Available online at www.sciencedirect.com
SCIENCE DIRECT®
ELSEVIER
Applied Animal Behaviour Science 96 (2006) 293–313
APPLIED ANIMAL BEHAVIOUR SCIENCE
www.elsevier.com/locate/applanim

Breed-typical behaviour in dogs—Historical remnants or recent constructs?

Kenth Svartberg *

Department of Zoology, Stockholm University, SE-10691 Stockholm, Sweden

Accepted 24 June 2005
Available online 1 August 2005

Abstract

Dogs show considerable variation in morphology, genetics and behaviour caused by long periods of artificial selection. This is evident in the large number of breeds we have today. Behavioural differences among breeds have often been regarded as remnants from past selection during the breeds' origin. However, the selection in many breeds has, during the last decades, gone through great changes, which could have influenced breed-typical behaviour. In order to investigate this, breed differences were studied using data from a standardized behavioural test from 13,097 dogs of 31 breeds from the Swedish dog population. Based on the test results, breed scores were calculated for four behavioural traits: playfulness, curiosity/fearlessness, sociability and aggressiveness. These traits have previously been found to be stable and valid, and hence regarded as personality traits in the dog. The present results suggested large differences between breeds in all of the investigated traits, even though there were within-breed variations. No relationships between breed-characteristic behaviour and function in the breeds' origins were found. Instead, there were correlations between breed scores and current use of the breeding stocks, which suggest that selection in the recent past has affected breed-typical behaviour. The breeds' use in dog shows, the dominating use in general, was negatively correlated with all investigated traits, both in sires and in dams. In contrast, use in Working dog trials was positively correlated with playfulness and aggressiveness in sires. Thus, these results suggest that selection for dog show use is positively correlated with social and non-social fearfulness, and negatively with playfulness, curiosity in potentially threatening situations and aggressiveness, whereas selection for Working dog use is positively correlated with playfulness and aggressiveness. Furthermore, correlation analyses show that popular breeds have higher sociability and playfulness

* Present address: Department of Anatomy and Physiology, Faculty of Veterinary Medicine and Animal Science, Swedish University of Agricultural Sciences, Box 7011, SE-750 07 Uppsala, Sweden.
Tel.: +46 18 67 28 21; fax: +46 18 67 21 11.
E-mail address: kenth.svartberg@afys.slu.se.

0168-1591/$ – see front matter
doi:10.1016/j.applanim.2005.06.014

scores than less popular breeds, suggesting that a positive attitude towards strangers is an important characteristic of a functional pet dog and desirable by dog owners. This indicates that selection towards use in dog shows may be in conflict with pet dog selection. Furthermore, these results suggest that basic dimensions of dog behaviour can be changed when selection pressure changes, and that the domestication of the dog still is in progress. A standardized behavioural test, like the one used in this study, is suggested to be highly useful as a tool in dog breeding programs.

Keywords: Dogs; Breed differences; Personality; Temperament; Fearfulness; Aggressiveness; Domestication

1. Introduction

Artificial selection can induce great behavioural changes in domestic species. This has been known at least since Roman times in Europe, and was perhaps already practiced by the early Neolithic farmers in ancient Egypt (Clutton-Brock, 1999). The domestic dog is probably the species that has been put under artificial selection during the longest period of time. The earliest archaeological finding of the domestic dog is dated to 14,000 year BP (Nobis, 1979, in Clutton-Brock, 1999), but results based on mitochondrial DNA suggest that the domestication of the dog may have begun 40,000 years from now (Savolainen et al., 2002). The domestication of the dog has resulted in considerable variety in morphology, genetics and behaviour (e.g. Scott and Fuller, 1965; Wayne, 1986; Wayne and Ostrender, 1999). The first evidence of distinct dog types is dated back to 3000–4000 year BP (Harcourt, 1974), and since then there has been increased variation and specialization. During Roman times, most of the dog types that we know about today – hunting dogs, guard dogs, sheep dogs and lap dogs – were well defined (Clutton-Brock, 1995). Varieties of each type have evolved since then, which is evident in the large number of recognized dog breeds seen today.

Even though studies on breed differences in behaviour are scarce, the existing results suggest that breeds differ in several aspects of behaviour. Breed differences have been found in traits such as emotionality and aggressiveness (Scott and Fuller, 1965; Cattell et al., 1973); the tendency to approach and withdraw in novel situations (Plutchik, 1971); activity and playfulness (Hart and Miller, 1985); predatory behaviour (Coppinger et al., 1987; Christiansen et al., 2001); agonistic signalling (Goodwin et al., 1997). Several authors, both in the non-scientific and scientific dog literature, have suggested that behavioural breed differences can be explained by differences in selection during the breeds' origin (e.g. Hart, 1975; Scott and Fuller, 1965). There are some results supporting this suggestion. Breeds selected for rat hunting and fighting – such as the Terriers – have been shown to be less fearful compared with breeds selected for bird hunting and Herding (Mahut, 1958). These breeds, together with working breeds, are also over-represented as initiators in dog-fights (Roll and Unshelm, 1997). This is supported by Bradshaw et al. (1996), whose results suggested that Working dogs/guard dogs and Terriers are more aggressive than other breeds. Bradshaw et al. (1996) also reported other differences between breed groups in the behavioural traits ''reactivity'' and ''immaturity'', which might be explained by differences in selection pressures in historical time. Seksel et al. (1999) reported breed group differences in social behaviour towards humans, where Gun

dogs were found to have high scores in handling and responsiveness tests compared to dogs of other breed groups. Thus, these results indicate that several aspects of breed-typical behaviour are evolutionarily conservative in the dog.

Due to cultural changes during the last century in modern Western societies, selection and use of dogs are today different to what they once were when the ancestors of the modern dog breeds evolved. The dog's practical functions have been and are gradually diminishing, and the dog's role as a companion and an object of affection has become more and more important (Clutton-Brock, 1995; Hart, 1995). In addition, selection for physical appearance has replaced selection for function, and is today assumed to dominate dog breeding (Willis, 1995; Lindsay, 2000). The start of breeding for appearance coincides with the beginning of organized dog shows and efforts to standardize dog breeds (Lindsay, 2000). In Sweden, there have been dog shows for more than 100 years, and in the UK for nearly 150 years (Grandjean et al., 2000). Even though these periods of time are short in evolutionary terms, it is reasonable to assume that basic emotional traits, such as fearfulness, may have been altered due to changes in selection pressures. These traits seem to be relatively strongly influenced by genes, and are assumed to have a relatively simple genetic base in dogs (Thorne, 1944; Scott and Fuller, 1965). Selection experiments in dogs and other canids have shown that social and non-social fearfulness can be rapidly altered in a few generations under intense selection (Murphree et al., 1969; Murphree, 1973; Kenttämies et al., 2002; Trut et al., 2004). Thus, changes in selection in the domestic dog during the last century may also have led to changes in breed-characteristic behaviour.

This study investigated breed-characteristic behaviour in 31 breeds using data from 13,097 dogs. The behavioural data was collected in a standardized test, from which scores for four behavioural traits related to social fear, non-social fear, play interest and aggressiveness were calculated according to previous results based on data from the same test (Svartberg and Forkman, 2002). These traits have been found to be stable over repeated tests (Svartberg et al., 2005) and have, with the exception of the aggressiveness trait, been validated against data from Working dog trials (Svartberg, 2002) and from owner reports of behaviour in everyday life (Svartberg, 2005). Based on this, these traits have been regarded as stable personality traits in the dog. In the present study, I compared similarity in breed-typical behaviour in breeds that have similar historical functions. This could give an indication whether these aspects of dog behaviour are conservative, and insensitive to recent changes in selection pressure. The current use of the breeding stock in the investigated breeds was also examined, and used as an index of recent selection. This, in turn, was compared with behavioural data to see if recent selection has influenced the typical behaviour of breeds today. Finally, the relationship between popularity of dog breeds and breed-typical behaviour was studied.

2. Methods

2.1. Subjects

Data from dogs that had carried out a standardized behavioural test (''Dog Mentality Assessment'', DMA) at 12–24 months of age were used in this study. The Swedish Kennel

Club (SKC) put the data from the behavioural test at my disposal. Because of a previously found relationship between owner experience from Working dog trials and trait scores (Svartberg, 2002), this was controlled in the present study: all dogs with owners who had merits from Working dog trials with previously owned dogs were excluded. This information was collected from the dog owner register by the SKC. Furthermore, all dogs with unknown owners, and dogs owned by the Swedish Police Force and the Swedish Army and Air Force were excluded. After these exclusions, all breeds with a minimum of 40 tested dogs, and at least 15 dogs from each sex, were included in the sample. Thirty-one breeds reached these criteria. In total, the sample included data from 13,097 dogs, where 6851 were males (52.3%) and 6246 were females (47.7%). The breeds and number of dogs per breed are presented in Table 1. An examination of the numerically smallest breeds (<100 tested dogs/breed) showed that each breed had been scored by at least ten observers, which minimized the bias of differences between observers.

2.2. The behavioural test

The data were collected by the Swedish Working Dog Association from January 19, 1997 to July 28, 2002, at 2426 tests using 213 observers. The behavioural test used, the DMA, included 10 subtests. A handler, usually the owner, accompanied the dog during the test. The handler was guided and instructed by a test-leader, and an official observer described the dogs' behavioural reactions in the subtests. Besides the test-leader and the official observer, two or three assistants were used in the test. All persons conducting the test had been trained and certified by the Swedish Working Dog Association. The subtests, in detail described in Svartberg and Forkman (2002), were:

Social contact: A stranger greeted, walked with, and made a physical examination of the dog. The dog's greeting behaviour, following behaviour and reaction to physical handling were described.
Play 1: A rag was thrown between the handler and the test-leader, and further away from the dog. The dog was then invited to play tug-of-war with the test-leader. The dog's interest in play, intensity in grabbing and interest in playing tug-of-war were described.
Chase: A small rapidly moving object (a rag attached to a long cord) ''fled'' in a zigzag pattern away from the dog. The test was repeated once. The dog's interest in chasing the object and grabbing it were described.
Passive situation: The handler remained in the same position during 3 min with the dog in a leash. The dog's activity level during this period was described.
Distance play: A stranger appeared at a distance, whereafter he invited the dog to play. The dog's interest in the person, aggressive reactions, exploratory behaviour, attempts to play tug-of-war and play invitations were described.
Sudden appearance: A human-like dummy was suddenly pulled up in front of the dog. The dog's startle reaction, avoidance and approach behaviour, as well as aggressive reactions, were described.
Metallic noise: A chain with large links was dragged over a sheet of corrugated metal close to the dog. The dog's startle reaction, avoidance and approach behaviour were described.

Table 1
The breeds included in the study

Breed name	*N*	Breed group	Yearly number of registred dogs, 2000–2002
Australian Kelpie	194	Herding dog	104.3
Australian Shepherd	177	Herding dog	138.0
Beauceron	54	Herding dog	37.0
Belgian Groenendael	165	Herding dog	107.7
Belgian Malinois	218	Herding dog	126.3
Belgian Tervuren	405	Herding dog	180.7
Border Collie	49	Herding dog	682.3
Bouvier des Flandres	165	Herding dog	77.7
Briard	384	Herding dog	193.3
Collie (rough)	551	Herding dog	596.0
German Shepherd Dog	3486	Herding dog	3072.3
Bernese Mountain Dog	480	Working dog	581.7
Boxer	988	Working dog	562.0
Dobermann Pinscher	427	Working dog	322.0
Great Swiss Mountain Dog	95	Working dog	22.0
Hovawart	436	Working dog	160.3
Leonberger	109	Working dog	369.3
Pinscher	71	Working dog	81.0
Giant Schnauzer	471	Working dog	269.3
Rottweiler	2564	Working dog	1104.7
American Staffordshire Terrier	63	Terrier	115.7
Irish Soft-coated Wheaten Terrier	233	Terrier	614.3
Parson Russell Terrier	61	Terrier	208.7
Dalmatian	50	Hound	228.3
Rhodesian Ridgeback	242	Hound	349.3
English Springer Spaniel	74	Gun dog	1026.7
Flat-coated Retriever	193	Gun dog	899.3
Golden Retriever	346	Gun dog	2791.7
Labrador Retriever	189	Gun dog	2258.3
Nova Scotia Duck Tolling Retriever	94	Gun dog	274.0
Poodle	63	Gun dog	541.7

Ghosts: Two persons, covered in white sheets, approached the dog slowly during several minutes. The dog's avoidance reaction, approach behaviour and aggressive behaviour were described.
Play 2: This subtest was a repetition of the first play test, with the exception of the tug-of-war part. The dog's interest in play and intensity in grabbing were described.
Gunshot: Gunshots were fired during activity (handler played with the dog) and during passivity. The dog's avoidance reaction was described.

The dog's behaviour was scored in a score sheet according to scales for the 33 predefined behavioural variables. The scales were, as far as possible, free from subjective opinions. The variables were scored from 1 to 5 according to the intensity of the reaction, where a low score equalled a low intensity in the dog's behavioural reaction. For a more thorough description of the subtests and the scoring of the dogs' behavioural reactions, see Svartberg and Forkman (2002).

2.3. Calculation of the breeds' trait scores

Previous results from factor analyses based on data from the behavioural test on a large number of dogs have revealed six primary factors, which have been interpreted as personality traits (Svartberg and Forkman, 2002). The traits were labelled ''playfulness'', ''curiosity/fearlessness'', ''chase-proneness'', ''sociability'', ''aggressiveness'' and ''distance-playfulness''. A study that investigated the validity and the relevance of the traits in everyday life (Svartberg, 2005) suggested that playfulness, curiosity/fearlessness and sociability were valid and relatively homogeneous traits. Chase-proneness and distance-playfulness shared aspects of these three traits, and were not related to any additional behaviour in everyday life. Based on this, playfulness, curiosity/fearlessness, sociability and aggressiveness were used as behavioural measures in this study (aggressiveness was included because of its relevance, despite that this trait was difficult to validate against behaviour in everyday life; Svartberg, 2005). According to the behavioural description in the DMA (Svartberg and Forkman, 2002) and the correspondence in behaviour in everyday life (Svartberg, 2005) these traits can be defined as dimensions reflecting characteristic behavioural strategies in different situations. Playfulness runs from low interest in playing with strangers to high interest (e.g. tug-of-war, running after thrown objects). Curiosity/fearlessness runs from high fearfulness (e.g. avoidance, flight) and a low tendency to explore in potentially threatening non-social situations, to low fearfulness and a high tendency to explore. Sociability runs from fearfulness and hostility towards strangers, to a positive attitude towards strangers (e.g. intense greeting). Aggressiveness can be regarded as a dimension ranging from low tendency to act threatening and aggressively in unfamiliar and potentially threatening situations, to a high tendency to threaten and act aggressively (e.g. raise hackles, bark, bite/bite intentions).

By using the dog's score from the variables representing each trait according to Svartberg and Forkman (2002), scores for each dog and trait were calculated. The variable scores were standardized (subtracting the mean and dividing by the standard deviation) before the calculation. Each dog's standardized score from the representing variables were then averaged and used as the dog's trait score. From the individual dogs' scores, the breed scores were calculated. First, the breed scores for each sex were calculated by averaging the scores for each trait, breed and sex. Correlation analyses (Spearman Rank Order Correlation Analysis) between the males' and the females' trait scores showed that they all were significantly correlated, with correlation coefficients ranging from 0.77 to 0.91 ($P < 0.001$). Therefore, I calculated general breed scores by averaging the males' and females' scores in each breed for each trait. In this way, potential sex differences in factor scores together with uneven sex ratios could not influence and bias the breed scores.

2.4. Classification of breeds according to historical usage

The classification of breeds according to historical use and function was based on breed nomenclatures from three internationally recognized dog organizations: the Federation Cynologique Internationale (FCI), the American Kennel Club (AKC) and the Kennel Club

in United Kingdom (KCUK). These classifications, which are similar to each other, are based on similarities between breeds regarding original function (Hart, 1975; Grandjean et al., 2000). Furthermore, these nomenclatures were compared to a breed classification of Dennis-Bryan and Clutton-Brock (1988), which reflect the breeds' development and geographical distribution. From this, the 31 breeds in the present study were classified in five groups: Herding dogs ($N = 11$), Working dogs ($N = 9$), Terriers ($N = 3$), Hounds ($N = 2$) and Gun dogs ($N = 6$). However, in the comparison between breed groups the Hound group was excluded because of the few representative breeds in the sample. The breeds and breed groups are presented in Table 1.

2.5. Current use and selection of dogs of different breeds

It is reasonable to assume that the use of the breeding stock in a breed reflects the selection criteria in that breed, i.e. if the breeding stock in a breed very often is used for a certain purpose, for example, hunting or herding, success in this type of use is regarded as important when choosing breeding animals. This has been assumed by Willis (1995), at least regarding selection for and use in dog shows. Thus, differences in what breeds are used for should reflect differences in selection criteria between breeds. Based on this assumption, the amount of merits of the breeding stock in different tests, trials and shows were used as a measure of recent selection in each breed. Data on merits of both sires and dams that were registered in the SKC and had produced litters born during three consecutive sample years (1997–1999) were collected from the SKC database. The merits were grouped into five categories: one category of merits from tests and trials related to the historical use of each of the four investigated breed groups,[1] and merits from dog shows. In total, the data included merits from 17 different types of tests/trials, in addition to merits from dog shows. The average number of merits (per breeding animal) for each category was calculated for each breed. This was done for both sires and dams, separately. The average number of merits was used as a measure of each breed's, compared to historical, more recent selection pressure in Herding, working use, Terrier hunting, Gun dog use and dog show use.

2.6. Breed-typical behaviour and registration numbers

To investigate the relationship between popularity of a breed and the breed's typical behaviour, correlation analyses were carried out. As a measure of popularity, the number of registered dogs per breed and year was used. To control random variation between years, the number of yearly registered dogs per breed during the years 2000–2002 was averaged, and used as an index of popularity.

[1] For all investigated breed groups, there are official trials/tests in Sweden that can be seen as analogous to the breed groups' original function. For Herding dogs there are different types of herding trials (sheep or cattle). For Working dogs a variety of working trials are held (Working dog trials, Schutzhund trials, Sled dog racing, Water rescue tests, Patrol dog tests, Search and rescue tests). Specific hunting trials are organized for the different types of hunting breed groups. For the two breed groups studied here – Terriers and Gun dogs – Badger hunting tests and different types of Field trials are organized for the respective breed group.

2.7. Data treatment and statistical analyses

The statistical analyses were carried out with non-parametric tests. Kruskal–Wallis tests were used in the comparison of trait scores between breeds, breed groups and clusters of breeds. A grouping of breeds based on breed-typical behaviour was made using cluster analysis. In this analysis, a non-hierarchical clustering procedure was used with a maximum of 10 iterations. The initial cluster centres were computed by first sorting the distances between all objects, and thereafter objects were chosen at constant intervals as initial cluster centres. Analyses of the relationship between the merits of the breeding stock and breed scores for the personality traits, and between the breed's yearly registration and breed trait scores, as well as the analyses of the internal consistency of the traits (the variable-to-trait correlations) were carried out by Spearman Rank Order Correlation Analysis. Sign test was used when the number of merits of different types was compared. The statistical package used was STATISTICA™, except for the analysis of breed differences, where SAS System v. 8 was used.

3. Results

3.1. Internal consistency of the traits

The average variable-to-trait correlation was 0.76 (range 0.74–0.79) for playfulness, 0.64 (0.52–0.72) for curiosity/fearlessness, 0.78 (0.74–0.83) for sociability and 0.64 (0.49–0.73) for aggressiveness. Even though one variable-to-trait correlation for aggressiveness fell below 0.5, which can be considered as a lower limit for acceptance of the internal consistency, this suggests that the traits have an adequate internal consistency.

3.2. Breed differences

There were significant differences between the 31 breeds in all investigated traits in both sexes (Kruskal–Wallis test, $N_{\text{males}} = 6851$, $N_{\text{females}} = 6246$; d.f. = 30; playfulness, males: $\chi^2 = 1037.2$; $P < 0.001$; females: $\chi^2 = 841.7$; $P < 0.001$; curiosity/fearlessness, males: $\chi^2 = 663.2$; $P < 0.001$; females: $\chi^2 = 572.3$; $P < 0.001$; sociability, males: $\chi^2 = 507.1$; $P < 0.001$; females: $\chi^2 = 477.5$; $P < 0.001$; aggressiveness, males: $\chi^2 = 430.1$; $P < 0.001$; females: $\chi^2 = 396.5$; $P < 0.001$). There were also relatively large variations within-breeds, and overlaps in trait scores between breeds were found. The average range of scores within the breeds were in all traits higher than 80% of the range found in the total sample (playfulness: 92.7%; curiosity/fearlessness: 87.8%; sociability: 82.0%; aggressiveness: 80.3%), and in no breed and for no trait the range was less than 52% of the range in the total sample. The distributions of curiosity/fearlessness scores in the highest and lowest ranked breeds in this trait (Labrador Retriever and Collie) are presented in Fig. 1, as an example of the variation within breeds. The 31 breeds' average trait scores, which are based on the average for males and females in each breed, are presented in Appendix A.

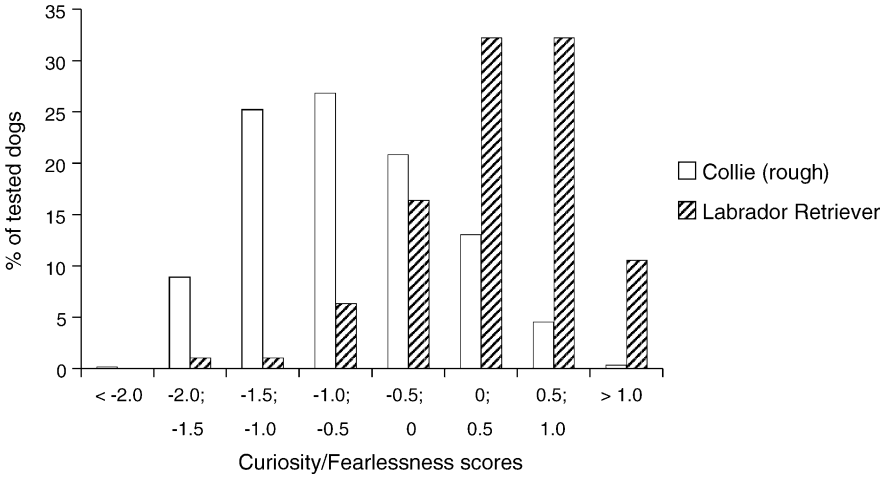

Fig. 1. The distribution of curiosity/fearlessness scores (males and females pooled) in the highest ranked breed—Labrador Retriever (shaded bars), and the lowest ranked breed—Collie (white bars).

3.3. Differences in breed-typical behaviour between breed groups

If historical selection is evident in the breeds' characteristic behaviour today, homogeneity within and differences between breed groups should be expected. To study this, I carried out a comparison of the breed trait scores between the four breed groups with at least three breeds represented (Kruskal–Wallis tests, d.f. = 3, Herding dogs: $N = 11$; Working dogs: $N = 9$; Terriers: $N = 3$; Gun dogs: $N = 6$). However, no significant differences in trait scores between breed groups were found (playfulness: $H = 1.72$, $P = 0.634$; curiosity/fearlessness: $H = 4.57$, $P = 0.206$; sociability: $H = 3.40$, $P = 0.334$; aggressiveness: $H = 3.28$, $P = 0.351$). The breed group scores for each of the four personality traits are presented in Fig. 2.

As a comparison, I carried out a cluster analysis with a four-cluster solution based on the breed scores for the personality traits. The cluster analysis resulted in a solution with 4–12 breeds in each cluster (Table 2). Kruskal–Wallis tests confirmed that the clusters differed in breed scores for all personality traits ($N = 29$, d.f. = 3; playfulness: $H = 19.07$, $P < 0.001$; curiosity/fearlessness: $H = 9.19$, $P = 0.027$; sociability: $H = 20.13$, $P < 0.001$; aggressiveness: $H = 13.11$, $P = 0.004$; see Fig. 3). The working and Gun dog breeds were distributed over all four clusters, whereas the Herding and Terrier breeds were found in three clusters. Thus, as Table 2 shows, the clusters of breeds showed poor correspondence to the breed groups based on historical use and selection. The trait scores for the clusters are presented in Fig. 3.

3.4. Recent selection

The data on merits of the breeding stock in the investigated breeds, presented in Table 3a and b, indicated that current use deviates from what could be expected according to the

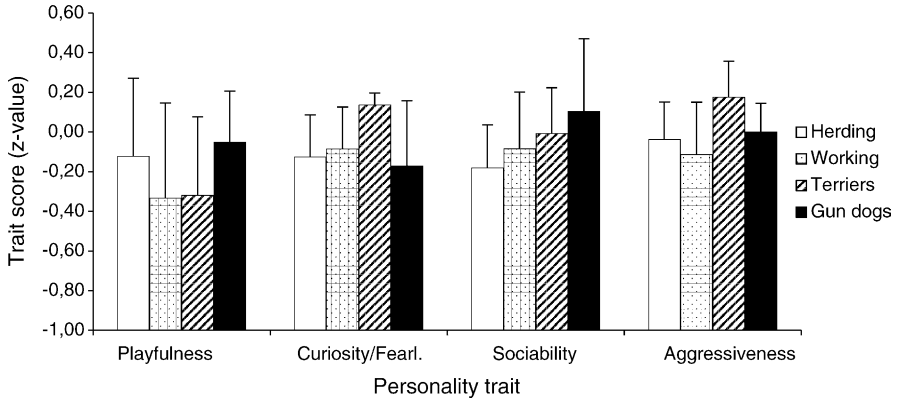

Fig. 2. Average breed trait scores for Herding dogs ($N = 11$), Working dogs ($N = 9$), Terriers ($N = 3$) and Gun dogs ($N = 6$). Kruskal–Wallis tests showed no significant differences between breed groups for any of the traits (error bars represent standard deviations).

grouping of breeds. Only 2 of 11 Herding breeds – Australian Kelpie and Border Collie – had merits from Herding trials. A similar pattern was found in the Working breed group, where a majority of the breeds had low or no merits from the related type of trials. As can be seen in Table 3a and b, the most common use for the breeding stock in general was in dog shows, both according to number of breeds that had merits (dams and sires in all 31 breeds had show merits) and according to the average number of merits per breed (12.1 in sires and 8.3 in dams). The second most common use was in Working dog trials, followed by use in field trials ('Gun dog merits'), Herding trials and Terrier hunting tests, in order. Also within the breed groups, the most common use was in dog shows. In three breed groups, there was a higher number of show merits than merits in the test/trial type that corresponded to original use (Sign test; Herding breed group, $N = 11$, sires and dams: $Z = 2.41$; $P = 0.016$; Working dog group, $N = 9$, sires and dams: $Z = 2.67$; $P = 0.008$; Gun dog group, $N = 6$, sires and dams: $Z = 2.04$; $P = 0.041$). There were too few Terrier breeds in the sample to test the significance of the difference in that breed group. In the Herding breed group, several breeds had a considerable number of merits from Working dog trials, which indicated recent selection towards use in Working dog trials in this breed group. An analysis showed that there was no difference between the number of merits from dog show and from Working dog trials in the Herding breed group (Sign test; $N = 11$, sires: $Z < 0.01$; $P = 1.000$; dams: $Z = 1.21$; $P = 0.228$).

3.5. Relationships between recent selection and breed-typical behaviour

To investigate the relationships between breed scores in the four traits and selection for dog show use, which was measured as the number of show merits for each breed's breeding stock during 1997–1999 (Table 3a and b), correlation analyses were carried out (Spearman Rank Order Correlation Analysis, $N = 31$). The results from these analyses showed significant and negative correlations between the number of show merits for each breed and the breed scores for playfulness (sires: $R_s = -0.42$, $P = 0.019$; dams: $R_s = -0.55$,

Table 2
Clusters of breeds from the cluster analysis based on breed-typical behaviour

Cluster	Breed	Breed group
1	Australian Kelpie	Herding
	Australian Shepherd	Herding
	Belgian Malinois	Herding
	Belgian Tervuren	Herding
	Border Collie	Herding
	German Shepherd Dog	Herding
	Giant Schnauzer	Working
	Golden Retriever	Gun dog
	Hovawart	Working
	Nova Scotia Duck Toll. R.	Gun dog
	Parson Russell Terrier	Terrier
	Rottweiler	Working
2	Beauceron	Herding
	Belgian Groenendael	Herding
	Briard	Herding
	Dobermann Pinscher	Working
	Poodle	Gun dog
3	American Staffordshire T.	Terrier
	Boxer	Working
	Flat-coated Retriever	Gun dog
	Labrador Retriever	Gun dog
4	Bernese Mountain Dog	Working
	Bouvier des Flandres	Herding
	Collie (rough)	Herding
	English Springer Spaniel	Gun dog
	Great Swiss Mount. Dog	Working
	Irish Soft-coated W.T.	Terrier
	Leonberger	Working
	Pinscher	Working

$P = 0.001$), sociability (sires: $R_s = -0.46$, $P = 0.009$; dams: $R_s = -0.42$, $P = 0.018$) and aggressiveness (sires: $R_s = -0.50$, $P = 0.005$; dams: $R_s = -0.41$, $P = 0.021$). There was also a negative correlation between the number of show merits for sires and the curiosity/fearlessness breed score ($R_s = -0.38$, $P = 0.033$), and a non-significant tendency for correlation between show merits for dams and curiosity/fearlessness breed score ($R_s = -0.34$, $P = 0.060$).

Sires from 25 breeds and dams from 28 breeds had merits from Working dog trials (Table 3a and b). Using correlation analyses, the relationships between breed trait scores and Working dog merits in the breeding stock in these breeds were investigated. The analyses showed that the average number of sire merits from working trials for each breed was positively correlated with breed scores for playfulness ($R_s = 0.40$, $P = 0.049$) and aggressiveness ($R_s = 0.46$, $P = 0.021$). Furthermore, there was a non-significant tendency for correlation between working merits in sires and curiosity/fearlessness ($R_s = 0.35$, $P = 0.086$). No correlations were found between sire merits in Working dog trial and

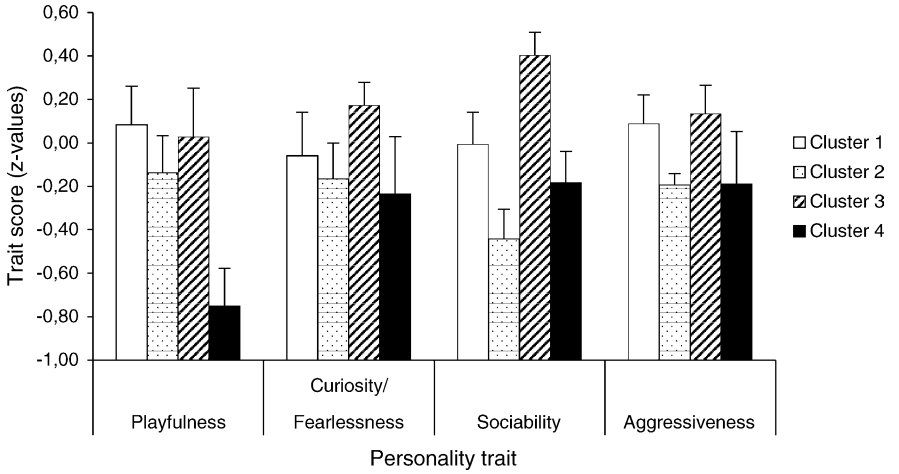

Fig. 3. Average breed trait scores for the four clusters of breed from the cluster analysis. For members of each cluster, see Table 2 (error bars represent standard deviations).

sociability ($R_s = -0.11$, $P = 0.611$), or between any of the breed trait scores and dam merits from working trials (playfulness: $R_s = 0.29$, $P = 0.141$; curiosity/fearlessness: $R_s = 0.08$, $P = 0.696$; sociability: $R_s = -0.01$, $P = 0.971$; aggressiveness: $R_s = 0.03$, $P = 0.901$). Only few of the 31 breeds had merits in tests related to Herding (2 breeds), Terrier hunting (1 breed) and gundog use (5 breeds), as presented in Table 3a and b. This made analyses of these selection pressures inappropriate.

3.6. Breed-typical behaviour and registration numbers

To investigate the relationship between breed-typical behaviour and popularity, correlation analyses between registration numbers for the breeds (presented in Table 1) and the breeds' trait scores were carried out (Spearman Rank Order Correlation Analysis, $N = 31$). These analyses showed a significant and positive correlation between registration number and breed trait score for playfulness ($R_s = 0.36$, $P = 0.047$) and sociability ($R_s = 0.45$, $P = 0.012$), but not for curiosity/fearlessness ($R_s = -0.01$, $P = 0.998$) or aggressiveness ($R_s = -0.08$, $P = 0.655$). One factor that can bias the use of registration numbers as a measure for popularity is that some breeds are newly introduced in Sweden. These breeds have low numbers of registrations due to this, but may be highly popular. According to the breed registration data from the Swedish Kennel Club, five of the sample breeds were introduced during the last 12 years (Australian Shepherd, Beauceron, Belgian Malinois, American Staffordshire Bull Terrier, Parson Russell Terrier). With these breeds excluded, the same significant relationships between breed-typical behaviour and registration numbers were found as in the previous analyses, but with higher degree of correlations ($N = 26$; playfulness: $R_s = 0.49$, $P = 0.010$; sociability: $R_s = 0.51$, $P = 0.007$; curiosity/fearlessness: $R_s = -0.10$, $P = 0.624$; aggressiveness: $R_s = 0.02$, $P = 0.935$).

Table 3
(a) The average number of merits of sires that bred litter 1997–1999 and (b) the average number of merits of dams that bred litter 1997–1999

Breed	Breed group	Herding merits	Working merits	Terrier hunting merits	Gun dog merits	Show merits
(a)						
Australian Kelpie	Herding	1.1	18.0	–	–	5.2
Australian Shepherd	Herding	–	9.1	–	–	6.9
Beauceron	Herding	–	2.6	–	–	14.2
Belgian Groenendael	Herding	–	4.1	–	–	17.5
Belgian Malinois	Herding	–	18.9	–	–	6.7
Belgian Tervuren	Herding	–	9.3	–	–	10.9
Border Collie	Herding	13.4	2.3	–	–	0.1
Bouvier des Flandres	Herding	–	3.1	–	–	11.6
Briard	Herding	–	1.8	–	–	23.7
Collie (rough)	Herding	–	0.9	–	–	7.6
German Shepherd Dog	Herding	–	8.8	–	–	2.5
Bernese Mountain Dog	Working	–	0.1	–	–	11.8
Boxer	Working	–	0.7	–	–	17.8
Dobermann Pinscher	Working	–	2.1	–	–	15.0
Great Swiss Mountain Dog	Working	–	–	–	–	7.2
Hovawart	Working	–	4.5	–	–	12.6
Leonberger	Working	–	0.3	–	–	20.1
Pinscher	Working	–	–	–	–	20.8
Giant Schnauzer	Working	–	8.6	–	–	11.9
Rottweiler	Working	–	3.0	–	–	8.6
American Staffordshire Terrier	Terrier	–	–	–	–	3.3
Irish Soft-coated Wheaten Terrier	Terrier	–	0.1	–	–	1.7
Parson Russell Terrier	Terrier	–	–	0.4	–	10.7
Dalmatian	Hound	–	–	–	–	15.6
Rhodesian Ridgeback	Hound	–	–	–	–	20.5
English Springer Spaniel	Gun dog	–	0.1	–	3.5	17.5
Flat–coated Retriever	Gun dog	–	2.0	–	7.9	16.6
Golden Retriever	Gun dog	–	0.3	–	2.3	9.4
Labrador Retriever	Gun dog	–	0.1	–	4.4	8.1
Nova Scotia Duck Tolling Retriever	Gun dog	–	0.8	–	0.9	8.6
Poodle	Gun dog	–	0.1	–	–	13.5
Average		0.5	3.3	<0.1	0.6	12.1
(b)						
Australian Kelpie	Herding	0.4	6.4	–	–	6.2
Australian Shepherd	Herding	–	2.9	–	–	5.5
Beauceron	Herding	–	1.1	–	–	7.4
Belgian Groenendael	Herding	–	1.3	–	–	10.8
Belgian Malinois	Herding	–	0.8	–	–	2.8
Belgian Tervuren	Herding	–	3.1	–	–	8.4
Border Collie	Herding	10.2	1.1	–	–	0.2
Bouvier des Flandres	Herding	–	1.3	–	–	9.2
Briard	Herding	–	3.6	–	–	15.0
Collie (rough)	Herding	–	0.2	–	–	4.4
German Shepherd Dog	Herding	–	3.5	–	–	2.2
Bernese Mountain Dog	Working	–	0.1	–	–	6.3

Table 3 (*Continued*)

Breed	Breed group	Herding merits	Working merits	Terrier hunting merits	Gun dog merits	Show merits
Boxer	Working	–	0.6	–	–	9.9
Dobermann Pinscher	Working	–	0.9	–	–	8.6
Great Swiss Mountain Dog	Working	–	–	–	–	8.8
Hovawart	Working	–	2.9	–	–	11.9
Leonberger	Working	–	0.1	–	–	13.7
Pinscher	Working	–	–	–	–	13.7
Giant Schnauzer	Working	–	3.8	–	–	6.6
Rottweiler	Working	–	1.3	–	–	6.1
American Staffordshire Terrier	Terrier	–	–	–	–	2.0
Irish Soft-coated Wheaten Terrier	Terrier	–	–	–	–	1.9
Parson Russell Terrier	Terrier	–	0.1	0.1	–	5.5
Dalmatian	Hound	–	0.1	–	–	13.9
Rhodesian Ridgeback	Hound	–	0.1	–	–	14.9
English Springer Spaniel	Gun dog	–	0.1	–	2.4	9.0
Flat-coated Retriever	Gun dog	–	0.5	–	6.5	11.8
Golden Retriever	Gun dog	–	0.1	–	1.1	5.9
Labrador Retriever	Gun dog	–	0.1	–	2.6	5.0
Nova Scotia Duck Tolling Retriever	Gun dog	–	0.1	–	1.3	7.7
Poodle	Gun dog	–	0.1	–	–	9.7
Average		0.3	1.2	<0.1	0.5	8.3

4. Discussion

The results in this study suggest large behavioural differences between breeds in the traits playfulness, curiosity/fearlessness, sociability and aggressiveness in the Swedish dog population, even though within-breed variations were found. No relationship was found between the breeds' typical behaviour and function in the breeds' origin. Instead, correlations between the breeds' average trait scores and modern use of the breeding stocks were found, indicating that recent selection has affected breed-typical behaviour. The breeds' use in dog shows – which was the most common use over all – was negatively correlated with all investigated traits, both in sires and in dams. In contrast, use in Working dog trials was positively correlated with playfulness and aggressiveness in sires. Popular breeds have higher sociability and playfulness scores than less popular breeds, which indicate that selection towards use in dog shows seems to be in conflict with selection for popularity. These results indicate that basic dimensions of dog behaviour can be changed when selection pressure changes, and that the domestication of the dog still is in progress.

According to the present results there are no differences between breed groups in the personality traits playfulness, curiosity/fearlessness, sociability and aggressiveness. Instead, a considerable variation of breed-typical behaviour was found within the breed groups. One striking example is the Retrievers in the Gun dog group, where the Labrador and Flat-coated Retrievers are ranked as number one and three in curiosity/fearlessness, whereas Golden Retriever and Nova Scotia Duck Tolling Retriever are among the five lowest ranked breeds for the same trait of the 31 investigated breeds. Another example is

the Belgian breeds within the Herding breed group, which in several other countries than Sweden are considered as varieties of one breed. They showed a considerable variation in breed scores, where the Malinois in all traits was ranked higher than the other two Belgian breeds Tervuren and Groenendael. As suggested by the result from the cluster analysis, a categorization of breeds according to similarity in breed-typical behaviour today should result in a very different nomenclature compared to a classification based on original use, like the nomenclatures of the international kennel clubs.

The present results are contrasted with previous results, where breed group differences have been found in traits similar to those studied here (e.g. fear: Mahut, 1958; playfulness and aggressivity: Bradshaw et al., 1996; social behaviour towards strangers: Seksel et al., 1999). This deviation might be explained by differences between populations, i.e. that the Swedish dog population differ compared to other populations. The Swedish dog population has for many years genetically been rather isolated from populations in other countries/continents due to quarantine regulations. However, this rule has not been applied to the UK, from where dogs have been imported regularly. Therefore, the dog populations in the UK and Sweden should not differ genetically, which makes it likely that there are other reasons for differences between the present results and the results from the UK dog population (Bradshaw et al., 1996; which has been found to correspond to the dog population in the USA: Bradshaw and Goodwin, 1998). A more plausible explanation for the deviating results regarding differences between typical behaviour in breed groups is methodological differences. Results that have been interpreted as breed group differences may be caused by differences between breeds, rather than breed groups. This is an obvious risk when only one breed per group is studied, from which generalizations about breed groups are made (e.g. Scott and Fuller, 1965; Plutchik, 1971). This risk also exists when individual dogs are classified into breed groups without any previous investigation of breed-typical behaviour (e.g. Seksel et al., 1999; Christiansen et al., 2001). All differences that are found by this procedure are inevitably interpreted as differences between breed groups, but could be caused by one or a few over-represented and extreme breeds. Another method that has been used in studies of breed-characteristic behaviour is ratings by authorities (i.e. veterinarians and obedience judges) according to predetermined traits. This has shown to be useful in studies of breed differences (Hart and Miller, 1985; Draper, 1995; Bradshaw and Goodwin, 1998). However, because of the subjectivity of this method, similarity between breeds within a group may be caused simply by the authorities' knowledge about how breeds commonly are categorized. Thus, this method may be less useful when differences between breed groups are studied, as in Bradshaw et al. (1996). In the present study, there is no reason to assume that different breeds are treated differently, or that some extreme breed could have biased the results. A possible problem with the present study, however, is the relatively few breeds in one of the breed groups, and that only four groups were compared. A higher number of breeds per group should have increased the statistical power of the analyses, and more groups investigated should have led to a higher general applicability of the results.

According to the data on merits of the breeding stock in the investigated breeds, dogs in general seem to be used very differently today compared to what function they had in the breeds' origin. Among the 11 Herding breeds only one was used in Herding trials to any relevant degree (the Border Collie), and none of the three Terrier breeds seemed to be

used as hunting dogs. Instead, there seem to be new functions for some of the breeds. Several former Herding breeds are now used as Working dogs (e.g. Australian Kelpie and Belgian Malinois). However, the use that seems to be the overall most common is in dog shows. The only exception from this was in the Herding dog group, where there was no difference between use in dog shows and use in Working dog trials. Thus, if the current use can be assumed to reflect selection during recent time (Willis, 1995), these results support previous assumptions that selection for dog shows may be the dominating selection pressure in modern dog breeding (Willis, 1995; Lindsay, 2000). Furthermore, the correlations found suggest that selection for current use is related to differences in breed-typical behaviour. Selection for use in Working dog trials is associated with high playfulness and aggressiveness, whereas selection for use in dog shows is related to low playfulness, low curiosity/fearlessness, low sociability and low aggressiveness. One interpretation of these results is that selection for what the breeds are used for today has created changes in breed-typical behaviour. This is supported by findings that suggest genetic influence on these traits, which is indicated by moderate to high heritabilities: between 0.15 and 0.23 for playfulness, curiosity/fearlessness and aggressiveness in German Shepherd and Rottweiler according to Strandberg et al. (2005), between 0.36 and 0.52 for all the investigated traits in German Shepherd according to P.-E. Sundgren (unpublished data) and approximately 0.40 for the broad Boldness dimension related to playfulness, curiosity/fearlessness and sociability (several breeds; L. Laikre, unpublished data). Previous results from selection experiments in canids suggest that fear-related traits, with heritabilities similar to the ones studied here, can be altered in a few generations when selection is intense (Murphree, 1973; Kenttämies et al., 2002; Trut et al., 2004).

The negative relationship between selection for show use and trait scores could indicate an adaptation to the situation that show dogs perform in. Generally, in dog shows, the dog, led by a handler, is shown running or walking in a ring together with other dogs (Grandjean et al., 2000). A judge also physically examines the dog, while the dog is in a passive standing position. This situation may favour dogs that show low social curiosity and aggressiveness, and high docility and passivity in general. However, the correlations found between behaviour and selection towards use in dog shows might also be due to some unknown correlating factor. For example, kennel owner's interest in dog shows could be correlated with a tendency to keep large numbers of dogs in an environment where calm and timid dog personalities are favoured (Scott and Fuller, 1965). Further studies are needed to understand the mechanisms causing these correlations.

The relationship between selection for Working dog use and playfulness is not surprising in the light of the results from a previous study (Svartberg, 2002). In that study, I found results suggesting that successful Working dogs have higher ''Boldness'' – a combined measure of playfulness, curiosity/fearlessness and sociability – compared to less successful dogs. Play is a commonly used reward in training of Working dogs in Sweden according to the dog training literature (Nordin, 1995; Mohlin, 2000; Järverud and af Klinteberg-Järverud, 2002), and may constitute a more valuable and efficient reward for dogs high in playfulness. Thus, selection for dogs high in the trait playfulness might be analogous with selection for trainability. The trait aggressiveness was not investigated in Svartberg (2002), but unpublished results suggest no relationship between

this trait and successful performance in Working dog trials (K. Svartberg, unpublished data). The relevance of this trait is unclear according to a comparison between test behaviour and typical behaviour in everyday life, where only a few and weak correlations were found between aggressiveness score and aggressive behaviour in everyday life (Svartberg, 2005).

Some questions could be raised on the validity of the selection measures used in this study. Regarding the merits in functional tests, it is possible that trial or test use is a poor predictor of the ''true'' use in a breed. However, it is likely to assume that breeds relatively often used in a specific type of functional test (i.e. Herding test) also are commonly used in the corresponding practical function outside the test situation (i.e. as a farmer dog in sheep or cattle work). Another issue is that it is reasonable to assume that other important selection criteria exist besides those investigated. One such is selection for life as a pet dog, which is difficult to estimate. However, the popularity of a dog breed may be an indication of how suitable the breed is for life as a pet dog. This is based on the assumption that most dogs in Sweden are used exclusively as companions and pet dogs, and that numerically large breeds are breeds that are adapted for pet dog living. Considering this, the results suggest that suitable pet dog breeds are characterized by high sociability and high playfulness. According to the results of a previous study (Svartberg, 2005), dogs with high scores in sociability are attracted to strangers, fearless of them and non-aggressive towards them. Dogs with high scores in playfulness are generally interested in playing with humans. Such attitudes in dogs are probably attractive for pet dog owners. Dogs with low sociability scores, i.e. hostile and socially fearful dogs, are probably far more difficult to handle, and breeds with that typical personality are less likely to attract new owners.

One risk of using correlations as indications for a directional relationship is the problem of determining the cause and the effect. The typical use of a breed, for example mainly in dog shows or mainly in Working dog trials, could systematically influence the environment that the dogs of the breed live in, and what stimuli the dogs are exposed to. An owner of a show dog may try to make the dog more docile and calm, and the Working dog owner may try to develop his or her dog's play interest. Thus, typical behaviour of a certain breed could be, at least partly, a reflection of the typical environment for dogs of that breed. However, there are several factors that support the suggestion that the breed scores in the present study reflect breed differences in genetic disposition, and not differences in environments between breeds. Firstly, the results are based on data where differences in owner experience in Working dog trials have been controlled, which is the only environmental factor that is known to be associated with trait scores (Svartberg, 2002). Secondly, the relatively high heritability for the traits suggests that the traits to a considerable degree are genetically influenced (Strandberg et al., 2005; L. Laikre, unpublished data; P.-E. Sundgren, unpublished data). Thirdly, previous results suggest high stability in adult dogs of the investigated traits over shorter periods of time (Svartberg et al., 2005), as well as stability over longer periods of time with the exception of aggressiveness (Svartberg, 2005), indicating low influence by environmental factors. Fourthly, traits related to fearfulness and confidence have been found to be stable from young age in dogs (Royce, 1955; Pfaffenberger et al., 1976; Goddard and Beilharz, 1986; Slabbert and Odendaal, 1999), as well as in cats (Lowe and Bradshaw, 2001), in wolves (Fox, 1972) and in humans (Kagan

et al., 1988). Thus, it is likely that the differences found in the investigated traits are not caused by environmental differences.

Another risk is that the dogs that are tested do not adequately represent their breeds. The Swedish Working Dog Association organize the tests, and therefore, the tested dogs could be more associated with Working dog trials – either by its owner's interest or by its disposition – compared to what is general for the breed. This could bias the breed scores. However, the control for owner experience in Working dog trials, which makes it unlikely that similarities in breed-typical behaviour is caused by similarities in dog owners' interest, and the large number of dogs in each breed suggest that the breed scores are to a reasonable extent representative and reliable.

5. Conclusions

In conclusion, the results suggest large between-breed differences in personality, and also within-breed variations in the Swedish dog population. Differences between breeds regarding several aspects of breed-typical behaviour – playfulness, social and non-social fearfulness, curiosity in potentially fearful situations, and aggressiveness – are not explained by past selection in the breeds' origin. Instead, correlations between current use of breeding stocks and breed-typical behaviour suggest that breed differences in behaviour, at least regarding the traits included in this study, are caused by more recent selection. Selection towards use in dog shows correlates positively with social and non-social fearfulness, and negatively with playfulness, curiosity and aggressiveness, whereas selection towards use in Working dog trials is positively correlated with playfulness and aggressiveness. Thus, even though the behavioural traits that are investigated here can be assumed to be evolutionarily stable, which the similarity between breed groups (Svartberg and Forkman, 2002) and correspondence to traits found in wolves (Fox, 1972) and other species (Gosling and John, 1999) suggests, rapid changes along these dimensions seem to be possible in a relatively few generations. It seems that the domestication of the dog is an ongoing process, which stresses the importance of behavioural considerations in dog breeding. This is an issue in the breeding of Working dogs of any type, but perhaps even more important in the breeding of pet dogs. A correspondence between the personality of dogs and the environment that dogs in a modern society live in decreases the risk of welfare problems, such as fear and anxiety. A behavioural test like the ''Dog Mentality Assessment'' used in this study can be a valuable tool for dog breeders and breed clubs in breeding programs, given that the test is standardized, have high test-to-test as well as inter-observer reliability, and is validated against relevant measures outside the test situation.

Acknowledgements

I am grateful for the help from the Swedish Kennel Club with supply of data. Furthermore, many thanks to Tommy Radesäter and Hans Temrin for valuable support during the preparation of the manuscript.

Appendix A

Breed scores that are based on the average scores for males and females in each breed, with standard errors (for both sexes pooled) and rank (in parenthesis).

Breed	Personality trait			
	Playfulness	Curiosity/Fearlessness	Sociability	Aggressiveness
Australian Kelpie	−0.133 ± 0.06 (17)	−0.166 ± 0.05 (19)	0.056 ± 0.07 (9)	0.079 ± 0.05 (12)
Australian Shepherd	0.002 ± 0.06 (13)	−0.191 ± 0.04 (23)	−0.055 ± 0.06 (13)	0.185 ± 0.05 (5)
Beauceron	−0.168 ± 0.09 (18)	0.014 ± 0.11 (13)	−0.428 ± 0.14 (27)	−0.132 ± 0.09 (21)
Belgian Groenendael	−0.017 ± 0.07 (14)	−0.112 ± 0.05 (16)	−0.571 ± 0.08 (31)	−0.191 ± 0.06 (24)
Belgian Malinois	0.542 ± 0.04 (1)	0.141 ± 0.04 (4)	−0.091 ± 0.07 (16)	0.320 ± 0.05 (1)
Belgian Tervuren	−0.044 ± 0.04 (15)	0.016 ± 0.03 (12)	−0.270 ± 0.04 (24)	0.077 ± 0.03 (13)
Border Collie	0.145 ± 0.09 (5)	−0.168 ± 0.10 (20)	0.165 ± 0.11 (6)	−0.075 ± 0.11 (20)
Bouvierdes Flandres	−0.789 ± 0.08 (27)	−0.161 ± 0.04 (18)	−0.333 ± 0.08 (26)	−0.197 ± 0.05 (25)
Briard	−0.267 ± 0.04 (20)	−0.179 ± 0.03 (21)	−0.219 ± 0.05 (23)	−0.170 ± 0.03 (23)
Collie (smooth)	−0.779 ± 0.04 (26)	−0.660 ± 0.03 (31)	−0.160 ± 0.03 (20)	−0.305 ± 0.03 (28)
German Shepherd Dog	0.177 ± 0.01 (3)	0.086 ± 0.01 (8)	−0.068 ± 0.01 (14)	0.009 ± 0.01 (17)
Bernese Mountain Dog	−0.604 ± 0.05 (24)	−0.187 ± 0.03 (22)	−0.026 ± 0.04 (12)	−0.421 ± 0.02 (30)
Boxer	0.043 ± 0.02 (11)	0.079 ± 0.02 (10)	0.446 ± 0.03 (2)	0.043 ± 0.02 (15)
Dobermann Pinscher	0.087 ± 0.03 (8)	−0.117 ± 0.03 (17)	−0.497 ± 0.04 (30)	−0.272 ± 0.03 (27)
Great Swiss Mountain Dog	−0.963 ± 0.09 (31)	0.123 ± 0.05 (7)	−0.100 ± 0.08 (18)	0.194 ± 0.07 (4)
Hovawart	−0.120 ± 0.04 (16)	0.032 ± 0.03 (11)	−0.092 ± 0.04 (17)	−0.016 ± 0.03 (18)
Leonberger	−0.835 ± 0.08 (28)	−0.463 ± 0.06 (30)	−0.193 ± 0.08 (21)	−0.468 ± 0.05 (31)
Pinscher	−0.880 ± 0.14 (30)	−0.337 ± 0.07 (25)	−0.443 ± 0.09 (28)	−0.344 ± 0.07 (29)
Giant Schnauzer	0.109 ± 0.03 (7)	−0.005 ± 0.03 (14)	0.052 ± 0.04 (10)	0.146 ± 0.03 (8)
Rottweiler	0.172 ± 0.01 (4)	0.123 ± 0.01 (6)	0.102 ± 0.01 (8)	0.129 ± 0.01 (9)
American Stafordshire Terrier	−0.286 ± 0.12 (21)	0.126 ± 0.08 (5)	0.249 ± 0.09 (4)	0.309 ± 0.08 (2)
Irish Soft-coated Wheaten Terrier	−0.728 ± 0.07 (25)	0.085 ± 0.04 (9)	−0.070 ± 0.04 (15)	−0.030 ± 0.04 (19)
Parson Russell Terrier	0.058 ± 0.14 (10)	0.201 ± 0.07 (2)	−0.197 ± 0.12 (22)	0.251 ± 0.06 (3)
Dalmatian	−0.258 ± 0.13 (19)	−0.053 ± 0.08 (15)	0.042 ± 0.11 (11)	0.146 ± 0.09 (7)
Rhodesian Ridgeback	−0.851 ± 0.06 (29)	−0.382 ± 0.04 (27)	−0.284 ± 0.05 (25)	0.103 ± 0.04 (10)
English Springer Spaniel	−0.413 ± 0.08 (23)	−0.281 ± 0.08 (24)	−0.127 ± 0.09 (19)	0.067 ± 0.07 (14)
Flat-coated Retriever	0.233 ± 0.04 (2)	0.160 ± 0.04 (3)	0.477 ± 0.05 (1)	0.026 ± 0.04 (16)
Golden Retriever	0.006 ± 0.03 (12)	−0.363 ± 0.03 (26)	0.215 ± 0.03 (5)	−0.143 ± 0.03 (22)
Labrador Retriever	0.122 ± 0.05 (6)	0.324 ± 0.04 (1)	0.444 ± 0.05 (3)	0.160 ± 0.05 (6)
Nova Scotia Duck Tolling Retriever	0.066 ± 0.07 (9)	−0.428 ± 0.07 (28)	0.106 ± 0.07 (7)	0.100 ± 0.06 (11)
Poodle	−0.312 ± 0.09 (22)	−0.431 ± 0.08 (29)	−0.487 ± 0.13 (29)	−0.199 ± 0.07 (26)
Average	−0.216	−0.102	−0.076	−0.020

References

Bradshaw, J.W.S., Goodwin, D., Lea, A.M., Whitehead, S.L., 1996. A survey of the behavioural characteristics of pure-bred dogs in the United Kingdom. Vet. Rec. 138, 465–468.

Bradshaw, J.W.S., Goodwin, D., 1998. Determination of behavioural traits of pure-bred dogs using factor analysis and cluster analysis; a comparison of studies in the USA and UK. Res. Vet. Sci. 66, 73–76.

Cattell, R.B., Bolz, C.R., Korth, B., 1973. Behavioral types in purebred dogs objectively determined by taxonome. Behav. Genet. 3, 205–216.

Christiansen, F.O., Bakken, M., Braastad, B.O., 2001. Behavioural differences between three breed groups of hunting dogs confronted with sheep. Appl. Anim. Behav. Sci. 72, 115–129.

Clutton-Brock, J., 1995. Origins of the dog: domestication and early history. In: Serpell, J. (Ed.), The Domestic Dog: its Evolution, Behaviour and Interactions with People. Cambridge University Press, Cambridge, pp. 7–20.

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

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

Dennis-Bryan, K., Clutton-Brock, J., 1988. Dogs of the Last Hundred Years at the British Museum (Natural History). British Museum (Natural History), London.

Draper, T.W., 1995. Canine analogs of human personality factors. J. Gen. Psychol. 122, 241–252.

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., 1986. Early prediction of adult behaviour in potential guide dogs. Appl. Anim. Behav. Sci. 15, 247–260.

Goodwin, D., Bradshaw, J.W.S., Wickens, S.M., 1997. Paedomophosis affects agonistic visual signals of domestic dogs. Anim. Behav. 53, 297–304.

Gosling, S.D., John, O.J., 1999. Personality dimensions in non-human animals: a cross-species review. Curr. Dir. Psychol. Sci. 8, 69–75.

Grandjean, D., et al. 2000. The Royal Canin dog encyclopedia. Royal Canin, Paris.

Hart, B.L., 1995. Analysing breed and gender differences in behaviour. In: Serpell, J. (Ed.), The Domestic Dog: Its Evolution, Behaviour and Interactions with People. Cambridge University Press, Cambridge, pp. 65–77.

Hart, E.H., 1975. Encyclopedia of Dog Breeds. TFH Publications, Neptune City.

Hart, B.L., Miller, M.F., 1985. Behavioral profiles of dog breeds. J. Am. Vet. Med. Assoc. 186, 1175–1180.

Harcourt, R.A., 1974. The dog in prehistoric and early historic Britain. J. Archeol. Sci. 1, 151–175.

Järverud, S., af Klinteberg-Järverud, G., 2002. Din hund söker. Brukshundservice Sverige AB, Farsta.

Kagan, J., Reznick, J., Snidman, N., 1988. Biological bases for childhood shyness. Science 240, 167–171.

Kenttämies, H., Valberg-Nordrum, N., Brenøe, U.T., Smeds, K., Johannessen, K.R., Bakken, M., 2002. Selection for more confident foxes in Finland and Norway: heritability and selection response for confident behaviour in blue foxes (*Alopex lagopus*). Appl. Anim. Behav. Sci. 78, 67–82.

Lindsay, S.R., 2000. Handbook of Applied Dog Behavior and Training. Adaptation and Learning, vol. 1. Iowa State University Press, Ames.

Lowe, S.E., Bradshaw, J.W.S., 2001. Ontogeny of individuality in the domestic cat in the home environment. Anim. Behav. 61, 231–237.

Mahut, H., 1958. Breed differences in the dog's emotional behaviour. Can. J. Psychol. 12, 35–44.

Mohlin, M., 2000. Lydnadsboken. Bilda förlag, Stockholm.

Murphree, O.D., 1973. Inheritance of human aversion and inactivity in two strains of the Pointer dog. Biol. Psychiatry 7, 23–29.

Murphree, O.D., Peters, J.E., Dykman, R.A., 1969. Behavioral comparisons of nervous, stable, and crossbred pointers at ages 2, 3, 6, 9, and 12 months. Condititional Reflex 4, 20.

Nobis, G., 1979. Der älteste Haushund lebte vor 14,000 Jahren. Umschau 19, 610.

Nordin, S., 1995. Spårhundsboken. Bilda förlag, Stockholm.

Pfaffenberger, C.J., Scott, J.P., Fuller, J.L., Ginsburg, B.E., Bielfelt, S.W., 1976. Guide Dogs for the Blind: their Selection, Development, and Training. Elsevier, Amsterdam.

Plutchik, R., 1971. Individual and breed differences in approach and withdrawal in dogs. Behaviour 40, 302–311.

Roll, A., Unshelm, J., 1997. Aggressive conflicts amongst dogs and factors affecting them. Appl. Anim. Behav. Sci. 52, 229–242.

Royce, J.R., 1955. A factorial study of emotionality in the dog. Psychol. Monogr. 69, 1–27.

Savolainen, P., Zhang, Y., Luo, J., Lundeberg, J., Leitner, T., 2002. Genetic evidence for an East Asian origin of domestic dogs. Science 298, 1610–1613.

Seksel, K., Mazurski, E.J., Taylor, A., 1999. Puppy socialisation programs: short and long term behavioural effects. Appl. Anim. Behav. Sci. 62, 335–349.

Scott, J.P., Fuller, J.L., 1965. Genetics and the Social Behavior of the Dog. The University of Chicago Press, Chicago.

Slabbert, J.M., Odendaal, J.S.J., 1999. Early prediction of adult police dog efficiency—a longitudinal study. Appl. Anim. Behav. Sci. 64, 269–288.

Strandberg, E., Jacobsson, J., Saetre, P., 2005. Direct and maternal effects on behaviour in German Shepherd dogs in Sweden. Livest. 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 familaris*). Appl. Anim. Behav. Sci. 79, 133–155.

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

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

Thorne, F.C., 1944. The inheritance of shyness in dogs. J. Genet. Psychol. 65, 275–279.

Trut, L.N., Plyusnina, I.Z., Oskina, I., 2004. An experiment on fox domestication and debatable issues of evolution of the dog. Russ. J. Genet. 40, 644–655.

Wayne, R.K., 1986. Cranial morphology of domestic and wild canids: the influence of development on morphological change. Evolution 40, 243–261.

Wayne, R.K., Ostrender, E.A., 1999. Origin, genetic diversity, and the genome structure of the domestic dog. BioEssays 21, 247–257.

Willis, M.B., 1995. Genetic aspects of dog behaviour with particular reference to working ability. In: Serpell, J. (Ed.), The Domestic Dog: Its Evolution, Behaviour and Interactions with People. Cambridge University Press, Cambridge, pp. 51–64.