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Genetic analysis of results of a Swedish behavior test on German Shepherd Dogs and Labrador Retrievers¹

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ABSTRACT: The objectives of this study were to estimate genetic parameters and the influence of systematic effects on behavior test results in dogs. Behavior test results on 1,813 Labrador Retrievers (LR) and 2,757 German Shepherd Dogs (GSD) were analyzed. The behavior test included observations on courage, defense drive, prey drive, nerve stability, temperament, cooperation, affability, and gun shyness. Sex and age influenced most of the traits, and seasons of birth and testing and litter size and composition influenced some of the traits. Apart from defense drive in GSD, and courage, nerve stability, hardness, and affability in LR, all traits were heritable, with heritabilities ranging from 0.14 for hardness to 0.38 for affability in GSD, and from 0.03 for affability to 0.56 for gun shyness in LR. Genetic correlations ranged from 1.00 (LR) and 0.95 (GSD) between courage and hardness to -0.01 (LR) and -0.03 (GSD) between gun shyness and defense drive. Most

genetic correlations were positive. Correlations with cooperation were mainly negative, especially in GSD. Genetic correlations between courage and defense drive in LR (0.26) and GSD (0.80), between courage and prey drive in LR (0.27) and GSD (0.65), between affability and nerve stability in LR (0.09) and GSD (0.64), between affability and temperament in LR (-0.24) and GSD (0.39), and between cooperation and hardness in LR (0.28) and GSD (-0.67) were significantly different between the breeds. Genetic parameters for defense drive and cooperation in GSD and hardness and gun shyness in LR were genetically different between the sexes. Results of this study indicate that correction for systematic effects is essential when making selection decisions. Estimating breeding values would be a good solution, incorporating both correction for systematic effects and using all genetic links. Genetic parameters need to be estimated for each breed separately.

Key words: behavior test, breed difference, dog, genetic parameter, sex difference

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INTRODUCTION

There is large variation among the many dog breeds in appearance, temperament, and behavior. These differences mainly originate from directional selection related to the different purposes for which the dogs were used. After all, what is required in a good hunting dog, for example, tends to be different from what is required in a good herding or guard dog. Because the dog arguably was the first animal species to be domesticated (Sutter and Ostrander, 2004), such directional selection has already taken place for a very long time. Consequently, selection has resulted in differences in

temperament and behavior among breeds and thus in the physiological background of these traits. Studies have revealed that genetic variation indeed exists for a large number of behavioral traits in various dog breeds (Wilsson and Sundgren, 1997b; Ruefenacht et al., 2002; Strandberg et al., 2005). There are indications that genetic correlations may differ between breeds (Saetre et al., 2005).

Apart from variation among breeds, there is also variation within breeds. Behavior is driven by a complex interaction of endocrine and neuroendocrine factors (Nelson, 2005). These factors are influenced by both genetics and environment and are largely comparable between males and females. There are several (neuro)endocrine factors, however, that have a function in sex-specific behavior (Feder, 1984; Nelson, 2005). Consequently, it is likely that some of the behavior in males and females, to some extent, will have a different genetic background.

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For this study, data were available on Labrador Retrievers (**LR**) and German Shepherd Dogs (**GSD**). The GSD is mainly used for guarding and police work. The LR is mainly used as a hunting and companion dog. This study had 2 main aims: first, to investigate systematic effects on behavior in a hunting dog (LR) and a herding-guarding dog breed (GSD) and second, to estimate genetic parameters in both breeds.

MATERIALS AND METHODS

The animals used in this research were all tested as part of the selection procedure for going into training to become a working dog. They were not part of any experiment. All was approved by the Swedish government.

Data

Behavioral test data from the Swedish Dog Training Centre (**SDTC**) were collected during the period 1980 to 2003 on 2,757 GSD from 144 sires and 172 dams and 1,813 LR from 159 sires and 233 dams. Most of the dogs were born at the SDTC. Information on littermates, as well as litter composition, was available. All dogs born that did not die before the age of testing were temperament tested. Litter size ranged from 1 to 13 in GSD, with a maximum of 10 males or 10 females in the litter, and from 1 to 11 in LR, with a maximum of 8 males or 8 females in the litter. Dams on average had 3.36 litters in GSD and 2.95 in LR, both with a range of 1 to 6. In GSD, 88% and in LR, 75% of the tested dogs were born from dams that had more than 1 litter. The dogs bred by the SDTC were placed in foster homes from 8 wk of age onward. Testing age ranged from 0.5 to 7.5 yr, but most dogs were tested between 1.5 and 2 yr of age. Because age appears to have an effect on the test results (Wilsson and Sundgren, 1997a), 3 age groups were defined, in which animals younger than 365 d at the time of testing were combined, as were animals in the range of 365 to 700 d of age and animals older than 700 d. Pedigree information of 5 generations deep was available for the majority of dogs. Dogs were selected for breeding based on an index compiled from partial indices for each of the behavioral traits, except for gun shyness. These partial indices for each dog were based on judgments of whether individual behavior test scores were more or less desirable than average (Wilsson and Sundgren, 1997a).

Behavior tests took place all year round. The results were used by the SDTC to select dogs, either bred by the SDTC or obtained from private breeders, for breeding and for training for various military and civilian work tasks. These tasks may include narcotic detection, police and protection work, or being a guide dog for the visually impaired. All behavior tests were judged by the same person. There was no information on whether the dogs were accepted for work or breeding, or whether or not the dogs were neutered. Details on the test have

Table 1. Trait description¹ (adapted from Wilsson and Sundgren, 1997a)

Trait	Description
Courage	The ability to overcome fear. Courage can only be interpreted in situations in which the dog actually becomes frightened. Score 1 (frightened) to 6.
Sharpness ²	The tendency to react with aggression (i.e., the tendency to use aggression to reach a certain goal). Score 1 (no aggression) to 3.
Defense drive ³	The tendency to defend itself or its handler. In most cases, defense drive is combined with aggression. However, a dog may show defensive tendencies without being aggressive, and aggressive behavior is not always combined with defensive tendencies. Score 1 (not defensive) to 9.
Prey drive	The willingness to engage in competitive games (e.g., tug of war), also called competitive drive or social competitive drive. In this study, the tendency to defend the object is also included in the character. Score 1 (unwilling) to 6.
Nerve stability	The appropriateness of the reaction of the dog to a certain situation. This includes the ability of the dog to adapt to various types of situations, to concentrate when highly aroused or in a situation of conflict, as well as its ability to relax and to overcome a frightening situation. Score 1 (unstable) to 8.
Hardness	The lack of lasting effect of a pleasant or frightening experience. A dog with a high score is very easily affected by corrections or a frightening experience, or both, whereas a dog with a low score is hard to affect. For training purposes, a dog with a medium score is preferable. Score 1 (hard) to 6.
Temperament	The degree of liveliness. Dogs with high temperament scores are more responsive to all types of stimuli. Score 1 (low) to 9.
Cooperation	The tendency to be influenced by the handler without being given a direct command or sign. Another often-used term is willingness to please. Score 1 (no influence) to 6.
Affability ⁴	The willingness of the dog to make contact with people. Score 1 (low) to 9.
Gun shyness	This characteristic is scored from 1 to 3, describing lasting fear (score = 1) to no sign of fear.

¹The traits were originally scored from high to low but were inverted for all traits to have a more intuitive score from low to high.

²Sharpness was scored on 2 scales: at the moment and an after reaction. These 2 scales have been combined into 1, resulting in a score from 1 to 3.

³Defense drive was scored on a scale 1 to 9, but some adjacent classes were combined into a score of 1 to 5 for statistical analysis.

⁴Affability was scored on a scale of 1 to 12 but has been transferred to a scale of 1 to 9.

been given by Wilsson and Sundgren (1997a), and trait descriptions taken from this study are in Table 1. The scale of some of the traits was adjusted compared with Wilsson and Sundgren (1997a). Adjustments have been indicated in the footnotes of Table 1. Affability was a difficult trait, because it combined social openness with both tendencies to be aggressive or afraid. A different score thus did not necessarily represent an increase or decrease but merely a change in the trait. Some traits were not normally distributed. However, there were no differences in heritabilities on the normal compared with log-transformed data (results not shown). The normal, untransformed data were, therefore, used for all analyses.

Statistical Analyses

Genetic Parameters. Factor analysis is often used in behavior genetics to combine traits with a potentially common background (Wilsson and Sundgren, 1997b; Strandberg et al., 2005). However, factors are unique for a specific data set and cannot be compared with factors obtained from analyzing another data set. Because, in the present study, results of 2 breeds are presented and compared, factor analysis was abandoned, and the original traits were analyzed instead. To determine which fixed effects should be included in the model to estimate genetic parameters, the GLM procedure in SAS (Release 9.1, SAS Institute Inc., Cary, NC) was used (PROC GLM). To keep the results comparable between breeds, a model was composed that could be applied to both breeds. Heritabilities were estimated in univariate analyses using ASReml (Gilmour et al., 2001), using the following animal model:

$$Y_{ijklmnopq} = \mu + s_i + ta_j + bs_k + ts_l + ls_m + nm_n + nm(ls)_{mn} + d_o + m_p + c_q + e_{ijklmnopqr}, \quad [1]$$

where μ = the mean; s_i = the fixed effect of the i th sex (1, 2); ta_j = the fixed effect of the j th test age (1 to 3); bs_k = the fixed effect of the k th season of birth (1 to 4), with the first season including December to February, the second March to May, etc.; ts_l = the fixed effect of the l th season of testing (1 to 4), with seasons defined as in season of birth; ls_m = the fixed effect of the m th litter size (1 to 11), with litters of 11, 12, and 13 combined into class 11; nm_n = the fixed effect of the n th male in the litter additional to the animal itself (1 to 8); $nm(ls)_{mn}$ = the litter composition, the fixed effect of number of males within a litter, resulting in 40 combinations (1 to 40); d_o = a random animal effect $\sim N(0, A\sigma_a^2)$, where A = the additive relationship matrix; m_p = a random maternal genetic effect $\sim N(0, A\sigma_m^2)$; c_q = the random effect of an early common environment for littermates $\sim N(0, I\sigma_c^2)$, where I = the identity matrix; and $e_{ijklmnopqr}$ = the random error term $\sim N(0, I\sigma_e^2)$.

Due to the limited size of the data sets, and due to the fact that the maternal genetic component in most cases was not significant, the covariance components between maternal and direct effects could not be estimated. Variance ratios were defined as:

$$c^2 = \frac{\sigma_c^2}{\sigma_p^2}, h_d^2 = \frac{\sigma_d^2}{\sigma_p^2}, \text{ and } h_m^2 = \frac{\sigma_m^2}{\sigma_p^2},$$

where c^2 = the common environment ratio related to littermates; h_d^2 = the heritability related to the direct genetic effect of the dog; and h_m^2 = the heritability related to maternal genetic effects. The phenotypic variance is defined as: $\sigma_p^2 = \sigma_d^2 + \sigma_m^2 + \sigma_c^2 + \sigma_e^2$.

Genetic and phenotypic correlations between traits were estimated in bivariate analyses, fitting only the additive genetic effect as described in model [2]. Omitting significant litter and maternal effects did not affect estimates of genetic correlations:

$$Y_{ijklmnopq} = \mu + s_i + ta_j + bs_k + ts_l + ls_m + nm_n + nm(ls)_{mn} + a_o + e_{ijklmnop}. \quad [2]$$

The systematic effects in this model were equal to model [1], and a_o = the random animal effect $\sim N(0, A\sigma_a^2)$. The overall heritability, ignoring common environment or maternal genetic effects, was estimated as $h_{overall}^2 = \frac{\sigma_a^2}{\sigma_p^2}$ and $\sigma_p^2 = \sigma_a^2 + \sigma_e^2$.

Comparison of Genetic Parameters Between Breeds. Because preliminary analyses showed that variance components for the same trait were not always of comparable size in GSD and LR, analyses were performed for each breed separately. To compare the results between breeds, and to see whether differences occur, estimates of heritabilities and genetic and phenotypic correlations were compared. Parameter estimates from the 2 breeds were defined as significantly different (i.e., a genotype $\times$ breed interaction) if they differed by more than the sum of the standard errors for each estimate.

Comparison of Genetic Parameters Between Sexes. Because preliminary analyses showed that the effect of sex was very large for some traits, genetic correlations and heritabilities were estimated for traits expressed in males and females. For each original trait, 2 new traits were defined: 1 for observations on the males and 1 for observations on the females. Each animal, therefore, had missing observations for their opposite sex variable. Parameter estimates from the 2 sexes were defined as significantly different (i.e., a genotype $\times$ sex interaction) if they differed by more than the sum of the standard errors for each estimate. Heritabilities and correlations between male and fe-

Table 2. Number of observations (n), mean, and SD of the traits considered in the analyses for the German Shepherd Dog and Labrador Retriever

Variable	German Shepherd Dog			Labrador Retriever		
	n	Mean	SD	n	Mean	SD
Females in litter, n	2,757	3.34	1.77	1,813	3.22	1.68
Males in litter, n	2,757	4.16	1.86	1,813	3.77	1.74
Litter size	2,757	7.92	2.37	1,813	7.50	2.21
Courage	2,756	2.99	0.67	1,804	3.09	0.65
Sharpness	2,757	1.25	0.45	1,805	1.11	0.33
Defense drive	2,757	2.73	0.77	1,805	2.34	0.57
Prey drive	2,756	3.57	0.68	1,806	3.54	0.66
Nerve stability	2,756	5.59	0.69	1,805	5.92	0.53
Hardness	2,756	2.26	0.51	1,805	2.34	0.58
Temperament	2,755	5.08	1.35	1,807	5.01	1.37
Cooperation	2,741	4.03	0.82	1,802	4.20	0.81
Affability	2,723	7.57	1.42	1,806	7.78	2.02
Gun shyness	2,096	2.87	0.38	1,415	2.94	0.23

male behavior were estimated using the reduced model [2], though leaving out the fixed effect of sex.

RESULTS AND DISCUSSION

Descriptive Statistics

The average test age was 1.48 yr for GSD and 1.43 yr for LR. Approximately equal numbers of dogs were born in each month of the year. Approximately equal numbers of dogs were tested in each month of the year, with the fewest dogs tested in December and July. In Table 2 are the means, SD, and number of observations for the traits considered in this study for the 2 breeds. In both breeds, the litters on average consisted of slightly more males than females, with an average litter size of 7.5 (LR) to 8 (GSD) pups.

Even though Svartberg (2006) may be correct that breed-specific behavior has decreased with the change in purpose of the various dog breeds, results from other studies show that differences between breeds are still present (Schmutz and Schmutz, 1998; Brenøe et al., 2002; Svartberg, 2002). It is not clear in the present study what the reason is for the small differences in mean score for the behavior traits between GSD and LR. Because all dogs considered in this study were STDC dogs, either bred by them or selected by them, these dogs may form a selected set and do not represent overall breed averages. In addition, it could be that the test judge was influenced by the fact that he was judging a GSD or a LR and, subconsciously, adjusted his judgment accordingly.

Effect of Sex. Males had greater scores than females for sharpness in GSD, for cooperation and gun shyness in LR, and for courage, defense drive, prey drive, nerve stability, and hardness in both breeds. The effect of sex on the behavior test results ranged from males scoring 5% of a SD greater for cooperation in LR to males scoring 58% of a SD greater for defense drive in GSD. These differences between sexes were highly

significant and suggest that sex-specific behavior is involved. Sex differences in behavior traits in dogs have also been reported by Wright and Nesselrode (1987), Svartberg (2002), and Courreau and Langlois (2005), in which males performed more extremely than females. Goddard and Beilharz (1985) reported an effect of sex only on fearful behavior, whereas Hoffmann et al. (2003) reported that sex had no significant influence on the performance of herding dogs. The traits considered in each of these studies, however, were different and thus hard to compare.

Although Courreau and Langlois (2005) concluded that male Belgian Shepherds perform better (i.e., more extreme) than females, Rooney and Bradshaw (2004) observed that their handlers had no preference, even though males are more often used for specialized detection work than females. The only difference between males and females was that the males were more aggressive toward other dogs. Aggression toward other dogs was not specifically tested in the present study, but in GSD, males on average were more aggressive (i.e., greater scores for sharpness) than females.

Effect of Age. Both in GSD and LR, younger dogs scored less than older dogs for defense drive and cooperation. More explicitly, animals of less than 1 yr of age scored less for nerve stability, temperament, and affability than older animals. The effect of age generally was large. The smallest and largest effects were both related to affability. Dogs younger than 1 yr of age scored 14% of a SD for affability in LR to 128% of a SD for affability in GSD less compared with dogs older than 2 yr of age. An effect of age was not found by Wright and Nesselrode (1987), in which the age of the dogs ranged from 0.25 to 11.5 yr.

The effect of age on performance was larger and more often present in GSD than in LR. In hardness, for example, younger dogs scored 59% of a SD greater than older dogs in GSD, whereas it was of no significant influence in LR. Also, younger dogs scored 128% of a SD greater for affability in GSD compared with

Table 3. Percentages of sires and dams born in each of the seasons for the German Shepherd Dog and Labrador Retriever

Season	German Shepherd Dog		Labrador Retriever	
	Sires	Dams	Sires	Dams
March to May	29	29	22	24
June to August	29	25	32	10
September to November	15	13	24	24
December to February	27	33	22	42

only 14% of a SD in LR. This smaller effect of age in LR may relate to the different desired behavior in LR and GSD. Selection for tame (friendly) behavior in silver foxes resulted in more juvenile behavior in adult animals (Trut, 1999). Because LR, in contrast to GSD, for many generations has been selected on friendly behavior, this selection strategy may have caused the behavior of LR to remain at a more adolescent level, thus explaining the small effect of age in LR.

Effect of Season of Birth. Season of birth was of significant influence on cooperation, prey drive, and temperament in GSD and on cooperation, defense drive, and courage in LR. Effects ranged from 12% of a phenotypic SD lesser scores for cooperation in LR born in March to May to 28% of a phenotypic SD greater for defense drive in LR born in March to May and for courage in LR born in September to November, both compared with dogs born in December to February.

Because the season of birth had an influence on the later performance of the dogs, this may have had an influence on the probability of being selected. Overall, approximately equal numbers of puppies were born in each of the seasons. In Table 3 are percentages of the sires and dams born in each of the seasons. For GSD, percentages in seasons 1, 2, and 4 are similar, whereas fewer sires and dams were born in season 3 (September to November). In LR, percentages of sires were approximately equal in all seasons. However, only 10% of the dams were born in season 2 (June to August), and 42% were born in season 4 (December to February). These results suggest that season of birth indeed has had an influence on selection.

Apart from structural differences in circumstances such as temperature or rainfall or whether trees have leaves, the seasons coincide with the fluctuation in hours of daylight. In Sweden, there is a distinct difference in number of hours of daylight between winter and summer, and because number of hours of light has an influence on behavior, it seems fair to assume that the change in behavior may be daylight-driven. In humans, there is a contrasting effect of season of birth on subsequent adolescent or adult behavior (Chotai et al., 2002, 2003). Until the age of 25, harm avoidance was greatest for women born around September. For women older than 25, harm avoidance was greatest when they were born around December (Chotai et al., 2003). Such mechanisms may exist in dogs as well.

Effect of Season of Testing. The effect of season of testing on the behavior test results ranged from 13% of a phenotypic SD lesser scores for cooperation in GSD tested in December to February to 22% of a phenotypic SD less for courage in GSD tested in June to August, both compared with GSD tested in September to November. Apart from the fact that the handler and the judge may be influenced by the season, which may have an effect on the test results of the dog, there may be 2 dog-related underlying mechanisms for these seasonal effects. First of all, as in the effect of season of birth, there may be a relationship with the hours of daylight. Compared with the autumn months of September to November, scores for courage, defense drive, nerve stability, temperament, and prey drive all are significantly less during the summer months. In human adults, serotonin and dopamine show marked seasonal fluctuations, with the least concentrations in December and January (serotonin) and autumn and winter months (dopamine; Lam and Levitan, 2000), resulting in increased incidence of depression and aggression. This may be the case in dogs as well.

A second explanation for seasonal fluctuation in some of the behavior traits in dogs is related to the reproduction cycle. Even though most domestic dogs have estrous cycles every 7 mo, Indian street dogs still only have a single annual reproductive cycle in the spring (Chawla and Reece, 2002). Becoming cyclic most likely is a threshold character so that the underlying physiology may be a continuous character. Domestic dogs, therefore, even though cyclic more than once per year, may still show variation in the underlying physiology, which may have an effect on behavior. Pal et al. (1998) reported a clear influence of reproductive season on behavior of free-ranging dogs. Effect of reproductive season may explain some of the decrease in courage, defense drive, prey drive, nerve stability, affiliability, and temperament in GSD, and in temperament and prey drive in LR during March to May and June to August.

Effect of Litter Size and Composition. In LR, dogs from litters with 3 pups scored 280% of a phenotypic SD greater for cooperation and 330% of a phenotypic SD greater for nerve stability than dogs from litters with 11 pups. There was no effect of litter size in GSD. There does not seem to be an obvious explanation for these large effects in LR, nor for the absence of them in GSD. In LR, there were 15 litters of 3 and

Table 4. Common environment (c^2), direct (h_d^2), and maternal (h_m^2) genetic heritabilities, heritability estimated with only the direct genetic effect in the model ($h_{overall}^2$), with SE and variance components estimated using the full model for the traits included in a behavior test for the German Shepherd Dog and Labrador Retriever

Trait	c^2	h_d^2	h_m^2	$h_{overall}^2$	σ_c^2	σ_d^2	σ_m^2	σ_e^2
German Shepherd Dog								
Courage	0.03 (0.03)	0.19 (0.04)	0.00 (0.02)	0.19 (0.04)	0.01	0.09	10^{-6}	0.35
Sharpness	0.01 (0.03)	0.16 (0.05)	0.03 (0.07)	0.19 (0.04)	0.00	0.03	0.006	0.16
Defense drive	0.04 (0.02)	0.07 (0.04)	0.06 (0.02)	0.14 (0.03)	0.02	0.04	0.03	0.47
Prey drive	0.06 (0.02)	0.21 (0.06)	0.02 (0.02)	0.23 (0.05)	0.03	0.09	0.01	0.32
Nerve stability	0.01 (0.02)	0.15 (0.05)	0.02 (0.02)	0.16 (0.04)	0.01	0.07	0.008	0.38
Hardness	0.03 (0.03)	0.14 (0.03)	0.00 (0.04)	0.14 (0.03)	0.01	0.25	10^{-6}	0.21
Temperament	0.00 (0.03)	0.18 (0.04)	0.00 (0.02)	0.18 (0.04)	0.01	0.05	10^{-6}	1.50
Cooperation	0.03 (0.02)	0.17 (0.04)	0.00 (0.03)	0.17 (0.04)	0.02	0.12	10^{-7}	0.51
Affability	0.00 (0.03)	0.36 (0.08)	0.03 (0.03)	0.38 (0.06)	10^{-9}	0.72	0.05	0.76
Gun shyness	0.07 (0.03)	0.21 (0.07)	0.02 (0.02)	0.22 (0.09)	0.01	0.03	0.003	0.11
Labrador Retriever								
Courage	0.07 (0.03)	0.13 (0.04)	0.00 (0.03)	0.13 (0.04)	0.03	0.05	10^{-6}	0.37
Sharpness	0.00 (0.03)	0.10 (0.06)	0.03 (0.03)	0.13 (0.05)	10^{-7}	0.01	0.004	0.09
Defense drive	0.04 (0.03)	0.19 (0.08)	0.03 (0.03)	0.21 (0.06)	0.013	0.06	0.008	0.22
Prey drive	0.00 (0.02)	0.32 (0.06)	0.00 (0.02)	0.32 (0.06)	0.002	0.13	10^{-9}	0.24
Nerve stability	0.06 (0.02)	0.09 (0.06)	0.07 (0.03)	0.15 (0.05)	0.02	0.03	0.021	0.24
Hardness	0.07 (0.03)	0.16 (0.05)	0.00 (0.02)	0.16 (0.05)	0.02	0.29	10^{-6}	0.28
Temperament	0.00 (0.03)	0.18 (0.05)	0.00 (0.03)	0.18 (0.05)	10^{-6}	0.06	10^{-8}	1.43
Cooperation	0.05 (0.03)	0.24 (0.08)	0.01 (0.03)	0.25 (0.06)	0.03	0.15	0.008	0.46
Affability	0.03 (0.02)	0.03 (0.03)	0.00 (0.02)	0.03 (0.03)	0.06	0.13	10^{-5}	2.06
Gun shyness	0.09 (0.03)	0.56 (0.09)	0.00 (0.02)	0.56 (0.09)	0.01	0.03	10^{-12}	0.03

12 litter of 11 pups and in GSD 19 litters of 3 and 28 litters of 11 pups, so that in each of the breeds, the effect could be estimated accurately. With respect to litter composition, dogs from litters with 1 or 2 males had much lesser scores for courage in GSD (1.2 to 2.0 phenotypic SD) and much greater scores for cooperation in LR (2.4 phenotypic SD) than dogs from other types of litters. These effects may have been caused by the fact that the males most likely were positioned next to a female in the uterus and thus showed less masculine behavior. Such effect of intrauterine position on behavior has been described in other species such as mice (Zielinski et al., 1992; Clark and Galef, 1995), rats (Hernández-Tristán et al., 1999), and gerbils (Clark and Galef, 1995).

Parameter Estimates

In Table 4 are the results of the univariate analyses. Common environmental effects have been reported to influence behavior traits in dogs (Courreau and Langlois, 2005; Strandberg et al., 2005). In the present study, common environment was of significant influence for defense drive, prey drive, and gun shyness in GSD and for courage, nerve stability, hardness, and gun shyness in LR. The maternal genetic effect was only significantly different from zero for nerve stability in LR. This suggests that the covariance between direct and maternal genetic effects would be small or nonexistent and that leaving the maternal genetic effect out of the model has not led to a large overestimation of genetic variances. This is confirmed by the fact that h_d^2 and

$h_{overall}^2$ were equal for all traits in both breeds except for nerve stability in LR. The heritabilities (direct genetic effect) were significantly different from zero for all traits but defense drive in GSD and courage, nerve stability, hardness, and affability in LR. In GSD, they ranged from 0.14 (hardness) to 0.49 (affability) and in LR from 0.19 (sharpness) to 0.47 (prey drive). Except for gun shyness, common environment influenced different behavior traits in the 2 breeds. The environmental variances for defense drive and nerve stability, and to a lesser extent for sharpness, prey drive, cooperation, and gun shyness, were larger in GSD than in LR. Possibly GSD were more sensitive to environmental influences than LR, resulting in larger environmental variation among the dogs (for comparison, see Mulder et al., 2007). This may also be reflected by the fact that the systematic effects (e.g., sex, age, litter composition) incorporated in the model had a larger influence in GSD than in LR.

The heritability estimates in the present study in general were less than those estimated by Wilsson and Sundgren (1997b). A first reason may be that the scoring of courage, sharpness, and affability in the present study was adjusted so that more alike scores were combined, which was not done in Wilsson and Sundgren (1997b). A second reason may be related to the different estimation methods: intraclass correlations between sibs within groups of full and half sibs (Wilsson and Sundgren, 1997b) vs. variance component estimation using an animal model (present study).

In Table 5 are the genetic and phenotypic correlations for the behavior traits in GSD and LR. Many of the

Table 5. Genetic (above diagonal) and phenotypic (below diagonal) correlations with SE for traits recorded in a behavior test for the German Shepherd Dog and Labrador Retriever

Trait	Courage	Sharpness	Defense drive	Prey drive	Nerve stability	Hardness	Temperament	Cooperation	Affability	Gun shyness
German Shepherd Dog										
Courage		0.25 (0.14)	0.80 (0.08)	0.65 (0.09)	0.62 (0.10)	0.95 (0.05)	0.25 (0.15)	-0.07 (0.15)	0.27 (0.13)	0.10 (0.15)
Sharpness	0.22 (0.02)		0.81 (0.07)	0.57 (0.10)	-0.28 (0.14)	0.22 (0.14)	0.54 (0.12)	-0.56 (0.11)	-0.51 (0.10)	-0.09 (0.15)
Defense drive	0.45 (0.02)	0.56 (0.01)		0.71 (0.08)	0.11 (0.15)	0.59 (0.62)	0.36 (0.15)	-0.39 (0.14)	-0.24 (0.13)	-0.03 (0.16)
Prey drive	0.35 (0.02)	0.36 (0.02)	0.49 (0.02)		0.02 (0.13)	0.62 (0.10)	0.79 (0.07)	-0.48 (0.11)	0.06 (0.12)	-0.11 (0.14)
Nerve stability	0.46 (0.02)	0.05 (0.02)	0.24 (0.02)	0.13 (0.02)		0.57 (0.11)	0.62 (0.11)	-0.33 (0.15)	0.64 (0.09)	0.35 (0.14)
Hardness	0.55 (0.01)	0.27 (0.02)	0.45 (0.02)	0.39 (0.02)	0.39 (0.02)		0.40 (0.14)	-0.67 (0.09)	0.09 (0.14)	-0.17 (0.16)
Temperament	0.14 (0.02)	0.21 (0.02)	0.21 (0.02)	0.41 (0.02)	0.36 (0.02)	0.21 (0.02)		-0.23 (0.14)	0.39 (0.12)	0.06 (0.16)
Cooperation	0.09 (0.02)	-0.11 (0.02)	-0.06 (0.02)	-0.13 (0.02)	-0.08 (0.02)	-0.54 (0.02)	0.03 (0.02)		0.48 (0.11)	0.18 (0.15)
Affability	0.09 (0.02)	-0.12 (0.02)	-0.06 (0.02)	0.05 (0.03)	0.24 (0.02)	-0.01 (0.02)	0.10 (0.02)	0.20 (0.02)		0.07 (0.14)
Gun shyness	0.17 (0.02)	0.04 (0.03)	0.13 (0.02)	0.11 (0.03)	0.32 (0.02)	0.05 (0.02)	0.16 (0.02)	0.02 (0.06)	0.00 (0.03)	
Labrador Retriever										
Courage		-0.14 (0.22)	0.26 (0.18)	0.27 (0.17)	0.77 (0.11)	1.00 (0.06)	0.09 (0.20)	0.20 (0.19)	0.39 (0.36)	0.45 (0.17)
Sharpness	0.05 (0.03)		0.85 (0.08)	0.62 (0.11)	-0.32 (0.17)	0.04 (0.19)	0.71 (0.12)	-0.53 (0.13)	-0.56 (0.25)	-0.01 (0.17)
Defense drive	0.32 (0.02)	0.43 (0.02)		0.62 (0.10)	-0.20 (0.16)	0.33 (0.15)	0.81 (0.09)	-0.51 (0.13)	-0.27 (0.28)	-0.01 (0.14)
Prey drive	0.08 (0.03)	0.21 (0.03)	0.33 (0.03)		-0.02 (0.15)	0.26 (0.15)	0.62 (0.10)	-0.50 (0.12)	-0.05 (0.27)	0.04 (0.13)
Nerve stability	0.46 (0.02)	-0.02 (0.03)	0.11 (0.03)	0.09 (0.03)		0.87 (0.08)	-0.18 (0.16)	0.58 (0.12)	0.09 (0.26)	0.53 (0.12)
Hardness	0.54 (0.02)	0.10 (0.03)	0.31 (0.03)	0.35 (0.03)	0.40 (0.02)		0.12 (0.18)	0.28 (0.17)	0.43 (0.32)	0.55 (0.15)
Temperament	0.03 (0.03)	0.18 (0.03)	0.22 (0.03)	0.37 (0.03)	-0.12 (0.03)	0.14 (0.03)		-0.49 (0.13)	-0.24 (0.19)	-0.17 (0.15)
Cooperation	0.20 (0.03)	-0.10 (0.03)	-0.04 (0.03)	0.16 (0.06)	0.34 (0.03)	0.07 (0.03)	-0.42 (0.02)	0.20 (0.02)	0.64 (0.23)	0.06 (0.14)
Affability	0.09 (0.02)	-0.05 (0.03)	-0.03 (0.03)	0.10 (0.03)	0.13 (0.03)	0.09 (0.03)	-0.06 (0.03)	0.04 (0.04)		0.03 (0.18)
Gun shyness	0.19 (0.03)	0.04 (0.04)	0.07 (0.08)	0.11 (0.04)	0.32 (0.03)	0.20 (0.03)	0.11 (0.07)	0.07 (0.03)		

Table 6. Estimates of genetic correlations between performance in males and females, heritability in males, and heritability in females (SE) for the traits recorded in a behavior test for the German Shepherd Dog and Labrador Retriever

Trait	German Shepherd Dog			Labrador Retriever		
	$r_{\text{male,female}}$	h^2_{males}	h^2_{females}	$r_{\text{male,female}}$	h^2_{males}	h^2_{females}
Courage	0.92 (0.16)	0.19 (0.05)	0.26 (0.06)	0.63 (0.36)	0.23 (0.08)	0.08 (0.06)
Sharpness	0.81 (0.14)	0.23 (0.06)	0.24 (0.06)	0.99 (0.01)	0.26 (0.08)	0.18 (0.07)
Defense drive	0.47 (0.22)	0.28 (0.07)	0.19 (0.06)	0.96 (0.12)	0.41 (0.09)	0.37 (0.08)
Prey drive	0.91 (0.09)	0.31 (0.07)	0.40 (0.07)	0.90 (0.12)	0.59 (0.09)	0.44 (0.08)
Nerve stability	0.88 (0.17)	0.13 (0.04)	0.34 (0.07)	0.87 (0.16)	0.29 (0.09)	0.22 (0.08)
Hardness	1.00 (0.17)	0.19 (0.06)	0.22 (0.06)	0.46 (0.24)	0.36 (0.08)	0.24 (0.07)
Temperament	0.88 (0.17)	0.26 (0.06)	0.16 (0.05)	0.77 (0.20)	0.37 (0.10)	0.16 (0.07)
Cooperation	0.51 (0.18)	0.30 (0.06)	0.28 (0.07)	0.81 (0.17)	0.36 (0.09)	0.30 (0.08)
Affability	0.92 (0.09)	0.26 (0.06)	0.58 (0.09)	0.41 (0.86)	0.05 (0.05)	0.08 (0.06)
Gun shyness	1.00 (0.11)	0.14 (0.07)	0.18 (0.07)	0.68 (0.12)	0.70 (0.12)	0.66 (0.12)

genetic correlations are comparable between breeds. The genetic correlation between hardness and courage is close to 1, suggesting they have equal genetic background. Also, the genetic correlation between sharpness and defense drive is high (>0.8). In contrast, prey drive and nerve stability are uncorrelated (0.02). Genetic correlations with affability in LR were not significantly different from zero. However, this is most likely because there is no additive genetic variance for 1 or both of the traits involved (see Table 4 for significance levels of the heritability estimates), so there is no correlation. Genetic correlations with cooperation are generally negative, suggesting that genetic potential for a high score for cooperation (i.e., extreme focus on the handler) coincides with genetic potential for a lesser score for courage, sharpness, defense drive, prey drive, nerve stability, hardness, and temperament. In other words, dogs with a high reward dependence level (i.e., willingness to please) seem to also be more fearful, less aggressive, less defensive, less competitive, and more nervous. These results seem to agree with those of Belyaev (1978) and Trut (1999), who described that selection for tame behavior in silver foxes (i.e., selection for novelty seeking and against harm avoidance) resulted in animals that were less fearful, less aggressive, and more self-confident. Courage and temperament are uncorrelated, suggesting different underlying genetic mechanisms.

Even though most genetic correlations are in the same range in GSD and LR, a few are significantly different. The genetic correlation between defense drive and courage is significantly greater in GSD (0.80 in GSD, 0.26 in LR), whereas the genetic correlation between defense drive and temperament is significantly greater in LR (0.36 in GSD, 0.81 in LR). In both cases, the low estimates were not significantly different from zero. The same phenomenon was present in the phenotypic correlations but less obvious. Explanation for these seemingly contradictory genetic correlations in the 2 breeds may lay in the definition of defense drive. Defense drive includes aggression in most cases, which would explain the correlation with courage in GSD.

However, a dog may also show defensive behavior without being aggressive, which may explain the correlation with temperament (liveliness) in LR.

The genetic correlation between hardness and cooperation is different in the 2 breeds, and significantly greater and of opposite sign in GSD (-0.67 in GSD, 0.28 in LR) and nonsignificant in LR. In this case, the phenotypic correlations are also different (-0.54 in GSD, 0.07 in LR). This difference intuitively can be explained by the fact that GSD, in contrast to LR, has a history as a herding and defense, and later as a police, dog. It thus may not be easily or long-lastingly impressed by experiences and, consequently and perhaps unfortunately, by more subtle influences by the handler. This difference in correlations suggests the presence of a difference in underlying physiology in both breeds, most likely caused by the very long selection history for different temperaments. This hypothesis is supported by results by Parker et al. (2004), who showed LR and GSD are members of different genetic clusters. They placed GSD in the cluster of breeds related to the Mastiff, whereas LR was mainly part of the cluster with hunting dogs.

Genetics of Behavior in Males and Females

Table 6 shows genetic correlations between the behavior traits and the heritabilities for males and females in both breeds. In GSD, the genetic correlations between male and female behavior for defense drive (0.47) and cooperation (0.51) are different from 1. In LR, the genetic correlations between male and female behavior for hardness (0.46) and gun shyness (0.68) are different from 1. These estimates indicate that partly different genetic mechanisms are involved in these behavior traits in males and females. Heritability estimates in males and females tend to be greater than the overall estimates (Table 4), but with greater standard errors. Heritabilities for nerve stability and affability are significantly different for males and females in GSD and for courage and temperament in the LR. However, these differences in heritabilities relate

to different traits than those for which the correlations between males and females were different. That, and the fact that the traits for which the correlation between males and females is significantly different from 1 are different in the 2 breeds, suggests that additional proof from other data should be obtained before conclusions are drawn.

Conclusion

Results of this study indicate that behavior in dogs is influenced by several systematic environmental, as well as genetic, effects. Therefore, directional selection for certain desired behavior is possible. Systematic effects in some cases cause large upward or downward bias to the eventual phenotype. Not taking these effects into account when making selection decisions thus may have substantial influence on selection results. Estimating breeding values would be a good solution, incorporating both correction for systematic effects and using all genetic links. Because some of the correlations are significantly different in the 2 breeds, genetic parameters need to be estimated for each breed separately. Even though further evidence is required, use of overall estimates of genetic parameters for males and females most likely will not affect selection decisions.

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