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Should performance at different race lengths be treated as genetically distinct traits in Coldblooded trotters?

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Abstract

Speed, in the form of racing time per kilometre (km), is a performance trait of the Swedish–Norwegian Coldblooded trotter included in the joint Swedish–Norwegian genetic evaluation. A few popular stallions have dominated Coldblooded trotter breeding, which has led to an increasing average relationship between individuals in the population. This study investigated the scope for broadening the breeding goal by selecting for racing time per km over different race lengths (short: 1640 m, medium: 2140 m and long: 2640 m), as this could encourage the use of breeding sires that are less related to the population. Performance data on three- to 12-year-old Coldblooded trotters in all Swedish races run 1995–2021 were obtained from the Swedish Trotting Association. These data consisted of 46,356 observations for 8375 horses in short-distance races, 430,512 observations for 11,193 horses in medium-distance races and 11,006 observations for 3341 horses in long-distance races. Variance components and genetic correlations were calculated using a trivariate animal model with Gibbs sampling from the BLUPF90 suite of programs. Breeding values for the three traits were then estimated using univariate animal models with the same fixed and random effects as in the trivariate model. Heritability estimates of 0.27–0.28 and genetic correlations between racing time per km at the different distances of 0.97–0.99 were obtained. Despite the strong genetic correlation between the traits, there was some re-ranking among the top 10 and top 30 stallions based on distance-specific breeding values. Estimated rank correlation between breeding values for racing time per km in short- and medium-distance races was 0.86, while between short- and long-distance races and between medium- and long-distance races it was 0.61. Mean relationship within the top 10 and top 30 stallions based on breeding values for racing time per km at each distance was 0.31–0.33 and 0.23–0.24 while mean relationship to the rest of the population ranged from 0.17 to 0.18 for all groups, although the 10 and 30 top-ranking stallions differed somewhat in the traits. Estimated average increase in inbreeding was 0.1% per year of birth and 1.2% per generation. The strong genetic correlation between racing time per km at different distances did not support their use as genetically distinct traits. Re-ranking of stallions for racing time per km at different race lengths could favour the use of a larger number of stallions in breeding, but according to our results it would not promote the use of stallions that are less related to the total population. Other traits like longevity or health traits, for example, career length and orthopaedic status, may be more relevant in broadening the breeding goal and preventing a few sires dominating future breeding, and this would be interesting to study further.

KEYWORDS

genetic correlation, performance, race length, re-ranking, speed

1 | INTRODUCTION

The Coldblooded trotter, an indigenous horse breed in Sweden and Norway, has been bred for harness racing over many decades. The Swedish Coldblooded trotter was granted its own studbook in 1964, when the breed officially split from the North Swedish horse. The Norwegian Coldblooded trotter originates from the native Norwegian Dole horse (Bjørnstad & Røed, 2001), which is believed to be closely related to the North Swedish horse, and has had its own studbook since 1939 (FAO, 2023). Since 2000, there has been a joint breeding programme for Coldblooded trotters in the two countries and a large overlap and exchange of breeding animals. Today, there are about 10,000 Coldblooded trotters in Sweden (personal communication Olsson, 2023) and 15,300 in Norway (Norsk Hestesenter, 2022).

Effective population size for the breed, including both Swedish and Norwegian horses, is estimated to be 50 when including horses born until 2013 (Olsen & Klemetsdal, 2020). A downward trend in number of mares covered each year has occurred in both countries. In Norway, 1359 mares were covered in 2007 (Norsk Hestesenter, 2010), but only 792 in 2020 (Norsk Hestesenter, 2021). In Sweden, 684 mares were covered in 2007 (HNS, 2012) and 654 in 2020 (HNS, 2021).

Genetic evaluation of Coldblooded trotters is mainly based on performance in harness racing from 3 to 6 years of age (Svensk Travsport, 2023a). The traits contributing information in the current statistical model for estimation of breeding values (EBVs) are best annual racing time per km (average time per km taken for an individual to complete the race), summarized earnings, percentage of races with first or second place and racing status (whether the horse has completed at least one race as a 3- to 6-year-old).

The small number of popular stallions used for breeding has resulted in an increasing relationship and inbreeding in the population, for example, Klemetsdal (1998) reported significant negative correlations between earnings and inbreeding level in the population. Increased inbreeding level has also been associated with lower fertility in Coldblooded trotter mares (Klemetsdal & Johnson, 1989) and increased risk of bilateral carpal joint arthritis (Dolvik & Klemetsdal, 1994).

Olsen and Klemetsdal (2020) showed that the use of a few popular stallions in Sweden and Norway has contributed to a genetic bottleneck in the population of Coldblooded trotters. According to Olsen et al. (2013), optimal contribution selection (Meuwissen, 1997) could be a useful tool to prevent further increases in inbreeding in the Coldblooded trotter and overuse of a few stallions, but this has so far not been implemented. It is crucial for breeders to produce horses that are attractive to buyers. Choosing a stallion that is less popular may lead to unsold or underpriced horses. To avoid overuse of individual stallions, annual breeding quotas are in place and were reduced in 2021, from a maximum of 80 to 70 mares covered in Sweden and from a maximum of 30 to 25 mares covered in Norway for Swedish stallions, and vice versa for Norwegian stallions (Svensk Travsport, 2021). However, further limitations in the number of mares covered may have economic consequences for owners and keepers of breeding stallions. A system guiding mare owners to select stallions from a different family cluster within the breed has been suggested as a solution to maintain genetic variation (Olsen & Klemetsdal, 2020). Other than the costs of setting up such as system, as pointed out by Olsen and Klemetsdal (2020), this would require mare owners to recognize the value of choosing a stallion that is less related to the population rather than choosing the stallion based on performance only.

It has not yet been determined whether the genetic evaluation model from 1994 could be revised in such a way that it favours the use of a greater number of less closely related stallions, to keep the genetic variation from declining and to reduce the inbreeding rate. In Sweden, trotters compete in short-, medium- and long-distance races, most commonly 1640, 2140 and 2640 m, respectively. If performance measured as racing time per km for different race lengths are genetically distinct traits, and selection for performance at different race lengths favours different stallions, then one option would be to select for performance depending on race length. Dividing the trait racing time per km for different race distances into different traits could potentially distinguish between sprinters and stayers, which could broaden the breeding goal and enable selection of more stallions that are less closely related to each other and to the rest of the population. There are no previous studies on Coldblooded trotters, or trotting horses in general, investigating this issue.

The aim of this study was therefore to estimate genetic parameters and EBVs for racing time per km for Coldblooded trotters in short-, medium- and long-distance races, and to analyse the potential re-ranking of breeding sires based on their EBVs for racing time per km over the different distances. The study also aimed at comparing the average relationship among top-ranked stallions for the three race distances and their relationship with the rest of the population. The outcome of this study would aid in providing useful information for the trotting associations about whether broadening the breeding goal in this way would help to reduce inbreeding and loss of genetic variation in the breed.

2 | MATERIALS AND METHODS

2.1 | Data material

The data used for this study were provided by the Swedish Trotting Association and consisted of racing performance results from Swedish trotting races during the period 1995–2021. All data were on Coldblooded trotters, which compete in separate races from Standardbred trotters. Coldblooded trotters are allowed to race from 3 to 15 years of age, but horses older than 12 years were removed from the dataset owing to few observations for these age groups, so the final dataset covered horses born between 1983 and 2018. Individual records were removed if they were: (a) from ridden Monté races (1.9%), (b) from horses that had been disqualified in that race (11.6%) and (c) three standard deviations or more above the mean value for racing time per km for a given race distance, resulting in 270, 528 and 48 observations removed from short-, medium- and long-distance races, respectively.

Descriptive analysis and data editing were performed with RStudio (R Core Team, 2022). The final dataset consisted of racing results for 4653 mares and 7258 geldings or stallions. These 11,911 unique horses had in total 187,874 observations from races after filtering the data based on the conditions mentioned above (Table 1).

The original pedigree information included 118,239 horses. From this, a pedigree file including seven ancestral generations for each animal in the final dataset was extracted and used for estimation of variance components and breeding values, comprising a total of 23,965 animals. For analyses of relationship within the group of top-ranked stallions per race distance and their relationship to the rest of the contemporary population, a pedigree including seven ancestral generations for all animals born during 2005–2012 was used (including 32,716 animals). For estimation of inbreeding coefficient, the original pedigree file with all available ancestry information was used.

2.2 | Trait definition

The trait studied was racing time per km, defined as the average time per km taken for an individual to complete the race. The value is recorded in four-digit format, for example, 1308 means 1 min, 30 s and 8 tenths of a second. The raw time format was kept in the analyses for easier interpretation of the results for the industry, and because the number of minutes was one for all observations, so it did not make any difference for the analysis if it was changed into seconds or not. The actual start distances stated in race descriptions were used to divide races into the three distance groups, based on definitions used by the Swedish Trotting Association (Svensk Travsport, 2023b). For short-distance races (N = 46,356), the distance ranged from 1609

TABLE 1 Number of observations (N) per race distance, number of individual horses, mean age of horses, mean and maximum number of starts per horse, mean racing time per km, standard deviation, and minimum and maximum racing time per km.

				No. of starts per horse		Racing time per km[b]			
Race distance[a]	N	Individual horses	Mean age	Mean	Max	Mean	SD	Min	Max
Short	46,356	8375	7	6	69	1308	39	1179	1432
Medium	130,512	11,193	7	12	137	1321	37	1191	1434
Long	11,006	3341	7	3	31	1307	30	1221	1398

[a]Where short-, medium- and long-distance races most commonly are 1640, 2140 and 2640 m, respectively.

[b]Where 1308 refers to 1 min, 30 s and eight tenths of a second.

to 1700 m, for medium-distance races (N = 130,512), it ranged from 2040 to 2300 m and for long-distance races (N = 11,006), it ranged from 2460 to 2760 m.

Descriptive statistics for the three race distances are presented in Table 1. The highest mean racing time per km was found for medium-distance races. According to the data, 7712 of the horses had started in both short- and medium-distance races, 2952 horses had started in both short- and long-distance races, 3262 horses had started in both medium- and long-distance races, and 2928 horses had started in all three race distances. The phenotypic distribution of racing time per km for each distance was similar to a normal distribution (not shown), and therefore their residuals were assumed to be normally distributed and no transformation of the data was required.

2.3 | Estimation of variance components and breeding values

Several models including various fixed and random effects, and interactions between fixed effects, were tested with the HPMIXED procedure in SAS (SAS Institute Inc, 2016). The choice of factors in the final model, presented below, was based on the level of significance of the fixed effects or the proportion of variance explained by the random effects, and whether the model fulfilled the assumption of normally distributed residual errors. The models all included the random effect of horse, trainer and a year–season interaction. Pairwise differences between the levels of each main effect were computed with the LSMEANS statement in SAS and adjusted for multiple comparisons using Tukey's method.

2.3.1 | Description of fixed effects

Most Swedish Coldblooded trotters are located in the northern half of Sweden and the majority of races are held in that area. Therefore, the grouping of race dates into seasons was based on the meteorological length of the seasons in the city of Sundsvall according to the Swedish Meteorological and Hydrological Institute. Winter was defined as lasting from 1 December to 24 March, spring from 25 March to 24 May, summer from 25 May to 24 September and autumn from 25 September to 30 November. The number of observations per season ranged from 1962 to 57,168 (Table 2). In total, races were held on 35 race tracks and for every race, track conditions were noted as a measure of how heavy or light the track surface was for each race, expressed as: easy, somewhat heavy, heavy or winter track. For long-distance races, heavy tracks were grouped with somewhat heavy tracks owing to few observations (72 observations for heavy tracks). Most races were held on easy track conditions (Table 2). The number of observations per track ranged from 2 to 5578 for short-distance races, 3 to 14,614 for medium-distance races and 18 to 1854 for long-distance races. A maximum of 15 horses (15 different positions) can participate in each race, and the range of number of observations per racing position was 11–7415, 124–26,237 and 10–2429 for short-, medium- and long-distance races, respectively. If the horse galloped or not in the race was also registered, although gallop is not allowed, the horse is only disqualified if it: gains position or speed when it gallops, gallops a too long distance (depends on how far from start it happens), gallops repeatedly in the race or cross the finishing line in gallop (Svensk Travsport, 2023c).

Information about the driver and trainer of each horse at the races was also provided in the dataset. There were 1528 individual drivers and 5033 individual trainers in total. The level of the driver and trainer (professional or amateur) was stated for each race. Because of changes in the regulations for amateur and professional drivers and trainers over the years, these data were converted to the current definition of either amateur driver/trainer or professional driver/trainer (Svensk Travsport, 2023d) before analysis of the data (number of observations shown in Table 2).

2.3.2 | Statistical model

A trivariate model including the three traits (i.e. racing time per km values for short-, medium- and long-distance races) was created and used for estimation of variance components. The BLUPF90 suites of programs by Misztal et al. (2014) was used to estimate variance components and heritability values. Gibbs sampling was used to estimate variance components in the Gibbsf90+ program, due to problems with convergence when using REML for this purpose.

The final model used for estimation of variance components was:

$$y = Xb + Z_{ys}ys + Z_t t + Z_a a + Z_{pe}pe + e$$

where y is the vector of the observations (racing time per km) for the three traits; X, Z_{ys}, Z_t, Z_a and Z_{pe} are incidence matrices; vector b includes the fixed effects of sex (mare or gelding/stallion), age (3–12 years), year of the race (1995–2021), season (winter, spring, summer or autumn), country of the horse (registered in Sweden or Norway), gallop during the race (yes or no), track (35 different tracks), track conditions (easy, somewhat heavy, heavy and winter track), starting method (auto-start or circular volt-start), starting position on the track (1–15), driver level (professional or amateur) and trainer level (professional or

TABLE 2 Total number of individual horses and number of observations (in brackets) for each factor (excluding starting position and track) and its level for the three race distances[a].

		Individual horses (observations)					
Factor	**Levels**	**Short-distance**		**Medium-distance**		**Long-distance**	
Sex	Gelding or stallion	5184	(30,861)	6823	(44,829)	2402	(8665)
	Mare	3191	(15,495)	4370	(85,683)	939	(2341)
Age, years	3	1677	(2852)	3366	(11,217)	47	(52)
	4	2450	(4707)	4690	(18,346)	613	(867)
	5	3042	(6767)	4991	(21,078)	986	(1632)
	6	3115	(7396)	4774	(20,675)	1137	(2055)
	7	2855	(7025)	4.160	(17,933)	1039	(1795)
	8	2419	(6079)	3391	(14,849)	934	(1625)
	9	1848	(4478)	2590	(10,643)	705	(1244)
	10	1410	(3345)	1898	(7682)	492	(849)
	11	921	(2340)	1249	(5015)	334	(536)
	12	586	(1367)	775	(3074)	204	(351)
Season	Winter	3757	(8442)	6061	(25,826)	1376	(2341)
	Spring	4340	(9067)	6820	(24,609)	1286	(1962)
	Summer	6507	(21,108)	9419	(57,168)	2213	(4703)
	Autumn	3892	(7739)	6544	(22,909)	1208	(2000)
Country	Sweden	6558	(41,713)	7883	(117,825)	2818	(10,088)
	Norway	1817	(4643)	3310	(12,687)	523	(918)
Gallop	Yes	5875	(14,869)	8487	(40,201)	1591	(2757)
	No	6924	(31,487)	9946	(90,311)	2834	(8249)
Track conditions	Light track	8039	(40,265)	10,887	(113,082)	3141	(9795)
	Somewhat heavy track	2756	(4148)	5112	(11,359)	742	(915)
	Heavy track	309	(328)	950	(1112)		
	Winter track	967	(1615)	1871	(4959)	237	(296)
Starting method	Auto-start	4414	(13,249)	5352	(20,341)	801	(1278)
	Volt-start	7642	(33,107)	10,865	(11,0171)	3229	(9728)
Driver level	Professional	7158	(37,703)	9487	(105,025)	2853	(9292)
	Amateur	3558	(8653)	6335	(25,487)	1072	(1714)
Trainer level	Professional	3412	(14,911)	4910	(44,009)	1348	(4219)
	Amateur	6144	(31,445)	8360	(86,503)	2299	(6787)

[a]Where short-, medium- and long-distance races most commonly are 1640, 2140 and 2640 m, respectively.

amateur). The numbers of observations and of individual horses for each level of fixed effects included in the trivariate analysis are shown in Table 2. The same effects were included for all three traits; vector ys is the random effect of the year–season interaction; vector t is the random effect of the trainer; vector a is the random effect of the animal; vector pe is the random permanent environmental effect; and vector e is the random residual effect.

The (co)variance for year–season, trainer, animal, permanent environmental and residual error for short- (s), medium- (m) and long-distance (l) races was assumed to be:

$$\mathrm{Var}\begin{bmatrix} \mathrm{ys_s} \\ \mathrm{ys_m} \\ \mathrm{ys_l} \end{bmatrix} = \begin{bmatrix} \sigma^2_{\mathrm{ys_s}} & \sigma_{\mathrm{ys_{s,m}}} & \sigma_{\mathrm{ys_{s,l}}} \\ & \sigma^2_{\mathrm{ys_m}} & \sigma_{\mathrm{ys_{m,l}}} \\ \mathrm{sym.} & & \sigma^2_{\mathrm{ys_l}} \end{bmatrix} \otimes \mathbf{I_{ys}}; \mathrm{Var}\begin{bmatrix} t_s \\ t_m \\ t_l \end{bmatrix} = \begin{bmatrix} \sigma^2_{t_s} & \sigma_{t_{s,m}} & \sigma_{t_{s,l}} \\ & \sigma^2_{t_m} & \sigma_{t_{m,l}} \\ \mathrm{sym.} & & \sigma^2_{t_l} \end{bmatrix} \otimes \mathbf{I}_t;$$

$$\mathrm{Var}\begin{bmatrix} a_s \\ a_m \\ a_l \end{bmatrix} = \begin{bmatrix} \sigma^2_{a_s} & \sigma_{a_{s,m}} & \sigma_{a_{s,l}} \\ & \sigma^2_{a_m} & \sigma_{a_{m,l}} \\ \mathrm{sym.} & & \sigma^2_{a_l} \end{bmatrix} \otimes \mathbf{A}_a; \mathrm{Var}\begin{bmatrix} \mathrm{pe_s} \\ \mathrm{pe_m} \\ \mathrm{pe_l} \end{bmatrix} = \begin{bmatrix} \sigma^2_{\mathrm{pe_s}} & \sigma_{\mathrm{pe_{s,m}}} & \sigma_{\mathrm{pe_{s,l}}} \\ & \sigma^2_{\mathrm{pe_m}} & \sigma_{\mathrm{pe_{m,l}}} \\ \mathrm{sym.} & & \sigma^2_{\mathrm{pe_l}} \end{bmatrix} \otimes \mathbf{I_{pe}};$$

$$\mathrm{Var}\begin{bmatrix} e_s \\ e_m \\ e_l \end{bmatrix} = \begin{bmatrix} \sigma^2_{e_s} & 0 & 0 \\ & \sigma^2_{e_m} & 0 \\ \mathrm{sym.} & & \sigma^2_{e_l} \end{bmatrix} \otimes \mathbf{I}_e$$

Several runs using different numbers of iterations, burn-in and thinning were analysed before the final parameters were set. In total, 400,000 iterations were run with a burn-in period of 125,000. Every 40th sample drawn was stored, which resulted in 6875 samples being passed to posterior analyses. Post-Gibbs analysis was performed with postgibbsf90 to obtain posterior standard deviation and posterior statistics. Visual inspection of trace plots in RStudio was performed to determine whether the chains had reached convergence.

Heritability estimates (h^2) for racing time per km in short-, medium- and long-distance races were calculated as:

$$h^2 = \frac{\sigma_a^2}{\sigma_t^2 + \sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2}$$

where σ_a^2 is the estimated additive genetic variance, σ_t^2 is the estimated trainer variance, σ_{pe}^2 is the estimated permanent environmental variance and σ_e^2 is the estimated residual variance.

Repeatability (r) for racing time per km in short-, medium- and long-distance races was calculated as:

$$r = \frac{\sigma_a^2 + \sigma_{pe}^2}{\sigma_t^2 + \sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2}$$

Using the variances estimated with the trivariate model, univariate models including the same fixed and random effects were run with Blupf90+ to obtain EBVs with standard error for racing time per km for each race distance.

The accuracy (r_{TI}) of each EBV was calculated as:

$$r_{TI} = \sqrt{1 - \frac{PEV}{\sigma_a^2}}$$

where PEV is prediction error variance for short-, medium- or long-distance races.

2.4 | Rank correlations and proportion co-selected

Spearman's rank correlation ρ was estimated for rank position of breeding stallions based on EBVs for the three distances, using cor.test in RStudio (R Core Team, 2022). Re-ranking of the top 10 and top 30 stallions (born during 2005–2012, with at least one offspring) for the three race distances was then studied. The proportion of co-selected stallions among the top stallions for the three traits was calculated.

2.5 | Relatedness and inbreeding coefficient

Pedigree data were analysed using the CFC software (Sargolzaei et al., 2006). The average pairwise relationship within three groups of stallions born during 2005–2012 and ranked among the top 10 and top 30 on EBVs for the different race distances, together with their relationship to the rest of the population from the same birth year period, was estimated. Calculations of average relationship within and between groups in the CFC software were based on the methods described by Colleau (2002).

Using the full pedigree, individual inbreeding coefficient was estimated for each animal. Horses were grouped based on the year of birth to estimate the average inbreeding per year from 1940 to 2021 and the average number of discrete generation equivalents.

3 | RESULTS

3.1 | Fixed effects and least squares means for fixed effects

The fixed effects included in the final model analysed in SAS were all highly significant ($p < 0.0001$) for racing time per km in the three distances, except for trainer level for medium-distance races ($p = 0.0004$), starting method for long-distance races ($p = 0.0153$) and starting position in long-distance races ($p = 0.1559$). Least squares means (LSM) for each level of the fixed effects sex, season, country, gallop, track conditions, starting method, starting position, driver level and trainer level are shown in Table 3 (LSM for tracks is not shown). Based on the data, males were on average faster than females, the summer season and easy track conditions gave the lowest LSM for racing time per km, and Norwegian horses racing in Sweden were on average faster than Swedish horses. The main improvement in racing time per km with age occurred from age three to six, and thereafter the curve flattened out (Figure 1). The LSM for racing time per km improved by 3.5 s in short-distance races from 1995 to 2021, while in medium- and long-distance races it improved by 4.1 s and 3.6 s, respectively (Figure 2).

3.2 | Estimated variance components, heritability and repeatability

In preliminary analysis of variance, driver and trainer were both included as random effects in the model.

TABLE 3 Least squares mean and standard error (SE) of racing time per km for each level of different fixed effects (age, year and track not included).

		Short-distance[a]		Medium-distance[a]		Long-distance[a]	
Factor	**Level**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Sex	Mare	1331	1	1351	1	1336	1
	Gelding or stallion	1321	1	1340	1	1325	1
Season	Winter	1335	1	1354	1	1341	1
	Spring	1328	1	1347	1	1330	1
	Summer	1319	1	1339	1	1324	1
	Autumn	1322	1	1342	1	1328	1
Country	Sweden	1337	1	1356	1	1339	1
	Norway	1315	1	1335	1	1322	1
Gallop	Yes	1332	1	1350	1	1334	1
	No	1319	1	1341	1	1327	1
Track conditions	Easy	1314	1	1333	1	1323	1
	Somewhat heavy	1326	1	1346	1	1338	1
	Heavy	1342	1	1361	1		
	Winter track	1322	1	1342	1	1331	1
Starting method	Auto-start	1321	1	1343	1	1330	1
	Volt-start	1330	1	1348	1	1331	1
Starting position	1	1323	1	1343	1	1328	1
	2	1324	1	1344	1	1329	1
	3	1324	1	1344	1	1329	1
	4	1325	1	1344	1	1330	1
	5	1325	1	1345	1	1330	1
	6	1325	1	1344	1	1330	1
	7	1325	1	1345	1	1330	1
	8	1326	1	1345	1	1329	1
	9	1326	1	1345	1	1330	1
	10	1326	1	1346	1	1330	1
	11	1327	1	1346	1	1330	2
	12	1327	1	1346	1	1330	2
	13	1326	1	1346	1	1333	3
	14	1335	5	1350	2	1336	4
	15	1326	1	1349	1	1332	4
Driver level	Professional	1323	1	1343	1	1328	1
	Amateur	1329	1	1348	1	1333	1
Trainer level	Professional	1324	1	1345	1	1328	1
	Amateur	1328	1	1346	1	1333	1

[a]Where short-, medium- and long-distance races most commonly are 1640, 2140 and 2640 m, respectively.

However, the driver effect did only account for 2% of the total variation explained for racing time per km in all three distances. This was the case both in the preliminary analysis in SAS as well as in the model used for estimation of variance components in Gibbsf90+. In 37% of the observations, the driver and trainer was the same person and the driver effect could therefore be confounded with the trainer effect. Because of this, only trainer was retained in the final model used for estimation of variance components. The estimated variance explained by the random effect of trainer in the final model was lower than the estimated variance of the additive genetic or permanent environment effects (Table 4).

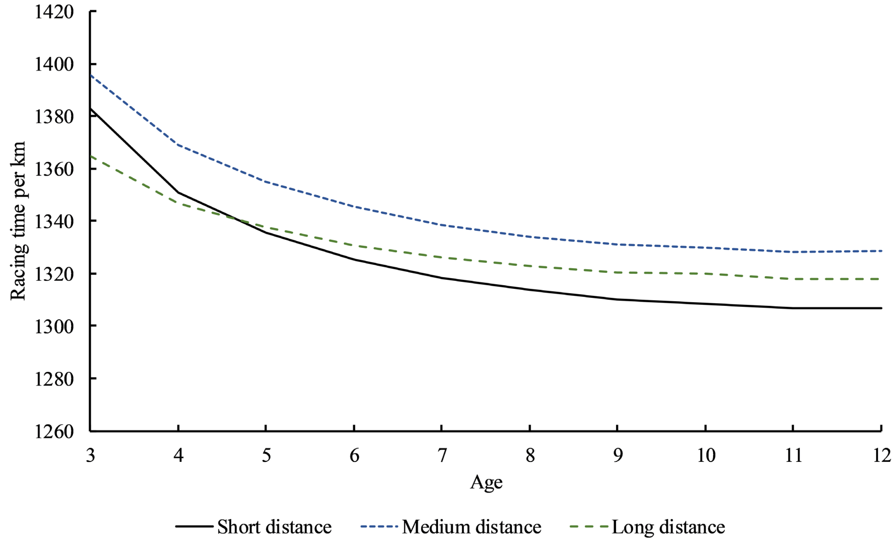

FIGURE 1 Least squares mean of racing time per km in short-, medium- and long-distance races as a function of horse age (years). Racing time per km expressed in four-digit form, where 1380 means 1 min, 38 s and 0 tenths of a second. [Colour figure can be viewed at wileyonlinelibrary.com]

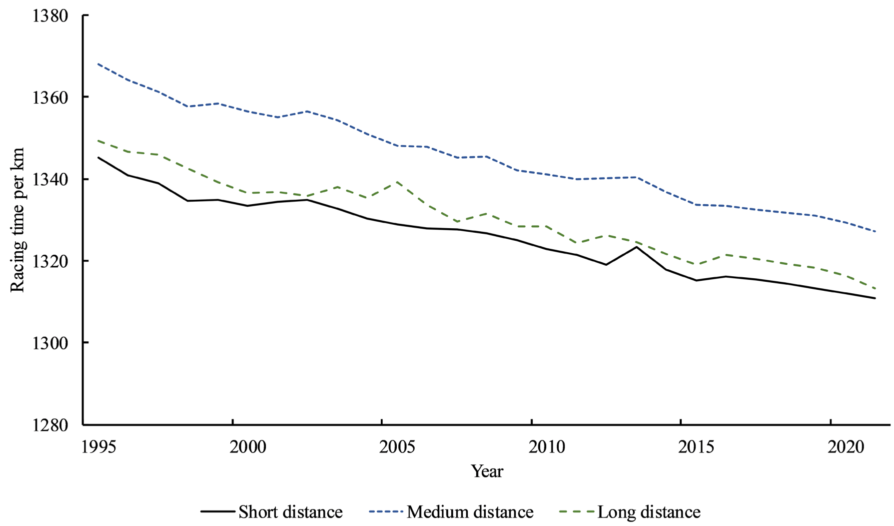

FIGURE 2 Least square mean of racing time per km in short-, medium- and long-distance races as a function of year. Racing time per km expressed in four-digit form, where 1380 means 1 min, 38 s and 0 tenths of a second. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Posterior means for additive genetic (σ^2_a), trainer (σ^2_t), permanent environmental (σ^2_{pe}) and residual (σ^2_e) variance, mean heritability (h^2) from post-Gibbs analysis and repeatability[a] (r) for racing time per km in short-, medium- and long-distance races[b].

Trait (racing time per km)	σ^2_a	σ^2_t	σ^2_{pe}	σ^2_e	h^2	r
Short distance	$285.2_{22.0}$	$117.4_{5.5}$	$384.9_{15.6}$	$250.0_{1.8}$	$0.275_{0.019}$	0.65
Medium distance	$282.7_{20.7}$	$123.5_{5.1}$	$362.1_{13.6}$	$226.5_{0.9}$	$0.284_{0.018}$	0.65
Long distance	$206.9_{16.0}$	$91.1_{6.3}$	$301.4_{12.6}$	$159.4_{2.4}$	$0.273_{0.019}$	0.67

Note: Posterior standard deviations shown as subscripts.

[a]Defined with σ^2_a and σ^2_{pe} in the numerator.

[b]Where short-, medium- and long-distance races most commonly are 1640, 2140 and 2640 m, respectively.

The Post-Gibbs analysis revealed moderate posterior mean heritability (range 0.273–0.284) for racing time per km in short-, medium- and long-distance races (Table 4). Median heritability was the same as the mean for all traits, while the mode ranged in value from 0.269 to 0.283. Posterior distributions of the heritability estimates for the three traits were visually close to normally distributed. The repeatability for the three traits was high and ranged from 0.65 to 0.67 (Table 4).

Estimates of genetic correlations between the traits are shown in Table 5. Mean genetic correlations r_g were very strong (range 0.97–0.99) for racing time per km over the three race distances. Mean correlation for trainer as well as for permanent environment effects were also very

TABLE 5 Posterior mean, standard deviation (SD), 95% posterior standard deviation (PSD) interval, median and mode of genetic correlation (r_g) in racing time per km between short-, medium- and long-distance races[a].

Traits (racing time per km)	Mean	SD	95% PSD interval	Median	Mode
Short–medium distance	0.99	0.002	0.99–1.00	0.99	0.99
Medium–long distance	0.99	0.003	0.99–1.00	0.99	0.99
Short–long distance	0.97	0.009	0.95–0.99	0.97	0.97

[a] Where short-, medium- and long-distance races most commonly are 1640, 2140 and 2640 m, respectively.

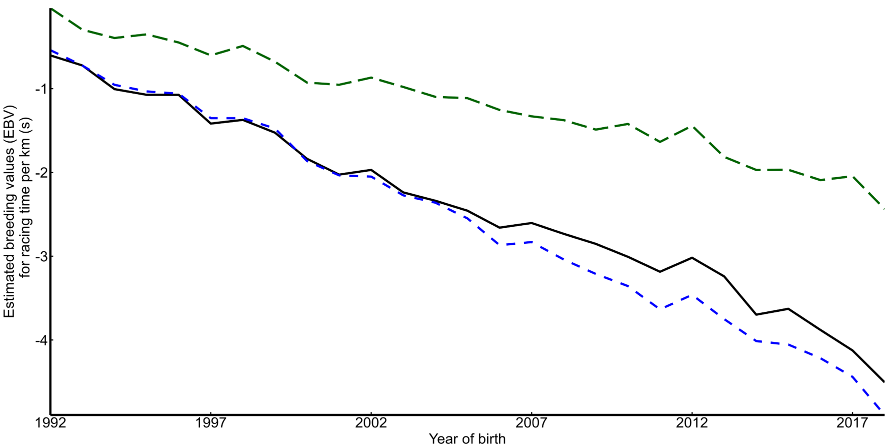

FIGURE 3 Estimated breeding values (EBVs) for racing time per km (transformed to seconds) for short- (black solid line), medium- (blue dashed line) and long-distance races (green longdashed line) for horses born during 1992–2018. [Colour figure can be viewed at wileyonlinelibrary.com]

strong (range 0.98–1.00 and 0.96–0.99, respectively) for racing time per km over the three distances (results not shown).

3.3 | Genetic trends

In short-distance races, the genetic improvement from 1992 to 2018 was −3.9 s per km (Figure 3). For medium-distance races, the genetic improvement during this period was −4.4 s, while for long-distance races it was −2.4 s. This corresponds to an annual change of −0.008, −0.009 and −0.006 genetic standard deviations for racing time per km in short-, medium- and long-distance races, respectively. The improvement per generation would then be −0.09, −0.11 and − 0.06 genetic standard deviations for short-, medium- and long-distance races, respectively.

3.4 | Rank correlation and re-ranking

The rank correlation between EBVs for racing time per km in short- and medium-distance races for all stallions with at least one offspring, without restriction on birth year, was 0.86. The corresponding rank correlation between the EBVs for racing time per km in short- versus long-distance races, and in medium- versus long-distance races, was 0.61 for the same group of stallions.

In total, 64, 70 and 47 stallions (born during 2005–2012 and with at least one offspring) included in the records for short-, medium- and long-distance races, respectively, received EBVs. The number of stallions co-selected among the top 30 for short-, medium- and long-distance races are shown in Figure 4. Of the top 30 stallions for short-distance races, 25 were also in the top 30 for medium-distance races. Of the top 30 stallions for long-distance races, 23 also had an EBV in the top 30 stallions for short-distance races and 21 had an EBV in the top 30 stallions for medium-distance races. Of the seven horses with an EBV in top 30 for short-distance, but not long-distance races, five were excluded from the top 30 for long-distance races because they, or their offspring, had not started in a race of this length. The corresponding number for medium- and long-distance races was 6. The top three stallions were the same in the short- and medium-distance groups, but the best stallion dropped to fifth place in the ranking for long-distance races. The stallion ranked second was the same for the three distance groups. The stallion ranked third for short-and medium-distance races was the top-ranked stallion for long-distance races.

There were four stallions co-selected among the top 10 for racing time per km in the three race distances (Figure 4). Of the top 10 stallions for short-distance races, six were also in the top 10 for medium-distance races. Of the top 10 stallions for long-distance races, five stallions were in the top 10 for short-distance races and six had an EBV among the top 10 for medium-distance races.

Accuracy of EBVs for the top 30 stallions ranged from 0.69 to 0.94 for short-distance races, 0.73 to 0.95 for medium-distance races and 0.54 to 0.90 for long-distance races. For the top 10 stallions, accuracies ranged from 0.73 to 0.94 for short-distance races, 0.72 to 0.95 for medium-distance races and 0.66 to 0.90 for long-distance races.

3.5 | Relatedness

Results from the pedigree structure analysis with all pedigree data included showed that the average family size for full sibling groups was 2.22 (range 2–11). Of the 118,240 horses in the complete pedigree, 106,379 horses had both dam and sire known. The average numerator relationship between stallions born during 2005–2012 with an EBV among the top 10 for racing time per km was 0.31–0.33 and between those among top 30 it was 0.23–0.24, for all three race distances. The relationship between the rest of the population born in the same period and the top-ranked stallions was 0.17–0.18. The average relationship between the top-ranked stallions was higher than within the rest of the population (0.16).

Average inbreeding coefficient (F) in the population of Coldblooded trotters born during 1940–2021, based on the dataset with all pedigree information included, is shown in Figure 5. Average estimated inbreeding coefficient for horses born in 2021 was 0.083. The change in inbreeding per year during the period covered by the data was estimated by regressing ln(1-F) on birth year to 0.001, which gave 0.012 per generation (ΔF) when the generation interval was assumed to be 11.5 years (following Olsen and Klemetsdal (2020)). This corresponded to an effective population size (Ne) of 42.

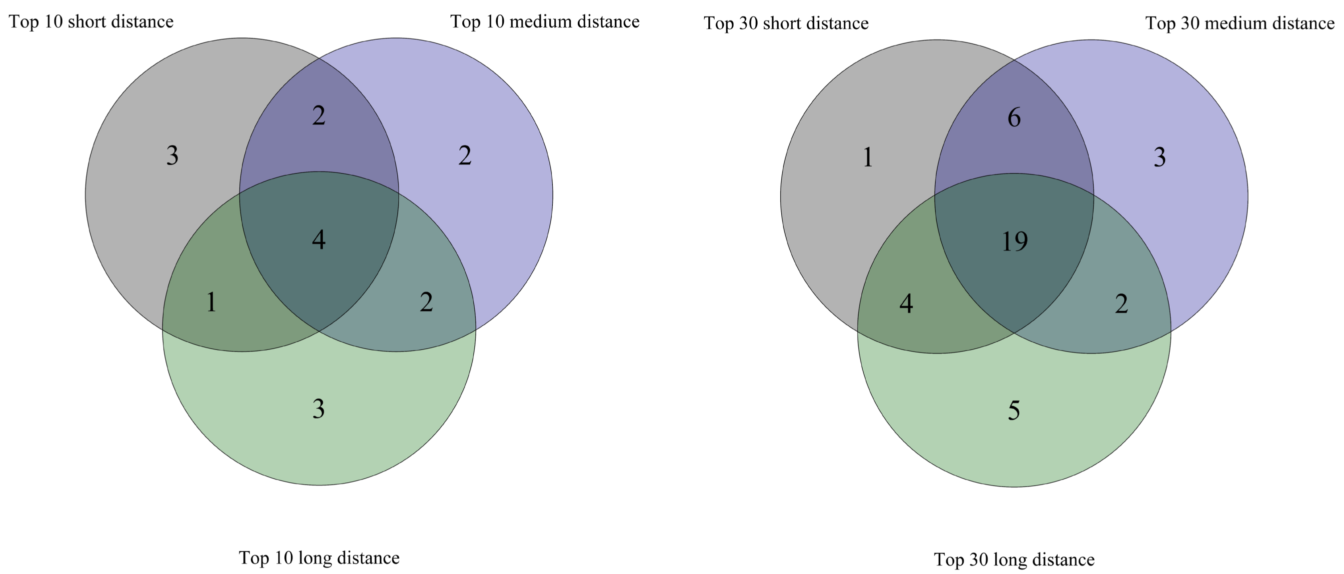

FIGURE 4 Venn diagram representing the number of stallions co-selected in the top 10 (left-hand side) and top 30 (right-hand side) for the trait racing time per km in short-, medium- and long-distance races, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

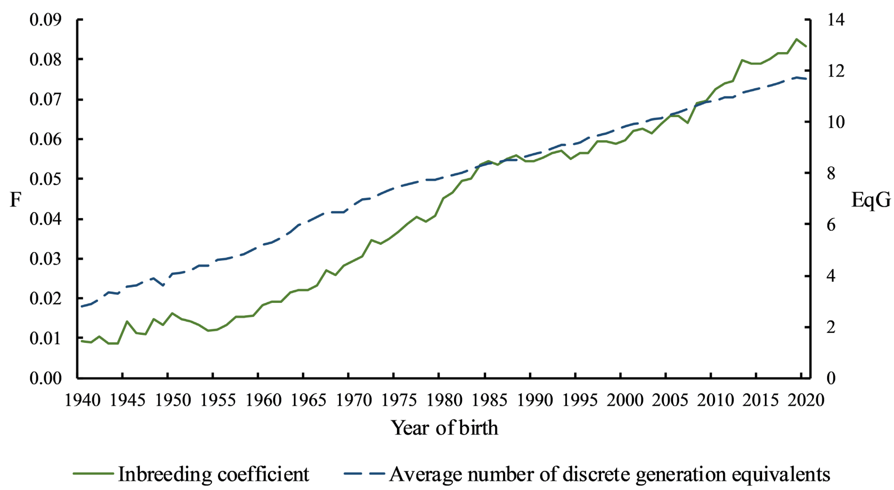

FIGURE 5 Average inbreeding coefficient (F) and average number of discrete generation equivalents (EqG) for Coldblooded trotters born during 1940–2021 including all pedigree information. [Colour figure can be viewed at wileyonlinelibrary.com]

Average number of discrete generations per year of birth for the same period (1940–2021) is also shown in Figure 5. The average number of discrete generation equivalents (EqG) in 2021 was 11.7. For animals born during 2005–2012, the average number of discrete generation equivalents was >10.2 for all year groups when no restriction was placed on number of generations included.

4 | DISCUSSION

4.1 | Genetic parameters for racing time per km in short-, medium- and long-distance races

The estimated heritability (0.27–0.28) of racing time per km in the three race distances was slightly lower than the heritability value of 0.35 used in the current routine genetic evaluation for best annual racing time per km (Árnason, 2021). The discrepancy between lower heritability when dividing the trait into three as in the current study and the heritability used in the genetic evaluation is probably a result of using a repeated records model including all racing data, compared with only the fastest racing time per km per horse. The lower heritability could also be a result of that horses aged 3–12 years were included in the present study, whereas the racing time per km trait used in the official index only includes records for horses aged 3–6 years. Older horses are more influenced by training and management, and can be assumed to be more pre-selected. Moreover, the rather complex model used in this study may have transferred variation explained by the horse to the random trainer effect, resulting in lower additive genetic variance. Finally, the variance components used in the current routine genetic evaluation are not based on the most recent data. The repeatability for the three traits (range 0.65–0.67) was similar to what has been found for racing time per km in Coldblooded trotters previously (0.64–0.65) (Klemetsdal, 1988). In Thoroughbreds, heritability for speed has been estimated to be 0.12 for short-distance (1006–1408 m) and medium-distance (1609–2414 m) races, and 0.07 for long-distance races (2816–4023 m) (Sharman & Wilson, 2023).

4.2 | Genetic correlations and genetic gain

The very strong genetic correlations (0.97–0.99) found between racing time per km in short-, medium- and long-distance races indicate that the traits are not genetically different from each other, and can continue to be treated as one trait. However, it should be noted that the number of stallions receiving EBVs for long-distance races was relatively small, because of the low number of horses competing in this race distance (Table 1). In Thoroughbreds, Sharman and Wilson (2023) also found a very strong genetic correlation between short- and medium-distance races and medium- and long-distance races (0.87 and 0.84, respectively), and a lower genetic correlation (0.47) between short- and long-distance races. It should be noted that the difference in length between short- and long-distance in Swedish trotting races is much less than between short- and long-distance in Thoroughbred races.

The genetic improvement for best annual racing time per km was low until the 1980s, when the first BLUP animal model genetic evaluation of Coldblooded trotters was established (Árnason, 2021). The favourable trend in racing time per km in the early 1990s, as seen in Figure 3, corresponds well with the updated genetic evaluation launched in 1994, when both Norwegian and Swedish Coldblooded trotters were included in a joint evaluation for the first time (Árnason, 2021). The largest genetic improvement in seconds per km over time was seen in short- and medium-distance races (Figure 3). The smaller improvement seen for long-distance races may partly be due to additional pre-selection of the somewhat older horses that start in long-distance races and partly to the focus on results for 3- to 6-year-olds in the official genetic evaluation. The Swedish Trotting Association devotes most of its effort and prize money to short- and medium-distance races, to meet the demand of easier races for younger horses. For 3- and 4-year-olds, the Coldblooded trotter criteria are held and the national derby for these two age groups awards a prize of 500,000 and 700,000 SEK (currently 42,300 and 59,200 EUR), respectively, for the winner over 2140 m of distance (Kallblodsklassikern, 2023). These are the two most prestigious races for a Coldblooded trotter. Interest in competing in long-distance races could probably be increased by distributing more of the prize money to this race length. Another contributing factor could be that the additive genetic standard deviation is roughly 15% lower for racing time per km in long-distance races than for racing time per km over the other two distances.

Even though the best racing time per km is included in the routine genetic evaluation, the total index presented for Coldblooded trotters combines EBVs start status and summarized earnings. The annual absolute change of 0.006–0.009 genetic standard deviations for the three traits analysed in this study is very low, and it should be noted that the generation interval in horses tends to be long. In comparison to the expected genetic gain in dairy cattle (although achieved by genomic selection), the corresponding change per year is 0.467 genetic standard deviations (Schaeffer, 2006). For the trait racing time per km, one should take into consideration the potential limit in how fast the horses can become and that the genetic improvement may slow down with time as shown in Swedish Standardbred trotters by Árnason (2001).

4.3 | Genetics behind best race distance

While the genetic correlations estimated in the present study were close to unity, other studies have shown that different genetic variants can favour performance at different racing distances. In Thoroughbreds, different variants of a single nucleotide polymorphism (g.66493737C>T) in the *myostatin* gene, which is linked to muscle mass, have been shown to be important for racing performance in short- or long-distance races (Hill et al., 2010). Like Coldblooded trotters, Thoroughbreds compete over different race distances, where so-called 'stayers' run >2400 m and 'sprinters' run up to 1400 m (Svensk Galopp, 2023). A study by Hill et al. (2010) found that the T/T genotype was beneficial for stayers and the C/C genotype for sprinters. The C allele has been associated with a smaller proportion of the slow type 1 muscle fibre and larger proportion of the fast and explosive type 2B muscle fibre in the Quarter horse, which is a breed selected for speed over short distances (400 m) (Petersen et al., 2013). However, the frequency of the C allele has been found to be very low in Coldblooded trotters (Velie et al., 2018). In trotting, even short-distance races are relatively long, usually 1640 m in Sweden (Svensk Travsport, 2023b), and it is possible that the same type of muscle fibre is beneficial in all the different race distances.

4.4 | Re-ranking

The results obtained in this study could be used to present EBVs for racing time per km in short-, medium- and long-distance races, which would make it possible for mare owners to choose stallions expected to give good offspring for racing at short and/or long distance. The rank correlation between short- and long-distance races, and between medium- and long-distance races of 0.61, indicates that, despite high genetic correlations, in practice there would be some re-ranking of stallions for racing time per km in long-distance compared with short- and medium-distance races. Selection based on EBVs for racing time per km in long-distance races could possibly promote the use of other stallions than those selected for performance in short- and medium-distance races. However, we found that the same two stallions were ranked in the top three for all three distances. If these were to be even more favoured than at present, due to their superiority for all distances, this could have a negative effect on efforts to promote the use of more stallions.

4.5 | Relatedness

The relationship between stallions with an EBV in the top 10 and top 30 for racing time per km for all three race distances was higher (0.31–0.33 and 0.23–0.24) than the average relationship between animals in the rest of the population (0.16). The fact that the top approved breeding stallions on average had a relationship almost at the level of half siblings is worrying. The trend seen in average inbreeding over the years (Figure 5) was not unexpected. Within the overall period, three time periods (1955–1985, 1985–2005 and 2005–2021) showed slightly different trends, similar to those presented previously by Olsen et al. (2013) and Olsen and Klemetsdal (2020). The average inbreeding coefficient for animals born in 2021 was estimated to be 8.3%, compared with 6.4% for Coldblooded trotters born in 2009 according to Velie, Jäderkvist Fegraeus, et al. (2019). The results in the present study show that the rate of inbreeding is still an ongoing problem. It is important to manage the increase in relatedness and inbreeding to avoid loss of genetic variation within the breed.

4.6 | Potential new traits to broaden the breeding goal

Our results did not provide genetic reasons to justify the inclusion of distance-specific racing time per km in the breeding goal for Coldblooded trotters. However, it would be interesting to study if other traits, for example, affecting health or longevity, may be relevant to consider when broadening the breeding goal to maintain a sustainable Coldblooded trotter population. Starting the career early has been shown to be important for racing longevity in Coldblooded trotters (Velie, Solé, et al., 2019) and in Standardbred trotters (Solé et al., 2017; Tanner et al., 2011). In Standardbred trotters, Ringmark et al. (2016) showed that having a symmetrical locomotion pattern and a good orthopaedic status are important factors for starting the career early. Although, increased training intensity and introduction of new training methods might increase the risk of lameness and asymmetric locomotion (Ringmark et al., 2016). Also, both conformational traits and orthopaedic traits are shown to be of importance for performance such as number of races in Swedish Standardbred trotters (Magnusson & Thafvelin, 1990). The number of horses that compete decreases with age. In the present study, only 775 Coldblooded trotter horses competed in races of medium length at the age of 10, in comparison with 4991 horses competing as 4-year-olds over the same distance (Table 2). It would therefore be interesting to study longevity and its genetic correlations to racing performance traits in the Coldblooded trotter. In Swedish Standardbreds, the number of completed races is included in the genetic evaluation, with a heritability of 0.18 (Árnason, 2021), but this is at present not the case for the Coldblooded trotter. According to Árnason (1999), there is no clear correlation between the number of races and success in other performance traits, such as number of placings, racing time per km or earnings, partly because the very best horses may only compete in a few prestigious races with large prize money.

When discussing health traits, it should be noted that Coldblooded trotter stallions considered for breeding are subjected to a thorough health inspection by two veterinarians and there is a zero-tolerance policy for osteochondrosis and ossification of ungular cartilages (Svensk Travsport, 2023e). Health inspections of young horses have previously been shown to be valuable in general, for example results from palpation and flexion tests on 4-year-olds have been shown to be significant for life length in Swedish Warmblood horses (Wallin et al., 2001).

5 | CONCLUSIONS

In this study, there was some re-ranking of top stallions based on EBVs for racing time per km over different race distances, but the distance-specific traits did not prove to be genetically different from each other. Based on these results, selection based on racing time per km in different race lengths would not promote the use of stallions that are less related to the rest of the population.

AUTHOR CONTRIBUTIONS

All authors contributed to designing the study. S. Andonov, E. Strandberg and S. Eriksson supervised the work. P. Berglund performed the data analyses and drafted the manuscript. All authors read, edited and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the Swedish Trotting Association. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the author(s) with the permission of the Swedish Trotting Association.

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