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Variance components, heritability estimates, and breeding values for performance test traits in Old Kladruber horses

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ABSTRACT: The Old Kladruber horse is an important Czech genetic resource. In the current study, two categories of traits were evaluated – the first, a numerical score for Type and Gender Expression and the second, 11 traits describing performance divided into four categories: (1) Rideability (Overall Impression, Rideability), (2) Gaits (Walk, Trot, Canter), (3) Carriage Drivability (Dressage Test, Obstacle Driving Test, Marathon Test), and (4) Reliability in Tug (First Tug, Second Tug, Third Tug). The original data set contained records from 700 individuals from the period 1995–2014, each horse having 3–5 performance evaluations for the suite of traits. Our objective was to identify a suitable model for the estimation of genetic parameters and prediction of breeding values. Only one model was examined for the Type and Gender Expression trait, whereas three models were compared for the analysis of each performance trait. Criteria for choosing the most appropriate model were minimal values for the deviance information criterion (DIC) statistics, low ratios of residual variance to phenotypic variance, and maximal heritability estimates. The heritability estimate for Type and Gender Expression was 0.18. For the performance traits, the model with the fewest sources of variation (model 1) was more appropriate than two alternatives with more sources of variation. Heritability estimates from this model ranged from 0.08 to 0.40, while estimates for various performance traits from the other models were in the range 0.08–0.24. Low heritabilities for several of the performance traits suggested that selection for their genetic improvement would likely be unsuccessful. In order to maintain genetic variability, inbreeding, and fitness in the Old Kladruber population we suggest to use breeding value estimation using the heritabilities and the method presented in this paper.

Keywords: harness horse; genetic parameters; performance test; genetic resource

INTRODUCTION

The Old Kladruber horse is an important Czech genetic resource. The National Stud Kladruby nad Labem was founded by Emperor Rudolf II who in 1579 imported Old Spanish and Old Italian horses from which the Equus Bohemicus breed was established. The breed was stabilized around the end of the 18th and the onset of the 19th century. The Old Kladruber horse belongs to several endangered horse breeds in the Czech Republic (SOKH 2015).

In recent years the population has been located in the Kladruby stud (grey variety) and the Slatiňany stud (black variety). One-half of the population is kept in the National Stud Kladruby nad Labem and the remaining animals are spread in private studs. Horses are selected mostly on type of galakarossier (carriage horse used for ceremonial and representative purposes). The primary goal of the breeding program is conservation of the gene pool with respect to conformation, gait, and sport performance, especially for carriage driving and dressage.

For Lipizzan horses the breeding goals are different (Zechner et al. 2002). The Italian population of Lipizzan horses is kept as a genetic reserve, while in the other Lipizzan populations the improvement

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in sport performance for dressage or carriage driving is emphasized. The Lusitano is the most important native equine breed in Portugal, and selection is based on functional traits including use in bullfighting (Vincente et al. 2012). The Noriker is an autochthonous Austrian draft horse breed in which selection is focused on conformation traits (Druml et al. 2008). Spanish heavy horses play an important role in maintaining the ecological and social integrity of rural areas. Gomez et al. (2012) conducted analyses of body conformation and results implementability into conservation strategies. Many of the populations they studied were small, closed and/or approaching endangered status. Breeding programs typically were based on pedigree analysis, maintenance of genetic variability, and controlling the rate of inbreeding.

Currently, there are approximately 1700 Old Kladruber horses registered in the Czech Republic, and only 30% of living animals underwent performance testing. Most of the models in the genetic parameter and evaluation studies of Gerber Olsson et al. (2000), Ducro et al. (2007a, b), and Viklund et al. (2008) included fixed and random effects for sex, location, and year of test (or their combination), date of test, age, thoroughbred percentage, classifier, and animal. In the experiments of Olsson et al. (2008), Viklund et al. (2010), and Becker et al. (2011), heritability estimates for performance test traits of sport horses ranged from 0.37 to 0.46.

With regard to conservation and genetic improvement of the Old Kladruber horse breed, no genetic analyses of performance test data have yet been conducted, and systematic breeding value predictions have yet to be computed and used in selection decisions. The objectives of this paper were to select suitable models for the estimation of genetic parameters and prediction of breeding values for performance traits of the Old Kladruber horse.

MATERIAL AND METHODS

Performance test of the Old Kladruber horse. Performance tests of Old Kladruber stallions and mares last two days and have two parts. The first part is evaluation of Type and Gender Expression as a single numerical score, and the second is evaluation of performance for 11 distinct traits organized into 4 groups. Group 1 is "Rideability", with traits Overall Impression and Rideability. Group 2 is "Gaits", with traits Walk, Trot, and Canter. Group 3 is "Driveability of Carriage" with traits Dressage Test, Obstacle Driving Test, and Marathon Test. Group 4 is "Test Reliability in Tug" with traits First Tug, Second Tug, Third Tug. Rideability and Gaits are assessed under saddle, Driveability of Carriage is assessed in harness, and Reliability in Tug is assessed from the ground. Each individual trait is scored between 1 (very poor) and 10 (excellent), with assessment to one decimal place.

Data. The original data set was obtained from the Studbook of the Old Kladruber Horse and Central Register of Horses. Performance test data were from 700 individuals (151 stallions and 549 mares) from the period 1995–2014. Evaluations were conducted by panels of judges. Each animal typically had 3–5 evaluations per test, which were not averaged but rather were analyzed as distinct observations. For horses tested more than once, the composition of the judging panel did not necessarily remain constant across time. With repeated measurements, 2622 observations were in the data set. Because the Old Kladruber breed is generally considered late maturing, performance tests were conducted only after horses were four years of age or older. Four age groups were created: four, five, six, and seven and more years of age.

Pedigree. Including four generations of ancestors, 1362 horses (born between 1904 and 2010) were included in the pedigree file. Known ancestors represented 91% of the horses in the pedigree. For 9% of individuals, both the sire and dam were unknown.

Estimation of genetic parameters. Fixed effects were tested using the GLM procedure of SAS (Statistical Analysis System, Version 9.1, 2005). For all performance traits, the model for statistical analysis included effects of sex, age group, year of performance test, location of performance test, a combination effect of year*place of performance test, stud, and variety. For Type and Gender Expression, the model included the effects of sex, age group, and variety (black vs grey).

Based upon results from these GLM analyses, single trait models with the addition of repeatability (Table 1) were tested for performance traits (model 1 through model 3) and for Type and Gender Expression (model 4). Using Gibbs sampling algorithm GIBBS1f90 software (Misztal, Version 1.37, 2002), variance components were estimated

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Table 1. Description of fixed and random effects in alternative models to estimate genetic parameters for performance traits

	Sex	Age	Year	Place	Year*Place	Variety	Stud	Classifier	PE	Animal
Model 1		F	F	F				R	R	R
Model 2	F	F	F	F		F	F	R	R	R
Model 3	F	F			F	F	F	R	R	R
Model 4	F	F				F		R	R	R

F = fixed, R = random, Sex = effect of sex (stallion, mare), Age = effect of age group (4, 5, 6, 7+), Year = effect of year of performance test (1, …, 20), Place = effect of place of performance test (1, …, 64), Year*Place = interaction of year and place of performance test (1, …, 78), Variety = effect of colour variant (white, black), Stud = effect of stud (National Stud Kladruby nad Labem, private studs), Classifier = effect of classifier (1, …, 26), PE = effect of permanent environment ~ N(0, $I\sigma^2_{pe}$), Animal = effect of individual ~ N(0, $A\sigma^2_a$)

using single trait models for each trait. The data set was screened as follows: sires with fewer than 3 offspring and classifiers who judged fewer than 10 horses were excluded. Performance test locations hosting fewer than 10 distinct evaluation events were also excluded. Incomplete data (performance test with unknown horses, classifier, place and year of test) were excluded from the data set as well. After filtering, 958 results from 276 horses were used to estimate the genetic parameters.

In all genetic parameter evaluation runs, the length of chains was set to 700 000 and burn in to 100 000. Every hundredth iteration was sampled for estimation of the posterior. After the selected burn in, models had achieved stabilized results.

Criteria for choosing a suitable model were deviance information criterion (DIC) statistics (Spiegelhalter et al. 2002), magnitude of the heritability estimates, and ratios of residual to phenotypic variance (σ^2_e/σ^2_p).

Estimation of breeding values. Breeding values predicted by BLUPF90 software were standardized to a mean value of 100 and a standard deviation of 20.

RESULTS AND DISCUSSION

Statistical description of the traits. Descriptive statistics for performance test traits of the Old Kladruber horse are shown in Table 2. With the exception of Type and Gender Expression and Canter, each score of the entire 10 point range did occur in the recorded data. Mean scores for the traits ranged from 6.3 to 7.8, and standard deviations were in the range 1.8–3.0. These relatively low standard deviations may suggest an insufficient use of the whole range of score. For Marathon Test, and for the First, Second, and Third Tug, the most commonly recorded scores were between 7.6 and 10.0 (Figure 1). It is uncertain whether differences between the horses actually were this small or whether the low observed variability was an artefact of the testing protocol. Regulations in the breeding program stipulated that only horses with assessments greater than five points for Type and Gender Expression and four points for each of the performance traits were accepted for reproduction.

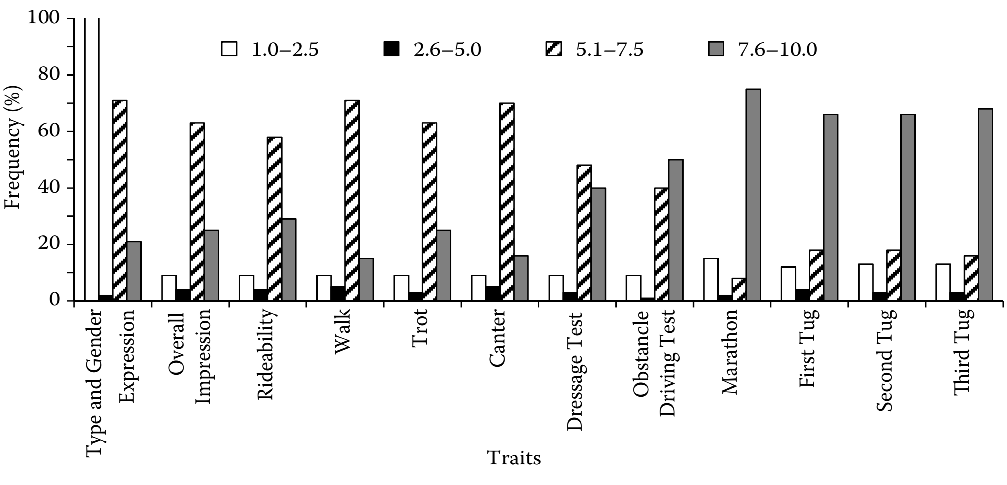

Figure 1. Range of score of all traits in performance test of the Old Kladruber horse

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Table 2. Mean, standard deviation (SD), minimum (Min), maximum (Max) values for traits evaluated in the performance test

Traits	Mean	SD	Min	Max	Skewness	Kurtosis
Type and Gender Expression	6.7	1.8	1	9	–2.4	5.1
Traits of performance						
Overall Impression	6.6	2.0	1	10	–1.9	3.0
Rideability	6.6	2.0	1	10	–1.9	2.9
Walk	6.3	1.9	1	10	–1.9	3.0
Trot	6.6	2.0	1	10	–1.9	3.2
Canter	6.3	1.9	1	9	–1.9	2.9
Dressage Test	6.9	2.1	1	10	–1.7	2.5
Obstacle Driving Test	7.2	2.2	1	10	–1.9	2.9
Marathon Test	7.8	3.0	1	10	–1.6	1.0
First Tug	7.5	2.8	1	10	–1.4	0.8
Second Tug	7.5	2.8	1	10	–1.4	0.8
Third Tug	7.7	2.9	1	10	–1.4	0.8

Pedigree data were available from 1904 to 2010 and documented four generations of ancestors of the performance tested horses. The average number of progeny registered per stallion was 6.2 with standard deviation 10.9. Figure 2 shows that about 70.5% of the stallions had fewer than 5 progeny each and only 7.4% had more than 20 progeny. Vincente et al. (2012) cited similar results in Lusitano horses – 52% of stallions had fewer than 5 registered progeny and only 10% had more than 40. Low numbers of progeny per stallion restrict the accuracy and utilization of genetic evaluation in endangered breeds because typically the population is small and closed, has a high degree of inbreeding, and often only natural mating is allowed (or insemination only to a limited extent).

Selection of a suitable model. For all four models, all of the fixed effects were statistically significant, explained from 31 to 46% of the total variability in the traits. In another study of the Old Kladruber horse (Vostry et al. 2012), fixed effects accounted for 15–34% of the total variability for linear type description. Vincente et al. (2014) indicated that in Lusitano horses, preliminary analyses of fixed effects for morphological and functional traits accounted from 14 to 35% of phenotypic variability.

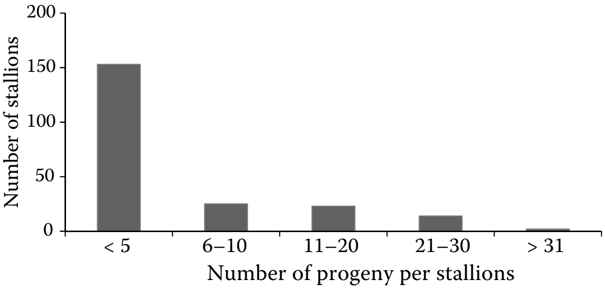

Figure 2. Number of progeny per stallion by classes for a four-generation pedigree of the Old Kladruber horse in performance test

The classification of various effects as random vs fixed varies among studies. The classifier effect is most often considered either fixed (Ducro et al. 2007b; Druml et al. 2008) or is modelled as an interaction of classifier with place or year (Druml et al. 2008). In our analyses, classifier was considered a random effect because each individual panel of classifiers made a relatively small number of assessments, possibly reducing confidence in accuracy of the estimated parameters. Additionally, preliminary analyses showed that when classifier was included as a fixed effect, heritability estimates did not change, but values of DIC were higher than if classifier was included as a random effect. In other investigations, models typically joint year and place of performance test effect (Gerber Olsson et al. 2000; Viklund et al. 2008). In our analyses of variance, the effect of year/place combination was highly significant. However, in comparisons of model 1 through 3 results, model 3 (with the combination year and place effect) was not superior to the other models. This may be attributed to the large number of years (20) and places (64) within a relatively small data set (958). The com-

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Table 3. Heritability estimates (h^2), ratios between residual and phenotypic variance (σ_e^2/σ_p^2), and values of deviance information criterion (DIC) for performance traits

Traits of performance	Model 1			Model 2			Model 3		
	h^2	ratio (%)	DIC	h^2	ratio (%)	DIC	h^2	ratio (%)	DIC
Overall Impression	0.33	42.75	2100	0.14	51.04	2225	0.08	44.03	2101
Rideability	0.40	35.42	1904	0.24	41.22	2010	0.14	35.82	1912
Walk	0.15	44.27	1924	0.08	50.01	2031	0.07	41.81	1927
Trot	0.25	46.13	2061	0.12	53.65	2171	0.08	46.29	2064
Canter	0.20	44.43	2026	0.13	50.77	2121	0.08	44.75	2025
Dressage Test	0.14	33.25	2171	0.13	34.88	2262	0.11	31.47	2192
Obstacle Driving Test	0.16	35.96	2158	0.15	37.54	2250	0.13	33.14	2186
Marathon Test	0.09	18.02	1782	0.19	18.71	1978	0.21	12.44	1840
First Tug	0.10	26.11	2292	0.09	26.90	2334	0.09	24.23	2353
Second Tug	0.10	23.09	2258	0.10	23.64	2309	0.14	20.47	2308
Third Tug	0.08	22.32	2300	0.10	22.45	2354	0.11	19.54	2354

parison of models for performance traits shows that the ratios of residual to phenotypic variance are the lowest in four cases for model 1; whereas heritability estimates were highest in eight cases (Table 3) for this model. Model 3 had the lowest residual to total phenotypic variance ratio in seven cases and the highest heritability estimate in three cases. Reduced residual variance (ratio) in model 1 and increased heritability for Overall Impression, Rideability, Trot, and Canter is a beneficial result. Novotna et al. (2014) used a similar approach to identify the most suitable variables and model for estimating genetic parameters and breeding values in sport horses in the Czech Republic. Vostry et al. (2011) tested the appropriateness of models and data set based on the values of residual variance and Akaike information criterion (AIC). In the current study, a Bayesian approach was used to test appropriateness of the models, with DIC values also taken into account. Utilizing DIC, models differing in numbers of random and fixed effects can be compared. Spiegelhalter et al. (2002) determined that values of DIC should vary by no more than two. In our study, values of DIC from model 1 were lowest in ten cases.

Based upon comparison of models 1 through 3 of heritability estimates, ratios of residual variance to phenotypic variance and DIC values (Table 3), we concluded that model 2 was clearly the least appropriate for subsequent analyses because it generally had higher residual variance proportions and lower heritability estimates than models 1 and 3. Model 3 accounted well for a variation of fixed effects (lower ratio proportions) but also lower heritability estimates if compared to model 1. Consequently, model 1 was chosen for further analyses, and subsequent results are based only on those results.

Heritability estimates. The highest heritability estimates were for Rideability and Overall Impression, 0.40 and 0.33, respectively. For the Gaits category of traits, estimates were 0.15 for Walk, 0.25 for Trot and 0.20 for Canter. Suontama et al. (2011) reported somewhat lower heritabilities for Walk and Trot (0.08 and 0.19) for Finnhorse and Standardbred trotter foals. Heritability estimates in other studies were slightly higher. For example, Gerber Olsson et al. (2000) and Olsson et al. (2008) reported heritabilities ranging from 0.39 to 0.46 for performance traits in Swedish Warmblood stallions, while Viklund et al. (2008) published estimates ranging from 0.37 to 0.45 for performance traits and from 0.31 to 0.41 for riding quality test of young German warmblood horses. As well, Becker et al. (2011) reported heritability ranging from 0.33 to 0.49 for performance test traits in German warmblood mares. Possible reasons for these slightly higher heritabilities than those in the current study are that Old Kladruber horses are evaluated in field performance tests; whereas in the previously cited reports, testing was conducted under breeding station conditions, which may have reduced incidental sources of variation. Heritability estimates in the current study for Dres-

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Table 4. Solutions for the fixed effects of sex and age estimated in genetic analysis of traits evaluated during performance tests of Old Kladruber horses

Traits	Sex		Age of horse (years)			
	S	M	4	5	6	7+
Type and Gender Expression	1.64	1.35	1.45	1.45	1.11	1.32
Traits of performance						
Overall Impression	1.16	0.92	1.00	1.00	0.84	0.78
Rideability	1.18	0.90	1.02	0.99	0.87	0.87
Walk	1.06	0.91	0.98	0.97	0.95	0.68
Trot	1.12	0.92	1.00	0.97	0.87	0.76
Canter	1.14	0.87	0.96	0.97	0.82	0.73
Dressage Test	1.22	0.97	1.00	1.08	0.88	0.93
Obstacle Driving Test	1.25	1.02	1.08	1.12	0.91	1.04
Marathon Test	1.27	1.15	1.26	1.30	0.98	1.34
First Tug	1.38	1.02	1.04	1.23	1.39	1.07
Second Tug	1.41	1.03	1.00	1.31	1.47	1.15
Third Tug	1.41	1.04	1.00	1.30	1.49	1.13

M = mare, S = stallion

sage Test, Obstacle Driving Test, and Marathon Test were 0.14, 0.16, and 0.09, respectively. First, Second, and Third Tug had low estimates of 0.10, 0.10, and 0.08.

Our heritability estimate for trait Type and Gender Expression in the Old Kladruber horse was 0.18. Suontama et al. (2011) reported substantially higher estimates (0.28 to 0.38) for Finnhorse and Standardbred trotter foals, and Viklund et al. (2008) reported heritability estimates ranging from 0.33 to 0.38 for Riding Horse Quality Test in three time periods for Swedish Warmblood horses.

Differences among heritability estimates for gaits and Type and Gender Expression may be magnified because the Old Kladruber horse population is small, many of the animals are related, and many are substantially inbred, leading to an expected reduction in genetic variance, leading to reduced additive genetic variance, leading to a lower numeric value of heritability. Another possible reason that heritability estimates in the current study are lower than those in investigations cited above may be that pre-selection of horses could significantly reduce additive genetic variance and lead to underestimated heritabilities in the population of interest (Janssens et al. 1997; Viklund et al. 2010). Pre-selection did occur in our study population in that only 30% of the population of Old Kladruber horses had undergone a performance test. Other investigations that have reported substantial pre-selection and its potential impacts include those of Gomez et al. (2012) in the Spanish heavy horse, Druml et al. (2008) in Noriker draught horses, and Vostry et al. (2012) in the Old Kladruber horse.

Estimation of breeding values. Solutions for the fixed effects of sex and age group in our statistical analyses are shown in Table 4. These results are

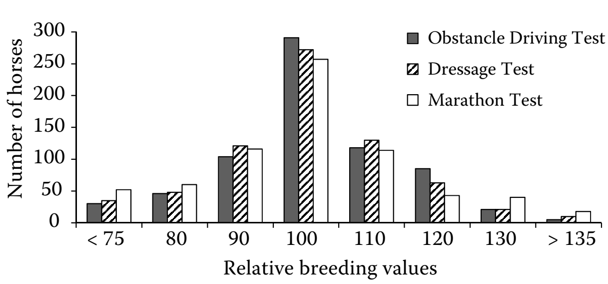

Figure 3. Distribution of relative breeding values for carriage driveability

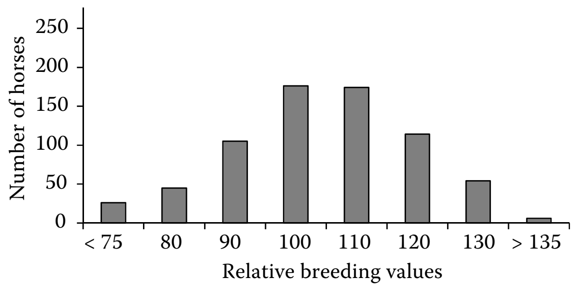

Figure 4. Distribution of relative breeding values for Type and Gender Expression

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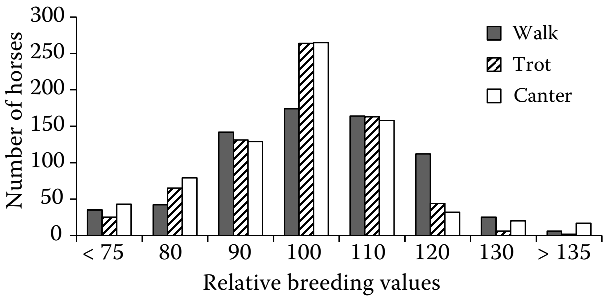

Figure 5. Distribution of relative breeding values for gaits

estimated breeding values (without standardization), for the whole population i.e. stallions, mares, four-year olds, etc. Stallions are more pronounced for Type and Gender Expression than mares. The best manifestation had four- and five-year-old horses except Reliability in Tug. The results in this trait suggested that six-year-old horses were more reliable (stronger) than four- or five-year olds. Viklund et al. (2008) reported that five-year-old horses were slightly higher scoring in the Riding Horse Quality Test than four-year-old horses. This small difference may be attributable to a longer training period and advanced maturation of the horse.

Distributions of estimated breeding values for some traits are shown in Figures 3–5. The observed distributions were approximately normal for all traits. In Figure 4, the majority of estimated breeding values ranges from 90 to 120, suggesting that the characteristics of the breed – type and gender expression – are maintained.

CONCLUSION

The results of this study showed that the statistical model (model 1) which contained effects for age, year, place of test, classifier, permanent environment, and additive genetic effect was more suitable for the estimation of genetic parameters than alternative models. It had the lowest values of DIC, the highest heritability estimates, and the lowest ratios of residual variance to phenotypic variance. Heritability estimates from this model were moderately high only for the traits Overall Impression (0.33) and Rideability (0.40). Heritability estimates ranging from 0.08 to 0.25 were found for the other performance traits. The heritability estimate for Type and Gender Expression was 0.18. These heritability and estimated breeding value results are a function of the animal population (which is small and closed to outside breeding) and its breeding program (pre-selection of animals to be tested). Primarily attention must be given to maintaining genetic variability, minimizing the rate of inbreeding, and maintaining fitness of the population. Selection among horses using estimated breeding values would allow maintaining the characteristics of the breed such as type and gender expression or trot (action of the legs, cadence) which is in accordance with the breeding objective, i.e. conservation of the Old Kladruber horse as working breed with primary use in sporting events such as carriage driving performance and dressage.

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