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The genetic contribution to canine personality

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The domestic dog may be exceptionally well suited for behavioral genetic studies owing to its population history and the striking behavior differences among breeds. To explore to what extent and how behavioral traits are transmitted between generations, heritabilities and genetic correlations for behavioral traits were estimated in a cohort containing over 10 000 behaviorally tested German shepherd and Rottweiler dogs. In both breeds, the pattern of co-inheritance was found to be similar for the 16 examined behavioral traits. Furthermore, over 50% of the additive genetic variation of the behavioral traits could be explained by one underlying principal component, indicating a shared genetic component behind most of the examined behavioral traits. Only aggression appears to be inherited independently of the other traits. The results support a genetic basis for a broad personality trait previously named shyness–boldness dimension, and heritability was estimated to be 0.25 in the two breeds. Therefore, breeds of dogs appear to constitute a valuable resource for behavioral genetic research on the normal behavioral differences in broad personality traits.

Keywords: Behavioral genetics, behavioral test, *Canis familiaris*, dog, genetic correlations, heritability, personality trait

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Personality refers to the behavioral characteristics of individuals that describe and account for consistent patterns of normal behavior that are stable across time and situations (Plomin & Caspi 1999). There are several working models for human personality traits, including the three-factor models proposed by Eysenck and Eysenck (1985) and Tellegen (1985) and the five-factor model proposed by Goldberg (1990). Research focused on comparative animal personality has revealed a number of trans-species personality traits including fearfulness, exploration, sociability, aggressiveness and activity level, suggesting that some personality traits have been evolutionary conserved (Gosling 2001; Gosling & John 1999). The complex personality phenotypes are thought to be influenced by many environmental factors and multiple genes (Bouchard 1994; Plomin *et al.* 1994). Currently, only a handful of genes have been associated with personality traits in humans, and their effect on the variation of normal behavioral phenotypes is usually limited (Benjamin *et al.* 1996; Caspi *et al.* 2002; Murphy *et al.* 2001). However, animal models offer a promising approach to detect the genetic components of complex behavioral traits (Flint 2003).

An often-overlooked resource for behavioral genetics is the domestic dog. This species is an exceptional organism in that it has been bred specifically for different behaviors (Ostrander *et al.* 2000). During the domestication of dogs, there have been a variety of selective pressures (Clutton-Brock 1999), and as a result, modern breeds of dogs display striking behavioral differences such as emotionality, aggressiveness, activity and predatory behavior (Coppinger & Schneider 1995; Coppinger *et al.* 1987; Hart & Miller 1985; Murphree *et al.* 1977; Overall 2000; Scott & Fuller 1966; Shekhar *et al.* 2001). Moreover, the recent history of many breeds is characterized by narrow bottlenecks and population expansions (Ostrander *et al.* 2000; Ostrander & Kruglyak 2000), and the existing population of purebred dogs (>300 breeds recognized by both Fédération Cynologique Internationale and the American Kennel Club) may be described as a collection of partially inbred genetic isolates. Some of the breed-specific morphological characteristics, inherited diseases and behaviors are likely to be the result of pronounced founder effects (Chase *et al.* 2002; Ostrander & Kruglyak 2000; Ostrander *et al.* 2000; Overall 2000).

Since 1989, the Swedish Working Dog Association has carried out a standardized behavioral test called Dog Mentality Assessment (DMA), and each year, thousands of dogs representing more than 180 breeds are being scored in six test situations called social contact, play, chase, sudden appearance, metallic noise and ghost. In each test situation, the animal is presented to a stimulus, and several behavioral traits are scored simultaneously. Svartberg and Forkman (2002) used factor analysis to explore the phenotypic correlation structure of DMA test results from a wide array of breeds and aggregated the scored behavioral traits into higher order composite traits. However, in animal research where behavior is assessed across several test situations,

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the correlation of behavioral traits scored in the same test situation tend to be larger than the correlation of behavioral traits scored in different test situations, presumably due to environmental events that occur just before or during the test situations. Thus, factor analysis on phenotypic correlations can result in factors mainly discriminating between test situations, which may obscure less-pronounced cross-test behavioral consistencies (Henderson *et al*. 2004).

An alternative way to define higher order behavioral traits is to use information on the genetic structure of the measured behavioral responses for the definition of composite traits (Flint 2003). When the genotype of animals is unknown, the co-inheritance (or genetic correlation) of two or more behavioral traits indicates that there are shared genetics and possibly a common biological mechanism underlying the behavioral traits. In this study, the genetic correlations between 16 measured behavioral traits were estimated in a cohort of DMA-tested German shepherd and Rottweiler dogs, using the pedigree register kept by the Swedish Kennel Club (Egenvall *et al*. 1999). The genetic correlation structure was compared between the two breeds and to previously defined personality traits. This data set, containing over 10 000 related and behaviorally tested dogs, is to our knowledge the largest data set that has been used for this purpose.

Materials and methods

The Dog Mentality Assessment test

This study is based on German shepherd and Rottweiler dogs that have been tested in a standardized behavioral test called DMA by the Swedish Working Dog Association. They initiated their testing of dogs in 1989, and in September 2001, more than 24 000 dogs from more than 150 breeds had been tested. The test was originally developed as a tool for selective breeding of working dogs and is today considered as a general behavioral test by many breeding clubs in Sweden. In the test, dogs are exposed to several test situations, and in each test situation, the intensity of one or more reactions (behavioral traits) are scored from 1 to 5 by an official observer, according to a standardized score sheet (see Supplementary material for details). All functionaries (observers and test leaders) have been trained and certified by the Swedish Working Dog Association, and the performance of the observers has been tested to assure a maximum of inter-rater reliability.

In 1997, the test was modified, and the number of test situations, as well as the number of scored behavioral traits, was expanded. In this study, personality trait scores have been calculated from the 16 behavioral traits that were scored in six test situations (social contact, play, chase, sudden appearance, metallic noise and ghost) that existed and were similar before and after the revision of the test. The scoring scale for four of these behavioral traits had been slightly altered after the revision of tests, and thus, the score from the earlier version of the test was adjusted to the intensity scale of the second version (for details see Strandberg *et al*. 2005).

Sampling and data preparation

German shepherds and Rottweiler were the two most numerous breeds, constituting over 50% of all tested dogs. The sample was restricted to dogs that had a complete score in all 16 investigated behavioral traits and dogs that had been scored by a judge that had scored at least 9 other dogs. In total, 182 official observers (judges) were involved scoring the dogs for this data set. For the dogs that had been tested twice, only the results from the first test occasion were analyzed. Because no more than 10 Rottweiler and nine German Shepard dogs had been tested more than once, the repeatability was not estimated. Furthermore, because the test occasions were typically separated by 12 months or more for dogs that had been tested twice, the results from a second test could not be expected to be a good repeated measure, owing to the possible learning effect and the possibility of specific training in the intervening period. These criteria resulted in a sample of 5964 German shepherds and 4589 Rottweilers (Table 1). To estimate the genetic correlations and heritabilities, untested relatives to the tested dogs were included to the level of grandparents. As a result, 3646 untested German shepherds and 1255 untested Rottweiler dogs were added to the pedigree files including all tested German shepherds and Rottweilers respectively. The pedigree information was retrieved from the registries of the Swedish Kennel Club.

Estimation of genetic correlations and heritability

To estimate the heritability of the 16 scored behavioral traits and the degree to which they are co-inherited (genetic correlations, R_A), we analyzed the behavioral traits in all possible pairwise combinations with a bivariate variance component model. This is a mixed linear model in which the column vector of phenotypic values of n individuals ($\mathbf{y}$) is expressed in terms of its additive genetic value and other random and fixed effects:

$$\mathbf{y} = X\mathbf{b} + Z\mathbf{a} + W\mathbf{c} + \mathbf{e} \tag{1}$$

where $\mathbf{b}$, $\mathbf{a}$, $\mathbf{c}$ and $\mathbf{e}$ are vectors of fixed effects, additive polygenic effect (breeding values), litter effect and residuals, respectively, with all observations for trait 1 coming first, followed by all for trait 2, and X, Z and W are the corresponding design matrices (Henderson 1984; Mrode 1996). A statistical analysis package (DMU, version 6, release 4) developed for quantitative genetics analysis (Madsen & Jensen 2000) was used to fit the models.

The fixed effects included in $\mathbf{b}$ were sex, age at test in months (12–25), test version (1 or 2), test year (1989–2001), calendar month of testing (1–12) and judge scoring the dog (1–182). The expectation of random effects were all zero with the following distributions:

Table 1: Background information and population structure of tested German shepherd and Rottweiler dogs

	Breed	
	German shepherd	Rottweiler
Total number of tested dogs	5964	4589
Original test (1989–96)	2180	2117
Revised test (1997–2001)	3784	2472
Test age in months	17.2 (14–17)	16.5 (14–17)
Males	3128	2248
Females	2836	2341
Fathers of tested dogs	818	434
Tested fathers	110	151
Tested dogs with tested fathers	863	2051
Mothers of tested dogs	1697	785
Tested mothers	280	343
Tested dogs with tested mothers	1465	2352
Number of litter	2265	1207
Inbred dogs (of tested dogs)	5734	4092
Inbreeding coefficient	2.9% (1.3–4.1)	3.2% (1.0–4.3)
Untested relatives included	3646	1255

Mean and range (first to third quartile) are given for age (in months) and inbreeding coefficient. Inbreeding coefficients are given for inbred animals only, and the estimates are based on the last 10 generations.

$$\mathrm{var}(\mathbf{a})=\begin{bmatrix}\sigma^2_{a1} & \sigma_{a1a2}\\ \sigma_{a2a1} & \sigma^2_{a2}\end{bmatrix}\otimes\mathbf{A},\mathrm{var}(\mathbf{c})=\begin{bmatrix}\sigma^2_{c1} & \sigma_{c1c2}\\ \sigma_{c2c1} & \sigma^2_{c2}\end{bmatrix}\otimes\mathbf{I}_c$$

$$\text{and}\,\mathrm{var}(\mathbf{e})=\begin{bmatrix}\sigma^2_{e1} & \sigma_{e1e2}\\ \sigma_{e2e1} & \sigma^2_{e2}\end{bmatrix}\otimes\mathbf{I}$$

where the two traits are indexed by 1 and 2, **A** is the additive relationship matrix including available information on all relationships among all individuals, and $\mathbf{I_c}$ and **I** are identity matrices of sizes equal to number of litters and observations, respectively. The genetic correlation was defined as $\sigma_{a1a2}\big/\sqrt{\sigma^2_{a1}\sigma^2_{a2}}$. The heritability was calculated as $\sigma^2_a/(\sigma^2_a+\sigma^2_c+\sigma^2_e)$, averaging over all 15 bivariate analyses of the behavioral variable. The fixed effects included in the model were selected from a preliminary analysis using a linear model excluding the additive polygenic and litter effects with the GLM procedure (Proc GLM) in the SAS software (SAS/STAT® software, version 8.02, SAS institute Inc., Cary, NC). Typically, three to five of the six fixed effects included in the model had a significant influence on the score of a behavioral trait. The effect of judge was always highly significant ($P < 0.0001$). For German shepherd, the effect of sex was significant for 12 of the 16 behavioral traits, and the effects of age, test, year and month were significant for 11, 2, 15 and 11 of the 16 behavioral traits, respectively. For Rottweiler, the effect of sex, age, test, year and month were significant for 14, 7, 1, 7 and 7 of the 16 behavioral traits, respectively. For simplicity, the same model was used for all behavioral traits. The random factors (direct genetic and litter effects) were selected based on previous model evaluation of DMA personality traits in German Shepard (Strandberg *et al.* 2005).

Analysis of genetic correlation matrix

The significance level of $\alpha = 0.01$ was chosen for the estimated genetic correlations. Under the null hypothesis, we expect to find approximately one significant correlation in each breed by chance, because we are studying 120 genetic correlations. This corresponds to a false discovery rate of approximately 0.016 in German shepherd and 0.023 in Rottweiler. Principal component analysis (Proc Princomp, SAS/STAT® software, version 8.02, SAS institute Inc.) was used to explore the structure of the genetic correlation matrix. The relative importance of principal components was assessed with a scree diagram (Cattell 1965).

Evaluation of personality rating model

In previous studies, Svartberg (2002) and Svartberg & Forkman (2002) used phenotypic correlations to group the behavioral variables scored in the DMA test into several specific personality traits and one higher-order personality trait called Shyness–Boldness. We used five of these predefined composite personality traits (Table 2) to predict the genetic correlation pattern and compared it to the observed genetic correlation. For the predictions, it was assumed that the behavioral traits contributing to a composite personality trait are co-inherited and that the contribution of each trait is equally strong. Similarly, it was assumed that behavioral traits that do not contribute to the same composite personality traits are

Table 2: Definition of four specific and one broad personality trait created from 16 behavioral traits scored in a standardized behavioral test for dogs

		Specific personality traits				
Test situation	Scored behavior	Playfulness	Chase-proneness	Curiosity/fearlessness	Aggressiveness	Boldness
Social contact	Greeting	0	0	0	0	+
Play	Interest	+	0	0	0	+
	Grabbing	+	0	0	0	+
	Tug-of-war	+	0	0	0	+
Chase	Following	0	+	0	0	+
	Grabbing	0	+	0	0	+
Sudden appearance	Startle reaction	0	0	–	0	–
	Exploration	0	0	+	0	+
	Remaining avoidance	0	0	–	0	–
	Aggression			0	+	0
Metallic noise	Startle reaction	0	0	–	0	–
	Exploration	0	0	+	0	+
	Remaining avoidance	0	0	–	0	–
Ghost	Startle reaction	0	0	–	0	–
	Exploration	0	0	+	0	+
	Aggression	0	0	0	+	0

Scores for the personality traits are calculated by summing the representative behavioral traits, with a positive or negative sign as indicated in the table. For details on the calculations, see Svartberg (2002).

inherited independently, i.e. are genetically uncorrelated. Firstly, the genetic correlation pattern was predicted, assuming the existence of four genetically independent personality traits (supplementary Table S1). Next, the genetic correlation pattern was predicted for the higher order trait shyness–boldness, implying that shared genetics is underlying all behavioral response except aggressive behavior (supplementary Table S2). The predicted correlation pattern was fitted to the observed correlation patterns with a regression model (Proc GLM, SAS/STAT® software, version 8.02, SAS institute Inc.) estimating the strength of the genetic correlations (β_i). The model fit was assessed with the fraction of explained to total variation (r^2).

Results

We estimated the genetic correlation matrix corresponding to the DMA test for two breeds, German Shepard and Rottweiler, with a bivariate variance component models (mixed linear models) for all pair-wise combinations of 16 scored behavioral traits (Table 3). The overall correspondence of genetic correlations between the two breeds was high, with a $r^2 = 0.79$, and a slope close to one (Fig. 1). However, there were some differences between the breeds: genetic correlations tended to be stronger in German Shepherd than in Rottweiler, as evident from the average genetic correlation for each breed (0.53 vs. 0.45, $P = 0.01$) and from the number of significant ($P \leq 0.01$) correlations (77 vs. 53). Specifically, the genetic correlations associated with following and grabbing in the chase test situation and with the startle reaction in the metallic noise and the ghost test situations appeared to be weaker in Rottweiler than in German shepherds (Table 3).

In both breeds, most of the additive genetic variance underlying the correlation matrix could be explained by one underlying trait, as revealed by principal component analysis (Fig. 2a). The first principal component explained 58 and 53% of the total additive genetic variance of German shepherd and Rottweiler respectively, and the loadings of behavioral traits on the first principal component (PC1) were very similar in both breeds except for aggressive response (Fig. 2b). The average (absolute) value of loadings on PC1 for all behavioral traits, except the two associated with aggression, were 0.8 and 0.75 for German shepherd and Rottweiler, respectively. Behavioral traits associated with playfulness, chase-proneness and exploration had positive loadings, whereas behavioral response associated with startle reaction or remaining fear loaded negatively on the first principal component (Fig. 2b). The eigenvalues and the variation explained by the remaining principal components were very small compared with that of the first component (Fig. 2a), and therefore, higher order

Table 3: Genetic correlations between 16 behavioral traits in German shepherd and Rottweiler dogs, estimated from bi-variate variance component models

			German shepherds															
	Test situation	Scored behavior	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	Social contact	Greeting	0.05															
2	Play	Interest	0.51*	0.19*														
3		Grabbing	0.49	1.00*,†	0.14*													
4		Tug-of-war	0.44	0.98*,†	0.86*,†	0.19*												
5	Chase	Following	0.36	0.70*	0.80*	0.61*	0.06*											
6		Grabbing	0.39	0.67*	0.86*	0.70*	0.94*,†	0.09*										
7	Sudden appearance	Startle reaction	−0.69*	−0.32*	−0.50*	−0.40*	−0.24	−0.34	0.17*									
8		Exploration	0.28	0.48*	0.61*	0.51*	0.26	0.31	−0.89*,†	0.18*								
9		Remaining avoidance	−0.61	−0.76*	−0.92*	−0.64*	−0.50	−0.62*	0.76*,†	−0.87*,†	0.07*							
10	Metallic noise	Startle reaction	−0.45	−0.38*	−0.45*	−0.36*	−0.58*	−0.50*	0.78*,†	−0.71*,†	0.73*,†	0.14*						
11		Exploration	0.58	0.70*	0.71*	0.58*	0.60*	0.49*	−0.72*,†	0.87*,†	−0.79*,†	−0.75*,†	0.10*					
12		Remaining avoidance	−0.45	−0.74*	−0.92*	−0.66*	−0.70*	−0.72*	0.50*,†	−0.73*,†	0.85*,†	0.75*,†	−0.89*,†	0.07*				
13	Ghost	Startle reaction	−0.29	−0.40*	−0.39*	−0.43*	−0.61*	−0.46*	0.67*,†	−0.52*,†	0.56*,†	0.73*,†	−0.60*,†	0.25†	0.18*			
14		Exploration	0.46	0.57*	0.48*	0.58*	0.68*	0.48*	−0.95*,†	0.89*,†	−0.80*,†	−0.78*,†	0.67*,†	−0.48*,†	−0.77*,†	0.11		
15	Sudden appearance	Aggression	0.13	0.24	0.26	0.22	0.57*	0.35	−0.27	0.21	−0.03	−0.21	0.28	−0.12	−0.45*	0.11	0.10*	
16	Ghost	Aggression	0.00	0.23	0.23	0.27	0.21	0.25	−0.35	0.22	−0.29	−0.29	0.37	−0.25	−0.31	0.21	0.71*,†	0.12*
			Rottweilers															
	Test situation	Scored behavior	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	Social contact	Greeting	0.09*															
2	Play	Interest	0.55*	0.14*														
3		Grabbing	0.57	0.97*,†	0.07													
4		Tug-of-war	0.72*	0.82*,†	0.97*,†	0.11*												
5	Chase	Following	0.07	0.62*	0.67*	0.02	0.10*											
6		Grabbing	0.35	0.62*	0.72*	0.32	0.78*,†	0.12*										
7	Sudden appearance	Startle reaction	−0.38	−0.40	−0.64*	−0.47	−0.05	−0.32	0.13*									
8		Exploration	0.57*	0.67*	0.79*	0.76*	0.35	0.62*	−0.69*,†	0.10*								
9		Remaining avoidance	−0.70*	−0.78*	−0.95*	−0.96*	−0.34	−0.33	0.69*,†	−0.63*,†	0.08*							
10	Metallic noise	Startle reaction	−0.16	−0.13	−0.25	−0.22	−0.08	0.00	0.81*,†	−0.28†	0.34†	0.09*						
11		Exploration	0.83*	0.71*	0.77*	1.00*	0.37	0.50*	−0.49*,†	0.84*,†	−0.94*,†	−0.70*,†	0.09*					
12		Remaining avoidance	−0.54	−0.62*	−0.76*	−0.84*	−0.06	−0.01	0.34†	−0.45†	1.00*,†	0.92*,†	−0.85*,†	0.04				
13	Ghost	Startle reaction	−0.30	−0.27	−0.76*	−0.27	−0.27	−0.24	0.48*,†	−0.48*,†	0.20†	0.36†	−0.38†	0.34†	0.16			
14		Exploration	0.58*	0.43*	0.93*	0.52*	0.27	0.33	−0.61*,†	0.73*,†	−0.38†	−0.54*,†	0.66*,†	−0.60*,†	−0.88*,†	0.14*		
15	Sudden appearance	Aggression	−0.19	−0.08	−0.24	−0.09	−0.10	−0.27	0.20	−0.21	0.22	−0.17	0.19	−0.23	−0.07	−0.08	0.10*	
16	Ghost	Aggression	−0.16	0.08	−0.11	0.32	0.09	0.14	0.17	0.07	−0.29	−0.16	0.24	−0.14	−0.47	0.33	0.52*,†	0.06*

Heritabilities are given on the diagonal.

*Statistically significant estimates ($P \leq 0.01$).

†The grouping of behavioral traits into four previously defined specific personality traits.

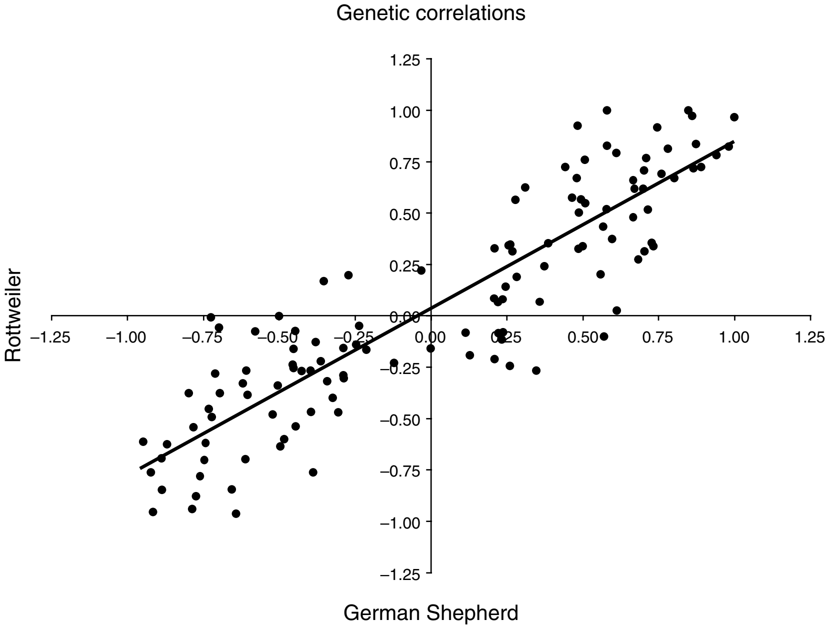

Figure 1: Genetic correlations (r_A) of 16 behavioral traits scored in a standardized behavioral test for dogs in two breeds of dogs. The estimate of 120 genetic correlations in Rottweiler is plotted as a function of the corresponding estimate in German shepherd. The correspondence of estimates in the two breeds was high, with a linear regression slope of 0.98 (SE = 0.05) and $r^2 = 0.79$.

components were not further analyzed. The first principal component suggested that there is shared genetics behind all behavioral traits except in those related to aggression, and thus, supports the previously defined higher order personality trait shyness–boldness (Svartberg 2002).

We then specifically studied the genetic correlations of the behavioral traits that are grouped together in DMA personality rating system. We noted that the behavioral traits that are used to calculate the personality trait playfulness (interest, grabbing and tug-of-war) were all strongly ($r_A > 0.8$) positively correlated (Table 3). The genetic correlations for the behavioral traits associated with chase-proneness (following and grabbing) and aggressiveness (aggression in the sudden appearance and ghost-test situations) were also positive and statistically significant, although the correlations were not strong (Table 3). For the composite personality trait exploration/fearlessness, the signs of the genetic correlations between behavioral traits agreed with expectations from the definition of the trait. That is, behavioral traits that are summed with equal sign were positively correlated to each other, whereas behavioral traits that are summed with different signs were negatively correlated. In German shepherds, all but one of the 28 genetic correlations associated with exploration/fearlessness were statistically significant. However, in Rottweiler, one-third of the correlations were relatively weak ($|r_A| \leq 0.45$) and not significantly different from zero (Table 3). Taken together, the correlation pattern expected from all four of the specific personality traits could only explain 46 and 39% of the variation of observed genetic correlations in German shepherd and Rottweiler, respectively. However, the predicted correlation pattern for the broad personality trait shyness–boldness fitted the observed data much better, and the predicted correlation pattern from shyness–boldness explained 85 and 77% of the variation of observed genetic correlations in German shepherd and Rottweiler, respectively.

The heritability values of the 16 behavioral traits are shown as the diagonal numbers in Table 3. These values ranged from 0.04 (remaining fear) to 0.19 (tug-of-war), and the genetic variance was significantly different from zero for all but one trait in German shepherd and two traits in Rottweiler. The heritability of the higher order personality trait shyness–boldness was higher, 0.25 and 0.27 for German shepherd and Rottweiler respectively.

Discussion

Behavioral genetic research on personality in dogs was pioneered by Scott and Fuller at the Jackson Laboratory in Bar Harbor (Maine, USA) during the 50s and 60s (Scott & Fuller 1966). They demonstrated a significant genetic contribution to almost all investigated traits, and by analyzing the behavior in five dog breeds, several broad behavioral traits were also identified that were associated with fearfulness, aggressiveness, reactivity and general activity (Brace 1961; Cattell & Korth 1973; Royce 1955). Behavioral testing of dogs is now widely used in breeding programs around the world, for example, for selecting service dogs. A standardized behavioral test, the DMA, has been used by Swedish Working Dog Association since 1989; and each year, thousands of dogs representing more than 180 breeds are being tested. To explore to what extent and how behavioral traits are transmitted between generations, we have estimated heritabilities and genetic correlations for behavioral traits in a cohort containing over 10 000 behaviorally tested German shepherd and Rottweiler dogs.

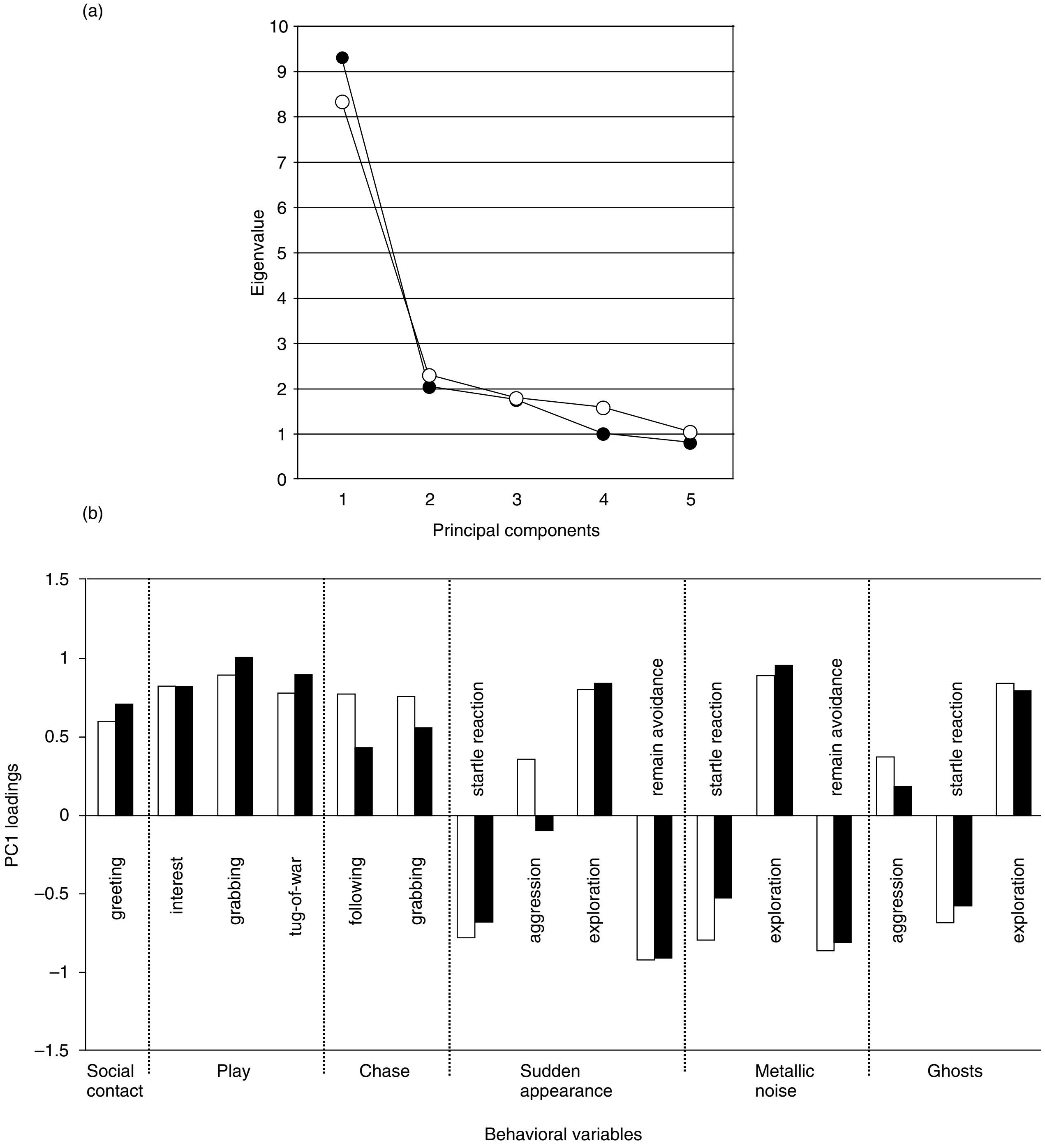

Figure 2: Principal component analysis of the genetic correlation matrix of 16 behavioral traits. (a) The first principal component (PC1) explains explains 58 and 53% of the total additive genetic variation for German shepherds [black circles (●)] and Rottweilers [white circles (○)], respectively. Only marginal additional variation is explained by higher order principal components. (b) Loadings of 16 behavioral traits on the first principal component for German shepherds [black rectangles (■)] and Rottweilers [white rectangles (□)]. Loadings have been scaled so that the squared loadings sum up to the eigenvalue of the first component.

In the study, we investigated 16 behavioral traits (variables) scored in the DMA test in the two breeds of dogs. It was shown that the reaction in one test situation is not genetically independent from the reactions in other test situations. In fact, our analysis provides evidence that there may be substantial shared genetics underlying most of the behavioral response in all of the test situations. The exception to this is aggressive behavior, which is genetically correlated across two test situations but only weakly correlated to other behavioral traits. We also note that the overall structure of the genetic correlations is very similar between the two breeds. For the broad personality trait shyness–boldness, the expected pattern of co-inheritance was very similar to the observed pattern of genetic correlations. The predicted correlation pattern explained 85% of the observed correlation in German shepherds and 77% in Rottweiler. Furthermore, shyness–boldness was found to explain almost twice as much of the variation of genetic correlations as the four genetically independent personality traits playfulness, chase-proneness, curiosity/fearlessness and aggressiveness. The existence of a partly genetically determined broad behavioral trait that can explain a significant part of the behavioral response in all the test situations, with the exception of aggressive behavior, is further strengthened by the fact that the heritability estimates of boldness (0.25 and 0.27) exceeded those of the individual behavioral traits in both breeds (0.04–0.19).

The DMA test has been designed to meet the demands from breeders of working dogs, and the resulting data cannot be regarded as direct observational data in a strict sense. For example, recording a behavioral response in a five-point intensity scale is obviously a crude and over-simplified description of underlying behavioral responses that clearly depends on the description of the intensity scale. However, the collected data comprise a much larger number of dogs than would ever be possible to test under more strict conditions. The behavioral scores derived from DMA personality rating have also been shown to have a high test–retest consistency (Svartberg *et al*. 2005a) and a good predictive power for behaviors outside the test situation and for performance in working dog trials (Svartberg 2002; Svartberg 2005b). Also, in spite of using crude test methods, general tests measuring similar aspects of dog personality still contribute to our knowledge about basic patterns in dog behavior and have proved to be useful in the selection of potential working dogs (Wilsson & Sundgren 1997).

There are several previous studies indicating the existence of a broad personality trait in dog similar to the shyness–boldness dimension. For example, Brace in Scott and Fuller (1966) identified one general behavioral dimension related to activity, confidence and performance in several test situations. This personality trait was labeled 'Activity–success' and was uncorrelated to aggressive behavior. Goddard and Beilharz (1985) studied the social behavior of dogs and identified a personality trait that was labeled 'Confidence', which was uncorrelated to aggression–dominance behavior. Wilsson and Sundgren (1997) identified a personality trait associated with courage, nerve stability and hardness across several different test situations that was only weakly correlated to aggressive behavior (sharpness) and defense drive in German shepherds and Labrador retrievers. Finally, Svartberg and Forkman (2002) using similar data as in this study identified the broad personality trait boldness, which was stable across a large number of breeds and unrelated to aggressiveness. We also note that Svartberg has shown that DMA boldness scores are related to performance in working dog trials, suggesting that the broad personality trait predisposes trainability in general (Svartberg 2002) and that boldness scores can predict behavioral response in the home environment, including interest in playing with humans, behavior towards strangers and non-social fear (Svartberg 2005b).

Shyness–Boldness is a personality dimension that is also readily recognized in humans (Kagan *et al*. 1988; Matthews & Deary 1998; Zuckerman 1991) as well as in other mammals such as rats (Pellis & McKenna 1992), hyenas (Gosling 1998) and marmots (Armitage 1986). There are also indications that the shyness–boldness continuum exists in the dog's wild ancestor, the wolf (Fox 1972). It has been suggested that \variation in boldness and shyness can be maintained in a population by frequency-dependent selection, in which the relative frequency of bold (risk-prone) phenotypes is dependent on the relative frequency of shy (risk-averse) phenotypes in a population (Wilson *et al*. 1994). The fact that the shyness–boldness dimension has been found in a large number of breeds (Svartberg & Forkman 2002) and has a clear genetic basis in the two investigated breeds in this study supports the previous suggestion that this trait has survived the varied selection pressures encountered during domestication.

References

Armitage, K.B. (1986) Individuality, social behavior, and reproductive success in yellow-bellied marmots. *Ecology* **67**, 1186–1193.

Benjamin, J., Li, L., Patterson, C., Greenberg, B.D., Murphy, D.L. & Hamer, D.H. (1996) Population and familial association between the D4 dopamine receptor gene and measures of novelty seeking. *Nat Genet* **12**, 81–84.

Bouchard, T.J. Jr (1994) Genes, environment, and personality. *Science* **264**, 1700–1701.

Brace, C.L. (1961) *Physique, Physiology, and Behavior: An Attempt to Analyze a Part of Their Roles in the Canine Biogram.* PhD Disertation, Department of Anthropology, Harvard University.

Caspi, A., Mcclay, J., Moffitt, T.E., Mill, J., Martin, J., Craig, I.W., Taylor, A. & Poulton, R. (2002) Role of genotype in the cycle of violence in maltreated children. *Science* **297**, 851–854.

Cattell, R.B. (1965) Factor analyis: an introduction to essentials. II. The role of factor analysis in research. *Biometrics* **21**, 405–435.

Cattell, R.B. & Korth, B. (1973) The isolation of temperament dimensions in dogs. *Behav Biol* **9**, 15–30.

Chase, K., Carrier, D.R., Adler, F.R., Jarvik, T., Ostrander, E.A., Lorentzen, T.D. & Lark, K.G. (2002) Genetic basis for systems of skeletal quantitative traits: principal component analysis of the canid skeleton. *Proc Natl Acad Sci USA* **99**, 9930–9935.

Clutton-Brock, J. (1999) *A Natural History of Domesticated Mammals.* Cambridge University Press, Cambridge, UK.

Coppinger, R. & Schneider, R. (1995) Evolution of the working dogs. In Serpell, J. (ed.) *The Domestic Dog*. Cambridge University Press, Cambridge.

Coppinger, R.J., Glendinning, E., Torop, C., Matthay, C., Sutherland, M. & Smith, C. (1987) Degree of behavioral neoteny differentiates canid polymorphs. *Ethology* **75**, 89–108.

Egenvall, A., Hedhammar, A., Bonnett, B.N. & Olson, P. (1999) Survey of the Swedish dog population: age, gender, breed, location and enrollment in animal insurance. *Acta Vet Scand* **40**, 231–240.

Eysenck, H.J. & Eysenck, M.W. (1985) *Personality and Individual Differences.* Plenum, New York.

Flint, J. (2003) Analysis of quantitative trait loci that influence animal behavior. *J Neurobiol* **54**, 46–77.

Fox, M.W. (1972) Socio- ecological implications of individual differences in wolf litters: a developmental and evolutionary perspective. *Behaviour* **41**, 298–313.

Goddard, M.E. & Beilharz, R.G. (1985) Individual variation in agnostic behaviour in dogs. *Anim Behav* **33**, 1338–1342.

Goldberg, L.R. (1990) An alternative 'description of personality': the big-five factor structure. *J Pers Soc Psychol* **59**, 1216–1229.

Gosling, S.D. (1998) Personality dimensions in spotted hyenas (*Crocuta crocuta*). *J Comp Psychol* **112**, 107–118.

Gosling, S.D. & John, O.P. (1999) Personality dimensions in nonhuman animals: a cross-species review. *Current Directions Psychol Sci* **8**, 69–75.

Gosling, S.D. (2001) From mice to men: what can we learn about personality from animal research? *Psychol Bull* **127**, 45–86.

Hart, B.L. & Miller, M.F. (1985) Behavior profiles of dog breeds. *J Am Vet Med Assoc* **186**, 1175–1180.

Henderson, C.R. (1984) Applications of linear model in animal breeding. University of Guelph Press, Guelph, Canada.

Henderson, N.D., Turri, M.G., Defries, J.C. & Flint, J. (2004) QTL analysis of multiple behavioral measures of anxiety in mice. *Behav Genet* **34**, 267–293.

Kagan, J., Reznick, J.S. & Snidman, N. (1988) Biological bases of childhood shyness. *Science* **240**, 167–171.

Madsen, P. & Jensen, J. (2000) A User's Guide to DMU, Version 6, release 4th ed. Danish Institute of Agriculture and Science, Tjele, Denmark.

Matthews, G. & Deary, I.J. (1998) *Personality Traits.* Cambridge University Press, Cambridge.

Mrode, R.A. (1996) *Linear Models for the Prediction of Animal Breeding Values.* CAB International, Wallingford, UK.

Murphree, O.D., Angel, C., Deluca, D.C. & Newton, J.E. (1977) Longitudinal studies of genetically nervous dogs. *Biol Psychiatry* **12**, 573–576.

Murphy, D.L., Li, Q., Engel, S., Wichems, C., Andrews, A., Lesch, K.P. & Uhl, G. (2001) Genetic perspectives on the serotonin transporter. *Brain Res Bull* **56**, 487–494.

Ostrander, E.A. & Kruglyak, L. (2000) Unleashing the Canine Genome. *Genome Res* **10**, 1271–1274.

Ostrander, E.A., Galibert, F. & Patterson, D.F. (2000) Canine genetics comes of age. *Trends Genet* **16**, 117–124.

Overall, K.L. (2000) Natural animal models of human psychiatric conditions: assessment of mechanism and validity. *Prog Neuropsychopharmacol Biol Psychiatry* **24**, 727–776.

Pellis, S.M. & McKenna, M.M. (1992) Intrinsic and extrinsic influences on play fighting in rats: effects of dominance, partner's playfulness, temperament and neonatal exposure to testosterone propionate. *Behav Brain Res* **50**, 135–145.

Plomin, R. & Caspi, A. (1999) Behavioral genetics and personality. In Pervin, L.A. & John, O.P. (eds), *Handbook of Personality: Theory and Research*, 2nd edn. Guilford, New York.

Plomin, R., Owen, M.J. & Mcguffin, P. (1994) The genetic basis of complex human behaviors. *Science* **264**, 1733–1739.

Royce, J.R. (1955) A factorial study of emotionality in the dog. *Psychol Monograph* **69**, 1–27.

Scott, J.P. & Fuller, J.L. (1966) *Genetics and the Social Behavior of the Dog.* University of Chicago Press, Chicago.

Shekhar, A., Mccann, U.D., Meaney, M.J., Blanchard, D.C., Davis, M., Frey, K.A., Liberzon, I., Overall, K.L., Shear, M.K., Tecott, L.H. & Winsky, L. (2001) Summary of a National Institute of Mental Health workshop: developing animal models of anxiety disorders. *Psychopharmacology (Berl)* **157**, 327–339.

Strandberg, E., Jacobsson, J. & Saetre, P. (2005) Direct genetic, maternal and litter effects on behaviour in German shepherd dogs in Sweden. *Livestock Prod Sci* **93**, 33–42.

Svartberg, K. (2002) Shyness–boldness predicts performance in working dogs. *Appl Anim Behav Sci* **79**, 157–174.

Svartberg, K. & Forkman, B. (2002) Personality traits in the domestic dog (Canis familiaris) *Appl Anim Behav Sci* **79**, 133–155.

Svartberg, K., Tapper, I., Temrin, H., Radesäter, T. & Thorman, S. (2005a) Consistency of personality traits in dogs. *Anim Behav* **69**, 283–291.

Svartberg, K. (2005b) A comparison of behavior in test and in everyday life: evidence of three consistent boldness-related traits in dogs. *Appl Anim Behav Sci* **91**, 103–128.

Tellegen, A. (1985) Structure of mood and personality and their relevance to assessing anxiety, with emphasis on self report. In Tuma, A.H. & Maser, J.D. (eds), *Anxiety and the Anxiety Disorders*. Erlbaum, Hillsdale, NJ.

Wilson, D.S., Clark, A.B., Coleman, K. & Dearstyne, T. (1994) Shyness and boldness in humans and other animals. *Trends Ecol Evol* **9**, 442–446.

Wilsson, E. & Sundgren, P.-E. (1997) The use of a behaviour test for the selection of dogs for service and breeding, I: Method of testing and evaluating test results in the adult dog, demands on different kinds of service dogs, sex and breed differences. *Appl Anim Behav Sci* **53**, 279–295.

Zuckerman, M. (1991) *Psychobiology of Personality*. Cambridge University Press, Cambridge.

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Supplementary material

The following material is available online at www.blackwell-synergy.com

Table S1: (A) Genetic correlation pattern predicted from a model assuming four genetically independent personality traits.

(B) Genetic correlation pattern predicted from a boldness model, assuming that all behavioral response, except aggressive behavior, is co-inherited.

Appendix S1: Supplementary methods.