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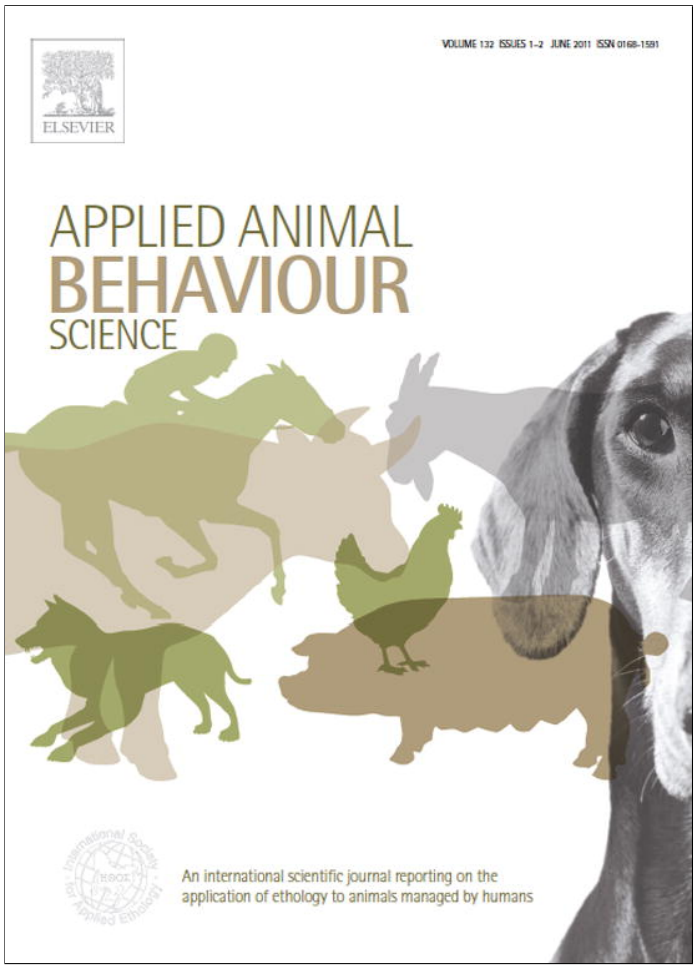

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Trainability and boldness traits differ between dog breed clusters based on conventional breed categories and genetic relatedness

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ABSTRACT

Modern dog breeding has given rise to more than 400 breeds differing both in morphology and behaviour. Traditionally, kennel clubs have utilized an artificial category system based on the morphological similarity and historical function of each dog breed. Behavioural comparisons at the breed-group level produced ambiguous results as to whether the historical function still has an influence on the breed-typical behaviour. Recent genetic studies have uncovered genetic relatedness between dog breeds, which can be independent from their historical function and may offer an alternative explanation of behavioural differences among breeds. This exploratory study aimed to investigate the behaviour profiles of 98 breeds, and the behavioural differences among conventional breed groups based on historical utility and among genetic breed clusters. Owners of 5733 dogs (98 breeds) filled out an online questionnaire in German. Breed trait scores on trainability, boldness, calmness and dog sociability were calculated by averaging the scores of all individuals of the breed. Breeds were ranked on the four traits and a cluster analysis was performed to explore behavioural similarity between breeds.

We found that two of the behaviour traits (trainability and boldness) significantly differed both among the conventional and the genetic breed groups. Using the conventional classification we revealed that Herding dogs were more trainable than Hounds, Working dogs, Toy dogs and Non-sporting dogs; Sporting dogs were also more trainable than Non-sporting dogs. In parallel, Terriers were bolder than Hounds and Herding dogs. Regarding genetic relatedness, breeds with ancient Asian or African origin (Ancient breeds) were less trainable than breeds in the Herding/sighthound cluster and the Hunting breeds. Breeds in the Mastiff/terrier cluster were bolder than the Ancient breeds, the breeds in the Herding/sighthound cluster and the Hunting breeds. Six breed clusters were created on the basis of behavioural similarity. All the conventional and genetic groups had representatives in at least three of these clusters. Thus, the behavioural breed clusters showed poor correspondence to both the functional and genetic categorisation, which may reflect the effect of recent selective processes. Behavioural breed clusters can provide a more reliable characterization of the breeds' current typical behaviour.

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1. Introduction

The dog (*Canis familiaris*) was the first domesticated species, and descended from the gray wolf (*Canis lupus*) at least 15,000 years ago (Savolainen et al., 2002; Dayan, 1994). Modern dog breeding over the past few hundred years has generated great variation in morphology, physi-

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ology and behaviour, which has giving rise to more than 400 dog breeds (Clutton-Brock, 1995) recognized today by official dog kennel organisations around the world. Due to modern breeding rules and strict breed standards, dog breeds have become morphologically homogeneous, genetically isolated breeding units (vonHoldt et al., 2010). It is not clear whether the term "breed" refers only to the genetic/morphological component or whether breeds are also uniform in their behaviour. Breed differences have been described predominantly in terms of behavioural traits, which are recognized as derived features of context independent behavioural functions, such as aggressiveness (Duffy et al., 2008) and nerve stability (Wilsson and Sundgren, 1997a). However, researchers have also found great individual variability within a single breed (e.g. aggressiveness: Podberscek and Serpell, 1996 in English Cocker Spaniel; nerve stability: Ruefenacht et al., 2002 in German Shepherd Dog).

Surveys have been conducted to obtain behavioural profiles of dog breeds by ranking the breeds on different behaviour traits (Hart and Miller, 1985), or clustering breeds on the basis of their behaviour (e.g. Bradshaw and Goodwin, 1998; Hart and Hart, 1985; Takeuchi and Mori, 2006). The concordance rate between two particular surveys, which used almost identical methods for clustering breeds, was 50–60% (Bradshaw and Goodwin, 1998; Takeuchi and Mori, 2006). This result could reflect a real basis for breed-typical behaviours, but also suggests possible cultural differences. Thus our first aim is to characterize dog breeds on the basis of their typical behaviour.

Behavioural differences between breeds are usually explained by their historical function. Before the emergence of dog kennel clubs at the end of the 19th century, breeds (or certain type of dogs) were selectively bred to optimize their performance in several tasks (e.g. herding, hunting, and guarding), which required selecting for specific morphological and behavioural features. Representatives of a given breed are generally suitable for a specific function (e.g. herding), due to breed specific behavioural skills (see also Coppinger and Coppinger, 2001; Spady and Ostrander, 2008). For example, livestock guarding dogs should not show any predatory motor patterns (giving eye, stalking and chasing) toward sheep or cows, while the presence of these behaviour patterns is important in herding dogs (Coppinger and Schneider, 1995). Accordingly, breeds with similar historical functions should behave generally more comparably than breeds with different functions. One problem which arises when using conventional grouping methods to categorise breeds by function, is the lack of scientific evidence on the history and function of most dog breeds. The currently recognized breed groupings were created by different national kennel club organisations, like the Fédération Cynologique Internationale (FCI) or the American Kennel Club (AKC), and are based on morphological similarity, anecdotal information about the breeds' behavioural utility, and scarce historical evidence. However, dogs today are usually regarded as family members or as companions in Western-cultures (Kubinyi et al., 2009; Serpell, 2003) and are generally no longer utilised in their original role. Behavioural traits, which had been the primary target for many hundreds of years, play little role in the breed standards today (McGreevy and Nicholas, 1999). This may explain why the behavioural comparisons at the breed-group level produced ambiguous results. For example, Svartberg (2006) did not find behavioural differences in curiosity/fearlessness, aggression, playfulness, and sociability among four FCI-based breed groups, whereas Ley et al. (2009) reported differences in five questionnaire scales in seven breed groups recognised by the Australian National Kennel Council. Taken together, it is still an open question whether the historical function of a breed affects their behaviour. Thus, our second aim is to compare the behaviour of breeds in conventionally recognized breed groups.

Genetic relatedness could also account for behavioural similarity among breeds (e.g. Takeuchi and Mori, 2006). Many reports have provided evidence for genetic variation of behavioural traits in dog breeds (e.g. fearfulness: Goddard and Beilharz, 1982, 1983; activity: Wilsson and Sundgren, 1998). Accordingly, closely related breeds should behave generally more similarly than genetically more distant breeds. The application of modern genetic methods based on similarity in DNA sequences has allowed a more precise estimation of genetic relatedness among breeds. However, this analysis has not revealed a true phylogenetic relationship among breeds in the usual (evolutionary) sense because of multiple cross-breeding events. Nevertheless, recent genetic studies have been aimed at analysing the hierarchical relationships between breeds. For example, Parker et al. (2004) have generated four genetic breed clusters from 85 breeds on the basis of 96 microsatellite loci. According to their analysis, a subset of breeds with ancient Asian and African origins have split off from the rest of the breeds with modern European origins, and shows the closest genetic relationship to the wolf. The modern European breeds were later divided into three clusters corresponding to the Mastiff, Herding and Hunting breeds. A more recent study based on a larger sample size of 132 breeds (Parker et al., 2007) identified a fifth 'Mountain' cluster containing mostly large mountain dogs separated from the Hunting cluster. More detailed analysis of breed relationships revealed smaller closely related sub-clusters within these five clusters, suggesting additional levels of relatedness among some breeds (Parker et al., 2007). Little is known about the effects of genetic relatedness on the behaviour of dog breeds, thus, our third aim is to compare the behaviour of breeds in different genetic breed clusters.

Traditionally two approaches have been used to characterize the behaviour of dog breeds: breed rating (e.g. Notari and Goodwin, 2007) and individual-based methods. We followed the latter method, and used several individuals per breed and breeds per breed group. Individual-based methods use two types of measurements: direct observational methods and questionnaire-based ratings of dogs by their owners. Behavioural tests measure a restricted set of objectively described behaviour units (e.g. growling and tail wagging) in a few, controlled situations, whereas questionnaire surveys are based on the owners' knowledge and familiarity with their dogs' everyday behaviour. The questionnaire method offers ease of data collection, a larger and more diverse sample, and therefore meet the requirements of this study. However there is some subjec-

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tivity in these assessments, such as the differing experience the owners have with dogs in general (Bennett and Rohlf, 2007, but see Tami and Gallagher, 2009). By combining the responses of many independent owners, such individual bias can be overcome (Jones and Gosling, 2005). The second source of subjectivity is the possible influence of breed stereotypes. Owners may tend to associate breeds or breed groups with certain behaviour-types (i.e. assess their dogs' behaviour on the basis of stereotypical beliefs). This subjectivity seems to be unavoidable; however, as Kwan et al. (2008) pointed out, the judgments of dogs do not simply reflect breed stereotypes, but take into account each individual's behavioural features.

In this study, our main aims are (1) to characterize dog breeds on four complex behavioural traits (trainability, boldness, calmness and dog sociability) using owner reported assessments on a large sample of dogs and (2) to test whether dog breeds' behavioural differences could be ascribed to the breeds' historical function (conventional breed groups) and/or genetic relatedness. Since not much research has been done on this topic and these issues we addressed have not been clearly defined, this study should be considered explorative by nature.

2. Materials and methods

2.1. Subjects

The analyses of the present study are based on a subset of the database provided by Kubinyi et al. (2009) in which 14,004 questionnaires were collected by the German "Dogs" magazine (published by Living at Home Multi Media GmbH, Hamburg, August 2007 issue) and the magazine's own website (www.dogs-magazin.de) from August 2007 to January 2008. From this database we extracted all adult pure-bred dogs whose breed presented at least 10 representatives. Altogether, 5733 questionnaires from 98 breeds were analysed. The dogs were on average 4.0 ± 3.0 years old, and 57.6% of them were males. Thirteen breeds were represented by at least 100 individuals, and the most frequent breed was the Labrador Retriever with 517 individuals.

2.2. Procedure

We used an online questionnaire adapted for dogs by Jesko Wilke based on a 48-item Human Personality Inventory (de.outofservice.com/bigfive). This questionnaire consists of 24 items in which owners are asked to score their dogs using a 3-point scale. Previous results (based on a larger sample from the original database) using principal component analysis have revealed that 17 items belonged to four components, labelled as trainability, boldness, calmness and dog sociability (Kubinyi et al., 2009) (Table 1). Dogs that scored low regarding the trainability trait are described by their owners as uninventive and not playful, whereas dogs that scored high on this trait are regarded as intelligent and playful. Boldness was related to fearful and aloof behaviour with a low score corresponding to a high degree of fearfulness/aloofness, and vice versa. The calmness trait describes the dogs' behaviour in stressful/ambiguous situations. A low score on this trait indicated stressed and anxious behaviour in these situations, while a high score referred to calm and emotionally stable dogs, according to the owner. Finally, dog sociability refers to their behaviour toward conspecifics, with a low score indicating a high tendency for bullying or fighting and inversely high scores related to a low tendency. The internal consistency and stability of these traits as well as the test–retest reliability of the questionnaire was reported earlier in Kubinyi et al. (2009).

Scores for individual traits were calculated by averaging the scores from the variables representing each trait, according to Kubinyi et al. (2009) (Table 1). The scores were then averaged for each breed regarding each behavioural trait in order to obtain the breed trait scores (Svartberg, 2006).

Hierarchical cluster analysis based on the breed trait scores was used to investigate the behavioural similarity between breeds. Hierarchical cluster analysis is an exploratory method used to identify relatively homogeneous groups of cases based on selected characteristics. In our sample, six breeds split off separately from the rest of the breeds (see Appendix A) and the 92 remaining breeds were divided into six clusters after visual examination of the hierarchical structure.

The classification of breeds according to historical function was based on the internationally recognized system of the American Kennel Club (AKC, www.akc.org). Eight breeds which are not recognized by the AKC (Bavarian Mountain Hound, German Bracke, German Hunting Terrier, Hovawart, Kromfohrländer, Landseer, Spanish Greyhound, White Swiss Shepherd Dog), were assigned to whichever AKC breed group most closely matched their classification by the Fédération Cynologique Internationale (FCI, www.fci.be). The 98 breeds present in this study were therefore classified into seven groups (Table 2).

To analyse the effect of the breeds' genetic relatedness in some behaviour traits, we categorised the breeds into five clusters according to Parker et al. (2007) (Table 3).

2.3. Statistical analyses

As the residuals of the breed behaviour trait scores were not all normally distributed and the variances were not homogeneous in all groups, nonparametric statistical methods were used. Kruskal–Wallis tests with Dunn post-hoc tests were used to compare the trait scores between breeds, and between the seven conventional breed groups and the five genetic breed clusters. A cluster analysis based on the behavioural traits was performed using the hierarchical agglomerative method. Distances between breeds were calculated from the four traits by squared Euclidean distance and breeds were clustered based on the between-groups average linkage method. With this method, a breed's behaviour has to be within a certain level of similarity to the cluster's average to be included in that cluster (Aldenderfer and Blashfield, 1984). Since the different breed frequencies in our sample may bias the breed trait scores, we randomly chose 10 individuals from each breed and ran the analyses on this balanced sample as well. SPSS 13.0 was used for all the analyses except the Dunn

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Table 1
The 17 questions, belonging to four traits: trainability, boldness, calmness and dog sociability.

Trainability	Calmness
Is ingenious, inventive when seeks hidden food or toy	Is calm, even in ambiguous situations
Is intelligent, learns quickly	Can be stressed easily[a]
Is very easy to warm up to a new toy	Is emotionally balanced, not easy to rile
Often does not understand what was expected from him/her during playing[a]	Is cool-headed even in stressful situations
Is not much interested except in eating and sleeping[a]	Is sometimes anxious and uncertain[a]

Boldness	Dog sociability
Is rather cool, reserved[a]	Fights with conspecifics frequently[a]
Is unassertive, aloof when unfamiliar persons enter the home[a]	Is ready to share toys with conspecifics
	Is bullying with conspecifics[a]
Is sometimes fearful, awkward[a]	Gets on well with conspecifics

[a] Scoring was reversed.

Table 2
Breed distribution according to conventional categorisation.

Conventional group name and description		Number of breeds	Number of individuals
Sporting dogs	Include pointers, retrievers, setters and spaniels; mostly used for cooperative hunting.	15	1197
Hounds	Include scenthounds, greyhounds and dachshunds; being used for independent hunting.	11	528
Working dogs	Were bred to perform such jobs as guarding livestock or pulling sleds.	20	1025
Terriers	Middle or small sized breeds, used for independent hunting.	14	808
Toy dogs	Small sized breeds with the main function: companionship.	11	561
Non-sporting dogs	Diverse group in terms of size and utility	12	492
Herding dogs	Middle or large sized breeds used for control the movement of other animals.	15	1122
All groups		98	5733

post-hoc tests, for this we used GraphPad Instat statistical software.

3. Results

3.1. Breed differences in behavioural traits

There were significant differences between breeds in all four traits (Kruskal–Wallis test, $N = 5733$, d.f. = 97, trainability $\chi^2 = 641.405$; boldness $\chi^2 = 417.126$; calmness $\chi^2 = 455.005$; dog sociability $\chi^2 = 687.035$, $P < 0.001$ for all).

The breeds were ranked on the basis of these traits (Appendix A). The five most popular breeds ($N \geq 200$: Beagle, German Shepherd Dog, Golden Retriever, Jack Russell Terrier, and Labrador Retriever) had no higher or lower scores than the population mean ± SD in calmness and trainability. However, the Beagle and Labrador Retriever scored higher than the mean on dog sociability, while the German Shepherd Dog and Jack Russell Terrier obtained lower scores. Jack Russell Terriers and Labrador Retrievers also scored higher on boldness.

3.2. Behavioural similarity between breeds

Breeds were clustered on the basis of their behaviour using hierarchical cluster analysis. Six breeds (three breed pairs) with extreme trait scores split off from the other breeds (Appendix A). The first pair consisted of the Newfoundland and the Landseer, known to be strongly genetically related. The AKC and the Kennel Club in the

Table 3
Breed distribution according to the genetic relatedness (Parker et al., 2007).

Genetic cluster name and description		Number of breeds	Number of individuals
Ancient breeds	Breeds with ancient Asian or African origin, mainly primitive type dogs	7	192
Mastiff/terrier cluster	Mastiff-type breeds or breeds with mastiff-type ancestors and terriers	13	1019
Herding/sighthound cluster	Breeds used as herding dogs and sighthounds	10	674
Hunting breeds	Breeds with relative recent European origin, primarily different hunting dogs	29	1974
Mountain cluster	Large mountain dogs and a subset of spaniels	11	958
All groups		70	4817

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UK classify them as coat colour varieties of a single breed, although the FCI recognizes them as distinct breeds. Both breeds were highly ranked in boldness, calmness and dog sociability. The next pair comprised of the Akita and the German Bracke and both breeds scored extremely low in regards to the dog sociability trait. The third pair, the German Pincher and the Spanish Greyhound, only slightly related to each other. Both breeds scored low on calmness, and the Spanish Greyhound ranked also low on boldness and trainability and high on dog sociability.

The remaining 92 breeds were divided into six clusters with 2–32 breeds in each cluster (Table 4), according to the dendrogram. The clusters differed from each other in each of the four traits (Kruskal–Wallis test, $N = 92$, d.f. = 5, trainability $\chi^2 = 43.409$; boldness $\chi^2 = 53.208$, calmness $\chi^2 = 45.790$, dog sociability $\chi^2 = 49.507$, $P < 0.001$, for all) and were characterized as low, medium and high on each trait, based on the post-hoc differences between them (Table 4).

3.3. Differences among conventional breed groups

Significant differences in the trainability and boldness scores were observed between the breed groups (Kruskal–Wallis test, $N = 98$, d.f. = 6, trainability $\chi^2 = 31.025$, $P < 0.001$; boldness $\chi^2 = 19.325$, $P = 0.004$); nevertheless, the differences between the groups regarding calmness and dog sociability traits were not significant (Kruskal–Wallis test, $N = 98$, d.f. = 6, calmness $\chi^2 = 11.522$, $P = 0.074$; dog sociability $\chi^2 = 12.111$, $P = 0.06$) (Fig. 1A and B).

According to the post-hoc tests, Herding dogs were reported by their owner to be more trainable than Hounds ($P < 0.01$), Working dogs ($P < 0.01$), Toy dogs ($P < 0.05$) and Non-sporting dogs ($P < 0.001$). Sporting dogs were also more trainable than Non-sporting dogs ($P < 0.05$).

Terriers scored higher on boldness than Hounds ($P < 0.01$) and Herding dogs ($P < 0.05$) (Fig. 1A).

3.4. Genetic relatedness

The five genetic clusters (identified by Parker et al., 2007) differed also in trainability and boldness (Kruskal–Wallis test, $N = 70$, d.f. = 4, trainability $\chi^2 = 10.153$, $P = 0.038$; boldness $\chi^2 = 14.497$, $P = 0.006$). The cluster of Ancient breeds was less trainable than the Herding/sighthound cluster and the cluster of Hunting breeds ($P < 0.05$ for both).

The Mastiff/terrier cluster was bolder than the Ancient breeds, the Herding/sighthound cluster and also the Hunting breeds ($P < 0.05$ for all) (Fig. 2A).

No significant differences in calmness and dog sociability traits were found between these clusters (Kruskal–Wallis test, $N = 70$, d.f. = 4, calmness $\chi^2 = 7.915$, $P = 0.095$; dog sociability $\chi^2 = 2.785$, $P = 0.594$) (Fig. 2B).

The analyses of the random sample of 980 individuals (10 individuals per breed, as mentioned in Section 2) led to the same differences between genetic breed clusters and similar differences between the conventional breed groups. The differences in calmness and dog sociability traits among conventional breed groups were significant in this sample compared to the trend difference observed in the whole sample. Nevertheless, this finding supports that the different breed frequencies in this study only minimally influenced the results.

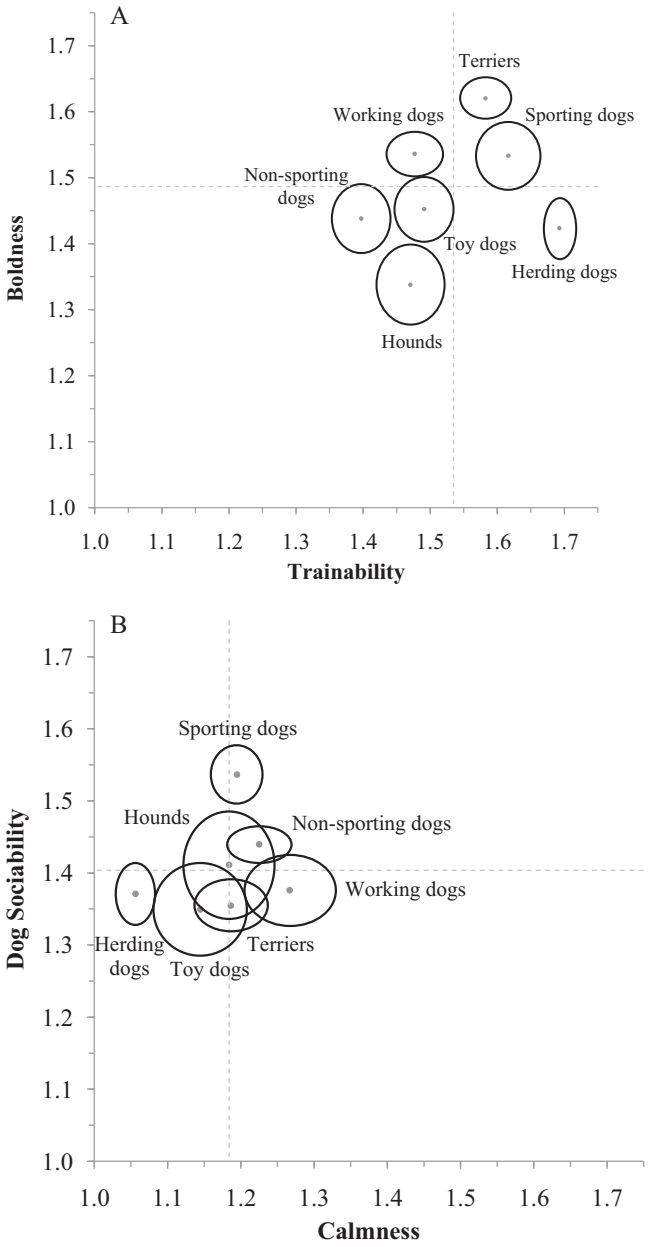

Fig. 1. Behaviour profiles of the conventional breed groups in (A) trainability and boldness and (B) calmness and dog sociability traits. Data points are group averages, the diameters of the ellipses represent the SE of trainability/calmness, the heights the SE of boldness/dog sociability. Dashed lines represent the population means. Kruskal–Wallis test showed significant differences between the groups in trainability and boldness and trend differences in calmness and dog sociability traits.

4. Discussion

The main focus of this study was to discover the typical behaviour of dog breeds and specific breed groups. Our aims were (1) to characterize a large number of breeds and explore their behavioural similarity and divergence, and (2) to test whether dog breeds' behavioural differences could be ascribed to the breeds' conventional

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Table 4
Clusters of breeds from the cluster analysis based on the trainability, boldness, calmness and dog sociability traits. The numbers links to the breeds represent the conventional breed groups and genetic clusters, respectively. The characteristic features of each cluster are presented.

Cluster 1 high calm, medium trainable, high sociable, high bold					
4;2	Airedale Terrier	3;5	Greater Swiss Mountain Dog	3;5	Saint Bernard
1;4	American Cocker Spaniel	5;.	Havanese	7;3	Shetland Sheepdog
2;4	Beagle	1;4	Irish Setter	5;4	Shih Tzu
7;3	Bearded Collie	1;2	Labrador Retriever	3;1	Siberian Husky
3;5	Bernese Mountain Dog	3;5	Leonberger	1;.	Small Munsterlander
6;2	Bulldog	4;4	Miniature Schnauzer	4;2	Soft Coated Wh. Terrier
5;4	Cavalier King Charles Spaniel	7;3	Old English Sheepdog	4;2	Staffordshire Bull Terrier
6;2	French Bulldog	5;4	Pekingese	2;3	Whippet
1;4	Golden Retriever	1;4	Pointer		
1;4	Gordon Setter	5;4	Pug		
Cluster 2 low calm, high trainable, low sociable, low bold					
4;2	American Staffordshire Terrier	1;5	English Cocker Spaniel	4;.	Parson Russell Terrier
7;3	Australian Shepherd	7;.	Entlebucher Mountain Dog	6;5	Poodle
2;.	Bavarian Mountain Hound	4;.	German Hunting Terrier	3;5	Rottweiler
7;3	Belgian Malinois	7;5	German Shepherd Dog	3;4	Standard Schnauzer
7;3	Border Collie	1;.	German Wirehaired Pointer	6;1	Tibetan Terrier
4;2	Border Terrier	3;4	Giant Schnauzer	1;4	Vizsla
3;2	Boxer	3;3	Great Dane	4;2	Welsh Terrier
4;4	Cairn Terrier	3;.	Hovawart	4;4	West Highland Wh.Terrier
2;4	Dachshund	4;2	Irish Terrier	2;.	Wirehaired Dachshund
6;4	Dalmatian	4;4	Jack Russell Terrier	6;4	Wolfspitz
3;4	Doberman Pinscher	5;5	Miniature Pinscher		
Cluster 3 high calm, high trainable, high sociable, high bold					
1;4	Flat-Coated Retriever	1;4	German Shorthaired Pointer		
Cluster 4 low calm, high trainable, medium sociable, low bold					
7;.	Appenzeller Sennenhund	5;.	Kromfohrländer	2;5	Rhodesian Ridgeback
7;.	Beauceron	2;.	Miniature Dachshund	6;1	Shiba Inu
7;.	Briard	5;4	Miniature Poodle	1;4	Weimaraner
7;3	Collie	7;.	Polish Lowland Sheepdog	7;.	White Swiss Shepherd
2;4	Ibizan Hound	7;.	Pyrenean Shepherd		
Cluster 5 low calm, low trainable, low sociable, medium bold					
1;4	Brittany	6;.	German Spitz	5;.	Yorkshire Terrier
4;.	Bull Terrier	5;5	Maltese		
5;4	Chihuahua	3;2	Perro de Presa Canario		
Cluster 6 high calm, low trainable, medium sociable, low bold					
3;1	Alaskan Malamute	6;.	Coton de Tulear	6;.	Eurasier
3;.	Anatolian Shepherd Dog	3;.	Dogue de Bordeaux	2;3	Irish Wolfhound
6;1	Chinese Shar-Pei	1;4	English Setter	6;1	Lhasa Apso

grouping based on historical function and/or genetic relatedness. We derived complex breed-related behavioural traits by averaging the behaviour scores of individual dogs within a given breed. This was based on the assumption that the complex behavioural traits might distinguish not only individual dogs, but also typical for larger population of dogs representing breeds or special breed groupings. Individual dog behaviour was measured by an owner-reported assessment, and four behavioural traits were obtained, namely trainability, boldness, calmness and dog sociability. Similar traits were previously detected by several other researchers (e.g. trainability: Bradshaw and Goodwin, 1998; Hsu and Serpell, 2003; boldness: Svartberg and Forkman, 2002; neuroticism (reverse to our calmness): Ley et al., 2009; dog-directed aggression (reverse to our dog sociability): Hsu and Serpell, 2003). The four behavioural traits found in this study correspond to the seven personality dimensions of dogs summarized in Jones and Gosling (2005) (see also in Kubinyi et al., 2009).

4.1. Breed differences in behavioural traits

Significant breed differences were observed in all the four traits. The behavioural profiles of the breeds are to some extent in accordance with the reports of other studies, but there is some dissimilarity. For example in the study of Duffy et al. (2008) the Akita, Dachshund, Chihuahua and Jack Russell Terrier were reported to be highly aggressive toward other dogs, whereas the Whippet, Collie and Bernese Mountain Dog were at the opposite end of the scale. Accordingly, the former four breeds ranked low in dog sociability in this study (lower than the population

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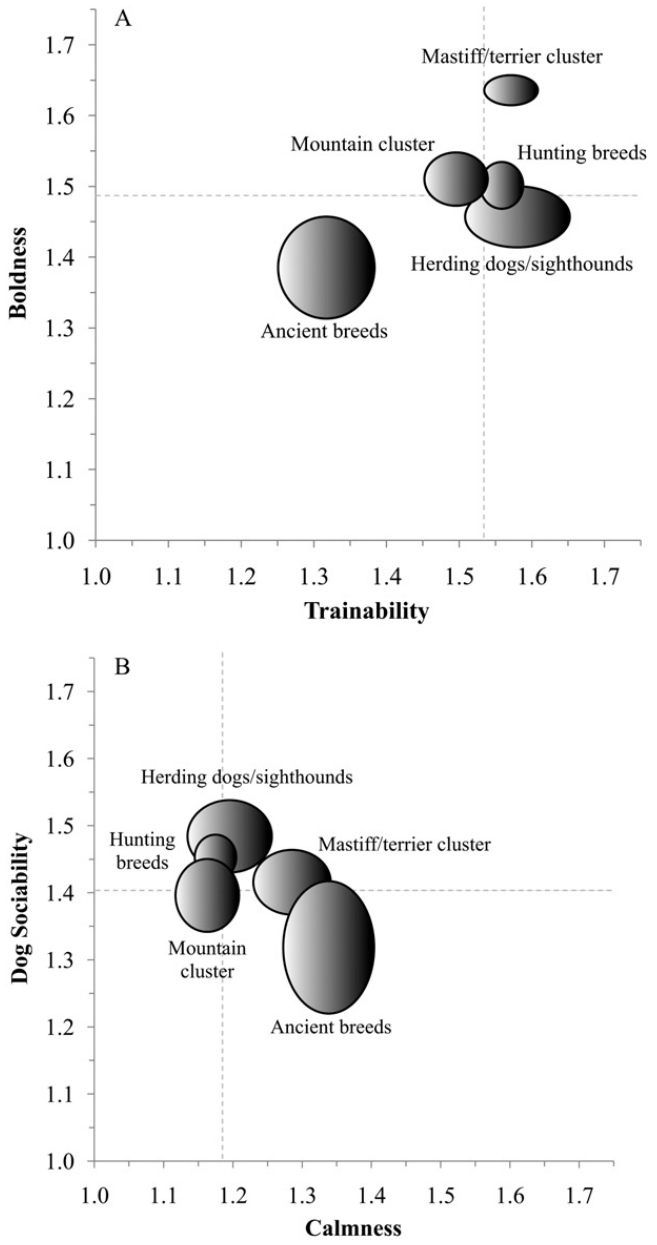

Fig. 2. Behaviour profiles of the genetic breed clusters in (A) trainability and boldness and (B) calmness and dog sociability traits. Data points are group averages, the diameters of the ellipses represent the SE of trainability/calmness, the heights the SE of boldness/dog sociability. Dashed lines represent the overall mean of the factors. Kruskal–Wallis test showed significant differences between the groups in trainability and boldness and trend difference in calmness traits.

mean ± SD), but from the later three, only the Whippet and Bernese Mountain Dog were ranked high, and the Collie was in the middle section of the dog sociability rank order.

Breed standards of kennel clubs usually contain a short description about the favourable behavioural characteristics of a given breed. For example, according to its FCI breed standard, Anatolian Shepherds are "steady and bold without aggression, naturally independent, very intelligent and tractable, proud and confident" (www.fci.be). Moreover, one of the eliminating faults of this breed is signs of aggressiveness or shyness. Contrary to this description, the Anatolian Shepherd breed in this study was described as low trainable, highly shy and not sociable with other dogs. Another example is the Spanish Greyhound (Galgo Espanol), which, according to its breed standard, should not be aggressive or overly shy (one of the eliminating faults), here was found to be the least bold breed of all. These examples show that even the vague characteristics described in the breed standards do not always reflect reality.

The dendrogram of the cluster analysis based on the four behavioural traits (Appendix A) illustrates the highly complex relationship between breeds. We divided the breeds into six clusters which either show or do not show strong correspondence to the conventional categories or the genetic breed clusters of Parker et al. (2007). There is some correspondence with the behavioural breed clusters in other studies. For example, eight of the nine breeds which were represented in our sample from the Svartberg's (2006) Cluster 1 also clustered together in this study. The Border Collie and Australian Shepherd had a highly similar behavioural profile which corresponded well to their genetic and functional similarity. In contrast, the Shetland Sheepdog and the Collie were related both in their historical function and genetically (Neff et al., 2004; Parker et al., 2007) but were clustered far from each other in their behavioural profiles. Given the explorative nature of our study and the applied statistical method, the behavioural relationship between breeds described in this study should be interpreted with caution; more studies are needed to confirm our findings.

4.2. Conventional categorisation

Dog breeds were grouped based on the systems provided by two internationally recognized kennel clubs, presupposing that these systems reflect the breeds' historical function. The seven groups differed in both trainability and boldness traits.

Trainability: Herding dogs were more trainable than Hounds, Working dogs, Toy dogs and Non-sporting dogs. Sporting dogs were also more trainable than Non-sporting dogs. Similar behavioural differences were previously shown in several surveys. Indeed, both Seksel et al. (1999) and Ley et al. (2009) found that breeds from the Pointing dogs group (here classified as Sporting dogs) were highly trainable, while Toy dogs scored low on that scale. Additionally, Ley et al. (2009) reported that Hounds were also relatively less trainable compared to Pointing and Herding dogs. Serpell and Hsu (2005) constructed a rank order among different breeds and found that the most trainable breeds were either the representatives of Herding or Pointing groups. The authors explained their results on the basis of the cooperative versus independent type of work that the breeds were originally bred for. Indeed, Herding and pointing dogs were bred for cooperative tasks with continuous visual contact with their human partner, while hounds were to hunt independently, out of the view of humans (see Gácsi et al., 2009). The Working dog group consists of sled dogs, guarding dogs and livestock guarding dogs, which require some human guidance to execute their tasks successfully, however most of these breeds were selected for independent working.

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Other factors, such as the differences regarding the general size or physical abilities of dogs could also be responsible for the breed/breed-group differences (Helton, 2010). For instance, the low trainability of the Toy dogs group could be explained by the typically small physical size of this group (Bennett and Rohlf, 2007), since larger dogs are more likely to attend formal obedience training, possibly because disobedience or behavioural problems could be more serious in larger dogs (Kobelt et al., 2003).

Non-sporting dogs appear to be the most difficult to train. This group contains highly diverse breeds in terms of size or historical function and is dominated by breeds with ancient Asian origin. The close genetic relatedness of these breeds with wolves (Parker et al., 2004) may account partly for the low trainability skills observed in this group.

Boldness: Terrier breeds scored higher on boldness than Hounds and Herding dogs, in line with previous studies in which terriers are described as typically energetic, excitable and reactive dogs (Hart, 1995; Ley et al., 2009; Scott and Fuller, 1965).

The historical function and utility of dog breeds seem to still have an effect on breeds' typical behaviour. However, explaining breed differences in terms of their function solely would presuppose that dogs are bred on the basis of their performance regarding these functions; which is usually not the case. Indeed, in modern dog breeding, most animals are selected on the basis of their success and judgement at dog shows. Dogs are evaluated at these shows according to strict breed standards which reflect mostly on morphological requirements. It is however important to note that breeds are often separated into working and show "lines" or "types", based on divergent selection criteria (e.g. Border Collie, Chang et al., 2009). In working lines, the performance plays the most important role for breeding. Accordingly, the behaviour of working line individuals could differ from that of the show lines (Duffy et al., 2008).

The differences between the conventional breed groups in calmness and dog sociability were rather small (trend differences in the whole sample and significant group differences in the random sample), although there were large differences between breeds in both traits. These characteristics are not strictly related to the breeds' original function, however, they might have been important for some breeds. For example, some breeds from the Hound group which were used for hunting in groups should show low aggression toward conspecifics as a requirement in these breeds; whereas other functions like herding might not have required direct selection for tolerant behaviour toward conspecifics.

However, the differences between the conventional breed groups in trainability and boldness are in contrast with the findings of Svartberg (2006), who did not find any breed group differences in four traits measured by behavioural tests. He suggested that recent selection criteria are more important in shaping the behaviour of dog breeds than their historical function. The differences between the two studies might reflect real breed differences between countries due to genetic isolation (Notari and Goodwin, 2007) or the different attitudes toward dog breed standards and present utility as well as various environmental effects (e.g. keeping conditions, neutering) in each country (Houpt et al., 2007). Different breed representations between countries and breed popularity could also potentially affect dog breeds' behaviour (Svartberg, 2006). However, it is also possible that our results only reflect the owners' stereotypic beliefs about breeds and breed groups of different historical functions.

4.3. Genetic relatedness

Breeds were grouped into five clusters (Parker et al., 2007) presupposing that the classification based on 96 microsatellite loci reliably mirrored the breeds' genetic relatedness. To our knowledge the present analysis is the first to investigate the effect of genetically supported grouping on the behavioural traits of dogs. The five clusters differed in trainability and boldness traits.

Ancient breeds were less trainable than breeds in the Herding/sighthound cluster and Hunting breeds. Breeds from the Mastiff/terrier cluster were bolder than the Ancient breeds, the breeds from the Herding/sighthound cluster and the Hunting breeds.

It seems that the genetic separation of the Ancient breeds from the other four breed clusters representing modern European breeds is paralleled by differences in behaviour. The Ancient breeds show the closest genetic relationship with the wolf (Parker et al., 2007) which might explain some part of these differences. The high score in the boldness trait of the Mastiff/terrier genetic cluster parallels the high boldness score of the Terriers and Working dogs in the conventional categories (Fig. 1). There is some evidence in the literature on the genetic basis of behavioural traits which are related to fearfulness (e.g. Murphree et al., 1969; Peters et al., 1967), for example, Goddard and Beilharz (1983) found relatively strong (0.46) heritability for this trait. However, much lower heritability was reported for 'courage' in German Shepherd and Labrador Retriever (0.25 and 0.28, respectively) (Wilsson and Sundgren, 1997b), and for boldness in German Shepherd and Rottweiler (0.25–0.27, respectively) (Strandberg et al., 2005; Saetre et al., 2006). Finally, trainability showed even lower heritability (0.01–0.16, reviewed in Ruefenacht et al., 2002).

The differences found between the genetic clusters were not independent from those found between the conventional breed groups, since genetic relatedness is often associated with morphological and functional similarity and shared geographic origin (Parker et al., 2004; vonHoldt et al., 2010). For example, conventional categorisation revealed that Terriers were bolder than Herding dogs. In parallel dogs in the genetic cluster of Mastiff/terrier breeds scored higher than the breeds in the Herding/sighthound cluster. It is not evident yet, if there is a causal relationship between these two results and if so, what is the direction of the causality. Overlaps between the conventional and the genetic groups are not obvious, because more recent breeds, especially in the Working dogs and Toy dogs groups were frequently bred from combinations of other breeds, independently of their historical function and genetic relatedness (vonHoldt et al., 2010).

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One limitation of the present study was that the owners' assessment of their dog could be biased by subjectivity and stereotypical beliefs. Another limitation is that dog keeping practices, which could affect the dogs' behaviour (Bennett and Rohlf, 2007; Kobelt et al., 2003), may vary systematically among breeds, producing false similarities or discrepancies in the perception of their typical behaviour. However, the diversity and the large number of dogs investigated in this study may help to minimize these biases.

5. Conclusion

We found large differences among dog breeds in four behavioural traits. Our results showed that the differences in breed-specific behaviour in trainability and boldness are partly determined by genetic factors and differences in the historical function of the breeds. However, breed clusters with similar behavioural characteristics corresponded neither to the presently recognized functional (conventional) classification nor to the genetic clusters of breeds. Behavioural divergence of seemingly related dog breeds could be associated to either cross-breeding with other breeds characterised by different behavioural traits (e.g. selection for toy dogs, vonHoldt et al., 2010), ceasing selection for the original function, or changes in function that was associated with a novel selective environment. Other factors like early period of socialization, dog keeping practices, and the behaviour of the owner might also play an important role in shaping the dogs behaviour, and these factors can modify the behaviour of individual dogs from the core characteristics typical of their breeds. Nevertheless, our study, although explorative by nature, might help owners to choose the appropriate breed as a pet on the basis of real breed-typical behaviour, which is beneficial not only for the owner but also for the welfare of the dog. Studies such as this one may be significant in contrasting the typical behaviour of "real" dog breed populations with the often 'ad hoc' description used by kennel clubs. It would be advantageous to use such data to make more precise official breed descriptions to help ensure a better match between a prospective owner and their pet.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.applanim.2011.03.006.

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