

CHAPTER 1

Introduction to dog behavior

Julie Hecht¹ and Alexandra Horowitz²

¹ Department of Psychology, The Graduate Center, City University of New York, Horowitz Dog Cognition Lab, Barnard College, New York, USA

² Department of Psychology, Barnard College, New York, USA

Domestic dog evolution and behavior

Dog evolutionary history

What is a dog? The answer can come in the form of a description of the dog's characteristic behavior, physical description, or evolutionary history. We will begin with the latter. The domestic dog, *Canis familiaris*, is a member of the Canidae family, genus *Canis*, along with such territorial social carnivores as the gray wolf (*Canis lupus*), the coyote (*Canis latrans*), and the jackal (e.g., *Canis aureus* and *Canis mesomelas*). The dog is the only domesticated species of the genus: that is to say, the only canid for whom artificial selection (selective breeding) by humans has usurped natural selection as a prime mover of the species.

A debate rages about how long ago, and where, a distinct species of dog appeared, given conflicting evidence from archeological sites and genetic analyses. There is much more agreement on one point: that dogs descended from wolves. *Canis lupus*, the present-day gray wolf, is the domestic dogs' closest living ancestor, as both species are descended from some proto-wolf some tens of thousands of years ago. Archeological evidence suggests that the divergence between wolf and dog began up to 50,000 years ago, with the advent of early human agricultural societies (Clutton-Brock 1999). Whether the divergence was a singular, one-time event or whether it happened at different times and multiple locations is still in debate (e.g., Boyko *et al.* 2009; Larson *et al.* 2012; Thalmann *et al.* 2013). Genetic evidence, from mitochondrial DNA, suggests that wolves and dogs began diverging much earlier, even 145,000 years ago (Vilà *et al.* 1997).

Dogs' domestication probably began with a human interest in animals who were relatively docile, perhaps willing to approach—or at least not flee from or attack—humans. The social nature of canids contributes to their interest in others, as well as the proto-dogs' flexibility in seeing humans as nonthreatening. This hypothesis was famously tested by the geneticist Dmitry Belyaev by creating a kind of “domesticated” fox out of a Siberian farm-fox population simply by selectively breeding only

those who reacted without fear or aggression to human approach. Over 40 generations, he had created foxes which looked and acted in many ways like familiar domestic dogs (Belyaev 1979; Trut 1999).

For millennia, dogs were bred for use for tasks (e.g. guarding and hunting) or as companions. Quite recently, in the 19th century, artificial selection began to be driven by an interest in creating pure breed lines, for show and competition in dog “fancies,” dog shows. Thus, the diverse array of breeds seen today is a result of specific breeding over the last century and a half for physical traits and temperament which suited the newly formed breed “standards” (Garber 1996). While some current dog breeds resemble ancient representations of dogs in art, no breed can be traced to those ancient dogs. As we will discuss, the diversification into breeds, some with exaggerated physical features, has led to the rise of inherited diseases which can be painful or even fatal (Asher *et al.* 2009). Isolated populations of purebred dogs now serve as useful models for naturally occurring cancers and diseases found in both humans and dogs (Breen & Modiano 2008).

Dog behavior in an evolutionary context

The story of domestication is informative because it gives the observer of dog behavior the background with which to interpret what she sees. That is, the dog is by no means a wolf but will share some behaviors with present-day wolves. Present-day dogs are highly designed by humans, have many behavioral and physical traits as a direct consequence of this design, and the affiliation between dogs and people is longstanding. Dogs are veritably members of human society and families (Horowitz 2009c).

Knowledge of the behavior of dogs' wild cousins, gray wolves, helps give clearer explanation for many common dog behaviors. For instance, viewed in the context of a human family home, a dog's propensity to sniff at the genital area of visitors to the home may seem odd, intrusive, or even “impolite.” Viewed in the context of canid social interaction, though, it is clear that the dog's sniffing is analogous to all canids' olfactory

investigation of the genital and anal areas of conspecifics (Sommerville & Broom 1998). These regions are rich with glandular secretions which carry information about the identification, and perhaps recent activities and health, of the individual. The dog in the human household is simply trying to find out about this human visitor (Filiatre *et al.* 1991).

Another dog behavior, the dog's licking of an owner's face upon the owner returning home, is commonly viewed as an expression of love. Indeed, many owners refer to this behavior as dog "kisses." Looking at wolf behavior again clarifies the interpretation. Wolves, living in family packs, approach and greet any wolves who are returning to the pack after hunting. The packmates lick—"kiss"—his or her face. Their licks are prompts for him to regurgitate some of the kill that he has just ingested. Similarly, a dog's "kiss" is a greeting, to be sure, but it is also a vestigial interest in whatever it was an owner might have consumed since leaving the house (Horowitz 2009c).

On the other hand, dogs' artificial selection history is explanatory of important differences in the behavior of wolves and dogs. Foremost among them is the dog's ability to (and desire to) look at the eyes of humans for information or to solve a problem. Since mutual gaze is a vital part of human communication, dog behavior which seemed to match this human behavior may have been preferred and selected (Horowitz & Bekoff 2007). Indeed, the modern dog's eyes are more rounded and forward-facing than those of wolves (Clutton-Brock 1999), and their faces have many neotenuous (baby-like) features which human adults are predisposed to find appealing and human-like (Hecht & Horowitz 2013). The dog's eye-gaze enables much of the species' success at tasks of social cognition, such as following a human's gaze or pointing arm or hand to a source of food or interest (e.g., Agnetta *et al.* 2000; Soproni *et al.* 2001), something characteristic of human-human interaction but quite unusual in nonhuman animal populations, in which to stare at another's eyes is a threat (Fox 1971).

An understanding of the development of different dog breeds, and each's use and habitual behaviors, is also explanatory in looking at the "average" dog's behavior. In early domestication, breeding would have been somewhat haphazard, but by the time of the Romans, there were physically distinct breeds bred for particular functions: as guard dogs, sheep dogs, and companion (lap) dogs (Clutton-Brock 1995). The kinds of breeds and the uses for breeds multiplied in the Middle Ages and through the present day extending to employing dogs as both herders and as guarders of livestock; as hunting dogs—tracking, pointing at, or retrieving game; as load-carriers (e.g., sled dogs); as assistance dogs (in guiding blind persons or aiding those with other physical disabilities); and as therapeutic companions. In some cases, successful job performance may require extensive breeding (sled dogs) or training (glycaemia alert dogs) (Huson *et al.* 2010; Rooney *et al.* 2013).

When selective breeding for physical traits and behavioral tendencies of specific, named purebreds began in earnest, in the late 19th century, modifications occurred which, while useful in carrying out the desired task, may be undesired in nonworking contexts. Moreover, given the degree of inbreeding, these behaviors are often intractable and tenacious (as described further in section "Breeds and behavior"). Even in mixed breeds, some degree of these behavioral tendencies may endure.

Dog interspecific social cognition

Among social species, dogs are unique: They have the potential to interact as smoothly with a separate species as with their own. *Canis familiaris* and *Homo sapiens* engage together in everything from the seemingly mundane—sitting side-by-side on a park bench—to the complex—running an agility course, working together to detect explosives or locate animal scat, or alerting a deaf person to a ringing telephone. Even village dogs, who often retreat when approached by humans, live in the vicinity of people (Ortolani *et al.* 2009).

Companion dogs are often described by owners as having clear constructed identities, particularly that they are "minded, creative, empathetic, and responsive" (Sanders 1993). Relationships with dogs run so deep that they are sometimes mentioned in obituaries along with other survivors of the departed (Wilson *et al.* 2013)—suggesting that for many, dogs are placed within the familial structure (Hart 1995).

Magic is not behind humans' feelings of connectedness toward dogs. Instead, companion dogs display social behaviors that support and reinforce the relationship, such as sensitivity to human actions and attentional states, and acting in accordance with humans in coordinated and synchronized ways. For example, dogs unable to access a desired item will alternate their gaze between the item and a nearby person (i.e., the behavior dogs perform when a ball rolls under the couch and you ultimately get it for them) (Miklósi *et al.* 2000). Dogs readily respond to human communicative gestures, whether stemming from our hands, face (e.g., eyes), or other body parts (Reid 2009). Dogs take note of our attentional states, particularly eye contact as well as head and body orientation—a dog being more likely to remove a muffin from a countertop if an owner's back is turned or eyes are closed than if the owner is sitting in a chair with eyes fixed on the dog (Schwab & Huber 2006). Dogs also attend to the tone of human voice and behave appropriately (according to humans) when spoken to in a cooperative or a forbidding tone (Pettersson *et al.* 2011).

While training can enhance a dog's ability to perform in social interactions (e.g., guiding-eye dogs and detection dogs), there are everyday examples of dogs showing complex, synchronized social exchanges with people. Kerepesi *et al.* (2005) found that companion dogs—not specifically trained—were able to engage in a cooperative interaction with their human partners that allowed for the completion of a joint task. In this study, people

asked their dog for blocks to help them build a tower, and dogs provided the blocks in a nonrandom fashion that indicated cooperation. Similarly, companion dogs show a great deal of social anticipation, which can enhance synchronization and feelings of mutual cooperation. Dogs even adopt new routines established by people, such as a short, pointless detour made by owners upon returning home after a walk (Kubinyi *et al.* 2003). Over time, dogs in this study even began to perform the pointless detour before their owner. Social coordination is also found in play, a common inter- and intraspecific activity. Play is essentially marked by coordinated movements and synchronized interactions. Dogs and humans attend to each other's play signals, and a dog's play bow—or a person's play lunge—is responded to meaningfully (Rooney *et al.* 2001).

While popular media often spotlight breed differences relating to social behavior, trainability, or “intelligence” (Coren 2006), research is mixed as to how artificial selection affects companion dog performance in human-guided tasks. In one study, dogs bred for cooperative interactions outperformed those bred for independent work on a human-guided task to locate hidden food (Gácsi *et al.* 2009). At the same time, there can be substantial differences between dog lines still selected and maintained for the original function and members of the breed not under continued election for performance (i.e., the difference between show dogs versus field dogs). In another study, subject dogs' ability to follow a human-demonstrated detour was independent of breed (Pongrácz *et al.* 2005). Udell *et al.* (2014) found that breed-specific predatory motor patterns predicted dog success in following human pointing gestures, with Border Collies and Terriers outperforming Anatolian Shepherds, a breed selected for behavioral inhibition. At the same time, Anatolian Shepherds significantly improved their performance with little training. On that score, Border Collies Betsy, Rico, and Chaser have been empirically shown to possess extraordinary facility with human language, but so too have Bailey (a Yorkshire Terrier) and Sofia (a mixed breed) (Hecht 2012).

Dog interspecific attachment

Another meaningful mechanism underlying the dog–human relationship is that of *attachment*, a concept initially introduced to describe the affectionate bond between a human infant and a caregiver (Bowlby 1958). Initial examination of attachment relied on the “Strange Situation Test” (SST), a behavioral experiment in a novel environment designed to investigate specific behaviors from the infant toward the mother as opposed to a stranger (Ainsworth & Bell 1970). Attachment is evidenced through infant “behavioral preferences” for a figure of attachment (e.g., mother), such as proximity maintenance, distress upon separation, as well as comfort and increased exploration in her presence.

Ethological studies suggest that attachments form in many species, not just humans. A modified version of

the SST was conducted between dogs and their owners (Topál *et al.* 1998). Like infants, dogs showed activation of attachment systems when in the presence of a stranger versus their owner, as well as the “secure base effect” where dogs were more likely to explore their environment in the presence of the owner than a stranger (Horn *et al.* 2013).

Subsequent studies found that for dogs, attachments can form later in life and even multiple times. Shelter dogs participated in the modified SST with someone assigned the role of “stranger” and another person assigned the role of “owner” (designated by three short interactions with the dog). Shelter dogs showed similar attachment behavior toward the newly appointed “owner” (Gácsi *et al.* 2001). Service dogs, like guide dogs for the blind, experience numerous early-life relationships and show attachment behavior toward their subsequent blind owner, who they met later in life (Fallani *et al.* 2006; Valsecchi *et al.* 2010).

These studies appear to be in tension with the initial assumption that for human-directed attachments to develop, dogs should be brought into the new owner's home at 8 weeks of age (Scott & Fuller 1965). Instead, while it is recognized that early-life exposure to humans is important for normal *social* development, dog *attachment* relationships can form later in life, multiple times, and toward multiple people.

Physiological mediators also underlie dog–human relationships. The peptide hormone oxytocin (OT) is involved in affectionate bonds and may help to mediate dog–human social behavior. For example, Kis *et al.* (2014) found an association between OT polymorphisms and human-directed social behavior in German Shepherds and Border Collies. Owners and dogs who engage in petting and light play both show OT increases (Odendaal and Meintjes 2003). While simply seeing a known person can raise dog OT levels, it is often the *quality* of the interaction that matters. Rehn *et al.* (2014) found that a familiar person engaging in “physical and verbal contact in a calm and friendly way” when greeting a dog was associated with a *sustained* increase in dog OT levels. In another study, owners who engaged in longer periods of gaze with their dog and reported a higher degree of satisfaction with their dog had increased OT levels over owners who did not report similar satisfaction and did not display high levels of gaze (Nagasawa *et al.* 2009). (Importantly, while owner OT levels increased, dog hormone levels were not examined, and it is plausible that what is enjoyable for people is not always the same for dogs, such as prolonged or persistent direct eye contact.) At the same time, Jakovcovic *et al.* (2012) found that dogs characterized as highly sociable gazed longer at an experimenter's face, even when the behavior (gaze) was no longer being reinforced.

Dog relationships with conspecifics and other nonhuman species appear to differ from the relationships dogs form with humans. Behavior toward the dam and members of a litter are not customarily described as

attachment relationships (Pettijohn *et al.* 1977). A study of older dogs living in the same house did not find behavioral indicators of an attachment bond between cohabitating dogs, although activation of the stress response was reduced when in the presence of the companion dog (Mariti *et al.* 2014). On the other hand, in a novel setting, shelter dogs showed diminished stress response, not in the presence of known kennelmates, but in the presence of a known person (Tuber *et al.* 1996). At the same time, when a companion dog dies, some owners report behavioral change on the part of the remaining dogs, such as change in appetite, sleeping, solicitation of affection, and use of space (Schultz *et al.* 1995; Walker *et al.* 2013).

Taken together, dogs have complex and long-standing relationships with members of their own and other species. They have preferred play partners (Ward *et al.* 2008) and engage in mutual resting and grooming with members of their own and other species—for the latter, particularly if the non-dog species was introduced early in the dog's life (Fox 1969; Feuerstein & Terkel 2008). Dogs can have meaningful and successful lives within the human environment, and their potential for success starts from the very beginning of life.

Dog development and behavior (early and late life)

Unlike *precocial* species (e.g., zebras, sheep, and some birds), born capable of moving around and caring for themselves soon after birth, *altricial* species (e.g., canids and humans) require substantial dependent care while they pass through a number of developmental stages in their first months of life. This time is marked by physiological maturation and the growth of sensory abilities that facilitate structured motor patterns and, ultimately, the presentation of adult dog behavior. During this time of intense physiological and sensory development, dogs are most malleable. They are essentially sponges, taking in information and readily updating and changing their behavior.

While the natural ecological niche for dogs is the human environment (Miklósi 2007), within this general environment, dogs are exposed to a wide diversity of anthropogenic settings. For example, there are an estimated one billion dogs on the planet, and the majority live as stray or village dogs (Lord *et al.* 2013): They live on the streets, scavenge from human refuse sites, and move and interact with conspecifics and other species on their own accords. In other parts of the world, dogs have entirely different surroundings and different roles to play. Dogs live in over one-third of US homes (AVMA 2012); many sleep in a bed with a person at night and are expected to stay home, possibly alone, during workdays (Horowitz 2014). Companion dogs are often expected to be leashed, urinate, and defecate in specified locations and interact (in a “civilized” manner) with a changing array of conspecifics and people. As mentioned, dogs can also perform a wide variety of

working functions, and some dogs serve as subjects in medical labs. What is expected of dogs varies considerably based on the specific human environment in which the dog finds himself. Early-life experiences are instrumental to successful environmental integration.

In these early months, young puppies need considerable social support and stimulation—both from conspecifics and from humans—in preparation for the expectations that will be applied to them. The support and environmental inputs that puppies do or do not receive affects their developing personality and later behavior. A 20-year study at the Jackson Laboratory in Bar Harbor, Maine, set out to explore the behavioral and genetic underpinnings of behavior. The researchers found that “critical” or “sensitive” periods of development—specific weeks or months in which dogs develop particular abilities—along with early-life environmental inputs, were instrumental to normal development (Scott & Fuller 1965).

While developmental periods have a clear progression (a dog will not play bow before it has opened its eyes), transitions between each stage are more gradual than initially thought (Bateson 1979). The following periods are instead guidelines—without hard-and-fast beginning and end points—and individual dogs will move quicker or slower from one phase to the next. Rates of development (heterochrony) can differ between breeds as well as between individuals.

Neonatal period: birth to approximately week 2

Dogs enter the world unable to survive on their own. Direct contact with the mother, the dam—who provides food and initiates elimination by tactile stimulation—allows pups to proceed with physical and neurological development. Neonatal pups are without vision, hearing, or coordination and rely on tactile and simple olfactory sensations (Scott & Fuller 1965; Lord 2013). Unable to self-regulate temperature, newborns spend most of their time sleeping and in physical proximity with the dam and littermates. Although most elements of their sensorium are underdeveloped, neonatal pups appear responsive to olfactory cues. Wells and Hepper (2006) found that neonatal pups (tested at 15 min and 24 h after birth) preferred water with the flavor aniseed when the dam had consumed aniseed during the pregnancy. Puppies did not show similar preference for vanilla, a different novel scent that the dam had not been exposed to—suggesting that gestational exposure (which has also been found in other mammals) is behind this neonatal preference.

While the majority of the neonatal period is spent prostrate (in a flat, pancake-like pose), newborn pups show behaviors associated with attaining food: “kneading” or “swimming” behavior directed at the teat or milk source. They also show discomfort: If isolated, pups display distress vocalizations, high-pitched calls—whines or yelps—that are frequently described as care-soliciting behavior (Elliot & Scott 1961). These early vocalizations later transform into other vocalizations

that are contextually similar. For example, adult dogs produce high-pitched, high-frequency “alone barks” that may also elicit attention (Yin & McCowan 2004; Pongrácz *et al.* 2006).

Transitional period: week 2 to week 3

The maturation process of the first few weeks of life becomes more evident at 14–21 days, when puppies spend less time in a flat, pancake state and more time moving toward presenting typical dog-like behavior. Pup eyes and ears open, allowing for a startle response (Scott 1958). Motor patterns and social behaviors like walking and tail wagging begin, as do rudimentary elements of play. Because of dog’s increased sensorium, now is the time to start introducing novel items, and “exposing puppies to normal household sounds, smells, and sights; daily handling; petting; and gentle brushing” (Case 2005).

Sensitive or Socialization period: week 3 to weeks 12–14

This is a period of considerable growth (particularly of species-specific social behaviors) and many experiential and learning opportunities. Socialization is described as the process of adopting “behavior patterns appropriate to the social environment in which [an individual will] live, allowing them to coexist/interact with other individuals” (Blackwell 2010). Attention to a dog’s individual experiences during this period, particularly a dog destined for companionship, is essential.

Motor patterns develop and adult-like behaviors are expressed in a more coordinated manner. Social behaviors like approach and avoidance emerge, as do tail wagging, growling, and additional play behaviors (Bekoff 1974). Vocalizations become more complex and are incorporated into social situations. Adler and Adler (1977) suggest that as soon as puppies have the physical capacity to recognize conspecifics, social learning is possible. Puppies who watched their mother perform in narcotics detection during this developmental period were more likely to work in narcotics detection themselves (Slabbert & Rasa 1997). Pups also show attention to and interest in humans which includes affiliative, social behaviors like approach and tail wagging. Dog propensity to follow human gaze or pointing cues increases as dogs age (Riedel *et al.* 2008; Dorey *et al.* 2010).

Dogs are weaned in the first part of this period, between approximately weeks 4 and 8, though there are considerable individual differences in weaning behavior even within breed (Rheingold 1963). A study of the weaning of German Shepherd puppies and their dams found that when puppies attempted to nurse, dams responded with “inhibited bites” or growls, mouthed threats, nibbles, and licks (Trivers 1974). In response, pups showed social behaviors, such as withdrawal and passive submission (Schenkel 1967). Dams also began to show “inhibited bites” toward puppies during play. Such social experiences are important for later social exchanges, see Appendix A.7.

This period is commonly referred to as a “sensitive” social period because pups can notice and interact with other species and novelty without hesitation—particularly before 5 weeks of age. Dogs show considerable exploratory behavior and approach novelty without hesitancy between 3 and approximately 5 weeks. As they grow, they can show hesitation to novel stimuli, and at about 8–10 weeks, this change magnifies, and some puppies display decreased comfort with new stimuli, like people, sounds, objects, and contexts (Case 2005). This presentation of fear could be modulated by both genetics and early-life experiences (Freedman *et al.* 1961; Uhde *et al.* 1992), and caution should be taken against exposure to noxious stimuli and situations, particularly during weeks 8–10.

Socialization in dogs

Socialization from week 3 to about week 14 is paramount. The American Veterinary Society of Animal Behavior recently issued a Position Statement recommending puppies start socialization classes early as 7–8 weeks and with a minimum of one set of vaccines (AVSAB 2008). As in other social mammals, early-life restrictions—both environmental and experiential—hinder later-in-life behavior and coping strategies and are associated with fear and anxiety (Scott & Fuller 1965). For example, puppies exposed to premature maternal separation were found to show higher prevalence of “destruction of objects, excessive barking, fearfulness on walks, fear of noises, possessiveness of toys, attention seeking, aversion towards people of unusual appearance, play biting, tail chasing, pica, possessiveness of food, aggression towards unfamiliar people, and house soiling” than control dogs who remained with dams until 2 months of age, that is, through weaning (Pierantoni & Verga 2007).

Daily tactile contact is important, and there are benefits to starting even earlier than the third week. Daily gentle tactile stimulation and handling of puppies’ bodies between days 3 and 21 was associated with more exploratory behavior when alone, and such puppies were less quick to vocalize than puppies that were not handled (Gazzano *et al.* 2008). Daily engagement of the senses promoted dogs who were more active, sociable, and less neophobic than puppies not handled as such (Fox & Stelzner 1966).

Careful, early exposure to potentially noxious stimuli could help with later-in-life coping. Newborn rats handled and exposed to mild stressors showed less stress activation and more exploratory behavior than unhandled rats when exposed to novelty as adults (Núñez *et al.* 1996). Pluijmakers *et al.* (2010) found that exposing puppies to audiovisual playback—consisting of animate and inanimate objects and noises at normal volume—between 3 and 5 weeks of age was associated with decreased fear to novel objects and unfamiliar settings. Puppies without exposure to the audiovisual condition show increased crouching, increased arousal—as indicated by rapid tail wagging—and increased locomotion, all of which are

associated with stress or fear (Beerda *et al.* 1997). This early-life exposure is aimed to combat the fear response that can develop after 5 weeks. Still, socialization should not be performed by throwing dogs off the deep-end and into overstimulating situations, such as street fairs or lengthy social gatherings. Small doses of successful and enjoyable experiences are key, and dog behavior should be continually monitored for low-level indications of discomfort and distress (see section “Patterns of communication”). Classical and operant techniques can be used to increase comfort during socialization.

Because of the importance of inter- and intraspecific interactions and exposure to stimuli and social experiences, shelters with puppies under their care should prioritize early-life socialization or find appropriate housing outside the shelter that can.

While restricted early-life environments can elicit profound behavioral changes in dogs, there is room for later-in-life behavioral flexibility. A recent study found that dogs who had lived in commercial breeding establishments, commonly referred to as “puppy mills” or “puppy farms,” were described by subsequent owners as displaying higher rates of “fear, house-soiling and compulsive staring” than a matched sample of dogs (McMillan *et al.* 2011). In 2013, the American Society for the Prevention of Cruelty to Animals (ASPCA) began a study investigating whether exposing fearful dogs to in-shelter counter-conditioning, habituation, and desensitization training plans could effectively mitigate dogs’ fear response before being placed into homes (ASPCA 2013). The ongoing success of the programs is a reminder that while experiences during early life are important to later-in-life behavior, dogs are malleable even beyond the sensitive period of socialization.

Aging dogs

The behavior and cognition of aging dogs is not typically considered part of the stages of dog behavioral development, but the realities of aging can be incredibly important to dog well-being. Just as young dogs undergo notable changes early in life, so do they experience changes later in life. Since adult and aged dogs are members of the shelter population (Shore & Girrens 2001), their unique position in life, as it relates to normal, successful aging versus cognitive dysfunction, merits consideration.

Considering age-related changes in dogs, researchers are attempting to discriminate the normal aging process from canine cognitive dysfunction. Some describe the behavioral changes resulting from normal aging as a “rate of cognitive deterioration that does not affect the day-to-day functioning of the individual” (Salvin *et al.* 2011). Owners of dogs 8 years and older describe certain trends associated with normal aging, such as deterioration of “play levels and response to commands” and increase in “fears and phobias.” Older dogs showed less enthusiasm “for eating and chewing” and an increase in water consumption, most likely as a function of

age-related health factors like teeth and mouth diseases, as well as renal problems.

Cognitive dysfunction, on the other hand, is characterized by behavior changes relating to deterioration of cognitive functioning and recognition, and the acronym DISHA describes changes like “Disorientation, altered Interactions with people or other pets, Sleep–wake cycle alterations, House-soiling and altered Activity level” (Landsberg *et al.* 2003). These challenges can play out in increased destructive behavior, house soiling, and increased vocalizations, unrelated to earlier-life behavior (Chapman & Voith 1990). These changes, particularly relating to memory, have made dogs models for human aging and dementia (Cummings *et al.* 1996). As in humans, therapeutic products are being tested and developed to treat cognitive dysfunction in senior dogs, some with validated efficacy (Landsberg 2005).

Normal dog behavior

Listen to people talk about companion dogs, and you are apt to hear descriptors like “crazy” or “bonkers.” While anyone who has ever lived with a dog might commiserate and find these labels at times appropriate, the labels do not offer much insight into what the dog is actually doing. Is the dog heating up a frying pan and preparing brunch for the family? That would be “crazy.” When the doorbell rings, does the dog assume the role of Olympic runner and high-jumper, taking laps around the living room and finishing the routine by jumping on entering guests? This is less “crazy” and more *normal* dog behavior performed in a context not always appreciated by humans.

What is behavior?

Dutch ethologist Niko Tinbergen—cowinner of the 1973 Nobel Prize in Physiology or Medicine—proposed an integrated approach to the study of behavior, characterizing two kinds of questions that researchers may ask and attempt to answer. “Why Questions,” commonly described as questions relating to ultimate causes of behavior, explore evolutionary forces behind behavior; “How Questions,” or questions relating to proximate causes of behavior, focus on a behavior’s immediate prompts, in both mechanistic and developmental terms (Tinbergen 1963). This approach, accepted by most researchers as a sound guide, expects that an individual’s behavior is a product of an individual’s life experiences (proximate explanations) and evolutionary history (ultimate explanations).

Thus, dog behavior can be framed first in the context of their species-specific characteristics: a gregarious, social canid with behaviors that support both inter- and intraspecific communication, as well as a species affected by recent artificial selection on the part of humans. Additionally, proximate factors such as dog individual life experiences and individual development are relevant for dog behavior.

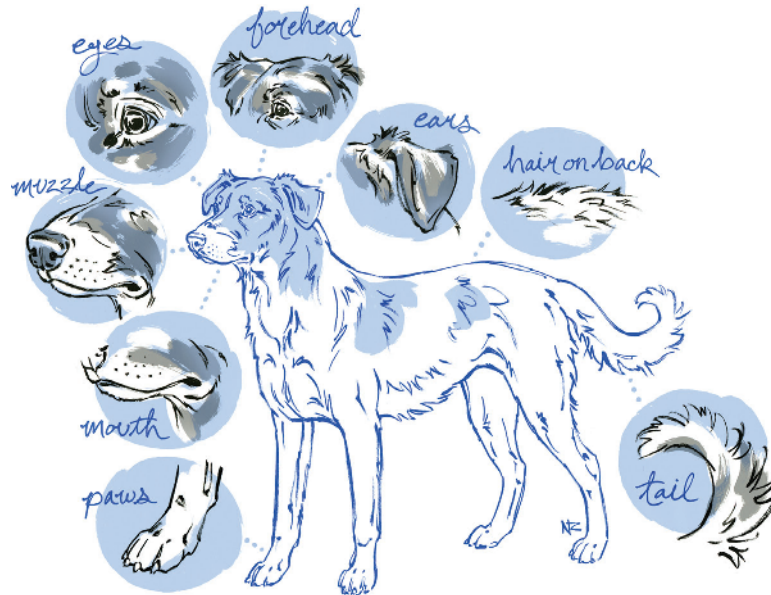


Figure 1.1 Know where to look for clues. Reproduced with permission of Natalya Zahn. © Natalya Zahn.

Dogs, like all species, come with a “normal” repertoire¹ of things they do, that is, possible behaviors. To name a few, dogs have the potential to play growl, sniff, and run in circles, but they cannot fly or sleep underwater. Even when a dog witnesses a bird flying, he cannot learn to perform that behavior. Underlying the concept of “normal” behavior is the concept of “behavior” itself. Behavior does not have a universally accepted definition (Levitis *et al.* 2009), although Tinbergen offers that behavior is “the total movements made by the intact animal” (Tinbergen 1951). This definition does not ignore that physiological processes (neuronal firing, hormone secretion, etc.) underlie behavior, but it does highlight that behavior is observable and measurable, which makes the study of dog behavior within reach.

There are many ways to scientifically describe dog behavior (see Miklósi 2007 for review). Species-specific behavior can be split into different categories, often determined by the topic of interest (Altmann 1974; Martin & Bateson 2007). For example, a dog could be described as engaging in “locomotion” to describe any type of lateral or vertical movement, or movement could be described based on quality—such as walking, running, or trotting. Behaviors can be examined separately, a “yawn” or a “paw raise,” or pooled together to describe behavioral states such as “play” or “aggression.” Behavior can also be described by its sequence as well as frequency, duration,

and intensity. Dogs mainly engage in visual, acoustic, and olfactory communication, and each plays an important role in inter- and intraspecific communication.

Visual communication

The initial step to visual communication is knowing which parts of the body convey meaningful information. For example, unlike peacocks in which eyespots or train length could affect mate choice (Petrie *et al.* 1991; Hale *et al.* 2009), a dog’s piebald facial coloration is apparently not an informative detail in dog–dog visual communication but is instead a by-product of domestication (Trut 1999). Instead, other body parts and visual signals are meaningful in canine communication (Figure 1.1).

Behavior not morphology

The body parts that contribute to visual communication merit discussion because research finds that people do not readily look at actual dog behavior. Instead, dog physical appearance, not behavior, often captures people’s attention. Physical appearance has been associated with dog adoption rates (Weiss *et al.* 2012), and physical appearance has been shown to be responsible for personality attributions. One study found that an image of a yellow-coated dog was rated as more agreeable, conscientious, and possessing emotional stability than an image of the same dog with a black coat (Fratkin & Baker 2013).

¹p. 21 “normal” repertoire: Behavior described as “abnormal” usually describes a normal behavior that is performed at a rate or frequency that impairs normal functioning. A dog who spends considerable time spinning in circles at the expense of other activities, like resting, eating, or playing, would be described as performing an abnormal behavior. Note that tail-chasing is not in and of itself abnormal.

In another study, attributions to dogs differed based on who the dog was with. Place a pit bull-type dog with an elderly woman or child, and people offered more positive ratings of the dog than if the dog was with a “rough” male (Gunter 2013). Furthermore, Horowitz and Bekoff (2007) suggest that people are attracted to dogs that exhibit seemingly human-like characteristics, such as flexuous facial features like raising the eyebrows or appearing to smile, both of which have been supported by recent studies (Hecht & Horowitz 2013; Waller *et al.* 2013). Overall, people construct meaning out of the way dogs look, often to the neglect of the way dogs behave.

Tails

If there is a body part people do take note of, it is the tail (Tami & Gallagher 2009). Charles Darwin points out that it is hard for a human to ignore a tail held high or one that is tucked deep beneath (Darwin 1872). Tails are mobile and can assume a range of heights and positions or swing at different speeds, each providing different information. At the same time, recent research finds that tail use might be even more complex and nuanced than initially thought.

Tails hold important information, especially in dog–dog communication. Simply the absence of the tail can affect communication, as can docked tails. Researchers who designed a mechanical dog outfitted with tails of different lengths (long or short) which were able to move or be still found that dogs were more likely to approach the robot dog when the tail was long and wagging as opposed to when it was long and still (Leaver & Reimchen 2008). Absent any other communicative cues, a wagging tail in this context appears to be interpreted by dogs as “friendly.” On the other hand, a short tail, whether still or wagging, was approached similarly, suggesting that short tails might be harder for dogs to interpret.²

The direction of a tail wag is also an informative detail. Tails that wag more to the right or left side of the dog’s body are called “lateralized” and may be connected to the dog’s emotional state. Typically, movements on the left side of the body correspond to right-hemisphere brain activation, and movements on the right side of the body correspond to left-hemisphere brain activity. Generally speaking, these hemispheres of the brain are associated with different behavioral outputs—approach (behavior on the right-/left-hemisphere activation) or avoidance (behavior on the left-/right-hemisphere activation) (Rogers 2009). For example, chicks forage for food with their right eye (left-hemisphere activation, i.e., approach) and look for predators with their left eye (right-hemisphere activation, i.e., avoidance) (Rogers 2000).

Dogs presented with stimuli of positive valence, such as an owner, wag more to the right side, or left-hemisphere

activation (i.e., approach), whereas an unknown dog prompts more left-bias wags, or right-hemisphere activation (i.e., avoidance) (Quaranta *et al.* 2007). While this research has been extended to suggest that dogs can even attend to the side of another dog’s tail wag (Siniscalchi *et al.* 2013), it remains unclear whether dogs in real-life settings are picking up on these subtleties.³

Dog tails vary in flexibility and expressiveness, and some are not easily seen, either because of breeding or other human interventions (Bennett & Perini 2003). Other tails have a normal position that is curled, tucked, or naturally falling to one side. Because of their variable physical appearance, tail movement is studied from the base, not the tip, and tail-wagging musculature moves the rump more than the tail.

The base of the tail, closest to the dog’s rump, gives details as to whether the tail is being carried along the midline or is raised or tucked. Relaxed tails are commonly held in a neutral position, extending from or dropped below the midline, although the “neutral position” will vary from dog to dog. Generally speaking, a high tail indicates excitement or arousal, and a high tail can be seen in a variety of approach-oriented behaviors, ranging from greeting and playing to fighting and threatening (Kiley-Worthington 1976). Tucked tails, on the other hand, indicate some degree of fear, submission, or appeasement. Tails can be held in a stiff, still position at all heights and could be the dog’s natural tail or a postural display. Stillness is common in dog interactions: For example, play incorporates many pauses interspersed within fluid movements and play signals. But a still tail without such indicators could suggest fear or aggression.

Probably, the most noticeable and heavily generalized part of the tail relates to movement. “A wagging tail indicates a happy dog,” it is often stated. If only it were so simple (or true). A tail wagging wholeheartedly, fluidly, and generously from side to side (usually at the level of the midline) is most readily associated with greeting or excitement. This is the “happy” tail we are so familiar with, and it might be accompanied by jumping, licking, running in circles, or other behaviors of arousal.

A tail wagging low and quickly indicates nervousness or timidity. Again, the tail is wagging, but its position and rate could indicate fear, submissiveness, or a dog in conflict—sometimes referred to as a “mixed motivational state.” Dogs who perform a low wag upon being approached, and then flip over to expose their underside, are displaying *passive submission*; for other dogs, a low wag and a low body posture are part of their normal greetings and are part of *active submission* (Schenkel 1967). A low wag should not be

²p. 24 *interpret*: Models are useful in the study of dog behavior insofar as dogs treat representations—to varying degrees—like their real counterpart. This can prove useful in applied or experimental investigations, such as intra-dog aggression, where dogs are apt to display similar behaviors toward a stuffed dog as they would toward a real dog.

³p. 25 *subtleties*: The field of lateralized behavior continues to grow and extend to practical applications. Dogs who ultimately succeed in guide-dog training tend to exhibit a right-paw preference and counterclockwise chest whirl (Tomkins *et al.*, 2012). Dogs lacking a paw preference are apt to be more sound-sensitive than dogs with a paw preference to either side (Branson and Rogers, 2006).

considered in isolation because its meaning takes shape only in the context of the dog's entire body. Low wags should always be considered within the dog's environmental context and behavior as a whole. High, fast wags indicate arousal, but they should also be viewed with some caution. Arousal can take different forms, such as general excitement, interest in interacting, or even aggression. There are many individual variations of tail wag—circling; going more counterclockwise than clockwise; banging—but whose meaning or significance has not been studied (and should not be assumed).

Overall, tail behavior should be considered in relation to the tail's normal, relaxed position, which will differ from dog to dog. For dogs in a shelter, watching the tail and its postural changes over time can provide a better estimation of the "neutral" tail position for that dog. The nuances of dog tails are important to learn and convey to the general public.

Piloerection

Piloerection is a physical response akin to getting goose bumps. Hackles tend to raise (i.e., hair tends to stand up) in areas from the base of the tail to the shoulders and down the spine. While it can be a meaningful indicator that a dog is excited (either happily or in alarm), this behavior is not within the animal's control (London 2012).

Research has not specifically investigated whether raised hackles is associated with different emotional states, although it is often associated with aggression or fear. The location of the raised hackles may be informative about an underlying emotional state: Some suggest that hackles raised near the base of the tail could be associated with "a high level of confidence" and a dog "more likely to go on the offensive" (London 2012). On the other hand, piloerection around the shoulder region may suggest that the dog is fearful, and hackles raised by both the shoulders and the base of the tail could indicate "an ambivalent emotional state and feeling conflicted" (London 2012).

Because raised hackles indicate arousal generally, the presence and location of piloerection should be considered in conjunction with ear, tail, and mouth position and overall body leaning and posture to assess the specifics of that aroused state.

Ears

Like the tail, ears are incredibly nuanced in natural presentation and carriage. Some are permanently pricked, while others droop to the side. Like tails, ear carriage is evidenced by looking at the base of the ear. Ears can flatten to varying degrees toward the head, and even in long-eared breeds like Basset Hounds, "ears back" can be noted by paying attention to the base. *Ears pressed back* are generally associated with greater levels of fear, submission, retreat, or even defensive aggression. *Ears forward* are the opposite, suggesting interest, attention, alert, and approach as opposed to withdrawal.

Mouth

While the mouth and muzzle are not often described in behavioral studies, these body parts are explicitly attended to during shelter behavior assessments of dogs (see ASPCA SAFER Glossary). The position of the mouth holds valuable information about what a dog might do next. *Open* versus *shut* is the first consideration, and further qualitative elements provide more detail. An *open, relaxed mouth* indicates a comfortable dog, while a *tight mouth* could indicate discomfort, fear, or simply a neutral position. The corners of the mouth, or labial commissure, is also important. What is sometimes described as a "long lip," where the commissure pulls back toward the ear, is often seen in fear, stress, or appeasement displays. In a *submissive grin*, the lips are retracted and the teeth are visible, but the eyes may be squinty and the forehead smooth. A "short lip" is pushed forward, forming a tight "c" shape of the mouth, as if a wind source behind the dog is pushing the facial features forward. This is part of an aggressive display, and the top of the muzzle is wrinkled, and the eyes are open and hard.

Tongue

Dog tongues are known to hang generously out of mouths during play, but they can also serve as indicators of discomfort. A tongue extended and retracted quickly is a *tongue flick*: Like the raised hackles, it may be a reflexive response to discomfort. Dogs also use tongues socially, to investigate substrates and surfaces (urine on the street, you after a run), as well as in greeting where dogs are apt to lick the mouth of both dogs and people.

Eyes

As previously mentioned, physical appearance can strongly relate to dog personality attributions. This is relevant for dog faces where eyebrows, depending on color and flexibility, can make a dog appear "angry" or "elated" without much concern for actual behavior. Dog eyes demand our attention, particularly when they take the form of what the ASPCA SAFER Glossary defines as "hard eye: dog's eye is large and the whites are likely observable." This hard, direct, unwavering appearance indicates threat, and the whale eye (with white sclera visible) can indicate discomfort or nervousness. A stiff, unwavering body posture often accompanies this type of eye presentation, and caution should be taken. Eyes can also assume a soft, squinty, more almond-shaped appearance leading McConnell (2007) to title sections of a book "Wrinkles Are Good," and "Warm Eyes, Warm Heart."

Paws

Like tails, paws do a lot of social "talking" although paws are much less noticed than tails. People who interact with companion dogs often take note of paws for parlor tricks like "high five" or "give paw." These gestures bear no social meaning for dogs, apart from the possible resulting food reward or social praise. Instead, for dogs, "offering a

paw” is a submissive or appeasing display (Lorenz 1954). Watch a dog respond to an upset owner (e.g., “Guilty Look” videos on YouTube), to see a paw raise used appropriately in a social context. Raising a paw is part of many social exchanges, see Appendices A.4, A.7, and A.9.

Body weight distribution and distance management

In social interaction, dog behaviors can be characterized as those associated with “coming closer” (distance between animals decreasing) or “backing up” (distance increasing). A dog’s body weight distribution offers subtle, yet important information. A dog with weight shifted forward, upper body pressed over the front legs, shows forward momentum, interest, confidence, or alertness. If a dog leans forward toward another dog—and the receiver leans back, looks away, or moves away—the second is engaging in conflict avoidance.

Similarly, “submissive” displays in canid social behavior aid in the prevention or reduction of fighting, aggression, or conflict. Submissive postures involve a reduction in perceived size, through lowered body and tail, pressing ears back, and, possibly, exposure of the inguinal region (Schenkel 1967), see Appendices A.4 and A.5. A dog being attacked in these postures is rare. A dog who continues to be approached could respond in defensive aggression if their initial tactic—leaning back, decreasing size, turning head—did not stop another’s advance, see Appendix A.6. Unfortunately, if dog signals go unheeded, dogs can learn to increase the use of defensive aggression over time and even fade out the use of distance-increasing signals.

Challenges to visual communication

Given the extreme morphological diversity of dogs, not all dog body parts will be visible all the time, nor are all body postures physically possible for all dogs (Price 1999). For instance, the hair or fur of some dogs prevents visible piloerection. Other dogs, particularly brachycephalic dogs, lack the highly flexible or expressive face of a German Shepherd-type dog (Bloom & Friedman 2013). Some dogs may thus be unable to signal, or their signal may not be noted. This diminishment of social signaling capacity is noteworthy because communication, as well as interpretation of communicative signals, is integral to modulating social interactions. As a result, individual dog behaviors should be considered in light of what is possible *for that dog*. It might be that something as trivial as shifting one’s weight back, or turning one’s head, is highly outwardly expressive for a particular dog.

Acoustic communication

Social animals tend to have more vocal nuances than those that are asocial, and dogs make a lot more noise than other canids, both in quality and quantity. Dogs whine, yelp, growl, howl, and bark (Tembrock 1976; Pongrácz *et al.* 2010), in addition to other less-described vocalizations such as laughing and grunting, to name a few (Simonet *et al.* 2001; Lord *et al.* 2009).

Barks and howls

Barks and howls are loud and noisy and can garner considerable attention. Howls carry for long distances, while barks are used for shorter-range communication (Feddersen-Petersen 2000). Howls and barks can be socially facilitating and can attract attention and participation from other dogs (Adams & Johnson 1994). Although, some dogs appear to bark more than others, even in the presence of the same stimulus.

Barks vary in duration and acoustic properties, but each bark is repetitive and loud. The acoustic properties of barks differ between contexts so barks performed in a disturbance (“stranger approaching”), isolation, or play context will sound different from one another (Yin & McCowan 2004). As a result, human listeners are able to characterize barks and describe tonal and high-pitched barks as indicating “fear” or “desperation” (e.g., “alone” bark), while low-pitched barks that are harsher with little amplitude modulation are described as “aggressive” (e.g., “stranger approaching” bark) (Pongrácz *et al.* 2006). For dogs, like other vocal mammals, vocalizations associated with affiliation and approach (high-pitched and tonal) sound different from those associated with withdrawal (low-pitched and atonal) (Morton 1977).

These acoustic rules can be applied to successful communication between humans and dogs. McConnell (1990) found that short, rapidly repeating notes were more successful in provoking dog movement than long, descending notes. This research can be put into practice in shelter settings, and volunteers should consider that tone and pitch can be more meaningful to dogs than the actual meaning of uttered words (ASPCA Webinar 2013).

Dog barks are one of the lesser-appreciated vocalizations and are associated with dog relinquishment and “misbehavior” (Senn & Lewin 1975; Wells & Hepper 2000). Owner problems with barking can stem from bark quantity (frequency) or quality (style or context) (Pongrácz *et al.* 2010). While barking has contextually specific acoustic properties—“meanings”—barking is a behavior that can be put under operant control, depending on the consequences that follow from the behavior. Applied Behavior Analyst, Susan Friedman, PhD, explains, “Once this idea is [understood], it opens the door to changing the duration, intensity and frequency of the behavior by changing the consequences” (Hecht 2013). Understanding that barking can be a learned behavior—and increased or decreased in particular contexts—allows people living with dogs to work with them to modulate barking when necessary (Juarbe-Díaz 1997). At shelters, everyone might benefit if dogs could learn to be quieter (see section “Shelter environment”).

Growls

Growls, too, have received scientific scrutiny. Once described simply as an “aggressive or distance-increasing call” (Haupt 2011), growls are more nuanced than initially thought (Yeon 2007). For example, growls can provide

information about the growler's size (Faragó *et al.* 2010a; Taylor *et al.* 2010), and they are performed in not just agonistic but also play contexts. In one study (Faragó *et al.* 2010b), growls were recorded in three different contexts: guarding a bone, growling at an approaching stranger, and during play. Growls were then played to dogs as they approached a bone that had been placed in front of concealed speakers. Dogs responded differently toward the bone depending on the growl played, suggesting that growl acoustic properties are meaningful for dogs. Dogs were more likely to retreat for a "my bone" growl than when hearing growls associated with a threatening stranger.

Olfactory communication

Dogs are known for their noses, and with good reason. Compared with relatively anosmic or "poor-smelling" animals like humans, dogs have the ability to detect and discriminate a huge number of odors (Horowitz 2009c) due to physiological structures that prioritize smelling. Scent particles enter the nose by both sniffing and regular breathing (Neuhaus 1981). These particles then enter the nasal cavity where a mucus lining covers the olfactory epithelium and mediates olfaction—smelling (Furton & Myers 2001). Considerably more genes code for olfactory receptors in dogs than in humans (Quignon *et al.* 2003).

The dog's nose is a powerful tool readily harnessed for detection, discrimination, and identification (Gadbois & Reeve 2014). To name a few, dogs can be trained to identify cancerous from noncancerous tissue samples, scat of particular species, and even whether a now-absent dead body had been lying on a carpet (Willis *et al.* 2004; Long *et al.* 2007; Oesterhelweg *et al.* 2008). In a study of dog ability to detect the direction of a track, German Shepherd dogs inspected a small number of footprints for 3–5 s and used this information to follow the track in the right direction (Thesen *et al.* 1993). This ability suggests that a dog's nose attends to minute differences in scent molecules that ultimately provide information on which footprint was laid more or less recently. Research in this area continues to grow, particularly studies investigating which training methods foster faster detection and scent learning (Hall *et al.* 2013).

Although dogs hold the potential for great olfactory acuity and discrimination, dogs are not necessarily relying on their sense of smell all the time (Horowitz *et al.* 2013). Factors such as dehydration and increased temperatures—that increase panting—can impair detection (Gazit & Terkel 2003). Additionally, differences between dogs with respect to the position of the olfactory lobe could affect dog olfaction (Roberts *et al.* 2010).

While dogs might enjoy engaging their noses to serve human purposes, dogs have species-specific uses for olfaction. Dogs have a secondary molecule-detection organ, the vomeronasal organ (VNO), which is directly involved in social communication and assessment of pheromones (Adams & Wiekamp 1984). Distinct from the main olfactory epithelium, the VNO is located below the nasal cavity, and its receptors also carry information to the

olfactory bulb. This chemosensory organ is ordinarily viewed as responsible for pheromone detection in urine, feces, and saliva, as well as glands in the anogenital region, mouth, and face. Olfaction plays an important role in intra- and interspecific social encounters, discussed further in section "Real-world interactions."

Olfaction is essential to the dog *umwelt* or perceptual world (Horowitz 2009c). The job of humans, as their caretakers and observers, is to know that the dog's nose is in play, regardless of whether we can see the nostrils twitching ever so slightly.

Patterns of communication

When interacting with dogs, people need to be aware of dog visual, acoustic, and olfactory communication. The following patterns of dog communication are particularly relevant for shelter and foster-care settings.

Stress

To live is to encounter "stressors." Widely discussed since the early 1900s, endocrinologist Hans Selye defined stress as "the nonspecific response of [an] organism to a noxious stimulus" (Mariti *et al.* 2012). While stress can be considered deleterious, "stress is an environmental effect on an individual which over-taxes its control systems and reduces its fitness" (Broom 1988) stress is also functional. It serves to activate the body for protection and action. If a zebra did not perceive and respond immediately to a stressor (a lion approaching), the zebra could be killed (Sapolsky 2004). At its core, stress can promote survival.

That being said, prolonged or repeated activation of the stress response—chronic stress—can have adverse consequences. Research has found relationships between stress and increasing levels of arousal, fear, and aggression (Mills 2002; Dreschel & Granger 2005); decreased immune functioning (Glaser & Kiecolt-Glaser 2005); and decreased life span (Dreschel 2010). Attending to the physiological and behavioral aspects of stress can help ameliorate or prevent stress in the future. At the same time, there are challenges to stress identification, such as individual variability in physiological and behavioral responses, as well as a lack of correlation between behavioral and physiological stress measures (Rooney *et al.* 2007; Hekman *et al.* 2012).

Stress response

Assessment of a stressor prompts immediate physiological changes. The fight-or-flight response prepares the body for immediate action: Pupils dilate, respiration and heart rate increase, and blood moves into limbs readying the body for immediate action. Stress also produces a hormonal response—effectively preparing the individual for sustained exertion—characterized by a cascade of hormonal responses resulting in the production of the glucocorticoid, cortisol which is the most common in mammals. Cortisol levels elevate during times of stress, regardless of whether it is eustress—"good" stress, as when playing—or distress,

“bad” stress. Cortisol measures—customarily collected from saliva, blood, and urine, but also feces and hair—along with behavior can offer insights into a being’s assessment of a situation. When the stressor is removed or perceived to be removed, normal bodily functions—such as food digestion, regular breathing and heart rate—return. Unfortunately, if an individual lives in a continual state of change and stressors (or perceives as much), levels could remain elevated and indicate chronic stress (Beerda *et al.* 1997, 1998).

Stress behaviors

Dog owners frequently refer to overt changes in dog behavior as indicators of stress, such as piloerection, trembling, and panting (Mariti *et al.* 2012). Research suggests that behavioral indicators of stress are less than straightforward and can vary between individuals. Thus, there is no definitive list of signs of stress (Rooney *et al.* 2009). Generally speaking, stress-related behaviors overlap with those associated with fear, anxiety, appeasement, and conflict. They can take on the appearance of behaviors associated with flight, freezing, or even fight.

Starting from the dog’s head, oral behaviors could include subtle snout/lip licking, yawning, and panting. Dogs may avoid eye contact or look away. Trembling and body shaking are often indicators of high psychological stress and could be accompanied by a lowered body posture, cowering, and hiding (Rooney *et al.* 2009). Dogs paw-lift in both asocial and social contexts, when alone and distressed, and also during social (inter- or intraspecific) conflict, confusion, or fear (for instance, of punishment) (Schilder & van der Borg 2004; Rooney *et al.* 2009). Periods of continual barking, whining, and howling suggest frustration or distress, although vocalization could also be socially mediated (Rooney *et al.* 2009).

Displacement behaviors are also important to attend to as they constitute normal behaviors performed in an “inappropriate” context (Falk 1977). Displacement behaviors are often associated with motivational conflict or frustration and could have crossover with stress-related behavior. For example, the appearance of another dog outside a dog’s run might increase yawning, a behavior not typical for dog–dog greetings.

Veterinarians mention lack of urination or defecation, or even dry mouth, as associated with stress, and one study even described “a characteristic breath odor” in distressed dogs (Mills *et al.* 2006). Human anxiety is associated with increased production of volatile sulfur compounds (Calil & Marcondes 2006), and persistent panting and/or drooling in dogs could alter the smell of dog breath.

Interestingly, water consumption could be an indicator of enhanced coping, as one study found that dogs who consumed water on the first day at a shelter had lower cortisol levels than dogs not observed to drink water (Hiby *et al.* 2006). In another study, dogs who were quicker to rest had lower cortisol levels than those who were more active (Batt *et al.* 2009). At the same time,

dogs experiencing stress could be anywhere from shut down and inactive to highly active (Hiby *et al.* 2006). Sociability could be another indicator as dogs more sociable with humans had lower cortisol levels than those described as less sociable (De Palma *et al.* 2005). Taken together, dogs who are inactive but showing overt or subtle social avoidance should also be considered as possibly experiencing increased stress levels.

Challenges associated with stress

Even for people living with dogs, subtle dog behaviors are not necessarily attended to, and global body movements and vocalizations may be easier to recognize (Tami & Gallagher 2009; Mariti *et al.* 2012). Because of the overlap between stress, fear, and aggressive behaviors, subtle indicators of stress are important to observe. Dogs often behave in a graded fashion and a lip lick, head turn, avoid gaze, and freeze may come prior to a bite. Unfortunately, by not attending to these subtle behavioral indicators, an aggressive display might seem to come “out of nowhere.”

Another major challenge in attending to stress in dogs is that there is intense variation in perception of stressors, as people living in multi-dog households may know. One dog might find loud noises terrifying, while another lounges on the couch during fireworks. From an early age, dogs appear to display individually distinct coping strategies (Riemer *et al.* 2013), “characterized by consistent behavioral and neuroendocrine characteristics” (Koolhaas *et al.* 1999). Coping strategies are often described as “proactive” and “reactive,” the former characterized by boldness exploration, and fight-or-flight in response to stressors, while reactive individuals tend toward freezing when encountering aversiveness.

Ultimately, individual monitoring and attention to individual coping strategies is useful to detect a stress response. Researchers concerned with the welfare of dogs have noted the importance of “[paying] attention to individual dogs and [noting] any changes in their behavior” (Rooney *et al.* 2009).

Stereotypic behavior

Stereotypic behavior has traditionally been defined as behavior patterns that are repetitive, unvarying, and seemingly functionless (Mason 1991) and that manifest differently between species. Behaviors could include repetitive spinning, jumping, pacing, licking, and self-biting, among others. Abnormal behaviors can develop as a coping mechanism to poor environments and can maintain even in the face of environmental improvement. As a general matter, they may indicate poor welfare, but on an individual level, these behaviors could offer individuals a type of “do-it-yourself” enrichment, and nonstereotyping individuals in poor environment could be in a worse state than stereotyping individuals (Mason & Latham 2004). Studies of the conditions under which repetitive behaviors are performed by kennelled (and shelter) dogs can give further insight into their meaning

and indicators for welfare (Denham *et al.* 2014). As a result of their complicated presentation and meaning, simply thwarting such behaviors could increase distress or the frequency of new deleterious behaviors. Repetitive, unvarying behaviors necessitate attention.

Fear and aggression

The outward appearance of aggression—loud noises, teeth bared and flashing—is hard to miss. But the precursors to aggression are many, and given the novelty of shelter environments for dogs, fear, and fear-related aggression, are noteworthy.

Fear is an emotional response evident in both physiologic and behavioral responses when something is perceived as frightening or indicative of danger (Boissy 1995). Fear-related behaviors at the veterinary clinic have been described as “fixed stare, lowered or tucked tail, crouched body posture, hiding, pressing into owner, attempt to jump off table” (Döring *et al.* 2009). Whereas confident or calm dogs have a high or mid-length tail and raised or neutral posture, fearful dogs are marked by low tail, depressed posture, and ears back (Darwin 1872) (see Appendices A.3 and A.6).

Fear and aggression are often connected. If pressed, dogs exhibiting fearful postures may freeze, continue to withdraw, or even flip onto their backs in a display of passive submission (Schenkel 1967). But others with a more “reactive” coping strategy may display a defensive attack. This posture differs from an offensive aggressive display in that the defensive dog’s posture is pulled back, with ears back and tail tucked; while he might bark, bare teeth, and lunge forward, ultimately the dog is retreating, attempting to escape or decrease proximity.

Dogs displaying more offensive aggression may lean forward with a fixed stare, raised tail, and stiff or frozen body, giving a “hard eye” with a closed mouth or offensive pucker: in a sense making themselves appear bigger.

Fear and aggressive behavior, like stress-related behaviors, can be a functional response to try to increase distance from a feared object or animal. But animals experiencing *unrelenting*—chronic—fearful or aggressive states can have decreased well-being. There can be a strong relationship between fear and stress, as dogs who crouch when exposed to frightening stimuli have higher cortisol levels than those who maintain an upright posture (King *et al.* 2003).

Dogs exhibiting continual fear, anxiety, and frustration might have increased arousal (whether subtle or overt) and have a lower threshold for aggression (Panksepp 1998). Sadly, dogs living with chronic stress or fear may have negatively impacted health and decreased length of life (Dreschel 2010).

Dominance

The term “dominance” is readily used by the general public and applied to everything from dogs being “disobedient” (jumping up, stealing food, etc.) and scuffles between dogs and dogs appearing to show aggressive or

assertive behaviors. The term is readily applied without consideration for contextual learning or preceding behaviors.

Unfortunately, these “definitions” of *dominance* do not have scientific merit. When used in animal behavior contexts, “dominance” is not an attribute of an individual; instead, it is commonly used to describe a dyadic relationship (Drews 1993). “Dominance relationships”—in which one individual is more assertive and the other is more submissive—are not set in stone and are malleable. For example, motivations for particular resources (e.g., resource-holding potential) differ between individuals and affect outcomes (Bradshaw *et al.* 2009).

Unfortunately, the idea of dominance has been widely overstated and oversimplified as it relates to the dog-human relationship. Owners and dog handlers sometimes use forceful methods to deter dogs from “asserting dominance.” Unfortunately, confrontational methods such as the “alpha roll” and “dominance down” can be associated with an aggressive response on the part of the dog (Herron *et al.* 2009).

When investigating the complex interplay between life experience and individual dog behavior, it becomes apparent that while a concept like dominance may enter into the social behavior of dogs, their individual behaviors are not defined by it. For example, a dog who is described as “dominant” because he guards food could, likely, learn to stop guarding food (Wood 2011). Thus, the utility of this label is questionable.

Play

As any observer of dogs knows, dogs play—a lot. Young dogs may spend up to one-third of their awake life in object play, social play, or running, locomotor play; and among dogs, play continues, albeit at a reduced rate, into adulthood—a rare and perhaps singular phenomenon among animals (Horowitz 2002). While “play” may seem to be trivial, play behavior is an integral part of social and physical development for dogs (Rooney & Bradshaw 2014). Dogs not only play with other dogs, but readily, and often, with humans and even other species. While play might be seen as “just something that dogs do,” it has unique characteristics that could offer a snapshot into the dog’s mind. Researchers breaking down the nuances of play find that it is marked by “a dizzying series of synchronous behaviors, active role swapping, variations on communicative displays, flexible adaptation to others’ attention, and rapid movement between highly diverse play acts” (Horowitz 2009c). The patterns of behaviors in play indicate that dogs have some rudimentary understanding of the minds and perspectives of other dogs (Horowitz 2009a) (Figure 1.2).

“Rough and tumble” play—the most characteristic dog-dog play—uses behaviors from nonplay contexts, such as biting, mounting, and jumping, and takes away their functional roles (such as to harm or eat, engage in sex, or attack). These behaviors are moderated in force and, importantly, are framed by the use of “play signals,”

behaviors which signal and sustain play, and seem to indicate “I want to play,” or request “Would you like to play?”. They include “the high-rumped crouch of a ‘play bow,’ an open-mouthed ‘play face,’ a more subtle ‘face paw,’ and a ‘teasing,’ ‘chase me’ posture” (Bekoff 1972, 1974) (see Appendix A.8). These signals are not directed randomly, but instead are presented most often toward dogs looking at them, and are used to begin play and at pauses or miscues. When individuals are not paying attention, dogs use “attention-getting behaviors,” including an “exaggerated retreat,” “in your face,” “present,” “bite,” “bite-at,” and “nose” (Horowitz 2009a) (Table 1.1).

Given the overlap of certain behaviors found in play and aggressive encounters, new owners may have difficulty distinguishing the two. But close examination of the suite of behaviors dogs use in play can distinguish it from an aggressive encounter. To understand and allow for play is important: play is not only rewarding for the dog and part of normal social life, it can be used as a

reward in training and has been seen to be a strong indicator of health and good welfare (Rooney & Bradshaw 2014).

Influences on dog behavior

Ask a Beagle to herd some sheep, and you will come face-to-face with genetic influences on behavior. Within the general canid behavioral repertoire, dogs can display more rigid behavioral displays based on artificial-selective pressures. We see genetic selection in its outward appearance—some dogs were selected for short legs—as well as in their behavioral characteristics—some dogs were selected for speed, others to herd.

Though genetic influences are strong, they are also just *tendencies*, not inevitabilities. While a Border Collie is a better bet to herd sheep than a Beagle is, not every Border Collie will excel in herding. Behavior is complex, a mixture of genetic influences, prenatal, and early-life factors working together to develop the behavior in question. For instance, livestock-guarding dogs who are not exposed to livestock early in life do not perform their expected duties (Coppinger *et al.* 1983). “Companion” dogs who are not exposed to people early in life will not necessarily be socially companionable.

Breeds and behavior

While dogs have been in existence as a separate species for some thousands of years, for most of that time, dogs were not comprised of different breeds. Ancient art and writing does suggest that there were distinctive types of dogs, from Mastiff-type dogs and Saluki-shaped dogs to small Terrier-like lapdogs. However, these were not “purebred” dogs as considered today. Dogs were selected for their function: for instance, for herding, guarding, hunting, and as companions (Grier 2006). The contemporary dog, by contrast, is made up of an estimated 400 breeds, as well as “mixed” breeds. A “breed” is a genetically closed population of animals that share



Figure 1.2 A dog play bow. Reproduced with permission of Natalya Zahn. © Natalya Zahn.

Table 1.1 Sample play signals and attention-getting patterns commonly occurring in dog play.

Behavior	Description	Behavior	Description
<i>Play signal</i>		<i>Attention getting</i>	
Exaggerated approach	Loose, rolling, running approach	Exaggerated retreat	Backward leap with head toward play partner
Play bow	High rump, forelimbs down, tail high and either wagging or erect	Bump	Body makes physical contact with partner
Chase me	A withdrawal while looking back; movement at a reduced pace	Present	Moving rear to other's face with possibility for contact
Open mouth	Teeth and lips showing but no biting	In-your-face	Very close self-presentation
Play pant	Breathy exhalation	Paw	Paw directed to partner's body or face

Adapted from Horowitz (2009a). Reproduced with permission from Springer. © Springer.

many physical and behavioral traits. While early dogs were the result of normal evolutionary processes, geographic segregation, as well as some human selection, “purebred” dogs are entirely the result of “artificial” selection; that is, dogs are specifically bred with other dogs of the same genetic lineage (Serpell & Duffy 2014). The rise of developing purebred dogs began in the late 18th century, with the advent of dog breed clubs and dog shows, also known as dog fancy. In contrast with the function-based selection of early dogs, modern dogs have been largely bred for appearance. Dogs with desirable traits and appearance were bred with dogs of similarly desirable features. Some look like the ancient dogs, but there is no evidence of a continuous link between the purebred Mastiffs and Salukis of today and the ancient versions. The result of just a few hundred years of specific breeding has made dogs as diverse in size and morphology as the Great Dane and the Maltese. Appearance-based variations have driven the breeding of dogs with markedly different body size, head size and shape, nose length, weight, leg length, coat, and tail length and shape (Bateson 2010). As discussed earlier, changes in “communicative anatomy” can affect intraspecific social behavior (Horowitz & Hecht 2014).

Purebred dog breeding encourages “registration” of breeds—and any dog who is registered as a member of a breed must come from parents who were themselves registered. “Mixed” breeds are simply those dogs whose parents (and perhaps their parents) come from different breeds. By design, the purebred dog comes from a “closed breeding population,” meaning that they are necessarily the result of inbreeding—breeding closely within a family (Wayne & Ostrander 2007; Serpell & Duffy 2014) to maintain a breed “standard.” Unfortunately, even with conscientious breeders, inbreeding has inevitable deleterious effects, including developmental disturbances, problems in fertility and birthing, diminished life expectancies, lowered immune system function, and various inherited physical disorders (Asher *et al.* 2009; Bateson 2010). Both gigantism and dwarfism can lead to impairments. In the former group, large dogs are predisposed to skeletal dysplasia as a result of trying to support their own great weight. Dogs with large heads, such as the Boston Terrier and Bulldog, must be delivered surgically, since they cannot fit out the birth canal of their mothers (Bateson 2010). With respect to the latter, the small skull of the Cavalier King Charles Spaniel predisposes it to syringomyelia, a painful swelling of the brain as a result of its ill-fittedness in the small skull. Numerous other predispositions to disorders have been bred into dogs—often as part of breeding dogs to the breed standard: from ulcerative eyes to skin fold dermatitis; from spina bifida (Pug) to dermoid sinus, a neural tube disorder (Rhodesian Ridgeback); from deafness (Dalmatian) to hip dysplasia (German Shepherd) (Asher *et al.* 2009).

The history of inbreeding dogs has resulted in distinct behavioral tendencies in various breeds. These behaviors are not inevitabilities, but they do reflect a genetic

change which often leads to certain behaviors, given an environment which supports that behavior. For instance, the Border Collie, often used and bred as a herding dog, shows actions like “showing eye” (fixing gaze at an animal), “stalking” (creeping toward the animal while maintaining eye), and chasing (Coppinger & Schneider 1995). The dog’s predisposition to do these actions can be molded into sheep-herding behavior. Other examples of breed tendencies abound: the pointer’s tendency to “point” with his body toward game; the retriever’s ability to fetch and retrieve game in water or on land; a hound’s vocalizations while tracking an animal with his nose; coursing dogs’ running pursuit of game. Many breeds have a “guard” tendency: vocalizing with assertive posture at a disruption or intruder.

Most contemporary dogs are not working dogs, however, and their behavioral tendencies may be more problematic than functional. For instance, a Border Collie without sheep to herd may take to stalking and chasing bicyclists and small children running. Pursuit of and nipping at motion of feet in the vicinity will be undesired and even perceived as “aggressive.” A guard dog’s barking at legitimate guests may be considered inappropriately “dominant” or “territorial.” Owners may wield ill-suited measures to try to fend off this perceived threat to their authority (Herron *et al.* 2009). In both cases, the tendencies that humans have bred into the dogs are re-characterized as “misbehavior” in a companion-dog context. Giving a new owner some understanding of the breed tendencies of a dog will go far in helping her work appropriately with what could otherwise be considered puzzling dog behavior at home.

Dog temperaments may also have genetic influences. In Scott and Fuller’s classic longitudinal studies of five breeds of dogs (Sheltie, Cocker Spaniel, Basenji, Beagle, and Fox Terrier), they noticed distinct differences between the breeds on scales of emotional reactivity, trainability, problem-solving behavior, and other capacities (Scott & Fuller 1965). At the same time, the researchers stated, “it does not follow that behavior is genetically determined; only that some of the *variation* in behavior is genetically determined...genetics does not put behavior in a straightjacket” (Scott 1985, p. 416). More recently, researchers have developed a questionnaire which has dog owners describe their dogs’ behavior along specific lines. The Canine Behavioral Assessment and Research Questionnaire (C-BARQ) has found reliable differences between breeds on various measures, including trainability, attention-seeking, excitability, and aggression. For instance, Golden Retrievers tend to rank highly on trainability while the Beagle ranks low; Huskies rank low on attention-seeking, while Dachshunds and Toy Poodles rank high (Serpell & Duffy 2014). As with behavioral tendencies, breed temperament biases should also be taken into account by owners and handlers when considering the source of perceived misbehavior by dogs.

Spay and neuter and behavior

Early sterilization—spaying and neutering—is now well established as normal, even preferable, for owned domestic dogs. In the US animal protection groups and humane societies advocate dog sterilization, and it is required for dog adoption from many animal shelters (Humane Society of the United States 2010). A common argument for sterilization is that it improves the welfare of the animal. More accurately, sterilization could be described as intended to aid the welfare of the species, not the individual animal, in light of the major ostensible benefit of reducing the population of unwanted animals. Whether there are benefits for individual dogs, or whether it is a detriment to individual dogs, is debated. Medical concerns have been raised about increased rates of obesity, hip dysplasia, incontinence, and stunted growth, although the research on these points is equivocal (Bushby & Griffin 2011). A recent paper found higher rates of various cancers, cruciate ligament tears, and hip dysplasia in sterilized Golden Retrievers than in intact members of the breed, with the rates varying depending on the date of surgical spaying or neutering (Torres de la Riva *et al.* 2013). On the other hand, veterinarians frequently advocate sterilization, citing health benefits including a lower risk of mammary tumors (Kustritz 2007; Bushby & Griffin 2011).

With respect to the behavioral effect of sterilization, the debate continues. Some describe a benefit in the perceived “elimination or reduction of highly objectionable behaviors, including scent marking, spraying, fighting, and roaming,” with an added benefit of early surgery that it is easier and less expensive for the surgeon than late surgery (Bushby & Griffin 2011). By contrast, others note that the evidence of these behavioral changes is also equivocal; in particular, aggression, while influenced by gonadal hormones, may not diminish in neutered dogs. Most dog bites come from males, and the majority of these from unneutered males (Lockwood 1996), and there is a correlation between sterilization and a decrease of typically “male” behaviors (Kustritz 2007). But this is not airtight evidence that sterilization diminishes aggression any more than it would be a sound argument for culling male dogs. What is clear is that sterilized dogs have been “deprived of the ability to perform one of the most fundamental natural behaviours” (Rooney & Bradshaw 2014), which, with the health and behavioral effects still debated, may most robustly reflect a cultural aversion to dog sexual practices (Horowitz 2014).

Shelter environment

Shelters are best characterized as novel environments filled with new sights and social encounters (both with conspecifics and people), “loud” smells and sounds, and general unpredictability (Hennessy *et al.* 1997). While dogs are less neophobic than their wild-type progenitors, novelty in all its many forms can still act as a stressor for dogs (Tuber *et al.* 1996). Shelter stressors have the

potential to present themselves as physical, environmental, psychological, and even social. These are some of the factors that can affect dog in-shelter behavior.

Prior experience

Dogs with prior kenneling or sheltering showed a less-activated stress response when introduced to a new kennel environment (Rooney *et al.* 2007). By contrast, dogs lacking prior kennel habituation maintained elevated cortisol levels. Another study found that dogs relinquished from homes without known prior exposure to a shelter showed an increased physiological stress response without adaptation during the first week; meanwhile, dogs marked as strays and returns showed a decreased physiological stress response during that time (Hiby *et al.* 2006).

People and conspecifics

For some dogs, relinquishment is characterized by separation from a figure of attachment, leaving dogs without social stability and social predictability. Shelter staff and volunteers are often not consistent, and dogs can be exposed to a slew of new people, possibly people they have not been familiarized to, like men or children. People interacting with shelter dogs should look at dog behavior to assess how they are perceived by the dog.

Pair- or group-housing of dogs is often recommended (Hetsts *et al.* 1992; Hubrecht *et al.* 1992). The presence of conspecifics can offer more social complexity—in terms of social interactions and even olfactory composition of the environment, which could decrease stereotypic behavior and mitigate stress (Hubrecht *et al.* 1992; Taylor & Mills 2007). While aggression or fights are offered as reasons against group-housing, these concerns have not been substantiated (Mertens & Unshelm 1996).

Smells

Given the complexity of their nose, shelter smells certainly do not go unnoticed by dogs. Dogs placed in sleeping compartments during kennel cleaning barked and showed cortisol increases. Moving dogs to a different area during cleaning (possibly for a walk, exercise, or training) is beneficial (Rooney *et al.* 2009). On the other hand, the addition of particular scents can enhance well-being. Dogs in the shelter exposed to diffused lavender and chamomile rested more and were less active than dogs exposed to no scent or rosemary or peppermint scents (Graham *et al.* 2005).

Sounds

Shelter acoustics generally include husbandry-oriented noises, people talking at varying decibels, barking, and even loud music. Shelter noise levels are in the area of 85–120db, comparable with a subway, jackhammer, and propeller aircraft (Coppola *et al.* 2006). Noises, depending on their regularity and acoustic properties, can promote acute or chronic stress (Sales *et al.* 1997; Beerda *et al.* 1998). The presence of heavy metal music significantly increased dog body shaking, whereas classical music was

associated with more resting behavior (Wells *et al.* 2002; Kogan *et al.* 2012). People speaking in shelters are recommended to consider how the sound of their voice is interpreted by dogs and whether they are contributing soothing or stressful elements (ASPCA Webinar 2013)

Lack of predictability and control

Lack of predictability and control over contingencies are known welfare challenges (Bassett & Buchanan-Smith 2007), and both typically characterize the experiences of dogs spending time in shelters. Dogs living on the streets or in homes build up expectations and associations in relation to a known environment. A certain type of shuffling at the door signals either the mailman or an owner, each receiving a unique response. A street dog might associate a door opening around a particular time with food. The imposition of daily cleaning, feeding, and walking schedules, as well as consistent interactions, can offer shelter dogs a sense of predictability.

In shelters, dogs lose control at every level, from what and when they eat to who they interact with. Control is further diminished in that space allowances limit their agency to flee or retreat. As a result, new, possibly undesirable, behaviors can develop if distance increasing is thwarted.

While control might be a challenging concept to introduce in shelters, it has been incorporated into farm settings in creative ways, such as call feeding stations for pigs (Ernst *et al.* 2005) or opportunities for animals to seek instrumental learning opportunities. Creating motivations for dogs to perform particular behaviors for particular rewards could enhance welfare, and positive affective states could be achieved as a result of self-directed problem-solving (McGowan *et al.* 2014).

Identifying potential shelter stressors provides an opportunity to ameliorate them and make them predictable or controllable or decreased by intensity, frequency, or duration. Providing dogs with less sensitization during their stay at shelters can help them refrain from developing behaviors and habits that prospective dog owners might find distasteful.

Real-world interactions

Greetings and interactions with dogs

As a result of a larger olfactory bulb, nasal receptors, and a VNO, dog olfaction differs from that of humans, both in quantity and in quality. This is most evident in dogs' preference for smelling, contrasted with humans' general preference for seeing. In comparison with humans, dogs access a much wider set of contextual and social information through smell. Dogs actively seek out direct olfactory contact with inanimate objects and living beings.

Dog–dog encounters are marked by close olfactory inspection, particularly of the head and anogenital area, see Appendices A.9 and A.10. Attention can vary based on sex, with females seeming to focus more attention to

the head and males to the anogenital region (Bradshaw & Lea 1992).

Communication via scents is common by depositing secretions and excretions in the environment. Urination is more than waste expulsion, and canids gain valuable social information by attending to these splatterings. For example, upon entering an area with other dogs (e.g., a dog run), dogs are apt to urinate which could aid in the decrease of direct social investigation from other dogs in the vicinity (Lisberg 2013). Scent marks can be visual, olfactory, or even auditory, as a dog scratching (auditory) after excretion also leaves visual and olfactory marks (Bekoff 1979; Cafazzo *et al.* 2012).

Depending on the shelter, direct encounters between dogs can be rare. Dogs tend to be on leash (or in kennels) when seeing other dogs, and interaction might be thwarted due to shelter regulations. Dogs might experience tension, restraint, or frustration upon seeing other dogs which could affect subsequent intraspecific interactions.

While pet dogs walking off-leash show more dog–dog interactions and direct olfactory investigation than leashed dogs, regardless, body sniffing is the most frequent interaction between dogs when they first meet (Bradshaw & Lea 1992; Westgarth *et al.* 2010). A recent study of shelter dogs found that while familiar dogs interacted, they interacted less than unfamiliar dogs (Pullen *et al.* 2013). After the initial encounter, the dogs investigated the environment instead of maintaining interaction, a phenomenon which has been described in other groups of free-ranging dogs. Shelter dogs appear to benefit from off-leash social interactions between vetted individuals.

Greetings and interactions with people

Given that dogs develop attachment relationships with people, it is important to consider the role that humans in shelters—staff, volunteers, and visitors—can play in the lives of dogs. Dog response to known people is what you might expect: The mere presence of a familiar person returning to a room can increase dog OT levels (Rehn *et al.* 2014). On the other hand, dogs experience varying degrees of comfort with different types of people, and some studies find that individual dogs show more comfort with women than men (Hennessy *et al.* 1997). It might be that dogs have had more experience with women or that the nature of the interactions provided by men differ from that provided by women. For example, Hennessy *et al.* (1998) found that when men emphasized quiet talk toward dogs, men were as effective as women in maintaining lower dog cortisol levels. Voice quality can differ between men and women, and so the type of acoustics one brings to the shelter's soundscape merit attention (ASPCA Webinar 2013).

Familiarity with particular people can also affect behavior. In one study, dogs in interactions with unfamiliar people were more “alert to their surroundings” (Pullen *et al.* 2012). In another study, dogs were apt to show fear-appeasement behavior, described as “tail down, ears down, and crouching,” upon an unfamiliar, friendly person's invitation to interact (Barrera *et al.*

2010). In that case, the shelter dogs maintained proximity to the unfamiliar person, and their behavior could indicate a mixed-motivational state.

While dogs appear to value human contact, it appears that quality of interaction might be the most important element. It is unfortunate that “humans frequently interact with pet dogs...as if vision was their predominant sense” (Berthoud 2010). As social primates, people greet with an outstretched hand or a hug, signals that could easily be misinterpreted by dogs (McConnell 2002). Given the opportunity, dogs rely heavily on smell when first interacting with people. Dogs begin interactions with unfamiliar people (both adults and children) by directing attention to the anogenital region (Filiatre *et al.* 1991). For familiar people, dogs focused

on the upper body. This suggests that left to their own devices, dogs choose to approach an unfamiliar person differently than those they know. Unfortunately, this behavior is often perceived as an “inappropriate” or nuisance behavior, and many dogs on leash are thwarted from making contact with this region.

There is another way that people may prevent direct olfactory investigation during greetings; people often descend a hand on top of a dog’s head instead of allowing the dog to approach and sniff. In these instances, observe the dog’s response to a hand falling from the sky. You are apt to see a dog turn his head, move his body away, or show other subtle distance-increasing behaviors. The dog’s behavior indicates this is not a “greeting” on dog terms (Figure 1.3a, b, c).

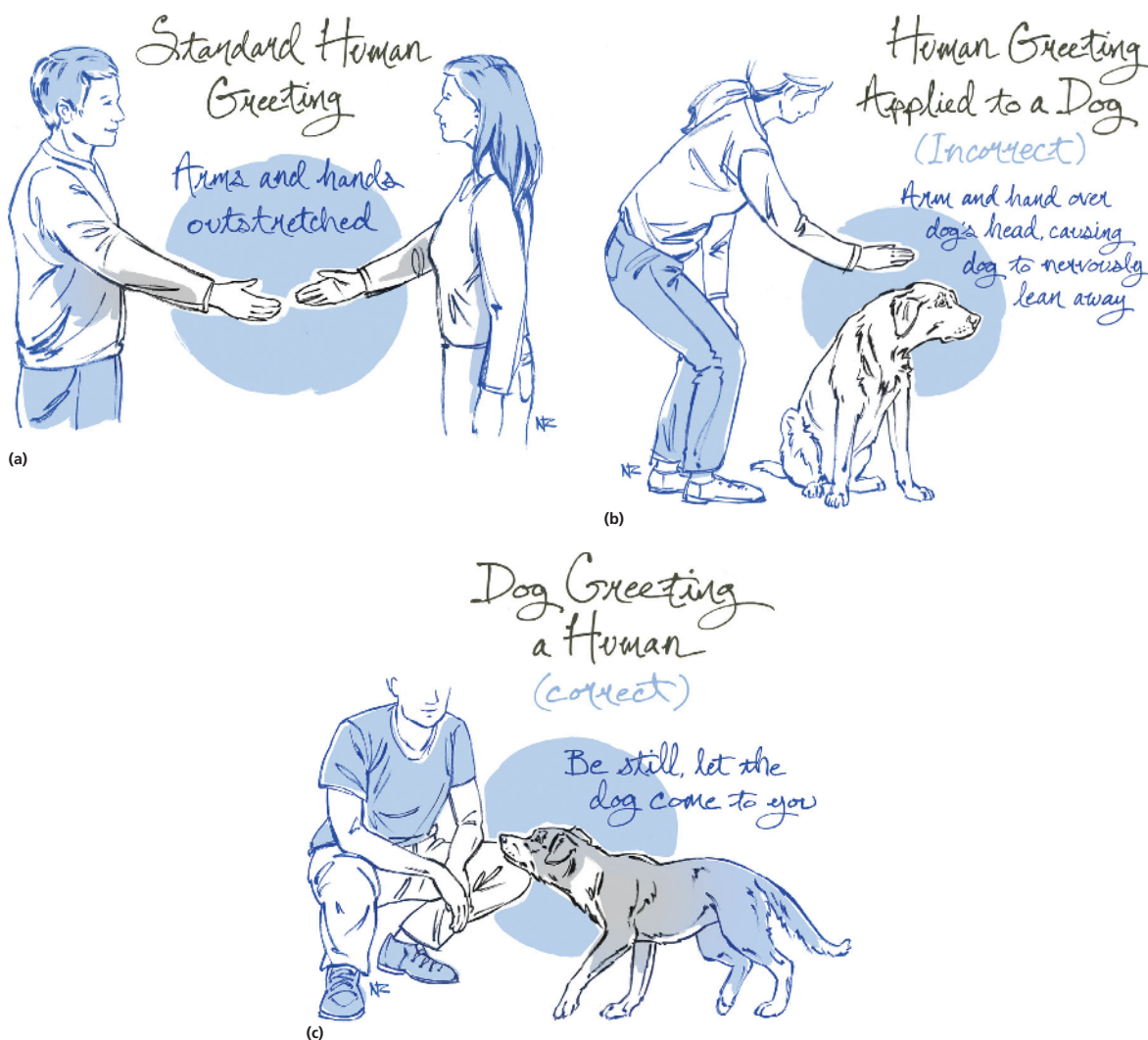


Figure 1.3 (a, b, c) An overview of dog-human greetings. Reproduced with permission of Natalya Zahn. © Natalya Zahn.

"Guilty look"

Dog owners and the media take a specific interest in the dog "guilty look," a widely revered expression supposedly indicating that a dog *knows* he has done something wrong (Horowitz 2009b; Hecht *et al.* 2012). For owners, the "guilty look" is clear: The dog freezes, approaches, or retreats with a depressed posture; presents a low and quick wag; has its ears back; and rolls onto the back or lifts a paw. Almost 75% of owners attribute guilt to companion dogs, far more than owners of other companion animals, like horses or cats (Morris *et al.* 2008) (Figure 1.4).

Research shows that, for dogs, the story is different. Dogs appear "guilty" when scolded by owners, regardless of whether they themselves performed the misdeed (Horowitz 2009b). Additionally, dogs look "guilty" in the presence of a "misdeed" that the dog himself did not perform (Vollmer 1977), calling into question whether the "guilty look" indicates a dog's *knowledge* of a misdeed. Instead, the "guilty look" is best viewed in an ethological context: Dogs show cohesive displays and appeasement postures toward an upset member of the social group or toward an owner in a context previously associated with scolding. In multipet households, a "guilty looking" dog might have gotten into trash, but the misdeed also might have been performed by a different dog (or cat).

Owners might observe a dog's "guilty look" as part of a ritual of forgiving the dog for the apparent misdeed. But "forgiving" a "guilty dog" could only obscure the real reason why the molding is in shambles or the trash has a new home on the kitchen floor. Was the dog anxious, scared, or bored? Those issues can be looked into and addressed. The supposed "guilty look" cannot.



Figure 1.4 A representation of the "guilty look" in dogs. Reproduced with permission of Natalya Zahn. © Natalya Zahn.

Reduce dog bites

Those involved in animal rescue, foster, or shelter work often have a high degree of affinity and affection for animals, but dogs do not have insight into those intentions. Instead, people easily initially fall into the category of "unfamiliar" or "stranger," which can elicit unintended dog behaviors. In one study, shelter dogs barked more and were more apt to maintain eye contact with unfamiliar men than unfamiliar women outside their kennel (Wells & Hepper 1999).

Attending to ladders of aggression, like that provided by Shepherd (2009), reveals that dog response to threatening or stressful stimuli (social, environmental or other) tends to be graded. A dog is apt to yawn, lick, look away, and move away before stiffening, growling, snapping, and finally biting. These behaviors, from what we might consider subtle to incredibly overt, aim to increase distance. Unfortunately, performing the latter set of behaviors, particularly in a shelter, can be detrimental to an individual dog's welfare. Subtle indications that a dog is less-than-comfortable demand attention because they suggest that a dog has the potential to respond with aggression if the perceived threat or stressor is not alleviated. Dogs whose subtle behaviors are continually ignored might learn that these behaviors are ineffectual, and they can resort to more overt distance-increasing indicators, like growling, barking, bearing teeth, lunging, and even biting, see Appendices A.3 and A.6.

Unfortunately, adults do not always attend to or agree when labeling or classifying aggressive behaviors, which makes bite prevention more challenging (Tami & Gallagher 2009). Young children are particularly susceptible to bites, and constitute a large number of those bitten (Reisner *et al.* 2011). Meints *et al.* (2010) found that young children tend to show considerable facial proximity and "leaning in" toward moving objects. This "intrusive facial proximity" could explain why young children are often bitten in the face.

It is important to note that aggressive displays are common during times of stress and change. A study of the prevalence of animal bites following a natural disaster found that the majority of bites were owner-directed suggesting that during times of chaos and upheaval, dogs can display the outward appearance of aggression even toward known individuals (Warner 2010). Dog bites also occur by known dogs in normal household settings, particularly when interactions are initiated by a child (Reisner *et al.* 2011).

Importantly, research finds that there are no universal characterizations of "aggressive" or "not-aggressive" dogs. Instead, a UK survey found that many factors influence the presence or absence of aggressive displays, and a dog who shows aggression in one context might not do so in another (Casey *et al.* 2014). Dogs in the survey tended to show aggressive behavior in only one context, suggesting that dog's

cannot necessarily be characterized as universally “safe” or universally “dangerous” as people would like. Instead, dogs need to be considered within the environment that they have been placed and their *in situ* presenting behaviors. Stephen Zawistowski, science adviser emeritus to the ASPCA, remarks, “Aggression is incredibly complex. It’s going to be both situation-dependent and dependent on the history of both the people and the dog” (Thompson 2014).

Consider aspects of the environment—social, resource-based, or other—that could elicit aggression. For example, valuable resources could be associated with behaviors like freezing, lunging, snapping, and biting, but dogs can also learn to stop resource-guarding behaviors, and this is now a common learning goal in shelters (Wood 2011; Mohan-Gibbons *et al.* 2012; Marder *et al.* 2013).

Conclusion

Just as people express preference for chocolate or vanilla, East Coast or West, people also express an affinity for particular companion animals, claiming allegiance as “dog people,” “cat people,” both, or neither (Gosling *et al.* 2010). Species affinity does not necessarily imply an understanding of that species’ biological and ethological underpinnings.

Companion dogs, in particular, are readily viewed in anthropocentric terms, assessed on our terms rather than theirs. Inferential reasoning, a common practice among humans, can be problematic when ascribed to other species because the inference does not necessarily translate across species boundaries. Humans readily anthropomorphize: We see ourselves in other beings, and we focus on behaviors and features that are human-like. For instance, dogs who show more “eyebrow raises” (a human-like feature) are adopted more quickly than other dogs (Waller *et al.* 2013). People show a preference for dogs with the human-like attributes of an upturned labial commissure—giving the appearance of a smile—as well as the presence of distinct, colored irises (Hecht & Horowitz 2013).

This chapter reminds us that dogs have a worldview that differs from that of the other companion species we reside with, whether cat, rabbit, bird, horse, or fish. Although dogs and humans have lived together for thousands of years, dogs maintain their own unique, species-specific behaviors and interests. They have not become more “human-like” just because they now have birthday parties or are taken to yappy hour. Dogs living on streets will scavenge, while dogs living in homes might be reprimanded for getting into the trash. Same behavior, interpreted differently due to context. This chapter asks that we view dogs on their terms, not ours, and pay direct attention to *in situ* behavior.

Acknowledgements

We thank Natalya Zahn for lending her artistic talents and eye for dogs to this project. Heaps of thanks to Merav Stein for taking on the unenviable task of citation compilation.

References

- Adams, G.J. & Johnson, K.G. (1994) Behavioural responses to barking and other auditory stimuli during night-time sleeping and waking in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science*, 39, 151–162.
- Adams, D.R. & Wiekamp, M.D. (1984) The canine vomeronasal organ. *Journal of Anatomy*, 138, 771–787.
- Adler, L.L. & Adler, H.E. (1977) Ontogeny of observational learning in the dog (*Canis familiaris*). *Developmental Psychobiology*, 10, 267–271.
- Agnetta, B., Hare, B. & Tomasello, M. (2000) Cues to food location that domestic dogs (*Canis familiaris*) of different ages do and do not use. *Animal Cognition*, 3, 107–112.
- Ainsworth, M.D.S. & Bell, S.M. (1970) Attachment, exploration, and separation: Illustrated by the behavior of one-year-olds in a strange situation. *Child Development*, 41, 49–67.
- Altmann, J. (1974) Observational study of behavior: Sampling methods. *Behaviour*, 49, 227–267.
- Asher, L., Diesel, G., Summers, J.F., McGreevy, P.D. & Collins, L.M. (2009) Inherited defects in pedigree dogs. Part 1: Disorders related to breed standards. *The Veterinary Journal*, 182, 402–411.
- ASPCA. (2013) *ASPCA opens behavioral rehabilitation center to help animal victims of cruelty*, <http://www.aspcapro.org/about-us/press-releases/aspcapro-opens-behavioral-rehabilitation-center-help-animal-victims-cruelty> [accessed March 17, 2013].
- ASPCA SAFER Glossary. (2014) <http://www.aspcapro.org/resource/saving-lives-behavior-enrichment-research-data/safer-glossary> [accessed March 1, 2014].
- ASPCA Webinar. (2013) *Patricia McConnell: Canine behavior and acoustics*. September 12, 2013. <http://www.aspcapro.org/webinar/2013-09-12-190000-2013-09-12-200000/canine-behavior-and-acoustics> [accessed June 10, 2014].
- AVMA. (2012) *U.S. pet ownership statistics. 2012 U.S. pet ownership & demographics sourcebook*. <https://www.avma.org/KB/Resources/Statistics/Pages/Market-research-statistics-US-pet-ownership.aspx> [accessed June 10, 2014].
- AVSAB. (2008) *AVSAB Position statement on puppy socialization*. American Veterinary Society of Animal Behavior. http://avsabonline.org/uploads/position_statements/puppy_socialization.pdf [accessed June 10, 2014].
- Barrera, G., Jakovcic, A., Elgier, A.M., Mustaca, A. & Bentosela, M. (2010) Responses of shelter and pet dogs to an unknown human. *Journal of Veterinary Behavior: Clinical Applications and Research*, 5, 339–344.
- Bassett, L. & Buchanan-Smith, H.M. (2007) Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science*, 102, 223–245.
- Bateson, P. (1979) How do sensitive periods arise and what are they for? *Animal Behaviour*, 27, 470–486.

- Bateson, P. (2010) *Independent inquiry into dog breeding*. University of Cambridge, Cambridge.
- Batt, L.S., Batt, M.S., Baguley, J.A. & McGreevy, P.D. (2009) The relationships between motor lateralization, salivary cortisol concentrations and behavior in dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*, 4, 216–222.
- Beerda, B., Schilder, M.B.H., van Hooff, J.A.R.A.M. & de Vries, H.W. (1997) Manifestations of chronic and acute stress in dogs. *Applied Animal Behaviour Science*, 52, 307–319.
- Beerda, B., Schilder, M.B.H., van Hooff, J.A.R.A.M., de Vries, H.W. & Mol, J.A. (1998) Behavioural, saliva cortisol and heart rate responses to different types of stimuli in dogs. *Applied Animal Behaviour Science*, 58, 365–381.
- Bekoff, M. (1972) The development of social interaction, play, and metacommunication in mammals: An ethological perspective. *Quarterly Review of Biology*, 47, 412–434.
- Bekoff, M. (1974) Social play and play-soliciting by infant canids. *American Zoologist*, 14, 323–340.
- Bekoff, M. (1979) Ground scratching by male domestic dogs: A composite signal. *Journal of Mammalogy*, 60, 847–848.
- Belyaev, D.K. (1979) Destabilizing selection as a factor in domestication. *Journal of Heredity*, 70, 301–308.
- Bennett, P.C. & Perini, E. (2003) Tail docking in dogs: A review of the issues. *Australian Veterinary Journal*, 81, 208–218.
- Berthould, D. (2010) Communication through scents: Environmental factors affecting the urine marking behaviour of the domestic dog, *Canis familiaris*, kept as a pet. PhD Thesis, Anglia Ruskin University, Cambridge.
- Blackwell, E. (2010) Socialization. In: D.S. Mills *et al.* (eds), *The Encyclopedia of Applied Animal Behaviour & Welfare*. CAB International, Oxfordshire.
- Bloom, T. & Friedman, H. (2013) Classifying dogs' (*Canis familiaris*) facial expressions from photographs. *Behavioural Processes*, 96, 1–10.
- Boissy, A. (1995) Fear and fearfulness in animals. *The Quarterly Review of Biology*, 70, 165–191.
- Bowlby, J. (1958) The nature of the child's tie to his mother. *International Journal of Psycho-Analysis*, 39, 350–373.
- Boyko, A.R., Boyko, R.H., Boyko, C.M. *et al.* (2009) Complex population structure in African village dogs and its implication for inferring dog domestication history. *Proceedings of the National Academy of Science*, 106, 13903–13908.
- Bradshaw, J.W. & Lea, A.M. (1992) Dyadic interactions between domestic dogs. *Anthrozoös*, 5, 245–253.
- Bradshaw, J.W.S., Blackwell, E.J. & Casey, R.A. (2009) Dominance in domestic dogs—Useful construct or bad habit? *Journal of Veterinary Behavior: Clinical Applications and Research*, 4, 135–144.
- Branson, N.J. & Rogers, L.J. (2006) Relationship between paw preference strength and noise phobia in *Canis familiaris*. *Journal of Comparative Psychology*, 120, 176–183.
- Breen, M. & Modiano, J.F. (2008) Evolutionarily conserved cytogenetic changes in hematological malignancies of dogs and humans—Man and his best friend share more than companionship. *Chromosome Research*, 16, 145–154.
- Broom, D. (1988) The scientific assessment of animal welfare. *Applied Animal Behaviour Science*, 20, 5–19.
- Bushby, P.A. & Griffin, B. (2011) An overview of pediatric spay and neuter benefits and techniques. *Veterinary Medicine*, 106, 83–89.
- Cafazzo, S., Natoli, E. & Valsecchi, P. (2012) Scent-marking behaviour in a pack of free-ranging domestic dogs. *Ethology*, 118, 955–966.
- Calil, C.M. & Marcondes, F.K. (2006) Influence of anxiety on the production of oral volatile sulfur compounds. *Life Sciences*, 79, 660–664.
- Case, L. (2005) *The Dog: Its Behavior, Nutrition, and Health*, 2nd edn. Blackwell, Ames.
- Casey, R.A., Loftus, B., Bolster, C., Richards, G.J. & Blackwell, E.J. (2014) Human directed aggression in domestic dogs (*Canis familiaris*): Occurrence in different contexts and risk factors. *Applied Animal Behaviour Science*, 152, 52–63.
- Chapman, B.L. & Voith, V.L. (1990) Behavioral problems in old dogs: 26 cases (1984–1987). *Journal of the American Veterinary Medical Association*, 196, 944–946.
- 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 University Press, Cambridge, MA.
- Clutton-Brock, J. (1999) *A Natural History of Domesticated Mammals*, 2nd edn. Cambridge University Press, Cambridge, UK.
- Coppinger, R. & Schneider, R. (1995) Evolution of working dogs. In: J. Serpell (ed), *The Domestic Dog: Its Evolution, Behaviour and Interactions with People*, pp. 21–47. Cambridge University Press, Cambridge, UK.
- Coppinger, R., Lorenz, J., Glendinning, J. & Pinardi, P. (1983) Attentiveness of guarding dogs for reducing predation on domestic sheep. *Journal of Range Management*, 36, 275–279.
- Coppola, C.L., Enns, R.M. & Grandin, T. (2006) Noise in the animal shelter environment: Building design and the effects of daily noise exposure. *Journal of Applied Animal Welfare Science*, 9, 1–7.
- Coren, S. (2006) *The Intelligence of Dogs: A Guide to the Thoughts, Emotions, and Inner Lives of Our Canine Companion*. Free Press, New York.
- Cummings, B.J., Head, E., Ruehl, W., Milgram, N.W. & Cotman, C.W. (1996) The canine as an animal model of human aging and dementia. *Neurobiology of Aging*, 17, 259–268.
- Darwin, C. (1872) *The Expression of the Emotions in Man and Animals*. John Murray, London.
- De Palma, C., Viggiano, E., Barillari, E. *et al.* (2005) Evaluating the temperament in shelter dogs. *Behaviour*, 142, 1307–1328.
- Denham, H.D.C., Bradshaw, J.W.S. & Rooney, N.J. (2014) Repetitive behaviour in kennelled domestic dog: Stereotypical or not? *Physiology & Behavior*, 128, 288–294.
- Dorey, N.R., Udell, M.A.R. & Wynne, C.D.L. (2010) When do domestic dogs, *Canis familiaris*, start to understand human pointing? The role of ontogeny in the development of inter-species communication. *Animal Behaviour*, 79, 37–41.
- Döring, D., Roscher, A., Scheipl, F., Küchenhoff, H. & Erhard, M.H. (2009) Fear-related behaviour of dogs in veterinary practice. *The Veterinary Journal*, 182, 38–43.
- Dreschel, N.A. (2010) The effects of fear and anxiety on health and lifespan in pet dogs. *Applied Animal Behaviour Science*, 125, 157–162.
- Dreschel, N.A. & Granger, D.A. (2005) Physiological and behavioral reactivity to stress in thunderstorm-phobic dogs and their caregivers. *Applied Animal Behaviour Science*, 95, 153–168.
- Drews, C. (1993) The concept and definition of dominance in animal behaviour. *Behaviour*, 125, 283–313.
- Elliot, O. & Scott, J.P. (1961) The development of emotional distress reactions to separation, in puppies. *The Journal of Genetic Psychology*, 99, 3–22.
- Ernst, K., Puppe, B., Schön, P.C. & Manteuffel, G. (2005) A complex automatic feeding system for pigs aimed to induce

- successful behavioural coping by cognitive adaptation. *Applied Animal Behaviour Science*, 91, 205–218.
- Falk, J.L. (1977) The origin and functions of adjunctive behavior. *Animal Learning and Behavior*, 5, 325–335.
- Fallani, G., Previde, E.P. & Valsecchi, P. (2006) Do disrupted early attachments affect the relationship between guide dogs and blind owners? *Applied Animal Behaviour Science*, 100, 241–257.
- Farágó, T., Pongrácz, P., Miklósi, Á., Huber, L., Virányi, Z. & Range, F. (2010a) Dogs' expectation about signalers' body size by virtue of their growls. *PLoS One*, 5, 15175.
- Farágó, T., Pongrácz, P., Range, F., Virányi, Z. & Miklósi, A. (2010b) 'The bone is mine': Affective and referential aspects of dog growls. *Animal Behaviour*, 79, 917–925.
- Feddersen-Petersen, D.U. (2000) Vocalisation of European wolves (*Canis lupus lupus* L.) and various dog breeds (*Canis lupus* f. *familiaris*). *Archiv für Tierzucht*, 43, 387–397.
- Feuerstein, N. & Terkel, J. (2008) Interrelationships of dogs (*Canis familiaris*) and cats (*Felis catus* L.) living under the same roof. *Applied Animal Behaviour Science*, 113, 150–165.
- Filiatre, J.C., Millot, J.L. & Eckerlin, A. (1991) Behavioural variability of olfactory exploration of the pet dog in relation to human adults. *Applied Animal Behaviour Science*, 30, 341–350.
- Fox, M.W. (1969) Behavioral effects of rearing dogs with cats during the 'critical period of socialization'. *Behaviour*, 35, 273–280.
- Fox, M.W. (1971) *Behaviour of Wolves, Dogs and Related Canids*. Harper and Row, New York.
- Fox, M.W. & Stelzner, D. (1966) Behavioural effects of differential early experience in the dog. *Animal Behaviour*, 14, 273–281.
- Fratkin, J.L. & Baker, S.C. (2013) The role of coat color and ear shape on the perception of personality in dogs. *Anthrozoös*, 26, 125–133.
- Freedman, D.G., King, J.A. & Elliot, O. (1961) Critical period in the social development of dogs. *Science*, 133, 1016–1017.
- Furton, K.G. & Myers, L.J. (2001) The scientific foundation and efficacy of the use of canines as chemical detectors for explosives. *Talanta*, 54, 487–500.
- Gácsi, M., Topál, J., Miklósi, Á., Dóka, A. & Csányi, V. (2001) Attachment behavior of adult dogs (*Canis familiaris*) living at rescue centers: Forming new bonds. *Journal of Comparative Psychology*, 115, 423–431.
- Gácsi, M., McGreevy, P., Kara, E. & Miklós, A. (2009) Effects of selection for cooperation and attention in dogs. *Behavioral and Brain Functions*, 5, 31.
- Gadbois, S. & Reeve, C. (2014) Canine olfaction: Scent, sign, and situation. In: A. Horowitz (ed), *Domestic Dog Cognition and Behavior: The Scientific Study of Canis Familiaris*, pp. 3–29. Springer Verlag, Heidelberg.
- Garber, M.B. (1996) *Dog Love*. Simon and Schuster, New York.
- Gazit, I. & Terkel, J. (2003) Explosives detection by sniffer dogs following strenuous physical activity. *Applied Animal Behaviour Science*, 81, 149–161.
- Gazzano, A., Mariti, C., Notari, L., Sighieri, C. & McBride, E.A. (2008) Effects of early gentling and early environment on emotional development of puppies. *Applied Animal Behaviour Science*, 110, 294–304.
- Glaser, R. & Kiecolt-Glaser, J.K. (2005) Stress-induced immune dysfunction: Implications for health. *Nature Reviews Immunology*, 5, 243–251.
- Gosling, S.D., Sandy, C.J. & Potter, J. (2010) Personalities of self-identified "dog people" and "cat people". *Anthrozoös*, 23, 213–222.
- Graham, L., Wells, D.L. & Hepper, P.G. (2005) The influence of olfactory stimulation on the behaviour of dogs housed in a rescue shelter. *Applied Animal Behaviour Science*, 91, 143–153.
- Grier, K.C. (2006) *Pets in America: A History*. Harcourt, Orlando.
- Gunter, L. (2013) Breed stereotype and effects of handler appearance on perceptions of pit bulls. *Interdisciplinary Forum for Applied Animal Behavior*, San Diego, CA.
- Hale, M.L., Verduijn, M.H., Moller, A.P., Wolff, K. & Petrie, M. (2009) Is the peacock's train an honest signal of genetic quality at the major histocompatibility complex? *Journal of Evolutionary Biology*, 22, 1284–1294.
- Hall, N.J., Smith, D.W. & Wynne, C.D.L. (2013) Training domestic dogs (*Canis lupus familiaris*) on a novel discrete trials odor-detection task. *Learning and Motivation*, 44, 218–228.
- Hart, L.A. (1995) Dogs as human companions: A review of the relationship. In: J. Serpell (ed), *The Domestic Dog, Its Evolution, Behaviour and Interactions with People*, pp. 161–178. Cambridge University Press, Cambridge, MA.
- Hecht, J. (2012) Do dogs understand our words? *The Bark*, 72 <http://thebark.com/content/do-dogs-understand-our-words> [accessed June 10, 2014].
- Hecht, J. (2013) Dog speak: The sounds of dogs. *The Bark*, 73 <http://thebark.com/content/dog-speak-sounds-dogs> [accessed June 10, 2014].
- Hecht, J. & Horowitz, A. (2013) Physical prompts to anthropomorphisms of the domestic dog (*Canis familiaris*). *Journal of Veterinary Behavior: Clinical Applications and Research*, 8, e30.
- Hecht, J., Miklósi, Á. & Gácsi, M. (2012) Behavioral assessment and owner perceptions of behaviors associated with guilt in dogs. *Applied Animal Behaviour Science*, 139, 134–142.
- Hekman, J.P., Karas, A.Z. & Dreschel, N.A. (2012) Salivary cortisol concentrations and behavior in a population of healthy dogs hospitalized for elective procedures. *Applied Animal Behaviour Science*, 141, 149–157.
- Hennessy, M.B., Davis, H.N., Williams, M.T., Mellott, C. & Douglas, C.W. (1997) Plasma cortisol levels of dogs at a county animal shelter. *Physiology & Behavior*, 62, 485–490.
- Hennessy, M.B., Williams, M.T., Miller, D.D., Douglas, C.W. & Voith, V.L. (1998) Influence of male and female petters on plasma cortisol and behaviour: Can human interaction reduce the stress of dogs in a public animal shelter? *Applied Animal Behaviour Science*, 61, 63–77.
- Herron, M.E., Shofer, F.S. & Reisner, I.R. (2009) Survey of the use and outcome of confrontational and non-confrontational training methods in client-owned dogs showing undesired behaviors. *Applied Animal Behaviour Science*, 117, 47–54.
- Hetts, S., Derrell, C., Calpin, J.P., Arnold, C.E. & Mateo, J.M. (1992) Influence of housing conditions on beagle behaviour. *Applied Animal Behaviour Science*, 34, 137–155.
- Hiby, E.F., Rooney, N.J. & Bradshaw, J.W.S. (2006) Behavioural and physiological responses of dogs entering re-homing kennels. *Physiology & Behavior*, 89, 385–391.
- Horn, L., Huber, L. & Range, F. (2013) The importance of the secure base effect for domestic dogs—Evidence from a manipulative problem-solving task. *PLoS One*, 8, e65296.
- Horowitz, A. (2002) *The behaviors of theories of mind, and a case study of dogs at play*. Unpublished doctoral dissertation, University of California, San Diego.
- Horowitz, A. (2009a) Attention to attention in domestic dog (*Canis familiaris*) dyadic play. *Animal Cognition*, 12, 107–118.
- Horowitz, A. (2009b) Disambiguating the "guilty look": Salient prompts to a familiar dog behaviour. *Behavioural Processes*, 81, 447–452.
- Horowitz, A. (2009c) *Inside of a dog*. Scribner, New York.
- Horowitz, A. (2014) *Canis familiaris: Companion and captive*. In: L. Gruen (ed), *The Ethics of Captivity*, pp. 7–21. Oxford University Press, Oxford.

- Horowitz, A.C. & Bekoff, M. (2007) Naturalizing anthropomorphism: Behavioral prompts to our humanizing of animals. *Anthrozoös*, 13, 23–35.
- Horowitz, A. & Hecht, J. (2014) Looking at dogs: Moving from anthropocentrism to canid *umwelt*. In: A. Horowitz (ed), *Domestic Dog Cognition and Behavior*, pp. 201–219. Springer-Verlag, Berlin.
- Horowitz, A., Hecht, J. & Dedrick, A. (2013) Smelling more or less: Investigating the olfactory experience of the domestic dog. *Learning and Motivation*, 44, 207–217.
- Houpt, K.A. (2011) *Domestic Animal Behavior for Veterinarians and Animal Scientists*. Wiley-Blackwell, Ames.
- Hubrecht, R.C., Serpell, J.A. & Poole, T.B. (1992) Correlates of pen size and housing conditions on the behaviour of kennelled dogs. *Applied Animal Behaviour Science*, 34, 365–383.
- Humane Society of the United States. 2010. *Spay-Neuter by State*. http://www.humanesociety.org/assets/pdfs/legislation/spayneuter_by_state.pdf [accessed June 10, 2014].
- Huson, H.J., Parker, H.G., Runstadler, J. & Ostrander, E.A. (2010) A genetic dissection of breed composition and performance enhancement in the Alaskan sled dog. *BMC Genetics*, 11, 71.
- Jakovcovic, A., Mustaca, A. & Bentosela, M. (2012) Do more sociable dogs gaze longer to the human face than less sociable ones? *Behavioural Processes*, 90, 217–222.
- Juarbe-Díaz, S.V. (1997) Assessment and treatment of excessive barking in the domestic dog. *The Veterinary Clinics of North America. Small Animal Practice*, 27, 515–532.
- Kerepesi, A., Jonsson, G.K., Miklósi, Á., Topál, J., Csányi, V. & Magnusson, M.S. (2005) Detection of temporal patterns in dog-human interaction. *Behavioural Processes*, 70, 69–79.
- Kiley-Worthington, M. (1976) The tail movements of ungulates, canids and felids with particular reference to their causation and function as displays. *Behaviour*, 56, 69–115.
- King, T., Hemsworth, P.H. & Coleman, G.J. (2003) Fear of novel and startling stimuli in domestic dogs. *Applied Animal Behaviour Science*, 82, 45–64.
- Kis, A., Bence, M., Lakatos, G. *et al.* (2014) Oxytocin receptor gene polymorphisms are associated with human directed social behavior in dogs (*Canis familiaris*). *PLoS One*, 9, e83993.
- Kogan, L.R., Schoenfeld-Tacher, R. & Simon, A.A. (2012) Behavioral effects of auditory stimulation on kennelled dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*, 7, 268–275.
- Koolhaas, J.M., Korte, S.M., De Boer, S.F. *et al.* (1999) Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews*, 23, 925–935.
- Kubinyi, E., Miklósi, Á., Topál, J. & Csányi, V. (2003) Social mimetic behaviour and social anticipation in dogs: Preliminary results. *Animal Cognition*, 6, 57–63.
- Kustritz, M.V.R. (2007) Determining the optimal age for gonadectomy of dogs and cats. *Journal of the American Veterinary Medical Association*, 231, 1665–1675.
- Landsberg, G. (2005) Therapeutic agents for the treatment of cognitive dysfunction syndrome in senior dogs. *Progress in Neuro-Psychopharmacology and Biology Psychiatry*, 29, 471–479.
- Landsberg, G.M., Hunthausen, W.L. & Ackerman, L.J. (2003) The effects of aging on the behavior of senior pets. In: G.M. Landsberg, W.L. Hunthausen & L. Ackerman (eds), *Handbook of Behavior Problems of the Dog and Cat*, 2nd edn, pp. 269–304. Elsevier, Edinburgh.
- 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 Science*, 109, 8878–8883.
- Leaver, S.D.A. & Reimchen, T.E. (2008) Behavioural responses of *Canis familiaris* to different tail lengths of a remotely-controlled life-size dog replica. *Behaviour*, 145, 377–390.
- Levitin, D.A., Lidicker, W.Z., Jr & Freund, G. (2009) Behavioural biologists do not agree on what constitutes behaviour. *Animal Behaviour*, 78, 103–110.
- Lisberg, A. (2013) Establishing new relationships through chemical signals: Status, scent-marks & anogenital investigation in unfamiliar dogs. Interdisciplinary Forum for Applied Animal Behavior, San Diego.
- Lockwood, R. (1996) The ethology and epidemiology of canine aggression. In: J.A. Serpell (ed), *The Domestic Dog: Its Evolution, Behavior and Interactions with People*, pp. 131–138. Cambridge University Press, Cambridge, UK.
- London, K.B. (2012) *Piloerection: What does it mean when a dog does this?* *The Bark*, [blog] April 4, 2012, <http://thebark.com/content/piloerection> [accessed March 17, 2014].
- Long, R.A., Donovan, T.M., Mackay, P., Zielinski, W.J. & Buzas, J.S. (2007) Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. *The Journal of Wildlife Management*, 71, 2018–2025.
- Lord, K. (2013) A comparison of the sensory development of wolves (*Canis lupus lupus*) and dogs (*Canis lupus familiaris*). *Ethology*, 119, 110–120.
- Lord, K., Feinstein, M. & Coppinger, R. (2009) Barking and mobbing. *Behavioural Processes*, 81, 358–368.
- Lord, K., Feinstein, M., Smith, B. & Coppinger, R. (2013) Variation in reproductive traits of members of the genus *Canis* with special attention to the domestic dog (*Canis familiaris*). *Behavioural Processes*, 92, 131–142.
- Lorenz, K. (1954) *Man Meets Dog*. Methuen & Co. Ltd, London.
- Marder, A.R., Shabelansky, A., Patronek, G.J., Dowling-Guyer, S. & D'Arpino, S.S. (2013) Food-related aggression in shelter dogs: A comparison of behavior identified by a behavior evaluation in the shelter and owner reports after adoption. *Applied Animal Behaviour Science*, 148, 150–156.
- Mariti, C., Gazzano, A., Moore, J.L., Baragli, P., Chelli, L. & Sighieri, C. (2012) Perception of dogs' stress by their owners. *Journal of Veterinary Behavior: Clinical Applications and Research*, 7, 213–219.
- Mariti, C., Carlone, B., Ricci, E., Sighieri, C. & Gazzano, A. (2014) Intraspecific attachment in adult domestic dogs (*Canis familiaris*): Preliminary results. *Applied Animal Behaviour Science*, 152, 64–72.
- Martin, P. & Bateson, P. (2007) *Measuring Behaviour: An Introductory Guide*, 3rd edn. Cambridge University Press, Cambridge.
- Mason, G.J. (1991) Stereotypies: A critical review. *Animal Behaviour*, 41, 1015–1037.
- Mason, G.J. & Latham, N.R. (2004) Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator? *Animal Welfare*, 13, S57–S69.
- McConnell, P.B. (1990) Acoustic structure and receiver response in domestic dogs, *Canis familiaris*. *Animal Behaviour*, 39, 897–904.
- McConnell, P.B. (2002) *The Other End of the Leash: Why We Do What We Do Around Dogs*. Ballantine Books, New York.
- McConnell, P.B. (2007) *For the Love of a Dog: Understanding Emotion in You and Your Best Friend*. Ballantine Books, New York.
- McGowan, R.T.S., Rehn, T., Norling, Y. & Keeling, L.J. (2014) Positive affect and learning: Exploring the “Eureka Effect” in dogs. *Animal Cognition*, 17, 577–587.

- McMillan, F.D., Duffy, D.L. & Serpell, J.A. (2011) Mental health of dogs formerly used as 'breeding stock' in commercial breeding establishments. *Applied Animal Behaviour Science*, 135, 86–94.
- Meints, K., Syrnyk, C. & De Keuster, T. (2010) Why do children get bitten in the face? *Injury Prevention*, 16, A172–A173.
- Mertens, P.A. & Unshelm, J. (1996) Effects of group and individual housing on the behavior of kennelled dogs in animal shelters. *Anthrozoös*, 9, 40–51.
- Miklósi, Á. (2007) *Dog Behaviour, Evolution, and Cognition*. Oxford University Press, Oxford.
- Miklósi, Á., Polgárdi, R., Topál, J. & Csányi, V. (2000) Intentional behaviour in dog-human communication: An experimental analysis of "showing" behaviour in the dog. *Animal Cognition*, 3, 159–166.
- Mills, D.S. (2002) Learning, training and behaviour modification techniques. In: D. Horowitz, D. Mills & S. Heath (eds), *BSAVA Manual of Canine and Feline Behavioural Medicine*, pp. 37–48. BSAVA, Gloucester.
- Mills, D.S., Ramos, D., Estelles, M.G. & Hargrave, C. (2006) A triple blind placebo-controlled investigation into the assessment of the effect of Dog Appeasing Pheromone (DAP) on anxiety related behaviour of problem dogs in the veterinary clinic. *Applied Animal Behaviour Science*, 98, 114–126.
- Mohan-Gibbons, H., Weiss, E. & Slater, M. (2012) Preliminary investigation of food guarding behavior in shelter dogs in the United States. *Animals*, 2, 331–346.
- Morris, P.H., Doe, C. & Godsell, E. (2008) Secondary emotions in non-primate species? Behavioural reports and subjective claims by animal owners. *Cognition and Emotion*, 22, 3–20.
- Morton, E.S. (1977) On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist*, 111, 855–869.
- Nagasawa, M., Kikusui, T., Onaka, T. & Ohta, M. (2009) Dog's gaze at its owner increases owner's urinary oxytocin during social interaction. *Hormones and Behavior*, 55, 434–441.
- Neuhaus, V.W. (1981) The importance of sniffing to the olfaction of the dog. *Z. Saugetierkunde*, 46, 301–310.
- Núñez, J.F., Ferré, P., Escorihuela, R.M., Tobeña, A. & Fernández-Teruel, A. (1996) Effects of postnatal handling of rats on emotional, HPA-axis, and prolactin reactivity to novelty and conflict. *Physiology & Behavior*, 60, 1355–1359.
- Odendaal, J.S.J. & Meintjes, R.A. (2003) Neurophysiological correlates of affiliative behaviour between humans and dogs. *The Veterinary Journal*, 165, 296–301.
- Oesterhelweg, L., Kröber, S., Rottmann, K. et al. (2008) Cadaver dogs—A study on detection of contaminated carpet squares. *Forensic Science International*, 174, 35–39.
- Ortolani, A., Vernooij, H. & Coppinger, R. (2009) Ethiopian village dogs: Behavioural responses to a stranger's approach. *Applied Animal Behaviour Science*, 119, 210–218.
- Panksepp, J. (1998) *Affective Neuroscience: The Foundations of Human and Animal Emotions*. Oxford University Press, Oxford.
- Petrie, M., Halliday, T. & Sanders, C. (1991) Peahens prefer peacocks with elaborate trains. *Animal Behaviour*, 41, 323–331.
- Pettersson, H., Kaminski, J., Herrmann, E. & Tomasello, M. (2011) Understanding of human communicative motives in domestic dogs. *Applied Animal Behaviour Science*, 133, 235–245.
- Pettijohn, T.F., Wong, T.W., Ebert, P.D. & Scott, J.P. (1977) Alleviation of separation distress in 3 breeds of young dogs. *Developmental Psychobiology*, 10, 373–381.
- Pierantoni, L. & Verga, M. (2007) Behavioral consequences of premature maternal separation and lack of stimulation during the socialization period in dogs. *Journal of Veterinary Behaviour*, 2, 84–85.
- Pluijmakers, J.J.T.M., Appleby, D.L. & Bradshaw, J.W.S. (2010) Exposure to video images between 3 and 5 weeks of age decreases neophobia in domestic dogs. *Applied Animal Behaviour Science*, 126, 51–58.
- Pongrácz, P., Miklósi, Á., Vida, V. & Csányi, V. (2005) The pet dogs ability for learning from a human demonstrator in a detour task is independent from the breed and age. *Applied Animal Behaviour Science*, 90, 309–323.
- Pongrácz, P., Molnár, C. & Miklósi, Á. (2006) Acoustic parameters of dog barks carry emotional information for humans. *Applied Animal Behaviour Science*, 100, 228–240.
- Pongrácz, P., Molnár, C. & Miklósi, Á. (2010) Barking in family dogs: An ethological approach. *The Veterinary Journal*, 183, 141–147.
- Price, E.O. (1999) Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science*, 65, 245–271.
- Pullen, A.J., Merrill, R.J.N. & Bradshaw, J.W.S. (2012) The effect of familiarity on behaviour of kennel housed dogs during interactions with humans. *Applied Animal Behaviour Science*, 137, 66–73.
- Pullen, A.J., Merrill, R.J.N. & Bradshaw, J.W.S. (2013) The effect of familiarity on behavior of kennel dogs during interactions with conspecifics. *Journal of Applied Animal Welfare Science*, 16, 64–76.
- Quaranta, A., Sinischalchi, M. & Vallortigara, G. (2007) Asymmetric tail-wagging responses by dogs to different emotive stimuli. *Current Biology*, 17, R199–R201.
- Quignon, P., Kirkness, E., Cadieu, E. et al. (2003) Comparison of the canine and human olfactory receptor gene repertoires. *Genome Biology*, 4, 80.1–80.9.
- Rehn, T., Handlin, L., Uvnäs-Moberg, K. & Keeling, L.J. (2014) Dogs' endocrine and behavioural responses at reunion are affected by how the human initiates contact. *Physiology & Behavior*, 124, 45–53.
- Reid, P.J. (2009) Adapting to the human world: Dogs' responsiveness to our social cues. *Behavioural Processes*, 80, 325–333.
- Reisner, I.R., Nance, M.L., Zeller, J.S., Houseknecht, E.M., Kassam-Adams, N. & Wiebe, D.J. (2011) Behavioural characteristics associated with dog bites to children presenting to an urban trauma centre. *Injury Prevention*, 17, 348–353.
- Rheingold, H.L. (1963) *Maternal Behavior in Mammals*. John Wiley & Sons, Inc, New York.
- Riedel, J., Schumann, K., Kaminski, J., Call, J. & Tomasello, M. (2008) The early ontogeny of human-dog communication. *Animal Behaviour*, 75, 1003–1014.
- Riemer, S., Müller, C., Virányi, Z., Huber, L. & Range, F. (2013) Choice of conflict resolution strategy is linked to sociability in dog puppies. *Applied Animal Behaviour Science*, 149, 36–44.
- Roberts, T., McGreevy, P. & Valenzuela, M. (2010) Human induced rotation and reorganization of the brain of domestic dogs. *PLoS One*, 5, 11946.
- Rogers, L.J. (2000) Evolution of hemispheric specialization: Advantages and disadvantages. *Brain and Language*, 73, 236–253.
- Rogers, L.J. (2009) Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 364, 943–954.
- Rooney, N. & Bradshaw, J. (2014) Canine welfare science: An antidote to sentiment and myth. In: A. Horowitz (ed), *Domestic Dog Cognition and Behavior*, pp. 241–274. Springer-Verlag, Heidelberg.

- Rooney, N.J., Bradshaw, J.W.S. & Robinson, I.H. (2001) Do dogs respond to play signals given by humans? *Animal Behaviour*, 61, 715–722.
- Rooney, N.J., Gaines, S.A. & Bradshaw, J.W.S. (2007) Behavioural and glucocorticoid responses of dogs (*Canis familiaris*) to kenneling: Investigating mitigation of stress by prior habituation. *Physiology & Behavior*, 92, 847–854.
- Rooney, N., Gaines, S. & Hiby, E. (2009) A practitioner's guide to working dog welfare. *Journal of Veterinary Behavior: Clinical Applications and Research*, 4, 127–134.
- Rooney, N.J., Morant, S. & Guest, C. (2013) Investigation into the value of trained glycaemia alert dogs to clients with type I diabetes. *PLoS One*, 8, e69921.
- Sales, G., Hubrecht, R., Peyvandi, A., Milligan, S. & Shield, B. (1997) Noise in dog kennelling: Is barking a welfare problem for dogs? *Applied Animal Behaviour Science*, 52, 321–329.
- Salvin, H.E., McGreevy, P.D., Sachdev, P.S. & Valenzuela, M.J. (2011) Growing old gracefully—Behavioral changes associated with “successful aging” in the dog, *Canis familiaris*. *Journal of Veterinary Behavior: Clinical Applications and Research*, 6, 313–320.
- Sanders, C.R. (1993) Understanding dogs: Caretakers' attributions of mindedness in canine-human relationships. *Journal of Contemporary Ethnography*, 22, 205–226.
- Sapolsky, R.M. (2004) *Why Zebras Don't Get Ulcers*, 3rd edn. Henry Holt & Company, New York.
- Schenkel, R. (1967) Submission: Its features and function in the wolf and dog. *American Zoologist*, 7, 319–329.
- Schilder, M.B.H. & van der Borg, J.A.M. (2004) Training dogs with help of the shock collar: Short and long term behavioural effects. *Applied Animal Behaviour Science*, 85, 319–334.
- Schultz, J., Anreder, P. & Zawistowski, S. (1995) *When the bond breaks*. *Animal Watch* (Winter), 15–17.
- Schwab, C. & Huber, L. (2006) Obey or not obey? Dogs (*Canis familiaris*) behave differently in response to attentional states of their owners. *Journal of Comparative Psychology*, 120, 169–175.
- Scott, J.P. (1958) Critical periods in the development of social behavior in puppies. *Psychosomatic Medicine*, 20, 42–54.
- Scott, J.P. (1985) Investigation behavior: Toward a science of sociality. In: D.A. Dewsbury (ed), *Leaders in the Study of Animal Behavior: Autobiographical Perspectives*, pp. 389–429. Associated University Presses, Cranbury.
- Scott, J.P. & Fuller, J.L. (1965) *Genetics and the Social Behavior of the Dog*. University of Chicago Press, Chicago.
- Senn, C.L. & Lewin, J.D. (1975) Barking dogs as an environmental problem. *Journal of the American Veterinary Medical Association*, 166, 1065–1068.
- Serpell, J.A. & Duffy, D.L. (2014) Dog breeds and their behavior. In: A. Horowitz (ed), *Domestic Dog Cognition and Behavior: The Scientific Study of Canis familiaris*, pp. 31–57. Springer-Verlag, Heidelberg.
- Shepherd, K. (2009) Ladder of aggression. In: D.F. Horwitz & D.S. Mills (eds), *BSAVA Manual of Canine and Feline Behavioural Medicine*, 2nd edn, pp. 13–16. BSAVA, Gloucester.
- Shore, E.R. & Girrens, K. (2001) Characteristics of animals entering an animal control or humane society shelter in a midwestern city. *Journal of Applied Animal Welfare Science*, 4, 105–115.
- Simonet P., Murphy M. & Lance A. (2001) *Laughing dog: Vocalizations of domestic dogs during play encounters*. Paper presented at the meeting of the Animal Behavior Society, Corvallis, OR.
- Siniscalchi, M., Lusito, R., Vallortigara, G. & Quaranta, A. (2013) Seeing left- or right-asymmetric tail wagging produces different emotional responses in dogs. *Current Biology*, 23, 2279–2282.
- Slabbert, J. & Rasa, O.A.E. (1997) Observational learning of an acquired maternal behaviour pattern by working dog pups: An alternative training method? *Applied Animal Behaviour Science*, 53, 309–316.
- Sommerville, B.A. & Broom, D.M. (1998) Olfactory awareness. *Applied Animal Behaviour Science*, 57, 269–286.
- Soproni, K., Miklósi, Á., Topál, J. & Csányi, V. (2001) Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *Journal of Comparative Psychology*, 115, 122–126.
- Tami, G. & Gallagher, A. (2009) Description of the behaviour of domestic dog (*Canis familiaris*) by experienced and inexperienced people. *Applied Animal Behaviour Science*, 120, 159–169.
- Taylor, K.D. & Mills, D.S. (2007) The effect of the kennel environment on canine welfare: A critical review of experimental studies. *Animal Welfare*, 16, 435–447.
- Taylor, A.M., Reby, D. & McComb, K. (2010) Size communication in domestic dog, *Canis familiaris*, growls. *Animal Behaviour*, 79, 205–210.
- Tembrock, G. (1976) Canid vocalizations. *Behavioural Processes*, 1, 57–75.
- Thalmann, 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.
- Thesen, A., Steen, J.B. & Døving, K.B. (1993) Behaviour of dogs during olfactory tracking. *Journal of Experimental Biology*, 180, 247–251.
- Thompson, D. (2014) *What makes an aggressive dog, and how you can spot one* (Health Day), <http://consumer.healthday.com/mental-health-information-25/behavior-health-news-56/dog-aggression-683735.html> [accessed May 29, 2014].
- Tinbergen, N. (1951) *The Study of Instinct*. Clarendon Press, New York.
- Tinbergen, N. (1963) On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20, 410–433.
- Tomkins, L.M., Thomson, P.C. & McGreevy, P.D. (2012) Associations between motor, sensory and structural lateralisation and guide dog success. *The Veterinary Journal*, 192, 359–367.
- Topál, J., Miklósi, Á., Csányi, V. & Dóka, A. (1998) Attachment behavior in dogs (*Canis familiaris*): A new application of Ainsworth's (1969) strange situation test. *Journal of Comparative Psychology*, 112, 219–229.
- Torres de la Riva, G., Hart, B.L., Farver, T.B. *et al.* (2013) Neutering dogs: Effects on joint disorders and cancers in golden retrievers. *PLoS One*, 8, e55937.
- Trivers, R.L. (1974) Parent-offspring conflict. *American Zoologist*, 14, 249–264.
- Trut, L. (1999) Early canid domestication: The farm-fox experiment. *American Scientist*, 87, 160–169.
- Tuber, D.S., Hennessy, M.B., Sanders, S. & Miller, J.A. (1996) Behavioral and glucocorticoid responses of adult domestic dogs (*Canis familiaris*) to companionship and social separation. *Journal of Comparative Psychology*, 110, 103–108.
- Udell, M.A.R., Ewald, M., Dorey, N.R. & Wynne, C.D.L. (2014) Exploring breed differences in dogs (*Canis familiaris*): Does exaggeration or inhibition of predatory response predict performance on human-guided tasks? *Animal Behaviour*, 89, 99–105.

- 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.
- Valsecchi, P., Previde, E.P., Accorsi, P.A. & Fallani, G. (2010) Development of the attachment bond in guide dogs. *Applied Animal Behaviour Science*, 123, 43–50.
- Vilà, C., Savolainen, P., Maldonado, J.E. *et al.* (1997) Multiple and ancient origins of the domestic dog. *Science*, 276, 1687–1689.
- Vollmer, P.J. (1977) Do mischievous dogs reveal their “guilt”? *Veterinary Medicine, Small Animal Clinician*, 72, 1002–1005.
- Walker, J., Phillips, C. & Waran, N. (2013) Companion animal owners’ perceptions of their animal’s behavioural response to the loss of an animal companion. In: *Proceedings, International Society for Anthrozoology*, Chicago, IL.
- Waller, B.M., Peirce, K., Caeiro, C.C. *et al.* (2013) Paedomorphic facial expressions give dogs a selective advantage. *PLoS One*, 8, e82686.
- Ward, C., Bauer, E.B. & Smuts, B.B. (2008) Partner preferences and asymmetries in social play among domestic dog, *Canis lupus familiaris*, littermates. *Animal Behaviour*, 76, 1187–1199.
- Warner, G.S. (2010) Increased incidence of domestic animal bites following a disaster due to natural hazards. *Prehospital and Disaster Medicine*, 25, 187–190.
- Wayne, R.K. & Ostrander, E.A. (2007) Lessons learned from the dog genome. *Trends in Genetics*, 23, 557–567.
- Weiss, E., Miller, K., Mohan-Gibbons, H. & Vela, C. (2012) Why did you choose this pet? Adopters and pet selection preferences in five animal shelters in the United States. *Animals*, 2, 144–159.
- Wells, D.L. & Hepper, P.G. (1999) Male and female dogs respond differently to men and women. *Applied Animal Behaviour Science*, 61, 341–349.
- Wells, D.L. & Hepper, P.G. (2000) Prevalence of behaviour problems reported by owners of dogs purchased from an animal rescue shelter. *Applied Animal Behaviour Science*, 69, 55–65.
- Wells, D.L. & Hepper, P.G. (2006) Prenatal olfactory learning in the domestic dog. *Animal Behaviour*, 72, 681–686.
- Wells, D.L., Graham, L. & Hepper, P.G. (2002) The influence of auditory stimulation on the behaviour of dogs housed in a rescue shelter. *Animal Welfare*, 11, 385–393.
- Westgarth, C., Christley, R.M., Pinchbeck, G.L. *et al.* (2010) Dog behaviour on walks and the effect of use of the leash. *Applied Animal Behaviour Science*, 125, 38–46.
- Willis, C.M., Church, S.M., Guest, C.M. *et al.* (2004) Olfactory detection of human bladder cancer by dogs: Proof of principle study. *BMJ: British Medical Journal*, 329, 712.
- Wilson, C.C., Netting, F.E., Turner, D.C. & Olsen, C.H. (2013) Companion animals in obituaries: An exploratory study. *Anthrozoös*, 26, 227–236.
- Wood, L.A. (2011) *Food for thought: Modifying food guarding behavior in the shelter environment*. *Animal Sheltering*, Iss. November/December 2011, 53–56.
- Yeon, S.C. (2007) The vocal communication of canines. *Journal of Veterinary Behavior: Applications and Research*, 2, 141–144.
- Yin, S. & McCowan, B. (2004) Barking in domestic dogs: Context specificity and individual identification. *Animal Behaviour*, 68, 343–355.