Universiteit Utrecht

The communicative relationship between human and dog

Understanding the relationship between domestic dogs (*Canis lupus familiaris*) and humans from a biological point of view

Master thesis; Environmental Biology – track Behavioural Ecology
Author: Sanne van Wingerden (3220427)
1ste supervisor: Dr. A. Ortolani
2nd supervisor: Dr. M.J.H.M. Duchateau
Department of Animals in Science and Society
Division of Animal Welfare and Laboratory Animal Science
Utrecht University
June 2012

Preface

This master thesis is the result of a literature research study done at the department of Animals in Science and Society, division of Animal Welfare and Laboratory Animal Science at the University Utrecht. The thesis is written under the guidance of Dr. A. Ortolani.
This paper is part of my master Environmental Biology with the track Behavioural Ecology at the University of Utrecht.
I hope this report will inspire people to do future research on the dog-human relationship because still little is known about this relationship and little empirical studies have been performed.

I would like to thank Dr. A. Ortolani for her excellent supervision during the process of making this thesis. I am grateful that she has read the drafts of the thesis during the weeks and I am thankful for her comments to improve the paper. Next I would like to thank all of those how have lend me articles and books to get information for this thesis.

Table of contents

Abstract

Dogs were probably the first animals that were domesticated and therefore have shared at least 10.000 years of mutual history with humans (Udell *et al*., 2008). Humans and domestic dogs interact with each other almost every day. For each species understanding the social communication of the other species is essential for the formation and maintenance of a good relationship (Bradshaw and Nott, 1995). In the last hundred years, we have begun to understand more about the behaviour of dogs and their relationship with humans.
The aim of the thesis is to take a closer look at the communicative relationship between domestic dogs (*Canis lupus familiaris*) and humans, and to understand this relationship from a biological point of view: how did of the relationship begin, understanding dog communication from a humans' point of view, understanding human communication from a dogs' point of view and the costs and benefits of the relationship for both species.
''Do humans understand dog communication as well as dogs seems to understand humans? Or is communication between these two species more one sided?''

Evidence of the beginning of the relationship between domestic dogs and humans seems to point more to the theory of Coppinger and Coppinger (2002): dogs have been domesticated themselves via natural selection by exploiting a new niche (e.g. the human garbage dump). New research argues multiple domestication events in the Middle Eastern wolves as the oldest ancestors (Gray *et al.,* 2010).
Domestic dogs use their social communicative signals in their relationship with humans. Humans do not always have the ability to understand these signals. Misunderstandings about these signals can arise because people tend to look only at one specific behaviour or one signal and forget that social signals used by dogs involve every part of the body, such as the ears, the direction of the eyes, the tail, the muzzle and the posture of the dog. When people misunderstand dogs' communicative signals, miscommunication can lead to problem situations.
The communicative interactions between domestic dogs and humans are well studied in the last decade. Dogs seem to be able to understand diverse human communicative signals, even when compared to other canid species. However, these experimental studies have also drawn criticism from other researchers and definite conclusions still cannot be drawn from these results.
The relationship between domestic dogs and humans seems to be unique. Both domestic dogs and humans have costs and benefits from their relationship. However, the benefits of the relationship are more obvious for humans while the benefits for dogs are less understood.

In summary, domestic dogs appear to be 'special' canid species in terms of social communication with humans. However, the communicative relationship between domestic dogs and humans seems to be skewed. Domestic dogs appear to understand more about human communicative cues than humans understand about dog communicative signals and misunderstandings do arise frequently. From a biological point of view, the relationship with humans began with self domestication of the dog and multiple domestication events have occurred. In terms of benefits, this relationship is more obvious for humans.

Keywords: Domestic dogs, Dog-human relationship, Communication, Canine evolution, Social cognition

Introduction

At some point in human history there were wolves, jackals, coyotes but no dogs. Some evolutionary process took place which caused the emergence of the domestic dog we know now a day (Coppinger and Coppinger, 2002). Dogs were probably the first animals that were domesticated and have shared a mutual living environment with humans for over 10.000 years (Udell *et al*., 2008).
In the 19th century, not much research was done on domestic dogs. Dogs were seen as: ''A loyal, true, and affectionate friend, but when we come to consider the psychical nature of the animal, the limits of our knowledge are almost immediately reached'' – Sir John Lubbock (1889, p.272). In the last hundred years, we began to understand more about the behaviour of dogs and their relationship with humans. Domestic dogs are an interesting species to investigate the potential influence of domestication on their communicative relationship with humans, because domestic dogs can be compared to their closest related wild canids, the wolves (*Canis lupus lupus)* (Udell *et al*., 2010).

Enormous numbers and diverse breeds of domestic dogs exist today (Coppinger and Coppinger, 2002). Humans keep over 1.8 million dogs as companion animals in the Netherland (Rijksoverheid, 2012). Domestic dogs live in a human social environment and interact with humans on a daily basis. Dogs are commonly referred to as 'man's best friend' and humans can develop a strong degree of attachment towards these companion animals (Cohn, 1997; Nagasawa *et al.,* 2009). Dog owners report strong emotional ties to their pets, see their pets as a part of their family and mourn the death of their pets (Kurdek, 2008; Lund *et al*., 2012). Owners might even start to treat their pets as human beings and attribute human characteristics to them, for example the 'guilty look' dogs can show, according to their owner, if they feel guilt after display unwanted behaviour (Horowitz, 2009). The relationship between domestic dogs and humans is complex and might be diverse in different countries and cultures (Coppinger and Coppinger, 2002).

The aim of this thesis is to give a critical overview of the present scientific literature on the human-dog communicative relationship and to understand this relationship from a biological point of view. ''Do humans understand dog communication as well as dogs seems to understand humans? Or is communication between these two species more one sided?''
In chapter one I will discuss the beginning of the relationship between domestic dogs and humans: the evolution of the domestic dog (*Canis lupus familiaris*). There are two main diverging theories about how the evolution of the domestic dogs occurred. According to Clutton-Brock (1995), people intentionally domesticated wolves, whereby they took wolf pups from their dens, brought them back to their villages and tamed them. According to Coppinger and Coppinger (2002), dogs have domesticated themselves via natural selection by exploiting a new niche (i.e. the human garbage dump) and only later artificial selection played an important role in creating diverse modern dog breeds.
In chapter two, I will discuss the ability of humans to understand dog communication. Domestic dogs can use a wide range of social signals to communicate with other species. 'Communication occurs when the action or cue given by one organism is perceived by and thus alters the probability pattern of behavior in another organism in a fashion adaptive to either one or both of the participants' (Wilson, 1975). Domestic dogs communicate using different signals and sensory systems, including vocal, vision, olfaction and audition (Wells, 2009). Some social communicative signals are similar to those of wolves, while other signals are only used by domestic dogs (Feddersen-Petersen, 2007). I

will discuss different types of social communicative signals used by domestic dogs and the ability of humans to interpret these signals correctly in the next chapter.
In the third chapter I will discuss the ability of dogs to understand human communication. Communication between domestic dogs and humans has been studied extensively in the last decade. Dogs' sensitivity to human gestural cues has been the focus of several studies. Dogs have been reported to respond to different signals given by humans (Elgier *et al*., 2009; Udell *et al*., 2010; Lakatos, 2011). For example, domestic dogs can use human gestures, such as pointing, head turning, body postures, touching, marking, gazing and nodding to locate hidden food items in an object-choice task (Hare and Tomasello, 1999; Soproni *et al*., 2001; Miklósi, 2003; Hare and Tomasello, 2005; Udell *et al*., 2008). Dogs can solve some of the researchers' tests even in their first attempt (Soproni *et al*., 2001; Riedel *et al*., 2008). However, these studies raise many questions. Do all dogs show these abilities or are the dogs studied just exceptions? Different examples of dogs' sensitivity to human communicative gestures in different studies will be presented in a critical way. The methods used will be discussed and compared. Subsequently hypotheses and potential explanations for these communicative abilities will be reviewed. There is a controversy in the literature regarding how dogs' communicative skills entered the canine repertoire. Different hypotheses have been proposed. On one hand, researchers claim that the behavioural adaptations that allow dogs to adapt to the human environment are caused by genetic changes during domestication and are not due to environmental influences or life experiences, the so called 'domestication hypothesis' (Hare *et al*., 2002). On the other hand, researchers claim that phylogeny (i.e. genetic changes during domestication) as well as ontogeny (i.e. development) both need to be taken into account when explaining the communicative abilities of domestic dogs (Udell *et al*., 2010).
In the last chapter I discuss the cost and benefits of the relationship between domestic dogs and humans, for both species. Domestic dogs have diverse roles in human society, such as companion dogs, guide dogs, rescue dogs, drug dogs and police dogs (Udell *et al*., 2008). There are also herding dogs, hunting dogs, dogs that locate birds for shooting, dogs that sit in humans' laps and dogs that are important in the lives of many human individuals (Udell *et al*., 2008). Dogs might have positive mental and physical health effects on humans: reducing cardiovascular risks, reducing feelings of loneliness or depression and give access to social encounters (McNicholas and Collis, 2000; Scheibeck *et al*., 2011; Arhant-Sudhir *et al*., 2011). On the other hand, dogs might also have costs for humans, such as transmission of diseases (zoonose), barking all day or destroying human property (Podberscek, 2006). Domestic dogs obtain food, shelter, companionship and veterinarian care from their owners (Podberscek, 2006). However, domestic dogs might incur costs from humans, such as behavioural problems, malnutrition, obesity and sterilization (German, 2006; Podberscek, 2006). Costs and benefits might also depend on cultural values and the relationship between dogs and humans might differ among different types of dogs (i.e. African village dogs, stray dogs, pet dogs and working dogs).
This thesis takes a closer look at the communicative relationship between domestic dogs (*Canis lupus familiaris*) and humans, so we can understand more about this relationship from a biological point of view.

Chapter 1. The beginning of the relationship between humans and domestic dogs

Domestic dogs are a successful canid species: they evolved from their ancestral form, the wolf, and have increased to enormous numbers and a large variety of breeds which are morphologically very diverse, from Chihuahuas to St. Bernards. There are approximately 400 million dogs living in the world today and over 150 breeds registered at the American kennel club and the European FCI (Coppinger and Coppinger, 2002; American kennel club, 2012; FCI, 2012).
Wolves and dogs differ in morphology and behaviour. Wolfs live in the wild, avoid people and hunt their prey for food. Dogs, on the other hand, live around people which provide either directly or indirectly (i.e. a human garbage dump) for their food (Coppinger and Coppinger, 2002).

1.1 The first domestic dog

At some specific moment in the past, more than 15.000 years ago, there were no dogs in human society. Some evolutionary process took place which transformed wild Canids into domestic dogs (Coppinger and Coppinger, 2002). Archaeological and genetic e evidence varies about the exact location and lineage of the first domestic dogs. Archaeologists argue that the earliest burials of domestic dogs are between 10.000 and 14.000 years old (Nobis, 1979). First cave art depicting dogs is found around 16.000 years ago (Delporte, 1990). First archaeological evidence of dogs being human companion animals dates back from 14.000 years before the present (Nobis, 1979). However, other researchers indicate that dogs are actually older, the gene sequences of wolves and dogs only differ 1 -2 % and these differences suggested that these animals separated about 135.000 years ago (Cohn, 1997; Vila *et al*., 1997). Around 10.000 years ago diverse images of dogs appear around the world and in Roman times different dog breeds were already recognized (Brewer *et al*., 2001).
Most recent genetic evidence argues multiple origin for the domestic dog; domestic dogs started to diverge from their ancestral from, the wolf at different places in the world (Sastre *et al.*, 2012). Recent archaeological and genetic evidence argue that the oldest dogs origins in the Middle East (Gray *et al.,* 2010) and most recent genetic evidence argues that the origin of dogs dates back from 20.000 years ago (Vilá, 2012).

1.2 The evolution of the domestic dog

Two main diverging theories have been proposed about the emergence of the domestic dog. People could have intentionally domesticated wolves by taking wolf pups from their dens, brought them back to their villages and taming them (Clutton-Brock, 1995), or dogs domesticated themselves by natural selection (Coppinger and Coppinger, 2002). According to Coppingers' theory, some wolves adapted to a new niche: the human garbage dump.
Darwin (1859) was the first to suggest that domestic dogs were selected by artificial selection: humans took wolves pups and tamed them. The emergence of domestic dogs by artificial selection is a popular view: humans took wolves pups from the wild, tamed these pups, trained them and eventually turned these wolf pups into pets (Clutton-Brock, 1995). According to Clutton-Brock (1995) the bones of wolves and early hominids were found at associated sites or caves around 150.000 years ago, suggesting that hunting activities of humans and wolves often overlapped. Humans hunted wolves but sometimes a wolf pup would be habituated to a family, be tamed and became a pet. Some of these wolf pets became more dominant and less submissive to humans when they matured and were likely to be killed. These dominant wolves had no opportunity to contribute to the gene pole of the domestic dog. Other wolf pets showed submissive behaviour and remained living in

human families. These submissive wolves bred with other tamed wolves and were likely the ancestors of the domestic dog. The remains of these tamed wolves, around 14.000 years ago, showed slight morphological differences compared with wild wolves: shortened facial region, compacted teeth and toe bones that were more slender. However, no measurements were taking from the remains of these early tamed wolves. Wolf skulls that have been found around 10.000 years ago (last Ice age at Alaska) also showed shortened facial regions. Around this time, also humans crossed the Bering Straits into North America, so it might be possible that humans tamed wolf pups around this time and in that location (Clutton-Brock, 1995).
These tamed wolves integrated into the social human environment and characteristics of the wild wolves disappeared, such as coat color, posture of the ears and tail, overall size and proportion of the limbs, and eventually a wolf became a dog. These characteristically changes are also found in the remains of the earliest domestic dog (Clutton-Brock, 1995).
Different researchers have criticized the wolf-pup theory of Clutton-Brock (1995). There is a difference between domestic dogs and tame dogs. Domestication of a species means that changes across generations make it easier for these species to adapt to live in a human environment and to accept humans. Tame species are reared as young to accept humans but are not genetically domesticated, so it would be difficult for tame wolf pups to evolve into domestic dogs (Udell *et al*., 2010).
The big difference between tame wolves and tame dogs is that dogs are genetically tamable and trainable and wolves can be taught a few of these tame qualities (Coppinger and Coppinger, 2002). Research about the tameness of wolves was done at Wolf Park in Indiana, where wolf pups were raised by humans. This research suggests that wolfs can be tamed until 19 days but dogs can be socialized until 10 weeks. Because dogs have an extended sensitive period for socialization, they have an increased opportunity to form a social bond with dogs but also with other species, like humans (Udell *et al*., 2010). Wolves can eventually accept humans but cannot be tamed like domestic dogs. Wolves and humans can form a relationship but this is difficult and only possible on wolfs' terms (Coppinger and Coppinger, 2002).
Frank *et al.* (1982) suggested that dogs and wolves learn differently. Canid problem solving strategies are different: wolves learn by insight and can solve problems by looking at another animal, but dogs learn by repetition and are poor observational learners. When training wolves, it has become evident that wolves may be better learners but cannot be taught to use instrumental conditioning: they cannot obey simple commands (Coppinger and Coppinger, 2002). Taming and training wolves might change the wolf slightly but their genes cannot be changed. These wolves cannot pass their trained and tamed characteristics to the next generation.
Moreover, if people had intentionally domesticated wolves, there should have been in the past a large population of wolves displaying a great variation of tame behaviour (i.e. flight distance to humans). Subsequently wolf individuals with this natural tame behaviour had to be isolated from the population and these tame wolves had to been bred for many generations. This hypothesis seems to be unlikely because it probably takes too much time for learned tame wolves to become genetically tame wolves. Besides this, there is no archeological evidence that people in the past had large enough populations with tamed wolves (Coppinger and Coppinger, 2002).
Along with behaviour, also morphological characteristics changed during the evolution of the domestic dogs. Dogs have smaller brains, smaller skulls and thicker skin than wolves. An adult dog, with the same head size of a wolf, has a 20% smaller brain and an adult dog with the same weight as an adult wolf has a 20% smaller head. The hypothesis that people intentionally domesticated wolves

seems to be unlikely because if people in the past wanted to create a wolf as companion hunting animal, it seems doubtful that they would have selected characteristics that are poor hunting qualities (Coppinger and Coppinger, 2002).

Coppinger and Coppinger (2002) proposed another evolutionary hypothesis as explanation for the origin of domestic dogs. They suggested the 'natural selection model': humans might have created a new niche by starting to live in aggregations that were permanent (i.e. villages), some 'wolves' entered the village and got access to a new food source (i.e. the human village garbage dump) which created safety and opportunities for reproduction. If some wolves were able to adapt to this new niche, they had to be genetically predisposed to show a lower 'flight distance' (i.e. greater tolerance of humans). These 'tame' wolves had selective advantages in the new niche and so could increase their survival. Therefore dogs might have domesticated themselves by exploiting a new niche. Different researchers have supported the theory of dogs' domestication by Coppinger and Coppinger (2002).

Boitani *et al*. (1995) suggested that this new niche (e.g. the human garbage dump) is an important food source for wolves. Wolves are naturally shy of humans and run away from the food source when humans come too close. The shyness of the animal and how far the animal is willing to retreat can be measured by their flight distance (Coppinger and Coppinger, 2002). Wolves have a large flight distance, which means that they run away fast and far. Because of this fact, wolves cannot compete with other animals at the garbage dump for food. Besides this, running away also cost a lot of energy. Dogs, which are naturally tame, have a shorter flight distance which gives them an advantage at the garbage dump: there is more available food when competing with animals that have a large flight distance.

According to Coppinger and Coppinger (2002), tame behaviour is an adaptation for wolves to feed at human garbage dumps. Because of the competition for food at this new niche, variation among wolves' behaviour developed. Wolves that were less nervous (i.e. less fearful and aggressive) had an advantage at the human garbage dump because they had the ability to exploit food sources when humans were nearby, which lead to higher fitness (Udell *et al*., 2010). The genes for tame behaviour were passed on to the next generation. Also other characteristics, like a small head, were adaptations to this new niche (Coppinger and Coppinger, 2002).

Also other researchers support the hypothesis that wolves domesticated themselves by exploiting a new niche. Ortolani *et al*. (2009) tested Ethiopian village dogs' attitude towards an unfamiliar person using a 'stanger-approach test'. Inter alia, the reaction of the dogs to the approach of the stranger and the approaching distance between the dogs and the observer were recorded. Coppingers' theory of dogs' self domestication suggested variation in flight distance towards humans (i.e. greater tolerance of humans) which leads to fully exploiting a new food source (i.e. a human garbage dump). Ortolani *et al*. (2009) found that these village dogs displayed different degrees of tolerance towards people, which might indicate that selection for tame behaviour in Ethiopian village dogs is still occurring.

In conclusion, dogs do not behave or look like wolves. Wolves can be tamed but not domesticated and forming a relationship with humans is very difficult. Both Coppinger and Coppingers' (2002) and Clutton-Brocks' (1995) hypotheses still have proponents and opponents but most evidence seems to point against the wolf-pup theory of dog domestication by Clutton-Brock (1995). Recent evidence

points more to the Coppinger and Coppinger (2002) theory, so it seems that dogs domesticated themselves by exploiting a new niche created by humans (i.e. the human garbage dump) and therefore this theory seems to explain the beginning of the interaction between humans and domestic dogs.

Chapter 2. Understanding dog communication from a humans' point of view

Understanding the social communication of domestic dogs is essential for the formation and maintenance of a good relationship with other species, such as their human caretaker (Bradshaw and Nott, 1995). Domestic dogs, like wolves, are social animals and use their communicative signals in their social relationship with humans (Feddersen-Petersen, 2007). Domestic dogs use a wide range of communicative signals involving different sensory systems, including vision, vocal, olfaction and audition (Wells, 2009). Frequently displayed social behavioural signals by domestic dogs are submission/dominance signals, aggression signals, play signals and stress, fear and anxiety signals (Feddersen-Petersen, 2007). Their closest ancestors, the wolves, are social pack living animals and developed social communicative signals to regulate their pack. This might be some pre-adaptation for domestication which has resulted in dogs' social signals to communicate with humans. Although similar social behaviour signals are displayed by both wolves and domestic dogs, dogs' social behaviour has changed over time, especially in some breeds as an adaptation to living in a human environment (Goodwin *et al*., 1997; Schilder, 2004; Feddersen-Petersen, 2007). Inter alia due to these changes in the social behaviour of dogs, humans might have difficulties interpreting communicative social behaviour signals of different dog breeds which might lead to miscommunication (Schilder, 2004).

2.1 Dominance and submissive signals

Many different forms of agonistic signaling (i.e. social behaviour associated with competition) have been observed in dogs, for example dominance and submissive behaviour. Vision plays an important role to communicate dominance or submission (i.e. posture, face, ears, mouth, tail etc.). Wolves use agonistic signals and visual communication to prevent escalations of aggression during social interactions in their pack (Bradshaw and Nott, 1995; Fatjó *et al*., 2007). Domestic dogs use dominance and submissive signals and postures to indicate aggression, dominance or submission (Goodwin *et al*., 1997; Fatjó *et al*., 2007).

Dominant postures in dogs are shown by displaying an upright body, a high head, a high tail and ears that are pricked. Submissive postures in dogs are shown by displaying a low body posture, ears that are flat and a low tail close to the body. This posture creates a smaller animal (Bradshaw and Nott, 1995; Goodwin *et al*., 1997; Bubna-Littitz, 2007; Fatjó *et al*., 2007).

These dominant and submissive postures include different types of signals. Dogs display dominance behaviour by using different types of signals including, growl (i.e. low-pitched noise), stand over (i.e. holds head or forepaw over opponents body), inhibited bite (i.e. place jaws around opponents body), stand erect (i.e. raise itself to fully height), body wrestle (i.e. stand on back paws and wresting with forepaws), aggressive gape (i.e. half open jaws and expose teeth), bare teeth (i.e. raises lips and expose teeth) and stare (i.e. look directly at opponent and remains eye contact) (Fox, 1970; Goodwin *et al*., 1997).

Dogs display submissive behaviour by using different types of signals including, muzzle lick (i.e. licking at the opponents' muzzle), look away (i.e. averts eyes and slowly turns its head away), crouch (i.e. lowers head and body), submissive grin (i.e. draw lips back and reveal teeth with closed jaws), passive submit (i.e. lies on back and belly exposed) and active submit (i.e. approaches in crouch position with tail between legs) (Fox, 1970; Goodwin *et al*., 1997).

People might have difficulties understanding dogs' dominance and submissive signals, especially in some modern dog breeds. Goodwin *et al*. (1997) suggested that some dog breeds have lost elements

of social signals in dominant and submissive behaviour. In their study, they selected ten dog breeds and videotaped different forms of agonistic signaling (i.e. signals shown during dominant and submissive interactions). Various threats signals were displayed by these dogs including growl, displace, stand over, inhibited bite, stand erect, body wrestle, aggressive gape, bare teeth and stare. These dogs also displayed submissive signals including, muzzle lick, look away, crouch, submissive grin, passive submit and active submit. The interactions of dogs with different types of stimuli (i.e. the owner, an unfamiliar person, food, toys, shelter, a familiar dog and an unfamiliar dog) were observed. These stimuli were supposed to evoke competition over resources between group members. The results suggested that different breeds displayed various types of dominance and submissive signals. Some breeds, like the Siberian husky and German shepherd, displayed all types of signals that were tested. Other breeds, like the Cavalier and the Norfolk terrier displayed only a few signals that were tested (i.e. growl, display and stand erect). This study suggests that some modern dog breeds have lost some elements of dominance and submissive signals.

Wickens (1993) preformed a similar study to compare visual social signals of domestic dogs and wolves during social interactions. Similar threat- and submissive signals were used as in the study of Goodwin *et al*. (1997). The results suggested a similar outcome: the frequency and type of visual signals varied greatly among different types of breeds, from none or few (i.e. Cavalier King Charles Spaniels or French bulldog) to many signals (i.e. Siberian Huskies). For example, Huskies displayed signals that were most similar to the signals displayed by wolves and there are little morphological differences between these species. On the other hand, Spaniels displayed signals that were least similar to the signals displayed by wolves and there are huge morphological differences between these species. This study suggests that threat signals and submissive signals are suppressed in frequency and intensity during social interactions among different dog breeds as compared to wolves.

The study of Feddersen-Petersen (2004) also suggests that breed groups can differ in social behaviour. Their study compared different groups of dog breeds and observed different types of social behaviour, inter alia: aggression, social play, social tolerance and coping with social conflicts. Some dog breeds (i.e. poodles) were not able to work together or compete in a group, suggesting that these breeds could not maintain a rank-order and solve conflicts. It has been suggested that these interactions between individuals were not functional and some individuals could not cope with the environment. Conflict solving is commonly seen in wolves to maintain their pack. However, some dog breeds (i.e. poodles) are not able to solve a conflict (here studied as to appease or inhibit the opponent) and the conflict might escalate into damaging fights. Other breeds (i.e. German shepherd, hunting dogs or Siberian huskies) might be able to better cope with social conflicts. This study suggests that dogs have lost some social signals to adapt to a life with conspecifics in a group.

The study of Feddersen-Petersen (2007) also suggests the loss of some social signals in dogs. They found around 60 different facial expressions in wolves. Due to the morphological differences in various dog breeds, domestic dogs use less facial expressions. Dogs have less numbers, less differentiation, reduced amplitude and less clearness of visual signals and body postures compared to the wolf. Reduced facial expressions might lead to problems in social communication, for example more group aggression. It has been suggested that dogs adapted to a life in a human environment and therefore aggression with humans might arise due to these reduced expressions.

People might misinterpret dogs' dominance and submissive social signals. Visual communicative signals displayed by dogs involve all parts of the body (i.e. direction of the eyes, ears, muzzle, tail, teeth exposure and standing position). Many of these displayed visual signals might not be

comprehensible, even for dog owners. For example, a belly display and roll over can be interpreted as submissive or fearful behaviour towards a dominant individual. However, these signals can also mean playful or sexual behaviour when these signals are ritualized by learning processes (Mugford, 2007).
The studies of Goodwin *et al*. (1997), Feddersen-Petersen (2004) and Feddersen-Petersen (2007) suggest that various dog breeds can display different types of dominance and submissive signals. This might be explained by artificial selection whereby morphological changes appeared in some dog breeds which might have caused changes in signaling abilities. For example the chow chow, which has stretched hind limbs and this might be a signal of demonstrative behaviour towards other dogs and humans (Bubna-Littitz, 2007).

2.2 Aggressive signals
Aggressive signals displayed by dogs can be observed in different situations: aggression related to fear, dominance, possessive, protection and territorial, predation, play, punishment, parental, redirected, pain or medical, learned, and intra-specific aggression. However, most times dogs display aggressive signals in more than one form (Borchelt, 1983; Reisner, 2002).
An aggressive posture displayed by domestic dogs include a stiff and upright tail, ears that are raised and forward, weight that is slightly forward, fur that is piloerected (most visible in the shoulder area and tail), pupils that are widened, lips that are curled, no lip retraction, nose that is wrinkled, teeth that are shown and the hind limbs are stretched. An aggressive posture displayed by domestic dogs (in the different situations) includes different types of aggressive signals: bare teeth, lift lip, aggressive growling, barking (short, rapid, high-pitch or growl-bark) biting, prey shake, snap, nip, lunge-bite, high activity (changes of locomotive states), flee, look away and shrink back (Bradshaw and Nott, 1995; Reisner, 2002; Bubna-Littitz, 2007; Fatjó *et al*., 2007; Mugford, 2007; van der Borg *et al.,* 2010).
Domestic dogs seem to have developed a wide range of vocal communicative signals for aggressive interactions (Feddersen-Petersen, 2007). Fox (1965) researched different types of vocalizations used by dogs. They found 5 types of auditory signals: infantile sounds (i.e. crying, whimpering and whining), howling, aggressive growing, submissive whining and territorial defensive barking. According to Bradshaw and Nott (1995), the most frequently used vocalizations in different contexts are: barking (defense, play, greeting and warning), grunt (greeting and sign of contentment), growl (warning, threat and play) and whine (submission, defense, greeting, pain and attention). Barking can be used as a threat signal in aggressive interactions between individuals. Domestic dogs seem to rely more on barking signals then other canid species, which might indicated that there is a selection pressure to display barking in dogs (Bradshaw and Nott, 1995). There are many different hypotheses why dogs frequently display barking as a threat signal. Barking is displayed when a dog is in conflict. When dogs are kept in a restrict environment (i.e. a humans' house), there are no opportunities to escape or run when a dog is confined or approached by an unfamiliar 'intruder'. Dogs use barking when they feel threatened in a certain situation (Lord *et al*., 2009).
Molnár *et al*. (2010) studied the ability of humans to interpret the emotional content of dogs' barks. Dog barks were recorded and played back to a group of blind people without any previous visual experiences, to a group of sightless people which had prior visual experiences and to a group of sighted people. All participating groups had never owned a dog. The barks were recorded in six different behavioural contexts: a stranger appeared, a fight was provoked (with aggressive barks), a walk was prepared by the owner, a favorite toy was held, a usual game was played with the owner

and the dog had to stay alone in the park. The participating people had to rank each bark to five different kinds of 'emotions' (i.e. aggression, fearfulness, despair, playfulness and happiness) and after hearing the barks for the second time, the participants had to guess the situation in which the barks were recorded. However, it is not clear how the researchers knew the dogs were displaying these types of emotions. The research suggested that blind people (i.e. without any canine visual experiences) could categorize different dog barks relying on the emotional content of the dog barks, almost as good as sighted people. These results suggests that people can recognize important motivational states in dog barks (i.e. interpret vocal communication in dogs), like aggression or fear, even without visual experiences.

Pongrácz *et al*. (2011) studied the classification of different dog barks by children and adults. In their experiment children and adults had to recognize recorded dog barks in three different contexts (i.e. stranger, play and alone) and had to characterize these dog barks by associating the bark with an emotion (i.e. angry, fearful or happy). However, it is not clear how the researchers knew the dogs were displaying these types of emotions. Overall, there were only minor differences between the performance of children and adults. However, older children could recognize and characterize more dog barks correctly as compared to younger children. Barks in the stranger context were more categorized as 'angry', while barks in the alone context were more categorized as 'fearful'. Play barks however were difficult to characterize. These findings suggest that correctly interpreting dog barks is present even at a very young age.

People, especially children, can also misinterpret dogs' visual signals on aggressive behaviour. Meints *et al.* (2010) found that children often misinterpret a dogs' aggressive face as a dog that is 'happy'. When a dog displays bare teeth, this might be misinterpreted as a humans' smile or grin. Children tend to make this mistake due to the differences between the anatomy of the faces of humans and dogs. Children are more likely to look only at the dogs' face and forget to look at every part of the body, therefore often misinterpret a dogs' face when a dog displays aggressive signals (Pongrácz *et al*., 2011).

Misunderstandings about aggressive signals displayed by dogs can also be related to different dog breeds. Some breeds might display different aggressive signals than other breeds. In the study of Duffy *et al.* (2008) different dog breeds were assessed on their aggressive responses towards strangers, owners and dogs in different situations. In the breed club sample, a total of 1553 questionnaires were filled out and 11 different breeds were tested. In the online sample, a total of 4952 questionnaires were filled out and 33 different breeds were tested. The results showed that some breeds displayed more aggression directed towards humans and dogs (i.e. the dachshunds and Chihuahua), while other breeds showed more aggression only towards other dogs (i.e. pit bull terriers). Dog breeds that displayed the most serious aggression towards humans (i.e. strangers or humans) were Jack Russell Terrier, dachshund and American cocker spaniel (i.e. towards owners). Breeds like Golden retriever, Labrador retriever and greyhounds displayed the least aggression towards humans and dogs. These findings suggest that the amount of aggression and aggressive signals might vary among different types of breeds.

2.3 Play signals

Domestic dogs display many pattern of social behaviour, including social play (one of the most important patterns of social behaviour). During social play dogs can learn the basic rules to adapt to a live in a social environment: how hard to bite, how rough they can interact, which are the codes of social behaviour and how to solve conflicts during play interactions with other individuals

(Feddersen-Petersen, 2007). Play behaviour includes elements of exaggerated, repeated and more variable 'functional' behavior (i.e. fleeing, fighting, sexual and predatory) as well as specific play behaviours (Rooney *et al*., 2001; Boissy *et* al, 2007).
Play postures displayed by domestic dogs include: crouch down with forelimbs nearly touching the ground, backside being up, tail that is erect and/or wagging, ears that are backward/erect, non-threatening postures, mouth that is open and tongue that might be exposed.
Play postures include different types of play signals (in the different situations): play bow, exaggerated approach, face pawing, leaping, withdrawal sequences, barking, play face, pawing with front paw, side-to-side head shake, twisting jumps, panting, staring, tail wagging, play biting, mouthing, standing over, chasing, tackles, chin over, forced down, muzzle lick and muzzle bite (Feddersen-Petersen, 1991; Bekoff, 1995; Rooney *et al*., 2001; Bauer and Smuts, 2007; Ward *et al*., 2008).
Play behaviours can be divided into different categories, for example: play-mounting (i.e. approaching another individual from the front and placing the forepaws on the back of the other individual, like a copulation pose in adults), play-fighting (i.e. including biting, pawing, wrestling, pushing and standing over), aggressive play (i.e. including chasing, attacking, bare teeth, stare, biting and circling), object play (i.e. biting object), and pseudo-sexual play (i.e. love play and sexual behaviour without copulation) (Pal, 2010). Also different forms of play activities are possible: object play, social play (i.e. agonistic behaviour due to contact), solitary play, dog-dog play and human-dog play (Feddersen-Petersen, 1991; Pal, 2010).
Some researchers studied the ability of dogs to respond to human play signals (Rooney *et al*., 2001; Rooney and Bradshaw, 2002). It is not clear however if humans are able to understand dogs' play signals. Dogs often display forms of play through contact and chase games or solitary play (Feddersen-Petersen, 2007). The game 'tug of war' is a popular game that owners often play with their dog. It has been suggested that during play the dominance relationship between dogs and humans is established. So it seems that the outcome of a game can influence the relationship between these two species (Rooney and Bradshaw, 2002). During these games, for example tug of war, play signals are displayed by both dogs and humans. When these play signals are misunderstood, the game might be misinterpreted as aggressive. For example, play signals displayed by humans, such as kiss the dog, pick up the dog or pull the tail of the dog might be misinterpret as threatening behaviour by dogs (Rooney *et al*., 2001).
Humans can also misinterpret other play signals used by dogs. Play signals displayed by dogs, like biting together with rapid side-to-side shaking of the head (which are also used during aggressive interactions) might be misinterpreted as real aggression by humans (Bekoff, 1995).
Play bows are used to indicate the beginning of a play session. Play bows are also used randomly during social play: dogs display play bows immediately before and after an action. Humans might misinterpret play bows as some kind of stop signal which might lead to the disruption of ongoing social play (Bekoff, 1995).

2.4 Stress, fear and anxiety signals

Stress signals displayed by dogs are categorized as behavioural, physiological or immunological. Previous scientific studies on behavioural responses in potential 'stressful situations' (i.e. noise, novelty, transport or restricted housing conditions) reported different stress signals displayed in dogs due to fear, stress and anxiety provoking stimulus (Beerda *et al*., 1997; Beerda *et al*., 1998; Beerda *et al*., 1999).

A fearful/stressful posture in dogs is shown by displaying a low head or head turned away, ears that are pulled back, a low tail or tail behind the legs, a low body posture and crouch near the ground to create a smaller animal (Bradshaw and Nott, 1995; Mugford, 2007; Feddersen-Petersen, 2007). Dogs display a fearful/stressful posture by using different types of stress signals including tongue out, snout lick, paw lift, body shake, vocalizations (i.e. yelping and whining), panting, increased restlessness, yawning, open mouth, increased auto-grooming and repetitive behaviour (Beerda *et al*., 1997; Beerda *et al*., 1998; Beerda *et al*., 1999). Other researchers studied stress signals in dogs using different potential 'stressful' situations, such as thunderstorm phobia, air blast, light/dark test, maze test, separation anxiety, noise phobia and time left alone. These studies reported different stress signals displayed by dogs including, excessive salivation, panting, hiding, trembling, elimination, yawning, change posture, teeth clapping, yelping, whining, paw lifting, auto grooming, nosing, freezing, avoidance, exploration, pacing, destructiveness, licking lips and tail wagging (King *et al.*, 2003; Dreschel and Granger, 2005; Haverbeke *et al*., 2008).

Not many studies focus on the ability of humans to understand dogs' fearful/stressful signals. Recently one study is performed, inter alia on humans' understanding of dogs' social signals. Ortolani *et al.* (2012) studied dogs' behavioural responses in a potential stressful situation, namely a visit to the veterinarian. The owners of the participating dogs had to fill out a questionnaire about the behavioural responses of their dogs in different situations, before entering the consultation room. Inter alia dog owners had to report the tension of their dog during a vet visit (measured on a scale of 1 to 5, with 1 'not at all tense' and 5 'extremely tense'). The behavioural responses of the dogs were videotaped during the vet visit. The results of the study showed that there was no significant correlation between the displayed stress signals of the dog during the vet visit (i.e. panting and licking lips) and the tension of the dog reported by the owner in the waiting room. Moreover, there seems to be an effect of the owners' nervousness: more nervous owners rank their dog as being more nervous. The study suggests that dog-owners cannot predict the emotional state of their dog at the veterinarian very well (pers. obs.).

It might be difficult for people to interpret dogs' stress/fearful signals. There is no standard definition of stress but stress can be seen as 'conditions where an environmental demand exceeds the natural regulatory capacity of an organism' (Koolhaas *et al.,* 2011). There is a wide variation of displayed stress signals in dogs and this variation is caused by differences in stressors and individual characteristics (Beerda *et al.,* 1997). Some stress signals (i.e. panting and licking lips) may help to identify stress but these behavioural signals can have different meanings in various dogs. For example panting, in previous studies this signal is well known as an indicator of stress but panting can also indicate fear or anxiety in dogs (Beerda *et al*., 1998). More severe stress may induce dogs to perform thermoregulatory behaviour (e.g. panting) (Beerda *et al*., 1997). Or for example licking lips, in previous studies this signal is well known to be an indicator of stress, but licking lips can also be an indicator of fear, submission, arousal or nervousness in dogs (Rehn and Keeling 2011; Ortolani *et al.,* 2012). Some stress signals can have different meanings in various situations, which might lead to misunderstandings about these signals between dogs and people.

2.5 Positive emotions

Emotions can be defined in many different ways. One definition might be: 'a mental state that arises spontaneously rather than through conscious effort en is often accompanied by physiological changes, a feeling' (The free dictionary). Research has focused on basic emotions in humans rather than in animals. According to Frijda (1986) and Ortony and Turner (1990) most frequently mentioned

basic emotions of humans are: happiness, surprise, anger, fear, sadness, disgust, joy, desire, hate, hope, love, grief and shame. The question still remains if animals, especially dogs, might also have these basic emotions.
According to Bekoff (2007) if you look at an animal, you can see that an animal can display emotions. Animals might display signs of pleasure, joy (during play), friendship or empathy, spite, gratitude, awe, grief and love. There are many anecdotes of different animals displaying these types of emotions. For example, elephants that mourn the dead of a group member or gorillas that holds wakes. However, there is no empirical evidence for these anecdotes.
Other researchers have argued that animals, especially dogs, can also display emotions due to the degree of similarity with humans. Humans and animals might have similarities in anatomy, brain structure and behaviour (van Rooijen, 1994). However, there is no empirical evidence from studies that measure emotions in dogs, only studies done on monkeys and great apes (Morris *et al.* 2008). Dog owners often use an anthropomorphic way (i.e. unjustified attribution of human qualities to animals) to argue that their dog shows emotions (Bradshaw and Casey, 2007). However, not much research has focused on the attribution of emotions to dogs.
One recent study of Morris *et al.* (2008) researched primary and secondary emotions in several companion animals. Inter alia dog owners (n=337) had to fill out a survey about the observed emotions of their pet and some owners were interviewed about the contexts and behaviours of the observed emotion 'jealousy'. The results suggested that the participating owners observed all primary emotions in their dog (i.e. interest, curiosity, fear, joy, affection, surprise, anxiety, sadness and anger), while secondary emotions were less frequently reported by the owners (i.e. embarrassment, shame, grief, guilt, empathy, pride and jealousy). Compared to owners with other pet animals, dog owners reported emotions displayed by their pet dog most frequently. In the second study, 81 % of the dog owners reported 'jealousy' in their dog. However, its behaviour could also be a form of attention-seeking behaviour. This study could not give evidence that dogs might display jealousy.
Owners might interpret dogs' emotions based on the 'social support hypothesis': interpretations on dogs' emotions are made on the assumptions of their own reaction to a certain situation and they might interpret signs of affection and dependence as if they were coming from other people (Bradshaw and Casey, 2007). However, there is still no clear empirical evidence which types of emotions might be displayed by domestic dogs.

In conclusion, domestic dogs display different signals of social behaviour (i.e. dominance and submission, aggression, play, stress, fear and anxiety) and use these social communicative signals in their relationship with humans. Understanding each other's social signals is essentially to maintain a good relationship.
It seems that humans do not always have the ability to understand the social signals displayed by dogs. People might recognize important motivational state in dog barks (i.e. aggression or fear) and it has been suggested that is present even at a very young age. On the other hand, owners cannot predict the emotional state (i.e. stress signals) of their dog at the veterinarian very well. Several researchers have studied the ability of dogs to respond to human play signals but it is not clear whether humans also understand dogs' play signals.
Misunderstandings about these social signals can arise due to the fact that people might look only at one specific behaviour or one signal and forget that social signals displayed by dogs involve all parts

of the body (i.e. direction of the eyes, ears, tail, muzzle, hair and posture).
Interpretation of dogs' social signals might be especially difficult by the fact that there are great morphological differences among dog breeds (i.e. extreme head- and body sizes), which can lead to differences in displaying signals of dominance, submission and aggression. People might also ignore some communicative social signals displayed by dogs, such as olfactory signals. They might not understand the importance of olfactory signals even though dogs are very sensitive to them. However, it is not clear if or how olfactory signals might influence the interaction between humans and dogs (Schilder, 2004).
When people fail to understand the communicative social signals that are displayed by dogs, they cannot appropriately respond and this might lead to problem situations. Podberscek (2006) and Feddersen-Petersen (2007) have suggested that dogs might get aggressive towards humans or might develop behavioural problems.

Chapter 3. Understanding human communication from a dogs' point of view

Today, many different definitions of communication are available. Wilson (1975) defines communication as follows: 'Communication occurs when the action or cue given by one organism is perceived by and thus alters the probability pattern of behavior in another organism in a fashion adaptive to either one or both of the participants'.
The communicative interactions between individuals are generally cooperative and mutually beneficial (Krebs and Dawkins, 1984). Communication is not limited to members of the same species, communication can also take place between different species, like domestic dogs (*Canis lupus familiaris*) and humans (*Homo sapiens*). Communicative interactions between domestic dogs and humans are well studied in the last decade. Research on dogs' sensitivity to human communicative cues have been reported that domestic dogs might be very skillful in understanding human gestural cues in many different independent studies (Hare and Tomasello, 1999; Soproni *et al*., 2002; Hare and Tomasello, 2005; Virányi *et al*., 2008; Udell *et al*., 2010). However, there is a controversy in the literature regarding the evolution of dogs' ability to understand human communicative cues (Elgier *et al*., 2009; Udell *et al*., 2010; Lakatos, 2011).

3.1 Dogs' understanding of human communication

Different scientific studies done on dogs' communicative abilities suggested that dogs can use different types of human gestures (i.e. pointing, head turning, body postures, touching, marking, gazing and nodding) to locate hidden food items in an object-choice task. (Hare and Tomasello, 1999; Miklósi, 2003; Hare and Tomasello, 2005; Udell *et al*., 2008). Domestic dogs might even solve these object-choice tasks at their first attempt and might use these human gestures from an early stage of age (i.e. puppies), which suggests that dogs might have unusual communicative skills (Soproni *et al*., 2001; Riedel *et al*., 2008). Some researchers have argued that the performance of dogs to respond to human communicative cues is better than the performance of wolves or even better than the performance of humans' closest relative, the chimpanzee (Hare and Tomasello, 2005; Bräuer *et al*., 2006).
Four different categories of human gestural cues used by domestic dogs to interpret human communication will be described: word learning, theory of mind, social learning and imitation, and following pointing gestures.

3.1.1. Word learning

Domestic dogs might respond to different auditory stimuli given by humans. The most frequently used auditory stimulus is words given by humans. Domestic dogs might have the ability to form a relationship between a word and an object that the word refers to, this is called 'word learning' (Kaminski *et al*., 2004). The study of Kaminski *et al*. (2004) suggested that Rico, a border collie, could recognize vocal labels for two hundred different items. When Rico had to retrieve an item, his choice was not influenced by the experimenter or the owner. When one of them gave a command to Rico, they both were standing in a room that was out of view for Rico. The Border collie could retrieve 37 out of 40 items correctly and could even learn to retrieve a new object in one single trail. A new object was placed among seven familiar objects and Rico had to retrieve the new one. Rico could retrieve the new object correctly in 70% of the trials, which suggested that Rico could pair an unfamiliar name with a new object and could even remember the name of the new object by a general learning mechanism (i.e. exclusion learning). The study suggests that Rico can label objects,

can use a general learning mechanism and has the ability to store the information in his memory. The mechanism of exclusion learning used by Rico has only previously been demonstrated in language learning in children.
However, other researchers have questioned the ability of using word learning in domestic dogs. The study of Kaminski *et al*. (2004) did not use different people to command Rico to retrieve a certain object. Besides this, retrieving objects can also be explained by a different mechanism instead of exclusion learning, for example simply by association (Markman and Abelev, 2004; Bloom, 2005). The question still remains if Rico is just an exception because no other dogs have been reported to retrieve so many different objects using word learning.

3.1.2. Theory of mind

Different definitions of 'theory of mind' have been proposed. Heyes (1998) defines this theory as follows: 'an animal with a theory of mind believes that mental states play a causal role in generating behaviour and infers the presence of mental states in others by observing their appearance and behaviour under various circumstances'. Most research has focused on theory of mind in non-human primates but recently studies also focus on domestic dogs (Udell *et al*., 2010).
The studies of Call *et al*. (2003) and Bräuer *et al*. (2004) have suggested that dogs can modify their behaviour when observing humans' attentional state by using theory of mind. These studies researched whether dogs might understand the visual perception of humans. The studies had created a situation whereby a human forbade the dog to take a piece of food (i.e. forbidden food). In the control condition, the human forbade the dog to take a piece of food and the human continued look at the dog because the human had a clear view of the dog and the food. In the other test conditions, the human forbade the dog to take a piece of food but the dog could take the forbidden food undetected because the human has left the room, the human turned their back towards the dog, the human was occupied in another activity or the human closed their eyes. The results suggested that the dogs could modify their behaviour in the various test conditions. When the human did not watched the dogs (i.e. in all test conditions, except for the control condition), the dogs were more willing to take the forbidden food undetected. The test conditions whereby the dogs were most willing to take the forbidden food undetected were: the humans' eyes were closed, the human has left the room, the humans' back was turned or the human was distracted. These studies suggests that dogs might be sensitive to the attentional state of humans: it seems that the dog knew when the human was looking at him so the human could see him taking the forbidden food and when the human was not looking at him so the human could not see him taking the forbidden food.
The studies of Gásci *et al*. (2004) and Cooper *et al*. (2003) researched the ability of dogs to recognize humans' attentional states by using facial cues. In the experiment of Gásci *et al*. (2004), two humans were holding a sandwich in their hands and the dog could choose to beg from one of them. The dog had to beg under varied test conditions. In the first situation, both women faced the dog but one woman had a blindfold on her head, mouth or ears and the other woman had a blindfold over her eyes. In the second situation one woman faced the dog, while the other woman turned her face away and turned her back towards the dog. The experiment of Cooper *et al*. (2003) tested also other restricted views: the human had a bucket on their head or was holding a book before their eyes. In both experiments the dog was given a reward, no matter where the dog begged. The results suggested that dogs begged significantly more from a human that could see, than from a human with restricted vision. Both experiments suggest that humans' body orientation and humans' visibility of the eyes might have an effect on the begging behaviour of a dog. These studies might provide some

evidence that dogs have a 'theory of mind' and might be able to adopt the mental state of other humans.
However, other researchers have questioned the ability of dogs to have a 'theory of mind'. Other theories might also explain the results of the above experiments. The performance of these dogs could also have been influenced by previous experiences. Begging for food when a human is looking can lead to reinforcement (i.e. receiving a reward). Begging for food when a human is not looking means no reinforcement, so begging will only be reinforced when a human is looking at the dog. Besides this, when a dog is forbidden to take a piece of food but still takes the food while the human is watching the dog, the dog is likely to be punished. On the other hand, if the dog takes a piece of food that is forbidden while the human is not watching, the dog is less likely to be punished and this action is probably more reinforced. It might be that dogs do not use a 'theory of mind' but just simple reinforcement (Udell *et al*., 2008).

3.1.3 Social learning and imitation

Several studies have suggested that domestic dogs can learn by observing humans. In the study of Pongrácz *et al*. (2001) dogs' behaviour was recorded in a 'detour test'. A favorite toy or food of the dog was placed behind a V-shape fence and the dogs had to find their toy or food. After some trials, the test set-up was changed whereby the dog was placed within the fence and had to find the toy or food that was places outside the fence. The results suggested that dogs were able to find their favorite toy or food but the dogs were more likely to find the object when the object was placed within the fence. However, after various trials the dogs were not able to find the object more rapidly. When the dogs were allowed to watch a human-demonstrator (i.e. owner or stranger) finding the object in the detour test, the dogs improved their task significantly within two or three trials. Dogs did not copy the path of the demonstrator in the detour test, but modified the observed detour behaviour. This study suggests that dogs can use observed information of human actions to solve a new task.
Rooney and Bradshaw (2006) studied the abilities of dogs to learn from the observations of human-dog interactions. The behaviour of a dog, which observed the interaction between a human and another dog (i.e. the demonstrator), was recorded. In the first experiment the dog watched the human and the demonstrator dog play the game 'tug of war'. The interactions between the human and the demonstrator could vary: 'the human won the game', 'the dog won the game' or 'petting' (i.e. control treatment) was observed. In both the conditions 'human won the game' or 'dog won the game' the dog observed play signals displayed by the human. In the control treatment, the human sat on a chair and petted the demonstrator dog. The results suggested that the dog, which observed the interaction between the human and the demonstrator dog, would approach the winner of the game first and more rapidly. The study suggests that winners of games would be more desirable as social partners. In the second experiment of the study of Rooney and Bradshaw (2006), the dog observed a combination of winning or losing (i.e. the game was lost or won by the dog or by the human) and a combination of signals or no signals were displayed (i.e. no play signals or vocalizations). When the human did not displayed play signals, the game context changed in a contest over resources. The results suggested that dogs that observed the interaction between the human and the demonstrator dog in a contest over resources would approach either the demonstrator dog or the human slower than in a game context. The study suggests that social partners in other contests are less desirable than partners in a game. These findings might suggest that dogs can gain information from observed behaviours of the human or of the demonstrator dog.

Topál *et al*. (2006) studied the ability of dogs to display imitative behaviour to an action of a human demonstrator. The dog had to imitate new actions displayed by the human demonstrator on the command 'do it'. The actions that were shown to the dog were as follows: the experimental design had six locations with plastic bottles, subsequently the owner picked up one bottle from one of the six locations and then placed the chosen bottle to a new location (i.e. one of the other five locations). The command 'do it' was given by the owner after the owner returned to its original position (i.e. behind the dog) and subsequently the dog had to performed the same action as he observed by the human demonstrator. The results suggested that the dog was able to copy the entire action of the human demonstrator above chance level, by reposition the bottle to the same 'new' position as demonstrated by the human.
Range *et al.* (2007) also studied selective imitation in domestic dogs. In his study, dogs watched a demonstrator dog pulling a rod with its paw instead of with its mouth, which is preferred by domestic dogs. The first group of dogs watched the demonstrator dog which carried a ball in its mouth. The second group of dogs watched a demonstrator dog with a 'free-mouth'. When the demonstrator dog was pulling the rod with its paw, only the second group of dogs imitated this non-preferred behaviour. The first group (i.e. the demonstrator had a ball in its mouth) did not adapt the non-preferred behaviour and still pulled the rod with their mouths, even after watching the demonstrator pulling the rod with its paw. These results suggest that dogs, like children, might use selective imitation by only adapting certain types of behaviour in certain situations.

3.1.4. Following pointing gestures

Pointing gestures are the most frequently studied human gestural cues. Dogs' responses to these gestures are usually tested in an object-choice task whereby dogs need to choose from one, two or more locations to find hidden food items by using human pointing cues (Udell *et al*., 2010). In such an object-choice task, a food item (i.e. reinforcing object) is hidden in one location: the target. The dog has to choose the 'right' location (i.e. the target) to get a reward. A human experimenter points at the target in the test area, while the dog observes. Alternative hiding places are controlled for smell, other cues, noise and human scent. When the dog is released in the test area, the dog can choose which location it wants to approach. If the dog chooses the location that the human is pointing out, the dog receives a reward. The dog can indicates its choice by touching or coming close (i.e. within pre-agreed distance) towards one of the locations (Udell *et al*., 2010). Many different forms of the object-choice task have been used to study dogs' ability to use human pointing gestures, including: pointing with one outstretched arm or hand, head turning, nodding, bowing and glancing with the eyes in the direction of the target (Hare and Tomasello, 1999; Miklóski *et al.*, 1998; Soproni *et al*., 2001; Udell *et al.,* 2008).
Miklósi *et al.* (1998) studied the ability of domestic dogs to use various human pointing gestures. In his object-choice test two bowls with hidden food were used. Which location was used as the target (i.e. location with the hidden food item) was determined by tossing a coin. When the experimenter hid the food under a bowl, the dog was out of sight. The experimenter was behind the bowls when the dog entered the room. The dog had to stand three meters away from the bowls when the experimenter made eye-contact and gave the predetermined gesture to the dog. Five different gestures were used (i.e. pointing, bowing (bending the upper torso), nodding, head turning and glancing with the eyes). After a specific gesture the dog was allowed to approach one of the bowls. When the dog had chosen the correct bowl (i.e. the bowl that was pointing out by the experimenter), the dog received a reward. When the dog had chosen the incorrect bowl, no reward was given to the

dog. The results suggested that the dogs were able to use the five different human gestural cues. The study suggested that domestic dogs can use all of these different gestures to locate the hidden food, without explicit training. Dogs could follow the gestures of a familiar person (i.e. the owner) or an unfamiliar person (i.e. the experimenter). Most dogs did performed above base-line, however there were still individual differences and the dogs performed better after training. This might suggest that not all dogs can use pointing gestures at the same level or associative learning might be involved. Subsequently many other studies (Hare and Tomasello, 1999; Soproni *et al*., 2002; Miklósi *et al.*, 2005; Hare and Tomasello, 2005; Miklósi and Soproni, 2006) have researched the ability of dogs to use other forms of human gestural cues. These studies have suggested that domestic dogs can use or can be trained to use different types of pointing gestures, including four categories of human pointing gestures: proximal points (i.e. the distance between the tip of the finger and the object is less than 40 cm.); distal points (i.e. the distance between the tip of the finger and the object is greater than 50 cm.); momentary points (i.e. the experimenters' arm and hand are extended towards the object and afterwards the arm has to returns back to a resting position before the dog can make its choice); and dynamic points (i.e. the experimenters' arm and hand are extended towards the object before the dog enters the trial and the arm and hand remain in the same place until the dog makes its choice)(Miklósi and Soproni, 2006).
Besides this, these studies also have suggested that domestic dogs might be able to use human pointing gestures, including pointing with an arm or extensions of an arm (Hare and Tomasello, 1999; Soproni *et al*., 2002; Miklósi *et al*., 2005), glancing (Soproni *et al.,* 2001), local enhancement when a human is present near the target (Hare and Tomasello, 1999), and when a human puts a marker on a target location (Hare and Tomasello, 2005; Udell *et al*., 2008*b*). The test conditions of these experiments could vary. In several experiments, the dog had to learn one gesture before another gesture would be presented. In other experiments, the order of gestures was varied (i.e. to avoid generalization) or new gestures were presented among learned ones (Udell *et al*., 2008). Besides the type of gesture, also the time that was giving to the dog to make a choice and the number of trails could vary. Even though the test conditions of these studies varied, all researchers propose that domestic dogs are able to use various forms of human pointing cues to locate a hidden food item in an object-choice task above chance level. This might suggest that domestic dogs are able to understand human communicative signals.

The ability to follow human pointing gestures is also studied in other species (i.e. wolves, foxes and cats) and can be compared to the performance of dogs. Dogs' performance of following human pointing gestures in an object-choice task has been compared to the performance of other canid species, like the wolf, wolf pups and foxes. Besides these species, also cats and apes have been compared in their ability to use human pointing gestures in an object-choice task.
Miklósi *et al*. (2003) studied the ability of dogs and wolves to locate a hidden food item by using human pointing cues. The results suggested that socialized wolves were able to locate a hidden food item when a familiar experimenter indicated the location by using touching and pointing cues. Wolves were able to learn some human gestures but their performance was, in general, worse than the performance of domestic dogs. Even when the test situations were similar and the test had a large individual variability. The results also suggested that dogs were able to gaze or look at the human experimenter when they were not able to solve the task (i.e. the task was manipulated and could not be solved). On the other hand, when socialized wolves had to 'solve' the manipulated task, they did not gaze or look at the human experimenter. It seems that wolves might perform worse on

the object-choice task because the willingness to look at the human experimenter was low. This study suggests that the differences in performance between wolves and dogs in an object-choice task might be explained by the fact that domestic dogs have the ability to look at the humans' face.
Virányi *et al*. (2008) studied the ability of hand-reared wolf pups and dogs pups (i.e. all species had the same age) to form eye-contact with a human experimenter and to follow pointing gestures in an object-choice task. The results of this study were in consistent with the results of the studies of Miklósi *et al*. (2003) and Riedel *et al*. (2007) and suggested that dogs pups were able to use distal pointing and other forms of pointing gestures (i.e. proximal pointing, touching and standing behind) to locate a hidden food item in an object-choice task, even without intensive socialization. Wolf pups, on the other hand, were not able to use these human pointing gestures in an object-choice task. However, when wolves were intensively trained and socialized, they were able to use simple forms of human pointing gestures, like touching or proximal pointing. The results also suggested that socialized wolves did not show the willingness to form eye-contact with the human experimenter. The study suggests that domestic dogs might have developed a more complex form of human-dog communication which cannot be accomplished by socialized wolves.
Hare *et al*. (2005) compared the ability of domestic dogs and foxes to use human communicative pointing gestures in an object-choice task. In the experiment the performance of foxes, which were selected against fear and aggression (i.e. experimental domestication) were compared to the performance of domestic dogs. The results suggested that foxes were able to use human gestures (i.e. pointing and gaze cues) in an object-choice task, the same way as domestic dogs were able to use these cues to find a hidden food item. The study suggests that experimental domesticated foxes are more skillful to use human pointing cues than foxes that are not bred for tame behaviour.
The ability to use human gestural cues is also studied in another domestic animal, such as the cat. Miklósi *et al*. (2005) studied the ability to use human pointing gestures in an object-choice task by comparing the performance of domestic dogs with the performance of domestic cats (*Felis catus*). Four different types of pointing gestures were compared (i.e. proximal pointing, distal pointing, momentary pointing and dynamic pointing). The results suggested that both domestic cats and domestic dogs were able to use human gestures to locate a hidden food item, but cats were slightly less successful than dogs. When the task was manipulated (i.e. the hidden food item was made inaccessible and so the task could not been solved) the results suggested that dogs were willing to look at the owner more often and for a longer period of time compared to cats. On the other hand, cats were willing to look only at the owner for a few times and spend more time trying to solve the task themselves. The study suggests that domestic cats seem to lack some degree of 'attention-getting behaviour' as compared to domestic dogs, which might indicate that there are species-specific differences in the ability to communicate with humans.
Itakura and Tanaka (1998), Call *et al. (*2000) and Bräuer *et al*. (2006) studied the ability of chimpanzees to solve an object-choice task by using human cues. The results suggested that although chimpanzees (*Pan troglodytes*) could use given cues (i.e. tapping on an object, gazing and pointing, gazing closely, gazing alone and glancing) to respond to an object-choice task, they were not able to use these cues to find a hidden food item. Chimpanzees are able to solve many non-social tasks but compared to the performance of domestic dogs, chimpanzees seem to be poor in using human pointing gestures in an object choice task. However, when individual chimpanzees were raised by humans their performance improved.
According to Hare and Tomasello (2005) domestic dogs can respond to human social cues and human pointing gestures in various human-guide tasks, much like human children do.

Several scientific studies have suggested that domestic dogs are able to use various human cues in different categories (i.e. word learning, theory of mind, social learning, imitation and following pointing). When comparing the performance of domestic dogs with the performance of other canid species or other animals, it has been suggested that domestic dogs might be unique in their communication with humans.

However, these experimental studies also have drawn criticism from other researchers. Previous results of different studies did not show a great variation among dogs. There might be breed differences and individual differences in the performance of, for example an object-choice task (Svartberg and Forkman, 2002; Udell *et al*., 2010). Some studies did not tested many species, some experiments only tested a couple of dogs or a couple of breeds (i.e. a low n was used; number of species in the experiment). Experiments need to test a great variation of dogs to identify individual differences and a large variation of breed types to indentify breed differences. However, several experiments just tested one type of breed and did not compare these results with other types of breeds. For example, some breeds might not have proper visual sharpness to distinguish between different pointing cues in an object-choice task (Coppinger and Coppinger, 2002). When domestic dogs do not perform above chance level in an object-choice task, this does not always means that they do not have the ability to use these cues. To draw significant conclusions, there need to be better control tests in every experiment and more dogs have to be tested in future studies (Udell *et al*., 2010).

It seems that domestic dogs are able to use human pointing gestures in an object choice task, but some experiments did not use a standard methodology. The above described experiments have used different forms of methodologies: there were large variations in distance between the object and the human pointing cues, variations in duration to show the pointing cue to the dog, variations in which body part of the human was shown as pointing cue and variation in the definitions used by researchers to describe the method. Because of the differences in methodologies, it is difficult to compare the performance among dogs or among other species because different things might be measured. For example, some researchers define gazing as only a movement of the eyes, while others define gazing as a movement of the entire head. Some dogs were able to use a movement of the entire head as a cue but were not able to use a movement of the eyes alone as a cue to locate the food item in an object-choice task (Udell *et al*., 2010).To draw significant conclusions on the performance of an object-choice task between different species or among the same species, there needs to be a well standardized methodology.

The environment of the test condition is of great importance and can influence the performance of an individual during an experiment. In several experiments described above the environment varied or was not well defined. For example, in one test situation wolves were tested behind a fence, while dogs were tested without this barrier. Differences in the performances of domestic dogs and other canid species in an object-choice task could be related to the fact that in some experiments dogs were tested indoors and wolves were tested outdoors (or vice versa) (Udell *et al*., 2010). In addition, some test conditions were not reported adequately. For example, several methodologies did not report whether dogs were tested inside or outside, whether dogs were tested in a new environment or in a familiar environment or how many people were present during the test trials. Dogs might be more distracted when they are tested outside, in a new environment or with many people present and might pay less attention to a cue that is giving by the experimenter (Udell *et al*., 2010). This might suggest that no good standardization of the test conditions and no adequately reporting of the test conditions can influences the test results, so no significant conclusion can be drawn.

Age might also be an important factor which can explain individual differences in performance during the above studies. In the above described experiments, some test dogs were in their sensitive period for social development during the experiment, while others dogs are not and this might explain the differences in performance among dogs. To draw significant conclusions, all studied individuals need to be of same age or in the same development stage (Udell *et al*., 2010).
Besides this, both phylogeny and ontogeny should be taken into account when testing human-dog communication (Udell *et al*., 2010). A dog will only perform certain behaviour, for example a response to a human pointing cues in an object-choice task, if that dog has the capacity of performing that behaviour and that performances will depend on environmental influences during development (Udell *et al*., 2010). However, not all experiments are based on these two concepts.

In conclusion, the communicative interactions between domestic dogs and humans are well studied in the last decade. It seems that domestic dogs have the ability to use various human communicative cues in different situation, even when compared to other canid species. However, these experimental studies have also drawn criticism from other researchers. Several previous scientific studies do not properly describe the test conditions and did not take factors like breed type, age, development stage and environmental influences in mind. Besides this, several studies have only tested a small variation of dog or just one breed type. Definite conclusions still cannot be drawn from previous results.

3.2 Evolutionary approaches to human-dog communication

There is a controversy in the literature regarding how dogs have adapted to a human communicative environment. Different hypotheses have been proposed. Several authors claim that genetic changes during domestication explain dogs' communicative skills. Hare *et al*. (2002) propose the so called 'domestication hypothesis'. On the other hand, researchers suggest that phylogeny alone cannot explain the communicative abilities of domestic dogs (Udell *et al*., 2010).

3.2.1 Inherited from the wolf

It seems that domestic dogs are able to use human cues (i.e. pointing gestures and gaze following) to locate hidden food items in an object-choice task (Hare and Tomasello, 1999), while wolves perform worse on this task (Miklósi *et al*., 2003). The difference between these species might be explained by the fact that wolves evolved as social pack animals. Wolves hunt in groups where gaze and body directions are of great importance for successful coordination. These group hunters need to know the social behaviour and the coordination of movements from their pack members and from their prey (Hare and Tomasello, 1999). Dogs descended from Old World wolves multiple times during history (Vila *et al*., 1997; Parker *et al*., 2004; Gray *et al.,* 2010), which suggests that the ability of domestic dogs to use human communicative cues might be inherited through common descent with the wolf.
However, these scientific studies also have drawn criticism from other researchers. Domestic dogs seem to be better in solving social-problem tasks than wolves, even when these wolves were socialized (i.e. wolves reared by humans) they were not as skillful as domestic dogs in locating hidden food items in an object-choice task by using human gestural cues (Hare *et al*., 2002).
Besides this, when hand-reared wolves and dogs both had to solve an impossible task (i.e. opening a

locked box with food inside), the results suggested that wolves did not give up and remained trying to solve the task by themselves. Domestic dogs, on the other hand, stopped trying to solve the task right after the beginning and directed their gaze to the human and the box (Miklósi *et al*., 2003). Most results from scientific studies do not support the hypothesis that dogs' communicative abilities are inherited through common descent with the wolf.

3.2.2 Domestication

Several researchers support the hypothesis that the ability of dogs to use human communicative cues might be evolved during the process of domestication. Dogs are adapted to a human communicative environment because of genetic changes during domestication and are not due to environmental influences and life experiences (Hare and Tomasello, 2005; Miklósi *et al*., 2007).These authors have proposed 'the domestication hypothesis': domestication is the main cause of dogs' sensitivity to human social cues. They claim that domestic dogs are more skillful than wolves in solving cognitive tasks by using human cues and experiences with humans do not affect these performances (Hare *et al.,* 2002; Miklósi *et al*., 2003; Hare and Tomasello, 2005).

This hypothesis was tested in various independent experimental studies. Several studies found a difference in the performance in solving an object-choice task between wolves and domestic dogs. Wolves that were reared by humans could not use more complex forms of human pointing cues (i.e. distal pointing or dynamic pointing), while domestic dogs were able to use all cues (Hare *et al*., 2002; Miklósi *et al*., 2003; Hare and Tomasello, 2005; Virányi *et al*., 2008).

In another study, the performance of experimental domesticated foxes and domestic dogs were compared in using pointing gestures and gaze following in an object-choice task. The results suggested that they both were equally skillful (Trut *et al*., 2004).

When the performances of other domestic species, like the domestic cat, were compared to the performance of domestic dogs, the results suggested that both species were able to use pointing signals in an object-choice task (Miklósi *et al*., 2005). However, when both species had to find food in an unsolvable task, cats were trying to solve the task by themselves and did not gaze at the human, while domestic dogs did gaze at the human (Miklósi *et al*., 2005).

Riedel *et al*. (2006) suggested that ontogeny does not play a role in the origin of dogs' ability to use human cues. They compared puppies of different age-stages in finding hidden food in an object-choice task. The results suggested that all puppies, independent of age, could solve the task. The results of these studies support the hypothesis that domestication (i.e. selection of genes) alone seems to play a critical role in the ability of dogs to use human communicative cues.

However, these scientific results also have drawn criticism from other scientist. Several studies do not take different stages of sensitive periods in mind when performing their experiment. Hare *et al*. (2005) performed their experiment with domesticated foxes that were still in their sensitive period (i.e. 3 months) and with undomesticated foxes that were not in their sensitive period (i.e. 1.5 month). These differences in sensitive periods might have an effect on the social development and behavioural responses of various species (Udell *et al*., 2010).

Age might also be an important factor in the development of dogs' abilities to use human cues (Udell *et al.,* 2010). When the performance of an object-choice task was compared between puppies of different age-stages, the results suggested that all puppies were able to solve the task but their performance improved with their age.

Recent evidence from scientific studies do not support the hypothesis that domestication alone have played a role in the development of dogs' sensitivity to human cues but also experiences during

ontogeny might have shaped dogs' communicative abilities (Wynne *et al*., 2008; Udell *et al.,* 2010).

3.2.3 Enculturation and socialization

Besides genetic influences, the socialization of dogs might also have played an important role in the development of dogs' communicative abilities (Itakure and Tanaka, 1998; Tomasello and Call, 2004). Domestic dogs might have developed social communication towards humans because they grew up in the same environment and could have learned from humans, depending on the amount of exposure to humans (Lakatos, 2011).

Call and Tomasello (1998) suggested that socialized apes (i.e. that were raised by humans) developed cognitive abilities due to living in a human social environment. Orangutans and chimpanzees were able to use human pointing cues in an object-choice task, even without previous training (Itakure and Tanaka, 1998).

Lakatos *et al*. (2009) suggested that domestic dogs display a similar performance compared to two-year-old humans in their ability to use pointing gestures. The study suggests that the performance of these species was similar due to the socialization of both species in the same human environment. However, other researchers have criticized the results of these studies. Even every young puppies (i.e. at the age of nine weeks) were able to use human pointing cues and gaze cues to solve an object-choice task. In the study of Hare *et al.* (2002), a group of puppies with exposure to humans in their early life was compared to a group of puppies with little exposure to humans in their early life, in the performances of an object-choice task. The results suggested that both groups were able to use human communicative cues to solve the task and both species were as skillful. The study suggests that domestic dogs do not need a certain amount of exposure to humans to be able to use human cues in an object-choice task.

3.2.4 Associative learning

Other researchers argues that the ability of dogs to use human cues in a cognitive test is the result of rapid learning and 'simple conditioning processes' (Lakatos, 2011).

Several other researchers have criticized this hypothesis. Learning might be important in the development of dogs' social communicative skills but associative learning alone cannot explain the ability of domestic dogs to use human cues. Various studies have suggested that domestic dogs are able to use many different forms of pointing gestures (i.e. the cue is giving at diverse distances or the cue is giving for diverse seconds), which are not learned. Besides this, when domestic dogs had to use non-social cues to discriminate a similar test situation, domestic dog were not able to learn the discrimination task, which suggests that dogs' ability to understand human communicative gestures cannot be the result of associative learning alone (Agnetta *et al.*, 2000).

3.2.5 Phylogeny and ontogeny

Udell *et al*. (2010) proposed 'the two stage hypothesis': phylogeny (i.e. genetic changes during domestication) as well as ontogeny (i.e. devolvement) are important factors for the ability of dogs to understand human gestures. The successful performance of domestic dogs in an object-choice task might be explained by the willingness of dogs to accept humans as social companions. Besides this, following the actions of humans leads to reinforcement (Udell *et al*., 2010).

When dogs are exposed to humans in their sensitive period of development dogs might accept humans as social companions. Experiences with humans during their sensitive period might lead to the ability of dogs to use humans' social cues. When dogs have the chance to form an association

between a specific human cue and the behavioural outcomes in their home environment (i.e. reinforcement by receiving food from a human hand), dogs would be able to perform above chance level in an object-choice task (Udell *et al*., 2010).

In conclusion, it seems dogs are able to understand various human communicative signals, even when compared to other canid species. Many different hypotheses have been proposed to explain the ability of dogs to understand human communicative signals. The two main diverging hypotheses in the literature are 'the domestication hypothesis' and 'the two stage hypothesis'. On one hand, researchers have claimed that genetic changes during domestication and not environmental influences or life experiences might have shaped dogs' ability to understand human cues. On the other hand, researchers have claimed that phylogeny (i.e. genetic changes during domestication) as well as ontogeny (i.e. development) both need to be taken into account when explaining the communicative abilities of domestic dogs. Domestication might have played a critical role in shaping dogs' understanding of human communicative cues, but experiences, ontogeny, socialization and environmental influences cannot be ruled out. Both hypotheses have drawn criticism from other researchers and definite conclusions still cannot be drawn from the results of scientific studies.

Chapter 4. Costs and benefits of the relationship between humans and domestic dogs

Different types of dogs are living today all over the world: village dogs, working dogs and companion dogs all coexist. These dogs might have a different type of relationships with humans: fully dependent, family dog or feral dog (Boitani *et al*., 2009).
The relationship between humans and domestic dogs seems to be a unique one. Both domestic dogs and humans have costs and benefits from their relationship. Domestic dogs can be helpful to humans: they might provide love, companionship and loyalty (Coppinger and Coppinger, 2002). However, in terms of benefits for dogs, the relationship is not well understood (Coppinger and Coppinger, 2002). Even though dogs seem to be beneficial for humans' lives, each year then thousands of dogs lose their home because owners cannot take care of them anymore, they are lost or dumped at shelters. Unfortunately some of these shelter dogs are euthanized because new homes cannot be found for them (Dierenbescherming, 2012).

4.1 Benefits of the relationship for people

Domestic dogs are popular pet animals and seem to be special companion animals compared to other species (Hart, 1995). The relationship between domestic dogs and humans might have benefits for both species, but in terms of benefits for humans many examples are known. Dogs can provide a service for people (e.g. detecting drugs, guarding homes or guiding humans) or they can make peoples' life in some way meaningful (Coppinger and Coppinger, 2002). Dogs can have a huge value for human society: they can save people, watch the household, guide the blind, help with police work and assist people (Coppinger and Coppinger, 2002).
Dogs can be part of a family and the main reasons reported by owners for having a dog are love, companionship, play, affection, physical qualities, entertainment and a good friend (Hart, 1995). Dog owners describe their dogs as accepting, trusting, loving and friendship giving. These owners reported that the benefits of being a dog-owner are protection, companionship, happiness or pleasure and their pet protects their home (Hart, 1995). Some family members reported to be even closer to their pet dog than to other human members in the family. Owners find it easy to give affection to their dog by stroking them and therefore might place their pet higher in ranking of importance than other family members (Hart, 1995).
Dogs' companionship might also have benefits for children's lives: dogs can give comfort and support, might improving self-esteem, might provide early experiences of live events and children might learn to care for others and develop more positive attitudes towards animals and humans in adulthood (Triebenbacher, 2000; Podberscek, 2006). Children might also be less afraid of doctors when a dog is present in the office (Coppinger and Coppinger, 2002). When children feel lonely or sad their dog can keep them company and play with them (Hart, 1995). When children can play and talk with a dog from early life, this might help them to make new friends, the willingness to make new friends and to be educated in forms of social relationships (Hart, 1995).
Pet dogs might also have benefits for foster children. Foster children might not have a secured position in the family and might be socially weak. Parents of foster children reported that the relationship with a dog improved their foster children's feelings about humans, decreased social barriers and improved their communication and mood (Hart, 1995).
Humans might develop positive feelings while caring for dogs because humans and dogs can form a bond which is similar to a mother-infant relationship (Serpell, 2003). Not only owing a dog, but also the degree of attachment towards a dog might be linked with humans' health and wellbeing

(Nagasawa *et al*., 2009). It has been suggested that oxytocin plays an important role in the degree of attachment behaviour and social bonding in animals. Oxytocin is a peptide hormone produced in the hypothalamus and is released by the pituitary during lactation and parturition (Nagasawa *et al*., 2009*b*). Nagasawa *et al*. (2009) have suggested that oxytocin levels in humans' urine can indicate attachment behaviour between humans and dogs. When dogs gaze at their owner, the urinary oxytocin concentrations of owners can increase, which might indicate social bonding and social attachment between humans and dogs.

Albert and Bulcroft (1988) found in a telephone survey in Rhode Island that dogs were the most popular pet animal and the most desired pets for owners that did not have a pet animal. When humans choose dogs as preferred pets in the survey, they reported to feel more attached to their pet dogs compared with humans that preferred other pets, like cats. Humans might have chosen dogs as their preferred pet in the survey because dogs might be more willing to play and humans might interact more actively with dogs (i.e. groom them, walk them, give special treats) compared with other pet animals (Hart, 1995). Humans and dogs might interact in a way that results in a high degree of attachment. Attachment behaviour has been reported as love, pleasure and protection, which might increases the owners morale- and self-esteem (Coppinger and Coppinger, 2002; Pehle, 2010).

Dogs as companion pets can also have physiological benefits for people. Humans that are ill reported that dogs might help them to distract them from their pain or their worries and dogs might help to cope with difficulties (Pehle, 2010).

Keeping dogs as companion animals have been reported to result in cardiovascular benefits. It has been suggested that when dog owners are petting a dog or see a dog entering the room, they can have reduced blood pressure and plasma cortisol. So the companionship of a dog might help to improve survival after a heart-attack (Hart, 1995; Arhant-Sudhir *et al*., 2011). Dogs' companionship might also improve the general health of humans. People with a dog seem to take longer walks then people without dogs. Dogs might increase the amount of exercise per day (Podberscek, 2006) and might stimulate the physical activity among patients (Epping, 2010). Dogs might also provide social encounters during walks: when dog owners walk their dog they can experience more positive social interactions and might have more social conversations then people that walk alone (McNicholas and Collis, 2000). Owners can receive social support through anthropomorphism of their dogs (Duvall Antonacopoulos and Pychyl, 2008). The relationship with pet dogs might reduce the feelings of stress, loneliness and depression, which has been reported to result in less doctor visits in a year (Siegel 1990; Hart, 1995; Scheibeck *et al*., 2011).

Companion dogs can also be useful in therapeutic settings: dogs might help patients to cope with difficulties (i.e. people in a wheelchair with a dog will join activities they otherwise might have avoided), they can stimulate playful contacts and might create a family atmosphere, they might distract humans from their illness, they can give people the feeling to discuss their fears and concerns, they might provide social contacts which promotes self-esteem and people spend less time alone (Hart, 1995; Coppinger and Coppinger, 2002; Podberscek, 2006; Pehle, 2010).

A study of Hart *et al*. (1987) assessed the attractiveness and acceptance of people with disabilities. The results suggested that disable people with a service dog had more friendly approaches during a trip outdoors compared to disable people without a service dog. Besides this, people in a wheelchair with a service dog received more social acknowledgments than people without a service dog. Domestic dogs seem to increase social responses and acceptance of disabled people and children (Hart, 1995).

4.2 Costs of the relationship for people

Although dogs seem to make humans lives more meaningful, the relationship between domestic dogs and humans might also have costs for people and for human society. Taking care of a pet dog is a huge investment of time and money. The main costs of the relationship with dogs are the disadvantages of behavioural problems and/or health issues.

Dogs can develop unwanted behaviour, including disobedience, aggression (to their owner, other people and dogs), separation problems, fears and phobias (Bradshaw and Nott, 1995; Wells and Hepper, 2000; Overall *et al*., 2001; Mills and Mills, 2003; Schilder, 2004; Podberscek, 2006). Aggression can have an impact on the owners' ability to travel or socializing with friends (i.e. visitors can be afraid of the dog) (Hart, 1995). Dogs' aggression might lead to dog-attacks and sometimes an owner is pressured to euthanize their dog (Podberscek, 2006). Dog-attacks can be a major problem in some countries due to dog zoonoses, such as rabies. However, in the Netherlands only 0,937% of the people are bitten by a dog each year (Commisie van Wijzen, 2008).

The risk of allergies and zoonoses (i.e. infection diseases transmitted from animals to humans) can be harmful for some people. Some owners can become allergic to dogs and might develop asthma, hay fever or rashes (McPherson *et al*., 2000; Podberscek, 2006).

Dogs might also cause distress to their owner when they get injured, ill or even die (Podberscek, 2006). Because owners might develop strong emotional bonds with their pets and even see their pet as part of the family, the grief of their pets dead can be very intense and can cause a lot of distress (Kurdek, 2008; Lund *et al*., 2012).

Owning a dog might also have costs for the society: dogs' diseases can be transmitted, humans can get attacked or bitten by a dog, the environment can be polluted, dogs can cause car accidents (i.e. when crossing roads), dogs can be predators towards other animals (i.e. kill or injure other pets) and dogs might bark all day and might destroy properties (Podberscek, 2006). The amount of urine and feces dogs produce every day is enormous. Feces in public places might cause many complains, pollution and minor health risks (Coppinger and Coppinger, 2002; Podberscek, 2006).

Taking care of a dog might be expensive, for example owners might have high costs for food (i.e. the amount of calories they really need), veterinarian care, management (i.e. collar, leash, fence etc), insurance, legislation, medicine, medical costs of dog bites, running animal shelters and police forces to find lost dogs (Coppinger and Coppinger, 2002). The average costs of owing a dogs is been estimated between 700 and 3000 dollar per year (Stregowski, 2012).

4.3 Benefits of the relationship for dogs

The relationship between domestic dogs and humans might have benefits for both species. However, in terms of benefits for dogs this relationship is less understood.

Dog owners might provide food, shelter, companionship and veterinarian care for their pets (Podberscek, 2006).

Besides this, people can also have a calming effect on some dog breeds (i.e. greyhounds). It has been suggested that if dogs are being pet, it will result in a drop of their blood pressure and heart rate (McGreevy *et al*., 2005).

From a biological point of view, survival and reproduction is beneficial for a species. Survival depends on basic needs: food, safety and reproduction. People might give access to these basic needs: they can provide food, safety, health, a home and care (Coppinger and Coppinger, 2002).

4.4 Costs of the relationship for dogs

The relationship between dogs and humans might also bring costs for dogs. People might provide the

basic needs for dogs, like food and shelter but sometimes their reproduction is well-arranged. However, most dogs in western society are sterilized and have no reproductive success (Coppinger and Coppinger, 2002).
When owners do not know the appropriate way to feed, train, handle and look after their dog, behavioural problems, malnutrition, obesity and diseases might develop. Owners might even abuse their dog in some cases (German, 2006; Podberscek, 2006). Some dogs might develop obesity, caused by extreme dietary intake due to inadequate feeding by owners. Owners might not realize the problems of obese dogs: orthopedic diseases, diabetes, urinary disorders, reproductive disorders and dermatological diseases which eventually might have harmful effects on the health and the length of the dogs' live (German, 2006).
Many dogs are euthanized because humans do not properly think about the consequences of having a dog. Owners need to get informed about: suitable breeds, backgrounds and history of the dog before buying a dog. Not thinking about the consequences might lead to faster abandon of new adopted puppies. The main reasons for people to abandon their dog were behavioural problems and lifestyle changes (Hart, 1995). Mader and Hart (1992) did a research in California on the age of dogs at time of death in different facilities (i.e. veterinarian clinics) compared with animal shelters. They found that when dogs are brought to animal shelters, their age of death seems to decrease (i.e. on average less than two years old) when compared to dogs living in a family home or veterinarian clinic (i.e. average age of death is 13 years).
In worse situations, humans might even abuse their pet dog. A link was found between abused dogs and children, suggesting that children and pets within the same family were both abused (Hart, 1995). There was also a link found between animal abuse and domestic violence in the Netherlands. Veterinarians have reported situations whereby both types of abuse occurred in their practice (Enders-Slegers and Janssen, 2009).
Dogs are trained to perform, but most tasks are complex, difficult and stressful and might not to be beneficial for them. For example wheelchair dogs need to pull a wheelchair from aside, which make the task of pulling more difficult (Coppinger and Coppinger, 2002).
Some household environments do not provide proper stimulation for dogs to display 'normal' behaviour. Owners often have no idea of the critical period of social development or requirements that are necessary to display proper behaviour (Coppinger and Coppinger, 2002). When dogs cannot display their behavioural needs, their welfare can be impaired directly (i.e. dogs often develop compulsive disorders), or indirectly by treating their dog inappropriately, bring them to shelters or have them euthanized (Podberscek, 2006; Ohl and van der Staay, 2011).
Humans intensively select specific desirable behavioural and physical traits and reduce the gene diversity by selecting against specific genetic problems. By selecting for one specific trait, more traits might be affected because one single gene can control more than one characteristic. In this way, the next generation can still have lots of genetic problems and breed-specific genetic diseases created by intensive breeding. Undesirable behaviours can occur in some breeds because of selection for specific looks, rather than the personality of the dog (Coppinger and Coppinger, 2002; Bateson, 2010). For example flank sucking (i.e. excessively sucking on the top of one of its hind legs which cause damage to the skin) in Dobermann pinschers (Hubrecht, 1995).
Breeders might also select for a typical look, for increased interest, for shows or for aesthetic. According to Bateson (2010) the most frequently mentioned dog breeds that are selected for exaggerated characteristics are the British bulldog and other breeds with a short muzzle, like the Pekingese. Due to intensive breeding, this breed can often barely breathe, barely chew, puppies

cannot be delivered normally and females are artificially inseminated. People want these specific dog breeds as pets due to their looks but do not think about the consequences of intensive breeding. Even though medical care is available for these breeds, they only need this medical care to survival because of intensive breeding by humans (Coppinger and Coppinger, 2002).
Other breeds are bred for exaggerated characteristics, like the chow chow which has been selected for diamond-shaped eyes. These dogs are in discomfort and sometimes might even need surgical correction (Hubrecht, 1995). Another example is tail docking (i.e. removal of a part of the dogs' tail), which is commonly seen in some dog breeds, for example boxers. Some people argue that tail docking reduces the risk of tail injuries (Diesel *et al*., 2010). However, dogs also communicate with their tail and tail docking might obstruct communication (Bradshaw and Nott, 1995; Bateson, 2010). In some extreme cause surgical procedures are done for desirable reasons instead of therapeutically reasons, for example tattooing, declawing, teeth-cutting and ear implants. These operations might affect their welfare in a negative way and are morally unacceptable (Hubrecht, 1995).

4.5 Forms of relationships

Many types of dogs (i.e. village dogs, working dogs, dog companion breeds) with morphological differences, adaptations to varied environments and functions are coexisting all over the world. According to Boitani *et al*. (2009), dogs can be divided in different groups based on their relationship with humans: -restricted dogs (i.e. fully dependent / restricted and all needs are provided by humans); -family dogs (i.e. fully dependent and semi-restricted); -stray or village dogs (i.e. have a social bond with humans and have different degree of tolerance/ fear towards humans); - and feral dogs (i.e. living in the wild and no socialization towards humans). However, these categories are not homogeneous and dogs' status and their relationship with humans can change over time. For example village dogs, due to the presence of a food source (i.e. a human garbage dump) they might become adopted in families and eventually become family dogs, although this is not the case for all village dogs (Boitani *et al*., 2009).
According to Coppinger and Coppinger (2002), four different types of relationships with humans are possible, also depending on culture and economical contexts. Dogs and humans can have a commensalistic relationship (i.e. one species gains benefit from the relationship and the other one is neutral), whereby dogs gain benefits from humans, they can reproduce, forage and survive at the niche humans created of waste food.
On the other hand, dogs and humans can have a mutualistic relationship, whereby both species gain benefits of the relationship (i.e. both species dependent on and adapted to the relationship). Humans believe that they provide safety and good care for their dogs and dogs might bring meaning to the lives of humans (Coppinger and Coppinger, 2002).
Another type of relationship is parasitism, whereby one species gain benefit at the cost of the other. Dogs have a lot of costs for people and human society, but dogs do not gain much biological benefit of the relationship with humans (Coppinger and Coppinger, 2002).
The relationship between dogs and humans can also be a form of amensalism (i.e. one species has a negative effect on the other, while the other is not affected by the interaction), whereby dog owners might treat their pet dog bad and are not biological good for their pet dog but dog owners themselves are not hurt in the relationship (Coppinger and Coppinger, 2002).
On the other hand, the relationship between humans and dogs can be reciprocal amensalism (i.e. both species have a negative effect on each other due to the interaction), whereby dogs are bad for the society due to economic and health problems and at the same time, the relationship is bad for

dogs (Coppinger and Coppinger, 2002).
I think that each type of relationship might fit to a different type of dog, so each type of dog might have a unique relationship with humans. It seems that a commensalistic relationship fit more to village dogs as they get benefits from humans by using human garbage dumps as a new niche to survive. A mutualistic relationship seems to fit more to family dogs (i.e. especially working dogs), although from a dogs' point of view the benefits of the relationship are more obvious for humans. Parasitism might not be applicable for the interactions between dogs and humans in western society but might fit to African village dogs. The last two types of relationships, amensalism and reciprocal amensalism, seem to be related to family dogs and restricted dogs, although dogs might also have benefits for humans.
The relationship between humans and dogs in western society, like pet dogs in the Netherlands seems to be a more complex form because both species seem to have costs and benefits from the relationship. However, the benefits of the relationship are more obvious for humans, while the benefits for dogs are less understood.

In conclusion, the relationship between dogs and humans seems to be complex because both species gain benefits and costs from their relationship. Dogs can have many different benefits for children, adults and human society. On the other hand, benefits for dogs seem to be less understood and even not applicable in biological terms.
Different types of dogs coexist today all over the world and each type of dog seems to have its own type of relationship with humans. For example, village dogs can form a social bond with humans, family dogs in western countries and working breeds live close together with humans and feral dogs are more independent of humans and might not even have a real relationship with humans.
It seems that dogs have a unique relationship with humans. Even though, the benefits of the relationship are more obvious for humans: dogs make people happy, dogs help people, and dogs change peoples' lives.

Conclusion

The aim of this thesis was to give a critical overview of the present scientific literature on the human-dog communicative relationship and to understand this relationship from a biological point of view. The research question of the thesis was: ‘‘Do humans understand dog communication as well as dogs seems to understand humans? Or is communication between these two species more one sided?’’ Conclusions can be drawn based on the discussion of the chapters from this thesis.

The first chapter discussed how the relationship between domestic dogs and humans began, namely the evolution of domestic dogs. Recent archaeological and genetic evidence argues multiple origin of the domestic dog. Besides this, the oldest dog origins in the Middle East and dates back from 20.000 years ago. There are two main diverging theories regarding the evolution of the domestic dog. According to Clutton-Brock (1995), people intentionally domesticated wolves, whereby they took wolf pups from their dens, brought them back to their villages and tamed them. According to Coppinger and Coppinger (2002), dogs have domesticated themselves via natural selection by exploiting a new niche (i.e. a human garbage dump). Recent evidence points more to the Coppinger and Coppinger (2002) theory, so it seems that dogs domesticated themselves by exploiting a new niche created by humans (i.e. the human garbage dump) and this seems to explain the beginning of the interaction between humans and domestic dogs. These ‘village’ dogs have become more integrated into the human environment due to artificial selection and over the curse of the centuries but especially in the last 100 years, hundreds of dog breeds have been created by humans.

Chapter two discussed the ability of humans to understand dogs’ communicative social signals. Domestic dogs use different social signals, for example dominance, submission, aggression, play, stress, fear and anxiety. Humans do not always have the ability to understand these communicative signals. For example, dog owners cannot predict stress signals of their dog at the veterinarian. However, there are researchers that proposed that humans can recognize motivational states, like aggression and fear in dog barks. Misunderstandings about dogs’ social signals do arise frequently. People, especially children, tend to look only at one specific behaviour or one signal and forget that social signals displayed by dogs involve all parts of the body (i.e. direction of the eyes, ears, tail, muzzle, hair and posture). Dogs’ signals, for example aggression, can be misinterpreted as a grin. Communicative signals can also be misinterpreted due to the great morphological differences among dog breeds (i.e. extreme body shape and docking of tail and ears). If people misunderstand dogs’ social signals, miscommunication can lead to problem situations, like the development of behavioural problems.

Chapter three discussed the ability of dogs to understand human communicative signals. Dogs seem to be able to understand varied human cues in different categories (i.e. word learning, theory of mind, social learning, imitation and following pointing gestures), even when compared to other canid species. However, these experimental studies have been criticized by other researchers: the results of different studies did not show a great variation, only a few dog breeds have been tested, a low number of dogs were tested, to many different methodologies were used, different definitions were used, the environment varied or the test conditions were not clear. Definite conclusions cannot be drawn from these studies. Future experiments need to be better standardized.

There are two main diverging theories regarding the evolution of dogs’ sensitivity to use human communicative cues: ‘the domestication hypothesis’ and ‘the two stage hypothesis’. On one hand, researchers have proposed that genetic changes during domestication and not environmental influences or life experiences might have shaped dogs’ ability to understand human cues. On the

other hand, researchers have claimed that phylogeny (i.e. genetic changes during domestication) as well as ontogeny (i.e. development) both need to be taken into account when explaining the communicative abilities of domestic dogs. Dogs' are influenced by the environment, development, experiences and socialization. Both hypotheses have drawn criticism from other researchers and definite conclusions still cannot be drawn from the results of scientific studies.
Chapter four discussed the costs and the benefits of the relationship between domestic dogs and humans. Both species gain benefits and costs from their relationship. Dogs might have benefits for children, adults and the society. On the other hand, benefits for dogs seem to be less understood and even not applicable in biological terms. The benefits of the relationship are more obvious for humans: dogs make people happy, dogs help people and dogs change peoples' lives.
Many different types of dogs coexist today and seem to have a unique relationship with humans. For example, feral dogs are independent of humans, village dogs can form a social bond with humans and family dogs live close together with humans.

In summary, it seems that domestic dogs are 'special' canid species in terms of social communication with humans. However, the communicative relationship between domestic dogs and humans seems to be skewed. Domestic dogs appear to understand more about human communicative cues than humans understand about dog communicative signals and misunderstandings do arise frequently. From a biological point of view, the relationship with humans began with the self domestication of the dog and multiple domestication events have occurred. In terms of benefits, this relationship is more obvious for humans.
Domestic dogs have adapted their social behaviour to a life in a human environment. They thereby reduced their social communication with conspecifics and it seems that modern breeds are better adapted to communicate with humans than with other dogs (Feddersen-Petersen, 2007).

Domestic dogs are commonly referred as ''man's best friend'' and research should focus more on the understanding of this relationship from a biological point of view.

References

Abrantes, R.A. (2009). 'The evolution of canine social behaviour'. Wakan Tanka Publishers, Naperville,, Illinois.

Agnetta, B., Hare, B. and Tomasello, M. (2000). 'Cues to food locations that domestic dogs (Canis familiaris) of different ages do and do not use'. Animal cognition, 3, pp 107-112.

Albert, A. and Bulcroft, K. (1988). 'Pets, families, and the life course'. Journal of marriage and the family, 50, pp 543-552.

American kennel club, 2012. 'Complete breed list', consulted on 19-04-2012 via http://www.akc.org/breeds/complete_breed_list.cfm

Arhant-Sudhir, K., Arhant-Sudhir, R. and Sudhir, K. (2011). 'Pet ownership and cardiovascular risk reduction: supporting evidence, conflicting data and underlying mechanisms'. Clinical and experimental pharmacology and physiology, 38, pp 734-738.

Bateson, P. (2010). 'Independent inquiry into dog breeding'. Report, University of Cambridge, pp 1-69.

Bauer, E.B. and Smuts, B.B. (2007). 'Cooperation and competition during dyadic play in domestic dogs, Canis familiaris'. Animal behaviour, 73, pp 489-499.

Beerda, B., Schilder, M., van Hooff, J. and de Vries, H. (1997). 'Manifestations of chronic and acute stress of dogs'. Applied Animal Behaviour Science 52, pp 307-319.

Beerda, B., Schilder, M., van Hooff, J., de Vries, H., and Mol, J. (1998). 'Behavioural, saliva cortisol and heart-rate responses to different types of stimuli in dogs'. Applied animal behaviour science 58, pp 365-381.

Beerda, B., Schilder, M., van Hooff, J., de Vries, H., and Mol, J. (1999). 'Chronic stress in dogs subjected to social and spatial restriction 1 behavioral responses'. Physiology and Behavior, 6 , (2), pp 233-242.

Bekoff, M. (1995). 'Play signals as punctuation: the structure of social play in canids'. Behaviour, 132, (5-6), pp 419-429.

Bekoff, M. (2007). 'Are you feeling what I'm feeling?'. New scientist, 194, pp 42-46.

Belyaev, D.K., Plyusnina, I.Z. and Trut, L.N. (1984). 'Domestication in the silver fox (vulpes fulves desm): changes in physiological boundaries of the sensitive period of primary socialization'. Applied animal behaviour science, 13, pp 359-370.

Belyaev, D.K. and Trut, L.N. (1975). 'Some genetic and endocrine effects of the selection for domestication in silver foxes. In 'the wild canids', edited by M.W. Fox. New York, van Nostrand Reinhold.

Bennet, P. and Rohlf, V. (2007). 'Owner-companion dog interactions: relationship between demographic variables, potentially problematic behaviours, training engagement and shared activities'. Applied animal behaviour science, 102, pp 65-84.

Bloom, P. (2004). 'Can a dog learn a word?' Science, 304, pp 1605-1606.

Boissy, A., Manteuffel, G., Jensen, M.B., Oppermann Moe, R., Spruijt, B., Keeling, L.J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., Aubert, A. (2007). 'Assessment of positive emotions in animals to improve their welfare'. Journal of Physiology and Behavior 92, pp 375-397.

Boitani, L., Ciucci, P. and Ortolani, A. (2009). 'Behaviour and social ecology of free-ranging dogs'. In: the behavioural biology of dogs, edited by P. Jensen, oxfordshire, pp 147-165.

Boitani, L., Francisci, F., Ciucci, P. and Andreolli, G. (1995). 'Population biology and ecology of feral dogs in central Italy'. In 'The domestic dog: its evolution, behaviour and interaction with people', edited by J. Serpell. Cambridge, UK: Cambridge university press.

Borchelt, P. (1983). 'Aggressive behaviour of dogs kept as companion animals: Classification and influences of sex, reproductive status and breed'. Applied animal ethology, 10, (1-2), pp 45-61.

Bowlby, J. (1969). 'Attachment and loss'. Attachment 1 New York: Basic books.

Bradshaw, J.W.S. and Casey, R.A. (2007). 'Anthropomorphism and anthropocentrism as influences in the quality of life of companion animals'. Animal welfare, 16, pp 149-154.
Bradshaw, J.W.S. and Nott, H.M.R. (1995). 'Social and communication behaviour of companion dogs'. In: the domestic dogs, its evolution, behaviour and interactions with people, edited by J. Serpell. Cambridge university press, pp 115-130.
Bräuer,J., Call, J. and Tomasello, M. (2004). 'Visual perspective taking in dogs (*Canis familiaris*) in the presence of barriers'. Applied animal behaviour, 88, pp 299-317.
Bräuer, J., Kaminski, J., Riedel, J., Call, J. and Tomasello, M. (2006). 'Making inferences about the location of hidden food: social dog, causal ape'. Journal of comparative psychology, 120, pp 38-47.
Brewer, D., Clark, T. and Phillips, A. (2001). 'Dogs in Antiquity. Anubis to Cerberus: the origins of domestic dogs'. Aris and Phillips.
Bubna-Littitz, H. (2007). 'Sensory physiology and dog behaviour'. In: the behaviour biology of dogs, edited by P. Jensen, CAB International, pp 91-104.
Byrne, R. (2003). 'Animal communication: What makes a dog able to understand its master?' Current biology, (13), pp 1-2.
Call, J., Agnetta, B. and Tomasello, M. (2000). 'Cues that chimpanzees do and do not use to find hidden objects'. Animal cognition, 3, (1), pp 23-34.
Call, J., Bräuer,J., Kaminski, J. and Tomasello, M. (2003). 'Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans'. Journal of comparative psychology, 117, (3), pp 257-263.
Call, J. and Tomasello, M. (1996). 'The effect of humans on the cognitive development of apes'. In Reaching into thought, Cambridge university press, pp 371-403.
Clutton-Brock, J. (1995). 'Origins of the dog: domestication and early history'. In, The domestic dogs, its evolution, behaviour and interaction with people, edited by J. Serpell, Cambridge university press, pp 7-20.
Cohn, J. (1997). 'How wild wolves became domestic dogs. Research sheds new light on the origin of humanity's most intimate quadruped ally'. BioScience, 47, (11), pp 725-728.
Commisie van Wijzen, (2008). 'Hondenbeten in perspectief. Een evaluatie van de RAD en aanbevelingen voor het terugdringen van bijtincidenten'. Minister van LNV, pp 1-109.
Cooper, J.J., Ashton, C., Bishop, S., West, R., Mills, D.S. and Young, R.J. (2003).'Clever hounds: social cognition in the domestic dog (*Canis familiaris*)'. Applied animal behaviour science, 81, pp 229-244.
Coppinger, R. and Coppinger, L. (2002). 'Dogs: a startling new understanding of canine origin, behaviour and evolution'. Scribner, New York, pp 1- 352 (book: 978-0684855301).
Case, L.P. (2010). 'Social behaviour and communication in dogs and cats'. In: canine and feline behaviour and training. A complete guide to understand our two best friends, Delmar engage learning, pp 44-70.
Delporte, H. (1990). 'L'image des animaux dans l'art prhehistorique'. Paris, France: Picard Editeur.
Dierenbescherming, 2012. 'Asielen'. Consulted on 2 March, 2012 via http://www.dierenbescherming.nl/asielen?gclid=CIXN5qaOyK4CFUNO3godTC9q_w
Diesel, G., Pfeiffer, D., Crispin, S. and Brodbelt, D. (2010). 'Risk factors for tail injuries in dogs in Great Britain'. Veterinary record, 166, (2), pp 812-817.
Dobney, K. and Larson, G. (2006). 'Genetics and animal domestication: new windows on an elusive process'. Journal of zoology, 296, pp 261-271.
Dorey, N.R., Udell, M.A. and Wynne, C.D. (2009). 'Breed differences in dogs sensitivity to human points: a meta-analysis'. Behavioural processes, 81, pp 409-415.
Dreschel, N.A. and Granger,D.A., (2005). 'Physiological and behavioral reactivity to stress in thunderstorm-phobic dogs and their caregivers'. Applied Animal Behaviour Science 95, pp 153-168.
Duffy, D., Hsu, Y. and Serpell, J. (2008). 'Breed differences in canine aggression'. Applied animal behaviour science, 114, pp 441-460.

Duvall Antonacopoulos, N.M. and Pychyl, T.A. (2008).' An examination of the relations between social support, anthropomorphism and stress among dog owners'. Anthrozoos, 21, (2), pp 139-152.
Duvall Antonacopoulos, N.M. and Pychyl, T.A. (2010). 'An examination of the potential role of pet ownership, human social support and pet attachment in the psychological health of individuals living alone'. Anthrozoos, 23, (1), pp 37-54.
Elgier, A., Jakovcevic, A., Barrera, G., Mustaca, A., Bentosela, M. (2009). 'Communication between domestic dogs (*Canis familiaris*) and humans: Dogs are good learners'. Behavioural precesses, 81, pp 402-408.
Enders-Slegers, M. and Janssen, M. (2009). 'Cirkel van geweld. Verbanden tussen dierenmishandeling en huiselijk geweld'. Stichting DierZijn, pp 1-81.
Epping, J.N. (2010). ' Dog ownership and dog walking to promote physical activity and health in patients'. Current sports medicine reports, 10, (4), pp 224-227.
Fatjó, J., Feddersen-Petersen, D., Ruiz de la Torre, J., Amat, M., Mets, M., Braus, B. and Manteca, X. (2007). 'Ambivalent signals during agonistic interactions in a captive wolf pack'. Applied animal behaviour science, 105, pp 274-283.
FCI, 2012. 'Fédération Cynologique international, standards and nomenclature'. Consulted on 19-04-2012 via http://www.fci.be/nomenclature.aspx.
Feddersen-Petersen, D. (1991). ' The ontogeny of social play and agonistic behaviour in selected canid species'. Bonner Zoologische Beitrage, 42, pp 97–114.
Feddersen-Petersen, D. (2004). 'Communication in wolves and dogs'. In: Bekoff, M. encyclopedia of animal behaviour, vol. 1., greenwood press, Westport, Connecticut, pp 385-394.
Feddersen-Petersen, D.U. (2007). 'Social behaviour of dogs and related canids'. Chapter 7 in the behavioural biology of dogs, edited by P. Jensen, oxfordshire, pp 105-119.
Fox, M.W. (1965). 'Canine behaviour'. 1ste edition, edited by C. Thomas, Springfield, Illinois.
Fox, M.W. (1970). 'A comparative study of the development of facial expressions in canids; wolf, coyote and foxes. Behaviour, 36, pp 49-73.
Frank, H and Frank, M.G.(1982). 'Comparison of problem solving performance in six-week-old wolves and dogs'. Animal behaviour, 30, pp 95-98.
Frijda, N.H. (1986). 'the emotions'. New York: Cambridge university press.
Gásci, M., Miklósi, A., Varga, O., Topál, J. and Csányi, V. (2004). 'Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention'. Animal cognition, 7, pp 144-153.
German, A.J. (2006). 'The growing problem of obesity in dogs and cats'. American Society of Nutrition, pp 1940S-1946S.
Goodwin, D., Bradshaw, J. W. S. and Wickens, S.M. (1997). 'Paedomorphosis affects agonistic visual signals of domestic dogs'. Animal behaviour, 53, (2), pp 297-304.
Gray, M.M., Sutter, N.B., Ostrander, E. A. and Wayne, R.K. (2010). 'The IGF1 small dog haplotype is derived from Middle Eastern grey wolves'. BMC Biology, 8, pp 16.
Hare, B., Brown, M., Williamsom, C. and Tomasello, M. (2002). 'The domestication of social cognition in dogs'. Science, 298, pp 1634-1636.
Hare, B., Call, J. and Tomasello, M. (1998). ' Communication of food location between human and dog (*Canis familiaris*). Evolution of communication, 2, pp 137-159.
Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R. and Trut, L. (2005). 'Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication'. Current biology, 15, pp 226-230.
Hare, B. and Tomasello, M. (1999). 'Domestic dogs (*Canis familiaris*) use human and conspecific cues to locate hidden food'. Journal of comparative psychology, 113, (2), pp 173-177.
Hare, B. and Tomasello, M. (2005). 'Human-like social skills in dogs?' Trends in cognitive sciences 9, (9), pp 439-444.
Hart, L. A. (1995). 'Dogs as human companions: a review of the relationship'. In: the domestic dog, its evolution, behaviour and interactions with humans. Edited by J. Serpell, Cambridge university

press, pp 162 -178.
Hart, L.A., Hart, B.,L. and Bergin, B. (1987). 'Socializing effects of service dogs for people with disabilities'. Anthrozoös, 1, pp 41-44.
Haverbeke, A., Diederich, C., Depiereux, E. and Giffroy, J.M. (2008). 'Cortisol and behavioral responses of working dogs to environmental challenges'. Physiology and Behavior 93, pp 59-67.
Heyes., C.M. (1998). 'Theory of mind in nonhuman primates'. Behavioural and brain science, 21, pp 101-134.
Horowitz, A. (2009). 'Disambiguating the 'guilty look': Salient prompts to a familiar dog behavior'. Behavioural processes, 81, pp 447-452.
Hubrecht, R. (1995). 'The welfare of dogs in human care'. In: the domestic dog, its evolution, behaviour and interactions with humans. Edited by J. Serpell, Cambridge university press, pp 180-198.
Itakure, S. and Tanaka, M. (1998). 'Use of experimenter- given cues during object-choice tasks by Chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*) and human infants (*Homo sapiens*)'. Journal of comparative psychology, 112, (2), pp 119-126.
Kaminski, J., Call, J. and Fischer, J. (2004). 'Word learning in a domestic dog: evidence for 'fast mapping''. Science, 304, pp 1682-1683.
Kaminski, J., Neumann, M., Bräuer, J., Call, J., Tomasello, M. (2011). 'Dogs, Canis familiaris communicate with humans to request but not to inform'. Animal behaviour, 82, pp 651-658.
Koolhaas, J.M., Bartolomucci, A., Buwalda, B., de Boer, S.F., Flügge, G., Korte, S.M., Meerlo, P., Murison, R., Oliver, B., Palanza, P., Richter-Levin, G., Sgoifo, A., Steimer, T., Stiedl, O., van Dijk, G., Wöhr, M. and Fuchs, E. (2011). 'Stress revisited: A critical evaluation of the stress concept'. Neuroscience and behavioural reviews 35, pp 1291-1301.
King, T., Hemsworth, P.H. and Coleman, G.J. (2003). 'Fear of novel; and startling stimuli in domestic dogs'. Applied animal behaviors science 82, pp 45-64.
Krebs, J.R. and Dawkins, R. (1984). ' Animal signals: mind-reading and manipulation'. In, behavioural ecology of evolutionary approach, 2nd edition, Oxford university press, pp 380-402.
Kurdek, L.A. (2008). ' Pet dogs as attachment figures'. Journal of social and personal relationships, 25, (2), pp 247-266.
Lakatos, G. (2011). 'Evolutionary approach to communication between humans and dogs'. Ann Ist Super Sanitá, 47, (4), pp 373-377.
Lakatos, G., Soproni, K., Dóka, A. and Miklósi, A. (2009). 'A comparative approach to dogs (*Canis familiaris*) and human infants' comprehension of various forms of pointing gestures'. Animal cognition, 12, (4), pp 621-631.
Lord, K., Feinstein, M. and Coppinger, R. (2009). 'Barking and mobbing'. Behavioural processes, 81, pp 358-368.
Lund, H.S., Eggertsonn, H., Jørgensen, A.M., Grøndahl, A. and Eggertsdóttir, A.V. (2012). ' Changes in the relationships between dogs, owners and veterinarians in Norway and Iceland'. Veterinary record, 165, pp 106-110.
Mader, B. and Hart,L.A. (1992). 'Establishing a model pet loss support hotline'. Journal of American veterinary medical association, 200, pp 270-274.
Markman, E.M. and Abelev, M. (2004). 'Word learning in dogs?' Trends in cognitive science, 8, (11), pp 479-481.
McGreevy, P.D., Righetti, J. and Thomson, P. (2005). 'The reinforcing value of physical contact on the effect on canine heart rate of grooming in different anatomical areas'. Anthrozoös, 18, (3), pp 236 -244.
McPherson, C.N.L., Meslin, F.S. and Wandeler, A.I. (2000). 'Dogs, Zoonoses and Public Health'. CABI Publishing, Wallingford, UK.
McNicholas, J. and Collis, G.M. (2000). 'Dogs as catalysts for social interactions: robustness of the effect'. British Journal of Psychology, 91, pp 61–70.

Meints, K., Racca, A. and Hickey, N. (2010). 'Child-dog misunderstandings: children misinterpret dogs' facial expressions'. In: proceeding of the 2nd canine science forum, Vienna, Austria, pp 99.
Miklósi, A., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z. and Csányi, V. (2003). 'A simple reason for a big difference: Wolves do not look back at humans, but dogs do'. Current biology, 13, pp 763-766.
Miklósi, A., Polgárdi, R., Topál, J. and Csányi, V. (1998). 'Use of experimenter-given cues in dogs.' Animal cognition, 1, pp 113-121.
Miklósi, A., Pongrácz, P., Lakatos, G., Topál, J. and Csányi, V. (2005). 'A comparative study of the use of visual communicative signals in interaction between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans'. Journal of comparative psychology, 119, (2), pp 179-186.
Miklósi, A. and Soproni, K. (2006). ' A comparative analysis of animals' understanding of the human pointing gesture'. Animal cognition, 9, pp 81-93.
Miklósi, A., Topál, J. and Csányi, V. (2007). 'Big thoughts in small brains? Dogs as a model for understanding human social cognition'. Cognitive neuroscience and neuropsychology, 18, (5), pp 467-471.
Mills, D. and Mills, C.B. (2003). 'A survey of the behaviour of UK household dogs'. Australian veterinary association conference, pp 97-99.
Molnár, C., Pongrácz, P. and Miklósi, A. (2010). 'Seeing with ears: Sightless humans' perception of dog bark provides a test for structural rules in vocal communication'. The quarterly journal of experimental psychology, 63, (5), pp 1004 - 1013.
Morris, P.H., Doe, C and Godsell, E. (2008). 'Secondary emotions in non-primate species? Behavioural reports and subjective claims by animal owners'. Cognitions and emotion, 22, (1), pp 3-20.
Mugford, R.A. (2007). 'Behavioural disorders of dogs'. In: the behaviour biology of dogs, edited by P. Jensen, CAB International, pp 225-242.
Nagasawa, M., Mogi, K., Kikusui, T. (2009). 'Attachment between humans and dogs'. Japanese psychological research, 51, (3), pp 209-221.
Nagasawa, M., Kikusui, T., Onaka, T. and Ohta, M. (2009*b*). 'Dog's gaze at its owner increases owner's urinary oxytocin during social interaction'. Hormones and behaviour, 55, pp 434-441.
Nobis, G. (1979). 'The oldest domestic dog lived 14.000 years ago'. Umschau, 79, pp 610.
Ohl, F. and van der Staay, F.J. (2011). 'Animal welfare- at the interface between science and society'. The veterinary Journal, in press.
Ortolani, A., Vernooij, H. and Coppinger, R. (2009). 'Ethiopian village dogs: behavioural responses to a stranger's approach'. Applied animal behaviour science, 119, pp 210-218.
Ortolani, A., *et al.* (2012). In press.
Ortony, A. and Turner, T.J. (1990). 'What's basic about basic emotions?'. Psychological review, 97, (3), pp 315-331.
Overall, K.L., Dunham, A.E. and Frank, D. (2001). 'Frequency of nonspecific clinical signs in dogs with separation anxiety, thunderstorm phobia, and noise phobia, alone or in combination'. Journal of the American veterinary medical association, 219, (4), pp 467-473.
Pal, S.K. (2010). 'Play behaviour during early ontogeny in free-ranging dogs (Canis familiaris)'. Applied animal behaviour science, 126, pp 140-153.
Parker, H.G., Kim, L.V., Scutter, N.B., Carlson, S., Lorentzen, T.D., Malek, T.B., Johnson, G.S., DeFrance, H.B., Ostrander, E.A. and Kruglyak, L. (2004). 'Genetic structure of the purebred domestic dog'. Science, 305, pp 1160-1164.
Pehle, M.A. (2010). ' Healing relationship with companion dogs in the therapeutic process: An exploratory qualitative study'. California Institute of Integral Studies, 107 pages; AAT 3406177.
Podberscek, A.J. (2006). ' positive and negative aspects of our relationship with companion animals'. Veterinary research communications, 30, (1), pp 21-27.
Pongrácz , P., Miklósi, A., Kubinyi, E., Gurobi, K., Topál, J. and Csányi, V. (2001). 'Social learning in dogs: the effect of a human demonstrator on the performance of dogs in a detour task'. Animal behaviour, 62, pp 1109-1117.

Pongrácz, P., Molnár, C., Dóka, A and Miklósi, A. (2011). ' Do children understand man's best friend? Classification of dog bark by pre-adolescents and adults'. Applied animal behaviour science, 135, (1-2), pp 95 - 102.
Power, T.G. (2000). 'Play and exploration in children and animals'. Lawrence Erlbaum associates, Hillsdale, New-Jersey, pp 48-49.
Prato-Previde, E., Custance, D., Spiezio, C. and Sabatini, F. (2003). 'Is the dog-human relationship an attachment bond? An observational study using ainsworth's strange situation'. Behaviour, 140, pp 225-254.
Range, F., Viranyi, Z. and Huber, L. (2007). 'Selective imitation in domestic dogs'. Current biology, 17, pp 868-872.
Reisner, I. (2002). 'An overview of aggression'. In: BSAVA Manual of Canine and feline Behavioural Medicine Eds. Horwitz, Mills and Heath, BSAVA, Gloucester, UK, pp 181-194.
Rehn, T. and Keeling, L.J. (2011). 'The effect of time left alone at home on dog welfare'. Applied Animal Behaviour 129, pp 129-135.
Riedel, J., Schumann, K., Kaminski, J., Call, J. and Tomasello, M. (2006). 'The early ontogeny of human-dog communication'. Animal behaviour 75, pp 1003-1014.
Rijksoverheid, 2012. 'Huisdieren'. Consulted on 22 February, 2012 via http://www.rijksoverheid.nl/onderwerpen/dieren/dierenwelzijn/huisdieren.
Rooney, N.R., Bradshaw, J.S. and Robinson, I.H. (2001). 'Do dogs respond to play signals given by humans?'. Animal behaviour, 16, pp 715-722.
Rooney, N.J. and Bradshaw, J.W.S. (2002). 'An experimental study of the effects of play upon the dog-human relationship'. Applied animal behaviour science, 78, pp 161-176.
Rooney, N.J. and Bradshaw, J.W.S. (2006). 'Social cognition in the domestic dog: behaviour of spectators towards participants in interspecific games'. Animal behaviour, 72, pp 343- 352.
Sastre, N., Ramos-Onsins, S., Brugada, V., de Mena, I., Sánchez, A., Francino, O., Lazuela, C. and Ramirez, O. (2012). 'Analysis of Y-chromosome DNA suggests a multiple-region origin of domestic dog'. In press.
Scheibeck, R., Pallauf, M.,Stellwag, C. and Seeberger, B. (2011).' Elderly people in many respect benefits from interaction with dogs'. European journal of medical research, 16, pp 557-563.
Schilder, M. (2004). 'Miscommunication in interactions between humans and their canine and feline pets'. In: FH de Jonge and R van den Bos (Eds): The human-animal relationship; Forever and a day. Animals in Philosophy and science, pp 98-109.
Scott-Phillips, T.C. (2008). 'Defining biological communication'. Journal of evolutionary biology, 21, (2), pp 387-395.
Serpell, J.A. (2003). ' Anthropomorphism and anthropomorphic selection- Beyond the 'cute response''. Society and animals, 11, (1), pp 83- 100.
Siegel, J.M. (1990). 'Stressful live events and use of physician services among the elderly: the moderating role of pet ownership'. Journal of personality and social psychology, 58, (6), pp 1081-1086.
Skinner, B.F. (1953). ' Science and human behaviour'. MacMillan, New York.
Soproni, K., Miklósi, A., Topál, J. and Csányi, V. (2001). 'Comprehension of human communicative signs in pet dogs (*Canis familiaris*)'. Journal of comparative psychology, 115, (2), pp 122-126.
Soproni, K., Miklósi, A., Topál, J. and Csányi, V. (2002). 'Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. Journal of comparative psychology, 116, (1), pp 27-34.
Stregowski, J. (2012). 'The Cost of Dog Ownership', consulted on 13 June, 2012 via http://dogs.about.com/od/becomingadogowner/a/costofdogs.htm
Svartberg, K. and Forkman, B. (2002).' Personality traits in the domestic dog (Canis Familiaris)'. Applied animal behaviour science 79 pp 133-155
Tomasello, M. and Call, J. (2004). 'The role of humans in the cognitive development of apes revisited'. Animal cognition, 7, pp 213-215.
Topál, J., Byrne, R.W., Miklósi, A. and Csányi, V. (2006). 'Reproducing human actions and actions

sequences: 'Do as I Do' in a dog'. Animal cognition, 9, pp 355-367.
Topál, J., Gácsi,M., Miklósi, A., Viránvi, Z., Kubinyi, E., csányi, V.(2005). 'Attachment to humans: a comparative study on hand-reared wolves and differently socialized dog puppies'. Animal behaviour ,70, pp 1356- 1375.
Tópal , J., Miklósi, A., Csányi, V. and Dóka, A. (1998). 'Attachment behaviour in dogs (Canis familiaris). A new application of Ainsworth's (1969) strange situation test'. Journal of comparative psychology 112, (3), pp 219-229.
Triebenbacher, S.L. (2000). 'The companion animal within the family system: the manner in which animals enhance life within the home'. In: A. Fine (ed), Handbook on Animal-Assisted Therapy: Theoretical Foundations and Guidelines for Practice (Academic Press, San Diego, USA), pp 357–374.
Trut, L.N., Plyusnina, I.Z. and Oskina, I.N. (2004). 'An experiment on fox domestication and debatable issues of evolution of the dog'. Russian Journal of Genetics, 40, pp 644-655.
Udell, M. and Wynne, C. (2008). 'A review of domestic dogs' (canis familiaris) humans-like behaviours: or why behaviour analysts should stop worrying and love their dogs'. Journal of the experimental analyses, 89, pp 247-261.
Udell, M. A.R., Giglio, R.F. and Wynne, C.D.L. (2008*b*). 'Domestic dogs (*Canis familiaris*) use human gestures but not nonhuman tokens to find hidden food'. Journal of comparative psychology, 122, (1), pp 84-93.
Udell, M., Dorey, N. and Wynne, C. (2010). 'What did domestication do to dogs? A new account of dogs' sensitivity to human actions'. Biol. Rev, 85, pp 327-345.
Van der Borg, J., Beerda, B., Ooms, M., Silveira de Souza, A., van Hagen, M. and Kemp, B. (2010). 'Evaluation of behaviour testing for human directed aggression in dogs'. Applied animal behaviour science, 128, pp 78-90.
Van Rooijen, J. (1994). 'Dogs have feelings'. The veterinary quarterly, 16, pp 52S.
Vila, C., Savolainen, P., Maldonado, J.E., Amorim, I.R., Rice, J.E., Honeycutt, R.L., Crandall, K.A., Lundeberg, J. and Wayne, R.K. (1997). ' Multiple and ancient origins of the domestic dog'. Science, 276, pp 1687-1689.
Vilá, C., (2012). 'Evolution of wild and domestic Canids'. In press.
Viránvi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D. and Miklósi, A. (2008). 'Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*)'. Animal cognition, 11, pp 373-387.
Ward, C., Bauer, E.B. and Smuts, B. (2008). 'Play partner preferences and asymmetries in social play among domestic dogs (Canis lupus familliaris) littermates. Animal behaviour, 76, pp 1187-1199.
Wells, D.L. (2009). 'Behaviour of dogs'. Chapter 14, in the ethology of domestic animals: an introductory text', edited by Per Jensen, 2nd edition, Oxfordshire.
Wells, D.L. and Hepper, P.G. (2000). 'Prevalence of behaviour problems reported by owners of dogs purchased from an animal rescue shelter'. Applied animal behaviour science, 69 (1), pp 55-65.
Wemelsfelder, F. (2007). 'How animals communicate quality of life: the qualitative assessment of behaviour'. Animal welfare, 16, pp 25-31.
Wickens, S.M. (1993). 'Social relationship in the domestic dog (Canis familiaris): the effect of learning and breed on behaviour within status relationships'. University of Southampton, pp 7.12-7.15.
Wilson, E.O. (1975). 'Sociobiology: the new synthesis'. Harvard university press, Cambridge.
Wynne, C., Udell, M. and Lord, K. (2008). 'Ontogeny's impacts on human-dog communication'. Animal behaviour, 76, pp 1-4.