

Selection on the Colombian paso horse's gaits has produced kinematic differences partly explained by the *DMRT3* gene

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Abstract

The Colombian paso horse, the most important horse breed in Colombia, performs specific and particular gaits (paso fino, trocha, and Colombian trot), which display different footfall patterns and stride frequencies. The breed has been selected for gait and conformation for more than 50 years and we hypothesize that this selection has led to kinematic differences of the gaits that can be explained by different genetic variants. Hence, the aims of the study were: 1. To identify if there are any differences in the kinematic and genetic variants between the Colombian paso horse's gaits. 2. To evaluate if and how much the gait differences were explained by the nonsense mutation in the *DMRT3* gene and 3. To evaluate these results for selecting and controlling the horses gait performance. To test our hypotheses, kinematic data, microsatellites and *DMRT3* genotypes for 187 Colombian paso horses were analyzed. The results indicated that there are significant kinematic and *DMRT3* differences between the Colombian paso horse's gaits, and those parameters can be used partially to select and control the horses gait performance. However, the *DMRT3* gene does not play a major role in controlling the trocha and the Colombian trot gaits. Therefore, modifying genes likely influence these gaits. This study may serve as a foundation for implementing a genetic selection program in the Colombian paso horse and future gene discovery studies for locomotion pattern in horses.

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Data Availability: All kinematic and genetic data are available from the figshare database (accession numbers [10.6084/m9.figshare.5877405](https://doi.org/10.6084/m9.figshare.5877405), [10.6084/m9.figshare.5877468](https://doi.org/10.6084/m9.figshare.5877468)).

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Competing interests: Gabriella Lindgren is co-inventor on a granted patent concerning commercial testing of the *DMRT3* mutation: A method to predict the pattern of locomotion in horses. PCT EP12 747 875.8. European patent registration date: 2011-05-05, US patent registration date: 2011-08-03. Miguel Novoa Bravo is personal of the company Genética Animal de Colombia Ltda. This funder provided support in the form of research materials, infrastructure, funding for research travel, and salary (after January the first 2018) for author MNB, but did not have any additional role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript. The specific roles of these authors are articulated in the 'author contributions' section. There are no further patents, products in development or marketed products to declare. This does not alter the authors' adherence to all the PLOS ONE policies on sharing data and materials, as detailed online in the guide for authors.

Introduction

The Colombian paso horse

The Colombian paso horse breed (CPH), also known as Colombian criollo paso horse, is the most important horse breed in Colombia. This breed is likely derived from a mix of Spanish horses brought by the conquerors to America starting in year 1493. This group of horses included the Spanish Jennet horse, which was known to perform ambling gaits [1]. In the beginning of the 20th century, the CPH population consisted of a mix of horses that performed several different stepping gaits [2]. The Colombian paso horses have been intensively selected for their gaits (paso fino, trocha and trot) since the 1980's [2]. Currently, the CPH breed is traditionally divided into four groups based on that they have been bred as separate populations during at least 30 years, which are not generally crossed, and also, their gaits: Colombian paso fino (CPF), Colombian trocha (CTR), Colombian trocha and gallop (CTRG) and Colombian trot and gallop (CTG) (www.fedequinas.org). Recently, the CPF group has been declared as a national genetic patrimony in Colombia (Law 1842 of 2017, <http://es.presidencia.gov.co/normativa>). This was the first CPH group distinguished outside Colombia and in the 20th century it was the group with the largest population size.

All the kinematic measurements were provided by Fedequinas. Thirteen anatomical landmarks were placed on the horses by the same operator (Fig 1). The landmarks were tracked using the Quintic Biomechanics® software. Measurements were taken for each side of the horse when the horse was in motion. A route was defined for each horse farm and every horse performed (by different riders) its gaits through that route 10 times. Five measurements per side were taken when the horse was perpendicular to the camera. This was recorded by a high-speed camera taking 240 frames per second. A metallic square of 1 X 1 meters was used in all the videos to calibrate the lengths of the measurements. The software automatically calculated the kinematic parameters. These were direct measurements on certain variables in locomotion, such as the angles of the fetlock joint flexion and extension, carpal joint flexion, elbow joint flexion and tarsal joint flexion (Fig 1). Also, the following parameters were measured: stride frequency (strides per minute), stride length (cm), fetlock front speed (cm/s), fetlock hind speed (cm/s) and hock speed (cm/s). The speeds were the mean (per side, left and right) of the maximum speeds registered for each route. The protraction and retraction measurements were defined as explained in Fig 2.

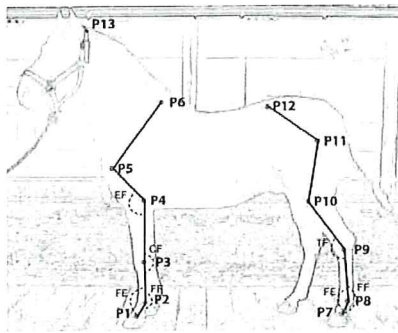


Fig 1. Anatomical landmarks location and angles measured on the horses in motion.

P1: Coronary band front, P2: Fetlock front (Metacarpophalangeal joint), P3: Carpal (Carpometacarpal joint), P4: Elbow (Head of radius), P5: Shoulder, P6: Scapula (Top of the withers), P7: Coronary band hind, P8: Fetlock hind (Metatarsophalangeal joint), P9: Tarsus (Tuber calcanei), P10: Stifle (Tibial tuberosity), P11: Hip joint (Summit of trochanter major), P12: Sacro-iliac joint (Tuber coxae), P13: Head (Wings of atlas bone). Angles measured during locomotion, FF—maximum fetlock flexion during the swing phase, FE—maximum fetlock extension during the stance phase, CF—maximum carpal flexion during the swing phase, EF—maximum elbow flexion during the swing phase, and TF—maximum tarsal flexion during the swing phase.
<https://doi.org/10.1371/journal.pone.0202584.g001>

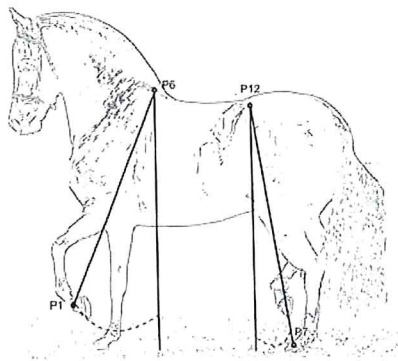


Fig 2. Protraction and retraction limbs angle measurements in a sample of the Colombian paso horse.

P1: Coronary band front; P6: Scapula (Top of the withers), P7: Coronary band hind, P12: Sacro-iliac joint (Tuber coxae). The dashed points show the angles measured when the horses were trotting without a rider. Protraction was the maximum angle between P1-P6 and the vertical plane when the forelimb was extended forward. Retraction was the maximum angle between P7-P12 and the vertical plane when the hind limb was extended backwards.
<https://doi.org/10.1371/journal.pone.0202584.g002>

SNP genotyping

Hair samples from 152 horses of the 187 horses described before (including 15 horses without phenotypic data), were selected from the repository in Fedequinas. To obtain DNA from the hair follicles, a previously reported Chelex–proteinase K protocol was used [11]. SNP genotyping was carried out with the StepOnePlus™ Real-Time PCR System (Life Technologies) using custom designed TaqMan SNP Genotyping Assays (Applied Biosystem) as previously described [9].

Statistical analysis

Selection of the kinematic parameters using asymmetry analysis.

using the function `gltDel` of the package `multcomp` for normally distributed parameters [21]. Dunn's post hoc test was done after the Kruskal-Wallis test using the package `dunn.test`. The homoscedasticity of all parameters was evaluated with the Levene test (`levene.test` function, `lawstat` package [22]).

Multivariate analysis.

A discriminant analysis was performed by using a stepwise selection to obtain a subset of the kinematic parameters that best summarized the differences among the groups. This was done with the function `candisc` of the package `candisc` [23,24], and `ida` function of the `MASS` package [25,26]. The figure of one dimension was obtained with the function `plot.cancor` of the `candisc` package [23,24].

Genetic analyses.

A genetic structure analysis based on 13 autosomal microsatellite markers (AHT4, AHT5, ASB17, ASB2, ASB23, HMS3, HMS6, HMS7, HTG10, HTG4, LEX3, LEX33, VHL20) for 149 of the 187 horses (horses that were genotyped for the *DMRT3* mutation) was performed to evaluate whether the horses were grouped in the same way as in a previous study that analyzed the microsatellite data of the whole registered CPH population [17]. This was done by estimating the number of possible populations in the sample based on Bayesian inference models [27] used by the software `STRUCTURE` 2.3.4. Also, the analysis of molecular variance (AMOVA) was performed to evaluate the genetic differentiation among CPH groups (CPF, CTR, CTRG, and CTG) with the `Arlequin` v3.5 software [28].

A Hardy-Weinberg equilibrium (HWE) test for the *DMRT3* genotypes was performed to estimate exact P-values using the Markov chain method with the `GENEPOP` v.4.3 software [29,30]. The associations between *DMRT3* genotypes and the different CPH groups were evaluated with the Pearson's chi-squared test using the function `VIII1` of the `StatR` package [19]. The associations between *DMRT3* genotypes and the footfall pattern (whether the horses performed a clear gait or not) in the diagonal gaits (trocha and Colombian trot gaits) were evaluated with Fisher's exact test using the function `VIII2` of the `StatR` package [19].

Results

Statistical analysis

Selection of the kinematic parameters using asymmetry analysis.

Sixty-nine out of 172 horses with at least one asymmetric limb were found. The kinematic parameters selected for further statistical analysis, based on our method described (Fig 3), are presented in Table 1. The parameters which presented no differences between symmetric and asymmetric limbs (within the left and right side) were highly correlated between both sides ($r > +0.5$, $P < 0.05$). Therefore, one side was randomly selected for further statistical analysis (Table 1). Also, for the parameters that presented differences between symmetric and asymmetric limbs for one of the sides (left or right), the parameter that presented no differences between symmetric and asymmetric limbs was selected for further statistical analysis (Table 1). The fetlock extension front in Colombian paso fino-CPF males group was the only parameter that presented differences between symmetric and asymmetric limbs for both sides (left and right). Therefore, the measurements of the asymmetric limbs ($n = 5$ for the left side and $n = 2$ for the right side) were removed. After that, both sides were correlated ($r > +0.5$, $P < 0.001$), therefore, one of the sides was randomly selected for further statistical analyses (Table 1).

Parameters which presented no differences for both sides in all the groups.	Parameters which presented significant differences for only one side per group.	Parameters which presented significant differences for both sides per group.
Carpal flexion	Fetlock extension front in CTRG females and CTR males	Fetlock extension front in CPH males
Elbow flexion	Fetlock extension front in CTRG females and males and CTR females	
Fetlock flexion—front	Fetlock extension front in CPH females and CTRG males	
Fetlock flexion—hind	Fetlock front speed in CTRG males	
Hock spread	Fetlock hind speed in CPH males and CTR females	
Protraction	Stride frequency in CTRG males	
Retraction	Stride length—front in CTRG females	
Stride length—hind	Fetlock flexion in CPH males and CTR males	

CPH: Colombian paso fino breed; CTR: CTR males per group; CTRG: CTRG females per group.
 CTRG: Colombian paso fino and gallop group; CTG: Colombian trot and gallop group.
 * P < 0.05.

<https://doi.org/10.1371/journal.pone.0202584.t001>

Table 1. The kinematic parameters selected based on the asymmetry analysis performed in the CPH breed.
<https://doi.org/10.1371/journal.pone.0202584.t001>

Mean and variation of the kinematics traits.

The variation and mean for the kinematic parameters stratified by horse group and sex, are presented in S1 Table. The SD for kinematics parameters was in the range of 0.33–6.07, the largest was found in stride length—hind in CTRG females, and the lowest in protraction—front in CPF males. In general, the variation coefficient for all the parameters was 3.52–33.95. All the parameters, except fetlock front speed (cm/s) and stride length for the front limb (cm) followed a normal distribution.

Correlations.

Table 2 shows the moderate to high ($r > +0.5$) significant ($P < 0.05$) correlations found for the different measurements in the CPH groups. The fetlock flexion for the front and hind limbs as well as the stride length, were the parameters with most correlations with other parameters. The stride frequency had the largest positive correlation with fetlock extension—front (CTR) and a negative correlation with protraction (CTR).

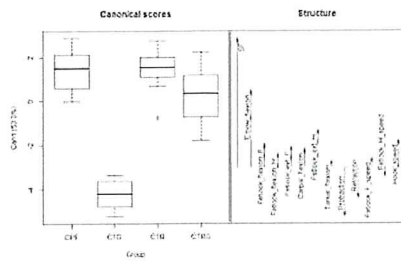


Fig 5. Canonical scores and the parameters that were selected for the first dimension of the discriminant analysis of the Colombian paso horse groups. CPF, Colombian paso fino group; CTR, Colombian trocha group; CTRG, Colombian trocha and gallop group; CTG, Colombian trot and gallop group. F, front; H, hind; ext, extension; SF, stride frequency. <https://doi.org/10.1371/journal.pone.0202584.g005>

In Fig 6 the results of the discriminant analysis are presented per gait instead of horse groups. This analysis resumed 100% of the variance in the two first axes based on the same parameters selected in the horse groups analysis (Fig 3).

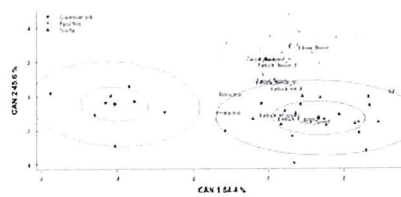


Fig 6. Discriminant analysis between the Colombian paso gaits using kinematic parameters. Each point represents an individual classified per gait. F, front; H, hind; ext, extension; SF, stride frequency. Ellipses show 0.5 (inner) and 0.95 (outer) level of significance for each gait. <https://doi.org/10.1371/journal.pone.0202584.g006>

Genetic analysis

The genetic structure analysis based on microsatellites showed a genetic difference between CPF group and diagonally gaited groups (CTR, CTRG, and CTG groups) (S1 Fig). Also, the AMOVA showed a genetic difference of 5.3% ($P = 0.02$) between CPF group and diagonally gaited groups.

The frequency of the mutant *DMRT3* A-allele in the whole CPH breed was 0.3 but there was a significant difference in the genotype distribution among the 4 horse groups ($P = 2.2 \times 10^{-76}$; Table 4). The mutant A-allele was fixed in the CPF group and the frequency of the mutation in the sample of the diagonally gaited horses (CTR, CTRG, and CTG group) was 0.04. The homozygous AA genotype was not found in the diagonally gaited horses. Also, there was a heterozygote excess ($P < 0.001$) in the diagonally gaited horses (CTR, CTRG, and CTG group). In addition, the number of horses which performed diagonal gaits with different *DMRT3* genotypes that performed a clear or unclear gait footfall pattern is presented in Table 5.

Colombian paso horse group	n	AA	CA	CC	P
Colombian paso fino	62	1.00	0.00	0.00	
Colombian trocha	26	0.00	0.02	0.98	
Colombian trocha and gallop	27	0.00	0.07	0.93	
Colombian trot and gallop	33	0.00	0.15	0.85	
Total	152	0.24	0.05	0.67	2.2×10^{-76}

Table 4. Genotype frequencies of the *DMRT3* mutation in a sample of Colombian paso horses. <https://doi.org/10.1371/journal.pone.0202584.t004>

Diagonal gait	Clear gait		Unclear gait		P
	AA	CA	AA	CA	
Diagonal	0	0	1	0	0.02
Diagonal and gallop	0	0	14	0	0.04

Table 5. Number of diagonally gaited horses with different *DMRT3* genotypes that perform a clear or unclear gait footfall pattern. <https://doi.org/10.1371/journal.pone.0202584.t005>

Discussion

Asymmetry

dissociations, which is the case for the trocha gait. In addition, similar results have been found in Icelandic horses when the speed increases. In that circumstance, the tölt gait tends towards lateral couplets (hind-first), but tölt with diagonal couplets was rarely presented [39]. Therefore, it seems that a gait with diagonal couplets or fore-first pattern (as the trocha gait), is not completely explained as a dissociation from trot or a deviation from a lateral couplet gait as the tölt gait is in Icelandic horses.

Regarding the second hypothesis, additional data provided by Fedequinas was analyzed, consisting of 2919 horses whose parents and grandparents all performed the trocha gait, all of them parentage tested. The registers showed that 94.75% of those 2919 offspring had the ability to perform the trocha gait, supporting the idea that the trocha is an inherited gait. Furthermore, there are other gaits like the foxtrot (Missouri fox trotter) and the marcha batida (Mangalarga marchador) gaits which have been described with the same footfall pattern as the trocha gait. However, in contrast to horses performing the trocha gait, the *DMRT3* mutant A-allele is fixed in horses performing foxtrot (100% vs 1% in horses performing the trocha gait) [15]. On the other hand, the *DMRT3* C-allele is fixed in horses performing the marcha batida gait as well as in horses performing the trocha gait, and a recent study proposed that there are likely other genetic mechanisms that explain the marcha batida gait [40]. This also support the hypothesis that the trocha is an inherited gait, and that there are other genes than *DMRT3*, or other mutations in the *DMRT3* gene, that influences these diagonally stepping gaits in horses.

Conclusions

The gaits within the CPH breed can be classified in different groups, using both kinematic data (stride frequency, fetlock extension and flexion, tarsal flexion, carpal flexion, fetlock front and hock speed measurements, and footfall pattern) and genetic data (microsatellite and *DMRT3* genotype frequencies). This makes it possible to implement genetic improvement programs and to establish kinematic parameters for each gait. Our data supports the hypothesis that the selection has produced kinematic differences between the Colombian paso horse's gaits, particularly between the Colombian trot and the other gaits (the paso fino and trocha gait). Also, the *DMRT3* mutation seems to explain the horses' ability to perform the paso fino gait but not the other diagonal coupled gaits (trocha and Colombian trot). However, there were no microsatellite or *DMRT3* genotype differences between horses performing the trocha and the Colombian trot gait. We propose that trocha is an inherited gait and its ambivalent position could be explained by other genes than the *DMRT3* gene, or other mutations in this gene, that influences this diagonally stepping gait. Therefore, it is very likely that other genetic factors are involved in regulating the trocha and the Colombian trot gaits in CPH horses. Finally, this study may serve as a foundation for implementing a genetic selection program in the Colombian paso horse and future gene discovery studies for locomotion pattern in horses.

Supporting information

S1 Video. Colombian paso fino horse performing paso fino gait.

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<https://doi.org/10.1371/journal.pone.0202584.s001>
(MP4)

S2 Video. Colombian trocha horse performing trocha gait.

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<https://doi.org/10.1371/journal.pone.0202584.s002>
(MP4)

S3 Video. Colombian trot and gallop horse performing Colombian trot gait.

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<https://doi.org/10.1371/journal.pone.0202584.s003>
(MP4)

S4 Video. Colombian trot and gallop horse performing gallop.

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<https://doi.org/10.1371/journal.pone.0202584.s004>
(MP4)

S1 Table. Mean and variation for kinematic parameters by horse group and sex in a sample of Colombian paso horse breed.

<https://doi.org/10.1371/journal.pone.0202584.s005>
(DOCX)

S1 Fig. Genetic structure analysis based on microsatellites of the Colombian paso horse sample.

Inferred ancestry of individuals (Y-axis) per horse (bar columns) in the CPH groups (X-axis). 1) Colombian trot and gallop group. 2) Colombian trocha and gallop group. 3) Colombian trocha group. 4) Colombian paso fino group.
<https://doi.org/10.1371/journal.pone.0202584.s006>
(TIF)

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