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Heritability Estimate for Temperament Scores in German Shepherd Dogs and Its Genetic Correlation with Hip Dysplasia

Stephen A. Mackenzie,[1] Elizabeth A. B. Oltenacu,[2] and Eldin Leighton[3]

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Temperament and hip dysplasia scores of 575 German shepherd dogs bred and evaluated by the United States Army's Division of Bio-Sensor Research between 1968 and 1976 were examined. The records represented 4 years, 18 sires, and 71 dams. Restricted maximum-likelihood procedures were used to obtain variance component estimates from which the heritabilities and genetic correlation were estimated. Heritability estimates for the temperament and hip dysplasia scores were 0.51 and 0.26, respectively. The genetic correlation between the two traits was estimated as −0.33. Males showed significantly higher temperament scores than females.

KEY WORDS: dogs; canine genetics; heritability; restricted maximum likelihood; German shepherds.

INTRODUCTION

The breeding of German shepherd dogs for working purposes such as military and police use involves selecting for suitable behavioral characteristics (often collectively referred to as temperament) and for a decreased incidence of hip dysplasia. Since both temperament and hip dysplasia are considered to be quantitative traits, mass selection in large colonies is the most efficient approach. Estimates of the heritabilities, variance components, and genetic correlation between the traits are necessary to obtain full benefit from best linear unbiased prediction (BLUP)

[1] Animal Husbandry Department, State University of New York at Cobleskill, Cobleskill, New York 12043.
[2] Department of Animal Science, Cornell University, Ithaca, New York 14853.
[3] Department of Animal Sciences, University of Maryland, College Park, Maryland 20742.

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techniques. BLUP can be used to predict the relative genetic worth of an individual dog, and these predicted values can, in turn, be quite useful as an aid in selecting replacement breeders.

Although hip dysplasia seems to be a moderately heritable trait (Leighton *et al.*, 1977), less is known of the heritability of temperament or its genetic correlation with hip dysplasia. Temperament is often a poorly defined trait, so that two studies using different methods of evaluating temperament may actually be studying two different sets of traits while using the same name to describe them. In the future, behavioral traits should be defined as objectively as possible. Meanwhile, it should be recognized that good genetic progress has been made using scores based on the subjective opinions of experienced workers, as demonstrated by Humphrey and Warner (1934).

Studies of the heritability of behavioral traits in dogs have shown conflicting results. Reuterwall and Ryman (1973) and Rosberg and Olausson (1976), working with the Army Dog Training Center in Solleftea, Sweden, and Pfleiderer-Högner (1979), studying German Schutzhund scores, report consistently low estimates of heritability for behavioral traits. The eight traits studied by Reuterwall and Ryman (1973) included affability (tested by having an unknown person confront the dog), disposition for self-defense (tested by having an unknown person attack the dog), disposition for self-defense and defense of the handler (tested by having an unknown person attack the dog and handler), disposition for fighting in a playful manner (tested by asking the dog to fight for a sleeve or stick), courage (tested by having a man-shaped figure approach the dog), ability to meet with sudden strong auditory disturbance (tested by firing shots at a distance and making noise with tin cans just behind the dog), disposition for forgetting unpleasant incidents (tested by scaring the dog at a certain location and then asking the dog to pass the location again), and adaptiveness to different situations and environments (tested by observations during other phases of the test). All scores were transformed and composite. Pfleiderer-Högner (1979) studied scores on tracking, obedience, man work, and character. Such scores are subjective in nature. Bartlett (1976), working with guide dogs in New Jersey, Goddard and Beilharz (1982), working with Australian guide dogs, and Fält *et al.* (1982), working with the National Dog School in Solleftea, Sweden, all report high heritabilities for certain behavioral components. Bartlett (1976) listed a heritability estimate of 0.49 for ear sensitivity (judged by how loud a vocal correction a new dog required). Goddard and Beilharz (1982) reported a heritability estimate of 0.58 for nervousness (fear, usually shown by withdrawal or inhibited movement with regard to people, traffic, or strange places). Fält *et al.* (1982) listed heritability estimates of 0.66 for yelp (time from the first separation of an 8-week-old puppy from its litter to the first distress call), 0.77 for contact 1 (tendency of the puppy to approach a strange person in a strange place after the separation), 0.43 for activity (number of squares entered when left in a marked arena), and 0.73 for fetch (pursuing a ball and picking it up in the mouth). This last trait is of most interest to this study since it involves chasing an object and biting it but not returning with it. The traits investigated in this study also involve an animal's tendency to chase and bite.

Studies of the genetic correlation between behavioral traits and hip dysplasia have been fewer and less conclusive. Bartlett (1976) reported a genetic correlation estimate of −0.22 between confidence and hip dysplasia, although it was not statistically significant. Rosberg and Olausson (1976) also listed a nonsignificant genetic correlation of −0.55 between behavioral traits and hip dysplasia.

METHOD

Records on the German shepherd dogs bred by the Division of Bio-Sensor Research, U.S. Army, between 1968 and 1976 were examined. The data were edited to include only those animals which had a temperament evaluation score, a hip dysplasia score, and the following information: sex, year of birth, height at 5 months of age (inches at the withers), sire, dam, and human handler. This reduced the number of records from 1059 to 575, representing 4 years, 18 sires, 71 dams, and 48 human handlers. The temperament evaluation scores were all assigned by the same person and ranged from 1 to 9, with half-scores possible. Higher scores reflected more desirable temperament (Castleberry *et al.*, 1975). The temperament score was a composite score indicating the animal's ability to chase and attack a decoy and the tendency to use its olfactory abilities. The score was assigned when an animal was between 4 and 8 months old and, along with the hip dysplasia score, was the major tool used to predict the future merit of each dog. Hip dysplasia scores were based on radiographs taken at 5, 8, or 11 months of age and were all assigned by Dr. Wayne Riser of the University of Pennsylvania's School of Veterinary Medicine. This time period covers the most frequent age for the appearance of hip dysplasia (3–8 months), during the pup's rapid growth phase (Foley *et al.*, 1979). Scores ranged from 1 to 9, with higher scores reflecting more desirable conditions as described by Leighton *et al.* (1977).

The model equation for the *ijklmn*th animal was

$$Y_{ijklmn} = \mu + x_i + r_j + b(F_{ijklmn} - \bar{F}) + s_k + d_l + h_m + e_{ijklmn},$$

where Y_{ijklmn} is the record of the *ijklmn*th animal, μ is a constant common to all records, x_i represents the effect of the ith sex, r_j represents the effect of the jth year, F_{ijklmn} represents the 5-month height of the $ijklmn$th animal, $\overline{F}$ represents the mean value of all the 5-month heights, s_k represents the effect of the kth sire, d_l represents the effect of the lth dam, h_m represents the effect of the mth handler and e_{ijklmn} represents the error associated with the $ijklmn$th record. The 5-month height was considered a covariate. Sires, dams, and handlers were considered random effects. The model equation in matrix notation was

$$Y = XB + Z_1u_1 + Z_2u_2 + Z_3u_3 + e,$$

where B represents the fixed effects (sex, year, and covariate), u_1 represents the sire effects, u_2 represent the dam effects, and u_3 represents the handler effects.

A restricted maximum-likelihood (REML) method was employed using the above model (Harville, 1977). The least-squares equations were set up in the general form. The fixed effects (sex, year, and covariate) were then absorbed and k_1, k_2, and k_3 added to the diagonal elements of the sire, dam, and handler equations, respectively. Estimates of k_1, k_2, and k_3 were not known at the beginning of the analysis, so guesses were used for their initial values. The solutions based on these guesses were then used to estimate new values for k_1, k_2, and k_3 and an iterative procedure was followed until all variance component estimates remained unchanged to two decimal places for three rounds in succession. At each round this procedure provided the following restricted maximum-likelihood estimates for the variance components:

$$\sigma_e^2 = (y'y - B'X'y - u'Z'My)/[N - r(X)],$$
$$\sigma_i^2 = [u'_iu_i + \sigma_e^2 tr(T_{ii})/p_i,$$

where ∂_e^2 is the error variance, ∂_i^2 is the variance of the ith random effect, $y'y$ is the total sum of squares, $B'X'y$ is the reduction due to the fixed effects, $u'Z'My$ is the reduction due to the random effects, N is the total number of observations, $r(X)$ is the rank of the design matrix for the fixed effects, u_i is the solution estimate for the ith random effect, and $tr(T_{ii})$ is the trace of the iith block of the generalized inverse of the coefficient matrix.

Estimates of heritability for temperament and hip dysplasia scores were calculated using the following formulas (Falconer, 1981):

$$h_s^2 = 4(o_s^2)/\sigma_t^2,$$
$$h_{sd}^2 = 2(\sigma_s^2 + \sigma_d^2)/\sigma_t^2,$$

where h_s^2 is the heritability estimate based on the sire component, h_{sd}^2 is the heritability estimate based on both the sire and the dam components,

$\hat{\sigma}_s^2$ is the estimate of the sire variance, σ_d^2 is the estimate of the dam variance, σ_h^2 is the estimate of the handler variance, and σ_t^2 is the estimate of the total variance, and

$$\sigma_t^2 = \sigma_s^2 + \sigma_d^2 + \sigma_h^2 + \sigma_e^2.$$

The genetic correlation between the temperament and the hip dysplasia scores was obtained using the following estimate of the genetic covariance between the two traits:

$$\text{cov}(A, B) = (\sigma_{A+B}^2 - \sigma_A^2 - \sigma_B^2)/2,$$

where cov(A, B) is the genetic covariance between the traits, σ_{A+B}^2 is the genetic variance obtained when the temperament and hip scores for each animal were summed to create a new variable for analysis, σ_A^2 is the genetic variance of the temperament scores alone, and σ_B^2 is the genetic variance of the hip dysplasia scores alone. The genetic variance for each trait was calculated as $4(\sigma_s^2)$. $\hat{\sigma}_{A+B}^2$ was calculated using the same model on the combined scores of the same animals.

The genetic variances and the genetic covariance between the two traits were then used to estimate the genetic correlation with the following formula (Van Vleck, 1979):

$$r_g(A, B) = \text{cov}(A, B)/[\text{sd}(A)\ \text{sd}(B)],$$

where $r_g(A, B)$ is the genetic correlation, cov(A, B) is the genetic covariance, sd(A) is the genetic standard deviation of the temperament scores, and sd(B) is the genetic standard deviation of the hip dysplasia scores. The genetic standard deviation for each trait was estimated as the square root of the genetic variance.

RESULTS

Solutions for the fixed effects (obtained from an analysis in which they were not absorbed) and their standard errors are shown in Table I. Males had significantly higher temperament scores than females ($P < 0.05$). Hip dysplasia scores were higher in females, though the difference was not significant ($P > 0.05$). The regression on 5-month height was significantly different from zero for both temperament and hip dysplasia scores ($P < 0.05$).

Table II lists the variance components, heritability estimates, and correlations between the temperament and the hip dysplasia scores. Sire and dam variances for the temperament scores were equal, suggesting that maternal effects were not important in those scores. The hip dysplasia scores, however, had a dam variance much larger than the sire variance, indicating that maternal effects were important in that trait.

Table I. Solutions and Standard Errors for the Fixed Effects

	Temperament		Hip dysplasia	
	Solution	SE	Solution	SE
Males[a]	0.0	0.0	0.0	0.0
Females	−0.630317	0.139968	0.107235	0.152507
Height	−0.001141	0.000576	0.001289	0.000632
Year 1	9.133635	1.225366	4.225495	1.333564
Year 2	9.360975	1.235873	3.625179	1.347941
Year 3	9.091844	1.197752	3.870095	1.302814
Year 4	8.959830	1.229957	3.574839	1.347103

[a] A constraint was placed on the males' equation.

Table II. Variance Components and Heritability and Correlation Estimates

	Temperament	Hip dysplasia
σ_s^2	0.39	0.23
σ_d^2	0.39	0.63
σ_h^2	0.03	0.02
σ_e^2	2.23	2.64
σ_t^2	3.04	3.52
h_s^2	0.51	0.26
h_{sd}^2	0.51	0.43
Phenotypic correlation	−0.56	
Genetic correlation	−0.33	

DISCUSSION

Differences between the sexes in behavioral traits have been noted previously by Humphrey and Warner (1934), Reuterwall and Ryman (1973), Pfleiderer-Högner (1979), and Goddard and Beilharz (1982). Other workers fail to mention the sex difference specifically yet calculate a separate heritability estimate for each sex, which demonstrates a respect for possible differences (Scott and Beilfelt, 1976; Bartlett, 1976; Fält *et al.*, 1982).

The heritability estimate of 0.51 for the temperament scores is high. The sire and dam variances for the temperament scores were equal in this study, indicating that maternal effects are not important in those scores. This is consistent with the findings of Goddard and Beilharz (1982), who reported no maternal effects present in behavioral traits in

Labradors. However, maternal effects in behavior traits have been reported by Scott and Fuller (1965), Scott and Bielfelt (1976), Pfleiderer-Högner (1979), and Fält *et al.* (1982). The key factor seems to be how long the puppies are left with the dam, as originally suggested by Scott and Fuller (1965). Puppies in the Bio-Sensor colony were weaned at 6 weeks of age (Linn, 1974). This apparently did not allow the dam enough time to greatly influence the puppies' behavior. The heritability estimate based on the sire variance of the hip scores (0.26) agrees closely with the estimate of 0.22 originally calculated by Leighton *et al.* (1977), working on the same trait in the same colony. The handler variance is small compared to the other components. This is of interest since the skills of the trainers and handlers working for the Bio-Sensor project were quite variable (Linn, 1983). The answer can be found in the description of the socialization procedures followed by the Bio-Sensor staff. The puppies were handled twice per week for a minimum of 15 min per session (Linn, 1974). It seems that this was not enough exposure for the skill of the handler to be reflected in the final product.

Both the phenotypic and the genetic correlation estimates between the temperament and the hip dysplasia scores are negative. The estimate of the genetic correlation was −0.33. If the temperament scores were merely a behavioral reflection of the hip condition, a positive correlation between the traits would be anticipated. This would stem from the fact that poor hips would have low scores and the pain in such hips would reduce the dog's desire and ability to chase and trail. This would result in low temperament scores which would create a positive correlation, not the negative correlation shown in this study. Other workers have listed nonsignificant negative genetic correlations between behavioral traits and hip dysplasia (Bartlett, 1976; Rosberg and Olausson, 1976). Significance was not tested in this study since it is an inappropriate procedure for REML estimates. Genetic correlations are thought to be sensitive to gene frequencies (Falconer, 1981). Therefore, other colonies may not have the same correlation between the two traits. More work needs to be done to determine whether or not this is a widespread problem.

In summary, it seems that certain components of behavior, even when judged subjectively, are highly heritable. This suggests that scores based on such highly heritable components are accurate descriptions of the animal's genotype and makes selection based on the animal's own records feasible. Not all behavioral components have high heritabilities, so care should be taken to select the proper scores for selection purposes. Contrary to the beliefs of early workers, who felt that there were no correlations between physical and mental traits, it now seems likely that hip dysplasia is associated with some behavioral components. It also appears that the correlation may be negative in some populations.

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