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Environmental effects and genetic parameters for measurements of hunting performance in the Finnish Spitz

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Introduction

The hunting ability of the Finnish Spitz, a hunting dog breed mainly used in grouse hunting, is judged by practical hunting ability tests. The purpose of these tests is to develop the quality of the breed for bird hunting. The selection of breeding individuals is based on their average test results or those of their progeny. Sometimes a good performance in a single, well-known hunting test is sufficient to lead to a demand for breeding purposes.

The tests are arranged outdoors in forests. The aim is to create circumstances that represent, as closely as possible, actual hunting situations. As the dogs are evaluated in nature, many environmental effects influence the test results. Dozens of different measures describing the hunting ability of the Finnish Spitz are evaluated in a test situation by one judge. Most of these measures are based on subjectively evaluated scores. As expected, heritability estimates for most of the measures were found to be low in a previous study (KARJALAINEN et al. 1994). However, they could be considered to be moderate for barking frequency and searching scores. Genetic differences between the dogs were also obvious in barking, following, total impression, total merit scores, and final scores.

The purpose of this study was to examine the effects of environmental factors on the seven most heritable measures of hunting performance, and to estimate their genetic parameters using bivariate REML analysis.

Materials and methods

Materials

The data set consisted of hunting test records for Finnish Spitz, from hunting trials in Finland, between 1978 and 1992. Over this 15-year period, a total of 12432 hunting test records were obtained from 1683 Spitzes. The average number of test records was 7.4 per dog, the maximum 67. However, 26.1% of the Spitzes tested had only one test record (Table 1).

The pedigree information used in the statistical analyses was the register of the Finnish Spitz, updated by the Finnish Kennel Club. The register included the identification (ID) number of the dog and its parents, the sex code, and the birth date if known. The total number of the Spitzes in the register was 28 370, of which 27 676 had known parents.

The proportion of Finnish Spitzes taking part in the hunting-performance tests was low, about 8.5%. The study was based on dogs born between 1978 and 1988, because they could have been evaluated in a hunting test during the years covered by the data.

In addition to the evaluated hunting-performance measures, the data included information on testing data and kennel district. Since 1988, the data also included information about weather conditions at the tests, i.e. wind and rain; these factors were recorded using codes.

The age of the Finnish Spitzes in the data set of hunting-performance records varied from

Test results (no.)	Dogs (no.)	Dogs (%)
1	440	26.14
2-4	498	29.59
5–9	312	18.54
10-19	262	15.57
20-29	123	7.31
30–70	48	2.85
Total	1683	100.00

Table 1. Distribution of dogs by the number of their test results

9 months to 11.8 years. The average age of the dogs in the hunting-ability tests was 4.2 years. Most of the dogs tested were 2–5 years old.

Testing for bird hunting starts in September and ends in the following February. Most of the dogs were tested in September. The number of hunting-test records per test year doubled from 1978 to 1992; in 1978 there were 439 test records from 176 dogs, in 1992 there were 1057 records from 386 dogs. The geographical distribution of test records and tested dogs was unbalanced. The numbers of test records and dogs were highest in southeastern and western Finland, and lowest in southern Finland.

The information on testing dates and kennel districts was missing for 623 and 679 test records, respectively. All test records with missing information were excluded from the data studied. After this, the data set consisted of 11 751 test records from 1625 dogs. Not all measurements of hunting performance were necessarily evaluated in a particular test situation, and this also caused restrictions to the data. Thus, the number of test records varied from 8 999 to 11 099, and the number of dogs from 1411 to 1594, depending on the measure. The research data set that included weather condition information was smaller, i.e. 3308–4150 test results obtained from 663–767 dogs.

Traits in the study

In the previous study (KARJALAINEN et al 1994), the total number of measures studied was 23. These were divided into four groups—calculated or measured traits, merit scores, fault scores, and total scores. Measures that could be considered as objectively recorded traits were in the group of calculated or measured traits. All subjectively recorded measures expressing the merit of dogs' hunting performance were in the group of merit scores. Correspondingly, all subjectively recorded scores expressing the mistakes made by the tested dog were in the group of fault scores. The sum of all merit scores (total merit scores), sum of all fault scores (total fault scores), and final scores, which were obtained by subtracting the fault scores from the total merit scores, were all in the group of total scores.

Seven measures of hunting performance with the highest estimates for heritability were selected and examined in detail in this study. The first, the frequency of barking, was 'calculated' or 'measured' and was the number of barks per minute. All other measures selected for further examination were subjectively recorded scores. Searching, barking, following, and total impression scores were from the group of merit scores, all with a maximum of 10 points. All these scores were in fact composed of more than one trait. When evaluating searching or following scores, both the speed of the dog and its distance from the owner are considered. Barking scores are composed of frequency and audibility of barking. Total impression, total and final scores are influenced by all measures evaluated in hunting ability tests.

Statistical methods

Variance and covariance components for the measures of hunting performance were estimated by applying the Restricted Maximum Likelihood (REML) method (PATTERSON and THOMPSON 1971). Environmental effects were submitted to the F-test, which employed residual variances from estimated mixed models that included and excluded the studied fixed effect. Solutions for the fixed effects were calculated with the animal model. Statistical analyses were done using the program package PEST (GROENEVELD 1990), including a variance component estimation program (GROENEVELD 1993) based on the derivate-free procedure.

The following linear model (model 1a) was assumed, when estimating the necessary variance and covariance components to calculate genetic parameters and solutions for the studied fixed effects:

$$y_{ijklmn} = \mu + sex_i + age_j + month_k + area - year_l + a_m + pe_m + \varepsilon_{ijklmn}$$

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=1-8), $month_k$ = fixed effect of the k^{th} testing month class (k=1-4), $area-year_l$ = fixed effect of the l^{th} testing area-year subclass (l=1-105), 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 e were assumed to be multivariate normal with zero means and with $Var(a) = A\sigma_a^2 Var(pe) = I\sigma_{pe}^2$ and $Var(\varepsilon) = I\sigma_e$. The covariances between a, pe, and ε were assumed to be zero.

The necessary (co)variance components for calculating heritabilities, repeatabilities and phenotypic and genetic correlations were estimated, assuming the bivariate model 1a. Due to the limitations in computer capacity, the pedigrees of the tested dogs were taken over four generations. Fixed effects were tested, and solutions for these effects were estimated assuming the univariate model 1a, making use of all relationships between animals. Solutions for the fixed-weather-condition effect were calculated using model 1b, which was similar to model 1a except for an additional fixed effect of combined wind-rain subclasses.

Classification of fixed effects

Model 1a included four fixed effects, i.e. sex, age, testing month, and combined testing area and year. There were two sexes (male and female) and eight categories for the age of tested dogs (1, 2, 3, 4, 5, 6, 7 and ≥8 years). Testing months were represented in four categories (1 = September, 2 = October, 3 = November, 4 = December, January, February). The area-year subclasses included the effects of testing areas, testing years, and the interactions between the areas and the years. The number of testing areas was 7 and the number of testing years was 15, which resulted in 105 area-year subclasses. The number of observations in different area-year subclasses varied from 24 to 235. The areas were composed of 17 kennel districts in Finland. Small kennel districts, situated geographically close to each other, were combined. There were probably interactions between all three effects, i.e. area, year and testing month, but it was impossible to estimate interactions between all three of these effects because of the low numbers of observations in each subclass.

Model 1b included the effect of the wind-rain subclasses, in addition to the fixed effects of sex, age, testing month, and combined testing area and year. Categories for sex, age, and testing month were the same as those in model 1a. Weather-condition information was available only from 1988 to 1992, resulting in 35 testing year-area subclasses in model 1b. The combined wind-rain effect was represented in four categories (1 = calm and dry, 2 = calm and rainy, 3 = windy and dry, 4 = windy and rainy).

Results and discussion

Means and variation

The mean values of the subjectively recorded scores were high (Table 2). The mean scores for searching and barking were > 8 points, with 10 being the highest possible score. Low points were rare in all subjectively measured scores. The coefficients of variation for all measures, except following scores and final scores, were less than 20%.

The inadequate registration of phenotypic variability of individual performances, as a result of too little differentiated between marks, was also reported by KREINER et al. (1992) who studied four Austrian Hound breeds.

Environmental effects

Differences between the sexes were statistically significant for frequency of barking (p < 0.001) and searching and barking scores (p < 0.01) (Table 3). Females scored higher for frequency of barking and in barking scores, whereas males scored higher for searching scores. In general, males seemed to have better scores for measures expressing the speed of the dog (searching and following scores), while females seemed to have better scores for traits that measured the skills of the dog when working with birds, for example barking, and total scores. However, the differences between the sexes were small at a practical level, in all measures.

The effect of age on the measures of hunting performances was statistically significant (p < 0.001) (Table 4). The differences between the age class with the poorest performance (1 year olds) and that with the best performance (6 year olds) were large for all measures of hunting performance. The dogs' test results improved after the age of 1 year up to the age of 6 years. After 6 years of age, the results did not improve. The improving results with age implied, in part, the importance of experience, training, and learning for hunting performance in the Finnish Spitz.

The effect of testing month was statistically significant (p < 0.001 or p < 0.01) for all measures of hunting performance (Table 5). Dogs produced the best results during winter for almost all measures. The exceptions were frequency of barking and barking scores, which produced the poorest scores during winter. The effect of testing month was probably due, in part, to seasonal differences in the behaviour of birds.

All seven measures of hunting performance were affected by area-year subclass effects. Differences between subclasses were statistically significant (p < 0.001) in searching, follow-

Table 2. Number of observations (N), means, standard deviations (SD), and coefficients of variation (CV) for the measures of hunting performance

Measure of hunting performance	N	Mean	SD	CV
Frequency of barking (no. barks/min) ¹	8999	98.17	15.19	15.5
Searching scores (pts 0-10) ²	11 099	8.09	1.33	16.4
Barking scores (pts 1–10) ¹	9251	8.16	1.17	14.3
Following scores (pts 1–10) ¹	9348	6.91	1.72	24.9
Total impression scores (pts 1–10) ¹	9341	6.95	1.29	18.6
Total merit scores (pts 1-100) ¹	9155	65.88	11.46	17.4
Final scores (pts 0–100) ³	10 030	61.29	17.78	29.0

¹ First barks > 0

²Barking opportunities >0

³ Barking opportunities > 1

Table 3. Effect of sex on the measures of hunting performance in relation to the performance of
males. N = number of observations; dev. = deviation from the results of males

	9	Sex	
	Males	Females	significance
Frequency of barking ¹			
N	4398	4601	
dev.	0.00	2.76	神神神
Searching scores ²			
N	5460	5639	
dev.	0.00	-0.15	并於
Barking scores¹			
N	4544	4707	
dev.	0.00	0.08	**
Following scores ¹			
N	4596	4752	
dev.	0.00	-0.08	NS
Total impression scores ¹			
N	4588	4753	
dev.	0.00	0.04	NS
Total merit scores ¹			
N	4503	4652	
dev.	0.00	0.81	NS
Final scores ³			
N	4933	5097	
dev.	0.00	0.59	NS

ing, total impression, total merit, and final scores. The effect of area-year subclasses was also important for frequency of barking (p < 0.05) and barking scores (p < 0.01). The interaction between testing areas and years was obvious, i.e. year-effect was different in different parts of Finland.

The effect of wind-rain subclasses was important for all measures of hunting performance, except barking frequency (Table 6). Differences between the subclasses were statistically significant (p < 0.001) in following, total impression, total merit and final scores, and also (p < 0.01) in searching and barking scores. The best test scores were obtained in calm and dry weather, whereas the test scores were poorest in windy and rainy weather. Scores were also poor in dry, windy weather. The effect of wind was clearly more important than the effect of rain on all measures of hunting performance.

Estimates of genetic parameters

Estimates of heritability were relatively low for the measures of hunting performance (Table 7). The highest estimates were for barking frequency ($h^2 = 0.15-0.17$) and searching scores ($b^2 = 0.14-0.15$). Estimates of heritability were somewhat lower for other measures of hunting performance, varying from 0.04 to 0.08. The repeatabilities were also low for the studied measures. The highest repeatabilities were for barking frequency and searching scores, which also had the highest heritabilities.

When total impression scores were analysed together with total merit scores or final scores in the bivariate analysis, heritability estimates for these measures were higher than those presented in Table 7. Repeatabilities were exceptionally low for total merit scores and

^{***, **} Significant at p < 0.001 and p < 0.01, respectively. NS = not significant

Table 4. Effect of age on the measures of hunting performance in relation to the performance of 1-year-old dogs. N = number of observations; dev. = deviation from the results of 1-year-old dogs

	Age (years)											
	1	2	3	4	5	6	7	≥8	significance			
Frequency of	f barking¹					.,						
N	291	1282	1668	1696	1529	1122	739	672				
dev.	0.00	1.80	2.77	3.64	3.63	3.92	3.73	2.49	特特特			
Searching sco	ores ²											
N	393	1686	2110	2057	1837	1340	872	804				
dev.	0.00	0.26	0.42	0.46	0.43	0.45	0.37	0.26	****			
Barking score	es ¹											
N	304	1321	1718	1746	1571	1147	755	689				
dev.	0.00	0.33	0.48	0.57	0.59	0.60	0.57	0.44	***			
Following sc	ores1											
N	315	1335	1742	1762	1583	1157	763	691				
dev.	0.00	0.29	0.52	0.61	0.59	0.70	0.51	0.43	***			
Total impress	sion score	es ¹										
N Î	312	1334	1733	1755	1589	1158	763	697				
dev.	0.00	0.29	0.49	0.55	0.56	0.65	0.61	0.52	特殊特			
Total merit s	cores1											
N	300	1308	1700	1730	1553	1134	748	682				
dev.	0.00	3.04	4.57	5.63	5.97	6.40	5.80	5.25	冷冰冷			
Final scores ³												
N	356	1511	1912	1857	1658	1216	790	730				
dev.	0.00	3.36	5.73	7.77	8.25	8.56	7.99	6.87	冷冷冷			
¹ First barks ² Barking opp ³ Barking opp *** Significar	ortunitie ortunitie	s > 1										

for final scores when these two measures were together in bivariate analysis. These anomalous estimates were probably due to the high correlation between the measures. However, most of the estimates of heritability and repeatability of the measures of hunting performance calculated assuming the bivariate model 1a, were in close agreement with the corresponding estimates based on the univariate model (KARJALAINEN et al. 1994).

Estimates of heritability and repeatability for the measures of hunting performance in this study differed to some extent from estimates published by VANGEN and KLEMETSDAL (1988). Their data was composed of the test results of the Finnish Spitz from 1978 to 1986, and genetic parameters estimated using the paternal half-sib correlation. Their estimates of heritability were lower for searching and barking scores, but somewhat higher than in this study for following, total impression and final scores. Repeatabilities were also slightly higher than in this study. However, the magnitude of the estimates was relatively small in both studies. Heritabilities and repeatabilities evaluated from field data were also relatively low for the measures from other hunting dog breeds, for example English Setter (VANGEN and KLEMETSDAL 1988) and four Austrian Hound breeds (KREINER et al. 1992).

The low estimates of heritability and repeatability were probably due in large part to random factors in the test situation. The tests are arranged in nature, in a way that represents, as closely as possible, the situations encountered in hunting. Therefore, it is obvious that many unexpected incidents affect the performance of a dog. Low repeatabilities imply also that the evaluation system of dogs is ambiguous. One judge has to evaluate dozens of measures that are open to interpretation. Also, one measure of hunting performance usually represents more than one trait. For example, two dogs having the same phenotypic value in

Table 5. Effect of testing month on the measure of hunting performance in relation to the performance in September. 1 = September, 2 = October, 3 = November, 4 = December, January February; N = number of observations; dev. = deviation from the results in September

		Statistical			
	1	2	3	4	significance
Frequency of barking ¹					
Ń	5614	1250	1486	649	
dev.	0.00	0.90	-0.98	-1.97	特殊特
Searching scores ²					
N	6745	1557	1972	825	
dev.	0.00	0.06	0.08	0.09	가장가
Barking scores ¹					
N	5722	1294	1559	676	
dev.	0.00	-0.02	-0.13	-0.18	特殊
Following scores ¹					
N	5771	1302	1585	690	
dev.	0.00	0.18	0.22	0.54	각착각
Total impression scores ¹					
N 1	5759	1303	1589	690	
dev.	0.00	-0.08	-0.08	0.19	外特殊
Total merit scores1					
N	5668	1279	1537	671	
dev.	0.00	-0.53	0.25	2.42	과장과
Final scores ³					
N	6242	1431	1665	692	
dev.	0.00	-1.03	-0.11	4.76	***

Barking opportunities > 0

searching scores may have very different ways of searching for prey. This inadequacy of the tests to be completely standardized and objective was also concluded from a study of four Austrian Hound breeds (KREINER et al. 1992).

Phenotypic (r_p) and genetic (r_g) correlations among the measures of hunting performance were positive, and usually moderate or high (Table 8). Genetic correlations were somewhat higher than phenotypic correlations. The highest correlations were among total impression, total merit scores, and final scores. Phenotypic correlations between these measures varied from 0.88 and 0.99, while genetic correlations were also close to 1, indicating that total impression, total merit, and final scores are measures of the same trait.

Correlations were lowest between barking frequency and searching scores ($r_p = 0.24$, $r_g = 0.31$) and between barking frequency and following scores ($r_p = 0.18$, $r_g = 0.35$). Also, barking frequency did not correlate very strongly with total impression or total merit scores. In addition, barking scores, which correlated strongly with frequency of barking, was less correlated with searching and following scores. Genetic correlations of frequency of barking and barking scores with other measures were low or moderate, thus indicating the necessity to consider one or other of these measures separately in the evaluation of breeding animals. The heritability of barking frequency was higher than that of barking scores, but in practice, barking frequency is considered to be fairly unimportant in evaluating the hunting ability of a dog.

Genetic correlations between the measures varied from -0.77 to 1.00 in the study reported by VANGEN and KLEMETSDAL (1988), and many of them were quite different

³ Barking opportunities > 1

^{***, **} Significant at p < 0.001 and p < 0.01, respectively

Table 6. Effect of weather conditions on the measures of hunting performance in relation to the performance in calm and dry weather. 1 = calm and dry, 2 = calm and rainy, 3 = windy and dry, 4 = windy and rainy; N = number of observations; dev. = deviation from the results in calm and dry weather

		Statistical			
	1	2	3	4	significance
Frequency of barking ¹					
N ,	2211	322	474	301	
dev.	0.00	-0.78	-0.71	-1.73	NS
Searching scores ²					
N	2693	404	598	455	
dev.	0.00	0.04	-0.14	-0.25	キキ
Barking scores ¹					
N	2277	329	487	317	
dev.	0.00	-0.03	-0.14	-0.18	가 가
Following scores ¹					
N	2307	331	487	324	
dev.	0.00	- 0.00	-0.45	-0.41	特斯特
Total impression scores ¹					
N	2301	330	490	324	
dev.	0.00	-0.03	-0.30	-0.34	가가가
Total merit scores ¹					
N	2259	326	482	314	
dev.	0.00	-0.69	-3.29	-4.54	外外外
Final scores ³					
N	2380	351	523	376	
dev.	0.00	-1.14	-4.59	-8.93	가 차 차

² Barking opportunities > 0

Table 7. Estimates of heritability (h²) and repeatability (r) for measures of hunting performance (model 1a, bivariate). Ranges are the estimates of genetic parameters from various bivariate analyses. N = number of observations

Measure of		No. of			
hunting performance	N	dogs	h^2	r	
Frequency of barking ¹	8999	1411	0.15-0.17	0.26-0.28	
Searching scores ²	11 099	1594	0.14-0.15	0.30	
Barking scores ¹	9251	1433	0.07-0.08	0.18-0.20	
Following scores ¹	9348	1442	0.07-0.08	0.14-0.17	
Total impression scores ¹	9341	1440	0.060.07	0.14-0.18	
Total merit scores ¹	9155	1419	0.05-0.06	0.14-0.17	
Final scores ³	10 030	1536	0.04-0.06	0.15-0.19	
¹ First barks > 0					
² Barking opportunities >0					
³ Barking opportunities > 1					

from estimates of correlations in this study. Only the genetic correlations between searching and following scores, and between final scores and other measures, were within the same

³Barking opportunities > 1

^{***, **} Significant p < 0.001 and p < 0.01, respectively. NS = not significant

hunting performance	1.	2.	3.	4.	5.	6.	7.
Frequency of barking ¹		0.31	0.87	0.35	0.56	0.52	0.72
2. Searching scores ²	0.24		0.49	0.83	0.73	0.72	0.64
3. Barking scores ¹	0.64	0.37		0.55	0.78	0.77	0.85
4. Following scores ¹	0.18	0.49	0.31		0.90	0.80	0.88
5. Total impression scores ¹	0.34	0.53	0.52	0.58		0.98	0.98
6. Total merit scores¹	0.36	0.53	0.53	0.59	0.88		1.00
7. Final scores ³	0.49	0.49	0.68	0.73	0.94	0.99	
¹ First barks > 0							
² Barking opportunities >0							
³ Barking opportunities > 1							

Table 8. Estimates of genetic correlations (above diagonal) and phenotypic correlations (below diagonal) among measures of hunting performance (model 1a, bivariate)

range in both studies. However, phenotypic correlations among the measures of hunting performance were similar in both these studies.

Conclusions

The means values were high for subjectively measured scores and the lowest scores were rarely used in the evaluation of hunting performance in the Finnish Spitz. The low estimates of heritability and repeatability for the measures of hunting performance indicate that many random factors affect evaluation in a test situation, and the evaluation system for dogs is ambiguous. In general, the scoring system should be less complicated. It could be simplified by decreasing the number of measures taken and by narrowing the scale of scores, for example from 1–10 to 1–5 points. The reliability of the evaluation system could be improved by defining measures more accurately and objectively.

The measures of hunting performance were affected by the age of the dog, testing month, testing area and year, and the interaction between the last two. Differences between the sexes were statistically significant for barking frequency, barking and searching scores, but were marginal. The effect of weather, especially wind, was important for all measures of hunting performance except frequency of barking. All environmental effects tested in this study are potential effects, when considering the statistical model for the evaluation of breeding values.

The selection of breeding animals in the Finnish Spitz based on performance testing is unreliable, because of low heritabilities and repeatabilities. The accuracy of evaluation would increase if the animal model BLUP method was used in the evaluation of breeding values. Genetic correlations among the measures were favourable, i.e., selection based on one measure results in genetic gain in other measures. Accounting for estimated heritabilities and genetic correlations and the importance of the measure in practice, the more representative measures needed to calculate breeding values for the individuals would be searching, barking, and following scores, and one out of the following: total impression, total merit scores or final scores.

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Summary

Genetic parameters for seven measures of hunting performance in the Finnish Spitz were estimated by applying the animal model and the Restricted Maximum Likelihood (REML) method to a data set, which consisted of 12 432 test results from 1683 dogs. Environmental effects on the measures of hunting performance were evaluated by the F-test, and the solutions for the fixed effects were calculated from the mixed animal model. All seven measures of hunting performance were affected by the age of the dog, testing month, testing area and season, and the interaction between area and season. Differences between the sexes were statistically significant for barking frequency, searching and barking scores. The combined wind and rain effect was important for all measures, except barking frequency. Heritability estimates were moderate for frequency of barking ($h^2 = 0.15 - 0.17$) and for searching scores ($h^2 = 0.14 - 0.15$), and somewhat lower for other measures of hunting performance. Phenotypic and genetic correlations between the measures of hunting performance were positive, and their magnitude was usually moderate or high.

Zusammenfassung

Umwelteinflüsse auf und genetiche Parameter von Jagdhundemerkmalen des Finnischen Spitz

Genetische Parameterschätzung für sieben Maße der Jagdhundeeignung wurde mit Tiermodell und mittels REML an 12 432 Testergebnissen von 1683 Hunden durchgeführt. Umwelteinflüsse wurden mittels F-Test geprüft und Lösungen für fixe Wirkungen mittels des gemischten Modells errechnet. Die sieben Merkmale für Jagdeignung werden beeinflußt von Hundealter, Testmonat, Testgebiet und Saison und der Interaktion zwischen diesen. Geschlechtsunterschiede waren signifikant für Häufigkeit des Bellens, Suchen und Intensität des Bellens. Die kombinierte Wirkung von Regen und Wind war für alle Merkmale außer für Häufigkeit des Bellens wichtig. Heritabilitätsschätzungen waren mäßig für Häufigkeit des Bellens (0,15–0,17) und für Suchpunkte (0,14–0,15) und etwas niedriger für die anderen Merkmale. Die phänotypischen und genetischen Korrelationen zwischen den Merkmalen waren mäßig bis stark positiv.

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