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Genetic variability in Hanoverian warmblood horses using pedigree analysis[1]

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ABSTRACT: A data set constituting a total of 310,109 Hanoverian warmblood horses was analyzed to ascertain the genetic variability, coefficients of inbreeding, and gene contributions of foreign populations. The reference population contained all Hanoverian horses born from 1980 to 2000. In addition, Hanoverian stallions born from 1980 to 1995 and Hanoverian breeding mares from the birth years 1980 to 1995 with registered foals were analyzed for the same genetic parameters. The average complete generation equivalent was approximately 8.43 for the reference population. The mean coefficient of inbreeding was 1.33, 1.19, and 1.29% for the reference population, stallions, and breeding mares, respectively. The effective number of founders was largest in stallions (364.3) and smallest in the reference population (244.9). The ratio between the effective number of founders and the effective number of ancestors was 3.15 for the reference population, 3.25 for the stallions, and 3.06 for the breeding mares. The effective population size in the Hanoverian warmblood reference population was 372.34. English Thoroughbreds contributed nearly 35% of the genes to the Hanoverian reference population and even slightly greater contributions (39%) to the stallions. Trakehner and Arab horses contributed approximately 8 and 2.7%, respectively, to the Hanoverian gene pool. The most important male ancestors were Aldermann I from the A/E line, Fling from the F/W line, and Absatz from the Trakehner line, whereas the breeding mare Costane had the greatest contribution to the reference population, stallions, and breeding mares. From 1996 onward, the stallions Weltmeyer and Donnerhall had the largest genetic impact on the Hanoverian horse population.

INTRODUCTION

The present Hanoverian breed is composed of approximately 19,000 registered breeding mares and 420 registered stallions; it is therefore the largest breed of warmblood horses worldwide and currently supplies Germany with the largest proportion of riding and sport horses of any breed. Moreover, the Hanoverian breed has greatly influenced other warmblood horse breeds through the exchange of breeding animals. The 7 breeding districts of the Hanoverian breed extend over the state of Lower Saxony and its neighboring regions. The original core breeding area of the "Hanoverian Marschzucht" was situated within the low-lying areas of the rivers Elbe, Weser, and Ems. The foundation of the royal stallion station (Landgestüt) Celle as early as 1735, the use of Andalusian, Napolitan, Holsteiner, Preußen, Mecklenburger, and English Thoroughbred stallions, and the introduction of a central registration of coverings and foalings marked the beginning of the breeding of the Hanoverian horse (Löwe, 1988).

A lack of knowledge exists concerning the present condition of the Hanoverian gene pool. Breeding programs based on prediction of breeding values using animal models and the intensive use of reproductive technologies such as artificial insemination in Hanoverian horses aim at the use of fewer superior animals, particularly of stallions. By using these advancements in horse breeding and the traditional strong emphasis on sire lines, there can be an increase in the genetic contributions of fewer ancestors and in the long-term rate of inbreeding. Therefore, the objective of this study was to monitor current levels and trends of inbreeding and the proportion of foreign blood in the Hanoverian population, and to determine the genetic contributions of important founders and ancestors to the current genetic structure.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database.

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Table 1. Number of animals in the entire pedigree and the reference population, pedigree depth and completeness, and number and birth years of founders for Hanoverian horses

Item	All horses	Stallions	Breeding mares
Total horses born 1920–2000, n	310,109	9,241	90,639
Reference population, n	167,063	1,925	33,119
Maximum generations traced, n	23	23	23
Pedigree completeness index	0.98	0.96	0.98
Complete generation equivalent	8.43	7.66	8.17
Founders, n	13,881	5,742	10,991
Average birth year of founders	1939	1920	1930
Range of birth year of founders	1861–2000	1861–1988	1879–1992

The data used in this study were provided by the Association of Hanoverian Warmblood Breeders (Verden/Aller, Germany). Horses born between 1980 and 2000 were defined as the reference population (n = 167,063), in which the pedigrees of the animals were traced back to the earliest recorded ancestors. This resulted in a data set constituting a total of 310,109 animals. The first ancestor recorded was traced to the year 1861 (Table 1). In addition to all registered horses, we distinguished breeding mares and stallions in the reference population. Breeding mares included in the reference population were dams with registered Hanoverian foals and born between 1980 and 1995 (n = 33,119). The stallion reference population includes sires with registered Hanoverian foals and born between 1980 and 1995 (n = 1,925).

The average coefficient of inbreeding, effective founder number, effective ancestor number, and effective number of founder genomes were estimated for all Hanoverian horses over a 20-yr period (1980 to 2000) and for breeding mares and stallions over a 15-yr period (1980 to 1995). Generation intervals were computed for the pathways sire to sire, sire to dam, dam to sire, and dam to dam by using the average age of the parents at the birth of their offspring that were kept for breeding.

The pedigree completeness index (**PEC**) proposed by MacCluer et al. (1983) describes the degree of completeness of pedigrees and quantifies the chances for detecting inbreeding in the pedigree:

$$PEC_{animal} = \frac{2C_{sire}C_{dam}}{C_{sire} + C_{dam}},$$

where C_{sire} and C_{dam} are contributions from the paternal and maternal lines.

The number of complete generation equivalents (**GE**) was computed for each individual j as

$$G_j = \sum n_i/2^g,$$

where n_i is the number of known ancestors in generation i and g is the number of known generations for individual j.

Ancestors with both parents unknown were considered as nonrelated founder animals. The total number of founders (f) contains limited information about the genetic diversity of the population, because some founders have been used more intensely and therefore make a greater contribution toward the reference population than other founders. The effective number of founders (f_e) is defined as the number of equally contributing founders expected to produce the same genetic diversity as in the population under study (Lacy, 1989) and is computed as

$$f_e = \left[\sum_{i=1}^{N_f} q_i^2 \right]^{-1},$$

where q_i is the genetic contribution of the ith founder to the reference population. When founders contribute to the reference population more equally, the effective number of founders is greater. If all founders contribute equally to the reference population, the effective and actual numbers of founders are the same.

A further measure of genetic diversity for populations, which accounts for the loss of allelic diversity since the foundation population, was proposed by Boichard et al. (1997). This parameter, the effective number of ancestors (f_a), also accounts for large contributions of all ancestors, not just founders, and is defined as the minimum number of ancestors explaining the complete genetic diversity of the current population. In contrast to the effective number of ancestors, the effective number of founders would overestimate genetic diversity in such situations.

Based on the marginal contribution of the 1,000 most influential ancestors, the effective number of ancestors is computed as

$$f_a = \left[\sum_{i=1}^{1000} p_i^2 \right]^{-1},$$

with p_i being the marginal genetic contribution of ancestor i and serving as a measure of genetic diversity. The marginal contributions of the ancestors are computed in a recursive procedure. The ancestor with the greatest contribution to the reference population is chosen, and then the contributions of all others are computed, conditional on the contribution of the ancestor

Table 2. Summary statistics of pedigree analysis of the Hanoverian reference population, Hanoverian stallions, and Hanoverian breeding mares

Item	All horses	Stallions	Breeding mares
Animals, n	167,063	1925	33,119
Average inbreeding coefficient, %	1.33	1.19	1.29
Effective population size, n	372.34	—	—
Effective founders, n	244.9	364.3	248.5
Effective ancestors, n	77.73	111.8	81.08
Effective founder genomes, n	34.69	49.07	35.49
Ancestors to explain 50% of gene pool, n	31	44	33
Ancestors to explain 75% of gene pool, n	109	189	123
Ancestors to explain 80% of gene pool, n	151	276	174
Ancestors to explain 90% of gene pool, n	347	627	462
Gene pool explained by 1,000 ancestors, %	96.22	95.08	94.12
Founders to explain 50% of gene pool, n	111	169	114
Founders to explain 75% of gene pool, n	349	555	373
Founders to explain 80% of gene pool, n	457	748	506
Founders to explain 90% of gene pool, n	930	1,509	1,136
Gene pool explained by 1,000 founders, %	90.79	84.44	88.73

chosen. Then, based on these marginal contributions, the next ancestor with the greatest contribution is chosen, and, in this way, the computations are continued. Hence, the marginal contributions are corrected for the contributions of ancestors already considered in the recursive process. Bottlenecks or the heavy use of a particular sire and his sons and daughters can be a reason for the loss of allelic diversity from the foundation population. Accordingly, the ratio of the effective number of founders and the effective number of ancestors can be used to indicate the importance of bottlenecks or the large influence of some breeding animals in the development of the population. If the ratio is close to unity, the population is stable in terms of the numbers of effectively contributing animals. If the effective number of founders is larger than the effective number of ancestors, then there are ancestors that have played a large role in population formation (Boichard et al., 1997). Because the marginal genetic contributions of ancestors ignore the generations when the contributions of ancestors are marginalized, the effective number of ancestors is dependent on the depth of the pedigrees.

The effective number of founder genomes (f_g) accounts for both unequal contributions of founders and random loss of alleles caused by genetic drift during bottlenecks (Lacy, 1989, 1995). It is defined similarly to the effective number of founders, with the difference that the genetic contribution of the ith founder to the reference population (q_i) is considered in relation to the proportion of the founder's genes that are retained in the reference population (r_i). Because ($1 - r_i$) quantifies the proportion of alleles from the founder that are not expected to be present in the reference population, f_g accounts for random loss of alleles during bottlenecks or unbalanced contributions of founders. The effective number of founder genomes is calculated as

$$f_g = \left[\sum_{i=1}^{N_f} \frac{q_i^2}{r_i} \right]^{-1},$$

With this definition, the interpretation is the number of equally contributing founders with no loss of founder alleles that would be expected to produce the same amount of diversity as in the reference population (Lacy, 1995). The Genedrop procedure described by Boichard et al. (1997) was used to compute the effective number of founder genomes. The effective number of genomes is sensitive to the depth of the pedigree, because breeding animals are used unequally in each generation, and thus alleles can be lost. The effective number of founder genomes is smaller than half the effective population size, the effective number of ancestors, and the effective number of founders.

The inbreeding coefficient (F) is defined as the probability of an individual having 2 identical genes by descent. F is computed by using the method of Van Raden (1992). The expected effective population size (N_e) was estimated based on the increase in inbreeding coefficient (ΔF) between the last generation of the reference population and the parents of these individuals [$N_e = 1/2\Delta F$] (Sölkner et al., 1998).

Gene contributions of foreign populations (English Thoroughbred, Trakehner horse, Holsteiner, Oldenburg warmblood, and Arab horses) were calculated for the reference population. The gene contribution calculation was based on the breed to which the founders belonged. From this calculation, the proportion of probabilities of gene origins for each animal was derived and was given as the percentage of the reference population in this study. The software PEDIG (Boichard, 2002) was used to calculate generation intervals, effective number of founders and ancestors, effective number of founder genomes, and marginal contributions of ancestors.

RESULTS

In this study, the pedigree completeness index was assessed for 5 generations. All individuals of the refer-

Figure 1. Average inbreeding coefficients (%) per birth year in the Hanoverian reference population, Hanoverian stallions, and Hanoverian mares.

ence population showed a PEC for 5 generations above 0.9. The average PEC was 0.98, 0.96, and 0.98 for the total reference population, stallions, and breeding mares, respectively (Table 1). The average complete GE for the total reference population with both parents known was obtained by averaging GE_j over the respective individuals and was 8.43, varying from 7.59 in 1980 to 9.35 in 2000.

The average inbreeding coefficient for the reference population was 1.33%. Stallions and mares had lower average inbreeding coefficients, with values of 1.19 and 1.29%, respectively (Table 2). There was no clear trend in inbreeding coefficients over the 20-yr period analyzed (Figure 1).

The effective population size was 372.34 for the reference population. The effective number of founders was largest in stallions and smallest in the reference population. The ratio between the effective number of founders and the effective number of ancestors was 3.15 for the reference population, 3.25 for the stallions, and 3.06 for the mares. The number of ancestors explaining 90% of the gene pool of the reference population of Hanoverian warmbloods was 347, whereas 90% of the gene pool of stallions was explained by 627 ancestors. To explain the same genetic diversity of the gene pool in mares, 462 ancestors were determined. The number of ancestors explaining the genetic variability was generally largest for the stallions. The percentage of gene pool explained by the marginal contributions of the 1,000 most influential ancestors was 96.22% for the reference population, whereas the same number of ancestors accounted for a smaller percentage of the gene pool of stallions and breeding mares.

The number of founders explaining the gene pool was larger than the number of ancestors. Like the number of ancestors, stallions showed the largest number of founders, and the gene pool explained by the marginal contributions of the 1,000 most influential founders was smallest for the stallions.

The generation intervals were 11.1 yr for the stallion-son and 8.9 yr for the stallion-daughter pathway. For the female offspring, the generation intervals were 10.7 yr for mares to sons and 9.3 yr for mares to daughters. The average generation interval over the 4 pathways was 10 yr.

English Thoroughbreds contributed nearly 35% of the genes to the Hanoverian reference population and made even slightly greater contributions (39%) to the stallions (Table 3). The second most important breed for the Hanoverian population was Trakehner, which accounted for 8% of the Hanoverian gene pool. Approximately 49% of the genes of the current population were

Table 3. Average gene contributions of foreign populations (%) to the reference populations for Hanoverian horses

Breed	All horses	Stallions	Breeding mares
Hanoverian warmblood	49.1	38.6	49.3
English Thoroughbred	34.8	38.9	34.6
Trakehner horse	7.9	7.9	8.0
Arab horse	2.7	2.7	2.8
Holsteiner warmblood	2.1	5.2	1.7
Oldenburg warmblood	0.5	0.8	0.5
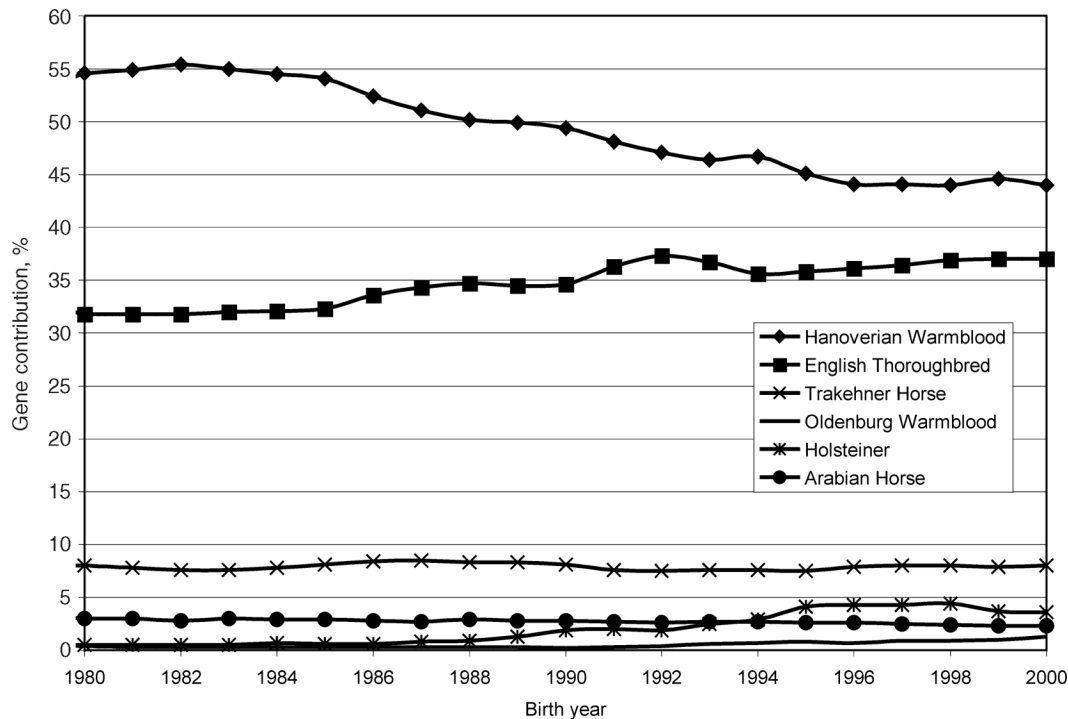
Figure 2. Average gene contributions of the different horse breeds per birth year in the Hanoverian reference population.

contributed by horses that were originally recorded as foundation animals of the Hanoverian breed.

By the early 1980s, the Holsteiner had been used only occasionally (0.5%), but showed an increase during the 1990s; therefore, its contribution to the reference population was 2.1% and its contribution to the stallion population was approximately 5%. The proportion of the Oldenburg warmblood was only 0.5%.

A similar tendency was seen in the population of breeding mares: the English Thoroughbred had the greatest influence of all foreign breeds (34.6%), followed by the Trakehner (8.0%), the Arab (2.8%), the Holsteiner (1.7%), and the Oldenburg warmblood (0.5%; Table 3). Looking at the time span from 1980 to 2000 for the reference population, a slight decrease in the Hanoverian gene proportion can be recognized, whereas the proportion of the English Thoroughbred increased to some extent. Both the Trakehner and the Arab had a more stable and unvarying influence (Figure 2). Similar observations could be made for mares (data not shown). In Hanoverian stallions, the Hanoverian and Thoroughbred represented between 35 and 45% of the gene proportions, whereas all other breeds had contributions of less than 10%. Genetic contributions from Trakehner and Holsteiner warmblood horses were the most important among these other breeds (Figure 3).

The 15 ancestors with the largest marginal genetic contributions were stallions and accounted for nearly 35% in the reference population and in mares, but accounted for only approximately 29% in stallions. The 15 most intensely used mares reached marginal genetic contributions of between 4.8 and 5.3% (Tables 4, 5, and 6). Most important ancestors were born in the first half of the 20th century. The 6 most important male ancestors belonged to the Hanoverian warmblood, whereas the 6 most important female ancestors belonged to 4 different breeds, Hanoverian warmblood, Thoroughbred, Oldenburg, and Holsteiner warmblood. The same 3 stallions, Aldermann I, Fling, and Absatz, had the greatest genetic impact in the reference population, as well as in mares and stallions. The breeding mare Costane was the most important breeding mare for all 3 populations (reference population, mares, stallions) and her marginal contribution was greatest in mares, with a value of 0.88%.

To show trends in genetic contributions over birth years in the reference population, we analyzed the marginal contribution of ancestors to the reference population in 5-yr intervals by birth dates. The greatest influence from 1980 to 1995 was from the stallions Aldermann I (A/E line) and Fling (F/W line). Their average marginal genetic contribution was consistently 3.8 to 4.1% and 3.7 to 3.9%, respectively; therefore, these 2 stallions contributed equally to the gene pool during this time span (Figure 4). The genetic contribution of the stallion Absatz (Trakehner line Abglanz-Absatz) showed an increasing trend from 2% in 1980 to 1985 to 3.5% in 1991 to 1995. The marginal genetic contributions of the stallions Weltmeyer (F/W line) and Donnerhall (D line) increased from 0.17 and 0.59% in 1986 to 1990 to 6.4 and 4.7%, respectively, in 1996 to 2000; therefore, these stallions had the greatest genetic im-
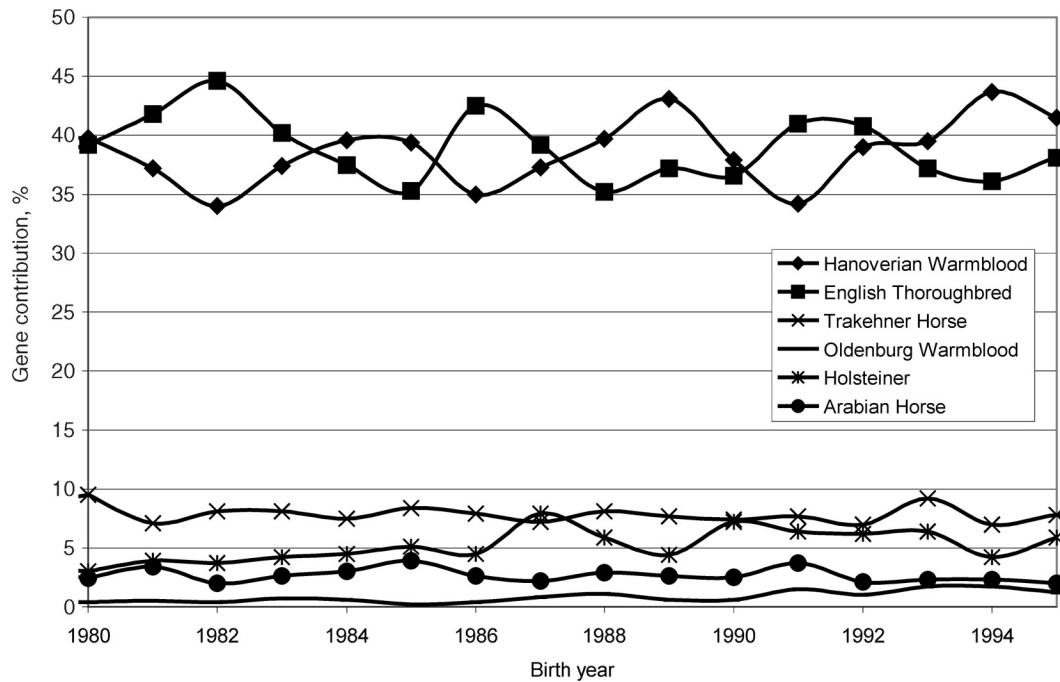
Figure 3. Average gene contributions of the different horse breeds per birth year in the Hanoverian stallions.

pact on the reference population from 1996 onward. The largest impact over the last 90 yr was by the stallion Alderman I, with an average marginal genetic contribution per birth year between 2.2 and 5.3%. No other stallion made such a consistently large contribution to the Hanoverian breed.

DISCUSSION

During the 19th century and until the First World War, Hanoverian breeding had to counterbalance strength and refinement. From then on, the Hanoverian breed was influenced by 2 main interests, first by the army's need to obtain a capable and efficient military horse, and second by the agricultural requirements of a robust carriage horse.

The first peak of English Thoroughbred use in Hanoverian breeding was around 1840; at that point in time, 35% of all stallions were English Thoroughbreds. However, the forced use of English Thoroughbreds led to disadvantages in exterior and disposition (Löwe, 1988) and was followed by a more careful use of English Thoroughbreds. The following period of selection for strength produced a strong and robust hardworking type. The period of refinement following the Second World War was a necessary process because of the general motorization of agriculture and transportation systems. This was achieved by employing Trakehner horses, of which several stallions had come to Hanover in the years 1944 to 1945 and again through the use of English Thoroughbreds. This is also reflected by the gene contributions (34.8% Thoroughbred, 7.9% Trakehner). The increase in the genetic proportion of the

Holsteiner warmbloods from 0.5 to 2.1% around the mid-1990s can be explained by the initiation of the Hanoverian Jumper Breeding Program in 1993, the starting point of an augmented use of the Holsteiner warmblood.

The average coefficient of inbreeding of the reference population of 167,063 horses (1.33%) was lower than in other population studies using similar large horse populations. In addition, the variation of the inbreeding coefficient over 20 birth years was small and did not exceed 0.3% in all horses and mares. In stallions, the mean inbreeding coefficient per birth year was between 0.9 and 1.58%. The overall coefficients of inbreeding reported in the literature were 8.48% for Andalusian horses (Valera et al., 2005), 6.59% for Italian Haflingers (Gandini et al., 1992), 8.99% for North American Standardbreds (MacCluer et al., 1983), 7.0% for Spanish Arab horses (Cervantes et al., 2008), 12.5% for Thoroughbreds (Mahon and Cunningham, 1982), 10.81% for Lipizzan horses (Zechner et al., 2002), and 2.40 (Thoroughbred) to 7.10% (Arab) for 5 horse breeds raised in France (Moureaux et al., 1996). Greater inbreeding coefficients were shown for smaller horse populations, such as 15.7% for Friesian horses (Sevinga et al., 2004), 7.75% for Kladruber horses (Volenec et al., 1995), 2.28% for South German coldblood horses (Aberle et al., 2004), 5.21% for Black Forest horses (Aberle et al., 2003a), 4.53% for Schleswig draft horses (Aberle et al., 2003b), and 1.73% for Rhenish German draft horses (Biedermann et al., 2002). Because most of these horse breeds were bred in closed populations, greater inbreeding coefficients were expected than in a population with more open access to other breeds. The magnitude of inbreeding coefficients was sensitive to pedigree depth and com-

Table 4. Total and marginal genetic contributions (%) of the 15 ancestors (stallions and breeding mares) with the largest marginal genetic contributions to the reference populations for Hanoverian horses

No.	Ancestor	Year of birth	Breed[1]	Sire line[2]	Total contribution	Marginal contribution
Stallion						
1	Aldermann I	1909	HAN	A/E	5.25	5.25
2	Fling	1911	HAN	F/W	4.72	4.72
3	Absatz	1960	HAN	*	3.63	3.46
4	Duellant	1943	HAN	D	3.04	2.47
5	Goldfisch II	1935	HAN	G	3.24	2.43
6	Ferdinand	1941	HAN	F/W	2.64	2.39
7	Der Löwe XX	1944	TB	*	2.00	2.00
8	Abendsport	1935	HAN	A/E	2.58	1.77
9	Feiner Kerl	1919	HAN	F/W	3.85	1.76
10	Frustra II	1943	HAN	F/W	1.79	1.57
11	Doemitz I	1944	HAN	D	1.79	1.51
12	Marcio XX	1947	TB	*	1.50	1.50
13	Abglanz	1943	TRAK	*	3.24	1.42
14	Woermann	1971	HAN	F/W	1.97	1.40
15	Waidmannsdank	1959	TB	*	1.29	1.29
All						34.94
Breeding mare						
1	Costane	1907	HAN		1.65	0.86
2	Altwunder	1950	HAN		1.21	0.58
3	Domgoettin	1961	HAN		1.28	0.49
4	Alexine	1933	HAN		1.47	0.48
5	Aversion XX	1914	TB		0.75	0.42
6	Ninette	1976	OLD		0.36	0.36
7	Faki	1938	HAN		0.41	0.32
8	Pechfackel XX	1943	TB		0.62	0.27
9	Bramouse XX	1936	TB		0.27	0.27
10	Gotensage	1948	HAN		0.80	0.25
11	Auerroeschen	1960	HAN		0.22	0.22
12	Square Note XX	1975	TB		0.21	0.20
13	Aussicht	1928	HAN		1.54	0.19
14	Golfkleid	1934	HAN		0.38	0.19
15	Ankerhirtin	1949	HAN		0.74	0.19
All						5.29

[1]HAN = Hanoverian warmblood; TB = English thoroughbred; TRAK = Trakehner; OLD = Oldenburg warmblood horse.

[2]An asterisk (*) indicates founder of a new sire line.

pleteness. The average complete GE of 8.34 in our study was similar to or larger than in other analyses. In an assessment of the Andalusian horse studbook, a value of 8.26 was obtained for the average complete GE resulting from 14.59 generations (Valera et al., 2005). Similarly deep and complete pedigree records were used in the studies of North American Standardbreds (MacCluer et al., 1983) and Thoroughbreds (Mahon and Cunningham, 1982). Pedigrees with a relative lack of information were analyzed by Cervantes et al. (2008) for Spanish Arab horses (5.7) or with a very high average complete GE of 15.2 for Lipizzans (Zechner et al., 2002). The low inbreeding coefficient in the Hanoverian population was clearly due to the large population size, the large number of founder animals of genetically diverse breeds, the balanced use of stallions from different sire lines, and the introgression of sire lines from other breeds, particularly English Thoroughbreds and Trakehners, in the breeding program. The traditional sire lines distinguished in the Hanoverian warmblood in-

clude the A/E line founded by Adeptus and his grandson Alderman I, the F/W line founded by Flick and his grandson Fling, the D line founded by Devil's Own XX and his descendant Detektiv, and the G line founded by Goldschaum XX and his descendant Goldfisch. Important new lines were founded after 1945 by using Trakehner, Thoroughbred, Anglo-Arab, Selle Francais, and Anglo Normanne stallions, such as Semper Idem (Trakehner) and his son Senator, Abglanz (Trakehner) and his son Absatz, Der Löwe XX, Matcho AA, Furioso II, and Cor de la Bryere and his son Calypso II. The concept of sire lines allowed the Hanoverian breeder to choose mating partners from other lines and allowed modest migration of sires from other breeds. Thus, inbreeding through the use of closely related mating partners could easily be avoided. An equilibrium value of an inbreeding coefficient of 1.33 for an effective population size of 372.34 was maintained, with a migration rate of 0.05. This means that approximately 19 immigrants per generation are sufficient to keep the inbreeding

Table 5. Total and marginal genetic contributions (%) of the 15 ancestors (stallions and breeding mares) with the largest marginal genetic contributions to the Hanoverian stallions

No.	Ancestor	Year of birth	Breed[1]	Sire line[2]	Total contribution	Marginal contribution
Stallion						
1	Aldermann I	1909	HAN	A/E	3.92	3.92
2	Fling	1911	HAN	F/W	3.74	3.74
3	Absatz	1960	HAN	*	2.70	2.57
4	Grande	1958	HAN	G	2.69	2.13
5	Gotthard	1949	HAN	D	2.45	2.06
6	Ferdinand	1941	HAN	F/W	2.08	1.89
7	Ramiro	1965	HOL	*	1.75	1.75
8	Dolman	1933	HAN	D	2.38	1.53
9	Der Löwe XX	1944	TB	*	1.44	1.44
10	Frustra II	1943	HAN	F/W	1.55	1.41
11	Cor de la Bryere	1968	AN	*	1.31	1.31
12	Ladykiller XX	1961	TB	*	1.29	1.29
13	Furioso II	1965	SF	*	1.28	1.28
14	Abendsport	1935	HAN	A/E	1.80	1.24
15	Feiner Kerl	1919	HAN	F/W	2.98	1.19
All						28.75
Breeding mare						
1	Costane	1907	HAN		1.20	0.64
2	Tabelle	1959	HOL		0.63	0.63
3	Warthburg	1962	HOL		0.61	0.50
4	Aversion XX	1914	TB		0.61	0.48
5	Ninette	1976	OLD		0.45	0.45
6	Altwunder	1950	HAN		0.83	0.34
7	Alexine	1933	HAN		1.04	0.33
8	Bramouse XX	1936	TB		0.29	0.29
9	Heureka Z	1960	HOL		0.27	0.27
10	Faki	1938	HAN		0.24	0.19
11	Pechfackel XX	1943	TB		0.52	0.15
12	Auerroeschen	1960	HAN		0.15	0.15
13	Kaiserwuerde XX	1945	TB		0.14	0.14
14	Square Note XX	1975	TB		0.18	0.14
15	Gotensage	1948	HAN		0.45	0.14
All						4.84

[1]HAN = Hanoverian warmblood; TB = English thoroughbred; TRAK = Trakehner; HOL = Holsteiner warmblood; AN = Anglo normanne; SF = Selle francais; OLD = Oldenburg warmblood horse.
[2]An asterisk (*) indicates founder of a new sire line.

coefficient of the total reference population at this level. Furthermore, the breeding concept is based on successful combinations among sire lines; thus, the breeder aims at finding the most successful combinations among his mares and the stallions. Many sires and dams obtain the opportunity to reproduce using this approach, and this fact largely prevents inbreeding through common sires. The studbook requires pure breeding, and only those breeds that are recognized as founder breeds of the Hanoverian warmblood are allowed to be registered. Examples include the English Thoroughbred, Arab, Anglo-Arab, Trakehner, Holsteiner, and other related warmblood breeds with a 50% gene proportion of Hanoverian warmblood or their founder breeds, or warmblood breeds originating from the Hanoverian warmblood, such as the Westphalian and Rhenish warmbloods. The effective number of founders in the Hanoverian reference population was much larger than those of 39.6, 39.5, 28, and 48.2 reported for the Carthusian strain of Andalusian horses (Valera et al., 2005), Spanish Arab horses (Cervantes et al., 2008), Thoroughbreds (Mahon and Cunningham, 1982), and Lipizzan horses (Zechner et al., 2002), respectively. This may also be the case for the 5 French horse breeds, the French trotter (70), Anglo-Arab (129), Arab (135), Thoroughbred (236), and Selle Francais (333), for which completeness and depth of pedigree were much lower (Moureaux et al., 1996). The contribution of ancestors to the gene pool in the Hanoverian warmblood was more balanced in comparison with Lipizzan horses (Zechner et al., 2002), Thoroughbreds (Cunningham et al., 2001), Andalusian horses (Valera et al., 2005), and Spanish Arab horses (Cervantes et al., 2008).

The average length of a generation interval in the present study was consistent with those reported for other horse populations, and thus cannot explain the low inbreeding coefficient. Moureaux et al. (1996) found average generation intervals in 5 horse breeds raised in France from 9.7 yr in Arabs to 11.8 yr in French trotters. Other average generation intervals reported for horse breeds were 9.7 yr for Icelandic Toelter horses (Hugason et al., 1985), 9.6 yr for Friesian horses (Sev-

Table 6. Total and marginal genetic contributions (%) of the 15 ancestors (stallions and breeding mares) with the largest marginal genetic contributions to the Hanoverian breeding mares

No.	Ancestor	Year of birth	Breed[1]	Sire line[2]	Total contribution	Marginal contribution
Stallion						
1	Aldermann I	1909	HAN	A/E	5.23	5.23
2	Fling	1911	HAN	F/W	4.74	4.74
3	Absatz	1960	HAN	*	3.28	3.12
4	Goldfisch II	1935	HAN	G	3.22	2.41
5	Duellant	1943	HAN	D	2.97	2.41
6	Ferdinand	1941	HAN	F/W	2.57	2.33
7	Der Löwe XX	1944	TB	*	1.94	1.94
8	Feiner Kerl	1919	HAN	F/W	3.90	1.79
9	Abendsport	1935	HAN	A/E	2.55	1.76
10	Frustra II	1943	HAN	F/W	1.7	1.49
11	Doemitz I	1944	HAN	D	1.75	1.48
12	Abglanz	1943	TRAK	*	3.10	1.46
13	Marcio XX	1947	TB	*	1.44	1.44
14	Waidmannsdank XX	1959	TB	*	1.35	1.35
15	Gotthard	1949	HAN	G	2.75	1.25
All						34.20
Breeding mare						
1	Costane	1907	HAN		1.64	0.88
2	Pechfackel XX	1943	TB		0.58	0.58
3	Altwunder	1950	HAN		1.19	0.57
4	Alexine	1933	HAN		1.41	0.49
5	Domgoettin	1961	HAN		1.19	0.45
6	Aversion XX	1914	TB		0.77	0.43
7	Faki	1938	HAN		0.39	0.31
8	Bramouse XX	1936	TB		0.28	0.28
9	Gotensage	1948	HAN		0.80	0.25
10	Auerroeschen	1960	HAN		0.22	0.22
11	Ankerhirtin	1949	HAN		0.73	0.20
12	Aussicht	1928	HAN		1.50	0.18
13	Golfkleid	1934	HAN		0.36	0.18
14	Spincka	1941	HAN		0.20	0.15
15	Angeberta	1907	HAN		0.37	0.13
All						5.30

[1]HAN = Hanoverian warmblood; TB = English thoroughbred; TRAK = Trakehner horse.
[2]An asterisk (*) indicates founder of a new sire line.

inga et al., 2004), 11.65 yr for Irish draft horses (O'Toole et al., 2001), and 10.11 yr for Andalusian horses (Valera et al., 2005). Taveira et al. (2004) reported an average value of 10.7 yr for Brazilian Thoroughbreds.

The generation intervals of stallions for their male offspring were on average 0.4 yr longer than those of the breeding mares. In contrast, the generation intervals of dams and sires toward female offspring showed a reversed relationship: breeding mares were on average 0.4 yr older at the time of the birth of their offspring than the respective stallions. The long generation intervals can be seen as a characteristic feature of horse breeding and are the consequence of the late onset of breeding use following a series of performance tests (30-d test, 70-d test of stallions, mare performance test), the long reproductive lifetime, and also their use in equestrian sports. The lengthening of generation intervals helps to keep inbreeding low and may be used to compensate for the number of stallions and breeding mares used. On the other hand, the time span is longer before an increase in inbreeding rate because the low

numbers of stallions and breeding mares used can be observed.

The effective population size of the Hanoverian population was 372.34, which is below the value published by the EAAP (European Association for Animal Production) Data Bank (N_e = 1,584). Sevinga et al. (2004) estimated a lower effective population size for the Friesian horse population (N_e = 27). Because a close relationship exists between the effective population size and all parameters derived from the probabilities of gene origin, conclusions can also be drawn from this for the effective number of founder genomes. The smaller the effective population size, the greater the decrease in the effective number of founder genomes per unit of time (Boichard et al., 1997). The number of founders in the total reference population was 13,881, but the effective number of founders was only 244.9 animals. Hence, it becomes evident that some founders were used more intensely than others, which is always critical in terms of loss of genetic diversity. The more intense use of some founders was also obvious from
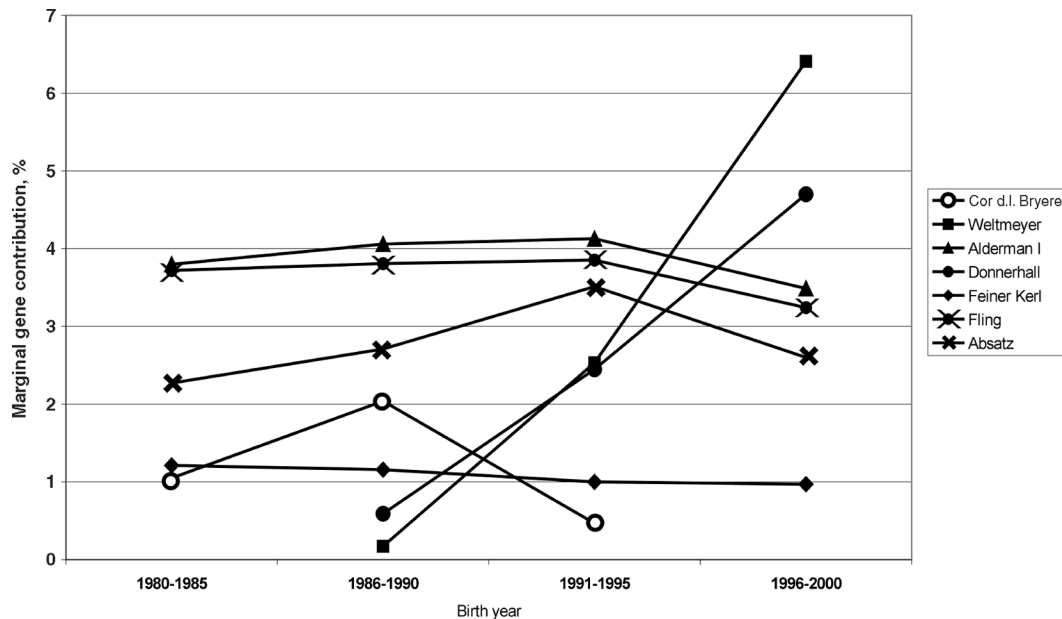
Figure 4. Percentage of marginal gene contributions from the most important stallions per birth year in the Hanoverian reference population.

the results of the analyses of the stallion and mare populations. There were 5,742 founders compared with 364.3 effective founders among the stallion population and 10,991 founders compared with 248.5 effective founders among the mare population. The most important male ancestor of the Hanoverian total reference population was Aldermann I (A/E line) has been used for 20 yr at the stallion station in Drochtersen, Germany, and has sired 110 approved sons, of which 71 remained in Hanover. This was the greatest number of sons ever registered in the Hanoverian breed (Löwe, 1988). Further important ancestors were the stallions Fling (F/W line) and Absatz (Trakehner line Abglanz-Absatz), with marginal contributions of 4.72 and 3.46%, respectively. Fling (F/W line) was thought to be the most important descendent in this line. Absatz (Trakehner line Abglanz-Absatz) was sire of 33 approved sons and 72 nationally awarded breeding mares in his 16 yr of breeding.

The ratio f_e/f_a was 3.15 within the total reference population, and 3.25 and 3.06 within the stallions and breeding mares, respectively, indicating a greater number of effective founders than effective ancestors. This result, as well as the fact that an inconsistent ratio of f_e/f_a existed, implies random loss of genetic diversity present in the founder animals within the Hanoverian population because of the heavy use of some sire lines in the past. Furthermore, the difference between the effective number of founder genomes and the effective number of ancestors indicated that random loss of alleles from founder animals had occurred, and this process continues as founders permanently enter into the Hanoverian warmblood. According to this difference,

the random loss of alleles had been larger in stallions and mares than in the reference population. In the breed history of the Hanoverian warmblood, drift caused the largest loss of alleles, and these losses were similar or even larger in comparison with Spanish Arab (3.04), Andalusian (2.4), and Lipizzan (1.84) horses. The reason for this large drift may be seen in the fact that the studbook is not closed for stallions and mares of other breeds as in most warmblood breeds; thus, many founder horses were used in the past. New founder horses are still introduced, and only a small proportion of these founder horses met the breeding goals and high standards required for athletic sport horses. Thus, we may assume that those alleles were particularly lost that did not seem useful for the development of the modern Hanoverian warmblood horse and its preferential use in sports. This random loss of allelic diversity in the founder generations did not increase inbreeding coefficients as new founder animals were introduced into the Hanoverian warmblood; thus, the number of founder animals has been kept nearly constant.

This study illustrates that breeding strategies in Hanoverian warmblood horses kept inbreeding at a low level over the last 20 yr. The differences between the effective number of founder genomes and half the effective population size, and the effective numbers of founders and ancestors indicate that the random loss of alleles of founders occurred to a large extent. We could identify 15 stallions with marginal genetic contributions in the breed history of approximately 35%, thus causing the ratio between the effective number of founders and ancestors to deviate from unity. The random loss of founder alleles was due to heavy use of some Hanoverian sires and sire lines. Active management of

sire lines and sires is necessary in the future to keep the rate of loss of genetic diversity low and to prevent single stallions from making large genetic contributions over a long time period to the Hanoverian warmblood population, given that the rate of inbreeding has increased in the last 10 yr.

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