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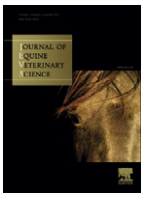

Original Research

Morphological and Genomic Differences Between Cutting and Racing Lines of Quarter Horses

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ABSTRACT

To investigate morphological and genomic differences between cutting and racing lines of Quarter Horses, 120 racing and 68 cutting animals of both sexes, registered at the Brazilian Association of Quarter Horse Breeders, were used. Blood samples were collected, and the following physical traits were measured: weight; height at withers; body length; length of the shank, pastern, rump, head, and neck; and chest, shank, and hoof circumference. For analysis of genomic differences, 54,602 single-nucleotide polymorphisms (SNPs) were genotyped using the Equine SNP50 BeadChip, and the quality of individual and SNP genotype data were evaluated. The fixation index, F_{ST}, was used to identify genome regions that were altered in the lines by selection. The results showed significant differences between the lines in all physical traits. Quality control led to the exclusion of four cutting animals with a call rate of <0.95. After filtering, 12,544, 13,815, and 13,370 SNPs were excluded for the whole population (n = 184), the 120 racing animals, and the 64 cutting animals, respectively. The number of informative polymorphisms detected in each line and in the whole population indicated that the Equine SNP50 BeadChip can be used in genetic studies of Quarter Horses. The fixation index, F_{ST}, identified 2,558 genome regions that may have been modified by divergent selection.

1. Introduction

As a breed of global importance, corresponding to 52% of all horses, Quarter Horses are important because of their great versatility in different equestrian events [1]. Quarter Horses were developed in North America in the 17th century from Arabian and Turkish horses brought by European settlers. The major development of this breed occurred during westward expansion when pioneers needed robust and versatile horses, fit for the saddle and for traction, in view of the difficulty to keep a varied stock of animals to satisfy diverse necessities [1].

The Quarter Horse breed is subdivided into different lines according to skills resulting from distinct selection objectives, including cutting and racing horses. The cutting line is destined for functional tests, exploring skills such as agility and obedience, which are important for cattle management in the field. The racing line is characterized by great sprinting speed over short distances on straight tracks. The cutting type is shorter and more compact and has muscular hindquarters, whereas the racing type is taller and has longer legs and a less prominent musculature.

The simultaneous study of thousands of DNA polymorphisms spread across the genome, known as genome-wide association analysis, has permitted the study of

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different populations of various domestic animal species [2-4], as well as the estimation of genetic divergence within and between populations [5]. During the process of domestication and breed formation, domestic animals were subjected to natural and artificial selection. These selection pressures led to an increase in the frequency of some mutations in specific regions of the genome, which generated more adapted animals or provided them with favorable characteristics to meet human needs. At the same time, the frequency of other polymorphisms decreased or they were completely eliminated [6]. In this respect, the comparison of allele frequencies between selected and unselected populations or between populations selected for different objectives provides insights into the regions of the genome that have been modified by selection.

According to Chowdhary and Raudsepp [7], one of the highlights from the analysis of the horse genome is its complete sequencing from a Thoroughbred animal (EquCab2.0) and, from this, the identification of 1,162,753 single-nucleotide polymorphisms (SNPs) in different breeds [8]. Designed to identify SNPs and genes that contribute to traits of interest in the major horse breeds raised today in the world, the Equine SNP50 BeadChip developed by Illumina, Inc., (San Diego, California, USA) represents a powerful platform for genetic studies of this species, permitting researchers to perform a variety of experiments that require the genotyping of DNA polymorphisms.

In view of these considerations, the aims of the present study were to investigate the genomic differences, using the Equine SNP50 BeadChip, and morphological differences between cutting and racing lines of Quarter Horses as a result of selection for different objectives.

2. Materials and Methods

2.1. Animals and Phenotypic Data

One hundred eighty-eight Quarter Horses of both sexes born between 1985 and 2009, including 120 racing horses and 68 cutting horses, registered at the Brazilian Association of Quarter Horse Breeders, were studied. All experimental procedures were conducted in accordance with the Brazilian legislation on animal welfare.

The following physical traits were measured according to Torres and Jardim [9]: weight; height at withers; body length; length of the shank, pastern, rump, head, and neck; and chest, shank, and hoof circumference. The measurements were performed by the same person using a tape measure and measuring stick, always on the right side of the animal, with the horse standing with front and rear legs perpendicular to the ground. For genotyping, a 5-mL sample of whole blood was collected from each animal by puncture of the left jugular vein in the neck region into vacuum tubes containing 7.5 mg ethylenediaminetetraacetic acid.

The animals of the racing line (18 male and 102 female horses), born to 48 stallions and 107 mares, belonged to five farms in the countryside of the State of São Paulo, Brazil. The animals of the cutting line (26 male and 42 female horses), born to 44 stallions and 64 mares, belonged to three other farms in the countryside of the State of São Paulo. In both lines, full sibs were avoided.

2.2. Genotyping of SNPs

Genomic DNA was extracted from the blood samples of Quarter Horses using the Illustra Blood Genomicprep Mini Spin kit (GE Healthcare, Little Chalfont, Buckinghamshire, UK) according to manufacturer instructions. DNA integrity was analyzed using 0.8% agarose gel electrophoresis, and DNA was quantified using a NanoDrop ND-2000 spectrophotometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA). The DNA concentration in the samples was adjusted to 40-60 ng/μL.

SNPs were genotyped on the HiScan system (Illumina Inc.) using the Illumina Equine SNP50 BeadChip at the Faculty of Agricultural and Veterinary Sciences, UNESP, Jaboticabal, São Paulo, Brazil. The chip contains 54,602 SNPs uniformly distributed across the entire genome of 15 horse breeds. The SNPs are distributed across the 31 autosomes and X chromosome. The mean interval between SNPs is 43,200 bp. This content is derived from the EquCab2.0 SNP Collection compiled by the Broad Institute's Equine Genome Sequencing Project, which identified >940,000 SNPs in Arabian, Andaluz, Akhal-Teke, Islandesa, Standardbred, Thoroughbred, and Quarter Horses.

2.3. Analysis of Morphological Differences and Differences in Inbreeding between Cutting and Racing Lines

Morphological differences between the two Quarter Horse lines (cutting and racing) were evaluated using a model that included the effects of sex and line, and age at recording as covariate. The general linear model (GLM) procedure of the Statistical Analysis System v.9.1 program (SAS Institute Inc., Cary, North Carolina, USA) [10] was used for statistical analysis, and means were compared using the Tukey test at a level of significance of 5%.

The inbreeding coefficient was calculated for each animal of the two lines based on pedigree records using the Relax2 program (MTT Agrifood Research Finland, Biometrical Genetics, Jokioinen, Finland) [11]. The relationship matrix contained 762 animals, with a depth of ancestry of four generations. The average inbreeding of consanguineous animals and of all animals of each line was estimated using the coefficients of inbreeding.

2.4. Quality of Genotype Data

The quality of individual and SNP genotype data was investigated using the Genome Studio program, version 2011.1 (Illumina Inc.). For individuals, call rate, heterozygosity, and gender estimation were determined. Animals with a call rate <0.95, heterozygosity of ±3 standard deviations from the mean, and errors in gender estimation were excluded from the sample. In addition, agreement between four replicates and parentage concordance (allele sharing) between four stallion/progeny and three stallion/mare/progeny pairs were evaluated.

With respect to the quality of SNP genotypes in the whole population and in each line, SNPs located on the X chromosome were excluded (filtered). SNPs with low genotyping quality (cluster separation <0.3), a call frequency <0.9, a minor allele frequency (MAF) <0.05 (including fixed alleles), and a Hardy–Weinberg $P < .001$ were also excluded.

2.5. Analysis of Genomic Differences between Cutting and Racing Lines

The fixation index, F_{ST}, was used to identify genome regions in the cutting and racing lines that have been modified by selection [12-14]. The $\vartheta = F_{ST}$ parameter was estimated for all SNPs that passed quality control (considering all individuals) using the Bayesian method proposed by Gianola et al. [15]. This method is a two-step procedure that eventually leads to clusters of ϑ values. The first step uses a simple Bayesian structure for removing samples from the posterior distribution of ϑ parameters without constructing Markov chains. This step assigns a weakly informative prior of allele frequencies and does not make any assumptions about evolutionary models. The second step considers samples from this posterior distribution as "data" and fits a sequence of finite mixture models to identify clusters of ϑ-statistics.

3. Results and Discussion

Selecting Quarter Horses for different objectives (racing or cutting) promoted significant changes in the physical traits of the animals. Table 1 compares the fitted means of the characteristics analyzed between the two lines. A significant effect of line ($P < .0001$) was observed for all traits. As expected, racing animals presented higher weight, height, body length, and body circumference than cutting animals. Thus, the phenotypic differences observed between the two lines have a possible genetic background. However, it is necessary to consider that phenotypes are also influenced by several environmental factors, such as feeding, training, and others. Although there are no other morphological studies characterizing Quarter Horse lines, the present investigation is important because it demonstrated a close relationship between physical characteristics and the function for which the animal is used. The different abilities of the breed, such as running, jumping, reining, and barrel racing, have resulted in an appropriate biotype for each modality, and differences in performance exist owing to morphological adequacy or inadequacy.

Among the 188 animals studied, 12 racing animals and one cutting animal were consanguineous. The mean coefficient of inbreeding (F) was 0.0028 or 0.28% for the whole population. In contrast, the mean coefficient of inbreeding was 0.0364 or 3.64% (0%-7.81%) for the 12 inbred animals of the racing line and 0.0036 (or 0.36%) for all racing animals. These coefficients were higher than those obtained for the only inbred animal of the cutting line (0.0078 or 0.78%) and for all cutting animals (0.0001 or 0.01%), suggesting a higher frequency of inbreeding in the racing line. Coefficients of 0.8% [16] to 1% [17] have been reported for Thoroughbreds, and of 10.3% for a population of Lipizzan mares [18]. In this research, as well as in the study by McCue et al. [19], the coefficients of inbreeding of Quarter Horses were found to be low when compared with other breeds, indicating that Quarter Horse breeders tend to avoid mating between closely related animals.

Quality control of individual genotype data led to the exclusion of four cutting animals from the sample because of a call rate <0.95 (95%). The remaining 184 animals (120 racing and 64 cutting animals) presented a mean call rate of 0.9929 ± 0.0054 (range: 0.9503-0.9979). Mean heterozygosity estimated for all individuals was 0.3468 ± 0.0148 (range: 0.3049-0.3788). The samples genotyped in duplicate showed ≥99.8% agreement (0.9979-0.9990). Similarly, parentage concordance between stallion/progeny and stallion/mare/progeny pairs was very high (0.9985-0.9995). Although some individuals were excluded because of a low genotyping rate, taken together, the present results indicate the lack of DNA contamination between samples and a generally successful hybridization between DNA and the chip.

Considering the whole population (n = 184) that passed quality control, 12,544 SNPs were excluded by the filtering process and 42,058 remained for further analysis. With respect to the 120 racing and 64 cutting animals, after filtering, 40,787 (13,815 excluded) and 41,232 (13,370 excluded) SNPs remained for analysis, respectively. Table 2 shows the number of excluded SNPs and the reason for exclusion for the whole population and for animals of the racing and cutting lines.

According to Wiggans et al. [20] and Ziegler [21], inconsistently genotyped SNPs or those that do not contribute to the accuracy of genetic evaluations should be excluded to reduce computational effort and the number of false results, as well as to improve precision of the estimates of the remaining polymorphisms. The numbers of excluded SNPs owing to an MAF <0.05 were similar in the racing line (8,925), cutting line (7,958), and whole

Table 1
Least-square means and standard errors of physical traits in racing and cutting Quarter Horses

Traits	Racing Line	Cutting Line
Body length (m)	1.8081 ± 0.0057[a]	1.6343 ± 0.0087[b]
Shank length (cm)	27.065 ± 0.0014[a]	24.478 ± 0.0014[b]
Pastern length (cm)	13.382 ± 0.0009[a]	12.231 ± 0.0009[b]
Rump length (cm)	62.032 ± 0.0032[a]	55.173 ± 0.0028[b]
Head length (cm)	62.170 ± 0.0020[a]	56.057 ± 0.0021[b]
Neck length (cm)	79.772 ± 0.0034[a]	73.333 ± 0.0049[b]
Weight (kg)	538.97 ± 3.7671[a]	450.69 ± 5.6902[b]
Height at withers (m)	1.5592 ± 0.0040[a]	1.4660 ± 0.0045[b]
Chest circumference (m)	1.9669 ± 0.0127[a]	1.8020 ± 0.0094[b]
Shank circumference (cm)	20.521 ± 0.0008[a]	18.812 ± 0.0009[b]
Hoof circumference (cm)	43.013 ± 0.0018[a]	39.751 ± 0.0027[b]

[a,b]Means in the same row followed by different superscript letters differ significantly at the 5% level (Tukey test).

Table 2
Number of SNPs excluded by quality control of genotype data considering the whole population, racing line, and cutting line of Quarter Horses and reason for exclusion

Category/Reason for Exclusion	Whole Population n	Racing Line n	Cutting Line n
Genotyped SNPs	54,602	54,602	54,602
Located on the X chromosome	2,539	2,539	2,539
Cluster separation <0.3	1,972	1,972	1,972
Call frequency <0.9	148	143	227
Fixed or with minor allele frequency <0.05	7,587	8,925	7,958
Hardy–Weinberg equilibrium—$P < .001$	298	236	674
SNPs selected for genetic analysis	42,058	40,787	41,232

population (7,587). Schröder et al. [22] reported a similar number in a study of Quantitative Trait Loci (QTL) for show jumping in Hanoverian Warmblood horses (7,875 excluded SNPs). In contrast, Lykkjen et al. [23] excluded 13,265 SNPs with an MAF <0.05 in a study identifying QTLs associated with osteochondrosis in Norwegian Standardbred trotters. In the present study, the number of informative SNPs in the two lines (racing animals: 40,787; cutting animals: 41,232) and in the whole population (42,058) were lower than the 47,699 SNPs found in Quarter Horses by McCue et al. [19]. This divergence of results is probably due to different criteria adopted in the filtering process of the genotyped SNPs used in their research, particularly the exclusion of polymorphisms with an MAF <0.01. In contrast, the present results were similar to those reported in studies that investigated other horse breeds using the Equine SNP50 BeadChip, such as Thoroughbreds (40,977) [24], Standardbreds (41,170) [23], Hanoverian horses (43,441) [22], and French trotters (41,249) [25]. Despite the difference in the number of informative SNPs between the racing and cutting lines, autosomal coverage, although higher in the latter, did not vary considerably.

Comparison of the mean MAF of the genotyped SNPs revealed no significant difference between the racing (0.2267 ± 0.1543) and cutting lines (0.2256 ± 0.1496; F test, $P > .05$). Similar values have been reported by Corbin et al. [26] and McCue et al. [19], who studied linkage disequilibrium (LD) in Thoroughbred (0.30 ± 0.12) and Quarter horses (0.232), respectively. However, the frequency of polymorphisms with an MAF <0.05 was higher in racing horses (17.87%) than in cutting horses (15.96%). Among these, the frequency of fixed (monomorphic) polymorphisms and those with rare alleles were 6.79% and 11.08% in racing animals and 5.11% and 10.85% in cutting animals, respectively. In addition, the number of informative SNPs (MAF ≥0.05) was higher in the cutting line (84.04%) than in the racing line (82.13%). Table 3 shows the number of SNPs according to MAF class. The higher frequency of polymorphisms with an MAF <0.05 in racing Quarter Horses might be explained by the more common practice of consanguineous mating and higher selection intensity in this line. Polymorphic SNPs that are associated with one population but not with the other, which were more frequent in the cutting line, might be used as informative SNPs for a line in particular. In contrast, highly informative SNPs (MAF = 0.4-0.5), which were more frequent in the racing line, are useful for individual identification by DNA testing (paternity and forensic tests).

Table 4 shows the distribution and density of informative SNPs (MAF ≥0.05) across the 31 autosomes in the sample of Quarter Horses studied. Considering the whole population, the largest number of informative SNPs was detected on chromosome 1 (3,502), and the smallest number, on chromosome 31 (492). With respect to genome coverage, the density of SNPs was 18.72 SNPs/million base pairs (Mb) or one SNP at an interval of 53,419 bp. This density varied between chromosomes, ranging from 16.82 SNPs/Mb (ECA12: average of one SNP at an interval of 59,453 bp) to 19.91 SNPs/Mb (ECA16: average of one SNP at an interval of 52,356 bp). In the racing line, chromosome 1 contained the largest (3,381) and chromosome 31 contained the smallest number of informative SNPs (486). The density was 18.15 SNPs/Mb or one SNP at an interval of 55,096 bp, ranging from 16.09 SNPs/Mb (ECA12: average of one SNP at an interval of 62,150 bp) to 19.44 SNPs/Mb (ECA31: average of one SNP at an interval of 51,440 bp). In the cutting line, ECA1 contained the largest (3,433) and ECA31 contained the smallest number of informative SNPs (496). The lowest SNP density was observed for chromosome 12, with 16.67 SNPs/Mb (average of one SNP at an interval of 59,988 bp), and the highest density was observed for chromosome 31, with 19.84 SNPs/Mb (average of one SNP at an interval of 50,403 bp), corresponding to a mean interval of 54,496 bp between SNPs distributed across the entire autosomal genome or to a density of 18.35 SNPs/Mb.

Equine chromosomes differ significantly in length, with the longest chromosome (ECA1) containing 186 Mb and the shortest chromosome (ECA31) containing 25 Mb [27]. Therefore, the higher frequency of informative polymorphisms on larger chromosomes and the lower frequency on smaller chromosomes observed in the two lines and in the whole Quarter Horse population indicate that the filtering process did not affect the uniformity of distribution of SNPs across the genome.

The F_{ST} mean estimated for the 42,058 SNPs in the two lines was 0.0342 ± 0.0403, with ϑ ranging from 0.0025 to 0.3556. This value was substantially lower than that reported by Gu et al. [28], who used microsatellite markers to identify genome regions that distinguish Thoroughbreds from non-Thoroughbred breeds and found an overall mean F_{ST} of 0.12. The low F_{ST} value found in the present study was expected, as fixation indices tend to be lower when lines instead of breeds are studied because of a theoretically lower genetic distance. Qanbari et al. [29], using F_{ST} to quantify genetic differentiation in *Bos taurus* cattle, found lower values within milk-producing (Holstein and Brown Swiss; 0.057 ± 0.076) and meat-producing breeds (Angus and Piedmontese; 0.022 ± 0.041) than between these breeds (mean of 0.278 ± 0.324).

The distribution of posterior means of the ϑ values (F_{ST}) in the two lines permitted classification of the 42,058 SNPs (loci) into seven clusters. According to Gianola et al. [15], the expectation is that these clusters are representative of

Table 3
Number and percentage of SNPs divided into four classes of minor allele frequency obtained for the racing and cutting lines of Quarter Horses and for the whole population

Line	Minor Allele Frequency			
	<0.05	0.05-0.5	0.05-0.4	0.4-0.5
Racing	8,925 (17.87%)	41,023 (82.13%)	31,580 (63.22%)	9,443 (18.91%)
Cutting	7,958 (15.96%)	41,906 (84.04%)	33,084 (66.35%)	8,822 (17.69%)
Whole population	7,587 (15.19%)	42,356 (84.81%)	32,985 (66.05%)	9,371 (18.76%)

Table 4
Distribution and density of informative SNPs (minor allele frequency ≥0.05) across the autosomes of racing and cutting Quarter Horses and of the whole population

Chromosome–Chromosome Size (Mb)	Informative SNPs			Density		
	Racing Line	Cutting Line	Whole Population	Racing Line (SNPs/Mb)	Cutting Line (SNP/Mb)	Whole Population (SNP/Mb)
1–186	3,381	3,433	3,502	18.18	18.46	18.83
2–121	2,238	2,197	2,289	18.50	18.16	18.92
3–119	2,213	2,213	2,261	18.60	18.60	19.00
4–109	1,980	2,053	2,059	18.17	18.83	18.89
5–100	1,773	1,794	1,826	17.73	17.94	18.26
6–85	1,474	1,451	1,510	17.34	17.07	17.76
7–99	1,792	1,782	1,834	18.10	18.00	18.53
8–94	1,720	1,722	1,767	18.30	18.32	18.80
9–84	1,529	1,555	1,578	18.20	18.51	18.79
10–84	1,478	1,484	1,527	17.60	17.67	18.18
11–61	1,102	1,128	1,134	18.07	18.49	18.59
12–33	531	550	555	16.09	16.67	16.82
13–43	739	754	776	17.19	17.53	18.05
14–94	1,703	1,777	1,764	18.12	18.90	18.77
15–92	1,759	1,703	1,767	19.12	18.51	19.21
16–87	1,675	1,676	1,732	19.25	19.26	19.91
17–81	1,492	1,511	1,546	18.42	18.65	19.09
18–83	1,405	1,462	1,455	16.93	17.61	17.53
19–60	1,151	1,144	1,166	19.18	19.07	19.43
20–64	1,184	1,208	1,225	18.50	18.88	19.14
21–58	1,044	1,052	1,087	18.00	18.14	18.74
22–50	904	969	953	18.08	19.38	19.06
23–56	975	986	1,016	17.41	17.61	18.14
24–47	885	882	908	18.83	18.77	19.32
25–40	703	740	738	17.58	18.50	18.45
26–42	765	765	792	18.21	18.21	18.86
27–40	676	719	721	16.90	17.98	18.03
28–46	860	847	885	18.70	18.41	19.24
29–34	599	616	614	17.62	18.12	18.06
30–30	571	563	579	19.03	18.77	19.30
31–25	486	496	492	19.44	19.84	19.68

different processes that occur in the populations, such as balancing, directional selection, and neutrality. Cluster 4, which consisted of 2,558 loci, presented the highest values of ϑ. The conditional probability of membership to this cluster was one for 271 loci. Fifteen of these loci, mapped to chromosomes 1, 2, 4, 5, 8, 9, 10, 16, 21, and 30, presented the highest values of ϑ (0.3013-0.3556), indicating genome regions that were more likely to have been subjected to divergent selection between lines.

Recently, genomic studies in the Quarter Horse got prominent. In the first sequencing of a horse genome by next-generation sequencing and the first genomic sequence of an individual Quarter Horse mare, Doan et al. [30] identified 3.1 milion SNPs, 193,000 insertion/deletion polymorphisms (InDels), and 282 copy-number variants in relation to the reference Thoroughbred genome. Additionally, these researches genotyped this Quarter Horse for gene mutations of known diseases and for gene variants associated with economically important traits, including racing performance. The four genes related to racing performance in Thoroughbred horses, *MSTN* (myostatin) [24,31-33], *PDK4* (piruvate dehydrogenase kinase, isozyme 4) [28,34], *CKM* (creatine kinase, muscle), and *COX4I2* (cytochrome c oxidase, subunit 4, isoform 2) [35], are located in equine chromosomes 18, 4, 10, and 22, respectively. These chromosomes are shown in this research as having 77 of 271 genomic regions (with conditional probability equal to one) selected divergently between racing and cutting lines. However, considering that the LD decrease in the Quarter Horse occurs between loci that are located at distances longer than 50-100 kb [19], none of the 77 regions close enough (in LD) to the gene polymorphisms associated with racing performance. Considering that speed is also a desirable trait in cutting animals, these results suggest the possibility that the same alleles of these gene polymorphisms have been selected in both lines of Quarter Horse.

4. Conclusions

Divergent selection of cutting and racing Quarter Horses promoted significant changes in the physical and genomic characteristics of these lines. The number of informative SNPs and SNP density found in the genome of cutting and racing Quarter Horses suggest that the Equine SNP50 BeadChip can be used for different purposes in the breed, such as genetic structure analysis, estimation of genetic divergence within and between populations, and identification of QTL and genome regions subjected to selection.

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