



Patterns of carnivores' communication and potential significance for domestic dogs

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INTRODUCTION

Animals communicate to convey information that can influence the behaviour of other animals, and consequently change their own environment (1, 2).

By communicating, animals may transmit information about their identity, emotional state, age, gender, health, social status, the ownership of the territory etc. (e.g. 3, 4, 5, 6, 7). Information may attract or repel, or may cause some long-term physiological changes in another individual (2).

Communication may occur between individuals of the same species or between different species (2, 8). Consequently, different kinds of information may be available for the conspecifics (e.g. reproductive status) and for individuals of different species (e.g. emotional state).

Information can be conveyed as visual, tactile, vocal, olfactory or seismic signals (e.g. 5, 7, 9, 10). Different signalling modalities are present in different species, depending upon their sensory capacity and the environment where they evolved (1). For example, in a noisy environment visual display can have higher importance, while in nocturnal animals, animals that live in an environment with low visibility or blind animal species, vocal and olfactory communication may be more applicable (1, 9, 11).

Communication is important for social and solitary animals (e.g. 7, 12, 13, 14, 15), although they may choose different modalities of communication. For example, visual display may be preferred for social animals with distinctive body parts that facilitate communication (3), whereas leaving long term scent marks may be preferred for solitary species (16).

Understanding animal communication has intrinsic value and has received a lot of research attention in recent decades. Nevertheless, the newer applied approach to animal communication tends to utilize acquired knowledge. For example, information about animal communication is used as a method in solving behavioural problems (e.g. use of pheromones for relaxing animals, e.g. 17), as environmental enrichment for zoo animals (18) and shelter dogs (19), or as a method to identify individuals in ecological studies (e.g. 20).

The objective of this paper is to summarize present knowledge of carnivores' communication, with a specific emphasis on canids and domestic dogs. Hence, it describes three main modalities of communication in carnivores, and gives a glimpse into the communicative world of domestic dog (*Canis familiaris*), our beloved pet.

SOCIAL LIFE OF CARNIVORES AND HOW THEY COMMUNICATE

In the order Carnivora both social and solitary species can be found, although they are predominantly solitary (14) or some may aggregate only during the breeding season (13). Moreover, the same species may have social and solitary individuals, which can be explained by ecological factors, such as food availability (21, 22).

In canids Fox (23) distinguished three types of social organisation. Type I include solitary animals that create temporary bonds only during the breeding season, and the male and female stay together only for 4 to 5 months to bring up offspring. In the Type II canids male and female form a permanent bond, while offspring may stay with their parents until the next breeding season. The most social canids belong to Type III. An example of Type III is the wolf (*Canis lupus*) pack, where male and female form a long term bond, and form a pack with their offspring and relatives (23).

Solitary carnivores may communicate to avoid contact and to defend territory (13), while in the breeding season communication is primarily needed for finding mates (16). They may rely more on the information that they can get from conspecifics by smell or sound, and visual communication patterns may be less developed (24, 25). Furthermore, leaving long-lasting olfactory signals may be even more advantageous than vocal signalling since quality and quantity of vocal repertoire may be small in less social animals (25).

In the course of evolution social carnivores developed more complex forms of communication necessary for formation and maintenance of cohesive pack structure. Efficient communication between pack members enables reduction in aggression and coordination in group activities, such as hunting or care for cubs (23, 24). The best example is the wolf pack, which has a highly structured hierarchy, with dominant alpha male and alpha female (23). However, it seems that social organisation in some other carnivores does not have to include hierarchy (25) and it may be speculated that even in wolves hierarchy is not so rigid (26).

Although the domestic dog (*Canis familiaris*) is a close relative of the wolf, its social organisation typically does not resemble the organisational level of wolves. Free-ranging dogs may be solitary and not territorial (27). Feral dogs, observed by Macdonald and Carr (22) and Boitani *et al.* (28), live in groups, but do not hunt together and males do not help females in raising young. Nevertheless, some other observations have shown that hierarchy in feral dogs can be recognised (29).

In social animals visual communication is more commonly used, where compound facial expressions, tail movements and ear positions can be enhanced by colouration of the coat (3, 21, 24, 25). Moreover, one signal may be used to boost another way of communication, such as tail movement that may enhance olfactory inspection of the glands in the anal region (24).

Living with humans has greatly influenced dogs' social lives. In contrast to wolves, their nearest relatives, dogs communicate with humans more than with conspecifics. In fact, humans have become the main social partners of dogs, while relations with conspecifics may often be scarce. Consequently, dogs may be better adapted for communication with humans than with other dogs (30). Dogs may understand signalling behaviour given by humans and no special attempt or adjustment in human behaviour is essential to achieve communication (*e.g.* 8, 31).

Other major changes present in domestic dogs as a consequence of domestication are neoteny and paedomorphosis. They have modified dogs' physical appearance and thereby affected communication (32). In the course of domestication dogs became more vocal, and in adulthood utilize some behavioural patterns typical of wolf cubs (5, 30, 33).

Auditory communication

In carnivores evolutionary development of vocalisation may result from social life, *e.g.* it has been observed that spotted hyenas (*Crocuta crocuta*) have a richer repertoire than brown hyenas (*Hyaena brunnea*) due to higher sociality (25). Equally, vocalisation may be influenced by species habitat, since it is more developed in black bears (*Ursus americanus*) than grizzly bears (*U. arctos*) due to their specialisation for forest life where vision is restricted (34). One of the most vocal carnivores is the domestic cat (*Felis catus*) (11, 35).

In nature wild canids, such as young wolves (*Canis lupus*), coyotes (*C. latrans*) and red foxes (*Vulpes vulpes*), vocalise during the first four or five weeks of life, but subsequently there is an inhibition of that behaviour outside the home den, probably due to the dangers for young animals outside the den (3). Adult canids may howl or bark and different kind of barks may be distinguished (25, 30). They are individually specific and therefore may serve for individual recognition (15).

Tembrock (36) classified canid vocalisation according to meaning and function in two broad groups, as vocalisation triggered by external events and vocalisation controlled by the internal state. He argued that externally triggered sounds are defensive, warning or alarm sounds. Furthermore, he considered acoustic behaviours controlled by the internal state as related to metabolism, reproduction or »the maintenance of orientation in space and time, including social system« (36).

Howling is a loud form of vocalisation, and it is employed to affect companions over greater distance. It serves to bring individuals together, to inform rivals of pack presence, and may indicate an animal's size and aggressiveness, and thus have a function in defence of territory (3, 6). As a form of communication, howling is present in social but not solitary canids (23).

In nature barking in wolves may serve as an alarm call for the entire social group, when they have to defend the group territory (6, 37). Similarly, in swift foxes (*Vulpes*

velox) barking is used for territorial defence, whereas higher intensity and shorter latency of responses may show higher levels of aggression in the vocalising animal (38). Barking may be used as a part of dominance/submission display (36). Furthermore, wolves, foxes and coyotes sometimes bark in captivity when they are aroused, to defend territory or a piece of meat, whilst barking may be preceded with a growl (3). On the other hand, since barking is used in many different situations, it presumably serves only to draw attention, while information that follows can be received through other sensory channels, i.e. visual and/or olfactory (37).

Domestic dogs are more vocal than all other Canidae and their barking can be considered as hypertrophied in comparison with wild relatives (3, 30). Excessive barking is considered as juvenile behaviour and in dogs it is thought that it is associated with pedomorphosis due to selective breeding of domestication (5, 33). Breeds differ according to their frequency of barking, possibly because their tendency to bark, that is the threshold or level of arousal necessary for animals to begin to bark, has been subjected to selective breeding (3, 39).

From the evolutionary point of view, it seems that by differentiating their barks dogs have become more adjusted to the human environment and vocalisation has become a tremendously important component of social interactions. Dogs develop many different sounds, distinguishing them from wolves (30). For the purpose of communication, dogs may produce sounds such as barking, groaning, growling, grunting, hissing, howling, meowing, panting, puffing, screaming, tooth snapping and chattering, whining, and yelping (5, 33, 40). Some of those sounds are more typical of puppies: grunting, meowing and partly screaming (33). Furthermore, adult dogs may howl in some situations, such as when some environmental sound is present (sirens, some types of music, aeroplanes flying overhead), and some dogs may howl when they are left alone, resembling the social function in wolves (5). Whining is considered a distress call; it may express dogs' emotional state, such as fear or pain, or may be a way of attracting attention (39). Dogs growl as part of aggression or in play (39, 41).

By measuring frequency and amplitude of barking, individual dogs can be distinguished, as well as their mood. In research conducted by Yin (42) and Yin and McCowan (43), by recording dog vocalisation in certain situations (disturbance, isolation, play), it was possible to divide dogs' barks into different subtypes, and humans were able to identify dogs by their bark spectrograms independent of the context of barking.

Scientists assume that for dog-dog communication vocalisation may be less significant than other forms of communication (33). Nevertheless, it seems that dogs can distinguish different barks (44). Furthermore, Simonet *et al.* (19) have shown that certain vocalisations have meaning for dogs: playing dog-laughter in shelters reduces unwanted distress behaviours. Finally, in research conducted by Adams and Johnson (45) the main

reason for dogs to wake up and bark during the night was barking of other dogs. Therefore, vocal communication may become as important as other forms of communication for dogs living separated from conspecifics in nearby households, as other forms of communication demand some kind of physical contact.

Visual communication

Visual communication may include eye contact, facial expressions, ear position, tail position, fur position (flat or raised), body postures and movements (e.g. 5, 12, 24). Increased sociability and proximity of conspecifics allows more sophisticated visual signals to develop in the course of evolution (23).

In canids eye contact can be used as a friendly greeting, but a direct stare is a threat, whereas subordinate dogs, wolves or coyotes avoid eye contact when they meet the direct look of a dominant individual (3, 33).

In a tranquil dog the mouth is relaxed and covers the teeth. In an aggressive dog the corners of the mouth are pulled forward and the lips are retracted vertically in snarling. As part of submissive display dogs may pull their lips back in a grin (33). Furthermore, a submissive dog may repeatedly extrude its tongue (tongue flick) signalling intention to lick (3, 33) and frequent licking is seen in anxious dogs (41). In foxes and coyotes a wide jaw-gape is seen as a component of threat expression (3), while dominant wolf or dog may grasp the muzzle or neck of a subordinate in an inhibited bite (33, 41).

Furthermore, in the canids the enlarged external ears, the pinnae, have been incorporated into facial expression and may convey different motivational states. In the alert or dominant canid the pinnae are shifted up and forward; in submission, fear or apprehension the ears may be flattened backwards, or in submission and greeting ears may be flattened sideways (3, 46).

In wild Canidae the colouration of the coat is adjusted to enhance visual communication. Therefore, in wolves, coyotes and red and grey foxes the sides of the face or cheeks are white, and the lips are black. In that way, black lips and their horizontal retraction are enhanced, giving facial expressions that can be seen in fear or aggression (3).

In canids the tail is used as an important visual signal. This is erected or arched when the animal is aroused and lowered in submissive animals (3). It may be loosely wagged for greeting, or stiffly in aggression. Moreover, the tail may be wagged more on the right side if the dog perceives pleasing stimuli and on the left side if the dog displays withdrawal tendencies (47). Therefore, it may be better to consider the tail wag as a context specific behaviour that may be used in different situations. Interestingly, according to Mills (25), colouration of tail may enhance communication in spotted hyenas, where their dark tail is in contrast with their lighter spotted body and has a function in communication, due to their social life.

In canids communicative body postures play a significant role. Confident animals display a body carriage that makes them look bigger, including rigid posture with head and tail up, and piloerection on the hackles (41). When a submissive dog, wolf or coyote approaches one of its own species or a human being in friendly greeting, it advances with the hind end lowered and the back arched in a »C« posture (3). Its head is lowered and tail tucked between the legs (46). In active submission a subordinate animal may approach a more dominant one showing the body signs of submission and lick the corner of its mouth in greeting (33). In passive submission a canid may lie down and roll over, exposing the belly, and additionally may urinate (5, 33).

One communicative body posture that is used to express play intention is the »play bow«. This play soliciting posture consists of lowering the front end of the body and raising the rear (48). The whole display includes the play bow, then a quick return to a standing posture, followed by some jumping around the intended playmate. During this display dogs may have so-called »play face« (33).

Canids' communicative displays are complex behaviour, which may include different body postures and other signals, integrated with movements. These patterns of compound signals may be seen in different contexts of canids' communications. For example, dominance and submission in wolves is generally signalled by body posture, but additionally may be signalled by movements of decreasing or increasing distance (46). Moreover, a more confident dog may display ritualised attack that may be oriented in the shoulder region, the hackles, whereas the hair in that region may be of a different colour, and erected during aggressive display (3). Head tossing, accompanied by chin markings display, as described for New Guinea singing dogs (*Canis hallstromi*), may be a signal of food soliciting or expression of frustration (49). Raised leg urination and ground scratching could be considered as visual signals for urine marking triggering olfactory inspection (50).

However, dogs can be in emotional conflict and show mixed signals (33), and the same ambiguity can be seen in wolves (46).

As in other canids, domesticated dogs use body postures and facial expressions to communicate changes in their motivational state, their state of mind or mood (3). Nevertheless, for many dog breeds the possibility to communicate precisely is lost due to an extreme diversity in morphological characters (30). Moreover, dogs' visual signals are impaired due to pedomorphosis (32). Although horizontal and vertical lip movements can be seen, in many breeds the effectiveness of such signals is reduced by a complete lack of white cheek marks, when the cheeks are of the same colour as the rest of the face, or covered in long hair, so the lips can not be clearly seen (3). Some breeds have large pendulous lips (e.g. boxers, St. Bernards) and may not be able to retract them efficiently (33). Furthermore, long-haired breeds can not

display piloerection on the hackles, or stare if their eyes are covered with hair (5).

In dogs, tails may be altered in comparison with wild canids. Dogs can be born with stump tails or their tails may be docked, or some may have permanently erect tails. That modification of signal structures, especially when the tail is docked and the animal is wagging the whole hind end, can have a detrimental influence on social communication in the dog (3).

Olfactory communication

In canids olfactory communication has a variety of forms since they have a remarkable sense of smell, i.e. they are able to detect small concentrations of odours and they can distinguish between them. Olfactory signals may include urine and faecal droppings, ground scratching, anal sac secretions, general body odour, rubbing certain body areas on a specific object, and rolling in noxious-smelling substances (5, 33, 40).

Olfactory cues are used for territory marking, individual recognition and as a method for leaving long term messages (3). Marks may be made on novel or familiar objects, territory, or scent marks of other individuals, or the animal may mark itself (6, 33, 51, 52). Unfamiliar urine, faeces or objects may be marked simply to reduce novelty (3). Feeding places can also be marked, probably increasing the efficiency of food source utilisation (6, 52).

In canids urination and defecation have evolved into a complex behaviour of territorial marking, through which one pack (of wolves) or one individual (a red fox) leaves a message about themselves and acquires information about other packs or individuals in a given region (3, 6). Canids urinate and defecate at particular places, inside and on the borders of their living area (3). In Ethiopian wolves (*Canis simensis*), urinations were frequently used for territorial border demarcation, but defecation predominantly occurred on latrines (6).

In feral dogs females marked more frequently near the nest side after litter production and when they were in oestrus (52). One of the messages that urine contains is about female reproductive status and oestrus females may urinate more, leaving long-distance messages for males. The urine of females contains a pheromone during the breeding season which is attractive to males, and may help them to localise the female in solitary species (3, 16).

Male urination can mostly be considered as scent marking (5, 52) and it is frequently accompanied by the leg-raised pattern (3). The reason for this behaviour may be that the raised-leg posture elevates the scent mark to nose height, allowing better dispersal of odour by wind, increased evaporating surface and minimizing the chances that the urine mark is going to be covered by snow or washed away by rain (33). Dogs that display raised-leg urination (RLU) may leave small quantities of urine on numerous places (5) or may deposit no urine (52). In a wolf pack a dominant individual may urinate more frequently and it may display leg-raised urination, while

subordinate males may urinate in infantile crouch position (3). However, observation of Ethiopian wolves conducted by Sillero-Zubiri and Macdonald (6), revealed that although the dominant pair of wolves marked the most frequently, other pack members may also display RLU and participate in scent marking of their territory. In domestic dogs the frequent leg-raising pattern in males is thought to be an example of behavioural hypertrophy in the domestic environment (3).

All canids possess paired small glands on each side of the anal sphincter. These glands, perianal or circumanal, release some of their contents when defecation occurs (3, 5). The secretion of anal sacs is highly individual-specific (5). In captive wolves, anal sac secretions on the faeces are mostly left by dominant males, signalling their status or territoriality (5).

Wild canids show interest in their own urine and faeces and that of other members of the same species. They may investigate urine or faeces by sniffing, and may urinate or defecate over or roll in this material (3). It is believed that dogs can get a lot of information about the animal that marked from the urine smell (33). Males are equally interested in urine of another males and females, but over-mark more frequently on other males' urine (51). In feral dogs the leading male may urinate frequently and immediately over the urine marks of oestrus females, which is termed by Pal (52) as »possessive urine marking«.

After urination or defecation, some canids may scratch the ground (6, 33). In wolves, coyotes and dogs, scraping with both fore and hind legs may occur after urination or defecation. This may be a visual display that attracts attention of conspecifics or a way to add odour from the paw glands after urination or defecation or may be used to mark the ground where the animal has eliminated, thus providing an additional territorial signal (3, 50). The probability of the occurrence of this behaviour increases when the individual is aggressively aroused (3).

General body odour is a product of glands on the dog's feet, head, anal region, the upper surface of the base of the tail and between the hind legs (5). Social investigatory behaviour in dogs is directed in those body areas. It starts when one dog approaches another and sniffs its head, inguinal and anal regions (3, 53). That kind of investigative behaviour is also seen in wolf cubs (3).

Dogs are prone to rolling in noxious smelly materials that they find (such as carcasses of dead animals). The function of that behaviour may be in collecting a desired smell or leaving their own smell (33). One possible explanation is given for wild canids, where an individual with a new smell will receive more social investigation by conspecifics after joining the pack, and that may reduce the possibility of agonistic interactions (3).

CONCLUSION

Animal communication is a well-studied field of science, but unfortunately there are still large gaps in our

knowledge. In social and solitary canids, communication has immense importance. They communicate with auditory, visual and olfactory signals. The research confirms the importance of olfactory communication for canids, while new research into vocalisation is bringing exciting results. Additionally, further research that investigates not only dog-dog communication, but also dog-human communication, and vice versa, may represent an intriguing new approach that may highly influence our understanding of dog-owner relationship.

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