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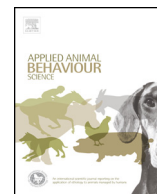


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Behavioral differences among breeds of domestic dogs (*Canis lupus familiaris*): Current status of the science

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ABSTRACT

In both popular media and scientific literature, it is commonly stated that breeds of dogs differ behaviorally in substantial, consistent and predictable ways. Since the mid-twentieth century, scientists have asked whether meaningful behavioral differences exist between breeds of dogs. Today, there are over 1000 identified dog breeds in the world, but to date, fewer than one-quarter of these are represented in studies investigating breed-specific behavioral differences. We review here scientific findings of breed differences in behavior from a wide range of methodologies with respect to both temperament traits and cognitive abilities to determine whether meaningful differences in behavior between breeds have been established. Although there is convincing scientific evidence for reliable differences between breeds and breed groups with respect to some behaviors (e.g., aggression, reactivity), the majority of studies that have measured breed differences in behavior have reported meaningful within-breed differences as well. These trends appear to be related to two main factors: the traits being assessed and the methodology used to assess those traits. In addition, where evidence for breed differences in behavior has been found, there is mixed consistency between empirical findings and the recognized breed standard. We discuss both the strengths and limitations of behavioral research in illuminating differences between dog breeds, highlight directions for future research, and suggest the integration of input from other disciplines to further contribute to our understanding of breed differences in behavior.

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1. Introduction

It is obvious that breed differences in behavior are both real and important in magnitude.

—Scott and Fuller (1965), p. 385.

To many, the above quotation from Scott and Fuller's classic *Genetics and the Social Behavior of the Dog* (1965) seems intuitively obvious. Over 1000 distinct dog breeds are in existence today (Morris, 2008), and of these, approximately 20% are recognized by various national and international kennel clubs. *Canis lupus familiaris* is a subspecies that exhibits extraordinary variation in morphological phenotype; it is assumed that breeds therefore differ widely in their behavioral phenotypes as well. Although the number of recognized dog breeds has grown substantially over the last century and a half, relatively little empirical research has targeted the behavioral characteristics that define breeds. As a result, dog breeding has been referred to as “a well-established art, but a crude, unestablished science” (Rine, 1991). Yet, it is widely acknowledged that different breeds have different and consistent behavioral predispositions due to selective pressure by humans (Howell and Bennett, 2011; Bradley, 2011; Serpell and Hsu, 2005).

The domestic dog – and the breeds that make up this diverse subspecies – is becoming an increasingly popular subject for behavioral research. The goal of this paper is to review and summarize research findings that have measured differences between dog breeds in temperament and cognitive performance in order to determine whether there is empirical evidence that dog breeds differ in substantial and systematic ways. We consider the historical understandings of breed origin, the diverse methodologies that have been used in empirical literature, their validity and appropriateness, the developmental history of subjects tested, and the extent to which specific breeds have been represented in the scientific literature. We hypothesize that (1) studies that have compared behavior between and within dog breeds suggest that within-breed differences are more evident than between-breed differences, and (2) where evidence for breed differences is found, the breed standard will be concordant with the empirical conclusions for the trait that was measured. Finally, we offer

conclusions about assessing breed differences in behavior and identify areas of research that need further investigation or replication.

2. Origins of dog breeds

The first evidence of distinctive dog breeds in the historical record appears around 3000 to 4000 years ago (Brewer et al., 2002; Harcourt, 1974). While many of the breed classes of dogs we know today, as well as their qualities and traits, were well defined by the Roman period (Clutton-Brock, 1995; Xenophon, 1897), the major era for the proliferation of dog breeds in Europe was the Middle Ages (Clutton-Brock, 1995). The unparalleled phenotypic variability between breeds led even Charles Darwin to believe that the domestic dog must have had at least two common ancestors (Darwin, 1859). In fact, it was during Darwin's lifetime that modern breeds became closed populations (Ritvo, 1987).

Biologically, dog breeds are groups of individuals within the subspecies *C. familiaris* that strongly resemble one another based on a series of characteristics that are identifiably different from other groups (Brewer et al., 2002). However, the most accurate way to define a breed based on behavior is still debated to a great extent. One hypothesis is that dog breeds originated as land races adapting to different environments in geographic isolation, with little to no human selective breeding (Coppinger and Coppinger, 2001). An alternative hypothesis is that artificial selection by humans was the fundamental basis of establishing dog breeds, accomplished by mating dogs with similar characteristics to produce similar future generations (Rine, 1991). The true origin of dog breeds is clearly a subject of considerable debate (Larson et al., 2012). This uncertainty has also prompted questions about how exactly a breed should be defined, and is in itself a source of disagreement among scientists today.

2.1. Defining the breed standard: The need for research

Regardless of how breeds may have originated, the wide variation in the dog breeds we know today is produced and maintained by ongoing human selection for specific

Table 1
 Breed groups (listed alphabetically) as defined by the American Kennel Club (AKC) and Fédération Cynologique Internationale (FCI).

Group title	Number of breeds	Historical roles	Characteristic behavioral traits (according to AKC)	Breeds represented in behavioral research
Herding	25	Driving livestock	Gentle herding, intelligent, trainable, excellent companions	Australian Cattle Dog, Border Collie, German Shepherd Dog, Shetland Sheepdog
Hound	28	Independent hunting of prey, vermin	Excellent scent-following ability, high activity, vocal	Basenji, Beagle, Dachshund, Greyhound
Non-Sporting	19	Varied	Varied; sturdy	Bulldog, Chow Chow, Dalmatian, Poodle (Standard and Miniature), Shiba Inu
Sporting	28	Cooperative hunting and other field activities	High activity, alert, companions	Cocker Spaniel, English Cocker Spaniel, English Springer Spaniel, Golden Retriever, Labrador Retriever
Terrier	30	Independent hunting and flushing vermin	High activity, high aggressivity toward other animals, eager	Bull Terrier, Miniature Schnauzer, Staffordshire Bull Terrier, Wire Fox Terrier
Toy	21	Companion	High excitability, low trainability	Cavalier King Charles Spaniel, Chihuahua, Italian Greyhound, Toy Poodle, Pug, Yorkshire Terrier
Working	29	Guarding, sled-pulling, rescue/service	Intelligent, high trainability	Akita, Alaskan Malamute, Bernese Mountain Dog, Boxer, Doberman Pinscher, Siberian Husky

Group title	Number of breeds (including subtypes)	Examples of breeds represented in behavioral research
(Group 1) Sheepdogs and Cattle Dogs	44	Border Collie, Belgian Sheepdog, Shetland Sheepdog, German Shepherd Dog
(Group 2) Pinschers and Schnauzers	52	Doberman Pinscher, Rottweiler, Miniature Schnauzer, Boxer
(Group 3) Terrier	34	Fox Terrier, Jack Russell Terrier, West Highland White Terrier, Staffordshire Bull Terrier
(Group 4) Dachshunds	3	Standard Dachshund, Miniature Dachshund
(Group 5) Spitz and Primitive Types	52	Siberian Husky, Norwegian Elkhound, Akita, Basenji
(Group 6) Scenthounds and Related Breeds	77	Beagle, Bloodhound
(Group 7) Pointing	37	Irish Setter, Pointer
(Group 8) Retrievers	22	Golden Retriever, Labrador Retriever, English Cocker Spaniel
(Group 9) Companion and Toy	30	Pug, Chihuahua, Cavalier King Charles Spaniel
(Group 10) Sighthounds	14	Afghan Hound, Deerhound, Greyhound, Whippet

mutations, and for variations in size, coat type and color (Coppinger and Coppinger, 2001; Scott and Fuller, 1965). Despite the long history of human selection for specific traits in dogs, ancient and modern breeds are not closely related because of to a loss of genetic diversity due to both historical (e.g., World Wars), cultural and geographic factors (Larson et al., 2012), and this has contributed to the debate of how to define a “breed.”

The opposing views on the proper definition of a dog breed are largely reflected in the two distinct ways in which breeds are categorized. The more recent approach groups breeds according to their genetic similarity. Parker and Ostrander (2005) used microsatellite DNA across the dog genome to genotype 85 breeds into four clusters – Asian/African breeds, mastiff-type dogs, herding dogs and sighthounds, and modern hunting dogs – with some breeds being assigned to more than one cluster. These clusters were identified as genetically distinct subpopulations based on patterns of allele frequencies, suggesting that breeds of dogs are local and temporal phenomena recently derived by crossbreeding, such that most modern breeds of dogs remain closely related (Larson et al., 2012; Wayne and Ostrander, 2007).

The more traditional and widespread method of categorizing breeds has been promoted by various national and international kennel club organizations, in which dog breeds are split into groups based on the nature of the

task with which the dogs are associated. While dozens of such organizations exist, empirical studies that have examined breed differences in behavior have largely focused on the categorizations determined by the American Kennel Club (AKC) (180 recognized breeds in seven breed groups) and the Fédération Cynologique Internationale (FCI) (365 breeds, 10 breed groups) (see Table 1 for all groups and descriptions). It is often claimed that some modern breeds were originally bred specifically for various physical attributes that also led to changes in behavior (e.g., Toy or Companion breeds as defined by the AKC), whereas other breeds may have been selected specifically for behavioral traits that are useful for a particular task and these traits subsequently came to characterize the different breeds of dogs (e.g., Herding breeds, livestock-guarding breeds) (American Kennel Club, 2012; Morris, 2008). It is worth noting that there is considerable overlap between the FCI breed groupings and the genetic clusters outlined by Parker and Ostrander (2005) relative to the groups employed by the AKC (Table 2).

Irrespective of different categorizations, there appears to be widespread agreement that dog breeds differ in behavior from one another in measurable and predictable ways; in other words, purebred dogs have a specific behavioral conformation, or “breed standard” (Coppinger and Coppinger, 2001). The breed standards for 153 recognized breeds are published by the AKC in *The Complete Dog Book*

Table 2
Breed groups based on genetic clusters (adapted from Parker et al., 2010).

Breed-type cluster	Examples of breeds in behavioral studies
Asian/ancient/African	Akita, Basenji, Chow Chow, Siberian Husky
Herding	Belgian Sheepdog, Greyhound, Shetland Sheepdog
Modern hunting	Golden Retriever, Labrador Retriever, English Cocker Spaniel, Border Collie
Mastiff	Rottweiler, Boxer, Bulldog, Miniature Bull Terrier

(2006) and on AKC's official website. For example, the Golden Retriever is described as "friendly, reliable, and trustworthy", while the German Shepherd Dog (GSD) has "a certain aloofness that does not lend itself to immediate and indiscriminate friendships". Although this terminology may appear consistent with popular conceptions of these breeds, such accounts are almost completely anecdotal. We will therefore examine not only the empirical evidence of breed differences in temperament and cognition in this review, but also whether these findings confirm or conflict with breed standards and other popular stereotypes.

3. Temperament and personality

The majority of empirical literature on breed differences in behavior deals with temperament. The term *temperament* may refer to either individual or breed behavioral differences that emerge early in development, are elicited in a range of situations, and remain relatively stable over time (Diedrich and Giffroy, 2006). Included in temperament are personality traits, although the terms *personality* and *temperament* are often used interchangeably (Jones and Gosling, 2005; McCrae et al., 2000). Although there is no universally agreed upon definition, personality are similarly defined as behavioral characteristics of individuals that are consistent and generalizable across settings and is the result of interaction between temperament and the environment (e.g., Jones and Gosling, 2005).

The study of personality traits in dogs has gained a great deal of empirical attention in recent decades. Personality may be assessed experimentally (i.e., a behavioral battery test, e.g., Jones and Gosling, 2005; Svartberg, 2002, 2007), observationally in a naturalistic setting (e.g., Goddard and Beilharz, 1983), or by indirect assessment via an informant (e.g., giving an owner a questionnaire used to rate personality traits, as in Jones and Gosling). Because we feel the term *personality* has anthropomorphic connotations (e.g., Jones and Gosling, 2005), we will generally use the term *temperament* in this review, but will refer to personality.

In dogs, personality has been assessed, for example, by the traits aggressiveness, sociability, curiosity/fearlessness, and playfulness (Svartberg and Forkman, 2002; Svartberg, 2006) or along the shyness-boldness spectrum (Svartberg, 2002). Similarly, temperament has been defined by the broad traits of aggressiveness, reactivity, and trainability (e.g., Hart and Hart, 1985; Takeuchi and Mori, 2006). Hart and Miller (1985) conducted the largest study to date on breed differences in temperament in which 48

veterinarians and 48 obedience judges ranked seven breeds chosen randomly from 56 breeds of dogs on 13 behavioral traits. A subsequent cluster analysis revealed that of these 13 traits, aggression, emotional reactivity and trainability were found to account for the most variance between breeds (Draper, 1995; Hart and Hart, 1985). Indeed, many studies on breed differences in temperament in dogs have investigated one or more of these three traits.

4. Aggression

Aggression is the most common and serious behavioral problem reported in dogs kept as companion animals (Borchelt, 1983; Fatjó et al., 2007). The effect of breed on the expression of canine aggression has been suggested by numerous experimental and survey-based studies (Duffy et al., 2008; Hsu and Sun, 2010; Scott and Fuller, 1965; Svartberg and Forkman, 2002). The measurement of aggression in dogs employs a wide range of sources, including dog bite statistics, surveys of dog owners, survey and referrals of general veterinary practitioners and databases from companion animal behaviorists (Duffy et al., 2008; Fatjó et al., 2007). Several topographies of aggression have been reported in a wide range of breeds and breed groups, making aggression one of the most complex canine behaviors to define in terms of context, intensity, and target.

4.1. Owner-directed aggression

Owner-directed aggression (ODA), or agonistic behavior that is directed toward people who are familiar to the dog, represents the most common cause of dog bite injuries reported (Overall and Love, 2001). Although no published direct assessments of breed differences in ODA exist, many indirect sources are available. Incident-based reports, including statistics on bite-related fatalities and veterinary caseloads, as well as owner-based questionnaires, yield inconsistent findings of breed differences in aggression. For example, Sacks et al. (2000) found that Pit Bull-type dogs and Rottweilers were involved in more than half of 238 total human deaths caused by a dog bite-related injury in the United States between the years of 1979 and 1998, whereas breeds that have been anecdotally considered to exhibit low ODA were ranked highest for bite-related fatalities where statewide breed-specific legislation is practiced (University of Colorado Denver (UCD), 2010). The difficulties with drawing definitive conclusions from bite statistics alone have been acknowledged (Sacks et al., 2000), as certain breeds and breed groups may be either over- and under-represented in different biting populations (Cornelissen and Hopster, 2010).

Owner-based surveys using the standardized questionnaire C-BARQ™ in the United States, Japan, and Taiwan have shown substantial discrepancies in breeds that exhibit high ODA. The highest levels of ODA have been reported in mostly small to medium-sized breeds (Duffy et al., 2008; Hsu and Sun, 2010), and many of the same breeds ranked high for ODA by Japanese dog owners also ranked high for snapping at children and exhibiting dominance over owner (Takeuchi and Mori, 2006). However, in a study by Hart and Miller (1985), breeds ranked by judges as showing the

greatest tendency to “exert dominance over their owners” or snap at children were not consistent with these more recent owner surveys.

Studies of veterinary caseloads consistently report the English Cocker Spaniel (Amat et al., 2009; Beaver, 1983; Borchelt, 1983; Fatjó et al., 2007; Wright and Nesselroete, 1987) and the English Springer Spaniel (Guy et al., 2001; Landsberg, 1991; Reisner et al., 1994) as exhibiting the highest levels of ODA.

These trends in ODA between breeds obtained by indirect assessments may be due to different perceptions of pet dog’s aggression between veterinarians and owners.

4.2. Stranger-directed aggression

There have been several direct behavioral assessments of breed-specific stranger-directed aggression (SDA). Bollen and Horowitz (2008) assessed over 2000 shelter dogs and found that failure on a behavioral evaluation (e.g., exhibiting serious aggression, including lunging while growling and snarling, and any attempts to bite) was significantly higher for “high risk” (Pit Bull, Rottweiler, Chow Chow, Husky) than for “low risk” (all other) breeds. It should be noted that these results may be confounded by a tester’s prior – and potentially biased – perception of the likelihood of these breeds to exhibit SDA. Breed groups did not differ in their reactions when dogs on-leash outdoors were approached by an unfamiliar person in a friendly manner (Vás et al., 2005). On breed level, Belgian Shepherds (Tervuerens and Groenendaels) exhibited significantly higher levels of avoidance behavior than both sled dogs (which included Malamutes and Huskies) and retrievers (which included Golden Retrievers and Labrador Retrievers) when approached by an unfamiliar human. The comparability of these experimental studies is limited, however, by differential inclusion of breeds, dissimilar testing situations and the inconsistency of measures to quantify SDA.

Breeds ranked high for SDA were consistent across owner surveys using C-BARQ™ (Duffy et al., 2008; Hsu and Sun, 2010), but were not consistent with experimental results. This is likely due to the relatively low diversity of breeds included in experimental studies and the results are not readily comparable between methodologies. Breeds that scored low on SDA on C-BARQ™, however, were consistent with the results reported by Vás et al. (2005). Relatively average scores were reported for SDA on C-BARQ™ among breeds commonly targeted in the media for human-directed aggression (e.g., Pit Bull-type breeds, Rottweiler, German Shepherd Dog).

There is evidence that behavioral differences within a breed may also be related to whether the individual dog of a particular breed has been bred for show or field work. Breeding for show has generally been associated with lower levels of aggression, curiosity, trainability (Serpell and Hsu, 2005) and playfulness, and with higher levels of fearfulness, while selection for field work was correlated with higher levels of playfulness and aggression (Svartberg, 2006). There is evidence of this pattern in ODA scores for Labrador Retrievers. The reverse effect was found for English Springer Spaniels, such that conformation-bred

individuals tended to be more owner-aggressive than field-bred individuals (Duffy et al., 2008). Aggressive individuals within a breed have also been linked to yellow coat color in Labradors (in Houpt and Willis, 2001; Kobelt et al., 2007) and golden coat color in English Cocker Spaniels (Amat et al., 2009; Podberscek and Serpell, 1996). This may be due to an overlap in the biochemical synthesis pathways of melanin and dopamine and other neurotransmitters (e.g., low levels of serotonin) that contribute to the expression of aggressive behavior (Hemmer, 1990). Associations between coat color and aggression seem breed-specific as no such effect was observed in Miniature Bull Terriers (Schalke et al., 2010) or Jindo Dogs (Kim et al., 2010).

4.3. Dog-directed aggression

Scott and Fuller (1965) were the first to systematically observe, measure, and document clear breed differences in the tendency to exhibit intraspecific aggression. Their experiments suggested that breeds defined as aggressive may be more likely to develop a linear dominance hierarchy. Their findings are similar to today’s AKC (2006 Guide) temperament standards for the five breeds tested in their experiments (Basenji, Beagle, Cocker Spaniel, Shetland Sheepdog, and Wire-Haired Fox Terrier). Importantly, Scott and Fuller reared several litters of each breed (with sample sizes ranging from 21 to 57 individuals for each breed) in controlled environments. In contrast, most of the empirical literature on breed differences in dog-directed aggression (DDA) is based on surveys and indirect reports, usually from owners, breed judges, veterinarians, and other animal care professionals. Generally consistent breed differences in intraspecific aggression have been found using the C-BARQ™ in the United States, Japan and Taiwan, with some exceptions. This is noteworthy, given both cultural differences in dog ownership, as well as restricted gene flow between distant geographic locales. In addition, the severity of injury resulting from intraspecific aggression has been attributed to breed-specific aggressiveness in an owner survey study in Germany (Roll and Unshelm, 1997). Relatively few veterinary caseloads have been published with respect to DDA, as most of these reports consist of dogs that exhibit human-directed aggression.

The tendency to exhibit behavioral precursors to DDA may be related to breed differences in social signaling. Draper (1995) found intraspecific aggression to be positively correlated with the uprightness of ear structure, whereas overall size was negatively correlated with reactivity. Overall morphology seems unrelated to the sending or receiving of any social signals (Kerswell et al., 2010), though some specific physical characteristics (e.g., snout length, reduced skull shape) have been correlated with signaling frequency (Roberts et al., 2010). Short-snouted (brachycephalic) dogs in particular may appear more juvenile and less threatening, and thus more likely to elicit play behaviors from other dogs. Such phenotypes may make it difficult for these breeds of dogs to communicate with other dogs. Breed differences have been found in the frequency of tail-wagging (Scott and Fuller, 1965), and across breeds the frequencies of dominant and submissive behavior patterns are positively correlated

with physical resemblance to the gray wolf (Goodwin et al., 1997). However, even between somewhat similar breeds, levels of conspecific interactions do not appear to be qualitatively different between Cocker Spaniels, Labradors, and Miniature Schnauzers except for in the first 3 min of an encounter when Cocker Spaniels show the least interactions (Pullen et al., 2013). The influence of morphological differences on social communication between breeds is in need of further research.

4.4. Summary of breed differences in aggression

Breed differences in aggression have been reported in numerous studies. Many breeds were differentially ranked for DDA, ODA, and SDA, suggesting that environmental stimuli, rather than breed alone, play a major role the propensity to exhibit aggression. Breed rankings for ODA are more consistent across methodologies than either DDA or SDA. Across aggression topographies, however, breeds exhibit differential levels across methodologies. Bite statistics are confounded in that bites from large dog breeds are more likely to lead to hospitalization and fatalities than bites from smaller breeds. Veterinary caseloads and owner surveys appear more consistent in breed rankings of aggression, but neither of these indirect methods of assessing breed-specific aggression are in agreement with experimental data. Few experimental studies have been conducted on aggression in dogs, with fewer different breeds studied compared to survey-based studies. The disproportionate amount of indirect assessments relative to experimental studies is likely due to ethical and practical difficulties with using aggression as a dependent measure. However, if behavioral precursors to aggression can be identified accurately and reliably, it may become possible to study aggression more frequently in controlled experimental studies.

The low reliability between direct and indirect methods for measuring aggression may also be attributed to different perceptions of what constitutes aggression. These perceptions may be influenced by experience with dogs of different breeds, the number of dogs owned, the size and appearance of the dogs, and the demographics of respondents. Across methodologies, however, assessments of breeds exhibiting low aggression (e.g., Golden Retrievers, Labrador Retrievers) are relatively consistent. Within-breed differences have been reported in direct, but not indirect assessments (e.g., owner surveys) of aggression. Owner surveys were not consistent with popular perceptions of breeds as portrayed in breed standards. All of these factors, however, further complicate the ability to draw conclusions about clear breed differences in aggression.

5. Emotional reactivity

Scott and Fuller (1965) defined reactivity as “the intensity of all responses, external and internal, made to a stimulus change” (p. 194). Emotional reactivity has been characterized by traits such as excitability, general activity, snapping at children, excessive barking, demands for affection (Draper, 1995; Hart and Miller, 1985), and fearfulness

or distress (Goddard and Beilharz, 1985a). We consider three major components of emotional reactivity here.

5.1. Excitability and general activity

Serpell and Hsu (2001) defined a dog high in excitability as, “high [in] energy, [and having] a very difficult time settling down and behaving quietly for extended periods of time.” (p. 351). Scott and Fuller found clear differences between breeds in their development of directly observable emotional reactions to human beings during social interactions (such as tail wagging, and distress vocalizations). Scott and Fuller measured behavioral and physiological indicators of emotional reactivity between breeds, by presenting dogs with different situations while briefly isolated from humans and conspecifics. An observer rated dogs’ behavioral responses on a 5-point intensity scale. Highly significant differences between all five breeds were found for shock response, escape activity, erect body posture, tremor, investigation, attention to observer, lip licking, vocalization, panting, tail wagging, resistance to forced movement, and biting. Elimination, heart rate change during bell ringing, and handler effect score were not significantly different between breeds. Individual differences within breeds were observed as well.

Indirect assessments have ranked the Miniature Schnauzer, Scottish Terrier, and West Highland White Terrier highest for all traits (e.g., playfulness, destructiveness, excitability, and excessive barking) that were considered to be indicators of reactivity (Hart and Miller, 1985; Notari and Goodwin, 2007). These findings have been relatively consistent with owner reports in the United States and the United Kingdom (Bradshaw and Goodwin, 1998). More recently, online owner reports have suggested significant differences between breed groups in measures of inattention and hyperactivity-impulsivity, with hounds having higher scores for inattention (also correlated with excessive barking, constant motion, and difficulty maintaining a stay) than other breed groups (Lit et al., 2010), and Herding group breeds scoring higher than Toy and Non-Sporting breeds for enjoying active play, constant motion and anticipation. These findings suggest that substantial breed differences may exist along different dimensions of a single trait.

Physiological and structural conformations may further substantiate differences in excitability between breeds, though such cross-disciplinary research in this area is still relatively sparse. Arons and Shoemaker (1992), for example, found differences in measured neurotransmitter levels (norepinephrine, dopamine, and epinephrine) between Border Collies, Siberian Huskies, and Shar Plaininetz (a livestock-guarding breed), which corresponded with excitability levels of these breeds (Arons and Shoemaker, 1992). Breed-specific dietary metabolism differences have also been found between Labrador Retrievers and Miniature Schnauzers in an experimental comparison between metabolite fingerprints generated from urine samples via flow injection electrospray (Beckmann et al., 2010). This may represent an additional physiological basis for breed differences in excitability and other measures of activity, as the ability to sustain high-intensity effort is

directly related to maximum energy consumption regulated through metabolic rate (Coppinger and Coppinger, 2001).

5.2. Exploratory behaviors: Avoidance and investigation

Differences between breeds of dog in fearfulness—defined as a “tendency to withdraw from intense and novel stimuli” (Goddard and Beilharz, 1985b), have been reported in numerous studies in a variety of contexts (Goddard and Beilharz, 1985b; Mahut, 1958; Plutchik, 1971; Scott and Fuller, 1965). Novel object and startle tests are commonly used to measure fear in dogs (King et al., 2003; Ley et al., 2007). In such procedures, subjects are presented with potentially fear-evoking stimuli (e.g., door banging, whistling, opening umbrellas) and the dogs’ responses are recorded. Fearful responses typically include withdrawal, crouched posture, or lowered tail position (Goddard and Beilharz, 1985a). Such behavioral tests are the most common in assessing temperament traits, including fearfulness, in dogs (Jones and Gosling, 2005).

Mahut (1958) experimentally determined significant breed differences in response to startle stimuli. Dogs of 10 different breeds were either kept as pets, kennel-reared (given access to the outdoors and other conspecifics, but not treated as pets), or cage-restricted (reared in isolation from humans and conspecifics). Kennel-reared dogs showed more avoidance responses than the other two groups. Similarly, Beerda et al. (2000) reported Beagles housed individually in kennels exhibited more oral behaviors and sighing after they were startled by a slamming door, that the authors termed “breed-specific” stress behaviors (p. 59). However, this effect was not observed in privately-owned Beagles or pair-housed kennel-reared Beagles, suggesting that within-breed differences may be due to learning of differential consequences based on dissimilar housing environments. For example, home-reared individuals may have more experience with learning that the consequences of a slamming door (e.g., the arrival or removal of a person) than would kennel-reared individuals. This suggests an environmental or ontogenic influence on reactivity rather than a genetic one. Similarly, Mahut (1958) also observed significant within-breed variation, yet concluded that there are clear breed differences in susceptibility to fear patterns. More recently, support for this claim has been found in that breeds bred for rat hunting and fighting exhibit less fearful responses to aversive stimuli than Sporting, and Herding breeds (Serpell, 1995), although it is important to note that the historical function of many breeds remains unproven. Another recent survey study reported that Herding breeds, Labrador Retrievers, Cocker Spaniels, English Springer Spaniels, and Toy Poodles, were at a significantly decreased risk for exhibiting fearful responses toward loud noises (e.g., fireworks, thunder, gunshots) (Blackwell et al., 2013).

Breed differences in emotional reactivity are especially important to the working and service dog industries. Dogs selected for guide dog work are typically high in confidence and low in aggression-dominance, whereas fearfulness is the most common reason dogs are rejected (Goddard and Beilharz, 1985a). Labradors were found to be the

least fearful in startling tests between 1 and 18 months of age, while German Shepherds were the most fearful (Goddard and Beilharz, 1985a). These experimental findings are consistent with breed differences in success rates for graduating as Seeing Eye guide dogs (Ennik et al., 2006), where Labrador Retrievers and Labrador–Golden Retriever crosses were the most likely to succeed in training whereas German Shepherd Dogs were the least likely. Furthermore, the topography of fearfulness, rather than the likelihood of its expression, may differ between breeds. For example, Kelpies and Boxers both displayed intermediate levels of fearfulness during startle tests; however, Boxers responded by becoming inhibited, whereas Kelpies responded with high activity (Goddard and Beilharz, 1985a).

Breeds reported as showing low fearfulness toward startle stimuli have been more frequently reported as potential sheep herding dogs when compared to other breeds (Christiansen et al., 2001). Green and Woodruff (1983) found that 11% of Komodorok and 78% of Great Pyrenees were successful in deterring predation in rangeland flocks of sheep, and observed that Great Pyrenees were not as playful with the sheep, less sociable to people and thus more apt to stay with the sheep rather than following the shepherd and adapted more readily to new people and terrain, whereas Komodorok were more reactive and immature. The relationship between working performance and response to startle stimuli has also been reported in racing dogs. King et al. (2003) found that Greyhounds with such histories displayed much less avoidance and aversion to novel stimuli than other breeds. Thus, breed differences in task performances by working and service dogs may be further explained by their tendency to exhibit neophobia or other types of reactivity to novel stimuli.

There is some evidence for breed differences in social investigation during human-dog play in experimental studies (Scott and Fuller, 1965) and sociability. Several experimental studies have found that Labrador Retrievers and Golden Retrievers are among the breeds that score higher in sociability and curiosity (Svartberg, 2006; Vás et al., 2005; Wilsson and Sundgren, 1997), whereas German Shepherd Dogs (Wilsson and Sundgren, 1997), and Poodles and Belgian Shepherds (Vás et al., 2005) were often among breeds with the lowest scores. Golden Retrievers have been reported to exhibit more indicators of stress (increased proximity-seeking behavior, locomotion and passive behavior, and decreased play and exploration) than Labrador Retrievers in experimental conditions in which the dogs were repeatedly separated from their owners (Fallani et al., 2007). This is likely related to the higher rankings for Labrador Retrievers than Golden Retrievers in startle or emotional reactivity tests and may furthermore have applications for trainability in service dog work. A longitudinal study in the United Kingdom found no breed differences in the prevalence of separation anxiety between Labrador Retrievers and Border Collies based on owner responses (Bradshaw et al., 2002), where both breeds are considered highly trainable as search and rescue dogs (Rooney and Bradshaw, 2004).

The personality dimension of shyness-boldness has been correlated with performance in working dogs, such that bolder dogs perform better during working dog trials;

though this has also been linked to the experience of the handlers (Svartberg, 2002). Svartberg (2002) observed that German Shepherd Dogs tended to perform better than Belgian Tervurens, but detected a threshold effect amongst high-performing dogs, such that no breed or sex differences were found. Breed-type had no predictive validity on working dog certification among German Shepherd Dogs, Belgian Malinois, and Dutch Shepherds (Sinn et al., 2010). Svartberg (2006) collected scores on a standardized test of responsiveness to diverse social and non-social stimuli of 31 breeds in five groups (Working, Terriers, Herding, Hounds, and Gundogs), and proposed that breed differences in fearfulness may be a consequence of recent selection for current breed stock, rather than of past selection in breed origin. Within-breed differences in reactivity have also been reported. In Swedish populations, selection of a breed for use in dog shows correlates positively with fearfulness and negatively with playfulness, aggressiveness, and curiosity; in contrast, breeding for working dog trials correlates positively with playfulness and aggressiveness (Svartberg, 2006).

6. Trainability

One of the most practical interests of dog owners regarding different breeds of dogs is their trainability—also referred to as obedience or “working intelligence” (Coren, 1995). Trainability may be defined as a dog’s willingness to attend to its owner and obey commands, with high motivation and resistance to correction, and low levels of distractibility (Serpell and Hsu, 2005). Although this area appears to have received less empirical attention than either aggression or emotional reactivity, trainability has been measured in different dog breeds with respect to quieting on command, leash training, housebreaking, obedience training, and habit formation in both experimental (Scott and Fuller, 1965) and survey (Hsu and Sun, 2010; Hart and Hart, 1985) studies. In addition, the ability to predict behavioral tendencies of different breeds is considered a powerful tool for cost-effective training of dogs for working dogs to be used in a variety of roles (Riva et al., 2012). Experimental studies have found breed differences in performance during leash training, quieting, and obedience (specifically, staying in one place on command), (Scott and Fuller, 1965). Breed differences in trainability have also been detected indirectly with owner reports and surveys (Serpell and Hsu, 2005). Extraversion and training focus were the only characteristics of trainability that were significantly different among the seven breed groups recognized by the Australian National Kennel Council (Ley et al., 2009). Herding breeds were reportedly the easiest to train, based on a cluster analysis of data obtained from an owner survey (Turcsán et al., 2011). Traits of trainability and boldness differed significantly between conventional and genetic groups, though behavioral breed clusters showed poor correspondence to both traditional and genetic categorization. Breed rankings of working intelligence are highly consistent with the results of other studies that have found breed differences in obedience training through survey responses by dog owners in both the United States (Hart and Miller, 1985) and Japan

(Takeuchi and Mori, 2006) and judges’ rankings in the United States (Coren, 1995).

Within-breed differences in trainability have been observed as a function of rearing styles. For example, Freedman (1958) tested puppies from eight litters and found within-breed differences in responses to reprimands in Beagles and Fox Terriers that were raised in “indulgent” environments (in which all activities the puppies engaged in were encouraged and they never received punishment) compared to “disciplined” environments (in which the puppies were restrained in the experimenter’s lap and trained (p. 585). There is a large disparity in physical differences among breeds and breed groups which may factor greatly into trainability differences among dogs. In a reanalysis of the data obtained by Hart and Hart (1985), taller dogs tended to rate higher for trainability than did shorter breeds (Draper, 1995), and breeds perceived as highly trainable according to Coren’s (1995) rankings were closer to the mean of all breed height standards sampled than breeds considered to exhibit the worst trainability, which included breeds at extreme ends of the height spectrum (Helton, 2010). Thus, differences in physical morphologies, rather than historical function, may allow some breeds greater advantages at some training tasks relative to others. Neophobia was found to influence trainability in dog breeds as well. Furthermore, existing studies on trainability are difficult to interpret because they include a diverse range of methodologies, dependent measures (e.g., rate, latency, performance criterion), and restrictive breed selection.

7. Cognition

Whereas the use of indirect assessments (e.g., questionnaires) is relatively popular for measuring temperament and personality, experimental studies are more commonly used in assessing breed differences in cognition. Although experiments on breed differences in cognitive abilities originated with Scott and Fuller (1965), this area has received less empirical attention than temperament. However, the scientific inquiry of canine cognition has been steadily developing over the past decade with a new focus—sensitivity to human cues. Thus, the literature on cognitive tasks in domestic dogs can be explored in two contexts: tasks that involve non-human stimuli and tasks that involve human interaction or response to human cues.

7.1. Physical problem-solving tasks

Much of the classic studies on both simple and complex learning in domestic dogs originated with physical problem-solving tasks. In a manipulation task conducted by Scott and Fuller (1965), Basenjis were consistently the most successful of the five breeds in removing a dish of food from within a covered wooden box that could only be reached by nosing or pulling the dish out through an open side, indicating that Basenjis are more skillful in manipulating objects. Cocker Spaniels consistently performed the worst, whereas Beagles, Wire-Haired Fox Terriers, and Shetland Sheepdogs were all intermediate in performance. All breeds improved with the presence of added

manipulanda to make the reward more accessible. More recently, studies have explored the role of morphological differences in accounting for breed differences in motor capabilities. McGreevy et al. (2010) found that short-snouted (brachycephalic) breeds (e.g., Pugs and Boxers) took less time than long-snouted (dolichocephalic) breeds (e.g., Whippets and Greyhounds) to complete a 100-paw criterion on a task of removing food from a cylindrical rubber Kong toy. This suggests that short-snouted dogs use their paws more in manipulation tasks, whereas dolichocephalic breeds may rely less on their paws because their relatively long muzzles allowed them to better extract food from the Kong toys. This was not found with Shetland Sheepdogs or Fox Terriers in Scott and Fuller's (1965) manipulation task, indicating that morphology is not in itself sufficient to explain differences in performance in manipulation tasks. Since it is unlikely that rearing histories played a large role in the differences between these two populations (puppies in both studies were under 16 weeks of age and attained from breeders), discrepancies may rather reflect breed differences in for example thresholds of stimulation.

Breed differences in spatial perception have been assessed using a detour task (Scott and Fuller, 1965), in which subjects had to move away from a visible dish containing food and walk around to the far side of a transparent barrier to attain the food. Breed differences in maze performance were found by Scott and Fuller in both performance, persistence (measured as number of attempts to get food) and improvement measures, though background variance was highly influential in average error and time scores (Elliot and Scott, 1965). It was concluded that breed differences in performance were largely due to differences in fear responses toward the apparatus between breeds (e.g., Basenjis exhibited the most fear responses, where Fox Terriers exhibited the fewest). Wide individual differences were observed. More recently, Head et al. (1997) found that the effect of age on open field activity is breed-dependent. In addition, exploratory behavior – measured by locomotor activity in an open field – correlated with behavioral indicators of cognitive function, measured by reversal learning, spatial learning, object recognition, and memory acquisition. More recently, differences in object permanence – the ability to locate an object that is no longer visible – were not found between breed groups (terriers, sporting, and working) (Gagnon and Doré, 1992). Rather, subjects were highly successful on visible displacement tests, but less successful on solving invisible displacement problems, suggesting that dogs solved these tasks on the basis of visual information.

There are several possible explanations for the relative success of different breeds in physical problem solving tasks. First, there may be breed-specific differential responses to frustrating or fearful situations. For example, Scott and Fuller (1965) reported that Cocker Spaniels would simply lie down and become inactive when they could not accomplish the detour task, whereas Basenjis remained active and were thus more likely to solve the problem by chance. In the maze test, the success of Beagles was attributed to their tendency to continuously investigate their surroundings, whereas Shetland Sheepdogs

appeared timid and hesitant in the maze and developed strong stereotyped habits – a trait they attributed to the central nervous system rather than environmental variables (Elliot and Scott, 1965). Morphological differences may also be a factor. For instance, the cranial morphology of some brachiocephalic dog breeds, (e.g., Pugs, Bulldogs) could affect a dog's sense of smell due to greater forward rotation of their brains and consequently lower repositioning of the olfactory lobe (Roberts et al., 2010), and thus influence their performance on odor or trailing tasks (Scott and Fuller, 1965), resulting in differential reliance on smell as a function of breed. The number of possible variables strongly suggests that understanding the causal factors for differences between breeds in physical problem solving is a complex task in itself.

7.2. Human-responsiveness tasks

Breed-specific differences in responsiveness to humans were documented beginning with Freedman's (1958) finding that punishment had a differential effect on social inhibition of eating in four breeds of dogs. Using eight litters (two litters per each breed), observers reported that Beagles and Fox Terriers were strongly oriented to the experimenter, whereas Basenjis showed increased activity levels but ignored the experimenter in favor of inanimate objects. In contrast, Shetland Sheepdogs exhibited avoidance due to fearfulness and exhibited lower activity levels (Freedman, 1958), and this is consistent with findings that Shetland Sheepdogs performed poorly on tests in which their emotional reactivity interfered with learning (Stafford (1996); Werboff et al., 1969; Takeuchi et al. (2001)). Recently, a number of studies have examined domestic dogs' ability to follow human cues to hidden food. Pongracz et al. (2005) did not find differences between breeds of dogs in their ability to follow a human point leading to a detour around a barrier. A meta-analysis compared 24 breeds – grouped by both the eight AKC categories and the four genetic clusters identified by Parker and Ostrander (2005) – used in 14 studies on a range of different pointing types, and found no differences between breeds in their ability to follow a human point to hidden food (Dorey et al., 2009). Wobber et al. (2009) found that working breeds (which included German Shepherds, Belgian Shepherds and Siberian Huskies) performed better in following human cues to food (including pointing and gazing) than non-working breeds (which included Toy Poodles and Basenjis), and the ability the follow such cues was not influenced by breeds' respective similarity to the gray wolf. Other studies have failed to observe differences in performance between herding and hunting dogs (Riedel et al., 2008) and between gundogs (Labrador Retriever, Golden Retriever, Cocker Spaniel) and non-gundogs (German Shepherd Dogs, Terrier mixes, and Poodles) (McKinley and Sambrook, 2000) in similar tasks. Most recently, Udell et al. (2014) reported that inhibition of predatory motor patterns predicts faster acquisition and higher levels of response accuracy on these tasks in breeds with exaggerated predatory repertoires (e.g., Border Collies) compared to breeds that do not (e.g., Airedale Terriers, Anatolian Shepherds). Given Scott and Fuller's findings that Basenjis

tended to be inattentive to the experimenter during social interaction following inaccessibility of food, it may be possible that Wobber et al.'s findings were due to behavioral idiosyncrasies of the particular breeds selected, rather than a characteristic of non-working breeds in general, especially given the relatively small likelihood that the one or two breeds chosen would be an accurate representation of an entire breed categorization. Comparing breeds that are believed to differ in their physical traits—including size (Helton and Helton, 2010) and motor selections, rather than historical roles, may be a more fruitful approach.

Human-directed gazing has also been an active area of canine cognition research. Most recently, breed differences in the acquisition of gazing at a person's face were not found (Jakovcevic et al., 2010), but Labrador Retrievers and Golden Retrievers gazed at the human face significantly more during extinction trials than did German Shepherd Dogs and Poodles. One explanation may be that cooperative breeds selected to work closely with humans are more skillful in cognitive tasks involving people than independent breeds and mixed-breeds (Gácsi et al., 2009). Svartberg (2006) argued that selection during recent decades may have led to great changes in breeds relative to their historical breed-typical behavior. Thus, breeds may show differences in their communicative skills not only because of different histories of selection, but also because their ability to learn such skills has been modified recently. Thus, the differential rates of extinction in gazing may be a reflection of training experience during a dog's lifetime, rather than phylogenetic influences. Passalacqua et al. (2011) found that Herding/Hunting breeds exhibited more human-directed gazing during an unsolvable task paradigm, than Primitive or Molossoid breeds, but suggested this was influenced by age and thus experience with interspecific social communication. Furthermore, training in agility and search-and-rescue tasks alters dogs' behavior on human responsiveness tasks (Marshall-Pescini et al., 2009). Another consideration is that social reinforcers may be particularly salient to certain breeds or breed groups, so that gazing could act as a conditioned reinforcer for one, but not another breed or breed group. A valuable area for future research would therefore be to investigate how breeds differ in their motivation for food, social, or tangible (e.g., toy) reinforcers, and how these differences influence performance on cognitive tasks.

7.3. Conclusions on breed differences in cognition

Many studies that have examined cognition in dogs have identified differences in performance among various breeds, though this has been more common in tasks involving sensitivity to human gestures rather than physical problem solving tasks. Where evidence in breed differences is found in the latter, authors have attributed their findings to breed differences in morphology, whereas in the former breed differences in sensitivity and propensity to follow human cues is attributed to artificial selection in certain breed or breed groups linked to their historical roles. This latter argument should be made with caution, as the intensity of selection for practical purposes has been fading as the importance of dog companionship and breeding

for appearance has risen, particularly in Western societies (Svartberg, 2006). Additionally, the lack of breed diversity in cognitive task studies presents another difficulty for making broad inferences about the cognitive abilities of certain breeds and breed groups relative to others. Of the 58 dogs in studies reviewed by Dorey et al. (2009), 19 were retriever or retriever mixes and 17 were German Shepherd Dogs or mixes, followed by 5 Dachshunds, with no other breed represented by more than three subjects. In addition, individual variation is an important consideration in comparing performance on cognitive tasks, and many authors do not report individual data. The discrepancies between breeds in many studies reviewed in this section may be due to ontogenetic differences between individual dogs, rather than to genetic breed differences. Ontogeny – in addition to phylogeny – plays a critical role in the ability of domestic dogs to respond to human gestures (Udell and Wynne, 2010). If studies aim to demonstrate breed-related differences in cognitive abilities, rearing and housing conditions for subjects must be as similar as possible, as these factors can have a major impact on at least some cognitive tasks (Dorey et al., 2009; Head et al., 1997; Udell and Wynne, 2010). Test situations should also be as standardized as possible.

8. Discussion

Does the current literature provide evidence for breed differences in behavior, as Scott and Fuller stated so surely in 1965? Our objective here has been to provide a comprehensive review of the many different sources of information available that claim evidence of breed differences in behavior, and to evaluate the validity of each of these sources. Specifically, we tested two hypotheses: that there is more evidence for within-breed variation in behavior rather than between breeds; and also, that where evidence for breed differences exist, the scientific findings will correspond to the breed standard for a given breed. We conclude that the question of breed differences in behavior is still very ripe for further investigation, and would most greatly benefit from an emphasis of certain themes, which we will discuss here.

8.1. Evidence for behavioral differences between breeds versus within-breed differences

Breed differences are more likely to be reported in survey-based studies and other indirect assessment methods than in experimental studies, and in certain temperament traits rather than cognitive abilities (Fig. 1). In studies measuring temperament, aggression and trainability are commonly assessed via surveys and other indirect methods, whereas most of the direct assessments of temperament in dogs have involved startle tests of emotional reactivity. However, the traits determined to have been representative of aggression, emotional reactivity, and trainability may not be ideal variables for delineating behavioral differences between breeds. Such traits may benefit not only from more operational definitions, but may not be entirely independent from other traits included in these studies.

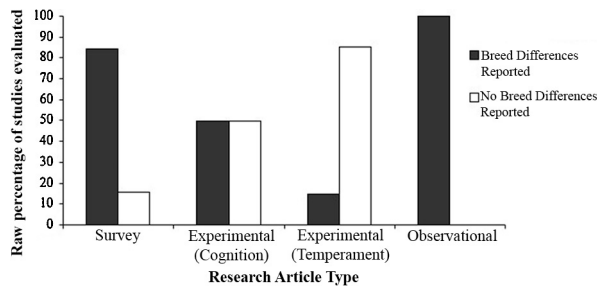


Fig. 1. Distribution of empirical research articles reporting breed differences and within-breed differences according to study type.

Survey-based studies may be extremely helpful in gaining information about breed-differences in behavior, largely because it allows researchers to sample from a wide range of breeds simultaneously. However, survey-based studies are also difficult to interpret for several reasons. First, there is a lack of baseline data on the relative numbers of dogs of different breeds in the sample populations, making comparisons of and representativeness less straightforward. In addition, respondents of surveys (which typically tend to be veterinarians, owners, judges, or other individuals with extensive dog experience) may be biased in their responses or may fail to accurately report the behavior of the dogs they interact with on a daily basis.

The validity of surveys and owner reports is a contentious issue: some argue that these assessments are unavoidably subjective (Duffy et al., 2008; Nederhof, 1985), while others contend that surveys are an acceptable method for assessing dog behavior (Block, 1961; Jones and Gosling, 2005). Miklósi (2007) has perhaps stated most articulately and accurately the relationship between the two methodologies: that while the use of questionnaires has been “fashionable” (p. 33) for collecting data on behavioral comparisons between breeds, this method should not be considered a substitute for research in which the behavior of the subjects is the dependent measure. Much work has already been done to develop robust, standardized questionnaires (e.g., C-BARQ™) for this purpose, but this research area is still relatively young.

Many of the studies reviewed here have reported not only substantial differences in behavior among breeds, but within breeds as well. Within-breed differences are likely related to environmental differences in rearing histories (e.g., Freedman, 1958) or certain contingencies that the individual has contacted throughout its lifetime. The fact that differences in temperament traits within breeds were also often reported, suggests the influence of either genetic isolation within breeds across different geographic locations or environmental factors, such as differential rearing conditions. For example, Mirkó et al. (2012) devised an individualized, adjective-based personality questionnaire for dog owners and trainers in Hungary, and compared stranger-directed sociability, activity, aggressiveness, and trainability) between the Hungarian Vizsla and the German Shepherd Dog—and found no difference between the two breeds after individuals were matched for demographic variables. In certain cases, systematic within-breed differences in temperament have been observed as a function

of whether the dog was bred for show or field work. Currently, the published sources that have reported breed differences in temperament traits have been largely quantified by empirical, yet indirect methods. We believe more experimental research needs to be conducted in this field, in order to address the inconsistencies reported among the more popular owner-based survey studies.

Comparison of empirical findings across studies is greatly hindered by the different rearing environments and demographics of the individuals within breeds being compared. Although the need to consider the interaction between ontogeny and phylogeny when making conclusions about canid social behavior is not a novel point (e.g., Coppinger and Coppinger, 2001; Fox, 1964; Scott and Fuller, 1965; Udell and Wynne, 2010) it appears to need considerable emphasis with respect to studies of breed differences in behavior. In contrast, much of the research reviewed here suggests that there has been a bias in scientific studies toward purely phylogenetic explanations for breed differences in behavior (Goodwin et al., 1997; Svartberg, 2006; Wobber et al., 2009). An example of this would be attributing performance to selective pressures during domestication. Yet, even in the most carefully controlled studies by Scott and Fuller nearly 50 years ago, individual differences between breeds were found (Cattell et al., 1973; Scott and Fuller, 1965), and it has since been noted that some behavioral traits may be more strongly influenced by genetics (i.e., excitability, aggression) whereas other traits (i.e., housebreaking ease) appear to be more influenced by environmental conditions (Hart and Miller, 1985). In modern studies, commonly carried out on pets reared in relatively uncontrolled environments, we expect environmental influences to have an even greater effect than in the older studies on kennel-reared dogs. In addition, inconsistencies in the results of many studies are not only due to different methodologies and rearing histories of the subjects, but are likely also the result of differential inclusion of breeds between studies. This is particularly true of the breeds used in Scott and Fuller’s experiments, relative to the breeds examined in more recent experimental and survey studies. Certainly, the number of breeds in existence today makes any sort of definitive and comprehensive examination of breed differences in behavior daunting and many studies have therefore only examined the most readily accessible and popular breeds. However, to seek differences among breeds in this way is shortsighted. One major problem with the literature claiming breed differences in behavior is that many breeds are grossly overrepresented and other breeds are virtually ignored. For example, although 202 breeds have been used in the studies we have cited in this review, Labrador Retrievers, German Shepherd Dogs, and Golden Retrievers were the most common breeds recruited (i.e., included in 30 or more scientific studies) (Fig. 2). In addition, this trend varies depending on the type of study being conducted, as has been acknowledged in reviews of studies of breeds responding to human gestures (Dorey et al., 2009), and temperament tests (Jones and Gosling, 2005). It is therefore premature and potentially misleading to study only readily accessible breeds of dogs and use these findings to make generalities about the

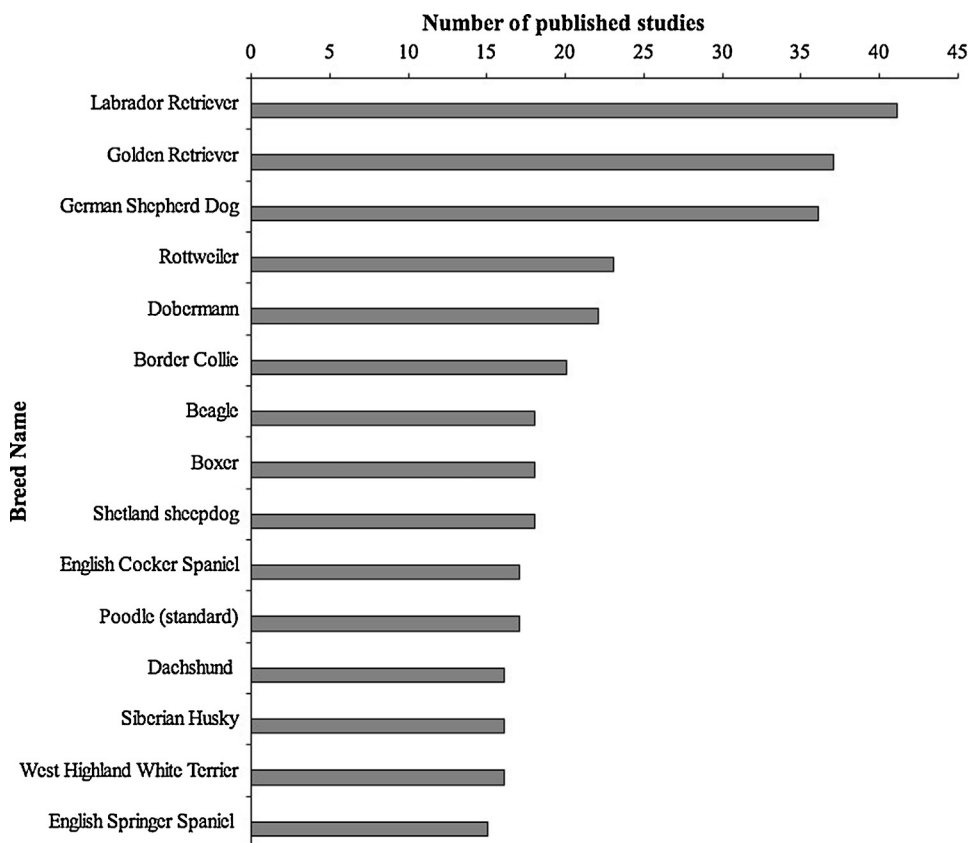


Fig. 2. Frequency of breeds represented in 20% or more of empirical behavioral studies. For veterinary caseloads, only breeds reported were included. Other names of breeds are denoted in parentheses in cases in which the same breed was referred to by two or more different names across studies.

domestic dog as a subspecies. The fact that only small and unrepresentative samples of different types of breeds have been tested, adds further emphasis to the need for caution when claiming breeds differ in systematic and fundamental ways. Future research should thus place an emphasis on investigating behavioral traits of breeds that are relatively under-represented in the literature.

The lack of operationalized dependent measures with which to assess behavior poses another difficulty for interpreting claims of breed differences in behavior. This is shown by the higher consistency in breed rankings from studies that measure highly operationally defined behaviors such as aggression and excitability compared to studies that attempt to measure less operationalized concepts such as trainability, intelligence, or impulsivity. As a result, replications of studies may be difficult to conduct and comparisons across studies may be more difficult if directly observable behavior is not among the primary measures being assessed, and the use of anthropomorphic terminology may hinder attempts to effectively explain why one breed is more likely to behave in one way compared to another (Wynne, 2007). Of particular interest may be cases in which certain breeds have been observed to exhibit relatively low food-motivation, because this may be erroneously interpreted as poor obedience training or trainability. In addition, there are also popular claims of breed-specific performance during particular tasks or

competitions, which have yet to be explored by experimental tests. Before claims of breed differences in performance on various tasks can be made, it must be ensured that the reinforcers used for each breed are indeed effective for that breed. More research clearly needs to be conducted in this area, as this is of direct relevance for assessing the trainability of breeds.

Another terminological concern in studying breed differences in behavior is the practice of generalizing behavioral traits into excessively broad behavioral categories. This likely leads to inconsistencies between studies, as behaviors that are only superficially related to each other are being considered as if they represent the same class of behavior and have related underlying causes. Defining aggression by structure or topography may not necessarily reflect the underlying behavioral cause of the aggression (i.e., aggression due to negative reinforcement – often termed *fear-based aggression* – compared to aggression due to positive reinforcement – often termed *dominance aggression*). In this case, we might argue that territorial aggression is maintained by negative reinforcement (the removal of an aversive stimulus contingent on aggressive responses, increasing the probability that aggressive responses will be exhibited in the future) (Skinner, 1938). Surprisingly, very few studies have examined breeds' responses to particular types of reinforcement, especially in cognitive tasks in which a breed's performance is the dependent

measure. Thus, describing breed differences in aggression in terms of function rather than topography not only eliminates the need to ascribe multiple levels of aggression, but also makes a functional treatment less cryptic. Therefore, assessing how breeds differ in their propensity to exhibit behaviors based on their function would be a constructive area for future research on breed differences in temperament. Similarly, the general term intelligence is perhaps breed-specific but not absolute; no breed is more or less intelligent in any general sense, but rather breeds differ in what they have a predisposition to learn (Coppinger and Coppinger, 2001). This is also true of measuring trainability and performance in cognitive tasks—as any individual dog's performance tends to be specific to particular test situations and is based on a large variety of capacities. Attempting to rank dog breeds on a single dimension of intelligence thus seems an overly simplistic method of determining the relative behavioral performance of breeds of dogs. A major argument against such rankings is that the intelligence of diverse breeds such as hunting or herding dogs cannot readily be compared, as their skills differ qualitatively, not quantitatively.

It is widely acknowledged that any individual's propensity to exhibit a certain behavior can be influenced by genetic selection (Bradley, 2011), and this can occur not only between breeds, but within breeds as well. It has been proposed that behavioral genetic research can be useful to understand the genetic bases of different traits, including temperament and personality (Saetre et al., 2006) and cognitive abilities (Dorey et al., 2009), but morphological differences among breeds may also inform those with an interest in behavioral differences among breeds. Such research could effectively translate these morphological differences into behavioral differences, bridging the gap between two scientific disciplines with a common interest. It may be the case that life experiences are highly important to all dogs, but that their behavioral tendencies are a reflection of biological predispositions, both as a result of evolutionary history and morphology, as well as breed. Behavioral research on breed differences in dogs may therefore be better suited to examine functional relations between a behavior of interest and environmental, rather than phylogenetic, variables. Given the effects of the environment on within-breed differences in dogs, behavioral assessments and treatments that address the environmental function of problem behaviors may prove especially useful.

8.2. Evaluating scientific evidence for the breed standard and breed categories

Based on our review of existing behavioral research, it appears that – contrary to our hypothesis – breed standards are largely unsubstantiated, for most breeds that have been studied. This is concerning, considering that breed is often used as a predictor of behavior when selecting dogs for working, or service roles, and even companion animals (Bradley, 2011), and schemas or negative stereotypes of particular breeds result in reduced likelihood of adoption from shelters (Wright et al., 2007). For instance, evidence from owner reports and veterinary referrals contradict the

“merry and affectionate” breed standard of the English Cocker Spaniel, which should exhibit an “even disposition” (American Kennel Club, 2012, AKC Meet the Breeds®: English Cocker Spaniel, para. 3). There are some exceptions. For example, Golden Retrievers have been found to exhibit relatively low aggression in numerous studies with a range of methodologies, which is consistent with the “friendly temperament” noted by the American Kennel Club. Definitive conclusions are prevented by the lack of diversity in breeds that have been used in experimental psychological studies, and these should be emphasized over indirect assessments, to provide some measure of cross-validation for the disproportionately large amount of surveys, referrals, and case studies that have examined breed differences in behavior.

A review of the literature on breed differences in behavior also suggests that both traditional and genetic methods of grouping breeds may not be validated by behavioral research, especially with respect to emotional reactivity and cognitive ability. The use of readily observable breed-typical behaviors as a means of defining breeds, or categorizing similar breeds may offer advantages, as some breeds or breed groups exhibit characteristic behavioral conformations that differ distinctively from other breed groups and are assumed to be predatory motor patterns modified under domestication (Coppinger and Coppinger, 1996). These predatory motor patterns include orient, eye, stalk, chase, grab-bite, kill-bite, dissect, and consume, each of which may be hypertrophied, ritualized, or suppressed. For example, livestock guarding dogs must exhibit highly suppressed predatory behavior in order to perform their task without posing a threat to livestock, and thus, rarely exhibit orient, eye, stalk, chase, grab-bite, or kill-bite (Coppinger and Coppinger, 1996). In contrast, hounds have hypertrophied orient, mark (as opposed to stalk), chase, grab-bite, and kill-bite, but lack eye, whereas retrievers exhibit hypertrophied orient and grab-bite but are at fault for kill-bite. Herders possess hypertrophied orient, eye, stalk and chase, but suppressed grab-bite and are faulted for kill-bite. Thus, these readily observable breed-typical behavioral conformations still have ties to the historical roles of breeds, but are more objective and directly exhibited by the dog than the more subjective breed standards that are often difficult to operationalize.

Furthermore, while an individual of a particular breed-type is genetically predisposed to exhibit breed-typical behaviors, the proper rearing environment with appropriate stimuli is also required for the expression of these behaviors (Coppinger and Coppinger, 2001). For example, the unique stalking posture of the Border Collie is exhibited by both trained and untrained individuals, but is refined by both training and experience (McConnell and Baylis, 1985). Given that much of the empirical literature on breed differences assumes phylogenetic determinants of behavior, the examination of breed-typical behaviors may represent a suitable direction for examining ontogenetic factors that contribute to behavioral differences both between and within breeds. In addition, differences in neurotransmitter levels (norepinephrine, dopamine, and epinephrine) have been found between Border Collies, Siberian Huskies, and Shar Plaininetz that are consistent with differences

in their respective predatory motor patterns (Arons and Shoemaker, 1992). More recently, differentially lower serotonin serum levels have been detected in aggressive English Cocker Spaniels relative to aggressive dogs of other breeds (Amat et al., 2013), which may provide a neurological reason for why this breed is often ranked as among the most likely to be seen by veterinarians and behaviorists for human-directed aggression. This is an important area for future research that will result in further scientific progress to understanding breed differences in behavior.

9. Conclusions

Our review of primary literature, empirical data, and published veterinary and public safety records, suggests that differences in behavior are evident among breeds of dogs. However, substantial within-breed differences in behavior also exist—even in the most controlled experimental studies. Breed differences in behavior are therefore influenced by both genetics, and by the environment and experience. Although breed and breed-group differences in behavior is evident in many cases, there is little evidence that these behavioral differences correspond to conventional and genetic categorizations of breeds. A more useful method of categorization may be based on directly observable breed-typical behaviors, which are genetically inherited, tied to historical roles of the breed, and can be modified by experience within an individual's lifetime. Different methodologies influence the results of studies, such that studies using owner-based surveys are more likely to conclude breed differences exist than experimental studies, likely due to the relatively small sample size and breed diversity in the latter. Interpretation of surveys conducted between different countries should be done carefully. Behavioral scientists need to be aware of the limitations of working with pet dogs with various rearing histories. Behavioral research is limited in its ability to make claims about breed differences for three major reasons. First, definitive claims about breed differences in behavior cannot be made without realizing that behavior is the outcome of complex interactions of phylogeny and ontogeny. Second, the large number of breeds to be examined today simply discourages inquiry in behavioral research; and finally, the definitions of many behavioral traits are subjective and structural, rather than objective and functional. It is the responsibility not only of researchers in the field of canine behavior and genetics, but also of professionals who work with dogs, including veterinarians, dog owners, breeders, obedience trainers and handlers of service dogs, and other parties interested in the effectiveness of breed-specific legislation, to address these issues if we are to further our understanding of the many different dog breeds that exist among us in the world today.

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