

Olfaction in the Order Carnivora: Family Canidae

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26.1 INTRODUCTION

This chapter reviews olfactory behavior in the Carnivora, concentrating on the family Canidae. Although there have been “pockets” of study on various aspects of olfactory behavior in other Carnivora (e.g., Mellon, 1993; Rozhnov and Rozhnov, 1998; Sliwa and Richardson, 1998; Soini et al., 2012), most research has focused on canids and it is these studies that form the focus of this review. Canids are also of interest because of their unique status in ‘serving’ humans using their sense of smell. Indeed, the olfactory abilities of wolves were recognized by early humans and used to aid hunting and this contributed to the development of cooperation between man and wolves and the process of the domestication of this species (Ruusila and Pesonen, 2004).

The chapter is divided into three main sections. First, aspects of the olfactory system that may contribute to the canids’ acute sense of smell are considered. Second, the olfactory behavior of canids is discussed, and, finally, the applications of dogs’ olfactory abilities are reviewed. We will use selective examples to illustrate olfactory behavior in canids and highlight issues which require further study in order to fully understand the role of odors for these species. With regard to terminology, we use the term “canid(s)” to refer to the family Canidae and “dog” when referring to the domestic dog, *Canis familiaris*, whether this be a pet, kennelled, or experimental animal. When referring to domestic dogs that are wild or feral, we use the term “free-ranging dog.”

26.2 CONSIDERATIONS OF OLFACTION IN THE CARNIVORA

We commence with two observations regarding olfaction in the Carnivora as a whole. First, olfactory behavior generally has been subjected to little study in this Order. As a result, caution must be exercised in making assumptions about the role, or lack of role, of odors in Carnivoran behavior. For example, studies of olfactory structures in Pinnipeds (walrus, seals, and sea-lions) indicate they are under-developed in comparison to other, land-based, Carnivora. This has led to a view that they have poor olfactory abilities and that odor plays little role in guiding their behavior. Recent research has challenged this notion. Psychophysical studies have demonstrated that South African fur seals and harbour seals have good olfactory discrimination abilities and sensitivity to various odors (Kowalewsky et al., 2006; Laska et al., 2008). Further studies have demonstrated the use of olfaction in the natural behavior of pinnipeds. Female Australian sea-lions distinguish their own pups from others by their odor (Pitcher et al., 2011) and the South American sea-lion locates its pups by smell (Trimble and Insley, 2010).

Second, the absence of study has led to some “facts” regarding the abilities of certain Carnivora becoming widely accepted. Perhaps the best example of this is the widely held view that bears have excellent olfactory abilities, for example, polar bears can smell a seal from over 1 km (Seaworld, 2012) or 30 km (Wiki, 2012) away. Whilst published papers report observations of bears in the wild using odors to detect prey (e.g., Blanco et al., 2011),

there are no reports demonstrating that the sense of smell in bears is more or less acute than that of other species. Whether the bear's olfactory abilities are exceptional, or better than other Carnivora, therefore requires experimental study.

Available evidence, albeit sparse, suggests that all members of the Order Carnivora have a rich olfactory-guided repertoire of behavior. However, much further scientific study is needed to evaluate the olfactory abilities of, and role played by odor in, various Carnivora species.

26.2.1 Olfactory Sensitivity

Early interactions between humans and wolves are speculated to have resulted from encounters when hunting the same prey. Observations of the hunting behavior of canids may have alerted man to the animals' use of odors and contributed to an association that lasts today. Interest in the olfactory abilities of the canids has arisen because of their reputed excellent sensitivity to smells, far superior to that of man. Evidence for this has been derived from observations of the dog being able to detect the presence of odors, such as explosives and drugs (see Section 26.4), at extremely low levels. Other studies have attempted to quantify the sensitivity of the dog's olfactory system through more conventional psychophysical tests. As a general conclusion, such experiments have found that dogs detect odors at a much lower concentration than do humans (e.g., Neuhaus, 1953; Marshall et al., 1981; Marshall and Moulton, 1981; Krestel et al., 1984; Walker et al., 2006).

A major issue in evaluating the threshold levels of olfactory detection reported by different studies is that varied methodologies have been used and give rise to different threshold estimates for the same odor. For example, when assessing thresholds for *n*-amyl acetate using a naturalistic "find the target task," Walker et al. (2006) reported threshold detection levels of 1–2 parts per trillion, over 30–20,000 times lower than those reported by Krestel et al. (1984) of 52–326,000 parts per trillion using a conditioned suppression paradigm. The performance of dogs may vary according to the paradigm used and also the training provided. A further significant factor is that different studies have used different breeds, e.g., standard schnauzer and Rottweilers (Walker et al., 2006), beagles (Krestel et al., 1984), and German shepherds and fox terriers (Marshall et al., 1981). Not only may there be breed differences in olfactory abilities, there may also be differences between individuals of the same breed (Marshall and Moulton, 1981).

Despite these problems, studies are consistent in indicating that dogs respond to odors at much lower levels (1,000–1,000,000 times lower) than humans. Much further study is needed, controlling for among other variables, test

paradigm and dog breed, to document the sensitivity of the dog's olfactory system.

26.2.2 A Canid is not just a Canid

One note of caution must be added here. The family Canidae comprises some 38 different species. The amount of study examining olfactory behavior in each of these species varies considerably. For example, the experimental studies described above examining olfactory sensitivity have focused exclusively on the dog. It is assumed that similar levels of sensitivity are displayed by other canids. Whether this is true, however, is unknown. The extent that findings found for one species of canid generalize to other canid species is an area requiring further investigation for all aspects of olfaction.

26.3 CANID OLFACTORY SYSTEM(S)

The excellent olfactory abilities of canids have long been established, but the question of what the underlying structural and/or neural mediation of these abilities are remains unknown. Although neural structures of the dogs' olfactory system were being uncovered at the start of the 20th century, more recent developments in genetic research may contribute to our understanding of the factors mediating its olfactory abilities. Here, we briefly review the olfactory system of the canids, focusing on those elements that may account for their acute olfactory sense. Having an excellent ability to detect odors suggests that there are scents present in the animal's environment that impart important information for the individual and its behavior. This section thus also discusses the odors produced by canids.

26.3.1 Olfactory Sensory Structures

The olfactory system of the canids, and indeed the Carnivora, is basically similar to that found in all vertebrates (Stoddart, 1980). Canids possess both main and accessory olfactory bulbs and a vomeronasal organ. Olfactory bulb volume, when compared to total brain volume, is higher in dogs (1.95%), than in herbivores (goat 0.77%) and humans (0.03%) (Kavoi and Jameela, 2011). Compared to rodents, the accessory olfactory bulb is less well developed and appears as a much simpler structure with less lamination (e.g., Salazar et al., 1994). Whilst dogs possess a vomeronasal organ that comprises both sensory and non-sensory epithelium and expresses markers of neuronal activity (Dennis et al., 2003), it is unclear whether the vomeronasal organ serves any function in canids. The characteristic facial expression associated with processing

chemosensory stimuli by the vomeronasal organ, flehmen, is not observed in the dog but is present in the coyote, jackal, and bushdog.

The area covered by the olfactory epithelium is much larger in dogs than in humans (e.g., German shepherd 150 cm² cf. humans 3–5 cm²), moreover the receptor cells appear to be more densely packed in dogs (Dodd and Squirrel, 1980). As a consequence, dogs possess a significantly greater number of olfactory receptor cells than do humans, 220 m–2 billion cf. to 12–14 million (Miklosi, 2007). Other structures implicated in transducing chemosensory stimuli, for example, the trigeminal nerve, the septal organ of Masera, Grueneberg ganglion, are all present in the canids (McCotter, 1913; Pettigrew et al., 2009). However, whether these have any functional significance for olfactory behavior in these animals is unknown.

26.3.2 Olfactory Receptor Genes

Since the discovery of olfactory receptor genes (Buck and Axel, 1991), there has been considerable interest in exploring the olfactory receptor gene repertoire of different animals, including the dog; such information may contribute to our understanding of their olfactory abilities. Current analysis has identified around 1100 olfactory receptor (OR) genes in the dog, of which 20–25% are thought to be pseudogenes (Quignon et al., 2012). The overall number of OR genes is higher than identified in humans (600–900), but lower than that found in the mouse (1200–1400) or rat (1600). A similar percentage of pseudogenes (20–25%) are observed in dogs as in rats and mice; humans, by contrast, have more (~50%).

OR gene proteins may be classified into families and sub-families according to their amino acid characteristics. Dogs exhibit a greater number of sub-families compared to the rat and mouse (300 cf. 280 and 246, respectively, Quignon et al., 2006). Two hundred of these genes are Class 1, a high percentage compared to other species. It has been suggested that this may be significant in mediating the olfactory abilities of the dog (Olender et al., 2004).

In contrast to OR genes, only nine intact vomeronasal VIR genes have been observed in the dog (Young et al., 2005). This is a similar number to that identified in humans, but significantly fewer than the 100 plus found in rodents. It is suggested that this smaller number is linked to the reduced structures of the accessory olfactory bulb and vomeronasal organ found in the dog (compared to rodents) and the associated decrease in functionality of these organs (Quignon et al., 2006). The same VIR pseudogenes are found in both the wolf and dog, suggesting that the reduction in the number of VIR genes is not a result of

domestication (Young et al., 2010) and may be a feature of canids more generally.

Exactly how the olfactory system of canids accounts for their acute olfactory abilities has yet to be determined. The greater number and more densely packed olfactory receptors may have a role in detection thresholds. The greater repertoire of OR gene sub-families may enable a greater range of odors to be transduced. Although more research is required, some preliminary studies do support the links between structures and function suggested above. For example, the olfactory ability of dogs differs widely between breeds. Boxers, which have a less acute sense of smell than poodles, possess a higher percentage of OR pseudogenes (Quignon et al., 2006). Breeds generally noted for good olfactory abilities (e.g., German Shepherd, Belgian Malinois) exhibit greater OR gene polymorphism compared to breeds with poorer olfactory abilities (e.g., greyhound and Pekingese) (Robin et al., 2009). Trained detection dogs that possess a glycine/arginine substitution at one specific locus on the cOR52N9 gene exhibit poorer performance on explosive detection tasks (Lesniak et al., 2008), indicating the potential importance of specific genes for the detection of specific odors. However, much more work is needed before the link(s) between structure/genes and olfactory function is fully elucidated. It should also be noted that the emphasis to date has been on peripheral sensory receptor mechanisms. Little attention has been paid to how more central processing of olfactory information may contribute to the dog's olfactory abilities.

26.3.3 Sniffing

Whilst the effective transduction of odors to neural impulses is a vital process, the odors have to be received by the receptors. It appears that the mechanism of delivery has been optimized through the form of the dog's nasal structures and its sniffing behavior.

The olfactory epithelium, situated in a recess at the rear of the canine nose, is separated by the *lamina transversa* from the main airways through which air traverses during breathing. This position enables air to travel across the epithelium in one direction during inspiration (allowing the possibility of spatial coding) and no movement of air during expiration, thus providing longer access for the odor molecules to the receptors (Craven et al., 2010). Sniffing is independent from respiration. Dogs sniff at a much higher rate than they respire, and sniffing rate may increase upon encountering novel or weak odors. Whilst breed size affects respiration rate, the rate of sniffing (3–12 Hz) is similar across all breeds of dog. It would thus appear that the odors are delivered to the receptor cells in a manner that optimizes their transduction, facilitating both detection and discrimination (Lawson et al., 2012).

26.3.4 Glands

As well as possessing structures to detect odors, canids also produce odors that may be important for guiding their behavior. Odors are produced by waste products: urine and faeces, and also from a variety of glands distributed over the animal's body. Canids possess sebaceous, apocrine, and eccrine glands (Harrington and Asa, 2003) which can be found singly or in aggregations and emit odor-producing secretions which can be detected by others. In many cases, little is known about the role these odors play or the functional chemicals emitted, and much more work is needed to understand their significance for canid behavior. Here we concentrate on describing the sources of odors and will deal with their possible functions in more detail later.

Sweat (eccrine) glands are found on the footpads and apocrine glands between the toes (Nielsen, 1953). Thus, the animals may leave an odor cue every time the paw comes into contact with a surface or through the specific behavior of ground scratching which may accompany urine or faecal scent marking. Apocrine glands are also spread over the hair-covered skin in most carnivores and may impart a distinctive whole body odor, for example, as noted in African wild dogs (van Heerden, 1981).

The anal region of some canids has three distinct odor producing areas: the supracaudal gland, situated on the top of the tail; the circumanal glands, which surround the anus; and the anal sac, situated internally with ducts to the anal canal. These odor sources are described in the following three paragraphs.

The supracaudal (tail) gland, or "violet" gland in the fox, is comprised of both sebaceous and apocrine cells, although it is the former that is regarded as the main odor-producing component (Albone and Flood, 1976). Most canids possess this gland; although it may be present in the dog, it appears not to function and is absent in the African wild dog. In the red fox, it produces a sweet, pleasant 'violet'-scented odor. The odor is weaker in wolves and coyotes, but smells similar to that produced by the red fox. In the gray fox, the odor is described as "musky" (Fox, 1971). The odor can be easily distinguished from that produced by the fox's anal gland (see below), which is described as "rancid," in contrast to the "pleasant" smell produced by the supracaudal gland. Although this gland is present in wolves, individuals do not appear to investigate this area in conspecifics (Harrington and Asa, 2003).

Anal sacs are paired reservoirs with ducts that lead to the anus and are found in most carnivores. The sacs are surrounded by smooth muscle and it is believed that, to a certain extent, secretions from the anal sac are under voluntary control (Harrington and Asa, 2003). Secretions can accompany some defecations, but not all, and may occur

on their own in the absence of defecation, especially when the animal is acutely stressed. In wolves, it is the dominant males that leave the majority of anal sac scent on their faeces (Harrington and Asa, 2003). In skunks and pole cats, anal gland secretions are sprayed on others as a means of defense. In beagles, consistent individual differences in the odors of anal sac secretions are present. Thus, a sharp acrid odor is associated with light colored, less viscous, and more rapidly secreted anal sac secretions, whereas a dull, somewhat neutral or slightly pleasant, dog-like odor is associated with dark, pasty, and less rapidly secreted anal sac secretions (Doty and Dunbar, 1974a).

Circumanal glands are located around the anus in canids and are made up of single apocrine glands, sebaceous glands, and hepatoid glands (Shabadash and Zelikina, 2002). With the concentration of odor sources distributed around the anal region, it is not surprising that this area receives significant investigation when conspecifics meet.

In addition to the anal region, the head provides a concentrated source of odors, and the head and muzzle region are sites of interest and investigation between conspecifics. Wolves appear to pay more attention to the head region than do dogs. Apocrine and sebaceous glands are found in high concentrations in the ears, where they combine to produce cerumen (ear wax). Eccrine (sweat) glands are found on the skinless end of the nose and saliva may be distributed around the mouth and jaw area.

Fox (1971) suggested that there is an inverse relationship between the intensity of body odor, especially that produced by the supracaudal gland, and the level of sociality exhibited by the animal. More intense odors are produced by the least social species. Thus foxes, which are less social than wolves and dogs, produce a more powerful odor. One exception to this is the African wild dog, which is highly social and produces a strong odor, but this may result from apocrine secretions on the body as opposed to anal region odors. A more intense odor may be required in more solitary species, as the opportunity for exposure to conspecific odors is poorer and therefore odors need to persist for longer to serve their communication function.

26.3.5 Summary

Whilst the role of some aspects of the canid's olfactory system that contribute to its sensitivity are understood, much still remains to be elucidated. The role of the animal's odors in shaping its olfactory system has yet to be explored. It may be that the information produced by various secretions requires a greater olfactory sensitivity to fully detect the information and this has, in part, driven the development of the canid's olfactory system.

26.4 OLFACTORY-GUIDED BEHAVIOR

The fact that canids have excellent olfactory abilities and possess a variety of sources for producing odors suggests that scent plays a significant role in canid behavior. The following section reviews olfactory-guided behavior in the canids. We consider the development of olfactory behaviors, the use of odors in social recognition, and scent-marking behavior. Again, the review will highlight areas where further research is needed.

26.4.1 Early Development of Olfactory Behavior

Dogs are able to detect chemosensory substances before birth and respond to these odors postnatally (Wells and Hepper, 2006). Dogs exposed to aniseed via their mother's diet prenatally exhibit a preference for this stimulus immediately after birth (Wells and Hepper, 2006). This preference is specific to the "odor" experienced before birth. Such learning may be important for the acceptance of milk (Wells and Hepper, 2006). At birth, pups exhibit rooting behavior, but whether this is controlled by olfactory stimuli is unknown. Pups detect and respond to olfactory stimuli at birth (e.g., aniseed, fish scent), even though the olfactory nerves are poorly myelinated (Scott and Marston, 1950; Jones, 2007). Day-old pups are able to acquire conditioned responses to olfactory stimuli (e.g., Volokhov, 1959). The odor of amniotic fluid may be important for mothers to accept pups, since mothers reject offspring which have been washed, but accept those bathed in amniotic fluid (Abitol and Inglis, 1997). Odors thus play an important role in canid behavior, beginning before birth and this continues throughout the individual's life.

26.4.2 Social Recognition

The ability of conspecifics to recognize others by individual, group or kinship cues is widespread amongst animals. There is no reason to expect these abilities are not present in the canids; however, little attention has been devoted to this issue.

It is generally believed that canids are able to recognize individual conspecifics by odors. It has been speculated that individually identifiable odors may originate from the faeces, urine, feet, anal sacs/gland, supracaudal gland, and skin. However, very little study has explored odor sources of individuality other than that presented by the animal's urine. Interestingly, dogs spend more time investigating the urine from a colony mate than they do their own urine, and longer again when presented with urine from a dog outside their colony (Dunbar and Carmichael, 1981). They also over-mark their own urine less than urine from another dog

(Bekoff, 2001). Wolves are able to discriminate individuals by differences in their urine (Brown and Johnston, 1983) and also increase urine over-marking upon encountering urine marks from conspecifics (Peters and Mech, 1975). Red foxes investigate both the urine and anal sac secretions of unfamiliar foxes more than familiar foxes (Blizard and Perry, 1979), although whether this reflects individual recognition, or recognition of familiarity, is unknown. There is additional evidence that dogs produce individually identifying odors. Wells and Hepper (2000) found that dog owners were able to identify their own dogs from their odors deposited on blankets. Detection dogs are able to identify individual maned wolves by their faeces (Wasser et al., 2009).

Dogs are able to recognize their siblings and mother at 5 weeks of age (Hepper, 1986, 1994), most likely using odor cues. Further, dogs recognize their mother by olfactory cues, even after two years of separation, although they only recognize unfamiliar siblings from whom they have been separated for two years if they have been living with another sibling during that time (Hepper, 1994). Contradictory evidence was obtained from a study of dogs examining the mother's ability to recognize her pups using a retrieval task: one female tested retrieved only her own pups, whereas another female retrieved both her own and alien pups (Dunbar et al., 1981). In a simultaneous choice task, mothers investigated their own 5-week-old pups more than unrelated offspring (Hepper, 1994).

Bitches in heat elicit much more investigation from sexually experienced male conspecifics than when not in heat, indicating their odor, especially urine, reflects their reproductive status (Beach and Gilmore, 1949; Doty and Dunbar, 1974b). Moreover, females urinate more when in heat (Beach and Gilmore, 1949), perhaps advertising their receptive status.

It is apparent that much more research is needed to determine the social recognition abilities of the canids. In particular, it will be of interest to establish if there are any differences between species that live in social groups (e.g., hunting dogs, wolves) and those that are more solitary (e.g., foxes).

26.4.3 Scent Marking

One behavior that has elicited investigation in the canids is scent marking. Scent marking, that is, the deposition of an odor through defecation, urination, and/or glandular deposits, is common to all canids. It has been argued that scent marks may signify individual or group identity and/or some aspect of current status, for example, dominance, reproductive state, age. These in turn may serve to determine ownership of territory, mark food caches, maintain group cohesion, and signal status. Whilst the behavior of scent marking has been documented amongst canids, the

information presented by marks and how this “acts” on the recipient has been less well elucidated.

Scent marking is not performed equally by all individuals. In most canid species, the dominant individual or pair is responsible for more acts of scent marking than lower ranked individuals, for example, coyotes (Gese and Ruff, 1997), gray wolves (Peters and Mech, 1975), dogs (Lisberg and Snowdon, 2011) and Ethiopian wolves (Sillero-Zubiri and Macdonald, 1998). It is unknown whether the marks contain information of dominance directly or by association, that is, others learn the individual identity of the dominant male/female and associate their individual signature left in the mark with their dominance status.

Individuals in groups or packs mark more than lone individuals, for example, coyotes (Gese and Ruff, 1997) and wolves (Mech and Boitani, 2003). Lone male wolves have been observed defecating away from paths used by packs, whereas packs tend to deposit marks on trails, especially at junctions (Peters and Mech, 1975), presumably places where others can find them. Males urine mark more than females, for example, dogs and free-ranging dogs (Pal, 2003), dholes (Paulraj et al., 1992) and wolves (Peters and Mech, 1975).

Marking may also be influenced by context. A higher rate of marking is observed during the mating season when females come into estrous, for example, dholes (Paulraj et al., 1992) and free-ranging dogs (Pal, 2003), suggesting that this behavior has a role in the maintenance of the pair bond (Rothman and Mech, 1979). Indeed, newly formed pairs exhibit an increase in marking. An increased frequency of urine marking is observed when the scent of other conspecifics is present, for example, as in dogs (Hart, 1974) and wolves (Peters and Mech, 1975). Some canids mark food caches that have been emptied with urine, for example, red fox (Henry, 1977), Arctic wolf (Mech, 2006), wolf (Harrington, 1981), and coyote (Allen et al., 1999).

Whilst wolf packs mark frequently in their own territory, they do not mark in the territories of their neighbors (Mech and Boitani, 2003). Increased marking is observed around the periphery of the animals’/group’s territory, for example, wolves (Peters and Mech, 1975), free-ranging dogs (Pal, 2003), coyotes (Allen et al., 1999), and foxes (Arnold et al., 2011), suggesting a role in territory demarcation. Faeces may be deposited in latrines throughout the territory, for example, golden jackals (Macdonald, 1979a), dholes (Davidar, 1975), and Ethiopian wolves (Sillero-Zubiri and Macdonald, 1998).

Scent marking by urination in male canids is accompanied by a specific raised leg urination posture and often only small amounts of urine are expelled (see Figure 26.1). This posture may be important as the animal sometimes displays this pose without urinating. The raised leg position may also serve to raise the position of the mark on the vertical object, perhaps reflecting something about the scent marker and



Figure 26.1 The characteristic ‘raised leg display’ posture adopted by male canids when depositing urine scent marks, here exemplified by the coyote (by permission J.W. Wall, jwallphoto.blogspot.com).

also to position the mark at nose height, thereby increasing the chances of detection. However, given the acute olfactory sense of the canid, this latter explanation seems unlikely and the function of raised leg urination is probably related more to its spatial position than odor. Canids, for example, red fox (Macdonald, 1979b), maned wolves (Macdonald, 1980), and black-backed jackals (Haywood and Haywood, 2010) deposit faecal marks on conspicuous, often raised, locations. Although the function of this is unknown, it is believed to increase the visual conspicuousness of the mark.

One specific pattern of urine marking that is observed is “double marking,” in which a scent mark deposited by one individual of a dominant pair is quickly over-marked by the other, for example, Arctic wolves (Harrington, 2006), gray wolves (Rothman and Mech, 1979), and coyotes (Gese and Ruff, 1997). It is speculated that this aids in courtship, the formation and maintenance of pair bonds, mate guarding, and territory formation (Macdonald, 1985). These hypotheses require further examination.

Observations of scent marking by canids are abundant and some of the parameters that affect marking, for example, dominance, and its context, edge of territories, are well established. As more studies emerge, increased variability in scent-marking behavior is becoming apparent. For example, the ground scratching rates of wolves in Poland (Zub et al., 2003) are much higher than those reported for wolves in North America (Peters and Mech, 1975). Individual differences are observed in marking behavior (Wirant and McGuire, 2004) and differences are seen between the behavior of captive and wild animals. The information provided by scent marks remains somewhat of a mystery. It is clear that these odor marks have a function and present information to other conspecifics. The nature of this information has yet to be elucidated. Such information is essential if the functions of scent marking are to be

fully understood. Scent-marking behavior is ubiquitous in canids yet much remains to be discovered about how scent marks exert their function.

26.4.4 Scent Rolling

A final behavior worth noting is scent rolling. Many canids roll in particularly pungent substances, such as rotten food or faeces (Reiger, 1979). Such rolling is often undertaken in a ritualistic manner. A number of possible functions have been suggested: to learn about the new odors; to camouflage and hide their own odors; to enhance their social standing; an evolutionary remnant of behavior that now serves no function; and, a comforting/reinforcing behavior. Much further work is needed to explore this. In African wild dogs, females roll in the urine of the males of packs they attempt to join (Frame et al., 1979). Presumably this enhances their acceptability, but exactly how remains to be determined.

26.4.5 Summary

Odors are important in guiding the behavior of canids, from birth and throughout their lives. However, our understanding of the full range of behaviors influenced by odors and how they function in different canid species remains sparse and much further work is needed before the extent of the role of odor in canids is fully understood.

26.5 USES OF THE DOG'S NOSE

The olfactory abilities of dogs, combined with their trainability, have led to their use to detect and discriminate odors in a wide variety of settings and for a variety of purposes. The following section will review these uses. First, however, a number of issues relating to the performance of dogs on these tasks are considered.

26.5.1 A Dog is Not Just a Dog

The use of dogs in applied settings is widespread, however factors that may affect their performance have yet to be fully explored. The performance of the dog will be influenced by two main factors: the individual animal and its training. These factors may singly, or in combination, influence how well the dog does on any particular task.

Different breeds of dog differ in their olfactory abilities, moreover, even within a particular breed, there are differences between individuals in their sensitivity and ability to discriminate odors. As yet, there has been no systematic study of breed or individual differences upon olfactory abilities within dogs. Related to this, is the dog's motivation to undertake the required task. Scott and Fuller (1965) assessed the interest of different breeds in locating

a live mouse in a 1 acre field. Beagles found the mouse in 1 minute, whilst fox terriers took 15 minutes. Scottish terriers never found the mouse and indeed it is reported that one even stood on the rodent but failed to notice it. Dogs will differ in their motivation and this also has to be factored in to assessments of performance.

The vast majority of detection dogs undergo training to ensure they are able to perform the required task. That said, one of the first reported instances of a dog detecting skin cancer was by an untrained animal (Williams and Pembroke, 1989). There are a number of issues surrounding training that should be considered. First, as with olfactory abilities, there are individual differences in the trainability of dogs (e.g., Maejima et al., 2007). Second, there is no standardized method for training dogs (e.g., Jezierski et al., 2010). Thus, the most appropriate procedure for obtaining optimum performance in dogs is unknown. Further, there is no standardized method for assessing performance (e.g., Rooney et al., 2007). Often organizations using dogs will have their own criteria, but these may vary between organizations and between applications.

Due to the potential variation introduced by these factors it is difficult to evaluate the meaning of a specific performance achievement (e.g., $x\%$ success rate) for any particular task. For example, if a dog is reported as being 80% successful, this does not necessarily reflect the absolute capability of *this* dog (e.g., training may have hindered its performance) or *all* dogs (e.g., this dog could have superior/inferior olfactory abilities). In the absence of standardized procedures for evaluating performance, the reported figures of success are little more than indications that, under some circumstances, a particular dog can complete, to some extent, the task required. Hence we do not report absolute success rates here. Comparisons within studies are reported where relevant as the same techniques (for good or bad) have been used and enable some conclusions to be drawn about relative performance.

The use of detection dogs is considered below under four main headings: forensic; economic, conservation, and health.

26.5.2 Forensic Applications

It has been widely assumed that one of the earliest uses of dogs by man was for tracking prey, thus assisting hunting. A variety of canids are reported to use odors (amongst other senses) in their hunting (Fox, 1975). Indeed dogs have been specifically bred for their ability to follow an odor trail. Romans found the Celtic tribes of the UK using the Agassian, a small dog renowned for its ability to air scent. In 2012, The Federation Cynologique Internationale recognized over 70 breeds of scent hounds.

Dogs have exceptional abilities to follow a route travelled by an individual on foot (e.g., Wells and Hepper,

2003). Dogs may use one, or a combination, of three methods to follow an individual (Hepper and Wells, 2005). They may: *track*, where they follow the route of the individual with their head down and nose very close to the ground; *trail*, when they follow the route with their head down when moving with the wind, but with their head up when moving into the wind; or *air scent*, where they follow the route with their heads up sampling the air.

The odor cues used by dogs may originate either from the individual directly or from ground disturbance (Hepper and Wells, 2005). The fact that individuals can follow the trail of one individual when crossed by many others suggests that there are individual odor cues that are available to the dog to use (Kalmus, 1955). The literature, however, is conflicting. Some studies suggest dogs cannot track in the absence of odor from ground disturbance (e.g., Budgett, 1933), others that dogs cannot follow a trail in the absence of the individual's odor (e.g., Pearsall and Verbruggen, 1982).

Whilst dogs can follow a track, exactly how they do so remains poorly understood. Some studies have attempted to explore how dogs use odor information to detect the direction of a track. For example, Hepper and Wells (2005) found that there was sufficient information contained in five consecutive footprints to determine the direction of a track. An evaluation of the time to deposit the five footsteps indicated that it took approximately 1.9 seconds from the 1st to the 5th step. Assuming that the dog makes some comparison between the footsteps (e.g., based on the quality of odor), then there is a change in the olfactory information presented by a time difference of under 2 seconds that is detectable by dogs. What also seems vital for dogs to track is discontinuity in the olfactory signal. Whilst dogs can easily determine directionality from a track formed of discrete footsteps, they find it much more difficult from a continuous track (Steen and Wilson, 1990). This is similar to insect behavior. Moths, for example, are unable to locate the source of odors when presented with a continuous plume, but can do so when the odor plume presents intermittent information (Justus and Cardé, 2002).

The ability of dogs to discriminate individuals (e.g., Hepper, 1988) has led to proposals that such animals may be used to detect individual odor "fingerprints" from crime scenes and use this information to match to the owner of the scent and possibly the perpetrator of the crime (Schoon, 1996). Scent identification line-ups, in which the dog is required to match the odor obtained from a crime scene to one of a number of odors presented in a row, is now accepted as part of proceedings in a number of European Courts (Schoon and Haak, 2002).

The ability of the dog to detect human odor is also used by search and rescue dogs, ranging from locating lost hikers to individuals buried under avalanches or earthquake debris. Others have been trained to locate cadavers and

parts of bodies (e.g., Komar, 1999). Of all the detections that the dog can perform, we still consider one of the most impressive to be the location of bodies submerged underwater (e.g., Osterkamp, 2011).

It is worth mentioning here another issue to be addressed in assessing detection dogs' performance. In most cases, dogs work as part of a team, the other team-member being their handler. It is known that handlers influence the reliability of their dog's performance (e.g., Lasseter et al., 2003). Thus, a further complication in assessing how well dogs perform is to assess the role of the handler. It may be appropriate to consider that in tasks in which the dog performs "off-lead," the animal is considered the unit of assessment, however when the dog performs the task "on-lead," it is the dog and handler that is considered the unit of assessment.

The ability of the dog to be trained and recognize specific odors has led to it being used in a number of forensic settings to detect the presence of a particular trained substance. Such detections include explosives (Gazit et al., 2005) and even the scent of the trip wires that trigger mines (Hayter, 2003). Following the detonation of explosives, for example, IEDs, dogs are able to match human odors obtained from the blast debris to the humans depositing scent on the device pre-explosion (e.g., Curran et al., 2010). Dogs are able to discriminate accelerants that have been used in arson, despite the presence of additional burnt material at the scene (e.g., Gialamas, 1996). Dogs are used to detect drugs, counterfeit and smuggled goods, and mobile phones in the prison population, amongst others. Indeed, with appropriate training, dogs appear able to detect virtually anything, provided it emits an odor at a level that can be detected by the dog.

26.5.3 Economic Applications

Detector dogs have been used in a variety of ways to reduce economic costs arising from damage to buildings or crops and to improve productivity. For example, dogs have been trained to detect the presence of dry rot fungi and decay caused by fungi (Kauhanen et al., 2002) and termite infestations (Brooks et al., 2003). Both causes of damage may be difficult to detect early and by visual inspection and result in considerable economic cost if not treated. When the performance of dogs to detect termites was compared against an electronic odor-sensing device, dogs performed better (81% vs 48–62% successful detection), but only when there was more than 50 termites present (Lewis et al., 1997). Below this number, the dog's performance became poorer, possibly due to the lack of sufficient odor.

Dogs have also been used in agricultural settings to detect the presence of insects that may damage crops, for example, red palm weevil (Nakash et al., 2000) and parasites which cause damage to livestock, for example,

screwworm and its pupae (Welch, 1990) and nematodes (Richards et al., 2008). Dogs can also, more effectively than other methods, determine estrous in dairy cows, thereby enhancing breeding success (Fischer-Tenhagen et al., 2011). Finally, dogs have been trained to detect bed bugs (Pfiester et al., 2008), a cause of concern for travellers and individuals prone to allergic reactions.

26.5.4 Conservation Applications

Detection dogs have found extensive use in conservation applications to detect the presence of other animals, a feat they perform more effectively than other methods. For example, Long et al. (2007) found that dogs were able to detect black bears, fishers, and bobcats from their faeces. Dogs detected more of these species than either hair snares or cameras; however they were more expensive to employ. Overall, however, the increased cost was more than made up for by increased detection rates and dogs were found to be the most cost effective method.

Dogs have been used to detect the presence of a wide variety of animals to enable assessment of their number in a particular area. This includes, for example, species large, Amur tiger (Kerley and Salkina, 2007), small, rats and mice (Gsell et al., 2010), and minute, fire ants (Lin et al., 2011). As well as detecting feces to provide estimates of numbers of animals, dogs have also been used to help humans detect and collect a sufficient quantity of fecal material to enable detailed testing to be undertaken to provide information on the health of the individuals, for example, Northern right whales (Rolland et al., 2006).

Dogs have been used to detect the presence of invasive species which may cause devastation to their new environment. For example, brown tree-snakes in Guam (Savidge et al., 2011), Quagga and zebra mussels in California (California Dept Fish and Game, 2009), and knapweed in Montana (Goodwin, 2010).

Finally, dogs may also be used to provide information about the effects of human changes to the environment on animal species. One area of concern has been the effect of wind farms on bird life. Dogs have been found to be far better at locating carcasses of birds around wind farms than humans, thus improving estimates of the impact of wind farms on the bird population (Paula et al., 2011).

26.5.5 Health and Medical Applications

One area of considerable interest in recent years has been the use of the dog's nose as a diagnostic instrument for evaluating human health (Wells, 2007). An initial paper (Williams and Pembroke, 1989) reported the case of a border collie/Doberman cross-breed persistently sniffing at a mole on the patient's skin. Following investigation,

the mole was found to be a malignant melanoma. The dog had undergone no training and appeared to be attracted to something about the odor of the mole. Since then, other studies have reported the ability of dogs to detect melanoma (Wells, 2012).

Based on the assumption that the presence of cancer changes the odor signature of the individual in a manner that is consistent across patients with the same condition, studies have explored the ability of dogs to discriminate samples from patients with cancer from those without. Dogs are able to detect the presence of bladder cancer from urine samples (Willis et al., 2004), although it has been questioned as to whether this is due to detecting the odor arising from the cancer or other factors that increase the risk of cancer, for example, smoking (Leahy, 2007). Dogs have been reported to be able to detect prostate cancer from urine (Cornu et al., 2011), breast and lung cancer from breath samples (McCulloch et al., 2006), colorectal cancer from breath or stool sample (Sonoda et al., 2011), and ovarian cancer from tissue (Horvath et al., 2008).

A second line of research has explored whether dogs can predict the onset of serious medical conditions. Based on owners' accounts of their dogs' untrained behavior, Wells et al. (2008) report that pet dogs displayed behavioral changes when their diabetic owners became hypoglycaemic, in many cases before the patients knew they were becoming low in sugar. Similar reports of dogs' behavior changing prior to the onset of migraine attacks have also been documented (Marcus, 2012). Studies indicate dogs can be trained to detect the onset of an epileptic seizure (Strong et al., 1999). Whether these alerts are based on the dog detecting changes in the individual's odor, as opposed to some other cue (e.g., visual), is unknown.

26.5.6 Summary

In summary, if it produces an odor the likelihood is that the dog can be trained to detect it and discriminate it from other odors. The key task is to correctly identify the odor for the dog. Despite many studies demonstrating that dogs undertake remarkable detections, the lack of standardization in, and standards of, training and appropriate evaluations of dog olfactory abilities preclude accurate assessment of the effectiveness of dogs, in general, performing these tasks. Further, great coverage is given when search and rescue dogs locate an individual alive following an appalling natural disaster. However, the fact that it is a natural disaster and a scene of devastation and confusion means it is virtually impossible to determine if dogs missed other individuals. Thus, assessing performance in the field may be difficult and this further emphasizes the need for standardized assessment and evaluation during training.

26.6 IMPROVING WELFARE THROUGH ODORS

Lately, some attention has been directed towards the use of so-called pheromones as a tool for enhancing animal welfare (see Doty, 2010, for a critique of the pheromone concept in mammals). Synthetic analogues of domestic species' facial secretions have been successfully produced to this end, with studies reporting efficacy in producing more normal patterns of behavior in animals who are exposed to them (e.g., Spielman, 2000). A "dog appeasing pheromone" (DAP, Ceva Sante Animale, France) has been reported to be useful in treating some behavior problems (e.g., firework phobia, travel-related excitement, separation anxiety) in pet dogs, although its effectiveness has been questioned (Frank et al., 2010). DAP has also been reported as useful in enriching the environment of captive canids. Thus, Tod et al. (2005) found a significantly reduced frequency of barking in sheltered dogs subjected to DAP exposure for 7 days, although maximum barking amplitude was not significantly altered.

Other odors have been used to provide enrichment for animals in captivity (e.g., cats and gorillas, Wells, 2009), but only one study has evaluated the use of odors for enriching the welfare of dogs (Graham et al., 2005). Odors were diffused into dogs' cages in a rescue shelter to assess whether they influenced the animals' behavior in ways suggestive of enhanced welfare. Lavender and chamomile encouraged more behaviors suggestive of increased relaxation (more resting and less barking), while peppermint and rosemary increased locomotion and barking. Given the significance of odors for canids, manipulation of their odor environment undoubtedly has the potential to improve their welfare. This is an area worthy of significant further study.

26.7 CANINE OLFACTION: A STUDY IN CONTRADICTION

Ever since man encountered canids, the acute olfactory sense of the wolf, and then the dog, has been recognized, selected for, and put to use. Recent years have seen the development of applications for the dog's nose, expanding from the earliest uses of tracking prey to the more recent detection of cancerous tumors. However, although the behavioral evidence is clear, our understanding of the factors underlying the canid's sense of smell and its functions is poor. Even basic questions, such as how good is the sense of smell across canids have yet to be answered. The challenge for future research is to explain what factors, both proximate and ultimate, have led to the acute sense of smell in the canid. We need to identify what information is provided by the olfactory cues left by canids, often in a stylised and ritualistic manner. This will not only enhance

our understanding of the olfactory world of the canid, but may also improve our opportunities to benefit from this sensory skill, thereby extending the cooperation that has been evident since *Homo* and *Canis* first encountered each other.

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