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Estimates of Genetic Parameters and Environmental Effects for Measures of Hunting Performance in Finnish Hounds¹

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ABSTRACT: Data from field trials of Finnish Hounds between 1988 and 1992 in Finland were used to estimate genetic parameters and environmental effects for measures of hunting performance using REML procedures and an animal model. The original data set included 28,791 field trial records from 5,666 dogs. Males and females had equal hunting performance, whereas experience acquired by age improved trial results compared with results for young dogs ($P < .001$). Results were mostly better on snow than on bare ground ($P < .001$), and testing areas, years, months, and their interactions affected results ($P < .001$). Estimates of heritabilities and repeatabilities were low for most of the 28 measures, mainly due to

large residual variances. The highest heritabilities were for frequency of tonguing ($h^2 = .15$), pursuit score ($h^2 = .13$), tongue score ($h^2 = .13$), ghost trailing score ($h^2 = .12$), and merit and final score (both $h^2 = .11$). Estimates of phenotypic and genetic correlations were positive and moderate or high for search scores, pursuit scores, and final scores but lower for other studied measures. The results suggest that, due to low heritabilities, evaluation of breeding values for Finnish Hounds with respect to their hunting ability should be based on animal model BLUP methods instead of mere performance testing. The evaluation system of field trials should also be revised for more reliability.

Key Words: Dogs, Behavior, Environment, Genetic Parameters

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Introduction

The Finnish Hound is the most popular dog breed in Finland, with approximately 4,400 pups registered each year. The great majority of Finnish Hounds are used actively in hunting, and thus the hunting properties of the breed are very important criteria when selecting breeding individuals. Hunting ability is judged in field trials, and the selection of breeding individuals is based mainly on dogs' own test results or those of their progeny.

There are over 30 measures to be evaluated in hunting trials, covering the most important aspects of hunting performance. The extent to which these measures actually describe genetic differences between dogs is unknown. Because the trials are held under "wild" conditions, many environmental effects influence trial results and thus obscure the evaluation

of the genetic level of dogs. In addition, most measures are subjectively evaluated scores; objective measures cannot readily be found for field circumstances. Thus, there is a need to clarify the present system of evaluation by finding the most suitable measures to describe important hunting traits.

The purpose of this study was to estimate heritabilities and repeatabilities for all measures of hunting performance. After screening of the most informative measures, genetic correlations among them and environmental effects on them were also estimated.

Materials and Methods

Field Trials for Finnish Hounds. The Finnish Hound is a scent hound that hunts singly, with its main game being hare and, to some extent, fox. Field trials are held separately for hare-hunting and fox-hunting dogs, but the vast majority of trials are for hare hunters only. The aim of the field trials is to create circumstances that represent actual hunting situations as closely as possible.

Trials consist of two to four heats per dog that are taken outdoors on normal hunting grounds, mainly forested landscapes. Heats can be run during the same day or on two consecutive days, but 2-d trials are most

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common. Trial areas are drawn for each heat so that only one dog at a time is running in each area, although the same areas may be used later for different dogs. All game in areas is naturally occurring. The dogs' hunting abilities are evaluated in a test situation by at least two judges, who award scores for various measures of hunting performance. The final result (i.e., the trial record of the tried dog) is formed by combining records of individual heats.

Measures of Hunting Performance. Search score describe a dog's overall performance when searching for trail and while trailing game before turning it out. Good search work resulting in high score is methodical and energetic, and the dog shows adequate cooperation with its handler. Duration of search, eagerness to work, range covered, and efficiency of search work are also recorded and evaluated separately.

Pursuit begins when the dog drives game to its feet. Pursuit score is the most important measure used to describe it, with long, continuous pursuit resulting in high score. Also duration of pursuit, general impression of a dog's style, speed on trail, and continuity of pursuit are recorded and evaluated separately.

A dog informs its handler of events during pursuit by giving tongue. In the evaluation of a dog's tongue score, good audibility and beautiful voice result in high score. Audibility, count of different tones in voice, frequency of barks, sex character of tongue (i.e., how typical the voice is for a dog's sex), and tonguing's descriptiveness of distance between dog and its game are evaluated separately.

A dog is to give tongue only during pursuit. Tonguing during search is considered a serious fault, because it misleads the handler into thinking game is out when the dog is only ghost trailing. In trials, ghost trailing is evaluated according to its seriousness either as excessive (resembles pursuit, continues long time) or slight (occasional tonguing during search). For this study, both were also combined as one ghost trailing score with two classes: no ghost trailing and ghost trailing to whatever extent.

When a dog loses trail, it is said to check. A good hunting dog works industriously to find the trail again, resulting in a high score for eagerness and effectiveness of check work. The dog's obedience, behavior toward its handler and other humans, ability to concentrate on its work, and cooperation with its handler are evaluated during the entire trial, with good character resulting in high scores.

Several important traits are summed for a merit score, fault score, and final score that form the final result for a dog in trial. Merit score consists of search score, pursuit score, general impression of pursuit, and tongue score. Fault score includes, in addition to ghost trailing, other faults of hunting work: backtracking, lack of endurance, and babbling (i.e., faulty tonguing during pursuit). The final score for a dog in trial is calculated as merit score minus fault score.

Materials. The data consisted of field trial records for Finnish Hounds between the years 1988 and 1992 from 2-d hare-hunting trials in Finland; 28,791 records were obtained with 5,666 Finnish Hounds. In some analyses records from individual heats were used as well. This data set included 82,064 records from individual heats on the 5,666 dogs. The data set used for each measure is indicated in Table 1 with a letter T (data set composed of trial records) or by a letter H (data set composed of individual heat records). Because all measures were not necessarily evaluated in every test situation, actual numbers of observations vary between measures as indicated in Table 1 (i.e., from 28,791 to 21,455 for trial record data set, and from 82,064 to 17,444 for the heat record data set).

Pedigree information used in the analyses was obtained from the register of Finnish Hounds updated by the Finnish Kennel Club. The register included the identification number of the dog and its parents, sex code, and birth date, if known. There were 84,337 Finnish Hounds in the register, of which 80,688 had known parents.

The percentage of Finnish Hounds that had taken part in the field trials was 18.8. The evaluation of the percentage of participants was based on dogs born between 1987 and 1989 because dogs could have been entered in trials before the age of 3 yr during the years the data covered. Average number of trial records per dog was 5.1, maximum number per dog was 40, and 27.6% of the dogs had only one record in the data set (Table 2).

The original pedigree and data sets were used when examining the effect of environment on the measures. However, due to limitations in computer capacity, data sets used in the estimation of genetic parameters had to be restricted. The data sets used for estimating heritabilities and repeatabilities included only records of dogs with at least three field trial records. Depending on measure, the number of trial records was thus reduced from 25,286 to 19,178, the number of heat records from 73,950 to 16,103, and the number of dogs from 3,223 to 2,863. The data sets used for estimating phenotypic and genetic correlations included only records of dogs with at least four trial records. The number of trial records was thus reduced from 23,751 to 17,980 and the number of tested dogs from 2,651 to 2,648. Pedigrees of the tested dogs could be taken into account only for two generations (parents and grandparents), resulting in 3,661 additional relatives included in the pedigree file when estimating heritabilities and repeatabilities and 3,350 additional relatives in the pedigree file when estimating genetic and phenotypic correlations.

The various measures of hunting performance were divided into six groups according to the specific hunting trait that they were supposed to describe (Table 1). The total number of the measures in this

Table 1. Measures of hunting performance and their number of observations (N), means, standard deviations (SD), and coefficients of variation (CV)^a

Measure of hunting performance	N	Mean	SD	CV
Search				
Search score, pts 1 to 10				
From trials (T)	28,532	7.31	1.98	27.1
From heats (H)	78,933	7.17	2.74	38.2
Duration, min 1 to 120 (H)	81,842	64.42	44.26	68.7
Eagerness, pts 1 to 9 (H)	34,746	6.56	1.37	20.9
Range, pts 1 to 9 (H)	36,193	5.65	1.33	23.5
Efficiency, pts 1 to 9 (H)	29,239	6.59	1.95	29.6
Pursuit				
Pursuit score, pts .1 to 70 (T)	21,455	40.45	16.99	42.0
Duration, min 1 to 120 (H)	56,722	72.85	35.53	48.8
General impression, pts 1 to 10				
From trials (T)	26,695	5.37	2.25	41.9
From heats (H)	56,758	5.62	2.65	47.2
Speed, pts 1 to 9 (H)	49,736	5.84	1.07	18.3
Continuity, pts 1 to 9 (H)	51,528	5.54	1.93	34.8
Tongue				
Tongue score, pts 1 to 10				
From trials (T)	26,800	6.86	.98	14.3
From heats (H)	57,859	6.91	1.06	15.3
Audibility, pts 1 to 9 (H)	57,260	6.56	1.30	19.8
Count of tones, pts 1 to 9 (H)	56,102	4.94	1.62	32.8
Frequency, pts 1 to 9 (H)	55,061	5.74	1.42	24.7
Sex character, pts 1 to 9 (H)	57,196	7.68	1.38	18.0
Descriptiveness, pts 1 to 9 (H)	17,444	5.91	1.52	25.7
Ghost trailing				
Excessive, binomial				
From trials (T)	28,791	—	—	—
From heats (H)	82,064	—	—	—
Slight, binomial (H)	82,064	—	—	—
Ghost training score, binomial (T)	28,791	—	—	—
Other traits				
Check work				
Eagerness, pts 1 to 9 (H)	31,101	6.78	1.28	18.9
Effectiveness, pts 1 to 9 (H)	27,605	5.61	1.70	30.9
Character				
Obedience, pts 1 to 9 (H)	56,181	6.55	1.41	21.5
Behavior, pts 1 to 9 (H)	68,804	6.64	1.15	17.3
Concentration, pts 1 to 9 (H)	29,388	6.54	1.14	17.4
Cooperation, pts 1 to 9 (H)	21,580	7.33	1.26	17.2
Combined traits				
Merit score, pts 1 to 100 (T)	24,150	55.59	24.01	43.2
Fault score, binomial (T)	28,791	—	—	—
Final score, pts 1 to 100 (T)	24,146	55.49	23.98	43.2

^aAbbreviations used: H, heats; pts, points; T, trials.

study was 28. Most scores were subjectively evaluated with a scale from 1 to 10 or 1 to 9 (Table 1).

Due to the skewness of the original distributions, measures describing ghost trailing were analyzed binomially. Dogs had been found to give tongue excessively during search in 7.4% of the trials and in 3.4% of the heats. Dogs received marks for slight tonguing during search in 5.4% of the heats. Overall, dogs exhibited ghost trailing at least to some extent in 17.2% of the trials. Restriction of the data set slightly increased frequencies of ghost trailing relative to the unrestricted data, but the differences were negligible.

In addition to the evaluated measures of hunting performance, the data included information on date of

trial, kennel district where the trial took place, and snow conditions during the trial. These were used to classify fixed effects for the model used in the analyses (i.e., age of dog, snow situation, and the combined effect of testing area, testing year and testing month).

Statistical Methods. Variance and covariance components for measures of hunting performance were estimated by applying the Restricted Maximum Likelihood (**REML**) method (Patterson and Thompson, 1971). Fixed effects were tested using the *F*-test. Necessary *F*-values were calculated using residual variances, which were estimated assuming mixed models that included and excluded the studied fixed effect. The (co)variance components were estimated,

Table 2. Distribution of dogs by number of records

No. of trial records	No. of dogs	%
1	1,562	27.57
2-4	1,941	34.26
5-9	1,227	21.66
10-19	817	14.42
20-29	112	1.97
≥30	7	.12
Total	5,666	100.00

and solutions for fixed effects were calculated based on the animal model. Statistical analyses were performed using the program package PEST (Groeneveld, 1990) and variance component estimation program REML VCE (Groeneveld, 1993), based on the derivative-free REML procedure. Standard errors for heritabilities, repeatabilities, and genetic correlations were calculated with program package REML VCE 3.2 (Groeneveld, 1996).

Univariate analyses were used for estimating heritabilities and repeatabilities, because computer capacity did not allow the use of "heat measures" in bivariate analyses. Likewise, genetic and phenotypic correlations were estimated with bivariate analyses instead of multivariate analyses. Further restrictions on data sets might have enabled the use of multivariate analyses, but it was feared they would eventually result in bias due to selectedness of dogs included, and they were rejected.

The following linear model was assumed in uni- and bivariate analyses when estimating variance and covariance components and solutions for fixed effects:

$$y_{ijklmn} = \mu + \text{sex}_i + \text{age}_j + \text{snow}_k + \text{area-year-month}_l + a_m + \text{pe}_m + \epsilon_{ijklmn}$$

where y_{ijklmn} = a record for a measure of hunting performance, μ = overall mean, sex_i = fixed effect of the i^{th} sex ($i = 1, 2$), age_j = fixed effect of the j^{th} age class ($j = 1-9$), snow_k = fixed effect of the k^{th} snow class ($k = 1, 2$), area-year-month_l = fixed effect of the l^{th} testing area-year-month subclass ($l = 1-75$), a_m = random additive genetic effect of the m^{th} animal, pe_m = random permanent environmental effect associated with the m^{th} animal, and ϵ_{ijklmn} = random residual effect.

The distributions of a , pe , and ϵ were assumed to be multivariate normal with zero means and with $\text{Var}(\mathbf{a}) = \mathbf{A}\sigma_a^2$, $\text{Var}(\mathbf{pe}) = \mathbf{I}\sigma_{\text{pe}}^2$, and $\text{Var}(\epsilon) = \mathbf{I}\sigma_\epsilon^2$. Covariances among \mathbf{a} , \mathbf{pe} and ϵ were assumed to be zero.

Classification of Fixed Effects. Sexes were coded as male or female. For age of the tested dogs there were nine categories (1, 2, 3, 4, 5, 6, 7, 8 and ≥9 yr). Snow situation was coded in two classes, bare ground or snow.

Area-year-month subclasses included the effects of testing area, testing year, testing month, and interactions between these effects. Testing areas were formed by grouping the 19 kennel districts of Finland into five areas; the criteria were the geographical closeness of districts and the general similarity of climate. Testing years were formed from testing seasons by combining records from January and February with records from the previous autumn, resulting in five classes (1988, 1989, 1990, 1991, and 1992). Testing months were combined in three categories (1 = September, October; 2 = November, December; and 3 = January, February). The number of testing areas, testing years, and testing month classes resulted in 75 area-year-month subclasses. The largest subclass included 814 observations and the smallest 54 observations.

Results and Discussion

Means and Variation. Means of most scores were high (Table 1). The sex character of tongue had the highest mean (almost 7.7 points, with a maximum score of 9), and various other scores also had means well over 6 points. Low points were rare in all subjectively measured scores. The high means were probably the result of judges unknowingly adjusting dogs' performance to unfavorable environment, trying thus to do justice to dogs. In some measures this was even recommended in rules, whereas it was forbidden to let good environment affect the judging negatively.

Coefficients of variation varied notably among measures, with CV of 25% dividing the measures approximately in half (Table 1). Measures describing different aspects of tongue as well as those describing the character of dog were least variable, with most dogs evaluated as "normal" and very few classified in either extremity. In contrast, the most objectively evaluated measures, especially duration of search and duration of pursuit, and the measures connected with them, showed considerable variation relative to their means.

Restrictions on the data set raised the means and lowered the standard deviations relative to those of the unrestricted data, as was to be expected due to the selectedness of dogs included. However, the changes were negligible.

Environmental Effects. For the examination of environmental effects on measures of hunting performance, five measures (considered as representative of the 28) were selected: search score, pursuit score, tongue score, binomial ghost trailing score, and final score.

The effect of sex was not statistically significant on any of the studied measures (Table 3). The effect of snow was highly significant on all studied measures except for ghost trailing (Table 3). Performances were poorer on bare ground except for tongue scores, which

Table 3. Effects of sex and snow, expressed relative to the performance of males or to the performance on bare ground

	Sex		Significance	Snow		Significance
	Males	Females		Bare	Snow	
Search score						
N ^a	13,903	14,629		15,519	13,013	
Dev	.00	-.16	NS	.00	.40	***
Pursuit score						
N	10,608	10,847		11,436	10,019	
Dev	.00	.47	NS	.00	7.35	***
Tongue score						
N	13,155	13,645		14,608	12,192	
Dev	.00	-.05	NS	.00	-.21	***
Ghost trailing score, binomial						
N	13,924	14,655		15,532	13,047	
Dev	.00	.01	NS	.00	.03	NS
Final score						
N	11,838	12,308		13,451	10,695	
Dev	.00	-.08	NS	.00	10.46	***

^aAbbreviations used: Dev, deviation from the comparison level; N, number of observations; NS, not significant.

*** $P < .001$.

were lower on snow. This was probably the result of snow muffling sounds in the forest and weakening the audibility of tongue. In practice, differences between snow classes were small in tongue as well as search scores. They were, however, very large in pursuit scores and in final scores, which were formed mostly of pursuit scores. Snow might have eased following the scent line for the dog and so enabled a continuous pursuit, which results in high scores.

The effect of age was highly significant on all studied measures (Table 4). Differences between the poorest age class (1-yr-olds) and the best age classes were also significant from a practical point of view, save perhaps for tongue score. Search and tongue scores improved up to the age of 4 yr and remained more or less constant after that, implying that these traits required a certain amount of experience to reach the potential of the dog but were not improved by further training. In contrast, measures related to pursuit improved throughout the career of the dog, and there were no signs of weakening performances even in the oldest age classes. The same trend was true for the binomial scores of ghost trailing, thus suggesting a possible association between good hunting performances and the habit of giving tongue during search.

The effect of area-year-month subclasses was highly significant on all studied measures of hunting performance. Differences between the extreme subclasses were very large, although most subclasses were close to each other. The difference between the best and the poorest subclass was almost 2 points for search score, over 20 points for pursuit score, almost .7 points for tongue score, and over 29 points for final score. The difference was remarkable also in ghost trailing score.

Interactions between the three effects were obvious (i.e., the effects of years and months were different in different parts of the country). However, results tended to be better in January and February than in the autumn months. Likewise, the kennel district of Southern Ostrobothnia, which alone formed one of the areas, was superior to other areas to a great degree.

Heritabilities and Repeatabilities. Estimates of heritability from univariate analyses were low for most measures of hunting performance (Table 5). This was mainly due to large residual variances, because almost all measures showed at least some additive genetic variation. This phenomenon was particularly noticeable for duration of search in spite of it being objectively measured. As expected, "trial-measures" that combined records of several heats tended to have reduced residual variances and higher heritabilities than "heat measures," but most measures proved to be of limited use for the evaluation of breeding values of Finnish Hounds because of their low heritabilities.

However, in almost every group there were some measures that had moderate heritabilities (Table 5). Most of these measures are considered relatively important when evaluating the hunting ability of a dog and would thus be well suited for intensified use in breeding. Even these heritability estimates were so low that performance testing alone is an unreliable method, and some other technique such as animal model BLUP should be used.

Repeatabilities were low for most measures of hunting performance, implying that the evaluation system of dogs' hunting ability might have been unreliable (Table 5). In general, measures that had highest heritabilities also had highest repeatabilities.

Table 4. Effect of age, expressed relative to the performance of 1-year-old dogs

	Age, yr									Significance	
	1	2	3	4	5	6	7	8	≥9		
Search score											
N ^a	370	2,939	5,013	5,322	4,906	3,985	2,799	1,702	1,496		
Dev	.00	.39	.48	.59	.57	.59	.71	.62	.53		***
Pursuit score											
N	271	2,206	3,773	3,987	3,678	3,036	2,111	1,280	1,113		
Dev	.00	3.63	5.97	8.34	10.40	12.57	13.65	13.90	15.49		***
Tongue score											
N	336	2,721	4,639	4,992	4,615	3,773	2,680	1,621	1,423		
Dev	.00	.12	.21	.28	.36	.30	.31	.28	.26		***
Ghost trailing score, binomial											
N	372	2,946	5,027	5,336	4,913	3,986	2,800	1,701	1,498		
Dev	.00	.00	.02	.05	.09	.11	.14	.19	.22		***
Final score											
N	324	2,534	4,268	4,481	4,131	3,395	2,355	1,412	1,246		
Dev	.00	5.67	9.32	12.70	15.20	17.72	19.54	20.00	21.42		***

^aAbbreviations used: Dev, deviation from the comparison level; N, number of observations.

*** $P < .001$.

This stresses the importance of reliable evaluation of measures if they are to be used to describe genetic differences between dogs. Objectivity of measures was not a guarantee of reliability, because the highest repeatabilities were for tongue, a subjective trait.

Low estimates of repeatability and heritability for measures of hunting performance were probably due to the great effect of environment on the field trial results, because trials are arranged in widely different areas, weather conditions, and even under slightly different rules. Some of the most important environmental effects could be taken into account in the model that was used in the estimation of parameters, but several possibly important factors had to be left out due to lack of information.

Because standardization of environment during field trials is not realistic, attention should be paid to collect more information on environmental factors. For example, more specific and objective information on weather conditions such as temperature or humidity, or information on judges who evaluated dogs in trials, could serve to reduce residual variance relative to other sources of variation. Genetic parameters should also be estimated for annually summarized field trial records in order to find out whether they show more genetic variation than the individual measures of hunting performance through the reduction of the effect of environment.

The most effective way to make the scoring system more a reliable source of information in breeding would be clarification of the system of evaluation. To ease the evaluation of traits for judges, the number of judged scores should be reduced to include only those scores that clearly portray genetic differences among dogs. The scale of points could be narrowed from 1 to 10 to 1 to 5. Judges should also be trained to use the

scale better. New, more objectively defined measures might be considered to improve the reliability of the scoring system as well. However, because the majority of measures are likely to remain more or less subjectively evaluated, heritabilities and repeatabilities evaluated from field trial data are also likely to remain relatively low. This has been a general tendency also in studies concerning other hunting dog breeds and their field trial results (Vangen and Klemetsdal 1988; Kreiner et al., 1992; Karjalainen et al., 1994).

Genetic Correlations. On the basis of the univariate analyses, five measures of hunting performance (search score, pursuit score, tongue score, binomial ghost trailing score, and final score) were selected to study correlations among them. The measures were chosen to represent the most important hunting traits of the Finnish Hound. Apart from search score, the chosen measures also had the highest heritability estimates among all measures of hunting performance.

Heritabilities and repeatabilities estimated assuming a bivariate model differed only marginally from corresponding estimates from univariate models (Table 6; data not shown for repeatabilities). Only heritability and repeatability estimates of pursuit score and final score were slightly affected when they were analyzed together, thus indicating a close correlation between these two measures.

Phenotypic and genetic correlations between pursuit score and final score were estimated to be 1.00 (Table 6). Final score was thus more or less an unnecessary source of information when used in connection with pursuit score. In practice, approximately 70% of dog's final score is formed of pursuit score, so the connection between these measures could be expected to be strong.

Table 5. Variances (σ_e^2 , σ_{pe}^2 , σ_a^2), repeatabilities (r), heritabilities (h^2), and standard errors (se_r , se_h^2) from univariate analyses

Measure of hunting performance	N	No. of dogs	σ_e^2	σ_{pe}^2	σ_a^2	r	se_r	h^2	se_h^2
Search									
Search score									
From trials	25,248	3,223	3.262	.096	.184	.08	.01	.05	.01
From heats	71,075	3,223	6.820	.144	.201	.05	.01	.03	.00
Duration	73,742	3,223	1,783.408	24.313	39.646	.03	.01	.02	.00
Eagerness	31,029	3,155	1.437	.176	.060	.14	.01	.04	.01
Range	32,279	3,157	1.397	.213	.118	.19	.02	.07	.01
Effectiveness	26,376	3,142	3.449	.107	.097	.06	.01	.03	.01
Pursuit									
Pursuit score									
Duration	19,178	3,195	182.426	10.848	28.995	.18	.02	.13	.01
Duration	51,519	3,221	980.129	57.611	76.228	.12	.01	.07	.01
General impression									
From trials	23,782	3,221	3.750	.315	.408	.16	.02	.09	.01
From heats	51,591	3,221	5.695	.330	.437	.12	.01	.07	.01
Speed	45,461	3,215	.964	.095	.044	.13	.01	.04	.01
Continuity	47,078	3,218	3.230	.161	.228	.11	.01	.06	.01
Tongue									
Tongue score									
From trials	23,878	3,221	.554	.198	.116	.36	.03	.13	.01
From heats	52,623	3,221	.777	.221	.117	.30	.02	.11	.01
Audibility	52,116	3,221	1.258	.293	.136	.25	.02	.08	.01
Count of tones	51,092	3,219	1.863	.469	.225	.27	.02	.09	.01
Frequency	50,142	3,221	1.422	.231	.280	.27	.02	.15	.01
Sex character	52,042	3,221	1.030	.794	.044	.45	.02	.02	.01
Descriptiveness	16,103	2,863	1.817	.267	.163	.19	.02	.07	.01
Ghost trailing									
Excessive									
From trials	25,286	3,223	.051	.012	.005	.24	.02	.07	.01
From heats	73,950	3,223	.028	.003	.001	.13	.01	.03	.01
Slight	73,631	3,223	.047	.003	.002	.09	.02	.04	.01
Ghost trailing score	25,286	3,223	.094	.028	.015	.32	.02	.12	.01
Other traits									
Check work									
Eagerness	28,227	3,185	1.265	.059	.063	.09	.01	.05	.01
Effectiveness	25,053	3,151	2.635	.081	.072	.06	.01	.03	.01
Character									
Obedience	51,173	3,217	1.645	.207	.037	.13	.01	.02	.00
Behavior	62,356	3,223	.605	.032	.009	.06	.01	.01	.00
Concentration	26,824	3,114	.804	.054	.011	.08	.01	.01	.01
Cooperation	19,571	2,918	1.159	.167	.031	.15	.01	.02	.01
Combined traits									
Merit score	21,479	3,216	371.287	25.540	48.550	.17	.02	.11	.01
Fault score, binomial	21,479	3,216	.067	.013	.004	.20	.01	.05	.01
Final score	21,477	3,216	371.662	24.552	48.052	.16	.02	.11	.01

Both final score's and pursuit score's correlations with search score were relatively high (Table 6). Because correlations between these measures were positive, selection based on pursuit and (or) final score would result in genetic gain in search score as well. However, phenotypic and genetic correlations of final and pursuit scores with tongue score and ghost trailing score were low; thus neither final nor pursuit scores alone represented all aspects of dogs' hunting abilities.

Correlations between tongue score and other measures were low, indicating that tongue traits are

separate from other hunting traits. This stresses the necessity to consider tonguing separately in the evaluation of breeding animals, as measures describing other hunting traits cannot be used to predict the level of dog in giving tongue. The same applies to ghost trailing score. However, the positive genetic correlations of ghost trailing score with pursuit score and final score may be strong enough to hamper the progress of breeding work when trying to lessen ghost trailing and at the same time improve pursuit results.

Table 6. Estimates of heritabilities (diagonal), genetic correlations (above diagonal) with standard errors in parentheses, and phenotypic correlations (below diagonal) from bivariate analyses

Measure of hunting performance	1.	2.	3.	4.	5.
1. Search score	.05	.60 (± .06)	.29 (± .08)	.05 (± .09)	.75 (± .05)
2. Pursuit score	.43	.12	.07 (± .08)	.44 (± .06)	1.00 (± .00)
3. Tongue score	.14	.22	.13	-.12 (± .08)	.26 (± .07)
4. Ghost trailing score, binomial	-.06	.14	.02	.12	.37 (± .07)
5. Final score	.63	1.00	.29	.11	.10

Implications

Because of the low heritabilities and repeatabilities, the evaluation of breeding values of Finnish Hounds should be based on animal model best linear unbiased prediction methods that combine information from all available relatives and simultaneously account for differences in environmental effects. The measures best suited for such use would be tongue, ghost trailing, and pursuit score. To allow a simple use in selection, single measures could be combined in an index representing a dog's overall genetic merit for hunting ability. The evaluation system of field trials should also be revised to improve reliability.

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