

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/271826897>

Dog Breeds and Their Behavior

Chapter · February 2014

DOI: 10.1007/978-3-642-53994-7_2

CITATIONS

46

READS

19,297

2 authors:



James A Serpell

University of Pennsylvania

192 PUBLICATIONS 6,397 CITATIONS

[SEE PROFILE](#)



Deborah L Duffy

Thomas Edison State University

32 PUBLICATIONS 1,686 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Maternal style, young adult temperament & cognition, and program outcome in a population of guide dogs [View project](#)



Canine comparative-genomics of behavior [View project](#)

Chapter 2

Dog Breeds and Their Behavior

James A. Serpell and Deborah L. Duffy

Abstract Domestic dogs display an extraordinary level of phenotypic diversity in morphology and behavior. Furthermore, due to breeding practices introduced during the nineteenth century, these phenotypic traits have become relatively ‘fixed’ within breeds, allowing biologists to obtain unique insights regarding the genetic bases of behavioral diversity, and the effects of domestication and artificial selection on temperament. Here we explore differences in behavior among the 30 most popular dog breeds registered with the American Kennel Club based on owner responses to a standardized and validated behavioral questionnaire (C-BARQ©). The findings indicate that some breed-associated temperament traits (e.g. fear/anxiety) may be linked to specific gene mutations, while others may represent more general behavioral legacies of ‘ancient’ ancestry, physical deformity, and/or human selection for specific functional abilities. They also suggest that previous efforts to relate dog breed popularity to behavior may have failed due to the confounding effects of body size.

2.1 Introduction

Despite much speculation, and an ongoing supply of somewhat contradictory molecular and archaeological discoveries, it is still not known precisely where or when the dog (*Canis familiaris*) was first domesticated. Based on available evidence it seems likely that domestication had occurred by around 15,000 years ago, but it remains unclear where it happened and whether it was a single, isolated event or the result of multiple domestications in different parts of Europe and Asia (Larson et al. 2012; Thalman et al. 2013). Regardless of location and timing,

J. A. Serpell (✉) · D. L. Duffy

Center for the Interaction of Animals and Society, School of Veterinary Medicine,
University of Pennsylvania, Philadelphia, PA 19104, USA

e-mail: serpell@vet.upenn.edu

however, it is likely that the process of domestication occurred in stages. Since the grey wolf (*Canis lupus*)—the putative ancestor—is typically more fearful or neophobic and potentially more aggressive towards humans than most dogs, the first stage in the process probably involved relatively intense selection for ‘tameness’ or docility (Coppinger and Schneider 1995). In a related canid, the domesticated silver fox (*Vulpes vulpes*), deliberate, experimental selection for tameness resulted within a few generations in dramatic reductions in human-directed fearfulness and aggression and increases in prosocial behavior, as well as a wide variety of correlated changes in physiology and morphology (Trut et al. 2009). It seems reasonable to postulate that early semi-domesticated wolves/dogs went through a similar process, and came out the other side of it looking and behaving quite different from the ancestral species (Coppinger and Schneider 1995). This new animal, the domestic dog, then experienced thousands of years of unprecedented diversification.

One of the unique things about dogs that distinguishes them from all other domestic animals is that they are, above all, products of human selection for behavior. The majority of domestic species—cows, sheep, pigs, chickens, and so on—are largely the consequence of selection for production-related traits, such as growth rates, feed conversion, muscle and/or fat mass, egg production, fur or hair quality, etc.¹ In contrast, dogs have traditionally been valued for their ability to perform an extraordinary variety of working and social roles, including that of security guards, hunting aides, beasts of burden, weapons of war, entertainers, fighters, shepherds, guides, garbage disposers, and pets, to name just a few. Thus, when we look at dogs as a whole, we see a species that has undergone a remarkably rapid adaptive radiation into a capricious ecological niche defined by the diverse instrumental and social demands of human beings. This history of adaptive radiation is to some extent still preserved in the genomes of what we now call ‘breeds’ of dog (Boyko et al. 2010), although the term itself is problematical and tends to mean different things to different people.

2.2 What is a Breed?

The domestic dog currently comprises a bewildering variety of different breeds—more than 400 according to some accounts—that differ dramatically in physical appearance and behavior. Judging from archaeological discoveries, early artistic representations and various written accounts, recognizable types of dogs—sight hounds, mastiffs, scent hounds, spaniels, terriers, lapdogs, and so on—have existed since ancient times (Clutton-Brock 1995). Most of these early dog types

¹ Although dogs have also been employed, from time to time, as food items or as a source of fiber, such uses were relatively limited and localized, and most of the types of dog developed for such purposes are now extinct (Serpell 1995).

represented *natural* breeds or *landraces* that evolved as a consequence of geographic isolation, random genetic processes such as ‘founder effect’ and ‘drift’, and local adaptation to both natural and artificial (human) selection. In general, the distinctive physical and behavioral characteristics of these natural breeds reflected their various functions within the human cultures in which they evolved. Most early accounts of dog breeds categorized them according to the various jobs they performed (Sampson and Binns 2006; Young and Bannasch 2006) and this system of classification according to ‘function’ is still retained by modern kennel clubs. The American Kennel Club’s current breed group classification into sporting, hound, working, terrier, toy, non-sporting, herding, and miscellaneous groups provides an obvious example.

Paleolithic and Neolithic humans may have had aesthetic preferences regarding the appearance of their dogs, but it is safe to assume that they were primarily concerned with the whole package of traits. In other words, they were seeking an animal that displayed the appropriate behavior—for herding sheep, protecting property, chasing hares, or whatever the task—while also possessing the right physical attributes, be it size, speed, visual acuity, coat length and quality, and so on, to enable it to perform these tasks well. In the sense that individual dogs were probably favored with extra food or access to mates when they did their jobs effectively, and were abandoned, traded or culled when they did not, these early ‘breeds’ were certainly products of human selection, but the process was largely unconscious rather than goal-directed, and little effort would have been made to prevent these animals from mating with whomever they chose. This somewhat haphazard approach eventually gave rise to the so-called ‘foundation’ breeds from which contemporary dogs are all ultimately derived.

Modern ‘purebred’ dogs are an entirely different story. In current dog breeding circles, the term “breed” refers to a population of closely related animals of similar appearance that is bred and maintained from a known foundation stock through genetic isolation and deliberate selection. For any modern dog to be successfully registered as purebred, both its parents and grandparents must also have been registered members of the same breed, which means that essentially all modern dog breeds are closed breeding populations (Ostrander 2007). The idea of ‘fixing’ the characteristics of dog varieties by genetic isolation and inbreeding is less than 200 years old, having originated from the hobby breeding of prize-winning poultry and livestock in England during the middle of the nineteenth century (Ritvo 1987). In some cases, it is claimed that modern purebred dogs are direct descendants of ancient or foundational stock but usually the genetic evidence for continuity is shaky at best (Larson et al. 2012). In reality, the lines of descent between modern and ancestral breeds have been thoroughly obscured by the effects of arbitrary selection for unusual or extreme aspects of physical appearance combined with deliberate hybridization between existing breed types to produce new, true-breeding strains that combine the attributes of the parental lines.

Despite this uncertainty, the remarkable phenotypic variation among modern dog breeds and their effective ‘fixation’ though genetic isolation presents biologists with a unique opportunity to explore both the genetic bases of canine

temperament and the impact of domestication and artificial selection on the evolution of behavior (Ostrander and Galibert 2006). Breed differences in behavior and temperament are also relevant to prospective dog owners who may wish to acquire an animal that is likely to be compatible with their own personalities and lifestyles.

2.3 Measuring Breed Differences in Behavior

When discussing breed differences in behavior, it is helpful to distinguish between *breed-specific* behavior patterns, such as the retriever's love of water, the pointer's 'point', or the Border collie's tendency to show 'eye', and more general breed differences in personality or temperament. The former are often viewed as unique or defining characteristics of particular breeds while the latter are considered aspects of each breed's overall character or behavioral 'style', and are often alluded to in the written standards for the breed. For example, the AKC temperament standard for the Belgian malinois states that this breed is, "confident, exhibiting neither shyness nor aggressiveness in new situations," is "reserved with strangers but is affectionate with his own people," is "naturally protective of his owner's person and property without being overly aggressive," and "possesses a strong desire to work and is quick and responsive to commands from his owner."

A variety of techniques have been used to measure these more general kinds of breed differences in behavior in dogs, including standardized behavioral tests (Scott and Fuller 1965; Svartberg and Forkman 2002; Svartberg 2006), expert opinions (Bradshaw and Goodwin 1998; Hart and Hart 1985; Hart and Miller 1985; Takeuchi and Mori 2006), and questionnaire surveys of dog owners and handlers (Duffy et al. 2008; Ley et al. 2009; Serpell and Hsu 2005; Turcsán et al. 2011). There are benefits and disadvantages to each of these approaches.

In theory, standardized behavioral tests ought to provide the most objective behavioral evaluations since they are based on direct observations of actual behavior. On the other hand, such tests are relatively laborious and time-consuming to conduct and, unless they are performed repeatedly on each dog over an extended period, the results are likely to be strongly influenced by the animal's emotional and motivational state at the time of testing (Serpell and Hsu 2001). In their pioneering early work, Scott and Fuller (1965) used a combination of behavioral observations and 'performance tests' to investigate the genetic basis for behavioral differences among five different dog breeds: basenjis, beagles, cocker spaniels, Shetland sheepdogs and wire-haired fox terriers. Puppies from each of these breeds were reared in identical conditions in order to reduce environmental influences on their behavioral development. Their performance was then evaluated at various ages on a series of standardized tests designed to measure such traits as overall emotional reactivity, response to handling and leash restraint, problem solving ability, trainability, aggressiveness, and tendency to bark. Analysis of variance by individual, litter and breed indicated strong and statistically significant

effects of breed on the expression of many of these traits. Scott and Fuller then carried out hybridization experiments using some of these breeds, such as basenjis and cocker spaniels, to produce F_1 and F_2 hybrids and backcrosses to each of the parent strains. Given the basic rules of Mendelian inheritance, the ways in which the different traits segregated out in these hybrid generations then provided clues to their genetic origins. For example, they found that the hybrid puppies' responses to approach and handling by a stranger (a trait the authors labeled 'tameness') were consistent with the actions of a single dominant gene for wildness in basenjis and a corresponding recessive gene for tameness in cocker spaniels. Other traits, such as problem-solving ability, were far more complex, however, and did not reveal any clear patterns of genetic inheritance (Scott and Fuller 1965).

Svartberg (2006) studied behavioral differences in 31 breeds of dogs subjected to a standardized test known as the Dog Mentality Assessment (DMA) that comprises 10 subtests and measures four distinct canine 'personality' traits: *playfulness*, *curiosity/fearlessness*, *sociability*, and *aggressiveness*. He found statistically significant breed differences in all of these traits, *although*, surprisingly, none of these differences were related to the breeds' original functional roles based on breed groupings (e.g. herding dogs, working dogs, terriers, and gun dogs). More recently, across-breed, genome-wide association (GWAS) studies have had some success identifying chromosome regions and possible candidate genes associated with canine personality traits such as *boldness* (Jones et al. 2008; Vaysse et al. 2011).

Hart and Hart (1985) pioneered the use of expert opinion as a technique for characterizing breed differences in behavior in dogs. In this method, canine 'experts' (e.g. obedience judges and veterinarians) are asked to rank a random subset of seven common breeds on 13 separate behavioral characteristics judged to be important to a majority of dog owners: e.g. watchdog barking, snapping at children, obedience training, destructiveness, excitability, etc. The respondents' rankings are then converted into deciles, each containing five or six breeds, with the highest decile representing the most extreme expression of the behavior. Analysis of variance subsequently determined that each of the traits could be used to discriminate between breeds, although some did so more reliably than others. Other researchers have since applied the same technique to examine breed differences in other countries, and have tended to find similar rankings for the same breeds (Bradshaw and Goodwin 1998; Notari and Goodwin 2007; Takeuchi and Mori 2006). It remains unclear, however, whether agreements among experts, either within or between countries, reflect true differences in breed behavior or shared opinions based on breed stereotypes (Duffy et al. 2008).

An alternative to canvassing the views of experts is to ask dog owners to provide personality or behavioral assessments of their dogs, and then use these assessments to investigate differences among breeds. While potentially more subjective than direct observations of behavior, such assessments are arguably less susceptible to cultural stereotypes than expert opinions, and, if large sample sizes are used, the effects of individual subjective biases can be greatly reduced (Jones and Gosling 2005). Such surveys can be divided into those that focus on relatively broad, overarching personality dimensions such as *boldness*, *sociability*, or

extraversion, and those that have investigated more specific phenotypic traits such *trainability* or particular types of aggression.

Ley et al. (2009) used the Monash Canine Personality Questionnaire (MCPQ) to explore breed differences in a sample of 455 Australian dogs. The MCPQ comprises a series of 41 descriptive adjectives that loaded on five personality subscales when subjected to factor analysis (*extroversion*, *motivation*, *training focus*, *amicability*, and *neuroticism*). Although not able to compare individual breeds due to small sample sizes, they investigated personality differences across the seven breed groups recognized by the Australian National Kennel Club. Relatively few significant differences were identified: working dogs and terriers were rated as significantly more extroverted, and toy breeds less extroverted. Working dogs and gundogs were rated significant higher for *training focus*, while toys and hounds were rated as lower for this subscale. The authors also noted that dogs' scores on the *neuroticism* subscale (a measure of fear and anxiety) correlated negatively with weight and height, while scores on *amicability* (a measure of sociability) correlated positively with weight and height.

In another study, Turcsán et al. (2011) invited the owners of 5733 dogs belonging to 98 breeds to rate their dogs on four broad personality traits: *Trainability*, *boldness*, *calmness*, and *dog sociability*. The results were then used to compare breeds belonging to the conventional breed groups recognized by the AKC (functional classification) and those identified as being more closely related according to genetic analyses (Parker et al. 2004). Significant breed differences in the four personality factors were observed. The results also indicated that dogs belonging to herding breeds tended to be significantly more trainable than hounds, working dogs, toys, and non-sporting breeds, and sporting breeds were more trainable than non-sporting ones. Terriers also scored higher for *boldness* than hounds or herding dogs. Neither the *calmness* nor *dog sociability* traits were able to discriminate reliably between breed groups. With respect to the five clusters of breeds identified as genetically related, the so-called 'ancient breeds' cluster was found to be less trainable than the herding/sighthound cluster, and dog breeds in the mastiff/terrier cluster scored higher for *boldness* than those in either the ancient breed, herding/sighthound, or hunting clusters. Again, *calmness* and *dog sociability* failed to discriminate between the clusters. The authors interpreted these results as indicating that some traits such as *trainability* and *boldness* are partly determined by genetic factors and by different histories of human selection for these functional traits. The distributions of the other two personality traits seemed to bear no relation to either functional or genetic breed classifications.

Three previous studies have used the *Canine Behavioral Assessment and Research Questionnaire* (C-BARQ) to investigate breed differences in behavior. (See below for further elaboration of this method.) Serpell and Hsu (2005) invited the owners of 1563 dogs belonging to 11 common breeds to assess them on the *trainability* factor of the C-BARQ. Highly significant breed differences in *trainability* were detected. In two breeds with distinct field and show-bred lines, show-bred dogs obtained significantly lower *trainability* scores. In general, sporting dog and working dog breeds (English springer spaniel, golden retriever, Labrador

retriever, poodle, rottweiler, and Shetland sheepdog) tended to obtain high scores for this factor while hounds (basset hound and dachshund), terriers (West Highland white terriers, and Yorkshire terriers), and the Siberian husky obtained low scores. The authors argued that these results were consistent with the differential effects of human selection for social cognitive skills in particular breeds, and lines within breeds, that historically tended to work in close partnership with people.

In a second study, Duffy et al. (2008) surveyed two separate samples of owners (1,521 breed club members and 3,791 pet owners) of 33 breeds of dog on the four aggression factors of the C-BARQ, and again found highly significant breed differences in behavior. Breeds that were common to both samples also ranked similarly on three of the four aggression factors. Small breeds, such as dachshunds, Chihuahuas and Jack Russell terriers, tended to obtain high scores on all or most aggression factors, while other breeds only displayed higher than average scores in specific contexts (e.g. *dog-directed aggression* in akitas and pit bulls). The authors concluded that aggression in small breed dogs was motivated primarily by fear, due to their greater vulnerability, and that owners of such breeds were also more tolerant of aggression due to the relatively limited risks of severe bites. In contrast, other breeds showed evidence of differential human selection for aggressive responses in specific contexts. The study also detected higher rates of *owner-directed aggression* in show-bred lines of English springer spaniels compared with field-bred dogs, and the reverse pattern for Labrador retrievers, a result the authors attributed to different popular sire effects in the two breeds.

More recently, McGreevy et al. (2013) explored the relationship between average C-BARQ factor and item scores and skull shape (cephalic index), body weight, and body size in a sample of 8,301 dogs belonging to 49 different breeds. A highly significant inverse relationship was detected between breed-specific body height and a large number of problematic behaviors including a range of fear/anxiety-related behaviors, *owner-directed aggression*, *attachment and attention-seeking*, and house-soiling when left alone. Body weight also correlated inversely with *excitability* and *hyperactivity*. These findings suggested that, across breeds, behavior tends to become more problematic as size decreases. The study also found that brachycephalic breeds tended to obtain lower scores for predatory *chasing*.

2.4 Current Study

As well as varying greatly in size, shape, and behavior, dog breeds also differ in popularity, with some breeds (e.g. Labrador retriever) maintaining rather consistent levels of popularity over time while others (e.g. Irish setter) have been subject to relatively sudden and rapid fluctuations in popularity (Herzog 2006). One possible explanation for this variation in dog breed popularity is that some breeds possess temperament traits that render them functionally better at serving as pets than others. In a recent study, Ghirlanda et al. (2013) used C-BARQ comparisons to test this hypothesis on a selection of 80 breeds of known popularity, but failed to

detect any association with breed behavioral characteristics. In the current study we use breed-specific C-BARQ data to re-examine this possible relationship by focusing on the behavioral traits of the 30 most popular breeds currently registered by the American Kennel Club (AKC).

2.4.1 Methods

2.4.1.1 The Sample

Table 2.1 provides the characteristics of the sample of breeds included in the present analysis. It consists of the 30 most popular breeds registered by the American Kennel Club (AKC), including both standard and miniature or toy-size variants of two breeds: the dachshund and poodle. It should be noted that, while there are no significant differences in sex ratio between the breeds sampled, breeds do differ significantly in terms of age and percent neutered. The values of N for each breed reflect the numbers available in the C-BARQ database at the time of sampling. The online version of the C-BARQ (<http://www.cbarq.org>) has been freely available to dog owners since it was created in 2006. Although initially publicized via notices sent to Philadelphia area veterinary clinics and the top 20 USA breed clubs (based on AKC registrations), the availability of the survey subsequently spread by word of mouth. The current sample of owner reports is therefore self-selected. While this may be considered a potential source of bias in the data, there is no *a priori* reason to believe that such biases would affect different breeds unequally.

2.4.1.2 About the C-BARQ

The ‘gold standard’ of behavioral measurement is the direct, unmediated observation and recording of all instances of an animal’s behavior over time (Martin and Bateson 1993). However, because most dogs in developed countries live inside people’s homes where it is impractical to observe them for extended periods, it is sometimes necessary to develop different kinds of measurement techniques in order to study their behavior. The *Canine Behavioral Assessment and Research Questionnaire* (C-BARQ) is one such technique that relies on measurement by proxy (Hsu and Serpell 2003). In other words, instead of observing and measuring the animal’s behavior directly, the C-BARQ records indirect behavioral information provided by the dog’s owner, guardian, or handler. This approach relies on two important assumptions: first, that the dog’s owner (or handler) knows more about its typical behavior than anybody else does, and second, that this knowledge of the dog’s typical behavior can be extracted from the person in a form that is quantitative, reliable, and reasonably accurate. The first of these assumptions seems intuitively reasonable given that the owner lives with the dog most of the

Table 2.1 Demographic characteristics of the sample of dogs used in the study

Breed	N	%	%	Age (+/- SD)
		Female	Neutered	
Australian Shepherd	406	48.3	74.9	4.28 +/- 3.13
Beagle	188	45.7	78.7	4.80 +/- 3.33
Boston Terrier	62	37.1	85.5	3.87 +/- 2.22
Boxer	206	49.0	74.8	4.39 +/- 2.93
Bulldog	49	57.1	61.2	3.84 +/- 3.04
Cavalier King Charles Spaniel	75	52.0	77.3	3.70 +/- 2.61
Chihuahua	273	45.8	61.2	4.03 +/- 3.23
Cocker Spaniel (American)	213	47.4	78.4	4.48 +/- 3.39
Dachshund	127	42.5	78.0	5.18 +/- 3.88
Dachshund (Miniature)	78	53.8	84.6	4.47 +/- 3.61
Doberman Pinscher	314	50.6	61.5	4.37 +/- 2.94
English Springer Spaniel	138	46.4	61.6	4.73 +/- 3.29
French Bulldog	34	47.1	70.6	3.55 +/- 2.76
German Shepherd	781	51.5	66.6	4.09 +/- 3.12
German Shorthaired Pointer	70	42.9	71.4	4.61 +/- 3.31
Golden Retriever	605	49.1	71.9	4.80 +/- 3.50
Great Dane	138	52.2	77.5	3.84 +/- 2.84
Havanese	121	48.8	58.7	2.94 +/- 2.56
Labrador Retriever	1120	49.7	76.2	4.06 +/- 3.19
Maltese	109	45.0	83.5	4.43 +/- 3.52
Mastiff (English)	196	34.2	54.1	2.53 +/- 2.04
Miniature Schnauzer	119	47.9	79.8	4.91 +/- 3.30
Pembroke Welsh Corgi	85	47.1	84.7	4.69 +/- 3.41
Pomeranian	140	41.4	57.1	4.13 +/- 3.52
Poodle (Standard)	314	45.2	67.8	4.46 +/- 3.28
Poodle (Toy)	70	50.0	61.4	5.47 +/- 4.05
Pug	105	47.6	79.0	4.33 +/- 2.90
Rottweiler	416	47.8	57.7	4.01 +/- 2.80
Shetland Sheepdog	179	48.0	71.5	5.16 +/- 3.37
Shih Tzu	133	45.1	74.4	5.16 +/- 3.76
Siberian Husky	150	47.3	73.3	4.61 +/- 3.41
Yorkshire Terrier	110	43.6	74.5	5.02 +/- 4.32

time and is likely to have observed its reactions and behavior across a wide range every day circumstances. The second assumption is more speculative and requires empirical verification.

The C-BARQ currently consists of 100 questionnaire items that ask respondents to use a series of five point ordinal rating scales (from 0 to 4) to indicate their dogs' typical responses to a variety of everyday situations and stimuli during the recent past. Depending on the type of behaviour being measured, the scales rate either severity (aggression, fear/anxiety, excitability) or frequency (all other categories of behavior) (Duffy and Serpell 2012). Participants are instructed to answer all

questions. However, if they are unable to answer a question because they have never observed the dog in the specified situation, they have the option to select “not observed/not applicable” and the item is then treated as a missing value. Using factor analysis, 68 of the original items were condensed into 11 behavioral factors. Two new factors (*energy* and *dog rivalry*) were added subsequently, and one of the original factors (*dog-directed aggression/fear*) was divided into two (*dog-directed aggression* and *dog-directed fear*) to create a total of 14 factors. This factor structure has been found to be remarkably consistent irrespective of breed, sex, or geographic location (Duffy et al. 2008; Hsu and Serpell 2003; Hsu and Sun 2010; Nagasawa et al. 2011; van den Berg et al. 2006, 2010). Twenty-two miscellaneous items are also included in the C-BARQ as stand-alone behavioral measures. High scores are less favourable for all items and factors with the exception of *trainability*, for which high scores are more desirable. For the purposes of analysis, each dog’s factor score is calculated as the average of its scores for the questionnaire items pertaining to that factor. Breed averages are based on the sum of the individual dog factor scores divided by the value of N for each breed (See Table 2.1).

To date, the various C-BARQ factors and items have been shown to have adequate internal reliabilities (Cronbach’s $\alpha \geq 0.7$), and acceptable test-retest and inter-rater reliabilities (Duffy et al. 2008; Duffy and Serpell 2012; Jakuba et al. 2013). Initially, 7 of the original 11 subscales were validated using a panel of 200 dogs previously diagnosed with specific behavior problems (Hsu and Serpell 2003). More recently, other studies have provided criterion validation of the C-BARQ by demonstrating associations between the various factor and item scores and, for example, training outcomes in working dogs (Duffy and Serpell 2012), the performance of dogs in various standardized behavioral tests (Barnard et al. 2012; De Meester et al. 2008; Svartberg 2005), and neurophysiological markers of canine anxiety and compulsive disorders (Vermeire et al. 2011, 2012).

2.4.2 Results

2.4.2.1 Aggression

Initial factor analysis of C-BARQ questionnaire data extracted three factors that measured different manifestations of aggression in dogs: *Stranger-directed aggression* (10 items), *owner-directed aggression* (8 items) and *dog-directed aggression* (4 items) (Hsu and Serpell 2003). As their names suggest, the first two of these factors measure aggression directed toward either unfamiliar or familiar people, respectively, while the third refers to contexts in which the dog directs aggressive threats or actions toward unknown or unfamiliar dogs. A fourth factor, *dog rivalry* (4 items), was later added to the C-BARQ to cover aggression directed toward other familiar dogs living in the same household (Duffy et al. 2008). Average scores on all of the C-BARQ aggression factors tend to be skewed toward

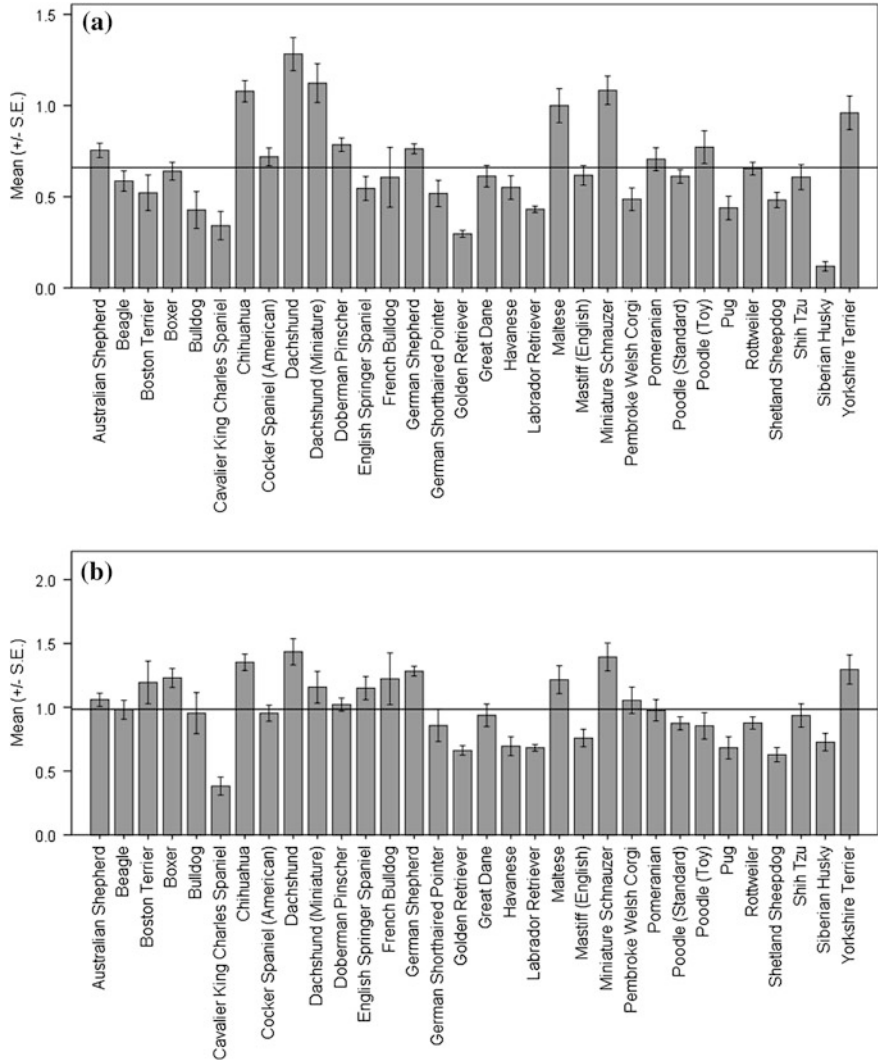


Fig. 2.1 Breed average C-BARQ scores for: **a** *stranger-directed aggression*, **b** *dog-directed aggression*, **c** *owner-directed aggression*, and **d** *dog rivalry* in the 30 popular AKC breeds (including miniature and toy variants of the dachshund and poodle). The horizontal line represents the average score for this population of dogs

zero (especially in the case of *owner-directed aggression*), hence the expanded Y axes in the charts (Fig. 2.1a–d). This probably reflects a history of relatively intense selection against disruptive levels of aggression in dogs, particularly when directed toward human members of the same household. Despite the limited variation in the data, breed differences for all four factors are statistically highly significant (Kruskal-Wallis P values < 0.0001).

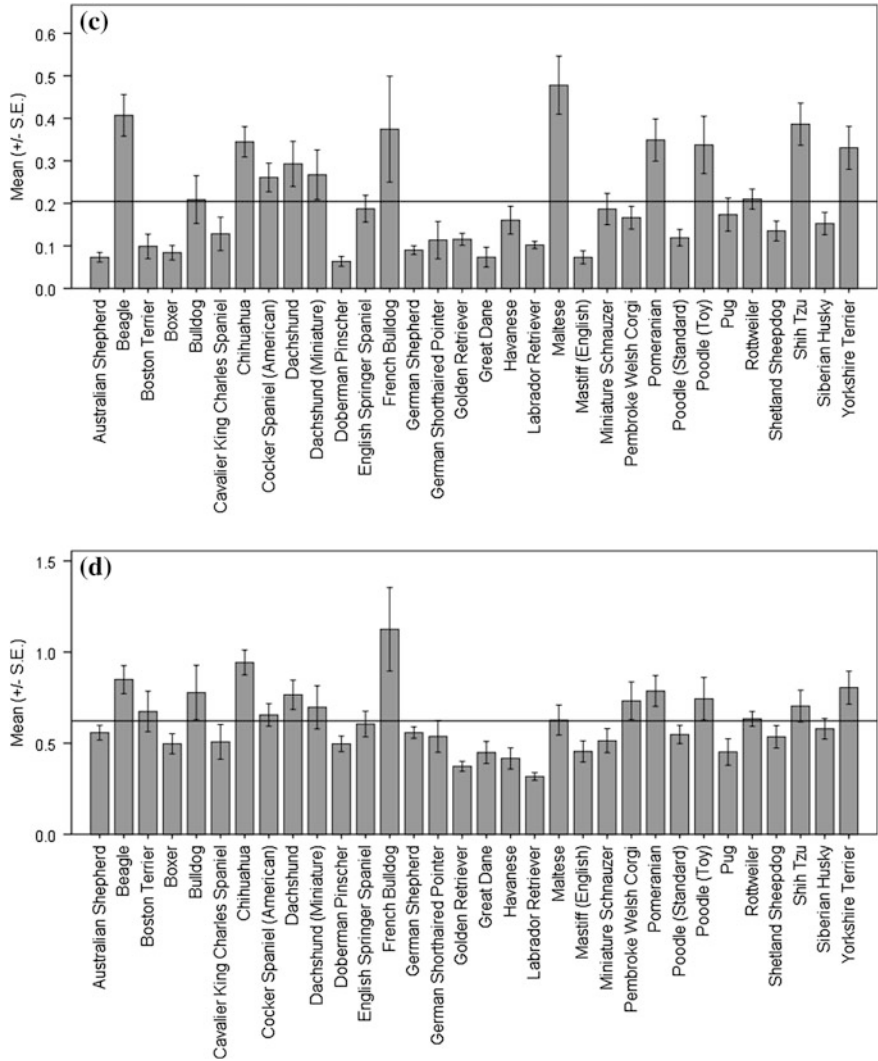


Fig. 2.1 continued

For *stranger-directed aggression*, several small or toy breeds stand out as having scores above the population average (e.g. Chihuahua, standard and miniature dachshund, Maltese, miniature schnauzer, toy poodle, and Yorkshire terrier). Two guard dog breeds, the Doberman and the German Shepherd, also obtain somewhat high scores on this factor, as does the Australian shepherd. In contrast, the bulldog, cavalier King Charles spaniel, golden retriever, Labrador retriever, pug, and Siberian husky all obtain below-average scores. A rather similar array of

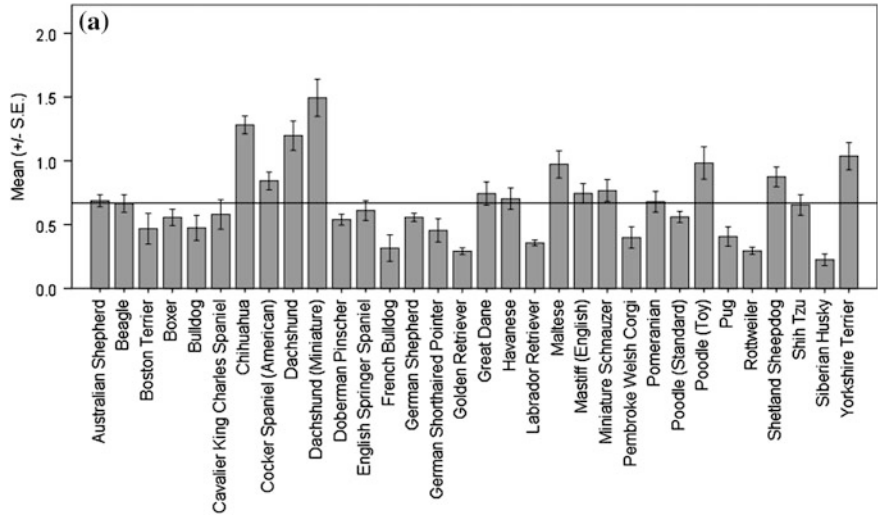


Fig. 2.2 Breed average C-BARQ scores for: **a** *stranger-directed fear*, **b** *dog-directed fear*, **c** *nonsocial fear*, **d** *separation related problems*, and **e** *touch sensitivity* in the 30 most popular AKC breeds

high and low breeds characterizes the *dog-directed aggression* factor, although in this case the boxer, English springer spaniel and French bulldog also join the ranks of the more aggressive breeds.

The *owner-directed aggression* and *dog rivalry* factors also show considerable overlap in terms of breed distribution. Again, small or toy breeds tend to score highest for these two types of aggression, particularly the beagle, Chihuahua, American cocker spaniel, both dachshunds, French bulldog, Maltese, Pomeranian, toy poodle, shi tzu and Yorkshire terrier, whereas all of the large or medium-sized breeds tend to score low on these factors.

2.4.2.2 Anxiety and Fear

Four distinct C-BARQ factors measure various dimensions of anxiety or fear. They include *stranger-directed fear* (4 items), (*unfamiliar*) *dog-directed fear* (4 items), *nonsocial fear* (e.g. loud noises, novel objects, etc.—6 items) and *separation-related behavior* (anxiety—8 items). A fifth factor, *touch sensitivity* (4 items), also appears to be an expression of fear in relation to being touched, handled, or groomed. Breed differences on all of these factors were highly significant (Kruskal-Wallis *P* value <0.0001) and, as with the aggression factors, scores for the various fear factors tend to be skewed toward zero; again presumably an effect of generations of selection in favor dogs that are less neophobic than their wild ancestor.

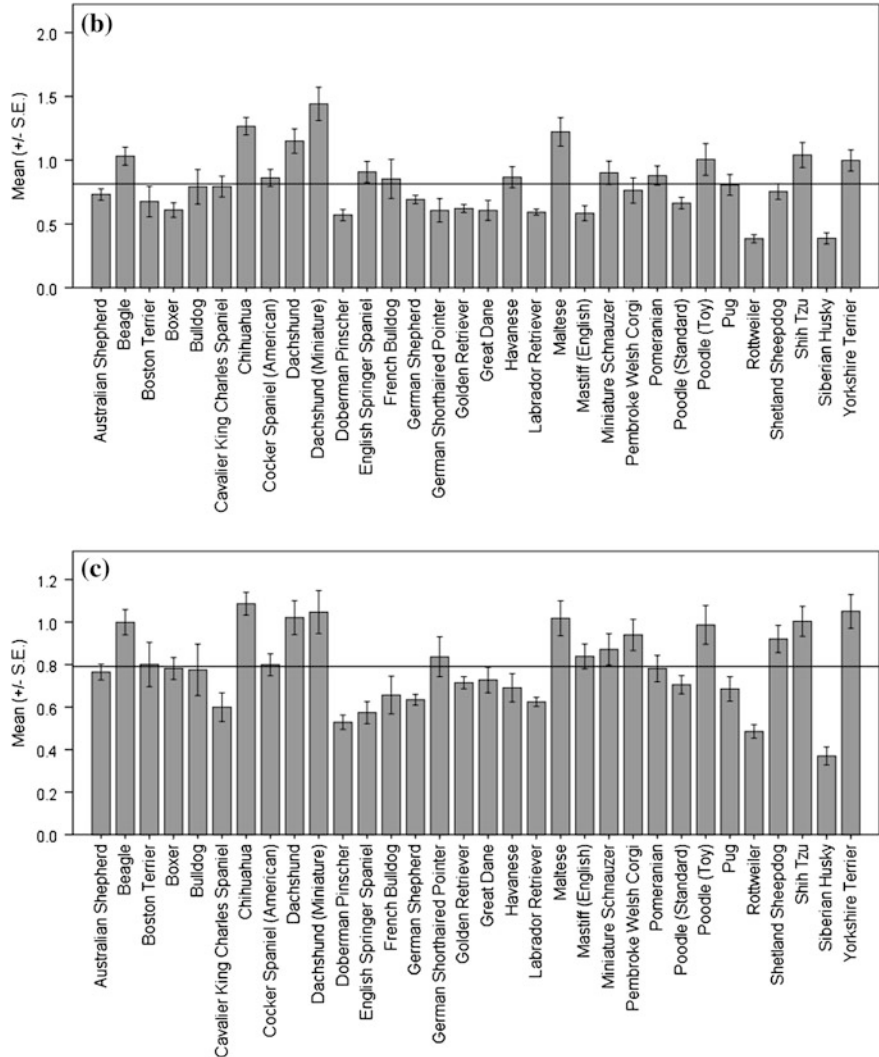


Fig. 2.2 continued

The most striking observation to be made from a cursory examination of the charts for these behaviors is the consistency with which the same group of breeds scores higher than the population average across the different contexts (Fig. 2.2a–e). Almost without exception they belong to either small or toy breeds, and, even within breeds, the dwarf or miniature versions (e.g. miniature dachshund and toy poodle) are significantly more fearful or anxious than their larger counterparts. Six of these breeds (Chihuahua, dachshund, miniature dachshund, Maltese, toy poodle, and Yorkshire terrier) score high in all five contexts, and two more (beagle and shih tzu) score high in four out of five.

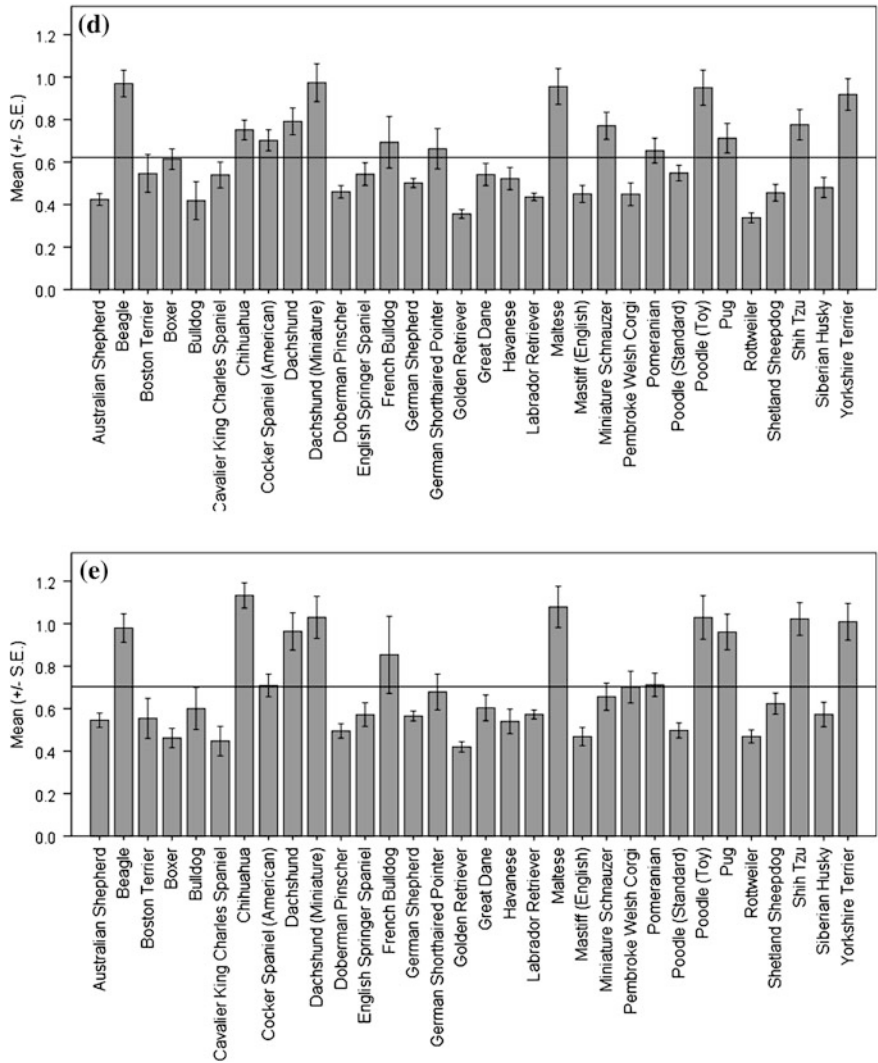


Fig. 2.2 continued

In contrast, many of the brachycephalic breeds (Boston terriers, bulldogs, French bulldogs, and pugs) tend to obtain low scores for fear, as do the golden retriever, Labrador retriever, rottweiler, and Siberian husky.

2.4.2.3 Attachment and Attention-Seeking

The C-BARQ *attachment and attention-seeking* factor comprises six questionnaire items. Dogs that score high on this factor tend to stay close to their owners, solicit

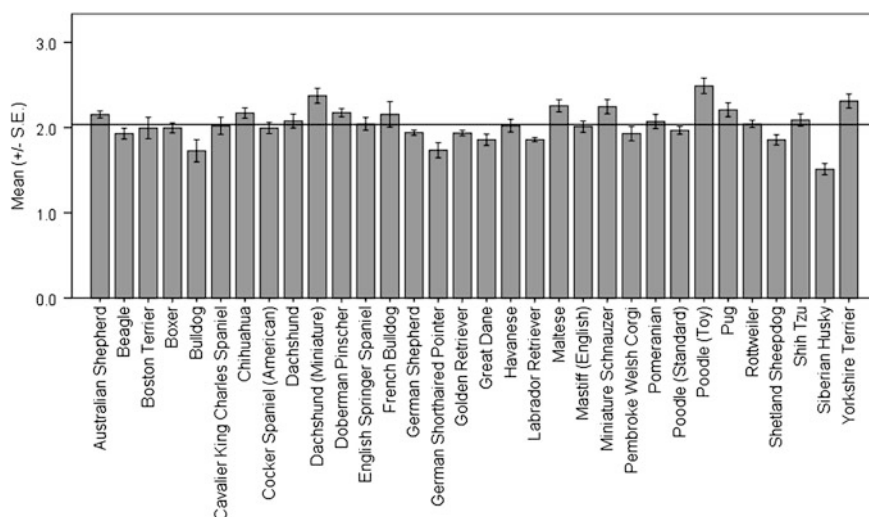


Fig. 2.3 Breed average C-BARQ scores for *attachment/attention-seeking* in the 30 most popular AKC breeds (including miniature and toy variants of the dachshund and poodle)

more affection and attention, and display agitation when the owner gives attention to third parties, such as other people or dogs (Hsu and Serpell 2003). Although breed differences for this factor are still highly significant statistically (Kruskal-Wallis P Value <0.0001), it is apparent from the chart (Fig. 2.3) that only a small number of breeds diverge markedly from the population average compared with most of the other C-BARQ factors, and only one—the Siberian husky—stands out. This breed is often described in the literature as being somewhat aloof, and its low score on this factor confirms this anecdotal observation. Interestingly, the breeds that tend to score higher for *attachment and attention-seeking* tend to be the same small or toy breeds that score high on the various aggression and fear factors (e.g. Chihuahua, miniature dachshund, Maltese, toy poodle and Yorkshire terrier). This might suggest that the *attachment/attention-seeking* behavior of these breeds is partly motivated by fear or anxiety.

2.4.2.4 Predatory Chasing

The C-BARQ *chasing* factor refers to the tendency of some dogs to display predatory chasing of cats, squirrels, birds, and/or other small animals, when given the opportunity. It comprises 4 questionnaire items. Again, there are large and highly significant breed differences in the expression of this trait (Kruskal-Wallis $P <0.0001$) with some breeds exhibiting high average scores (German short-haired pointer, miniature schnauzer, and Siberian husky) and others low (bulldog, Chihuahua, English mastiff, pug, and shih tzu) (see Fig. 2.4). Although the three

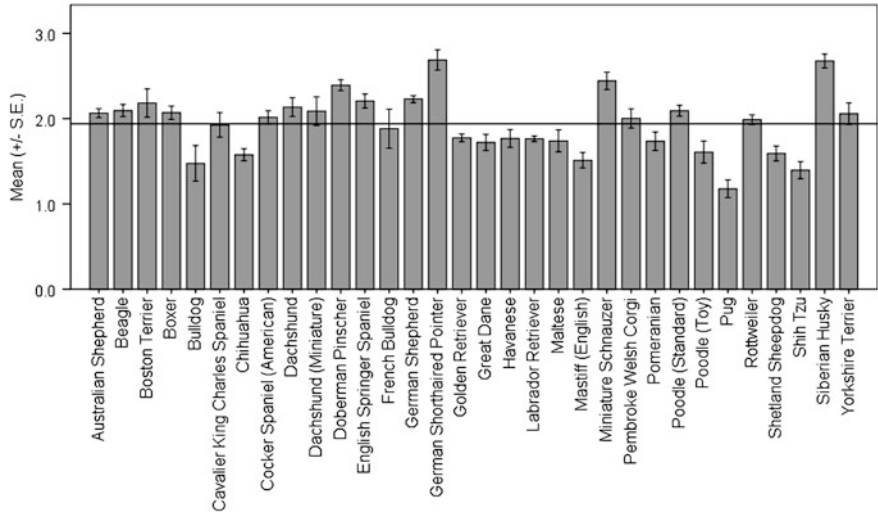


Fig. 2.4 Breed average C-BARQ scores for *chasing* in the 30 most popular AKC breeds (including miniature and toy variants of the dachshund and poodle)

highest scoring breeds have relatively little in common in other respects, all of them are known historically for their role in hunting or vermin control and their strong predatory drive. In the case of the lowest scoring breeds, anatomical and physical constraints may limit these dogs’ ability to chase potential prey species, even if they possess the inclination to do so.

2.4.2.5 Excitability

Dogs that obtain a high score on the C-BARQ *excitability* factor (6 items) tend to display strong reactions to potentially exciting or arousing events, such as going for walks or car trips, doorbells ringing, the arrival of visitors, or the owner arriving home after a period of absence. Such dogs also have difficulty calming down after such events (Hsu and Serpell 2003). As with *attachment and attention-seeking*, there is a surprising degree of uniformity among the selected breeds respecting their average scores on this factor, and no particular breed or breeds stands out, although there are highly significant breed differences (Kruskal-Wallis $P < 0.0001$). The three lowest scoring breeds (bulldog, English mastiff, and Siberian husky) are well known for being relatively ‘laid back’, and many of the high scoring breeds belong to the same group of small or toy breeds that also tend to score high for aggression, fearfulness, and *attachment and attention-seeking* (e.g. both dachshunds, Maltese, toy poodle, and Yorkshire terrier). In addition, the Pomeranian, miniature schnauzer, and many of the brachycephalic breeds (Boston terrier, boxer, French bulldog, and pug) tend to obtain higher than average scores for *excitability* (Fig. 2.5).

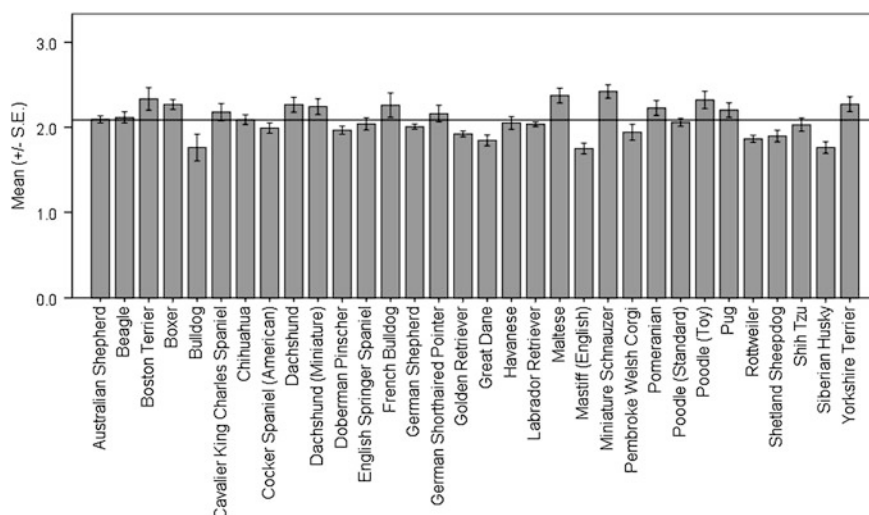


Fig. 2.5 Breed average C-BARQ scores for *excitability* in the 30 most popular AKC breeds (including miniature and toy variants of the dachshund and poodle)

2.4.2.6 Energy

The C-BARQ *energy* factor consists of just two questionnaire items: “playful, puppyish, boisterous” and “active, energetic, always on the go.” Although the majority of the selected breeds show average energy levels close to the population mean for this factor, several breeds stand out (Kruskal-Wallis $P < 0.0001$). In particular, the Australian shepherd, boxer, Doberman pinscher, German short-haired pointer and Maltese obtain relatively high average scores for *energy*, while the bulldog, Great Dane and English mastiff obtain relatively low scores (Fig. 2.6). With the exception of the Maltese, most of the former are originally working breeds so an abundance of energy may have been selected for. Among the latter, the bulldog’s various medical issues may account for its lack of energy, and the two giant breeds may also be lethargic for morphological reasons.

2.4.2.7 Trainability

Eight questionnaire items comprise the C-BARQ *trainability* factor. Dogs that score high on this factor are attentive to their owners and willing to obey basic commands, are not easily distracted, respond positively to correction, tend to be fast learners, and readily fetch or retrieve thrown objects/toys (Hsu and Serpell 2003). As with all C-BARQ traits, there are highly significant differences across the 30 most popular breeds in the expression of this factor (Kruskal-Wallis $P < 0.0001$), with some breeds (e.g. Australian shepherd, Doberman pinscher, English springer spaniel, golden and Labrador retrievers, standard poodle,

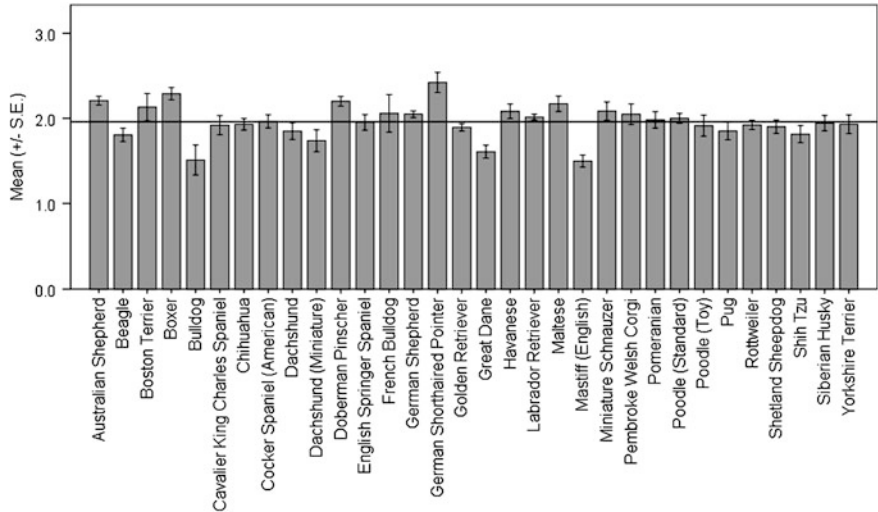


Fig. 2.6 Breed average C-BARQ scores for *energy* in the 30 most popular AKC breeds (including miniature and toy variants of the dachshund and poodle)

rottweiler and Shetland sheepdog) tending to obtain high average scores for *trainability*, while other breeds (e.g. beagle, dachshund, pug, and Yorkshire terrier) obtain relatively low scores (Fig. 2.7). In general, most of the breeds classified as belonging to the AKC’s hound, toy, terrier and non-sporting groups fall below the population average for this trait, whereas breeds belonging to the sporting and herding groups tend to be above the average. Breeds in the heterogeneous “working dog” group are inconsistent, with some obtaining a high average score (rottweiler) and others a low one (Siberian husky).

2.4.2.8 Miscellaneous Problems: Persistent Barking, House Soiling, Escaping/Roaming

In addition to the main factors, the C-BARQ also comprises a number of individual questionnaire items that were retained as sources of information about relatively specific patterns of behavior. Some of these items also reveal pronounced differences in behavior across breeds. For example, the item, “*barks persistently when alarmed or excited*” reveals striking differences across breeds (Fig. 2.8, Kruskal-Wallis $P < 0.0001$). All the small or toy breeds previously associated with aggression, fearfulness, *attachment and attention seeking*, and *excitability* exhibit higher than average levels of *persistent barking*, and in this they are joined by the miniature schnauzer and Shetland sheepdog, which displays the highest level of this behavior of any of the sampled breeds. Conversely, most of the larger and brachycephalic breeds display relatively low levels of barking, and the Siberian husky rarely barks.

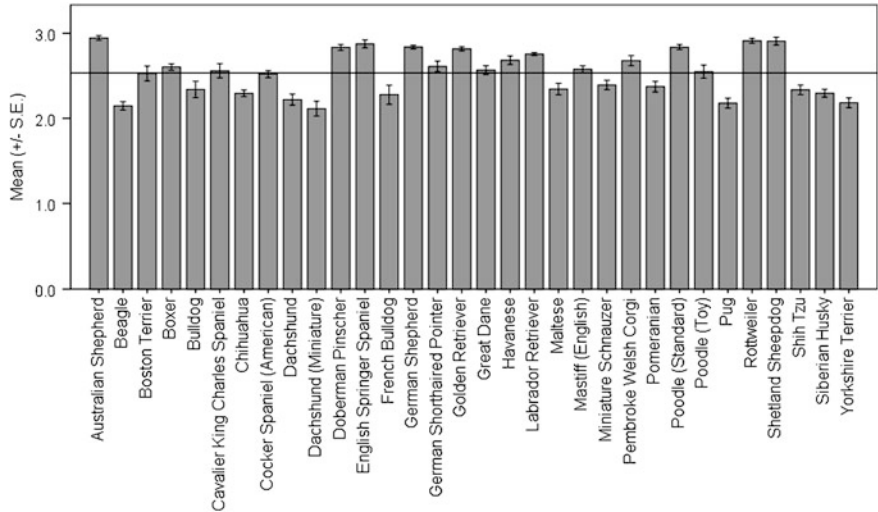


Fig. 2.7 Breed average C-BARQ scores for *trainability* in the 30 most popular AKC breeds (including miniature and toy variants of the dachshund and poodle)

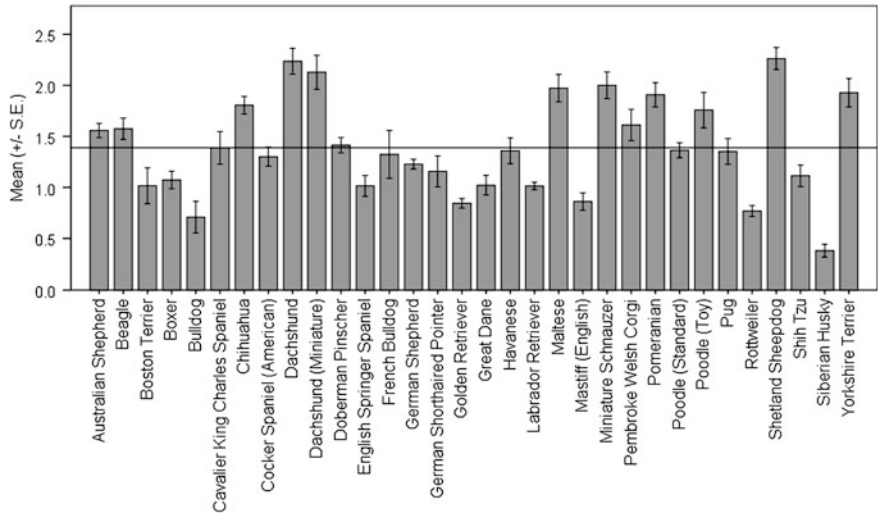


Fig. 2.8 Breed average C-BARQ scores for *persistent barking* in the 30 most popular AKC breeds (including miniature and toy variants of the dachshund and poodle)

Another C-BARQ ‘miscellaneous’ item, “*urinates when left alone at night or during the daytime,*” reveals an even more striking disparity between large and small breed dogs (Kruskal-Wallis $P < 0.0001$). With the exception of the beagle and the bulldog, all of the breeds with higher than average scores for this behavior are in the toy or miniature size range. Conversely, apart from the cavalier King

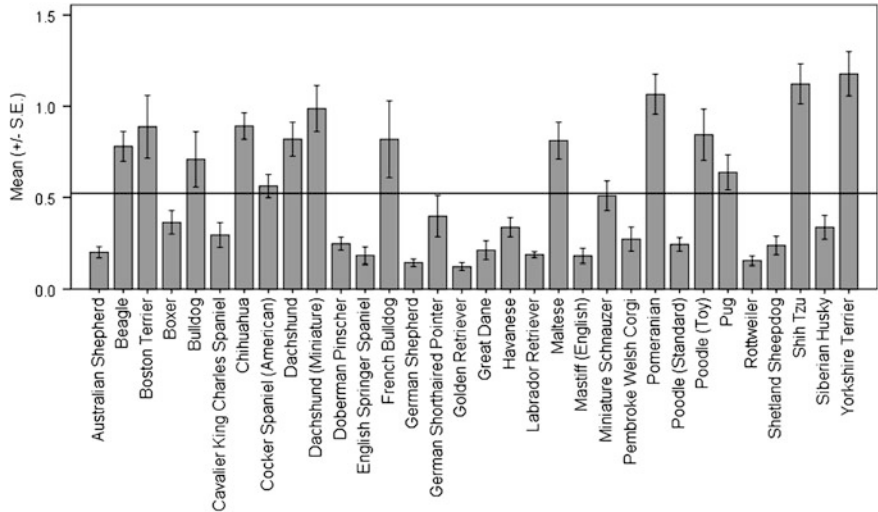


Fig. 2.9 Breed average C-BARQ scores for *urination when left alone* in the 30 most popular AKC breeds (including miniature and toy variants of the dachshund and poodle)

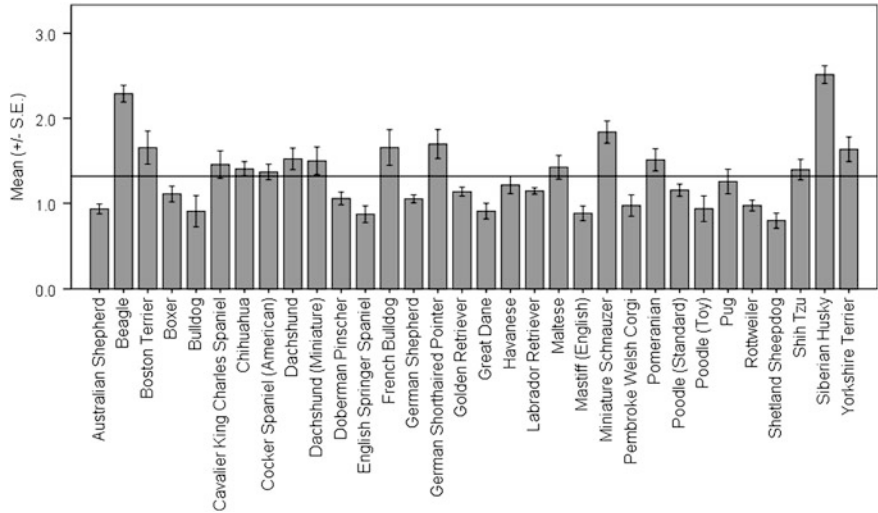


Fig. 2.10 Breed average C-BARQ scores for *escaping/roaming* in the 30 most popular AKC breeds (including miniature and toy variants of the dachshund and poodle)

Charles spaniel, Havanese and Shetland sheepdog, all of the low scoring breeds are medium to large breed dogs (Fig. 2.9).

Finally, the item, “*escapes or would escape from home or yard, given the chance,*” points to a distinctive flight risk for beagles and Siberian huskies compared with most of the other sampled breeds, as well as some risk for Boston Terriers, French bulldogs, German short-haired pointers, miniature schnauzers, and Yorkshire terriers (Fig. 2.10, Kruskal-Wallis $P < 0.0001$).

2.5 Discussion

In general respects, the observed breed differences in behavior in the present study resembled some of those obtained in previous analyses. For example, Hart and Hart (1985), Ley et al. (2009) and Turcsán et al. (2011) also found that herding and sporting dog breeds tended to obtain higher scores for *trainability* (although measured in different ways), and Ley et al. (2009) also detected positive associations between small body size and *neuroticism* (i.e. anxiety-related behavior) and less sociable personality. McGreevy et al. (2013) detected similar correlations, but this study was based on a comparable dataset to the one we used, so some overlap is inevitable. While replication of results by independent studies suggests that these apparent breed differences in behavior reflect some sort of underlying biological reality, it remains unclear the extent to which they are caused by specific genes; differential histories of human selection for functional traits; differences in the early environment, socialization and training of dogs of different breeds; and/or systematic biases in how the owners of different breeds evaluate them in behavioral surveys. Furthermore, it must be emphasized that individual variation in C-BARQ scores within breeds are often as great or greater than the differences between breeds, and this limits our ability to talk about breed-specific or breed-typical personality traits based on these kinds of measures.

Genes have certainly been demonstrated to play important roles in the expression of behavior in dogs (Scott and Fuller 1965; Mackenzie et al. 1986; Serpell 1987). Attempts to estimate the heritability of canine temperament and performance traits have typically obtained highest values for traits reflecting anxiety/fearfulness, sociability, boldness, and various forms of aggression (Goddard and Beilharz 1982; Liinamo et al. 2007; Pérez-Guisado et al. 2006; Saetre et al. 2006; Scott and Bielefeldt 1976; Willis 1995; Wilson and Sundgren 1998). In the present study, a possible direct genetic affect may help to account for the consistently higher levels of fearfulness and reactivity in the small or toy breeds of dog. For example, molecular geneticists have been able to identify alleles associated with the *Insulin-like Growth Factor-1 (IGF1)* gene that are present in all toy or miniature dog breeds, but absent from wolves and other wild canids, and very rare among large breed dogs (Sutter et al. 2007; Gray et al. 2010). Earlier studies also found significantly lower levels of circulating *IGF1* in the serum of miniature poodles compared with standard poodles, and in small breed dogs compared with larger ones (Eigenmann et al. 1984; Guler et al. 1989). More interestingly, in a study of German shorthaired pointers deliberately selected for nervousness/fearfulness,² an inverse linear correlation was detected between the severity of the dogs' fearful behavior and their serum *IGF1* levels (Uhde et al. 1992). This might suggest that, in addition to affecting growth and stature, the *IGF1* gene has pleiotropic effects on temperament that tend to make small dogs more fearful,

² This population of nervous pointers was created by researchers during the 1960s to serve as an animal model of human anxiety disorders.

more reactive and excitable, more likely to display defensive aggression and anxious attachment, and more likely to urinate when left alone. A genetic correlation between size and temperament might make sense from an evolutionary perspective since smaller individuals are likely to be more vulnerable than larger ones. However, it is also possible that the observed correlation between small size and fearful/anxious temperament is due to an environmental factor. Small breed dogs may learn to be more risk averse due to their greater vulnerability to harm or injury, and/or the owners and breeders of such dogs may be more tolerant of their behavioral issues because of their smaller size, and/or they may provide them with less early exposure to unfamiliar environments and social interactions during the sensitive period for socialization, thereby rendering them more fearful and anxious. Choosing between these various alternatives is beyond the scope of the present study but future investigations of this apparent ‘small breed effect’ might benefit from comparing small or toy breeds that show the effect consistently (e.g. Chihuahua, dachshund, toy poodle) with those that don’t (e.g. cavalier King Charles spaniel, Havanese).

Less specific genetic factors may also help to explain the relatively eccentric C-BARQ factor and item scores for the Siberian husky. This breed has been classified as an ‘ancient breed’ based on its apparent degree of genetic relatedness to the wolf (Parker et al. 2004). Its high scores for *chasing* and *escaping/roaming*, and low scores for *trainability*, *attachment/attention-seeking* and *persistent barking* certainly tend to render it more wolflike in behavior than any of the other popular breeds in our sample, although these traits might also reflect evolutionary convergence rather than genetic relatedness. In addition, it should be emphasized that this breed also displays exceptionally low levels of both social and *nonsocial* fear: a characteristic that would generally be considered atypical of wolves.

Several of the observed breed differences in the study are most plausibly accounted for by reference to the original functional (working) roles of the breeds involved. For example, the relatively low scores for the fear-related factors in Doberman pinschers, German shepherds, and rottweilers, and the high scores of two of these breeds for *stranger-directed aggression* make sense in the context of their widespread use as guard dogs. Similarly, the beagle’s apparent tendency to escape and roam is probably a legacy of its hound-like propensity to hunt by ‘following its nose’, while the high scores obtained for *chasing* in German short-haired pointers and miniature schnauzers may also reflect past selection for attention to, and pursuit of, potential prey. The breed differences identified for the *trainability* factor also fit within a functional framework. Because they traditionally performed relatively complex tasks in tandem with human partners, sporting and herding breeds have presumably been selected for social-cognitive skills that enhance their working performance. Such skills would likely include many of the elements of the *trainability* factor such as attention and focus, responsiveness to signals and directions provided by humans, and quickness to learn. In contrast, toy breeds are not required to work, and hounds and terriers typically work more or less independently of human direction.

Some breeds may also suffer from straightforward morphological and anatomical constraints on their behavior. The low scores for *chasing* and *energy* of the some of the brachycephalic and giant breeds are likely to be at least partly a consequence of their lack of stamina due either to their exceptionally large body size or congenital deformation of the respiratory tract and axial skeleton.

With respect to the issue of dog breed popularity, the current findings may also help to explain why Ghirlanda et al. (2013) were unable to detect any consistent relationship between popularity and behavioral characteristics in their study. Miniature and toy breed dogs have grown markedly in popularity throughout the last decade (Euromonitor International 2013), despite the evidence provided here that they are likely to display a range of more severe behavioral problems than larger breeds. Since the effects of canine behavioral problems, such as aggression, excitability, or house soiling, are likely to scale with body size, it follows that dog owners are going to be more tolerant of the same behavior problems produced by a small breed dog compared with a larger one. In which case, any underlying association between breed popularity and behavior will tend to be confounded by the effects of body size.

Finally, these results provide support for the use of the C-BARQ as a behavioral assay for measuring behavioral phenotypes in dogs. According to some authorities, the field of behavioral genetics has been held back in recent years by the lack of reliable behavioral phenotyping techniques (Hall and Wynne 2012; Spady and Ostrander 2008). Hopefully, future genetic association studies will help to determine whether the C-BARQ or other behavioral measurement techniques will be able to fulfill this important role.

References

- Barnard, S., Siracusa, C., Reisner, I., Valsecchi, P., & Serpell, J. A. (2012). Validity of model devices used to assess canine temperament in behavioral tests. *Applied Animal Behaviour Science*, 138, 79–87.
- Boyko, A. R., Quignon, P., Li, L., et al. (2010). A simple genetic architecture underlies morphological variation in dogs. *PLoS Biology*, 8, e1000451.
- 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. *Research in Veterinary Science*, 66, 73–76.
- Clutton-Brock, J. (1995). Origins of the dog: Domestication and early history. In J. Serpell (Ed.), *The domestic dog, its evolution, behaviour and interactions with people* (pp. 8–20). Cambridge: Cambridge University Press.
- Coppinger, R., & Schneider, R. (1995). Evolution of working dogs. In J. Serpell (Ed.), *Domestic dog, its evolution, behaviour and interactions with people* (pp. 22–47). Cambridge: Cambridge University Press.
- De Meester, R., De Bacquer, D., Peremans, K., Vermeire, S., Planta, D. J., Coopman, F., et al. (2008). A preliminary study on the use of the socially acceptable behaviour test as a test for shyness/confidence in the temperament of dogs. *Journal of Veterinary Behavior*, 3, 161–170.
- Duffy, D. L., Hsu, Y., & Serpell, J. A. (2008). Breed differences in canine aggression. *Applied Animal Behaviour Science*, 114, 441–460.

- Duffy, D. L., & Serpell, J. A. (2012). Predictive validity of a method for evaluating temperament in young guide and service dogs. *Applied Animal Behaviour Science*, 138, 99–109.
- Eigenmann, J. E., Patterson, D. F., Zapf, J., & Froesch, E. R. (1984). Insulin-like growth factor I in the dog: A study in different dog breeds and in dogs with growth hormone elevation. *Acta Endocrinology*, 105, 294–301.
- Euromonitor International. (2013). Passport global market information database, Retrieved September 11 2013.
- Ghirlanda, S., Acerbi, A., Herzog, H., & Serpell, J. A. (2013). Fashion vs. function in cultural evolution: The case of dog breed popularity. *PLoS ONE*, 8(9), e74770.
- Goddard, M. E., & Beilharz, R. G. (1982). Genetic and environmental factors affecting the suitability of dogs as guide dogs for the blind. *Theoretical and Applied Genetics*, 62, 97–102.
- Gray, M. M., Sutter, N. B., Ostrander, E. A., & Wayne, R. K. (2010). The IGF1 small dog haplotype is derived from middle eastern gray wolves. *BMC Biology*, 8, 16.
- Guler, H-P., Binz, K., Eigenmann, E., Jaggi, S., Zimmermann, D., Zapf, J., & Froesch, E. R. (1989). Small stature and insulin-like growth factors: Prolonged treatment of mini-poodles with recombinant human insulin-like growth factor I. *Endocrinologica (Copen.)*, 121, 456–464.
- Hall, N. J., & Wynne, C. D. (2012). The canid genome: Behavioral geneticists' best friend? *Genes Brain and Behavior*, 11, 889–902.
- Hart, B., & Hart, L. (1985). Selecting pet dogs on the basis of cluster-analysis of breed behavior profiles and gender. *JAVMA*, 186, 1181–1185.
- Hart, B., & Miller, M. F. (1985). Behavioral profiles of dog breeds. *JAVMA*, 186, 1175–1180.
- Herzog, H. (2006). Forty-two thousand and one Dalmatians: Fads, social contagion, and dog breed popularity. *Society and Animals*, 14, 383–397.
- Hsu, Y., & Serpell, J. A. (2003). Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. *JAVMA*, 223, 1293–1300.
- Hsu, Y., & Sun, L. (2010). Factors associated with aggressive responses in pet dogs. *Applied Animal Behaviour Science*, 123, 108–123.
- Jakuba, T., Polcova, Z., Fedakova, D., Kottferova, J., Marekova, J., Fejsakova, M., et al. (2013). Differences in evaluation of a dog's temperament by individual members of the same household. *Society and Animals*, 21, 582–589.
- Jones, A. C., & Gosling, S. D. (2005). Temperament and personality in dogs (*Canis familiaris*): A review and evaluation of past research. *Applied Animal Behaviour Science*, 95, 1–53.
- Jones, P., Chase, K., Martin, A., Davern, P., Ostrander, E. A., & Lark, K. G. (2008). Single-nucleotide-polymorphism-based association mapping of dog stereotypes. *Genetics*, 179, 1033–1044.
- Larson, G., Karlsson, E. K., Perri, A., et al. (2012). Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences USA*, 109, 8878–8883.
- Ley, J. M., Bennett, P. M., & Coleman, G. J. (2009). A refinement and validation of the Monash Canine Personality Questionnaire (MCPQ). *Applied Animal Behaviour Science*, 116, 220–227.
- Liinamo, A-E., van den Berg, L., Leegwater, P. A. J., et al. (2007). Genetic variation in aggression-related traits in golden retriever dogs. *Applied Animal Behaviour Science*, 104, 95–106.
- Martin, P., & Bateson, P. P. G. B. (1993). *Measuring behaviour*. Cambridge: Cambridge University Press.
- MacKenzie, S. A., Oltenacu, E. A. B., & Houpt, K. A. (1986). Canine behavioral genetics—a review. *Applied Animal Behaviour Science*, 15, 365–393.
- McGreevy, P., Georgevsky, D., Carrasco, J., Valanzuela, M., Duffy, D. L., & Serpell, J. A. (2013). Dog behavior co-varies with height, bodyweight and skull shape. *PLoS ONE*, 8(12), e80529.

- Nagasawa, M., Tsujimura, A., Tateishi, K., Mogi, K., Ohta, M., Serpell, J. A., & Kikusui, T. (2011). Assessment of the factorial structure of the C-BARQ in Japan. *Journal of Veterinary Medical Science*, 73, 869–875.
- Notari, L., & Goodwin, D. (2007). A survey of behavioural characteristics of pure-bred dogs in Italy. *Applied Animal Behaviour Science*, 103, 118–130.
- Ostrander, E. A. (2007). Genetics and the shape of dogs. *American Scientist*, 95, 406–413.
- Ostrander, E. A., & Galibert, F. (2006). Forward. In E. A. Ostrander, U. Giger & K. Lindblad-Toh (Eds.), *The dog and its genome* (pp. xiii–xix). Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.
- Parker, H. G., Kim, L. V., Sutter, N. B. et al. (2004). Genetic structure of the purebred domestic dog. *Science*, 304, 1160–1164.
- Pérez-Guisado, J., Lopez-Rodríguez, R., & Munoz-Serrano, A. (2006). Heritability of dominant-aggressive behaviour in English Cocker Spaniels. *Applied Animal Behaviour Science*, 100, 219–227.
- Ritvo, H. (1987). *The animal estate: English and other creatures in the Victoria age*. Cambridge, MA: Harvard University Press.
- Saetre, P., Strandberg, E., Sundgren, P-E., Pettersson, U., Jazin, E., & Bergström. (2006). The genetic contribution to canine personality. *Genes, Brain and Behavior*, 5, 240–248.
- Sampson, J., & Binns, M. M. (2006). The Kennel club and the early history of dog shows and breed clubs. In E. A. Ostrander, U. Giger & K. Lindblad-Toh (Eds.), *The dog and its genome* (pp. 19–30). Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.
- Scott, J. P., & Bielfelt, S. W. (1976). Analysis of the puppy testing program. In C. J. Pfaffenberger, J. P. Scott, J. L. Fuller, B. E. Ginsburg & S. W. Bielfelt (Eds.), *Guide dogs for the blind: Their selection, development and training* (pp. 39–75). Amsterdam: Elsevier.
- Scott, J. P., & Fuller, J. L. (1965). *Genetics and the social behavior of the dog*. Chicago: Chicago University Press.
- Serpell, J. A. (1987). The influence of inheritance and environment of canine behaviour: Myth and fact. *Journal of Small Animal Practice*, 22, 949–766.
- Serpell, J. A. (1995). The hair of the dog. In J. A. Serpell (Ed.), *The domestic dog: Its evolution, behaviour and interactions with people* (pp. 258–264). Cambridge: Cambridge University Press.
- Serpell, J. A., & Hsu Y. (2001). Development and validation of a novel method for evaluating behavior and temperament in guide dogs. *Applied Animal Behaviour Science*, 72, 347–364.
- Serpell, J. A., & Hsu, Y. (2005). Effects of breed, sex, and neuter status on trainability in dogs. *Anthrozoös*, 18, 196–207.
- Spady, T. C., & Ostrander, E. A. (2008). Canine behavioral genetics: Pointing out the phenotypes and herding up the genes. *The American Journal of Human Genetics*, 82, 10–18.
- Sutter, N. B., Bustamante, C. D., Chase, K., et al. (2007). A single IGF1 allele is a major determinant of small size in dogs. *Science*, 316, 112–115.
- Svartberg, K. (2005). A comparison of behaviour in test and in everyday life: Evidence of three consistent boldness-related personality traits in dogs. *Applied Animal Behaviour Science*, 91, 103–128.
- Svartberg, K. (2006). Breed-typical behavior in dogs—historical remnants or recent constructs? *Applied Animal Behaviour Science*, 96, 293–313.
- Svartberg, K., & Forkman, B. (2002). Personality traits in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science*, 79, 133–155.
- Takeuchi, Y., & Mori, Y. (2006). A comparison of the behavioral profiles of purebred dogs in Japan to profiles of those in the United States and the United Kingdom. *The Journal of Veterinary Medical Science*, 68, 789–796.
- Thalman, O., Shapiro, B., Cui, P., et al. (2013). Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science*, 342, 871–874.
- Trut, L., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: The domesticated fox as a model. *Bioessays*, 31, 349–360.

- Turcsán, B., Kubinyi, E., & Miklósi, A. (2011). Trainability and boldness traits differ between dog breed clusters based on conventional breed categories and genetic relatedness. *Applied Animal Behaviour Science*, 132, 61–70.
- Uhde, T. W., Malloy, L. C., & Slate, S. O. (1992). Fearful behavior, body size, and serum IGF-I levels in nervous and normal pointer dogs. *Pharmacology Biochemistry and Behavior*, 43, 263–269.
- van den Berg, L., Schilder, M. B. H., de Vries, H., Leegwater, P. A. J., & van Oost, B. A. (2006). Phenotyping of aggressive behavior in golden retriever dogs with a questionnaire. *Behavior Genetics*, 36, 882–902.
- van den Berg, S. M., Heuven, H. C. M., Van den Berg, L., Duffy, D. L., & Serpell, J. A. (2010). Evaluation of the C-BARQ as a measure of stranger-directed aggression in three common dog breeds. *Applied Animal Behaviour Science*, 124, 136–141.
- Vaysse, A., Ratnakumar, A., & Derrien, T. et al. (2011). Identification of genomic regions associated with phenotypic variation between dog breeds using selection mapping. *PLOS Genetics*, 7, e1002316.
- Vermeire, S. T., Audenaert, K. R., & De Meester, R. H. et al. (2011). Neuro-imaging the serotonin 2A receptor as a valid biomarker for canine behavioral disorders. *Research in Veterinary Science*, 91, 465–472.
- Vermeire, S. T., Audenaert, K. R., & De Meester, R. H. et al. (2012). Serotonin 2A receptor, serotonin transporter and dopamine transporter alterations in dogs with compulsive behavior as a promising model for human obsessive-compulsive disorder. *Psychiatric Research*, 201, 78–87.
- Willis, M. B. (1995). Genetics of dog behaviour with particular reference to working dogs. In Serpell J (ed), *The domestic dog, its evolution, behaviour and interactions with people* (pp. 51–64). Cambridge: Cambridge University Press.
- Wilsson, E., & Sundgren, P-E. (1998). Behaviour test for eight-week old puppies—heritabilities of tested behaviour traits and its correspondence to later behaviour. *Applied Animal Behaviour Science*, 58, 151–162.
- Young, A., & Bannasch, D. (2006). Morphological variation in the dog. In E. A. Ostrander, U. Giger, K. Lindblad-Toh (Eds.), *The dog and its genome* (pp. 47–65). Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.