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Heritabilities of a population of German Shepherd Dogs with a complex interrelationship structure

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Summary. Heritabilities of conformation characteristics of a German Shepherd Dog population were estimated. The interrelationship structure was complex, with more than one generation, some related parents, and some 'diallel' crossings. These problems were overcome by a simple, practical method of estimation of heritability. Relatively high heritability estimates were obtained.

Key words: German Shepherd Dog – Heritability technique – Conformation

Introduction

The breeding of dogs has occupied man for many years. In recent times the breeding techniques have advanced considerably, giving rise to new horizons in breeding. The use of advanced quantitative genetic techniques in dog breeding has mainly been restricted to the determination of the inheritance of various diseases. Despite the importance of conformation characteristics, there is only a limited amount of literature in the field of quantitative genetics in this area (Humphrey and Warner 1934; Pfaffenberger et al. 1976).

It is of interest and importance to know to what extent 'breed standards' have affected the homogeny (and therefore, heritability) of conformation within a breed. The potential for further breeding and selection of conformation characteristics of the German Shepherd Dog is explored here.

The population which was studied was not purely hierarchically structured. There were a few second generation crossings and several of the dams were crossed to more than one sire. The resultant population was one with a rather complex interrelationship structure (Fig. 2).

The problem of the use of more than one generation has been approached by King and Henderson (1954). In the analysis of poultry, the heritability of several hatches of chickens was determined by simply adding another level to the heirachal structure, namely 'hatches'. The interrelationships between hatches were then ignored. A similar approach was used in the present estimation of heritabilities.

Thompson (1977 a, b) presented a maximum likelihood method for estimating the heritability when more than one generation is available, and the progeny are non-inbred half sibs.

Hinkelmann (1969) has devised a method for a variance analysis of data with related dams. This method is for balanced data, but can be adapted for the unbalanced case with some assumptions (Hinkelmann 1969). Hinkelmann (1971) also provided formulation for complex, single generation, inbred situations. This method does not accomodate relationships between the sire and dam mated to the sire.

Combining the Hinkelmann (1971) method (which is relatively involved in the unbalanced case) with the method of Thompson (1977 a, b) is likely to result in complicated and considerable formulation, if it is at all possible. The latter would be even more involved with the additional 'diallel' situation (one dam mated to more than one sire), which exists in the data which was used.

Materials and methods

A number of characteristics (listed in Table 1) were measured on a total of 201 progeny [a thorough description of the mea-

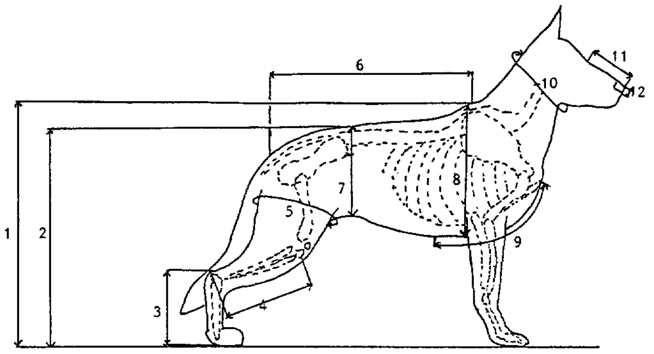

Fig. 1. Illustration of conformation characteristics (lateral view). *1* Front height, *2* Hind height, *3* Metatarsal length, *4* Tibia length, *5* Hind leg circumference, *6* Body length, *7* Abdomen height, *8* Chest height, *9* Chest length, *10* Neck circumference, *11* Snout length, *12* Nose height

Table 1. A summary of the pooled regression and correlation heritabilities

Characteristic	H^2	SE
Weight	0.41	0.17
Snout length	0.53	0.20
Nose breadth	0.41	0.14
Nose height	0.76	0.18
Neck circumference	0.44	0.19
Chest length	0.48	0.14
Front height	0.65	0.17
Hind height	0.47	0.17
Chest height	0.54	0.15
Chest width	0.81	0.15
Abdomen height	0.44	0.16
Abdomen width	0.32	0.13
Body length	0.44	0.18
Leg circumference	0.08	0.11
Metatarsal length	0.51	0.15
Hip breadth	0.62	0.15
Tibia length	0.67	0.14
Paw width	0.72	0.18
Head width	0.35	0.15
Size of dog	0.54	0.17

Table 2. The analysis of variance

Source	D.F.	SS	MS	EMS
Between groups	G[a]-1	SS_g	MS_g	[f]
Between sires in groups	S[b]-G	SS_s	MS_s	$\sigma_e^2 + K_2\sigma_d^2 + K_3\sigma_s^2$
Between dams in sires	D[c]-S	SS_d	MS_d	$\sigma_e^2 + K_1{}^{e}\sigma_d^2$
Between progeny	N[d]-D	SS_n	MS_n	σ_e^2

[a] G = no. of groups

[b] S = total no. of sires summed over groups

[c] D = total no. of dams summed over S

[d] N = total no. of progeny summed over D

[e] K_1 = as k1 in Becker (1975)

[f] The variance between groups is not used in the rest of the analysis

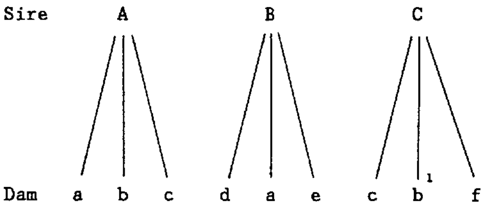

Fig. 2. An illustration of interrelationship problems between the dams. The dam 'a' is used twice and dam 'b' is related to dam 'b¹'

surements may be obtained in Verryn (1985); see also Fig. 1]. The data which was available here was unbalanced.

Variance analysis

As a result of the interrelationship problems which were discussed above, the normal variance analysis which is used in unbalanced hierarchal designs was modified for this analysis in the following way.

The data was divided into four groups, each group containing normal, hierarchical designs without interrelationship problems. In other words, the dams which were mated to more than one sire were only entered for one litter in any single group. No litter was entered more than once in the sum total of the data, however an individual parent may be present in more than one group.

The few litters which were interrelated, due to the presence of both first and second generation crossings, were placed in separate groups. Litters which had parents (dams) which were related were also placed in separate groups. The litters which did not have any of the problems concerning relationships were randomly placed in the various groups. There is a non-random element in the allocation of the other litters to their groups. This is done in an attempt to make more use of the available data.

The analysis of variance is presented in Table 2. The statistical model is:

$$Y_{ijkl} = \mu + \alpha_i + \beta_{ij} + \gamma_{ijk} + \varepsilon_{ijkl}$$

where

μ = the population mean,
α_i = the i-th group,
β_{ij} = the j-th sire in the i-th group,
γ_{ijk} = the k-th dam mated to the j-th sire,
ε_{ijkl} = the l-th progeny of the k-th dam.

The standard deviation and the lower 95% confidence limits were calculated the normal way, as presented by Becker (1975).

The values of K_2 and K_3 were not determined in the same way as in the usual three level structure. Using the general formula provided by Gates and Shiue (1962), the following is obtained:

$$K_2 = \{\Sigma(N_d^2/N_s) - \Sigma(N_d^2/N_g)\}/DF_d$$

$$K_3 = \{\Sigma(N_s^2/N_s) - \Sigma(N_s^2/N_g)\}/DF_s$$

$$= \{N_t - \Sigma(N_s^2/N_g)\}/DF_s$$

with

N_d = number of progeny in each dam,
N_s = number of progeny in each sire,
N_g = number of progeny in each group,
N_t = total number of progeny.

The heritability formulae used were the standard formulae:

$$h_s^2 = 4\sigma_s^2/(\sigma_s^2 + \sigma_d^2 + \sigma_e^2)$$

$$h_d^2 = 4\sigma_d^2/(\sigma_s^2 + \sigma_d^2 + \sigma_e^2)$$

$$h_{sd}^2 = 2(\sigma_s^2 + \sigma_d^2)/(\sigma_s^2 + \sigma_d^2 + \sigma_e^2)\,.$$

Naturally, the situation which is described here is not one of a random sample from a large population. This leads to an increase in inaccuracy. Only about one-half of the litters could be placed completely randomly in groups.

Regression analysis

As much of the parental data was available, a regression analysis was also undertaken. The data was organized in the same fashion as that for the variance analysis. Thus, some of the parent values appeared in more than one group. This repetition of parents is not abnormal, as a common method is the repeated parent technique, where the parent's value is repeated with each of the offspring.

The regression method used was that of Kempthorne and Tandon (1953), where each litter mean is weighted by a factor determined by the estimated correlation (t) and by the litter size. The correlation between members of families (t) is estimated by the method suggested by Falconer (1963). In the case of sire-progeny regressions, an expansion of the Kempthorne and Tandon method which is presented by Ollivier (1974) was used.

The heritability estimates from dam and sire regressions were weighted with the variances and pooled. The sire and dam correlation estimates were also pooled. The pooled regression and pooled correlation heritability estimates were then weighted (with the variances) and pooled. The upward bias of the dam correlation estimate and the correlations between the above two pooled heritability estimates were ignored.

Results

The heritability results are tabulated in Table 1. The mean of all the full sib correlation estimates is 0.62 and the mean of all half sib correlations is 0.41. This may indicate a relatively significant upward bias of full sib correlation estimates. The difference between half- and full sib heritability estimates may also be as a result of a more restricted selection of breeding sires (than of dams) being used in the breeding program. The variance between sires may be biased downwards as a result of selection. On the whole, the heritabilities are relatively high and suggest significant breeding potential, despite the possibility of an upward bias.

Discussion

By arranging data with a complex interrelationship structure into smaller groups of standard interrelationship designs, the analysis of the data may be much simpler. The variance as a result of the complex relationships (such as those of related dams, the same dams used with more than one sire, and second generation crossings) is included in the between group variance. It is obvious that too many groups would result in to great a loss in degrees of freedom. Thus, the number of groups should be kept to a minimum.

The analysis by this method may be less accurate and thorough, but it has the great advantages of simplicity and practicality.

On consultation of the heritability estimates, there appears to be considerable breeding potential in the conformation of German Shepherd Dogs. The potential could possibly be used in breeding German Shepherd Dogs of better stamina, speed and health (for a detailed study see Verryn 1985).

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