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**25,000 years of fluctuating selection on the leopard complex spotting (*LP*)
and congenital stationary night blindness (CSNB) in horses**

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Abstract

The leopard complex spotting is inherited by the incompletely dominant locus, *LP*, which causes congenital stationary night blindness in homozygous horses. We investigated an associated SNP in the *TRPM1* gene in 96 archaeological bones from 31 localities from Late Pleistocene to Medieval Times. The first genetic evidence West and East Europe dates back to the Pleistocene. We tested for temporal changes in the *LP* allele frequency and estimated coefficients of presumed selection by means of Approximate Bayesian Computation analyses. Our results show that the observed changes of frequency are congruent with shifts in artificial selection for the leopard spotted phenotype. In early domestic horses from Kirklareli-Kanligecit (Turkey) dating to 2700-2200 BC, a remarkably high number of leopard spotted horses (6 out of 10 individuals) was detected including one adult homozygote. However, *LP* seems to have disappeared during the late Bronze Age, suggesting selection against this phenotype in early domestic horses. During Iron Age *LP* re-appeared, probably by reintroduction into the domestic gene pool from wild animals. This picture of alternating selective regimes might explain how genetic diversity was maintained in domestic animals despite selection for specific traits at certain times.

Key words: ancient DNA, coat colour, domestication, Palaeolithic cave art, population genetics, *Transient Receptor Potential Cation Channel Subfamily M, Member 1*

Short title: 25,000 years of fluctuating selection in horses

Introduction

Leopard complex spotting has been a popular coat color phenotype of domestic horses already since ancient times (Figure 1). Horses with these phenotypes were most likely highly regarded, as they are depicted carrying royalty and noblemen from Early Medieval Times onward (Morales 2010). Today, leopard complex spotting phenotypes are frequently found in a range of breeds from Asia (Altai Horses, Mongolian Pony), America (Appaloosa, American Miniature Horse, Colorado Ranger Horse, Falabella, Pony of the Americas, Spanish Mustang) and Europe (British Spotted Pony, Knabstrupper, Noriker, Karabaier). Leopard complex spotting (*LP*) is inherited in an autosomal incomplete dominant mode. Despite its popularity, the underlying genetics of this phenotype was, for a long time, unknown. Recently, RNA-Seq data demonstrated that a 1378 bp insertion in intron 1 of the *Transient Receptor Potential Cation Channel Subfamily M, Member 1 (TRPM1)* gene is completely associated with *LP* in horses (Bellone et al. 2013). This insertion, a long terminal repeat (LTR) of an endogenous retrovirus, is located on horse chromosome 1, and several associated SNPs have been identified (Sponenberg et al. 1990; Terry et al. 2004; Bellone et al. 2008; Bellone et al. 2010a; Bellone et al. 2010b).

Homozygosity for *LP* has also been associated with congenital night blindness (CSNB) in Appaloosa and Miniature horses (Sandmeyer et al. 2007; Sandmeyer et al. 2011; Bellone et al. 2013; reviewed in Cieslak et al. 2011 and Reissmann & Ludwig 2013). In a natural environment, individuals affected by CSNB should be susceptible to predation. In an artificial environment, those individuals are known to be nervous, apprehensive, and sometimes difficult to handle in dusky or dark environments. Therefore, it seems likely that homozygotes were selected against in wild populations and potentially also in early domesticated populations, at least during times when practical considerations were more important than phenotypic ones. Interestingly, it was shown that the leopard complex spotted

phenotype was already present in pre-domestic Pleistocene and Holocene populations (Pruvost et al. 2011; Bellone et al. 2013). Here we extend these analyses to early domesticated horses by typing a SNP in the *TRPM1* gene (ECA1:108,249,293 C>T) that has found to be associated with both *LP* and CSNB in Appaloosa horses (Bellone et al. 2010b; Bellone et al. 2013) in 65 early domesticated horses from 19 localities from Siberia, China, Middle and Eastern Europe, and the Iberian Peninsula dating from the Early Bronze Age up to the Iron Age.

Materials and Methods

Samples: Overall, we included 96 horse (*Equus caballus*) bone and tooth specimens from 31 different localities from Siberia, Middle and Eastern Europe, China and from the Iberian Peninsula (Table S1). These samples cover a large time period from the Late Pleistocene to Medieval times and are all dated either by archaeological context or ¹⁴C dates (Table S2). Samples except those from Kirklareli-Kanligecit (n = 10) and Chicha (n = 6) were previously genotyped for 8 coat color loci (Ludwig et al. 2009) (Table 1).

Ancient DNA Extraction and Amplification: Approximately 250 mg of bone material was used for each extraction. External surfaces of bones were removed by abrasion to minimize environmental contaminations. Each sample was ground to powder with a freezer mill and incubated in 0.45 M EDTA (pH 8.0) and 0.25 mg/ml Proteinase K overnight at room temperature under rotation. After centrifugation for 5 min at 4,000 rpm in a Universal 320 centrifuge (Hettich), DNA was purified from the supernatant using a silica based method as previously described (Rohland & Hofreiter 2007a; b).

LP primers were designed based on the associated SNP previously reported (Bellone et al. 2010b; Sandmeyer et al. 2011) and added to our primer set detecting coat color SNPs.

Amplifications were performed in two steps using multiplex PCR combined with a singleplex PCR as previously described (Ludwig et al. 2009; Pruvost et al. 2012). PCR products varied in length between 52 bp and 78 bp (including primers; see Table S3). Four microliters of extract were used for each multiplex PCR. Negative extraction controls and negative PCR controls were used in each PCR. Amplification products were visualized on agarose gels.

Authentication: DNA sampling, extractions and pre-PCR preparations were carried out in laboratories dedicated to ancient DNA following the standard procedures to avoid contamination. Independent replications were carried out in a different laboratory (York) for seven bones positive for the SNP allele associated with *LP*.

Mutation analysis: *LP* locus: We used two different primer pairs to detect the point mutation in the *TRPM1* gene. These primers are designed for the pyrosequencingTM technology sequencing both strands in order to avoid false positive detection of mutation due to post mortem DNA degradation (Cytosine deamination).

Other coat colors gene: As previously described we used a set of eight SNPs in six genes for detecting basic colors (bay, black and chestnut), diluted phenotypes (silver and cream) and spotted or painted phenotypes (overo, tobiano and sabino). Primers are listed in Table S3.

Pyrosequencing: Biotinylated PCR products were prepared at the PyroMark Vacuum Prep Workstation according to the manufacturer's instructions. Amplicons for each SNP were sequenced using pyrosequencingTM technology on a PSQTM 96MA (Biotage). The SNPs were identified using PSQTM 96MA and automatically edited by the PSQTM 96MA SNP software. The results for the color determination are summarized in Table 1 and Table S4.

Allelic dropout: The probability (P) of a false heterozygote individual is calculated after n replicates: $P = K \times (K/2)^{n-1}$ where K is the observed number of allelic dropouts divided by all heterozygous individuals. For all genes we did a minimum of four replications except for

ASIP and *TRPM1* (six replications minimum) which reduced the risk of non-detection of a heterozygote individual to an average of 0.3 % ($P = 0.0078$ for *KIT13*, 0.0015 for *KIT16* and *MATP*, and 0.00012 for *MC1R*).

Estimating the allele frequency of missed alleles: We computed the upper bound of the allele frequency of a coat color allele having been present in the pre-domestication population but not observed in our samples assuming a binomial distribution. Given n samples, the likelihood was calculated that a color allele is not detected which had a frequency of $\leq 5\%$ (Table S5). This was taken into account for the simulation analysis (see below).

Testing temporal changes and selection coefficients estimation: The temporal change in the frequency of the *LP* allele between each consecutive pair of samples was investigated by means of a Bayesian simulation test (Sandoval-Castellanos 2010), in order to determine the periods when the changes observed cannot be attributed to genetic drift and sampling error alone. Considering that selection pressure due to CSNB could be present, this test was also applied with weak negative selection (selection coefficient of -0.01) exclusively on *LP* homozygotes. Afterwards, an Approximate Bayesian Computation (Bertolle et al. 2010) algorithm was employed for obtaining the joint posterior probability distribution of two parameters: (1) a coefficient of selection due to CSNB, which affected the survival of the *LP* homozygotes; and (2) a coefficient of artificial selection that increased/decreased *LP* alleles in the effective population size (as if it affected the reproductive success). Both selection coefficients were simulated from uniform priors (-1.0 to 1.0). The employed summary statistic (SuS) was the Euclidean distance between allele frequencies and rejection was stated whenever the simulated SuS was different from the observed one, so the posterior is exact and no regression adjustments were necessary (as in Beaumont et al. 2002). As Eurasian horse populations have increased since predomestication times (Cieslak et al. 2010) the census population size before the Copper Age was set to 10,000 diploid individuals and after those

times (3,600 BC) an exponential population growth was set, which resulted in a population of 80,000 individuals by the last sample time (Late Iron Age). A variable number of simulations (between 500,000 and 10 million) were run in order to yield at least 10,000 non-rejected iterations per comparison. Additional runs were performed for pilot assays, for optimization of the runs, and to check the robustness of the results to variation of fixed parameters and for exploring alternative scenarios.

The program used was a modification of the software TAFT v2.3 (Sandoval-Castellanos 2010) where initial allele frequencies are simulated from a Dirichlet distribution conditional to the observed frequencies. Considering a Wright-Fisher model, the intermediate generations have multinomial distribution but the sampling and the separating of the effective population from the total population have hypergeometrical distribution which is more appropriate (Pollak 1983).

Results

The samples investigated were genotyped for *LP* (*TRPM1* SNP ECA1:108,249,293 C>T) as well as for eight other coat color SNPs in six genes (*MC1R*, *ASIP*, *SILV*, *MATP*, *EDNRB*, *KIT*) including the basic coat colors (bay, black, chestnut), dilution phenotypes (cream, silver) and white spotting (tobiano, sabino, overo) (Table 1; S6). We were able to type 65 samples for the *TRPM1* SNP and identified the *LP* associated allele in eight individuals. The tobiano and sabino alleles were previously identified in eight and three of these early domestic samples, respectively (Ludwig et al. 2009).

Our results show that the presence of leopard complex spotted horses continues into early domestic times (Figure 2). At the archaeological site of Kirklareli-Kanligecit (Turkish Thrace) dating to the early Bronze Age (2700-2200 BC), six out of ten horses investigated

shared the *LP* associated SNP including one homozygote individual. Compared to pre-domestic horses in Europe, the change in the *LP* frequency (from 0.0556 to 0.350) represents a statistically significant increase ($p = 0.0151$) that becomes even more significant ($p = 0.0019$) if a negative selection coefficient (-0.01) is introduced to account for CSNB, which is linked with the *LP* allele (Sandmeyer et al. 2007). We assume a negative selection coefficient against CSNB in wild animals, because night blindness substantially increases risk of predation. Under these conditions, our estimate of an artificial selection coefficient accounting for the observed increase in *LP* frequency is positive and high (0.3652, 95% C.I. = 0.0 to 0.85). The high positive value for the estimated selection coefficient suggests that the horses from Kirklareli-Kanligeçit were domestic horses. This conclusion is further supported by their archaeological context and the fact that there is no archaeological evidence for wild horses in Turkish-Thrace during the Mid-Holocene (Benecke 2009).

Later during the Bronze Age, *LP* apparently disappeared from the domesticated horses of our sample set. This change is also significant ($p = 0.0081$), while the estimate of the artificial selection coefficient becomes negative (Figure 3; S7-S8). The phenotype reappears in our sample set during the Early Iron Age, with the first evidence originating from a single sample from the fortified settlement of Chicha (1400-1300 BC), one of the most important archaeological sites of the transitional period between the Late Bronze Age and the Early Iron Age in the forest steppe region of western Siberia. We also found evidence for another leopard complex spotted horse from Arjan (800 BC), an Iron Age Scythian grave from the Tuva region, western Siberia (Table 1 and Figure 2). Based on morphological characters of the skeleton, the horse with *LP* from Chicha was likely a wild animal, suggesting that this phenotype could have been reintroduced into the domestic gene pool from a wild population. Although being present in the domestic gene pool during Iron Age, leopard complex spotted horses seem to remain rare during this period with only 2 out of 33 individuals.

Discussion

Here we report that *LP* is not only the most common spotting pattern identified among the 96 ancient samples analyzed so far, it is also the only one which has been found in both pre-domestic and early domestic horses. Considering the archaeological record, the high allele frequency of *LP* and the positive selection coefficient for the *LP* allele found for the horses from Kirklareli-Kanligecit (Turkey), we conclude that these horses belonged to a domestic population. As no wild horse fossils have been found in this region from the time period the fossils date to it is reasonable to assume that these horses were not only domesticated, but probably also imported to this region. Previous studies on the population structure of pre-domestic horses indicated that they existed as a panmictic population ranging from the French Pyrenees to Siberia, with a second isolated (sub-)population inhabiting the Iberian Peninsula since glacial times (Cieslak et al. 2010; Warmuth et al. 2011). Given such population structure, it is not unlikely that leopard spotted horses were also present in Siberia. However, until now, this phenotype has only been found in pre-domestic horses from Western and Eastern Europe and is missing in the last remaining wild horse, the Przewalski horse, which is a possible ancestor of domestic horses (Lau et al. 2009; Lippold et al. 2011). Therefore, it is plausible to assume that the geographical origin of the *LP* allele in the domestic horses from Kirklareli-Kanligecit lies in Europe. After their initial domestication probably around 3,500 BC in the North-Caspian region (Outram et al. 2009), domesticated horses were distributed very rapidly all over Eurasia, offering the possibility of incorporating local genetic diversity of the wild population into the domestic gene pool. It has been previously suggested that the genetic diversity of domestic animal species has been augmented by backcrossing with their wild ancestors (Vilà et al. 2005), and a replacement of the original domestic mtDNA genomes with ones from local wild populations has been demonstrated in early domesticated pigs from

Europe (Larson et al. 2007). Similarly, the high mtDNA diversity found in domestic horses is generally explained by assimilation of local wild mares into the domestic gene pool. Therefore, the *LP* allele in domestic horses probably originated from interbreeding of domestic horses with local wild mares. Our results also add further evidence to a high diversity of coat color phenotypes early during the domestication process.

As we could only analyze horses from a single Early Bronze Age site, we cannot draw a conclusion about the high frequency of the *LP* allele observed at Kirklareli-Kanligecit being a general feature of domestic horses at this time or specific to the breeding practices and population of this specific site. However, the *LP* phenotype seems to be rare or disappear from the gene pool of domestic horses later during the Bronze Age, as we found no evidence for it in later Bronze Age horses. It is possible that at some point farmers became aware of the difficulties of rearing night blind animals, which may have been easy prey for predators and theft as well as difficult to handle in low light conditions, and therefore they selected against them. This argument is supported by two facts: 1) genetic drift alone is unlikely to explain the absence of the *LP* allele during the late Bronze Age ($p = 0.0081$; see supplementary information); and 2) the estimated selection coefficient in addition to negative selection due to CSNB was also strongly negative for this time period (-0.5176 , 95% C.I. = -1.0 to -0.05). Both factors argue for active human-mediated selection against the *LP* phenotype during the later Bronze Age, in the opposite direction of the selection coefficient suggested for the Early Bronze Age. Thus, the phenotypic and breeding preferences of early horse breeders seem to have changed over time, similar to changing preferences of recent animal breeders. For example, there is a documented increase in frequency of the leopard complex phenotype in the breed Noriker during the Baroque Age, which was achieved by cross-breeding with Spanish horses (Nissen 1999). The goal was to breed exotic colored gala horses. In the following centuries the *LP* phenotype went out of fashion and became very rare just like as

other painted phenotypes. Today, breeding efforts have intensified again because there is a growing interest in their restoration.

We cannot exclude that *LP* persisted at a low frequency in the domestic population at the late Bronze Age, although we did not find any evidence. Considering only the Bronze Age samples in our data set the probability that the *LP* allele frequency was lower than 0.15 is 95%, and 99% for a frequency below 0.22. However, the phenotype reappears in our sample set around 1,400 BC in a horse sample from Chicha (West-Siberia). While, based on its skeletal morphology, this horse almost certainly represents a wild horse; a second *LP* positive Iron Age sample originates from a Scythian grave dating to 800 BC clearly representing a domestic animal. Together, these results strongly argue for a successful reintroduction of the leopard complex spotting phenotype into the domestic gene pool from the wild population, further suggesting that cross-breeding between wild and domestic horses took place either accidentally or was a current practice of prehistoric breeders long after the initial domestication.

Although we did not investigate any medieval samples, leopard complex spotted phenotypes become increasingly abundant in texts and iconographies from this time, indicating its increased prestigious value. There are many famous paintings showing noblemen from Early Medieval Times onward on such horses (Morales 2010). Today, *LP* phenotypes are frequently found in many breeds testifying to their ongoing popularity. Thus, *LP* was not only re-introduced into the domestic horse population, but almost certainly selected for again at some point after the Iron Age, suggesting another swing in the selective preferences of horse breeders with regard to phenotype. Our modelling results further support this notion as the major shifts in allele frequency at the *TRPM1* gene over time almost certainly reflect changes in the selective regime (Figure 3), due to a combination of the negative effect of CSNB and fluctuating artificial selection on the color phenotype. Assuming

that this picture of alternating selective regimes holds also true for other loci, in combination with at least occasional cross-breeding of domestic animals with their wild conspecific, it might explain how genetic diversity was maintained in domestic populations despite extensive selection for specific traits during certain time periods.

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Figure 1: Examples of leopard complex horses in human artefacts and culture*.

*Pictures from left to right:

- a) The picture shows the panel of the dappled horses - "Le panneau des Chevaux ponctués", Cabrerets, Lot France (Photo from P. Cabrol ©, Centre de Préhistoire du Pech Merle).
- b) There are several examples of spotted horses in the art of ancient Egypt dating from 1500 - 1300 BC (<http://www.spanishjennet.org/history.shtml>).
- c) The mosaic from North Africa are from the *Dominus Iulius* at Carthage that appears in: Fradier (2001) " Mosaiques Romaines de Tunisie.", Cérés Éditions, Tunis (Fradier 2001).
- d) The Persian plateau passed from conqueror to conqueror until the arrival of the Muslims from the South in 640 AD. Art objects from that time to present show spotted horses in spite of Mohammed's teachings horses persisted in Persian art, leading to the conclusion that spotted horses were common in Persia since before the Muslim conquest (text and picture from (<http://www.spanishjennet.org/history.shtml>))
- e) China 600-900
- f) The mosaic (Spain 975 AD) is taken from the *Beato de Gerona Codex*, dated from 975 and attributed to the *Abad Domenicus* which appears in Williams (1993) "The Art of Medieval Spain - AD 500-1200.", Harry N. Abrams Inc., New York (Williams 1993).
- g) This painting from John Wootton titled "Lady Conaway's Spanish Jennet" is owned by the Marquess of Hertford.

Figure 2: Distribution of leopard spotted horses over time and region. The X-axis shows the number of individuals, the Y-axis summarizes temporal and geographical origin, with the oldest samples at the bottom and the youngest at the top.

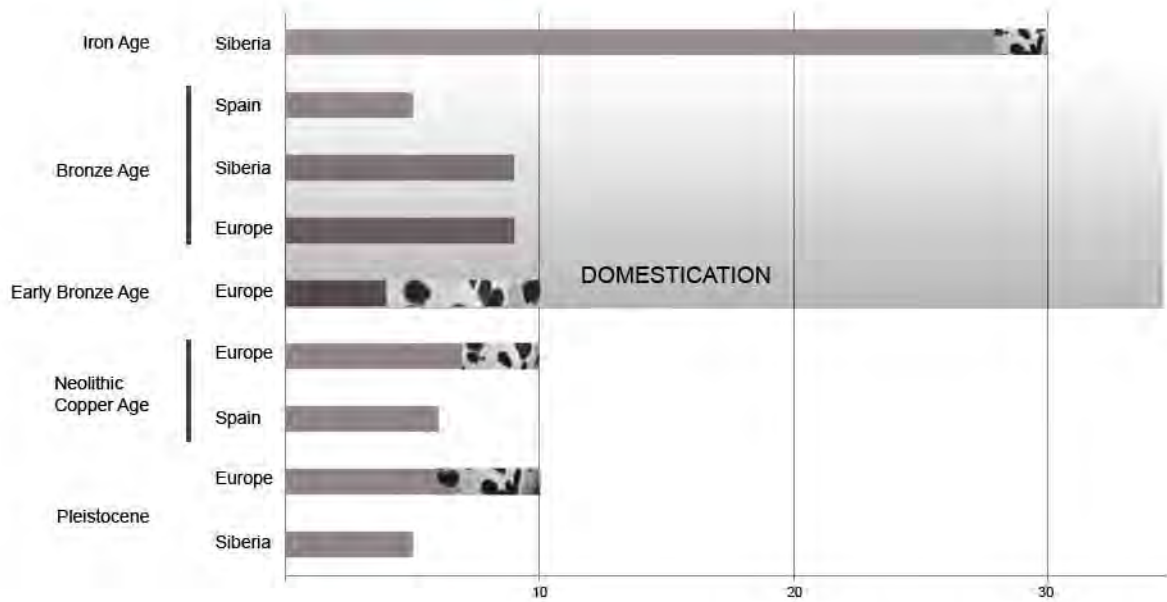


Figure 3: Changes in the allele frequency of *LP* (upper graph, scale at right) and estimated selection coefficients (*s*) obtained by simulations (bottom graph left scale) for the overall sampling (left) and for Eastern European samples (right). The blue line indicate changes in the artificial selection estimate, red line the changes in the selection caused by CSNB, and the black line the changes in the frequency of the *LP* allele. The vertical lines in blue or red indicate the 95% probability credible interval for the selection coefficients estimations. The numbers over the black line indicate significance of the changes in the allele frequency of *LP*.

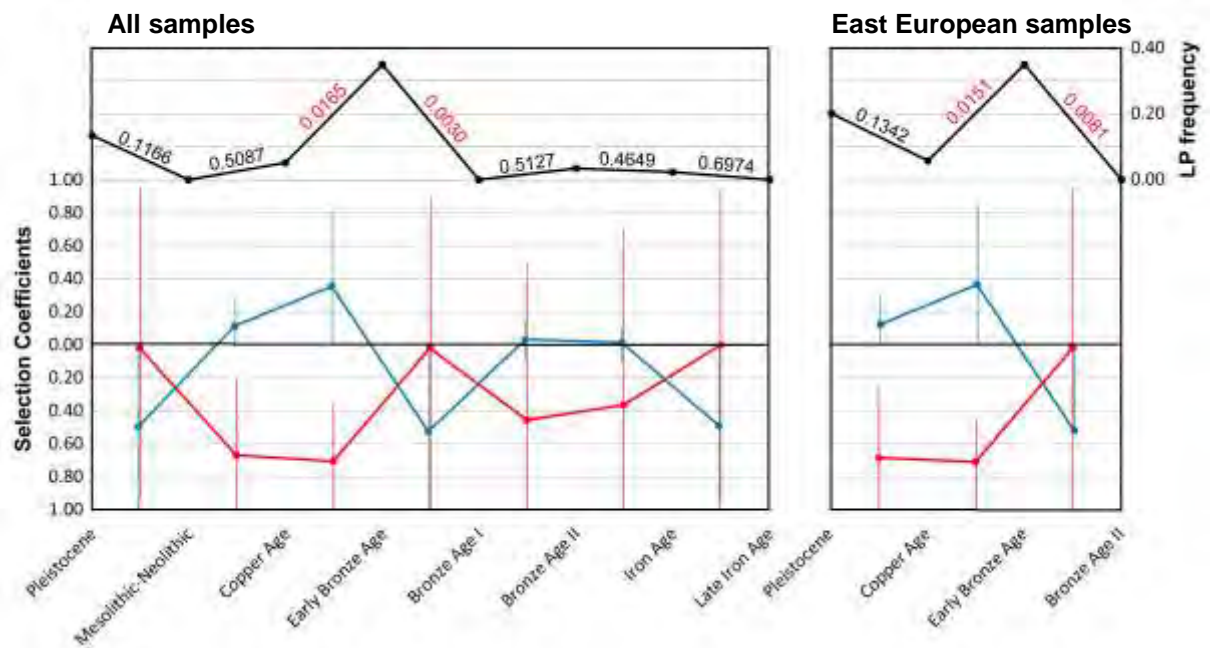


Table 1: Genotyping results for 9 coat color loci for the ancient samples investigated.

Phenotype is proposed based on the genotype at each of the 9 loci tested including basic coat color (bay, black, or chestnut), dilution (cream or silver), and spotting pattern (leopard complex, tobiano, sabino, or overo). Grey shading indicates that at least one allele differs from the proposed wild type. A horse that had more than one one spotting phenotype was not identified. In addition, we detected also no variation at the *EDNRB* locus (overo). Grouping as used for the statistic modeling is also shown.

Genetic and simulation analysis samples																									
Total	Siberia	Europe	Spain	Color		Spotting	Dilution	ASIP	EDNRB	KIT13	KIT16	MATP	MC1R	SILV9	SILV11	TRPM1									
Ple	Ple			Pleistocene	Siberia	SP1181A	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp							
						SP1181B	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp							
						SP1181C	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp							
						SP1181E	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp							
						SP1181F	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp							
	Ple					Europe	PET6	Bay	Leopard Complex	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	LP/lp						
							PET5	Bay	Leopard Complex	No	A/a	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	LP/lp						
							PET3	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
							PET2	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
							PET1	Bay	Leopard Complex	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	LP/lp						
							KG5	Bay	Leopard Complex	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	LP/lp						
							KG4	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
							KG3	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
							KG2	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
							KG1	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
							MNe				Mesolithic-Neolithic	Spain	44	Bay	No	No	A/a	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp
													3	Black	No	No	a/a	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp
													31	Bay	No	No	A/a	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp
													32	Black	No	No	a/a	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp
34	Black	No	No	a/a	ov/ov	KMO/KMO							sb1/sb1	C/C	E/E	z/z	z/z	lp/lp							
37	Bay	No	No	A/a	ov/ov	KMO/KMO							sb1/sb1	C/C	E/E	z/z	z/z	lp/lp							

BAII	BAII	BAII	BAII	Iron Age	Siberia	Mic1	Bay	Tobiano	No	A/a	ov/ov	KM1/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp					
						Mic2	Chestnut	No	No	A/a	ov/ov	KM0/KM0	sb1/sb1	C/C	e/e	z/z	z/z	lp/lp					
						Mic3	Black	No	No	a/a	ov/ov	KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp					
						Mic4	Bay	No	No	A/a	ov/ov	KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp					
						Mic5	Bay	Sabino	No	A/a	ov/ov	KM0/KM0	SB1/sb1	C/C	E/e	z/z	z/z	lp/lp					
						Gar2	Black	No	No	a/a	ov/ov	KM0/KM0	sb1/sb1	C/C	E/e	z/z	z/z	lp/lp					
						Gar3	Bay	No	No	A/a	ov/ov	KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp					
						CoA																	
						BAI	BAI	BAI	BAI	Siberia	BER1	Chestnut	No	No	A/A	ov/ov	KM0/KM0	sb1/sb1	C/C	e/e	z/z	z/z	lp/lp
											TAR1	Bay	No	No	A/a	ov/ov	KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp
											TAR2	Chestnut	No	No	a/a	ov/ov	KM0/KM0	sb1/sb1	C/C	e/e	z/z	z/z	lp/lp
TAR4	Bay	No	No	A/A	ov/ov						KM0/KM0	sb1/sb1		E/E	z/z	z/z	lp/lp						
TAR5	Bay	Sabino	No	A/A	ov/ov						KM0/KM0	SB1/sb1	C/C	E/e	z/z	z/z	lp/lp						
TAR7	Black	No	No	a/a	ov/ov						KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
TAR8	Bay	No	No	A/a	ov/ov						KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
TAR10	Black	No	No	a/a	ov/ov						KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
BAII	BAII	BAII	BAII	Spain	39	Bay	No	No	A/a	ov/ov	KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
					40	Bay	No	No	A/a	ov/ov	KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
					22	Black	No	No	a/a	ov/ov	KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
					24	Bay	No	No	A/a	ov/ov	KM0/KM0	sb1/sb1	C/C	E/e	z/z	z/z	lp/lp						
					25	Black	No	No	a/a	ov/ov	KM0/KM0	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp						
Iron Age	Siberia	CIC1	Bay	No	No	A/A	ov/ov	KM0/KM0	sb1/sb1		E/E	z/z	z/z	lp/lp									
		CIC2	Bay	Leopard Complex	No	A/A	ov/ov	KM0/KM0	sb1/sb1		E/E	z/z	z/z	LP/lp									

						ARZ14	Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/e	z/z	z/z	lp/lp
					China	Fen1	Bay	Tobiano	No	A/A	ov/ov	KM1/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp
				Fen2		Bay	No	No	A/a	ov/ov	KMO/KMO	sb1/sb1	C/C	E/e	z/z	z/z	lp/lp	
				Fen3		Bay	No	No	A/a	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp	
				Fen4		Bay	No	No	A/A	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z	lp/lp	
LIA						Spain	4	Black	No	No	a/a	ov/ov	KMO/KMO	sb1/sb1	C/C	E/E	z/z	z/z
				Med.	Spain	29	Chestnut	No	No	a/a	ov/ov	KMO/KMO	sb1/sb1	C/C	e/e	z/z	z/z	lp/lp