

Inbreeding and its effects on racing performance in Thoroughbred horses: A review of global evidence with insights from the Hungarian population

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Abstract: The Thoroughbred horse represents one of the most intensively selected domestic animal populations, developed through centuries of breeding focused on maximising racing performance. Originating from a limited number of founder animals and maintained as a closed studbook population since the late eighteenth century, the breed has experienced progressive increases in relatedness and inbreeding. This review examines the development of pedigree structure in Thoroughbred horses and evaluates the potential consequences of inbreeding for racing performance, with particular emphasis on studies assessing performance through race earnings and related indicators. Historical and genetic evidence describing the narrow genetic base of the breed and the subsequent formation of influential sire lines are summarised to provide context for understanding current levels of genetic diversity. The genetic principles underlying inbreeding and inbreeding depression are discussed, including the increase in homozygosity and the potential expression of deleterious recessive alleles affecting fitness and athletic ability. The review then synthesises findings from international studies, while focusing on research conducted in Hungary, that investigate the relationship between pedigree-based inbreeding coefficients and racing performance traits. Empirical results from the literature show varying degrees of association between inbreeding and earnings-based performance measures, with several studies reporting negative relationships consistent with inbreeding depression. Differences among populations, analytical methods, and performance indicators are also taken into account. Overall, the reviewed evidence underscores the importance of monitoring inbreeding levels and maintaining genetic diversity in Thoroughbred breeding programmes to sustain both racing performance and long-term population health.

Keywords: earnings; fitness; performance traits; recessive deleterious alleles; race

INTRODUCTION

Thoroughbred horses are primarily distinguished by their racing ability and speed. This feature not only makes them known as the most common breed for racing, but it has also brought much more

to humans. Consequently, breeding objectives in Thoroughbreds have focused primarily on racing performance rather than production traits such as reproductive output or growth rate. The focus is on optimal breeding strategies to produce elite racehorses with successful racing careers (Bailey

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et al. 2022). The introduction of Thoroughbred horses to Hungary dates back to the 1780s, when imports from England began, and organised Thoroughbred racing was established shortly thereafter (Bokor et al. 2013).

The origins of the Thoroughbred breed have long been debated, particularly regarding the number of horses that contributed to its foundation. Despite this uncertainty, it is widely accepted that the breed descended from a relatively limited number of founders. Historical documentation identifies many of these founders, which include Oriental horses along with those native to the British Isles horses (Willett 1970; Binns and Morris 2010). This selective breeding led to animals with high stamina and athletic ability, which are used to breed other horse populations as well (Petersen et al. 2013a). These facts have made the population of Thoroughbred horses one of the largest and, at the same time, closed populations (Todd et al. 2018). The small number of sire founders plus the human interference for athletic traits selection (Gu et al. 2009; Petersen et al. 2013a; McGivney et al. 2020) have shaped an inbred population with lower genetic diversity relative to other horse breeds (Cunningham et al. 2001; Petersen et al. 2013b; Metzger et al. 2015).

Inbreeding, which is a common phenomenon in closed and managed populations, can be considered as mating between related individuals. Wright (1922) formalised the inbreeding coefficient as the probability that the two alleles at a locus in an individual are identical by descent (IBD). As a result, homozygosity will be increased and will be followed by a rise in the expression of recessive deleterious alleles, producing reductions in mean performance or fitness that are termed “inbreeding depression” (Allendorf et al. 2022). This matter can cause economic issues for the Thoroughbred industry, but also many welfare concerns for the animals themselves.

PEDIGREE STRUCTURE IN THOROUGHBRED HORSES

Historical formation and genetic bottlenecks of the Thoroughbred

The origins of the Thoroughbred breed trace back to a narrow genetic base, though the exact number of founding horses remains disputed among

scholars (Willett 1975; Wright 1989; Evans et al. 1990; Cunningham et al. 2001). Despite this debate, consensus holds that only a limited group of horses laid the genetic foundation of today's Thoroughbred. Historical accounts consistently point to two major sources: about 200 imported Oriental horses, acquired through warfare, royal gifts, trade and illegal routes – principally Arabians, Turks, and Barbs from the Middle East and North Africa – and native British mares, including Galloway mares of diverse origins (Willett 1970; Binns and Morris 2010; Huggins 2019). In one of the most comprehensive analyses, Cunningham et al. (2001) examined the pedigrees of 200 British Thoroughbreds born between 1770 and 1990 to reconstruct the breed's genetic origins. Their study revealed that just 158 horses, born between 1665 and 1860, accounted for 81% of the genetic contribution to modern Thoroughbreds.

Building on the evidence of a narrow genetic foundation, molecular research has clarified the precise origins of the Thoroughbred's paternal and maternal lineages. Examination of male sex chromosomes proved that the dominant Y-chromosome haplotype was shared by nearly all modern Thoroughbreds, which originated from the Oriental horses introduced to Europe roughly 700 years ago (Wallner et al. 2017; Felkel et al. 2019). This genetic continuity aligns with historical breeding patterns: more than 95% of contemporary Thoroughbred stallions trace their paternal line directly to Eclipse, the great-great-grandson of the Darley Arabian (Cunningham et al. 2001). These findings confirm that the extensive importation and use of Oriental stallions between the 16th and 18th centuries were not isolated events but part of a sustained infusion of Eastern genetic material into the developing Thoroughbred population.

Complementary research on the maternal side paints a different picture. Bower et al. (2011) analysed mitochondrial DNA – passed down exclusively through mares – and found that modern Thoroughbred mares carry distinct mitochondrial genotypes not observed in Arabian horses. This indicates that native British and European mares, such as Irish Hobby horses and Galloways, made substantial contributions to the maternal foundation of the breed. Taken together, these genetic and historical insights show that the Thoroughbred was not derived exclusively from Arabian horses, but a hybrid born of crosses between Oriental stallions

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and British mares, refined over centuries through selection for speed, endurance, and power (Petersen et al. 2013a; Huggins 2019).

The establishment of the first General Stud Book in 1792 – recording 237 mares and 169 stallions – marked the formal beginning of the Thoroughbred as a closed breed. When the stud book was officially closed in 1793, registration was restricted to horses listed in that original document and their direct descendants, creating the Thoroughbred genetic pool. From that point onward, the Thoroughbred was developed under a rigorous and highly controlled breeding regime, with a singular goal: the enhancement of racing performance through selective breeding (Feher 1990).

Thoroughbreds began to arrive in Hungary from England in the 1780s, and their first race was held in 1814. After the expansion of the importation during the 1820s, Hungary's first official racetrack was inaugurated in 1827 (Bokor et al. 2013). The Hungarian Thoroughbred Stud Book was first published in 1823 (Feher 1990), formalising Hungary's participation in the international Thoroughbred registry system. Imported horses were accepted into the Hungarian registry under regulations approved by the International Stud Book Committee (2024), which require the possession of an official racehorse identity card and a certified pedigree issued by an accredited Stud Book Authority in their country of origin. The entrance criteria for the Hungarian Stud Book remained aligned with the International Federation of Horseracing Authorities (2024), ensuring that the Hungarian Thoroughbred population is recognised as a subpopulation within the broader English-Irish Thoroughbred lineage.

Pedigree-based parameters

Pedigree completeness and data depth. Complete and deep pedigree records improve the reliability of pedigree-based genetic estimates because fewer ancestors are unknown. Measures of inbreeding stand or fall on two pillars: how many generations are traced, and how few of those ancestors are unknown (Klein et al. 2022). Pedigree completeness reflects the amount of ancestral information available for each individual, expressed as the average number of generation equivalents known.

Bokor et al. (2013) analysed pedigree records from 3 043 Hungarian Thoroughbred horses – 1 559 stallions and geldings, plus 1 484 mares – that partici-

pated in gallop racing between 1998 and 2010, with 43 generations. On average, the pedigrees in the reference population were 92.79% complete for the first 15 generations, and 36.38% complete overall. The mean number of complete generations was 6.69 (ranging from 0 to 14), while the maximum number of generations traced averaged 28.96 (ranging from 0 to 43).

The Hungarian Thoroughbred reference population overall possesses remarkably deep and detailed pedigrees, similar to those reported for Lipizzan horses, with 32 generations and 15.20 complete generations. This reference showed 90% completeness until the first 10 generations, and then decreased (Zechner et al. 2002). Also, recently, 35 generations were traced in Lipizzan horses from the Lipica Stud Farm, with 100% pedigree completeness up to the seventh generation (Ferme et al. 2026). These results are consistent with those of Pavlik et al. (2014), with 100% completeness in Thoroughbreds for the first five generations, and then subsequently reduced. Moureaux et al. (1996) reported greater pedigree completeness in French Thoroughbreds than in the other breeds examined. The French Thoroughbreds' pedigrees were almost 100% complete in the first four generations and then remained 50% complete by the eighth generation.

Although extensive pedigree information is also available for Lipizzan horses, several other breeds have shown lower pedigree completeness than Thoroughbreds. For instance, French Trotter and French Saddle horses were more than 80% complete during the first five generations and only more than 50% for the first eight generations (Moureaux et al. 1996). In addition, a study of 1 374 Norik of Muran horses showed the highest pedigree completeness only in the first five generations, with almost no known pedigree after the 10th generation, and the maximum number of generations traced was only about 12.67 (Kasarda et al. 2019). These findings suggest that the long-established Thoroughbred studbook and breed structure allow more comprehensive pedigree analyses than what is possible in some other horse breeds.

Generation interval and its paths. The term generation interval is explained as the average age of parents when their progeny was born, and this offspring has been used for breeding, or in other words, the average time interval between a horse's birth and the birth of its replacing progeny (Bowling

1996). This value is dependent on two ages. First, the average age at the first mating and that of the animals' culling (Langlois and Maheut 1976).

This parameter was also measured by Bokor et al. (2013) through four different paths of sire-son, sire-daughter, dam-son, and dam-daughter. The average in general was measured as 11.41 years, and to compare both sexes, the paternal pathways showed generation intervals approximately 1.5 years longer than the maternal pathways, in contrast to the findings of Watanabe (1981) for the Thoroughbred population in Japan, with mares showing longer generation intervals than sires.

Among equine breeds, reported generation intervals vary considerably (Moureaux et al. 1996). In the case of Thoroughbreds, depending on the population studied, approximately 10.50 and 10.60 years were measured (Langlois and Maheut 1976; Moureaux et al. 1996). Therefore, in comparison, Bokor et al. (2013) demonstrated a longer generation interval. This might be due to keeping successful horses in racing longer and then breeding them, as mating for Thoroughbreds starts after they have completed their racing careers (Thiruvankadan et al. 2009). Also, the better pedigree completeness of the Hungarian population has given more reliable parameters.

INBREEDING

The genetic and theoretical basis of inbreeding

Inbreeding is a central concept in population and quantitative genetics and is relevant both as a population parameter and as a factor influencing the estimation and interpretation of genetic traits, as seen in the study of Oki et al. (2005), intended to assist in measuring the heritability of the tying-up syndrome in Thoroughbreds. Wright (1922) introduced the coefficient of inbreeding (F) to quantify the probability that an individual's two alleles at a locus are identical by descent from a common ancestor, resulting from matings between related individuals. This coefficient remains the theoretical foundation of inbreeding studies, linking pedigree structure with expected homozygosity in the genome. Increases in F elevate homozygosity, thereby increasing the probability of deleterious recessive alleles becoming expressed, resulting in reduced mean fitness or performance, a phenomenon known as inbreeding depression.

Extensions of Wright's coefficient have been developed to capture additional theoretical aspects of inbreeding. Ballou (1997) introduced the concept of ancestral inbreeding (F_{BAL}), which measures the proportion of an individual's genome that has already undergone inbreeding in previous generations. This refinement provides insight into whether deleterious alleles may have been purged by selection, since repeated exposure of alleles to homozygosity can allow natural or artificial selection to recognise and eliminate their negative effects. Kalinowski et al. (2000) further decomposed inbreeding into "new" inbreeding, which reflects recent autozygosity from unique ancestor paths, and "ancestral" inbreeding, which represents genome regions identical by descent from more distant ancestors. Their framework suggested that the effects of inbreeding depression could differ between new and ancestral components, with ancestral inbreeding potentially exerting weaker negative impacts if purging had already acted on harmful alleles. These theoretical distinctions are especially relevant in populations with long breeding histories, such as Thoroughbred horses, where multiple generations of selection and limited founder diversity contribute to complex patterns of homozygosity (Bokor et al. 2013).

In the study of Bokor et al. (2013), the inbreeding coefficient was estimated as 9.58%, which is lower than that of the English-Irish Thoroughbred population (Mahon and Cunningham 1982; Cunningham et al. 2001) and Lipizzan horses (Zechner et al. 2002), but considerably higher than that of the French Thoroughbred population (Moureaux et al. 1996) and Czech native endangered horses and draught horses, including Noriker horses (Vostra-Vydrova et al. 2018; Vostry et al. 2018). It would appear that the Hungarian and the English-Irish Thoroughbreds along with the Lipizzan horses exhibit the inbreeding coefficient among the highest reported values (Table 1), however, these comparisons should be interpreted in relation to pedigree depth and completeness, as more complete pedigrees allow more distant common ancestors to be identified and may therefore result in higher estimates of pedigree-based inbreeding.

Genomic characterisation of inbreeding

Runs of homozygosity (ROH) are continuous stretches of homozygous regions in the genome that can be used to identify chromosomal segments

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Table 1. Inbreeding coefficient (F) of Hungarian, English-Irish, French, Slovak and Iranian Thoroughbreds, Lipizzaners, and Czech horses

Horse population	F (%)	Reference
Hungarian Thoroughbreds	9.58	Bokor et al. (2013)
English-Irish Thoroughbreds	14.00	Cunningham et al. (2001)
English-Irish Thoroughbred broodmares	12.50	Mahon and Cunningham (1982)
French Thoroughbreds	1.02	Moureaux et al. (1996)
Slovak Thoroughbreds	0.86	Pavlik et al. (2014)
Iranian Thoroughbreds	0.30	Taned et al. (2025)
Lipizzan horses	10.80	Zechner et al. (2002)
Lipizzan horses (Lipica Stud Farm)	11.55	Ferme et al. (2026)
Czech native draught horses	4.65	Vostra-Vydrova et al. (2018)
Czech native horses	7.06	Vostry et al. (2018)

which are likely to be identical by descent (IBD). The proportion of the autosomal genome contained within ROH can be used to estimate genomic inbreeding (F_{ROH}). ROH patterns reflect the effects of recombination across generations, as chromosomal segments inherited from common ancestors are progressively broken down over time (Allendorf et al. 2022). Therefore, ROH can provide an additional genomic measure of inbreeding, complementary to the pedigree-based inbreeding coefficient. Recent whole-genome sequencing (WGS) studies in Thoroughbreds have provided further evidence about the level and development of genomic inbreeding in this population.

Bailey et al. (2024) analysed WGS data from 185 North American Thoroughbreds born between 1965 and 2020 and estimated the genomic inbreeding coefficient (F_{ROH}) from ROH. They found that the horses born between 2000 and 2020 had a significantly higher F_{ROH} (0.28) than the horses born between 1965 and 1986 (0.27). The WGS-based F_{ROH} was also only moderately correlated with pedigree-based inbreeding calculated from five generations, indicating that genomic data can provide additional information about the realised homozygosity of individual horses that may not be fully represented by pedigree records (Bailey et al. 2024). This difference is important for Thoroughbreds because their closed stud-book and repeated use of a limited number of successful ancestors can lead to the accumulation of autozygosity that is not completely described by conventional pedigree calculations. More recently, Asadollahpour Nanaei et al. (2026) investigated the demographic and genomic history of Thoroughbreds using a time-

stamped panel of WGS data, including horses from the early twentieth century to the present. Their results showed a significant increase in genomic inbreeding over recent decades, with the increase particularly related to long and very-long ROH. These results are in agreement with the findings of Bailey et al. (2024) and provide further evidence that the increase in genomic inbreeding in Thoroughbreds is associated with changes in breeding practices and the continued use of genetically influential animals.

As longer ROH, unlike short ones, stem from more recent common ancestors, there has been less time for meiotic recombination across generations. This introduces a greater chance of recessive deleterious alleles being expressed in the current reference population (Sumreddee et al. 2021). A recombination rate of 1.16 centimorgans per megabase (cM/Mb) was used for North American Thoroughbreds. Using this recombination rate, ROH of approximately 8, 4 and 2 Mb were estimated to reflect common ancestry approximately 5.4, 10.7 and 21.5 generations ago, respectively (Bailey et al. 2024). To investigate pregnancy loss in Thoroughbreds in the United Kingdom, Lawson et al. (2024) compared ROH patterns among pregnancy-loss groups and reported a greater number and longer total length of ROH in mares associated with mid- and late-gestation loss than in the early-gestation group. These findings suggest a stronger contribution of recent rather than ancestral inbreeding to these pregnancy-loss outcomes.

Hill et al. (2022) suggested that shorter ROH, which generally reflect more distant common ancestry, may have weaker negative effects than longer ROH. Moreover, they referred to a study

on Australian Thoroughbreds agreeing with the same statement by suggesting that the ancestral history coefficient of inbreeding has shown even positive effects on athletic and performance traits of horses (Todd et al. 2018). On the other hand, longer ROH from the more recent ancestors causes more depression, possibly because they contain a higher proportion of rare, deleterious alleles, which accumulate over generations (Hill et al. 2022). In summary, longer ROH may be more detrimental because they can contain rare deleterious alleles, and also because they have not gone through much recombination during meiosis.

Recently, a study of 233 Lipizzan horses from the Lipica Stud Farm reported a mean F_{ROH} of 0.16. The authors also identified ROH islands containing candidate genes previously associated with several biological functions and traits in horses, including reproduction, pigmentation, muscle function and locomotion. However, these associations were based mainly on previously reported functions of the candidate genes rather than direct measurements of these traits in the studied Lipizzan horses, and the authors emphasised that further studies are required to confirm the functional implications of these ROH regions (Ferme et al. 2026). In a similar study, the genomic inbreeding coefficients (based on ROH) of the Lipizzan populations of the Central European countries (Bosnia and Herzegovina, Slovenia, Croatia, Hungary, Slovakia and Czech Republic) lower values were reported, varying between 0.11 and 0.14 (Vostra-Vydrova et al. 2026).

Australian horses demonstrated 80% of their inbreeding due to a small number of ancestors, which can impact animals' fitness considerably. The reason for the negative relationship between inbreeding and performance is assumed to be due to the challenging recognition of those partially deleterious alleles that do not have lethal or other strong detrimental effects on the population (Todd et al. 2018). These alleles can arise from different factors, including the domestication of horses and the foundation of the Thoroughbred (Cunningham et al. 2001; Corbin et al. 2010; Schubert et al. 2014), or simply from inbreeding resulting from selective matings (Todd et al. 2018).

Effective population size

The effective population size (N_e) is a theoretical construction used to compare real populations

to an ideal model. The measured value of N_e is reflective of the pedigree quality, and lower values do not necessarily correspond with a more diverse population. The benchmark model is the Wright-Fisher population, a simplified, hypothetical group where only genetic drift shapes allele frequencies, and all genetic changes depend only on individuals within the population. The effective population size of a real population is the size that the Wright-Fisher model would need to have in order to produce the same rate of inbreeding and the same level of random fluctuation in allele variation that we actually observe in the real group being studied (Crow and Kimura 2017).

The inbreeding-based effective population size for three traditional Hungarian breeds with an open stud-book was measured in a range of 100–165 (Klein et al. 2022), and it was estimated not lower than 100 for Hungarian Thoroughbreds during the last 30 generations (Bokor et al. 2013).

Bazvand et al. (2024) measured the effective population size of Caspian, Kurdish, Arabian, Turkmen, Akhal-Teke, and Fell pony breeds in Iran as low as 54, 49, 37, 35, 27, and 26, respectively, with a declining trend in general for all these breeds. Consistent with this declining trend, a recent whole-genome sequencing (WGS)-based study by Asadollahpour Nanaei et al. (2026) highlights a marked historical decline in effective population size in Thoroughbreds, particularly during the mid-twentieth century, providing a genomic demographic context for the subsequent accumulation of autozygosity.

Inbreeding parameters

Rate of inbreeding. The rate of inbreeding describes the change in the inbreeding coefficient between generations or over a defined period; it was mostly increasing among the available studies; however, its speed is highly correlated with the pedigree completeness of the studied reference population. The inbreeding coefficient increased gradually over 3 decades (from ~0.68% to ~0.90%), with declining heterozygosity in Russian Thoroughbreds (Kalashnikov et al. 2020), aligned with the findings about the increase of this factor for Japanese Thoroughbreds (Watanabe et al. 2024), Hungarian Thoroughbreds (Bokor et al. 2013), and Binns et al. (2012) findings for Thoroughbreds. Remarkably, in Britain and Ireland, the rate of inbreeding accumulation was estimated as 0.58%

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for Thoroughbred broodmares and 0.17% for the Thoroughbreds in Slovakia (Mahon and Cunningham 1982; Pavlik et al. 2014), which show much slower trends than the above. Norik of Muran horses showed an inbreeding level of 0.23%, pedigree-wise and 0.11%, genomic-wise, suggesting a low intensity of inbreeding level, however the overall concerns regarding the rising trend of this parameter remain (Kasarda et al. 2019).

Apart from the pedigree-based analysis, WGS research in North American Thoroughbreds and the Thoroughbreds sampled across the 20th century support this general increasing trend in the rate of inbreeding (Bailey et al. 2024; Asadollahpour Nanaei et al. 2026).

Average relatedness. Average relatedness (AR) reflects how well an individual or group represents the genetic composition of the population by measuring the possibility that a randomly chosen allele from the population comes from a specific individual or group. Under random mating (panmixia), average relatedness serves as a suitable indicator of inbreeding. Therefore, comparing average relatedness with average inbreeding can reveal deviations from random mating and highlight the population's non-random mating structure (Goyache et al. 2003).

The average relatedness was estimated as 19.19% for the reference population of Hungarian Thoroughbreds (Bokor et al. 2013), which is higher than that of Slovak Thoroughbreds with AR at 0.91% (Pavlik et al. 2014), indicating a comparatively high level of relatedness within the Hungarian Thoroughbred population.

Inbreeding depression in theory

Rise in inbreeding affects genome-wide homozygosity and thereby increases the probability that deleterious recessive alleles are expressed, producing reductions in mean performance or fitness, as well as other issues such as pregnancy loss, which are termed “inbreeding depression” (Allendorf et al. 2022; Lawson et al. 2024). Inbreeding can contribute to mutational load (recessive deleterious mutations) as a significant part of the genetic load. Genetic load is an indicator of undesired genetic material, causing lower fitness in the population (Hedrick and Garcia-Dorado 2016). Therefore, inbreeding depression is a result of the increase in the genetic load, followed by the increase in mutational load. Epistatic interactions and reductions in fa-

vourable heterozygosity can also lead to inbreeding depression (Charlesworth and Willis 2009; Leroy 2014).

In horse populations, inbreeding has long been a concern due to closed studbooks and the intense use of a limited number of elite sires. Thoroughbreds represent an especially clear example as the studbook has been closed since the 18th century, and breeding practices have repeatedly favoured a narrow set of successful sire lines, leading to an increase in mean relatedness and a steady accumulation of inbreeding. Pedigree analyses of Thoroughbreds in Hungary confirmed these global patterns, reporting moderate but increasing levels of inbreeding, a small effective population size, and concentration of genetic contributions from a limited set of founders (Bokor et al. 2013). The consequences of inbreeding for performance traits in horses are theoretically predicted to mirror those in other domestic and wild species, where higher levels of inbreeding are associated with reduced survival, growth, or competitive ability (Allendorf et al. 2022). In mammals broadly, empirical studies confirm that inbreeding depression manifests across a wide range of fitness-related traits, although the magnitude can vary depending on trait type and population history (Ballou 1997).

RACING PERFORMANCE IN THOROUGHBRED HORSES

Racing performance is a complex trait that can be evaluated using several indicators. Different traits, such as variations of time, handicap, or similar performance ratings, the distance between the first-place winner and other horses, standard start index (SSI), and earnings, can all be considered (Watanabe 1974; Thiruvankadan et al. 2009). As well, ranking presents another option, making the measurements more precise for comparison of all the horses in each race, by considering the different environmental factors (da Gama et al. 2016).

During some studies (Gaffney and Cunningham 1988; Gardner 2006; Velie et al. 2015b), scientists estimated the inbreeding and training performance of Thoroughbreds by comparing the prominent race-time records. Following these measurements, values showed negligible improvement during re-

cent decades in Europe, pinpointing the shortcomings of relying on this trait only, while earnings have shown more solid results. However, there are mixed results for each trait, providing promising values within a specific study in support of its own purpose.

Bakhtiari and Kashan (2009) found that time and normalised ranking values were good indicators of heritability, genetic correlation, and repeatability in their case of Thoroughbred horses in Iran. Also, Iranian Thoroughbreds showed moderate heritabilities in race completion time and average speed of 0.25 and 0.23 (Taned et al. 2025). As well, Australian Thoroughbreds showed high heritability of around 0.61 for best race distance, alongside the log of cumulative earnings and the log of earnings per race start with heritabilities of 0.19 and 0.23, respectively (Velie et al. 2015a).

Earnings as a trait and its heritability

Several earnings-based measures, including cumulative earnings, log-transformed cumulative earnings, earnings per start and log-transformed earnings per start, have been used as indicators of racing performance (Bailey et al. 2022). Specifically, earnings are not normally distributed; prize money is typically restricted to the top five finishers and decreases sharply from first place downwards (Estes and Baumohl 1960a,b). Although this factor might be somewhat misleading, as not all the horses earn prize money, the measurement of this trait's heritability has resulted in a decreased estimate due to this fact (Burns et al. 2006). As inbreeding increases, the loss of genetic variance and expression of harmful recessive alleles can reduce this performance, making earnings especially vulnerable to inbreeding.

Heritability has shown moderate values in the case of earnings, making earnings and earnings per start reliable predictors of race performance (Thiruvankadan et al. 2009). Studies in France on horses born between 1995 and 1999 have found that measuring earnings on their own can give skewed information, especially because many horses do not receive any money in the race, making the evaluation challenging. Therefore, using logarithms of these estimations is a more appropriate statistical approach (Langlois and Blouin 2007).

Repeatability describes the consistency of repeated measurements within individuals and reflects both genetic and permanent environmen-

tal sources of variation. The repeatability of the log of earnings was measured to be around 0.24, 0.37 and 0.31 for Spanish, French, and Turkish horses, respectively (Chico 1994; Langlois 1996; Ekiz et al. 2005). As well, Bokor et al. (2007) estimated the same trait of approximately 0.27 for Thoroughbreds mixed with other breeds in France, and for Thoroughbreds in the United Kingdom and Ireland. The log of earnings per start was measured at about 0.31 for the Thoroughbreds in Czech Republic and 0.41 for the Thoroughbreds in Turkey (Ekiz et al. 2005; Svobodova et al. 2005).

Effects of inbreeding on racing performance in Thoroughbred horses

Todd et al. (2018) analysed 135 572 Australian Thoroughbreds and reported a negative relationship between the pedigree-based inbreeding coefficient (F) and racing performance, whereas the ancestral history coefficient (AHC) showed a positive association with performance. The ancestral history coefficient, which is a measure of the number of times that an allele has been IBD in the individual's pedigree (Baumung et al. 2015), introduces alleles that could expose either a positive or neutral effect, in contrast with the more recent IBD alleles. The reason for the positive relationship between AHC and fitness level is assumed to be due to the selection of some specific favourable mode of traits which has been repeated over time. Meanwhile, this strong selection throughout the pedigree has also led to some selective sweeps as well, since each allele might have carried the neighbouring alleles also (Gu et al. 2009; Hill et al. 2010). The study on Norwegian cold-blooded trotter also illustrated the same results, aligned with the improvement in the race performance associated with long-term selection (Klemetsdal 1998).

Cumulative earnings, earnings per start, career length, total starts and winning strike rate were the performance traits tested for Australian horses. In Figure 1, both F and AHC showed strong associations for the first two traits and the least for the winning strike rate (Todd et al. 2018).

Todd et al. (2018) identified 10 influential ancestors accounting for almost 80% of the IBD alleles in the modern Australian horses, who are also responsible for about 82% of AHC. They further examined founder-specific genetic load and proposed that a stronger reduction in performance among the descendants of a particular founder may indi-

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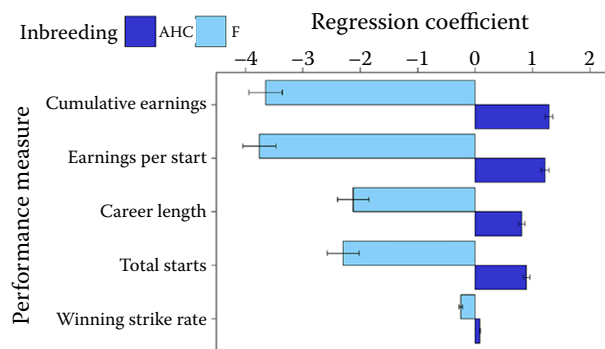


Figure 1. Relationship between racing performance traits and inbreeding in Australian Thoroughbreds

Error bars represent one standard error around the mean. Reproduced from Todd et al. (2018) under the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>)

AHC = ancestral history coefficient; F = inbreeding coefficient

cate a greater contribution of deleterious variation associated with that founder (Figure 2).

In the founder-specific analysis, Herod plays a distinct role compared to Eclipse, Stockwell, and Touchstone. Herod's descendants showed a weaker negative association with performance than descendants of the other three founders. Previous records also suggest that these stallions might have carried disease-related genes, which could have made their offspring more likely to develop health issues which

weaken racing performance, such as Touchstone (Fairfax-Blakeborough 1970) and Eclipse (Erickson et al. 2000). Stockwell has also been discussed in relation to laryngeal neuropathy, a condition reported in his maternal lineage and subsequently investigated genetically in Thoroughbreds (Dupuis et al. 2013; Boyko et al. 2014).

Todd et al. (2018) noted that each founder would have transmitted a mixture of favourable and deleterious alleles to descendants, so inbreeding for each individual would be the same. However, they stated that offspring probably have taken a different set of loci. Therefore, the overall amount of IBD alone may not fully describe the consequences of inbreeding, and understanding the founder-specific origin may also be important. They also explored the traits concerning genome-based analyses but did not find any specific results, which might be due to a smaller size of the dataset ($n = 122$). Building on evidence of a negative relationship between inbreeding and racing performance, Hill et al. (2022) investigated genomic inbreeding in 6 128 Thoroughbreds from Australia, New Zealand and Europe. They chose the traits of horses' career length and the number of races a horse can participate in, as these are robust health indicators (Flash et al. 2022). Genomic inbreeding was estimated using F_{ROH} , and they found that 10% lower or higher F_{ROH} can show a strong association with the positive or negative odds of racing.

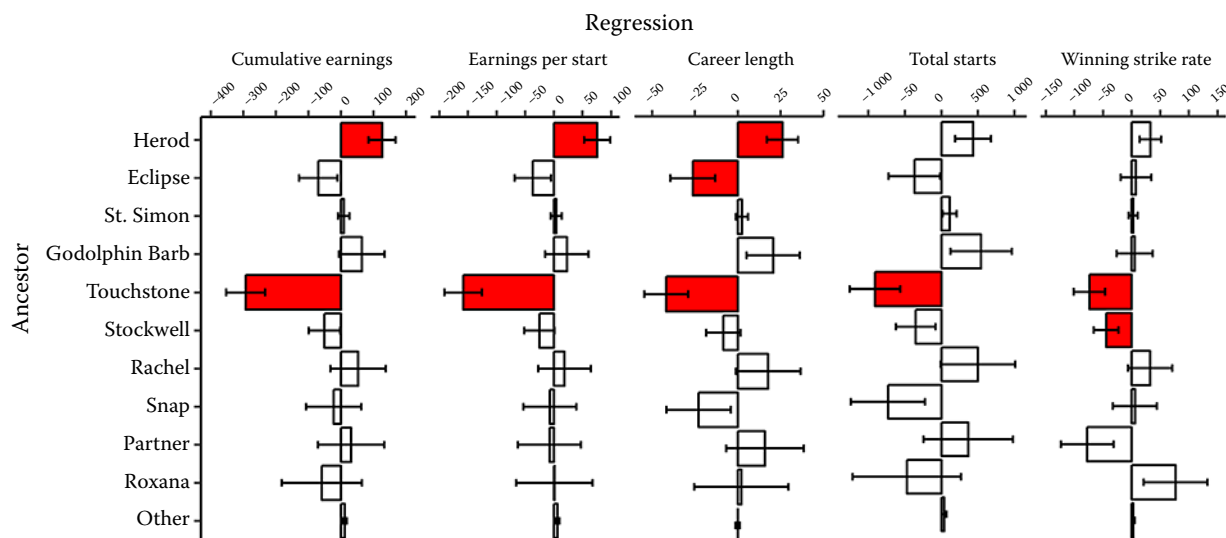


Figure 2. Relationship between the partial inbreeding coefficient and racing performance of Australian Thoroughbreds, representing the ancestors' genetic load

Error bars represent one standard error from the mean. Reproduced from Todd et al. (2018) under the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>)

The horse with the highest F_{ROH} (0.40) was estimated to have a 13% lower probability of ever racing than the horse with the lowest F_{ROH} (0.18). They also stated that long ROH threatens racing performance more than short ROH, indicating that recent alleles which have become IBD are more harmful to the traits (48% decrease in the odds of racing by a 10% increase in F_{ROH}). Agreeing with the effects of inbreeding on Thoroughbreds' racing performance, a more recent study on 768 North American Thoroughbreds showed that 10% more F_{ROH} has led to 3.5 fewer starts per race, compared to horses with average inbreeding (Hill et al. 2023).

CONCLUSION

Based on the literature reviewed, it can be stated that, despite the continuous development of molecular genetic techniques, genealogical information remains a valuable tool for evaluating inbreeding and population structure. However, the highly variable inbreeding levels, rates of inbreeding, and effective population sizes reported for Thoroughbred populations across different countries coincide with substantial differences in pedigree depth and completeness. Therefore, comparing these parameters without simultaneously considering pedigree quality may lead to misleading conclusions. This issue is especially relevant when comparing inbreeding levels among populations, where a lack of available pedigree information may be misclassified as a lack of inbreeding. Although WGS-based methods are generally expected to provide more direct estimates of genomic inbreeding and effective population size, additional methodological information, such as the length of ROH considered, is essential for meaningful comparisons among genotyped populations. Such information also facilitates more meaningful comparisons between pedigree-based and genomic parameters; for example, genomic inbreeding based on long ROH may reflect recent inbreeding captured by Kalinowski's new inbreeding coefficient.

The genetic structure of modern Thoroughbreds reflects a deep but highly unbalanced pedigree, shaped by a narrow founder base and repeated use of a few dominant sire lines. This has produced a population with strong historical bottlenecks, high average relatedness, and steadily increasing inbreeding levels. Although intense selection for

performance may have facilitated the removal of some harmful alleles, it has not prevented the accumulation of mildly deleterious variation, which contributes to measurable inbreeding depression.

Across multiple studies, recent inbreeding reduces the likelihood of racing, affects career length, and lowers earnings. These patterns demonstrate that the interaction between pedigree structure, genomic architecture, and selection continues to shape the fitness of the breed. However, the consequences of inbreeding are not uniform, as recent and ancestral inbreeding have shown different effects, while the genomic regions and deleterious variants responsible for inbreeding depression are still not fully understood. Future studies integrating pedigree information with whole-genome data could help distinguish these effects and identify the genomic regions associated with racing performance and other fitness-related traits.

Moving forward, sustainable management of Thoroughbred genetics will require balancing performance-driven selection with the preservation of genetic diversity. These findings can support breeding decisions aimed at reducing highly related matings, monitoring recent inbreeding, and avoiding excessive genetic contributions from dominant sire lines. Such strategies may help maintain racing performance while protecting the long-term genetic health of the population.

The conflict of interest

The authors declare no conflict of interest.

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