picard ($N_a=4.0$), German Pinscher ($N_a=4.91$) and Flat-Coated Retriever ($N_a=5.09$); similar to the Irish Red & White Setter ($N_a=6.39$) and Borzoi ($N_a=6.57$); but lower than large and genetically diverse breeds such as the Labrador Retriever ($N_a=7.78$), Miniature Poodle ($N_a=9.03$), and most importantly, the Italian Greyhound ($N_a=7.57$).

However, the average number of alleles is less important than the number of alleles that have the greatest genetic influence on heterozygosity, a figure known as average effective alleles/loci or N_e . In this cohort of Whippets, N_e was estimated at 3.26 effective alleles per locus. Therefore, approximately three alleles at each locus contribute to most of the heterozygosity within the breed. The observed (actual) heterozygosity of this group of 110 dogs was 0.63, while the expected heterozygosity (H_e) for a similar population in a state of Hardy-Weinberg equilibrium (HWE) was 0.65, yielding a coefficient of inbreeding (F) of 0.03 (i.e., only 3% more inbred than predicted for a random breeding population). Taken together, these standard genetic assessment values indicate that the breed has good genetic diversity, which has been sustained in a relatively random manner across the breed's history.

The number of effective alleles is also a measure of the number of individuals that are necessary to keep a free-breeding population in a state of HWE from one generation to the next. This number is also known as the effective population size. Pure breeds of dogs have

Ne values as low as 2.3-2.6 (Doberman Pinscher, Japanese Akita, Swedish Vallhund, Flat-Coated Retriever), 3.3-3.8 (Havanese, Labrador and Golden Retriever, Border Collie, Samoyed), and as high as 4.2 (Toy Poodle). The effective population size for Whippets from 1980-2000 has been calculated as 56.4 [14], which is just above the theoretical limit of 50 individuals necessary to maintain HWE. For comparison, the effective population size for Toy Poodles has been estimated at 136.3 [15]. The low Ne for Whippets suggests the need for breeders to maintain current heterozygosity as vigorously as possible by choosing dogs with different alleles at the 33 STR loci for their breeding programs.

Table 2. Standard Genetic Assessment of 110 Whippets based on 33 autosomal STR loci. SE = standard error.

	Na	Ne	Ho	He	F
Mean	6.36	3.259	0.633	0.649	0.026
SE	0.41	0.234	0.023	0.021	0.016

C. Standard genetic assessment values for individual STR loci

The allele frequencies can be also used to do a standard genetic assessment of heterozygosity at each STR locus (**Table 3**). This provides an estimate of genetic similarities in the specific regions of the genome that are associated with each STR marker. Phenotypic differences equate to genotypic differences. Therefore, alleles that are widely shared across the population are indicators that positive selection is occurring for certain desired traits. The Na values for an individual STR locus for this population of 110 Whippets ranged from a low of 2 (REN162C04) to a high of 13 (VGL1165, VGL2918) alleles per locus, while the Ne ranged from 1.57 (INU030) to 7.35 (VGL1165) effective alleles per locus (**Table 3**). It is important to remember that the number of different alleles identified in each STR across all dog breeds tested at the VGL range from 7-29 different alleles (avg. 15.4 alleles/locus) (see **section IIA**).

The observed heterozygosity (Ho) for an individual STR locus ranged from 0.32 (AHTh171-A) to 0.87 (VGL1165), while He ranged from 0.37 (INU030) to 0.86 (VGL1165) (**Table 3**). Based on these values, 23 STR loci had positive F values and 10 STR loci were negative. Additionally, five of the loci with positive inbreeding coefficients (REN64E19, AHT137, VGL1063, INU055, and AHTh171-A) had F values greater than 0.1, indicating over 10% excess of inbreeding (**Table 3**). This suggests that these loci were under a greater degree of positive selection than those with negative F values, and thus are presumably linked to regions of the genome more strongly associated with current desired breed-specific traits. However, the influences of these various inbred and outbred regions of the genome defined by these 33 STR loci have been kept in balance by breeders, as evidenced by a near zero F value for the overall population (**Table 2**). The degree of inbreeding or outbreeding for individual dogs in this group of 110 Whippets will be made apparent from internal relatedness (IR) scores (see **section E**).

Table 3. Standard Genetic Assessment of individual STR loci (n=33) for 110 Whippets.

#	Locus	Na	Ne	Ho	He	F
1	AHT121	7	4.59	0.79	0.78	-0.01
2	AHT137	7	2.9	0.57	0.66	0.134
3	AHTH130	6	3.22	0.67	0.69	0.024
4	AHTh171-A	5	1.84	0.32	0.46	0.291
5	AHTh260	9	3.46	0.7	0.71	0.012
6	AHTk211	4	2.17	0.49	0.54	0.099
7	AHTk253	4	2.95	0.62	0.66	0.06
8	C22.279	6	3.26	0.71	0.69	-0.03
9	FH2001	5	2.31	0.55	0.57	0.031
10	FH2054	7	3.84	0.69	0.74	0.062
11	FH2848	8	5.09	0.8	0.8	0.002
12	INRA21	4	2.6	0.61	0.62	0.004
13	INU005	5	2.51	0.66	0.6	-0.09
14	INU030	4	1.57	0.34	0.37	0.061
15	INU055	4	1.69	0.34	0.41	0.161
16	LEI004	5	2.02	0.6	0.51	-0.19
17	REN105L03	8	3.09	0.65	0.68	0.046
18	REN162C04	2	1.7	0.49	0.41	-0.19
19	REN169D01	6	2.25	0.51	0.56	0.082
20	REN169O18	5	3.66	0.7	0.73	0.037
21	REN247M23	4	2.59	0.57	0.61	0.066
22	REN54P11	7	2.97	0.65	0.66	0.022
23	REN64E19	5	2.74	0.56	0.64	0.121
24	VGL0760	7	3.59	0.78	0.72	-0.07
25	VGL0910	7	3.33	0.69	0.7	0.008
26	VGL1063	9	3.57	0.61	0.72	0.149
27	VGL1165	13	7.35	0.87	0.86	-0.001
28	VGL1828	8	5.6	0.78	0.82	0.057
29	VGL2009	5	3.62	0.69	0.72	0.054
30	VGL2409	6	3.19	0.72	0.69	-0.05
31	VGL2918	13	7.01	0.83	0.86	0.033
32	VGL3008	7	2.7	0.65	0.63	-0.03
33	VGL3235	8	2.57	0.67	0.61	-0.09

On average, the alleles identified in this group of 110 Whippets represented 41.3% ($6.36/15.4=0.413$) of alleles known to exist in all canids tested at the VGL. This is higher than the Flat-Coated Retriever (40%); similar to the Llewelin Setter (41.7%) and Newfoundland (42.5%); but lower than breeds such as the Italian Greyhound (49.2%), Standard Poodle (65.3%), and Havanaes (61.2%).

D. Differences in population structure as determined by principal coordinate analysis (PCoA)

PCoA measures the genetic relatedness of individuals in a population. The data is computed in a spherical form, but it is often presented in the two dimensions that most closely represent its three-dimensional form (usually coordinates 1 and 2). The more closely individuals cluster together around the XY axis, the more related they are to each other.

The 110 Whippets formed a single population (i.e., a pure breed) divided into three genetically distinguishable subgroups by PCoA (**Figure 1**). These subpopulations were comprised of dogs that were more related to each other than to dogs in the rest of the population. This feature indicates the use of bloodlines (i.e., line breeding) within a breed. Overall, PCoA results suggests that the 110 dogs chosen for this analysis were as genetically diverse as possible and likely to be representative of the entire breed.

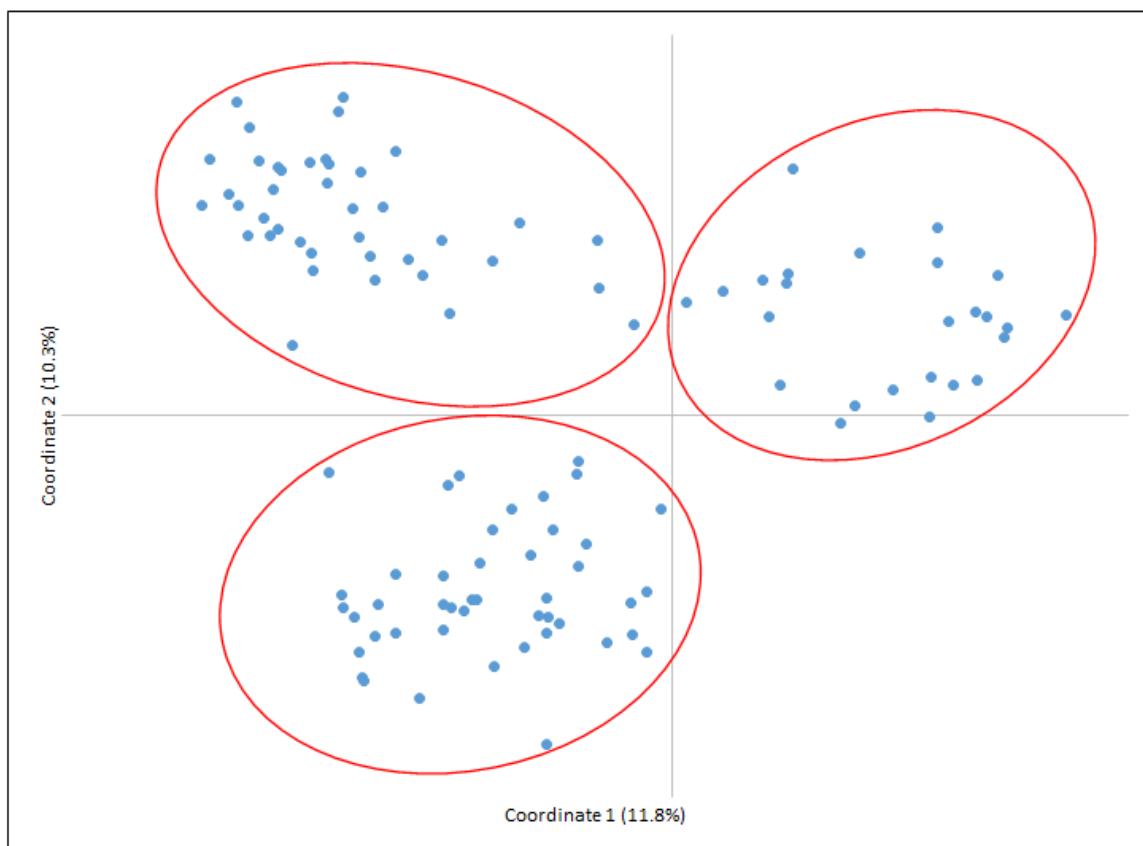


Figure 1. PCoA graph portraying the genetic relatedness of 110 Whippets included in this study. The population segregates by degree of relatedness into three subpopulations or bloodlines (circles).

The degree of relatedness of individuals within a breed can be further emphasized by comparing closely and distantly related breeds, such as the Whippet, Italian Greyhound, and Samoyed (**Figure 2**). Comparing related breeds with a genetically distant breed will enhance the degree of relatedness between related breeds (or varieties/bloodlines). **Figure 2** shows that Italian Greyhound (orange dots) are composed of two varieties: European

(circled in red) and North American. Moreover, when other breeds are added to the PCoA, Whippets (blue dots) are closely clustered as a single breed, and no longer divided into subgroups as in **Figure 1**. Samoyeds (grey dots), being genetically dissimilar to the two other breeds, are tightly clustered on the lower left quadrant at a significant distance from the Whippet and Italian Greyhound. It is also significant and expected that the Whippet and Italian greyhound are clustered nearest to each other, but it is even more significant that several Italian Greyhounds, especially those from Europe, are clustering within or closely adjacent to Whippets. This suggests that some outcrossing has occurred more recently between these two breeds.

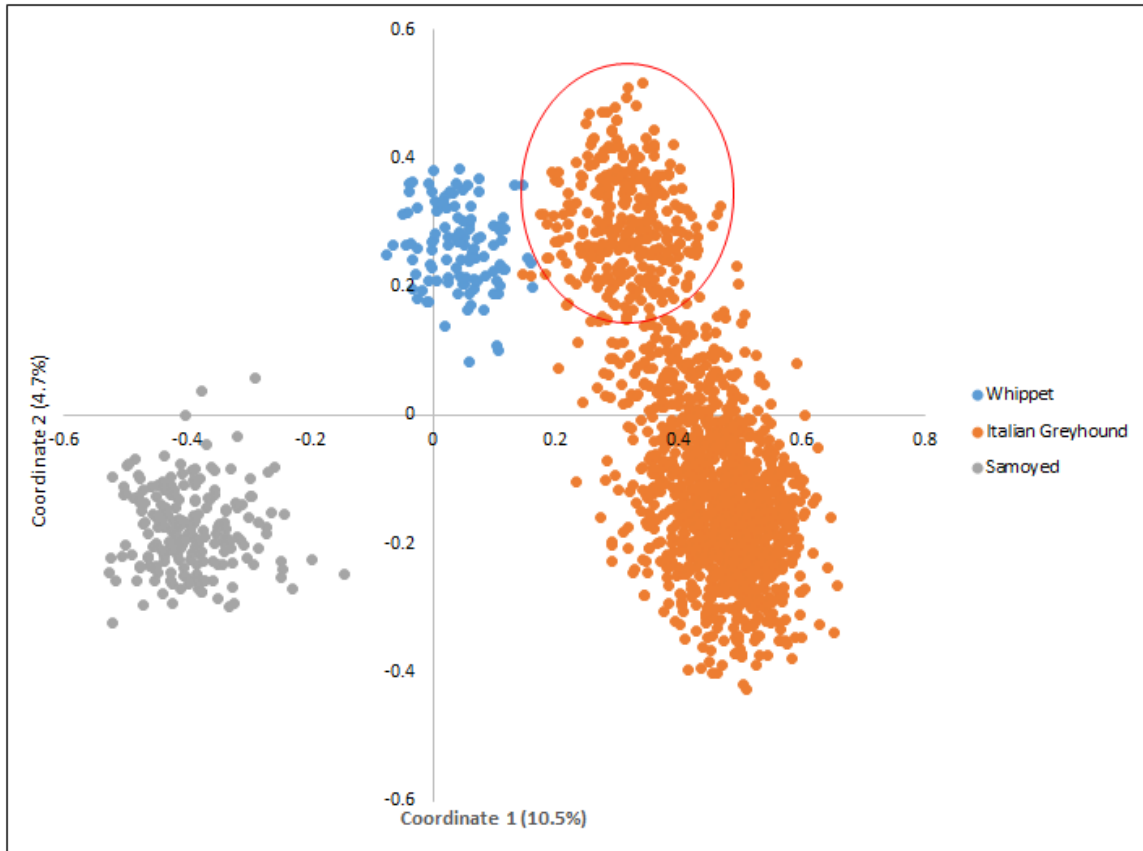


Figure 2. PCoA comparing Whippet (blue dots), Italian Greyhound (orange dots) and Samoyed (grey dots) based on alleles for 33 autosomal STRs. European Italian Greyhounds are circled in red.

E. Internal relatedness (IR) of individuals and the population as a whole

E1. IR testing

Genetic assessments such as those presented in Tables 1-3 are indicators of population-wide (average heterozygosity), and do not reflect the genetic diversity inherited by individuals from their parents. Internal Relatedness (IR) is a calculation that has been used to determine the degree to which the parents of an individual dog are related. The IR calculation takes into consideration homozygosity at each locus and gives more weight to rare and uncommon alleles. Rare and uncommon alleles would presumably be present in

more genetically diverse individuals. IR scores of all individuals in a population can be graphed to form a curve ranging from -1.0 to +1.0. A dog with a value of -1.0 would have parents that are totally unrelated at all 33 STR loci, while a dog with an IR value of +1.0 has parents that are genetically identical at all loci. An IR value of +0.25 would be found among offspring of full sibling parents from a random breeding population. IR values >0.25 occur when the parents of the full sibling parents are themselves highly inbred. The higher the IR value above 0.25, the more closely related are the parents and grandparents of the sibling parents. **Table 4** summarizes the IR values for the 110 Whippets tested in this study.

Table 4. Internal relatedness (IR) values calculated using allele numbers and frequencies in 110 Whippets. The IR values can be adjusted to reflect how these same dogs would score if they were to exist in a large population of village dogs (IRVD).

	IR	IRVD
Minimum	-0.2698	-0.0317
1st Quartile	-0.0248	0.2048
Mean	0.0343	0.2853
Median	0.0193	0.2606
3rd Quartile	0.1143	0.3762
Maximum	0.2663	0.6696

The 25% of most outbred dogs in the test population had IR scores of -0.025 to -0.269, while the 25% of most inbred dogs in the group had IR scores ranging from 0.114 to 0.266. The mean (average) IR score for the group was 0.0343. Therefore, IR values give a different picture than seen with the population average scores from the standard genetic assessment (**Table 2**). While the standard genetic assessments indicated a population in HWE (i.e., random breeding), the IR scores showed that a subset of individuals within the breed is very outbred, and a different group of dogs is very inbred. The most inbred dog in the group (IR=0.026) was interrelated to the same degree as offspring of full sibling parents. The more inbred dogs are balanced by outbred dogs, making it appear that the overall population was in a state of HWE. This is a common feature of all pure breeds of dogs.

E2. Adjusted IR values (IRVD) as a measure of genetic diversity lost during breed evolution from time of origin to the present time.

It is possible to determine the amount of canid genetic diversity a breed has retained as it evolved to present day. This is done by assuming that individual Whippets were members of the current village dog population found in the Middle East, SE Asia and the Island Pacific nations. The IR values and IR values adjusted to village dogs (IRVD) can then be graphed, and the IR and IRVD graphs are then overlaid (**Figure 3**). One-half of the dogs in this study have IRVD scores from 0.285 to 0.670 and one-half with IRVD scores of -0.031 to 0.285 (**Table 4**). Therefore, if this group of dogs were found among modern village dogs, three-fourths of them would be considered equally or more inbred than offspring of full sibling village dog parents. However, this degree of inbreeding is seen in most dog breeds.

As with all the other dog breeds tested at the VGL thus far, the IRVD curve for the Whippet (blue line) is shifted to the right of the IR curve (red line) (**Figure 3**). The area of overlap

was 32.5%, which corresponds to the percentage of retained village dog genetic diversity in the Whippet. All pure breeds of dogs have come from relatively small founder populations, which has limited genetic diversity from the time registries were created and closed. Greatly varying amounts of genetic diversity may have been lost subsequently through artificial genetic bottlenecks such as cataclysmic events (e.g., world wars) or inbreeding for a specific show conformation (e.g., popular sire effects and line breeding).

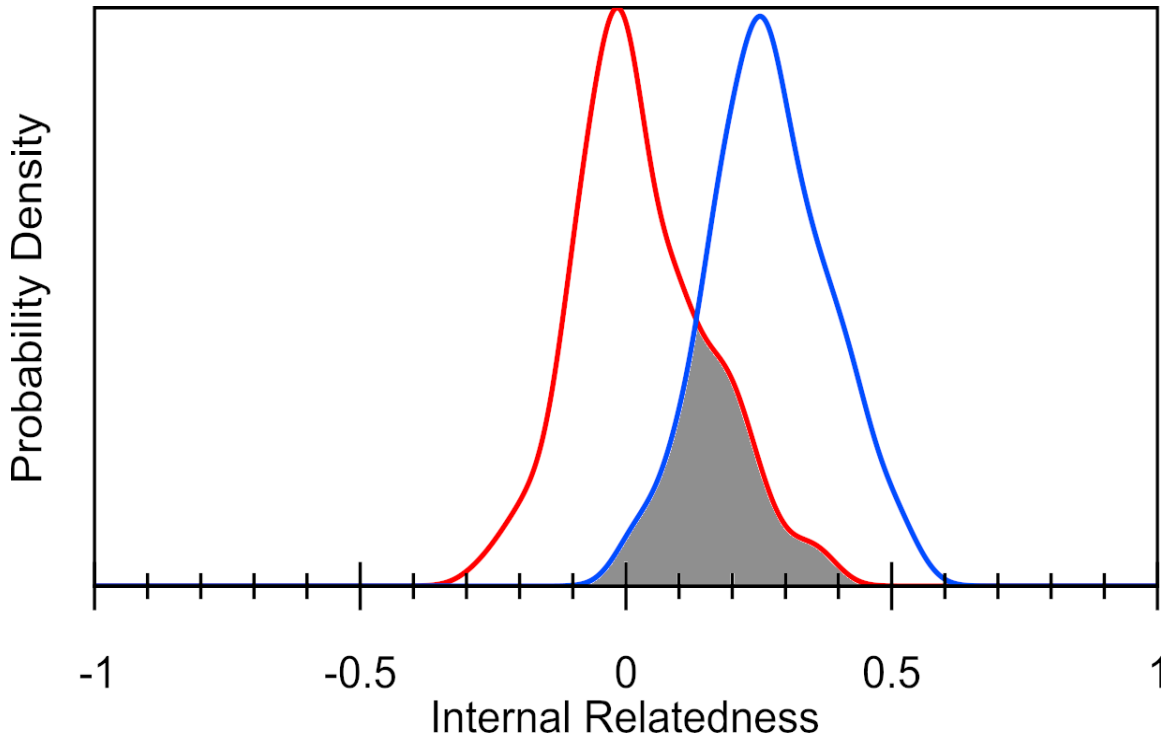


Figure 3. Distribution of IR (red line) and IR-village dog (IRVD) (blue line) values for the Whippet (n=110). The area under the curve (shaded in grey) represents the degree of allele sharing (32.5%) between Whippets and village dogs.

F. DLA Class I and II haplotype frequencies and genetic diversity

The DLA consists of four gene rich regions making up a small part of canine chromosome 12. Two of these regions contain genes that help regulate normal cell- (Class I) and antibody-mediated (Class II) immunity. Polymorphisms in these regions have also been associated with abnormal immune responses responsible for autoimmune diseases, allergies, and resistance/susceptibility to infectious diseases.

The Class I region contains several genes, but only one, DLA-88, is highly polymorphic (i.e., with many allelic forms) and is therefore most important for immune regulation. Specific alleles at the four STR loci associated with the DLA88 are linked together in various combinations, forming specific haplotypes (**Table 5**). Haplotypes are groups of genes (and consequently their alleles) inherited as a block, rather than individually.

The class II region also contains several genes, three of which are highly polymorphic: DLA-DRB1, DLA-DQB1 and DLA-DQA1. Specific alleles at these three STR loci associated with the three class II genes are strongly linked, and often inherited as a single haplotype (**Table 6**). An individual inherits one haplotype from each of the parents. The STR-based haplotype nomenclature used in this breed diversity analysis is based on

numerical ranking: class I haplotypes (originally identified in Standard Poodles) are named 1001, 1002, and so on; class II haplotypes are named 2001, 2002, etc. It is common for different dog breeds to share common and even rare haplotypes for these loci, depending on common ancestry.

F1. DLA class I and II haplotypes existing in Whippets

The 110 Whippets included in this study possessed 19 DLA class I and 11 DLA class II haplotypes (**Table 5**), which is a relatively high number of DLA haplotypes compared to other breeds tested at the VGL. No class I or II haplotype was dominant (>50% frequency) in the breed, which is somewhat different from many other breeds. Interestingly, three class I haplotypes (1247, 1248, and 1249) and one class II haplotype (2062) were unique to the breed (not shared with other breeds) (**Table 6**). This, combined with the number of class I (19) and class II (11) haplotypes identified, indicates that the breed has evolved from a relatively large and diverse founder population.

Table 5. DLA class I and II haplotypes identified in Whippets (n=110) with their respective frequencies. The haplotype with the highest frequency for each class is bolded.

DLA1 Haplotype	STR types	Frequency (%)
1002	380 365 281 181	8.6
1008	386 373 289 182	4.5
1012	388 369 289 188	3.6
1016	382 371 277 178	10.5
1033	382 379 277 181	0.5
1040	380 371 277 186	8.6
1045	376 371 277 186	0.5
1054	382 379 277 184	0.5
1056	386 373 289 190	6.8
1058	387 378 287 186	8.6
1066	376 375 277 178	21.4
1104	386 373 289 186	15.5
1142	376 379 277 180	0.5
1162	386 373 289 181	0.9
1208	386 373 277 181	5
1209	386 378 287 186	1.8
1247	376 373 289 190	0.5
1248	386 365 281 181	1.4
1249	388 379 289 190	0.5
DLA2 Haplotype	STR types	Frequency (%)
2001	343 324 284	10
2003	343 324 282	8.6
2006	339 325 280	5
2017	343 322 280	24.1
2018	339 324 284	0.5
2028	345 327 288	8.6

2031	339 322 282	10.5
2033	339 323 282	10.5
2037	341 327 280	0.5
2048	339 331 282	21.4
2062	345 327 282	0.5

F2. DLA haplotype sharing with other dog breeds

DLA haplotypes are much more conserved than most other regions of the genome, and each DLA region is inherited as a block of linked genes from each parent and passed on by descent to their offspring. Therefore, the number and incidence of DLA haplotypes found in a breed can be used to estimate the founder/founder lines that were used to create a breed, as well as the importance (influence) of the various lines in subsequent breed evolution over time.

The DLA class I and II regions are frequently shared among breeds, reflecting common distant ancestry and inheritance by descent (**Table 6**). As might be expected, the greatest sharing of DLA haplotypes was with the Italian Greyhound. However, a great deal of haplotype sharing was observed with European breeds such as Poodles, Golden and Labrador Retrievers, Magyar Agar, Border Collie, and English bulldog. As has been observed with almost all breeds studied, the Havanese also shares many of the same haplotypes as the Whippet. It is also noteworthy that DLA haplotype sharing was significantly broader with class I haplotypes than with class II haplotypes. Finally, Whippets share DLA haplotypes with 53 other breeds/varieties tested by the VGL, the highest amount of DLA sharing observed so far.

Table 6. Sharing of DLA class I and II haplotypes between Whippets (highlighted in blue) and other dog breeds tested at the VGL (n=53).

DLA I#	Whippet (n=110)	Whippet STR types (cont'd)	American Eskimo Standard (n=65)	American Eskimo Toy (n=38)	American Hairless Terrier (n=14)	American Pit Bull Terrier (n=186)	American Redbone (n=160)	American Shetland Sheepdog (n=582)	Alaskan Malamute (n=657)	Barbet (n=68)	Border Collie (n=65)	Beiger Picard (n=152)	Bernese Mountain Dog (n=151)	Black Russian Terrier (n=150)	Biewer Terrier (n=54)	Yorkshire Terrier (n=219)	Bleu de France (n=219)	Yorkshire Terrier (n=16)	Borzo (n=152)	Chinook (n=36)	Collie (n=49)	Dobberman Pinscher (n=254)	English Bulldog (n=163)	English Mastiff (n=31)	Flat Coated Retriever (n=875)	Great Dane (n=74)	Golden Retriever (n=882)	German Shepherd (n=38)		
1002 380 365 281 181	0.086	0.652	0.14	0.11	0.019	0.25	0.0578	0.066	0.0578	0.066	0.008	0.008	0.007	0.007	0.06	0.06	0.06	0.06	0.06	0.14	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	
1008 386 378 289 182	0.045	0.023	0.04	0.11	0.005	0.05	0.0578	0.054	0.0578	0.054	0.008	0.008	0.007	0.007	0.06	0.06	0.06	0.06	0.06	0.14	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	
1012 388 369 289 188	0.036	0.023	0.04	0.11	0.005	0.05	0.0578	0.054	0.0578	0.054	0.008	0.008	0.007	0.007	0.06	0.06	0.06	0.06	0.06	0.14	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	
1016 382 371 277 178	0.105	0.008	0.04	0.11	0.005	0.05	0.0578	0.054	0.0578	0.054	0.008	0.008	0.007	0.007	0.06	0.06	0.06	0.06	0.06	0.14	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	
1033 382 378 277 181	0.005	0.008	0.04	0.11	0.005	0.05	0.0578	0.054	0.0578	0.054	0.008	0.008	0.007	0.007	0.06	0.06	0.06	0.06	0.06	0.14	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	
1040 380 371 277 186	0.086	0.008	0.04	0.11	0.005	0.05	0.0578	0.054	0.0578	0.054	0.008	0.008	0.007	0.007	0.06	0.06	0.06	0.06	0.06	0.14	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	
1045 376 371 277 186	0.005	0.008	0.04	0.11	0.005	0.05	0.0578	0.054	0.0578	0.054	0.008	0.008	0.007	0.007	0.06	0.06	0.06	0.06	0.06	0.14	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	0.0008	
1054 382 379 277 184	0.005	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	
1058 386 378 289 190	0.068	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004
1058 387 378 287 186	0.086	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004
1066 376 375 277 178	0.214	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004
1104 386 378 289 186	0.155	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004
1142 376 377 277 180	0.005	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004
1162 386 378 289 181	0.009	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004
1208 386 378 277 181	0.005	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004
1209 386 378 287 186	0.018	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004
1247 376 373 289 190	0.005	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004
1248 386 365 281 181	0.014	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004
1249 388 378 289 190	0.005	0.008	0.21	0.32	0.003	0.03	0.2123	0.154	0.2123	0.154	0.154	0.154	0.095	0.095	0.204	0.078	0.078	0.078	0.078	0.38	0.96	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004	0.0004

DLAZ #	STR types	Whippet (n=110)	American Eskimo, Eskimo, Toy Miniature (n=38)	American Eskimo, Toy (n=14)	American Hairless Terrier (n=186)	American Akita (n=160)	American Japanese Akita (n=582)	Alaskan Klee Kai (n=657)	Barbet (n=68)	Border Collie (n=65)	Berger Picard (n=152)	Bernese Mountain Dog (n=151)	Black Russian Terrier (n=137)	Biewer Terrier (n=219)	Yorkshire Terrier (n=14)	Borzoi (n=152)	Chinoock (n=36)	Collie (n=49)	Doberman Pinscher (n=1254)	English Bulldog (n=163)	English Mastiff (n=31)	Mastiff (n=21)	Flat Coated Retriever (n=875)	Great Dane (n=74)	Golden Retriever (n=882)	German Shepherd (n=38)	
2001	343 324 284	0.1	0.662	0.14	0.11	0.126	--	--	0.159	0.138	--	0.013	--	0.249	0.38	--	0.14	--	0.0004	0.598	--	--	0.1457	0.007	0.0204	0.01	
2003	343 324 282	0.086	0.023	0.04	0.263	--	--	0.132	0.054	--	--	--	0.263	0.213	0.249	0.38	0.089	0.01	0.0004	0.598	--	--	0.1457	0.007	0.0204	0.01	
2006	339 325 280	0.05	--	--	--	0.005	0.009	0.0034	0.007	--	--	--	--	--	--	0.007	0.01	--	0.0004	0.598	--	0.29	0.0006	--	--	0.0385	0.43
2017	343 322 280	0.241	--	--	0.013	--	--	--	0.029	0.169	0.102	--	--	--	--	0.007	0.01	--	0.0004	0.598	0.21	0.29	0.0006	--	--	0.0385	0.43
2018	339 324 284	0.005	--	--	0.011	--	--	--	--	--	--	--	--	--	--	--	0.07	--	--	0.215	0.21	0.29	0.0006	--	--	0.0385	0.43
2031	339 322 282	0.105	--	--	0.011	--	--	--	--	0.008	--	0.033	--	--	--	--	0.07	--	--	0.037	0.21	0.29	0.0006	--	--	0.0385	0.43
2033	339 322 282	0.105	--	--	0.011	--	--	--	--	0.008	--	0.033	--	--	--	--	0.07	--	--	0.037	0.21	0.29	0.0006	--	--	0.0385	0.43
2037	341 327 280	0.005	0.008	--	0.005	0.013	--	--	--	0.008	--	0.033	--	--	--	--	0.07	--	0.0016	0.215	0.21	0.29	0.0006	--	--	0.0385	0.43
2048	339 331 282	0.214	0.031	0.26	0.25	0.016	0.178	0.2474	0.3714	0.085	--	0.287	0.029	0.009	0.059	0.09	--	--	0.0016	0.215	0.21	0.29	0.0006	--	--	0.0385	0.43
2062	345 327 282	0.005	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.0006	--	--	0.0385	0.43
DLAZ # (cont'd)	STR types (cont'd)	Whippet (n=110)	Havana Silk (n=49)	Havanese (n=1011)	Italian Greyhound (n=1424)	Irish Setter (n=60)	Irish Red and White Setter (n=109)	Irish Wolfhound Terrier (n=78)	Lakeland Terrier (n=141)	Labrador Retriever (n=295)	Llewellyn Setter (n=152)	Magyar Agar (n=78)	Newfoundland Sheepdog (n=199)	Toy Poodle (n=234)	Miniature Poodle (n=422)	Poodle (n=5237)	Rat Terrier (n=44)	Samoyed (n=192)	Saint Bernard (n=90)	Scottish Collie (n=124)	Shiba Inu (n=162)	Shikoku (n=87)	Greater Swiss Mountain Dog (n=59)	Shiloh Shepherd (n=69)	Shiloh Shepherd (n=273)	Cardigan Welsh Corgi (n=43)	
2001	343 324 284	0.1	0.006	0.05	0.0504	--	--	--	--	0.002	--	0.071	--	0.004	0.017	0.5991	0.01	--	0.017	--	0.012	--	--	--	0.004	--	0.23
2003	343 324 282	0.086	0.03	0.26	0.2117	--	--	--	0.762	0.022	--	0.004	--	0.425	0.507	0.10445	0.13	0.013	--	0.016	--	0.924	--	0.009	--	0.23	
2006	339 325 280	0.05	0.149	--	0.0015	--	--	--	0.028	--	--	0.192	--	0.002	0.03447	--	0.02	--	--	--	0.003	--	--	0.304	0.383	0.19	--
2017	343 322 280	0.241	0.002	--	0.0109	0.2124	--	--	0.016	--	--	0.449	--	0.002	0.001	0.0021	0.02	--	--	--	0.004	0.219	0.201	--	--	--	--
2018	339 324 284	0.005	--	--	0.0252	--	--	--	--	--	--	--	--	0.005	0.00057	0.1	--	--	--	--	0.004	0.219	0.201	--	--	--	--
2028	345 327 288	0.086	--	--	0.001	--	--	--	--	--	--	--	--	--	--	--	0.1	--	--	--	0.011	--	--	--	--	--	--
2031	339 322 282	0.105	0.041	--	0.0621	--	--	0.013	0.004	0.012	--	--	--	--	--	0.14	--	--	--	0.016	--	--	--	--	--	--	--
2033	339 322 282	0.105	0.038	--	0.0049	--	--	--	--	--	--	--	--	0.004	--	--	--	--	--	0.016	--	--	--	--	--	--	--
2037	341 327 280	0.005	0.367	--	0.0208	0.3	0.028	--	--	0.369	--	0.013	--	0.009	0.011	0.00048	0.06	--	--	0.004	--	--	--	--	--	--	--
2048	339 331 282	0.214	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
2062	345 327 282	0.005	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--

F3. Heterozygosity in the DLA region

The 7 loci that define the DLA class I and II haplotypes are in stronger linkage disequilibrium than other parts of the genome that are measured by the 33 autosomal STR markers. However, the expectation is that these loci have achieved an equilibrium with other loci in the genome with random mating and over enough time. This can be tested by doing a standard genetic assessment of each of the loci (**Table 7**), as well as using an average of all the loci taken together (**Table 8**). Standard genetic assessment of each of the 7 loci demonstrates values for F (inbreeding coefficient) that range from slightly negative (such as DLAI-3CCA) to slightly positive (e.g., 5ACA) across DLA loci (**Table 7**). The F values tend to balance out in the overall standard genetic assessment of all 7 loci, where F is 0.007 (**Table 8**). These values indicate that the DLA region is in equilibrium with the rest of the genome, and behaves similarly to what is expected for a random breeding population.

Table 7. Standard genetic assessment for Whippets (n=110) using each of the 7 STRs in the DLA class I and II regions.

Locus	Na	Ne	Ho	He	F
DLA I-3CCA	6	4.301	0.8	0.768	-0.04
DLA I-4ACA	7	4.597	0.82	0.782	-0.05
DLA I-4BCT	4	2.862	0.577	0.651	0.114
DLA1131	8	3.864	0.676	0.741	0.088
5ACA	4	2.389	0.555	0.581	0.046
5ACT	6	4.445	0.82	0.775	-0.06
5BCA	4	2.706	0.664	0.63	-0.05

Table 8. Summary of standard genetic assessment for Whippets (n=110) using 7 STRs in the DLA class I and II regions. Values are expressed as means (averages) with one standard error (SE).

	Na	Ne	Ho	He	F
Mean	5.571	3.595	0.701	0.704	0.007
SE	0.566	0.322	0.04	0.029	0.026

IV. What does this assessment of genetic diversity tell us about the contemporary Whippet

The Whippets tested constituted a single breed, albeit with some intra-breed genetic structure to the level of bloodline. The breed originated from dogs that shared many of their genomic alleles with village dogs currently found in the Middle East, SE Asia, and Island Pacific nations. Their DLA haplotypes are also shared with many other breeds that evolved mainly in England.

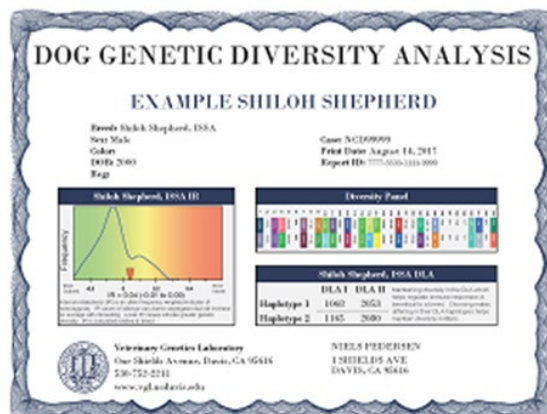
The anticipation is that the 110 dogs tested in this study will define almost all of the known autosomal alleles and DLA class I and II haplotypes for the breed. This is sufficient to provide a reasonable assessment of genetic diversity in the breed. Nevertheless, it is important to screen more Whippets, especially from parts of the world outside of the USA. Genetic diversity for the breed appears to be average, and slightly higher than other pure breeds tested at the VGL with fewer individuals. Thus, it is important to identify any additional diversity that might exist; breeders should also avoid using linebreeding in order to re-distribute the genetic diversity currently existing in the breed.

Whippets have maintained an average level of genetic diversity since founding. This knowledge is impetus for breeders to be as diligent as possible in maintaining and redistributing existing diversity through the following generations. A lack of genetic diversity is not in itself bad, providing the founder population was relatively free of deleterious genetic traits and breeders have been judicious in avoiding any artificial genetic bottlenecks that may cause either a loss or imbalance of original diversity. The breed is surprisingly clear of breed-specific heritable disease traits and enjoys a good lifespan. Breeds that lack genetic diversity must be managed much more closely to avoid further loss of genetic diversity and have less leeway in dealing with simple recessive or complex polygenic disorders that might arise. Elimination of deleterious traits may result in loss of genetic diversity, especially when diversity is already low.

V. Results of Diversity Testing

A. How will you be given the results of DNA-based genetic diversity testing on your dog?

After a sample is submitted for genetic testing, the identity of the dog and owner will be replaced by a laboratory barcode identifier. This identifier will be used for all subsequent activities and each owner will be provided with a certificate that reports the internal relatedness, genomic STR genotypes and DLA class I and II haplotypes for the dog(s) tested. The internal relatedness value for the dog being tested is reported in relation to others in the population. The alleles at each of the 33 STR loci are presented as numbers that correspond to those found in Table 1. Each locus will have two alleles, which can be different (heterozygous) or the same (homozygous). Each allele is inherited from one of the parents. Dogs from closely related parents will be homozygous for more alleles at each locus, or in regions of the genome that are under strong positive selection for phenotypic trait or traits mostly favored in the breed. Dogs with a predominance of rare (i.e., low frequency) alleles will be more distantly related to the bulk of the population than dogs that have a predominance of common (i.e., high frequency) alleles. A sample genetic diversity report is shown below.



B. What should you do with this information?

The goal for breeders should be to continue to produce puppies with IR scores close to zero, and as informed breeding decisions are made, even lower scores. Mates should be preferably selected to avoid homozygosity at any genomic loci or DLA class I and II haplotype; moreover, mating of dogs with less frequent genomic alleles or DLA haplotypes is encouraged. Maintaining existing genomic diversity will require using IR values of potential mates based on the 33 STR loci to assure puppies of equal or greater overall diversity. However, because IR values reflect the unique genetics of individuals, they cannot be used as the primary criterion for selecting ideal mates. Mates with identical IR values may produce puppies significantly more or less diverse than their parents. Conversely, breeding dogs with high IR values (providing they are genetically different) may produce puppies with much lower IR scores than either parent. A mating between a dog with a high IR value and one with low IR value, providing the latter has few alleles and DLA haplotypes in common, will produce puppies much more diverse than the highly inbred parent. Breeders should also realize that a litter of puppies could have a wide range of IR values, depending on the comparative contributions of each of the parents. The more genetically diverse and different the parents, the greater the range of IR values in their offspring.

The next step is to compare the DLA class I and II haplotypes of the mates. You want to avoid breeding dogs that will produce puppies homozygous for the same haplotypes; once again, less common haplotypes may increase breed diversity in relation to common ones.

Breeders who would like to predict the genetic outcome of puppies of certain sires and dams should screen them for genetic differences in alleles and allele frequencies for the 33 genomic STR loci. Rare alleles should be favored over common ones. This information is included on all certificates and on the breed-wide data found on the VGL website.

References

1. Wikipedia. Whippet. <https://en.wikipedia.org/wiki/Whippet>
2. American Kennel Club. Whippet. <https://www.akc.org/dog-breeds/whippet/>
3. American Whippet Club. About Whippets. <https://www.americanwhippetclub.net/about-whippets>,
4. Canadian Kennel Club. Whippet. <https://www.ckc.ca/en/Choosing-a-Dog/Choosing-a-Breed/Hounds/Whippet>.
5. Walsh EG and Lowe M. 2004. The English Whippet. Coch-Y-Bonddu Books. <http://6949ffa0ba48dd63b79067c6c9974fb8.mooselodge.ca/>
6. Federation Cynologique Internationale. Whippet. <http://www.fci.be/Nomenclature/Standards/162g10-en.pdf>
7. The Kennel Club. Pedigree Breed Health Survey 2004. Whippet. <https://www.thekennelclub.org.uk/media/16790/whippet.pdf>
8. Orthopedic Foundation for Animals. Whippet. <https://www.ofa.org/diseases/breed-statistics#detail>
9. The Kennel Club. Pedigree Breed Health Survey 2014. <https://www.thekennelclub.org.uk/media/749822/whippet.pdf>
10. Mosher DS, Quignon P, Bustamante CD, Sutter NB, Mellersh CS, Parker HG, Ostrander EA. A Mutation in the Myostatin Gene Increases Muscle Mass and Enhances Racing Performance in Heterozygote Dogs". PLOS Genetics. 2007, 3: e79.
11. Dog Breed Health. Whippet. <http://www.dogbreedhealth.com/whippet/>
12. American Whippet Club. Health Statement. <http://cdn.akc.org/Marketplace/Health-Statement/Whippet.pdf>.
13. Strain GM, Louisiana State University. <https://www.lsu.edu/deafness/incidenc.htm>
14. The Kennel Club. 2015. Population analysis of the Whippet breed. <https://www.thekennelclub.org.uk/media/686620/whippet.pdf>
15. The Kennel Club. 2015. Population analysis of the Toy Poodle. https://www.thekennelclub.org.uk/media/686304/poodle__toy_.pdf
16. Whippet Health Foundation. Investigation into Diet-Associated Dilated Cardiomyopathy in Dogs. <http://www.whippethealth.org>
17. AKC. Canine Health Foundation. Investigation into Diet-Associated Dilated Cardiomyopathy in Dog. 2019. http://www.whippethealth.org/AppFiles/AKCCHF_02661update.pdf

This report was generated by Shayne Hughes and Felipe Avila on 01/19/2024.