

People and Animals: The International Journal of Research and Practice

Volume 1 | Issue 1

Article 6


2018

How Wolves Turned into Dogs and How Dogs Are Valuable in Meeting Human Social Needs

Kurt Kotrschal

University of Vienna Department of Behavioural Biology, Wolf Science Center and University of Veterinary Medicine Vienna,
kurt.kotrschal@univie.ac.at

Follow this and additional works at: <https://docs.lib.purdue.edu/paj>

 Part of the [Anthropology Commons](#), and the [Other Animal Sciences Commons](#)

Recommended Citation

Kotrschal, Kurt (2018) "How Wolves Turned into Dogs and How Dogs Are Valuable in Meeting Human Social Needs," *People and Animals: The International Journal of Research and Practice*: Vol. 1 : Iss. 1 , Article 6.

Available at: <https://docs.lib.purdue.edu/paj/vol1/iss1/6>

This document has been made available through Purdue e-Pubs, a service of the Purdue University Libraries. Please contact epubs@purdue.edu for additional information.

How Wolves Turned into Dogs and How Dogs Are Valuable in Meeting Human Social Needs

Cover Page Footnote

Acknowledgements Much of my wolf-dog worldview I owe the input from, and discussion with, all our colleagues from the Wolf Science Center (WSC) in Ernstbrunn, notably Friederike Range and Zsófia Virányi. Our work there is made possible by the local land owner, Fürst Heinrich XVI Reuss, by the Veterinary University Vienna, by the University of Vienna and by the Land Niederösterreich.



How Wolves Turned into Dogs and How Dogs Are Valuable in Meeting Human Social Needs

Kurt Kotrschal¹

Keywords: human-animal bond, canines, domestication, hunter-gatherers, wolves, dogs

Abstract A wealth of recent behavioral, neurobiological, and genetic results allows us to draw a new, comprehensive picture of the human-wolf-dog relationship. Dogs originated from wolves 35,000 years ago, mainly via selection for tameness. Wolves were probably spiritual partners and hunting buddies of Paleolithic hunter-gatherers over wide areas of Eurasia. Coming together and staying together was probably facilitated by the close ecological and social match between wolves and humans. Both are cursorial hunters and scavengers living in cooperative but relatively closed family groups, which selected for very similar mentalities.

Parallel selection for tameness (i.e., being “nice”) in dogs and humans quickly and in a diverse way changed behavioral and anatomical phenotypes from wolf to dog, and social orientation from Stone Age to modern humans. Actually, dogs were the most important human companions in conquering the world. By adapting to the needs of diverse human societies and civilizations, a wide variety of dogs developed. Over long periods of history dogs were meant to be benign with their own humans, but not with strangers. Hence human ingroup-outgroup distinctions may explain why considerable aggressiveness may still be found in dogs and humans, although incompatible today with a globalized world and universal ethics. In dogs this can be easily controlled by selective breeding and in humans, less easily, by cognition. Actually, sledge dogs and modern hunting breeds were selected for tolerance in the past.

Most recent scientific results not only underline how closely dogs match human operational and social needs, but also find that most of the dog’s social behavior, cognition, and cooperativeness is direct wolf heritage and did not emerge in domestication, as previously thought. Dogs have adjusted to human needs in many subtle ways in the course of domestication. This makes dogs much better companions than tame wolves. Dogs are more easily socialized; they are strongly tuned toward people, respect human leadership, and are superior receivers and

(1) University of Vienna Department of Behavioural Biology, Wolf Science Center, and University of Veterinary Medicine Vienna

donors of emotional social support. Dogs actually became more obedient and respectful of social hierarchies than wolves, more dependent on human support, and better at inhibiting their impulses. Dogs diversified their barking for communicating with humans. They can read our emotions and adjust to them in an empathic way. Dogs are capable of human-like thinking, of taking a human perspective, and even of tricking us. Not least, they share a sense of fairness with wolves and humans.

Hence, dogs can be particularly valuable partners in meeting universal human social needs. Human-dog relationships are “essentialized,” lacking the cultural and symbolic complexities of relationships between humans. But the devotion of dogs is not unconditional; they do judge our moods and social conduct and make their choices accordingly. Dogs can boost the self-esteem and agency of their human partners and are excellent “social lubricants,” thereby connecting people. Actually, in their flexibility, social devotion, adaptiveness, and responsiveness, dogs are the stars among all animal companions. No wonder, as the human-dog relationship started in the early Paleolithic, tens of thousands of years before the domestication of other animals. Dog companionship seems increasingly important in a globalized and digitalized world. An ever accelerating pace of life may not always provide the conditions needed to keep people physically and mentally healthy. Living in good relationships with dogs can keep people connected with their social essentials.

Therefore, dogs are prime animal assistants in a wide range of activities, pedagogy, and therapy. Supported by human biophilia, the presence of a friendly dog may have strong calming and socializing effects on humans and may support communication and sociopositive behavior. Dogs are probably the most socially responsive of all companion animals, privately and in professional settings. In all such activities (for definitions please see the White Paper of the International Association of Human-Animal Interaction Organizations [IAHAIO], Jegatheesan et al., 2014), well-socialized and friendly dogs respond well to temporary and positive challenges, but must never be overburdened. It requires a suitable dog in a secure relationship with a sensitive and knowledgeable human partner. Furthermore, it has to be kept in mind that dog partners need regular veterinarian checks in the interest of the animals’ health and welfare and to minimize health risks (e.g., zoonoses) for the human partners. All activities and work need to conform to the IAHAIO Guidelines for Animal-Assisted Activities and Animal-Assisted Therapy (Prague, 1998) and with the IAHAIO White Paper (Jegatheesan et al., 2014).

Why Is Human-Wolf-Dog Important?

Dog keeping tends to be considered a private pastime. Correct, but this misses the point. Today it is known that the association between wolves (*Canis lupus*) and modern humans (*Homo sapiens sapiens*) started some 40,000 years ago in several areas of Eurasia (Frantz et al., 2016). Ever since, virtually all human societies have lived in some kind of partnership with dogs. A diverse range of cultures developed, and the world became a gigantic niche construction experiment (Wilson, 2012). Hence, to understand ourselves, that

is, the *conditio humana*, in a broad biological, psychological, anthropological, or philosophical sense, three related facts need to be considered: the evolutionary origin of humans from other animals, the peculiar affinity of humans to nature and other animals (biophilia in the sense of Wilson, 1984), and in particular, the enormously variable relationships with dogs. Humans and dogs are radically social. Individuals therefore need to be explained as nodes in complex and highly cooperative social networks. In all human societies, other animals are integrative parts of these networks (Serpell, 1990).

Wolves are the ancestors of all domestic dogs. Still, the two have never become discrete entities. From the very beginning of “dogification,” wolf genes continued to flow into dog genomes, for example, in the case of the dogs of the Great Plains Indians (Ulmer, 2010), or massively today, as it has become fashionable to breed and keep wolf-dog hybrids. But dog genes also trickle back into wolves (Anderson et al., 2009), particularly during wolf population bottlenecks (Randi et al., 2014) and under human influence (Newsome et al., 2017).

While wolves in the wild rely on cooperation-based survival (Range & Virányi, 2015), dogs are adapted to live and thrive in a human environment (Kotrschal, 2016a; Marshall-Pescini, Cafazzo, Virányi, & Range, 2017). Hence, dogs are not at all the “degenerate” descendants of the noble and perfectly adapted wolves, as some held till the middle of the 20th century (Lorenz, 1954). To the contrary, dogs have become immensely successful via the human vector: while roughly 200,000 wild wolves still roam the Northern Hemisphere, an estimated 1 billion dogs are spread over all continents, except for Antarctica, not least because dogs are extremely adaptable. Hence, in most societies since prehistory dogs rapidly developed according to specific human needs, which is reflected in dog genetics (Parker et al., 2004; Parker, Shearin, & Ostrander, 2010).

Desired traits in dogs have been emphasized by selective breeding (e.g., Coppinger & Feinstein, 2015; Coppinger & Schneider, 1995; Xenophon, 400 BCE). Even within societies, partnership diversifies into mutually nonexclusive working skills (hunting, guarding, rescue, etc.), always also featuring a measure of social companionship. Human-dog companionship itself can be diverse. For many, their dogs are valuable social partners, supporting self-esteem and social connectedness to other people; for others, dogs are buddies in sports or hunting; for still others, dogs may be mainly the visible representation of a marital phenotype. Nearly independent of breed, dogs remain amazingly adaptable to the personalities, interaction styles, and needs of their human partners, which they tend to reflect in their behavior toward the outside (Cimarelli, Turcsán, Bánlaki, Range,

& Virányi, 2016; Kotrschal, Schöberl, Bauer, Thi-beaut, & Wedl, 2009; Schöberl, Wedl, Beetz, & Kotrschal, 2017). Counterintuitively perhaps, dog keeping does not decrease in modern urbanized societies worldwide, but to the contrary, the importance of dogs as social partners seems to increase steadily (Serpell, 2016).

These few spotlights should suffice to clarify that in many ways, dogs are much more important for humans, as most people would still believe. This statement does not just reflect the author’s fondness for dogs; it is supported by recent scientific results in genetics and archaeology, behavioral biology, psychology, and comparative cognition (Kotrschal, 2016a). On the downside, dogs can of course do harm and trigger conflicts, and human-dog relationships may fail. In fact, to be mutually beneficial, that is, to promote an increase in well-being for both parties, the human-dog relationship should be reciprocal and persistent (Fine 2015; Russow, 2002).

Overwhelmingly, people living with dogs have better physical and mental health than comparable people without dogs (Headey, 1999; Headey & Grabka, 2007; Headey, Na, & Zheng, 2008). Dogs keep their human partners active and socially embedded and provide substantial emotional support (Beetz, Julius, Turner, & Kotrschal, 2012a; Julius, Beetz, Kotrschal, Turner, & Uvnäs-Moberg, 2012). Therefore, dogs can substantially assist humans in living a “good life” in the sense of Coan (2011), who found that the core factor for a long and healthy life is a balanced emotionality.

Aims of This Review

In the following, I will present evidence in support of this daring and potentially provocative statement. I will first summarize what dogs can do for us with regard to social connectedness, emotions, and health, and then I will try to answer the question of exactly why dogs developed into such a prominent role as companion animals. A first step will be a glance into prehistory, discussing the most likely scenarios of how wolves and people got together. This merges into a summary of the core facts of

wolf domestication to dog and to discussing whether wolves just changed into dogs, or whether humans experienced a parallel shift from the early Stone Age to today via a kind of “self-domestication” by selection for tameness (Belyaev, 1972; Hare, Wobber, & Wrangham, 2012). Did the dogs have a role in this “domestication” of the Paleolithic hunter-gatherers into modern humans? Discussing the mechanisms of domestication will shed light on the consequences it had for dog genetics and why selection for tameness and the occurrence of aggressive behavior in dogs are no contradiction. Recent results in alignment with Paleolithic prehistory show that wolves can be social and cooperative with humans. But I will discuss the idea that cooperative orientation, that is, the checks and balances of living with humans, changed during dogification.

What Dogs Can Do for Us

Living in a positive relationship with one or more dogs can, indeed, have astonishingly positive effects on well-being and health, which more than counterbalance the investment in time and money. In the following discussion the many potentially positive effects of dogs on their human companions are summarized, supporting the idea that dogs are superbly adapted to human social needs (Kotrschal, 2016a; Miklósi, 2015; Miklósi & Topál, 2013).

For roughly 35,000 years (Frantz et al., 2016; Guo-Dong Yang et al., 2016; Thalmann et al., 2013), dogs have been cooperation partners in a number of areas, for example, in hunting, warfare, and guarding (Serpell, 1990, 2016). Aside from these classical domains, dogs nowadays assist the police and the military; engage in all kinds of rescue operations; sniff out all kinds of substances, including insect pests or urinary bladder cancer; provide assistance for disabled persons or in various kinds of pedagogic and therapeutic settings; warn of epileptic seizures, and so on. Teaming up with dogs enhances human potential in a unique way. Humans contribute their conceptual mind, the dogs their detail-mindedness, their keen senses, and their urge to cooperate (Grandin & Johnson, 2005).

But at least as important seem the social effects of dogs (Kotrschal, 2014). As associates of children and adults, dogs may contribute to an atmosphere of pleasure and reduce anxiety. Thereby, dogs facilitate positive interactions and communication with pedagogues or therapists (Julius et al., 2012; Levinson & Mallone, 1997) and support prosocial behavior training. Effects are the more pronounced the younger the children (DeLoache, Pickard, & LoBue, 2011; Wedl & Kotrschal, 2009). Also, dogs motivate children to engage in physical activity, which is crucial for developing their “executive functions,” key for success at school and in society (Diamond & Lee, 2011). The mere presence of a dog can favorably influence the social and communicative atmosphere in groups of children and significantly increase school attendance (Kotrschal & Ortbauer, 2003), and may even improve learning success (Beetz, 2015; Gee, Gould, Swanson, & Wagner, 2012). Dogs can also be vital partners for the elderly (Fine, 2015), keeping them independent and socially connected, thereby counteracting old age depression by satisfying people’s basic social need of providing care and, in turn, receiving unconditional devotion.

Reviews of the scientific literature (Beetz, Uvnäs-Moberg, Julius, & Kotrschal, 2012b; Julius et al., 2012) draw an even wider picture of the positive social effects of living with dogs on social connectedness, emotions, and ultimately on salutogenesis (staying healthy). The support of good mood by dogs is not to be underestimated (Coan, 2011). Such mental effects come with decreased cortisol levels, blood pressure, and heart rate, which is potentially mediated by oxytocin (Julius et al., 2012). Emotional support from dogs improves immune functions, decreases susceptibility to illness (Beetz et al., 2012b), and has positive effects on owners’ physical activity, on the entrainment of health-supporting habits and routines, and on improved abilities to cope with pain and to trustfully relate to other people. If suffering from a heart attack, dog owners still survive for longer than non-dog owners. Most of these studies show significant effects, but at moderate effect sizes; still, the social company of a dog, in all its dimensions, seems to shift stress coping toward calming and to potentially help

in remaining mentally balanced. The combination of minor positive mental and physiological effects of dog companionship seems to positively affect the labile balance between health and illness.

Such a sweeping synthesis is not just positive inference from a meager database. The epidemiological studies of the Australian health economist Bruce Headey in Australia, China, and Germany (Headey, 1999; Headey & Grabka, 2007; Headey & Zheng, 2008) revealed that dog keepers in all these countries felt better, were objectively healthier, and made up to 18% fewer doctor visits than well-matched non-dog owners. Also, as shown particularly by the study on Beijing dog keepers (Headey & Zheng, 2008), this effect is not due to people adopting a dog already being healthier than those who do not.

The “special” nature of human-dog relationships evidently resembles parent-offspring relationships (Archer, 1997), even including dyadic attachment (Solomon, Beetz, Schöberl, Gee, & Kotrschal, 2018; Topál, Miklósi, Csányi, & Dóka, 1998). Dogs support their people’s self-confidence and efficacy. Dogs, even more than children, seem to function as the “extended phenotype” and “externalized ego” of their masters. In the company of friendly dogs, people are generally judged more positively by others and receive more trust (summarized in Kotrschal, 2016a). The potential of dogs acting as “ice breakers” and “social lubricants” is well known (Wells, 2004), catalyzing openness for communication and contact between people. Dogs show nearly unconditional affection and devotion, no matter whether their human companion is rich or poor, young or old, or shabbily dressed; this “Cinderella effect” is independent of race, gender, disability, religion, or political beliefs. But dogs judge the pleasantness and trustworthiness of their human companions and make their choices accordingly (Anderson et al., 2017; Catala, Mang, Wallis, & Huber, 2017); hence, their devotion is not really fully unconditional. In reverse, humans seem to interact in a more authentic way with dogs than with other people, which is indeed read by human bystanders. Sensitively interacting with a dog also creates trust in people (see Kotrschal, 2016a), and the “antisocial” behavior of dogs reliably indicates

the antisocial attitudes of their keepers (Ragatz, Fremouw, Thomas, & McCoy, 2009).

Living with dogs not only has social benefits and related physiological effects, but also seems to support the development and maintenance of a diverse and resilient microbiome (Se Jin Song et al., 2013). The microbiome consists of all the microbes inhabiting the gut, skin, and all mucosal surfaces. It is a first line of defense against infections and is, in a variety of ways, essential for survival, even affecting physical and mental health. Early contact with dogs and other animals may decrease the susceptibility to allergies later in life.

Humans are “biophilic,” which includes the urge to relate to and live with other animals (Julius et al., 2012; Kotrschal, 2014; Wilson, 1984). Hence, it remains an open question to what degree the positive effects described above are dog-specific, or whether they would also be produced by relating to other companion animals. Because the major mechanism of all domestications is selection for tameness (Belyaev, 1972; Wilkins, Wrangham, & Fitch, 2014), domesticated animals are generally much more suitable companions than most tame wildlife. Of all domesticated animals, dogs are with humans for the longest period of time. No wonder that they seem our closest social match of all companion animals (see below). But due to a wealth of social mechanisms shared between humans and other animals (Julius et al., 2012; Kotrschal, 2014), the differences in the positive effects when living with dogs as compared to other companion animals may be of degree rather than kind. However, this remains speculation, as comparative data are lacking.

In conclusion, people may benefit substantially from living with a dog with respect to quality of life, well-being, and health. In this respect dog keepers may also be regarded as role models for a live-in alignment with the universal human needs of connectedness and living in contact with nature and animals. Living with dogs has the potential of increasing people’s resilience in an environment characterized by a steady acceleration, by globalization, and by the digitalization of even our social lives (Kotrschal, 2016a, 2016b).

A Perfect Match? Why and How Wolves and Humans May Have Met

Human “biophilia” (Wilson, 1984), that is, an “instinctive” interest in nature and in other animals, is a human universal that is particularly evident in children (DeLoache et al., 2011). They appropriate the relevant items of their world by anthropomorphizing (Urquiza Haas & Kotrschal, 2015), particularly by employing their social-bio-psychological mechanisms. Also, humans can engage in social relations with other animals because of mechanisms that are widely shared among the vertebrates, notably mammals and birds (Julius et al., 2012).

Still, it remains a miracle of human biocultural evolution that early Paleolithic hunter-gatherer *Homo sapiens* engaged in a partnership with wolves (*Canis lupus*) some 35,000 years ago (Frantz et al., 2016), but not in such a close way with other animals, and that this quickly merged into the human universal of a durable companionship with dogs. Evidently, the main reason for this is that there is a closer ecological and social fit of humans with wolves than with any other animal species. Both humans and wolves are large-brained, ecologically broadly adaptable, hypercursorial hunter-scavengers/gatherers, organized in cooperative family clans, engaging in complex within- and between-clan relationships.

Within these groups of humans and wolves, relatively flat dominance hierarchies are characterized by mutual tolerance and respect for the clan elders, based on their competence (Barnard, 1998; Fogg, Howe, & Pierotti, 2015; Mech, 2012). Individuals engage in elaborate cooperation over hunting, raising offspring, and territorial defense (Kotrschal 2014, 2016a). In wolves, the offspring of the previous year generally help to raise younger offspring. Only the parental pair reproduces, but there are exceptions to this (see below). Occasionally, adult offspring disperse from these groups in search of partners to establish a new group, or to integrate into another group, which is comparatively more common and easy in human groups than in wolves. Human clans and wolf packs are relatively “closed” groups defending their resources and territories against neighboring groups,

which includes both skirmishes and killing “the others” as well as forming between-group alliances. Actually, a majority of wolves in the high-density Yellowstone area are killed by their neighbors (Casidy, Mech, MacNulty, Stahler, & Smith, 2017); in our Stone Age ancestors an estimated 30% of people died from the same cause (Schneider, 2014). Such pressure by conspecifics increases group cohesion. In Yellowstone, for example, high prey and pack densities produce packs of occasionally more than 40 members, with more than one female reproducing (Urbigit, 2008). Still, humans and wolves are not doomed to be killed; neighboring groups occasionally meet and spend time with one another in the case of wolves (Peterson, 1995), and they may form alliances, for example, by intergroup marriage in the case of humans. This match in the basic human lifestyle is greater with wolves than with any of the great apes or any other animal.

The main reason for this seems to be convergent evolution based on ecological similarity. Both species are adaptable generalists, coping with a range of habitats from sub-Saharan deserts to the Arctic, based on their cognitive abilities, social organization, and cultural versatility, which to some degree even applies to wolves (Musiani et al., 2007). Only the tropical rain forests with their low prey densities remained devoid of wolves and could only be permanently inhabited by specially adapted humans. This kind of social lifestyle may have exposed both species to the kind of “selection for tameness” that may account for the differences between chimpanzees and bonobos (Hare et al., 2012), or between early Stone Age and modern humans (see below).

However, this close match does not answer the question of how wolves and dogs actually diverged some 35,000 years ago. In a number of such events, virtually from Western Europe to Southeast Asia, people stayed together with wolves for a sufficient period of time to allow genomic changes toward dogs, with only a few of these lineages being the base for our modern dogs (Frantz et al., 2016; Guo-Dong Wang et al., 2016). From the human point of view, this attraction was “magical” (Kotrschal, 2016a; Shipman, 2015). Early Paleolithic *Homo sapiens*

practiced animistic spirituality, believing in a spirited nature and in a dualistic world: the one that is experienced and the domain of spirits (Barnard, 1998). Shamans mediated between the two; offenses against taboos and disrespect of spirits would have had dire consequences, such as injury, sickness, or death. These people connected with the game they hunted in a spiritual way, but also with animals they rarely hunted, such as wolves, which seemed to be important totems and connectors to the domain of spirits.

A model system in support of this view is found in the Great Plains indigenous people of North America, who did not hunt the wolves but considered them their brothers and teachers, symbols of wisdom and of a caring and defensive family life (Fogg et al., 2015; Ulmer, 2010). Even today animistic Mongolians engage in wolf cults and practice “sky burials” in which wolves are believed to transport the souls of the dead to the domain of spirits. The obvious close resemblance of wolves’ lifestyle and social organization with that of their human observers, as well as wolves’ curiosity and elaborate hunting and warfare tactics (Jiang Rong, 2008), may have been the background for the exceptional spiritual meaning wolves tended to have for early hunter-gatherers, and still have for some seminomadic pastoralists. Within a few thousand years, people repeatedly engaged in alliances with wolves a number of times, from Western Europe into Southeast Asia (Frantz et al., 2016; Guo-Dong Wang et al., 2016). Hence, a common spiritual culture of these Eurasian hunter-gatherers may have facilitated their teaming up with wolves.

This is also supported by mythology. A universal element in human spirituality is transformation/metamorphosis, also into animals (“therianthropy”; Hamel, 1969) or other mental and physical states. “Lycanthropy,” the werewolf mythos, is common to all Indo-Germanic ethnicities: it probably emerged with the wolf-human relationship in Eurasia (Kotrschal, 2012, 2016a). The shamans may have pioneered living with socialized wolves, thereby increasing their social prestige; alternatively, relating to wolves may have started as a kind of “pet keeping,” a human universal, also practiced by hunter-gatherers (Serpell, 1990).

Social prestige and spirituality alone are probably insufficient to explain the sustained teaming between wolves/dogs and humans. Very likely, ecological benefits for both partners were involved, potentially over hunting. Is it a coincidence that mammoth hunting started in parallel with the first changes from wolf to dog genomes some 35,000 years ago? Was this kind of hunting dangerous big game facilitated by the assistance of wolves? Such a partnership may have been one of the early key innovations that gave *Homo sapiens* a competitive edge over the sympatric Neanderthals (Shipman, 2015). In fact, isotope analysis of collagen from 30,000-year-old mammalian bones from the Predmosti site (Czech Republic) showed that *Homo sapiens* and wolves from this site ate mainly mammoth, the dogs mainly reindeer and horse (Bocherens et al., 2014). Whatever these results may mean, they indicate some close and complex association between humans, wolves, and dogs, potentially similar to that of the North American Great Plains people (Fogg et al., 2015; Kotrschal, 2016a; Ulmer, 2010).

But how did wolves and humans really come in contact? Did the wolves approach humans, as proposed by Coppinger and Feinstein (2015)? Possibly, as wolves are curious and people produce remains that are interesting food for wolves, such as remains of prey or feces; also, 35,000 years ago wolves may have been less shy of people than today. But this may not have been the only way into partnership. In fact, only hand raising of wolves from early pup age on results in trustful and cooperative companions (Frank & Frank, 1982; Klinghammer & Goodman, 1986; author’s experience). In the Paleolithic, this could only have been done by co-nursing wolf pups with human babies; in a way it is still practiced in parts of Africa and New Guinea with dog pups, piglets, and other animals (Serpell, 1990; Zimen, 1980, 1988). All our knowledge and experience indicates that a coordinated hunt would only be possible with socialized wolves. In fact, one of the reasons why it is easier to cooperate with dogs than with wolves is that dogs are more easily socialized with humans than wolves are (Scott & Fuller, 1965; Zimen, 1988), and dogs are less selective in their cooperative orientation toward

individuals they were socialized with during their upbringing (Kotrschal, 2016a).

Why did the human-wolf partnership not start in Africa? Actually, the so-called “Egyptian jackal,” distributed from east to west across north-central Africa, turned out to be the African gray wolf (Gaubert et al., 2012; Viranta, Atickem, Werdelin, & Stenseth, 2017). However, this wolf hardly lives in packs and may not have had the relevant mental disposition for associating with humans, and it may not have been sufficiently charismatic to people. Alternatively, it may have immigrated to Africa after *Homo sapiens* had emigrated some 60,000 years ago (Viranta et al., 2017). In Eurasia, humans met wolves with a social organization that closely matched their own. Also, the pack-living Eurasian wolves are top predators, hence their charismatic appeal to sympatric early humans.

How did Stone Age people deal with “their” wolves? It is unlikely that it was straight human domination and wolf subordination. First of all, early Paleolithic humans had no metal chains or wire mesh, and therefore could not force wolves into staying. Second, in contrast to dogs, wolves respond to punishment and forceful domination with immediate resistance (Klinghammer & Goodman, 1986). Cooperating with wolves in a complex way is only possible without force, punishment, or outright domination, which would cause fear and resistance. This would be particularly counterproductive when testing for cognition and cooperation (Kotrschal, 2012, 2016a), and because dominated wolves tend to revolt, this would create a safety problem. Actually, inappropriate handling resulted in the killing of a hand raiser by her wolves in Sweden’s Kolmarden Zoo in 2012. The zoo and its director were sentenced in 2016, basically because dominating wolves was considered by the court to be an unprofessional mistake in handling captive wolves. At the Wolf Science Center (WSC; Austria) wolf handling is based on positive reinforcement training (PRT), positive social relationships, and human leadership.

Hunter-gatherers lived in relatively “egalitarian” societies (Barnard, 1998). Similar to wolf packs, these humans were organized in kinship clans characterized by relatively respectful and intense within-group

communication (Barnard, 1998; Fogg et al., 2015; Serpell, 1990), as can be inferred from the mental characteristics of modern people (Stoeckel, Palley, Gollub, Niemi, & Evins, 2014). Animistic spirituality supports showing respect to most animals, including those that are hunted; wolves were probably not hunted (Fogg et al., 2015). Hence, the sociocultural practice of most Paleolithic societies was probably relatively adequate in dealing with wolves as a relatively independent and level ally.

Mechanisms of Domestication: Dogs Are Domesticated Wolves—Are Modern Humans Domesticated Stone Age People?

Dogs are “domesticated” wolves. This means that they are genetically changed, as compared to their wolf ancestors (Axelson et al., 2013; Parker et al., 2004; Parker et al., 2010). Two major groups of genes were particularly affected by mutations from wolf to dog, those involved in brain formation and in digestion. This makes dog brains different from wolf brains; and like humans after becoming sedentary, dogs improved in digesting starch and other components, which sedentary humans secondarily included in their diets. Also, dogs, like most domesticated animals, show the general “domestication syndrome” (Darwin, 1868; Herre & Röhrs, 2013), such as changed fur color, short snouts, small teeth, floppy ears, a relatively small forebrain, “tameness,” and so on. How can this happen?

Dimitri Belyaev (1972) selected silver foxes for tameness. After a few generations, these foxes were highly sociable with people and showed the Darwinian domestication syndrome. Hence, the main mechanism behind the immense morphological variability seen in domestic dogs was selection for tameness. It seems that this leads to mild neural crest stem cell deficits during embryonic development (Wilkins et al., 2014). Most of the modified traits in the domestication syndrome, both morphological and physiological, can be explained as direct or indirect consequences of this modification.

Intriguingly, selection for tameness may not only have turned wolves into dogs, but also early Paleolithic

hunter-gatherers into modern humans. In parallel to the “self-domestication hypothesis” explaining why chimpanzees and the very closely related bonobos are socially so different (Hare et al., 2012), it is reasonable to assume that some kind of “self-domestication” by selection for “being nice”/social competence also occurred in humans since the early Stone Age. Social organization became increasingly more complex, and social competence and excellent “executive functions” (i.e., the social cognition syndrome featuring the quality of inhibition/impulse control, episodic memory, strategic thinking, and the ability to flexibly adapt one’s behavior to context; Miyake, Friedman, Emerson, Witzki, & Howerter, 2000) are important preconditions for complex cooperation, particularly across kinship clans. Some authors even suggest that living with dogs had a role in the evolution of human cognition and language (Harari, 2014).

Alternatively, it has been assumed that humans have profited in developing their social skills by living with dogs (Schleidt & Shalter, 2003), in a kind of “co-evolution.” This, however, remains untestable, because there have been no ethnicities for 35,000 years without dogs; hence, there is no appropriate human control group. Moreover, major changes from wolf to dog include a greater readiness to accept domination and submit to human will in the latter (see above), supporting the view of an asymmetric adaptation process: dogs’ reproductive success depends on their match with human needs much more than the other way around. More likely, dogs and humans evolved in parallel, basically due to parallel selection for tameness.

But if modern dogs and people underwent a strong selection for tameness/being nice, why do we see so much aggressiveness in both species? In this respect it is useful to remember the clan organization of both wolves and Stone Age people. Associated dispositions are still to be found in modern humans and dogs (Stoeckel et al., 2014). Selection for tameness/being nice was mainly related to within-group cooperation, whereas for humans and even more for dogs, defense against strangers is still an important feature today. Humans are still engaged in warfare

and between-group aggression; and many breeding lines of dogs are still selected for guarding and defense against alien people and/or animals. This distinction between ingroup friendliness and outgroup aggression was made by Xenophon, an ancient Greek commander and philosopher, in his *Kynegiton* (400 BCE), where this sentence can be found: “A dog must be sweet and attached to his own people, but rejecting and cruel against strangers.”

There is an evident challenging mismatch of such behavioral dispositions with the demands of living in a globalized world under a global ethic, manifest, for example, in the UN’s Universal Declaration of Human Rights (1948). In dogs as well as in humans, the ingroup-outgroup mental reflexes need to be inhibited. At least in dogs this seems easily possible by selective breeding, which already has produced sledge dogs or modern hunting breeds, such as the golden retriever, that are reliably friendly with people and dogs in general, well beyond the groups they are socialized with. In humans, the prefrontal cortex is able to inhibit instinctive impulses, provided that it is empowered by proper early upbringing for exerting proper control over individual conduct (Diamond & Lee, 2011; Miyake et al., 2000).

The Kinds of Dogs Today

Today, dogs differ sufficiently from wolves (Miklósi, 2015; Serpell, 2016) to be assigned species status by some scientists (*Canis familiaris* instead of *Canis lupus familiaris*). Yet wolves and dogs still readily hybridize. In fact, wolf-dog always formed a genetically dynamic system. For example, black coat color in wolves and dogs is due to a mutation that happened an estimated 37,000 years ago in dogs (Anderson et al., 2009).

The domains of cooperation between humans and dogs and cultural backgrounds shaped dogs and left distinct genetic traces (Parker et al., 2004; Parker et al., 2010). In essence, every culture and society has dogs that fit their demands. Genetically, the four major groups of dogs are “wolf-like,” “herding dogs,” “Mollosser,” and the “big rest” of highly domesticated dogs, reflecting two basic domains

of human-dog cooperation, herding and warfare. Among the wolf-like dogs the radiation in “professions” parallels the highly domesticated dogs, including ancient hunting dogs such as the Afghan, sledge dogs such as the husky, and all kinds of Eurasian spitz-like dogs for hunting and guarding, with a particularly rich radiation in Japan.

A recent hype is the keeping of wolf-dog hybrids, reflecting the romantic desire of people to live with wolves. The rationale for this remains doubtful. It took dogs more than 30,000 years to adapt well to human needs. Hybridizing modern dogs with wolves means pushing the reset button and causes problems in keeping them and also welfare problems, because these animals are ill-suited to life in modern human environments. Hybrid lines acknowledged by the Fédération Cynologique Internationale (FCI) are the “Czechoslovakian wolf dog” and the Saarloos. They tend to be sensitive and often shy “dogs” and need experienced keepers. The new trend of keeping “high-end hybrids,” that is, timber wolves with some dog in them, has spilled over to Europe from North America, where seemingly hundreds of thousands of these hybrids are kept (Herzog, 2010). This often creates problems and risks due to unsuitable keeping and not least a considerable animal welfare problem, as many of these hybrids are destroyed at a young age. To satisfy the understandable desire of living with a tame wolf, I recommend picking a dog from the “wolf-like” group (Frantz et al., 2016; Parker et al., 2004), for example, a malamute, a spitz-like breed, or an Eurasier (www.eurasier-club-austria.at). These dogs still contain lots of wolf, but they are sufficiently domesticated to be easily kept.

How Dogs Adapted to Live with Humans

Dogs developed into our closest animal companions, matching human social behaviors and mentalities in an astounding way (e.g., Miklósi, 2015; Miklósi & Topál, 2013). Humans tend to be similarly caring toward their dogs as to their own children (Stoeckel et al., 2014) and also use baby talk to dogs (Lesch, 2016; Mitchell, 2001). Dogs usually respond with devotion and a great readiness to bond. In fact, a short contact

with shelter dogs sufficed to initiate bonding (Gácsi, Topál, Miklósi, Dóka, & Csányi, 2001). The basic neurohormonal mechanisms of bonding in dogs involve oxytocin in a way that is virtually identical to the way it works in humans and other mammals (Handlin et al., 2011; Julius et al., 2012; Kotrschal, 2014; Nagasawa et al., 2015).

Much insight into the human-dog relationship has come from recent work with pet dogs by groups at the Budapest Eötvös University, the “Clever Dog Lab” of the Vienna Veterinary University, groups in the United States, and at the Wolf Science Center in Austria, where equally raised and kept dogs were compared (reviewed in Kotrschal, 2016a). Results were particularly surprising in two respects: first, in revealing the close match between the social needs and skills of humans and dogs, and second, in deconstructing some scientific myths about how dogs would have changed as compared to their wolf ancestors. For example, it was suggested that dogs would be a “nicer,” that is, less aggressive and more cooperative, version of wolves within their kind and with humans (Hare & Tomasello, 2005; Hare et al., 2012). Today, it appears that the cooperative dispositions of dogs are directly inherited from the wolf (the “canine cooperation hypothesis”; Range & Virányi, 2015). However, cooperation has qualitatively changed from wolf-wolf and wolf-human to dog-dog and dog-human.

Dogs are “clever” in many ways, but they may be astonishingly “simple” in other respects. For example, dogs are capable of inferential reasoning (Erdohegyi, Topál, Virányi, & Miklósi, 2007), but they are less numerically competent than wolves (Range, Jenikejew, Schröder, & Virányi, 2014). Also, dogs are less tolerant and more aggressive among themselves (Range, Ritter, & Virányi, 2015) and respect dominance hierarchies more readily than wolves. Dogs “negotiate” and communicate less over access to resources than wolves. They rely more on hierarchy and tend to escalate aggressive interactions more rapidly than wolves. On the other hand, with their ability to express mood and context by barking, dogs have developed a differentiated means of communicating with humans and among themselves (Molnar, Pongracz, Farago, Doka, & Miklósi, 2009;

Pongrácz, Molnár, Dóka, & Miklósi, 2011; Pongrácz, Molnár, & Miklósi, 2010). Wolves do bark, but only in an aggressive context. Also, dogs may be better than wolves at inhibiting their impulses, allowing them to better concentrate on human-given tasks (Marshall-Pescini, Virányi, & Range, 2015; Müller, Riemer, Virányi, Huber, & Range, 2016). Although wolves were much better than dogs in learning a complex task by observing a conspecific (Range & Virányi, 2014), dogs excel in learning from their people (Kubinyi, Topál, Miklósi, & Csanyi, 2003), which seems to be facilitated by dog pups making gaze contact with people earlier and more readily than wolf pups (Range & Virányi, 2011). Wolves are generally more neophobic than dogs, but at the same time, more explorative (Moretti, Hentrup, Kotrschal, & Range, 2015) and more persistent in pursuing their goals (Marshall-Pescini, Rao, Virányi, & Range, 2017).

Although wolves were shown to be as attentive to relevant people as dogs (Range & Virányi, 2013), dogs are still more “tuned” to people and seem more dependent on human emotional social support and ostensive cueing (Topál, Miklósi, & Csanyi, 1997) than wolves. Still, relationship quality hardly affects dogs’ working performance (Naderi, Miklósi, Doka, & Csanyi, 2002). It seemed that dogs, sooner than wolves, would ask humans for help with unsolvable tasks (Miklósi et al., 2003; Virányi et al., 2008). However, when corrected for persistence, this difference vanished (Marshall-Pescini et al., 2017).

Actually, wolves are as easily obedience-trained via positive reinforcement training as dogs (Da Silva Vasconcellos et al., 2016). However, in the more complex task of trotting freely on a treadmill, wolves were even more easily trained than dogs (Kortekaas & Kotrschal, 2017), which may be related to the greater explorative motivation and persistence of wolves. Contrary to previous results, adult wolves are nearly as good as dogs in using human pointing cues (Udell, Dorey, & Wynn, 2008) and are even better than dogs in following human gaze (Range & Virányi, 2011). In the complex cooperative task of leash walking, wolves are nearly as synchronized and cooperative as equally raised and kept dogs (Kotrschal et al., 2014).

Many of the following, often astounding, social features and skills of dogs with people may also be found in adequately socialized wolves, but most of the relevant tests have not been done yet. Dogs often match their owners’ personalities and interaction styles, and in owner-dog dyads, partners mutually affect each other’s stress coping (Kis, Turcsán, Miklósi, & Gácsi, 2012; Konok et al., 2015; Kotrschal, 2016a; Schöberl et al., 2017). In general, dog personalities vary along a continuum between bold and shy (Svarterberg & Forkman, 2002; Svartberg, Tapper, Temrin, Radesaeter, & Thorman, 2005).

In many respects dogs think in a way similar to that of humans, based on similar mental representations. This, for example, has been shown in “Do as I Do” experiments (Topál, Byrne, Miklósi, & Csanyi, 2006), where dogs do not just reflexively imitate people, but do so in a meaningful way, and even after delaying their action. fMRI studies show responses of the human or dog caudate nucleus to the same pleasant stimuli (Berns, Brooks, & Spivak, 2013). Also, dogs do not just respond to the tone of our voice, but actually process words in a way similar to that of humans (Andics, Gácsi, Faragó, Kis, & Miklósi, 2014). Hence, they can be trained to know the meaning of hundreds of words, and they seem to employ the same learning mechanism as children (Kaminski, Call, & Fischer, 2004).

Dogs not only organize their social behavior via identical neurohumoral mechanisms (Kotrschal, 2014), but they also can, indeed, read people’s emotions, respond appropriately (Müller, Schmitt, Barber, & Huber, 2015), and may show emotional contagion with humans (Huber, Barber, Farago, Müller, & Huber, 2017; Min Hooi Yong & Ruffman, 2014), which is a major component of empathy. It has been shown that dogs can even extract information about the trustworthiness of people by watching them interact (Chijiwa, Kuroshima, Hori, Anderson, & Fujita, 2015). Dogs can take human perspectives (Catala et al., 2017) and can even trick people (Heberlein, Manser, & Turner, 2017). Hence, dogs are capable of complex social cognition, including inequity avoidance (Range, Horn, Virányi, & Huber, 2008), that is, responding similarly to humans to being treated unfairly. It has

been recently shown that wolves are inequity averse too (Essler, Marshall-Pescini, & Range, 2017); hence, the inequity aversion of dogs did not emerge during domestication. Dogs are capable of understanding the actions of human cooperators (Naderi, Miklósi, Dóka, & Csányi, 2001). This is not so surprising, as a sense of fairness is an important component of complex cooperation. In wolves, cooperation is tuned toward conspecifics, with an open door for human partners, whereas in dogs, this cooperation is qualitatively tuned toward humans (Miklósi & Topál, 2013).

Dogs in the Modern World

Their human-like social emotionality and cognition makes dogs valuable social/emotional supporters for modern people in urban environments, with lifestyles characterized by globalization, digitalization, and acceleration. Increasingly, this may cause mismatches with the biopsychological human universal demands, as indicated by a worldwide surge of psychological problems, particularly in technological societies. Such universal human demands include living in contact with nature and animals (Wilson, 1984), as well as in socially supportive relationships characterized by mutual care and devotion (Julius et al., 2012). Hence, dogs may decisively contribute to keeping people connected with their basic needs, not just as “social substitutes.” Rather, dogs are social catalysts and lubricants, keeping their people socially connected. From dogs’ perspective, living in a close social relationship with humans is also the ideal setting to which they are adapted. Still, a majority of the estimated 1 billion dogs live parallel to humans in growing cities and their peripheries worldwide, mostly in semiferal packs. The close social fit between dogs and the social neediness of biophilic humans may all contribute to the often astounding effects dog assistance has in a wide variety of therapeutic and pedagogic settings (Julius et al., 2012; Kotrschal, 2016b). Hence, the hunting companion and spiritual ally of the early Paleolithic today supports the well-being and health of people challenged by increasingly demanding lifestyles.

Humans always decisively influenced the ecologies of virtually all their habitats and increasingly do so today by their sheer numbers and presence. This significantly determines the distribution and behavior of wildlife (Ripple et al., 2014), which either avoids humans or profits from them. Generalized and bold carnivores, notably coyotes and wolves, seem to continuously adapt to human environments, profiting from resources of human origin, as was already the case some 35,000 years ago when wolves and humans met (Newsome et al., 2017). Hence, in many ways, our modern world with a human population just short of 8 billion experiences a steady increase in the significance and diversity of human-canine relationships.

Summary for Practitioners

The wealth of recent behavioral, neurobiological, and genetic results allows us to draw a new, comprehensive picture of the human-wolf-dog relationship. Dogs originated from wolves 35,000 years ago, mainly via selection for tameness. Wolves were probably spiritual partners and hunting buddies of Paleolithic hunter-gatherers over wide areas of Eurasia. Coming together and staying together was probably facilitated by the close ecological and social match between wolves and humans. Both are cursorial hunters and scavengers living in cooperative but relatively closed family groups, which selected for very similar mentalities.

Parallel selection for tameness (i.e., being “nice”) in dogs and humans quickly, and in a diverse way, changed behavioral and anatomical phenotypes from wolf to dog, and social orientation from Stone Age to modern humans. Actually, dogs were the most important human companions in conquering the world. By adapting to the needs of diverse human societies and civilizations, a wide variety of dogs developed. Over long periods of history dogs were meant to be benign with their own humans, but not with strangers. Hence human ingroup-outgroup distinctions may explain why considerable aggressiveness may still be found in dogs and humans,

incompatible today with a globalized world and universal ethics. In dogs this can be easily controlled by selective breeding and in humans, less easily, by cognition. Actually, sledge dogs and modern hunting breeds were selected for tolerance in the past.

Most recent scientific results not only underline how closely dogs match human operational and social needs, but also find that most of dogs' social behavior, cognition, and cooperativeness is direct wolf heritage and did not emerge in domestication, as previously thought. Dogs have adjusted to human needs in many subtle ways in the course of domestication. This makes dogs much better companions than tame wolves: Dogs are more easily socialized, they are strongly tuned toward people, they respect human leadership, and they are superior receivers and donors of emotional social support. Dogs actually became more obedient and respectful of social hierarchies than wolves, more dependent on human support, and better at inhibiting their impulses. Dogs diversified their barking for communicating with humans. They can read our emotions and adjust to them in an empathic way. Dogs are capable of human-like thinking, of taking a human perspective, and even of tricking us. Not least, they share a sense of fairness with wolves and humans.

Hence, dogs can be particularly valuable partners in meeting universal human social needs. Human-dog relationships are "essentialized," lacking the cultural and symbolic complexities of relationships between humans. But the devotion of dogs is not unconditional; they do judge our moods and social conduct and make their choices accordingly. Dogs can boost the self-esteem and agency of their human partners and are excellent "social lubricants," thereby connecting people. Actually, in their flexibility, social devotion, adaptiveness, and responsiveness, dogs are the stars among all animal companions. No wonder, as the human-dog relationship started in the early Paleolithic, tens of thousands of years before the domestication of other animals. Dog companionship seems increasingly important in a globalized and digitalized world. An ever-accelerating pace of life may not always provide the conditions needed to keep people physically and mentally healthy. Living

in good relationships with dogs can keep people connected with their social essentials.

Therefore, dogs are prime animal assistants in a wide range of activities, pedagogy, and therapy. Supported by human biophilia, the presence of a friendly dog may have strong calming and socializing effects on humans and support communication and sociopositive behavior. Dogs are probably the most socially responsive of all companion animals, privately and in professional settings. In all such activities (for definitions please see the IAHAIO White Paper, Jegatheesan et al., 2014), well-socialized and friendly dogs respond well to temporary and positive challenges, but must never be overburdened. It requires a suitable dog in a secure relationship with a sensitive and knowledgeable human partner. Furthermore, it has to be kept in mind that dog partners need regular veterinarian checks in the interest of the animals' health and welfare and to minimize health risks (e.g., zoonoses) for the human partners. All activities and work need to conform to the IAHAIO Guidelines for Animal-Assisted Activities and Animal-Assisted Therapy (Prague, 1998) and with the IAHAIO White Paper (Jegatheesan et al., 2014).

Acknowledgments

Much of my wolf-dog worldview I owe to the input from, and discussion with, all our colleagues from the Wolf Science Center (WSC) in Ernstbrunn, notably Friederike Range and Zsofia Viranyi. Our work there is made possible by the local landowner, Fürst Heinrich XVI Reuss, by the Veterinary University Vienna, by the University of Vienna, and by the Land Niederösterreich.

References

- Anderson, J. R., Buchera, B., Chijiwa, H., Kuroshima, H., Takimoto, T., & Fujita, K. (2017). Third-party social evaluations of humans by monkeys and dogs. *Neuroscience and Biobehavioral Reviews*. <https://doi.org/10.1016/j.neubiorev.2017.01.003>

- Anderson, T. M., et al. (2009). Molecular and evolutionary history of melanism in North American gray wolves. *Science*, 323, 1339–1343. <https://doi.org/10.1126/science.1165448>
- Andics, A., Gácsi, M., Faragó, T., Kis, A., & Miklósi, A. (2014). Voice-sensitive regions in the dog and human brain are revealed by comparative fMRI. *Current Biology*, 24, 574–578.
- Archer, J. (1997). Why do people love their pets? *Evolution and Human Behavior*, 18, 237–259.
- Axelson, E., Ratnakumar, A., Arendt, M. L., Maqbool, K., Webster, M. T., Perloski, M., . . . Lindblad-Toh, K. (2013). The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature*, 495, 360–364.
- Barnard, A. (1998). The foraging spectrum: Diversity in hunter-gatherer lifeways. *American Ethnologist*, 25, 36–37.
- Beetz, A. (2015). *Hunde im Schulalltag. Grundlagen und Praxis* (3rd ed.). München: Reinhardt Verlag.
- Beetz, A., Julius, H., Turner, D., & Kotrschal, K. (2012a). Effects of social support by a dog on stress modulation in male children with insecure attachment. *Frontiers in Psychology*, 3, 1–9. <https://doi.org/10.3389/fpsyg.2012.00352>
- Beetz, A., Uvnäs-Moberg, K., Julius, H., & Kotrschal, K. (2012b). Psychosocial and psychophysiological effects of human-animal interactions: The possible role of oxytocin. *Frontiers in Psychology*, 3, 1–16. <https://doi.org/10.3389/fpsyg.2012.00234>
- Belyaev, D. K. (1972). Destabilizing selection as a factor in domestication. *Heredity*, 70, 301–308.
- Berns, G. S., Brooks, A., & Spivak, M. (2013). Replicability and heterogeneity of awake unrestrained canine fMRI responses. *PLoS ONE*, 8, e81698. <https://doi.org/10.1371/journal.pone.0081698>
- Bocherens, H., Drucker, D. G., Germonpre, M., Laznickova-Galetova, M., Naito, Y. I., Wissing, C., . . . Oliva, M. (2014). Reconstruction of the Gravettian food-web at Predmostí I using multi-isotopic tracking (13C, 15N, 34S) of bone collagen. *Quaternary International*, 359–360, 211–228.
- Cassidy, K. A., Mech, D. L., MacNulty, D. R., Stahler, D. R., & Smith, D. W. (2017). Sexually dimorphic aggression indicates male gray wolves specialize in pack defense against conspecific groups. *Behavioural Processes*, 136, 64–72.
- Catala, A., Mang, B., Wallis, L., & Huber, L. (2017). Dogs demonstrate perspective taking based on geometrical gaze following in a Guesser–Knower task. *Animal Cognition*. <https://doi.org/10.1007/s10071-017-1082-x>
- Chijiwa, H., Kuroshima, H., Hori, Y., Anderson, J. R., & Fujita, K. (2015). Dogs avoid people who behave negatively to their owner: Third-party affective evaluation. *Animal Behaviour*, 106, 123–127.
- Cimarelli, G., Turcsán, B., Bánlaki, Z., Range, F., & Virányi, Z. (2016). Dog owners' interaction styles: Their components and associations with reactions of pet dogs to a social threat. *Frontiers in Psychology*, 7, 1–14. DOI: 10.3389/fpsyg.2016.01979
- Coan, J. A. (2011). The social regulation of emotion. In J. Decety & T. Cacioppo (Eds.), *Handbook of social neuroscience*. New York: Oxford University Press.
- Coppinger, R., & Feinstein, M. (2015). *How dogs work*. Chicago: University of Chicago Press.
- Coppinger, R., & Schneider, R. (1995). The evolution of working dogs. In J. A. Serpell (Ed.), *The domestic dog* (pp. 21–50). Cambridge: Cambridge University Press.
- Darwin, C. (1868). *The variation in animals and plants under domestication*. London: John Murray.
- Da Silva Vasconcellos, A., Virányi, Z., Range, F., Ades, C., Scheidegger, J. K., Möstl, E., & Kotrschal, K. (2016). Training reduces stress in human-socialised wolves to the same degree as in dogs. *PLoS ONE*, 11, e0162389. <https://doi.org/10.1371/journal.pone.0162389>
- DeLoache, J. S., Pickard, M. B., & LoBue, V. (2011). How very young children think about animals. In S. McCune, S. J. A. Griffin, & V. Maholmes (Eds.), *How animals affect us: Examining the influences of human-animal interaction on child development and human health* (pp. 85–99). Washington, DC: American Psychological Association.
- Diamond, A., & Lee, K. (2011). Interventions shown to aid executive function development in children 4 to 12 years old. *Science*, 333, 959–964.
- Erdohegyi, A., Topál, J., Virányi, Z., & Miklósi, A. (2007). Dog-logic: Inferential reasoning in a two-way choice task and its restricted use. *Animal Behaviour*, 74, 725–737.
- Essler, J., Marshall-Pescini, S., & Range, F. (2017). Domestication does not explain the presence of inequity aversion in dogs. *Current Biology*, 27, 1861–1865. <https://doi.org/10.1016/j.cub.2017.05.061>
- Fine, A. H. (2015). *Handbook on animal-assisted therapy: Theoretical foundations and guidelines for practice*. London: Academic Press.
- Fogg, B. R., Howe, N., & Pierotti, R. (2015). Relationships between indigenous American peoples and wolves 1: Wolves as teachers and guides. *Journal of Ethnobiology*,

- 35, 262–285. <https://doi.org/10.2993/etbi-35-02-262-285.1>
- Frank, H., & Frank, M. G. (1982). On the effects of domestication on canine social development and behaviour. *Applied Animal Ethology*, *8*, 507–525.
- Frantz, L. A. F., et al. (2016). Genomic and archaeological evidence suggests a dual origin of domestic dogs. *Science*, *352*, 1228–1231.
- Gácsi, M., Topál, J., Miklósi, A., Dóka, A., & Csányi, V. (2001). Attachment behavior of adult dogs (*Canis familiaris*) living at rescue centers: Forming new bonds. *Journal of Comparative Psychology*, *115*, 423–431.
- Gaubert, P., Bloch, C., Benyacoub, S., Abdelhamid, A., Pagani, P., Adeyemi, C., . . . Dufour, S. (2012). Reviving the African wolf *Canis lupus lupaster* in North and West Africa: A mitochondrial lineage ranging more than 6,000 km wide. *PLoS ONE*, *7*, e42740. <https://doi.org/10.1371/journal.pone.0042740>
- Gee, N., Gould, J. K., Swanson, C. C., & Wagner, A. K. (2012). Preschoolers categorize animate objects better in the presence of a dog. *Anthrozoös*, *25*, 187–198.
- Grandin, T., & Johnson, C. (2005). *Animals in translation. Using the mysteries of autism to decode animal behaviour*. New York: Scribner.
- Guo-Dong Wang, et al. (2016). Out of Southern East Asia: the natural history of domestic dogs across the world. *Cell Research*, *26*, 21–33. <https://doi.org/10.1038/cr.2015.147>
- Hamel, F. (1969). *Human animals, werewolves and other transformations*. New York: University Books.
- Handlin, L., Hydbring-Sandberg, E., Nilsson, A., Ejdebäck, M., Jansson, A., & Uvnäs-Moberg, K. (2011). Short-term interaction between dogs and their owners: Effects on oxytocin, cortisol, insulin and heart rate—an exploratory study. *Anthrozoös*, *24*, 301–315.
- Harari, Y. N. (2014). *Sapiens: A brief history of humankind*. Munich: Random House.
- Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, *9*, 439–444.
- Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*, 573–585.
- Headey, B. (1999). Health benefits and health cost savings due to pets: Preliminary estimates from an Australian national survey. *Social Indicators Research*, *47*, 233–243.
- Headey, B., & Grabka, M. M. (2007). Pets and human health in Germany and Australia: National longitudinal results. *Social Indicators Research*, *80*, 297–311.
- Headey, B., Na, F., & Zheng, R. (2008). Pet dogs benefit owners' health: A 'natural experiment' in China. *Social Indicators Research*, *87*, 481–493.
- Heberlein, M. T. E., Manser, M. B., & Turner, D. C. (2017). Deceptive-like behaviour in dogs (*Canis familiaris*). *Animal Cognition*. <https://doi.org/10.1007/s10071-017-1078-6>
- Herre, W., & Röhrs, M. (2013). *Haustiere—Zoologisch gesehen* (reprint, 2nd ed.). Berlin: Springer Spektrum.
- Herzog, H. (2010). *Some we love, some we hate, some we eat: Why it's so hard to think straight about animals*. New York: Harper.
- Huber, A., Barber, A. L. A., Farago, T., Müller, C. A., & Huber, L. (2017). Investigating emotional contagion in dogs (*Canis familiaris*) to emotional sounds of humans and conspecifics. *Animal Cognition*. <https://doi.org/10.1007/s10071-017-1092-8>
- IAHAIO Guidelines for Animal-Assisted Activities and Animal-Assisted Therapy. (1998). <http://iahaio.org/prague-declaration/>
- Jegatheesan, B., Beetz, A., Ormerod, E., Johnson, R., Fine, A., Yamazaki, K., . . . Choi, G. (2014). International Association of Human-Animal Interaction Organizations White Paper: The IAHAIO definitions for animal-assisted intervention and guidelines for wellness of animals involved. <http://iahaio.org/wp/wp-content/uploads/2017/05/iahaio-white-paper-final-nov-24-2014.pdf>
- Jiang Rong. (2008). *Wolf totem*. New York: Penguin.
- Julius, H., Beetz, A., Kotrschal, K., Turner, D., & Uvnäs-Moberg, K. (2012). *Attachment to pets: An integrative view of human-animal relationships with implications for therapeutic practice*. Göttingen and Cambridge, MA: Hogrefe.
- Kaminski, J., Call, J., & Fischer, J. (2004). Word learning in a domestic dog: Evidence for “fast mapping.” *Science*, *304*, 1682–1683. DOI: 10.1126/science.1097859
- Kis, A., Turcsán, B., Miklósi, A., & Gácsi, M. (2012). The effect of the owner's personality on the behaviour of owner-dog dyads. *Interaction Studies*, *13*, 373–385.
- Klinghammer, E., & Goodman, P. A. (1986). Rearing and socialization of wolves in captivity. In H. Frank (Ed.), *Man and wolf: Advances, issues and problems in captive wolf research* (pp. 31–59). Dordrecht: W. Junk.
- Konok, V., Kosztolányi, A., Rainer, W., Mutschler, B., Halsband, U., & Miklósi, Á. (2015). Influence of owners' attachment style and personality on their dogs' (*Canis familiaris*) separation-related disorder. *PLoS ONE*, *10*, e0118375. <https://doi.org/10.1371/journal.pone.0118375>

- Kortekaas, K., & Kotrschal, K. (2017). Wolves (*Canis lupus*) are quicker than dogs (*Canis lupus familiaris*) to freely use a treadmill, but dogs are more relaxed during training. In prep.
- Kotrschal, K. (2012). *Wolf—Hund—Mensch. Die Geschichte einer Jahrtausende alten Beziehung*. Wien: Brandstätter.
- Kotrschal, K. (2014). *Einfach beste Freunde. Warum Menschen und andere Tiere einander verstehen*. Wien: Brandstätter.
- Kotrschal, K. (2016a). *Hund-Mensch. Das Geheimnis der Seelenverwandtschaft*. Wien: Brandstätter.
- Kotrschal, K. (2016b). Do companion animals support social, emotional and cognitive development of children? In L. Freund, S. McCune, P. McCardle, L. Esposito, & N. Gee (Eds.), *Social neuroscience of human-animal interaction*. Washington, DC: NIH-Waltham.
- Kotrschal, K., Hampl, C., Auer, M., Heberlein, M., Virányi, Z., & Range, F. (2014). Wolves (*Canis lupus occidentalis*) are as cooperative as dogs (*Canis familiaris*) during leash walking. International Society of Anthrozoology (ISAZ) Annual Meeting, Vienna.
- Kotrschal, K., & Ortbauer, B. (2003). Behavioural effects of the presence of a dog in the classroom. *Anthrozoös*, 16, 147–159.
- Kotrschal, K., Schöberl, I., Bauer, B., Thibeaut, A.-M., & Wedl, M. (2009). Dyadic relationships and operational performance of male and female owners and their male dogs. *Behavioural Processes*, 81, 383–391.
- Kubinyi, E., Topál, J., Miklósi, A., & Csanyi, V. (2003). Dogs (*Canis familiaris*) learn from their owners via observation in a manipulation task. *Journal of Comparative Psychology*, 117, 156–165.
- Lesch, R. (2016). *Baby talk or command? How humans talk to their dogs*. Master's thesis, University of Vienna.
- Levinson, B. M., & Mallone, G. P. (1997). *Pet-oriented child psychology* (2nd ed.). Springfield, IL: C. C. Thomas.
- Lorenz, K. (1954). *Man meets dog*. London: Methuen.
- Marshall-Pescini, S., Cafazzo, S., Virányi, Z., & Range, F. (2017). Integrating social ecology in explanations of wolf–dog behavioral differences. *Current Opinion in Behavioral Sciences*, 16, 80–86.
- Marshall-Pescini, S., Rao, A., Virányi, Z., & Range, F. (2017). The role of domestication and experience in 'looking back' towards humans in an unsolvable task. *Scientific Reports*, 7, 46636. <https://doi.org/10.1038/srep46636>
- Marshall-Pescini, S., Virányi, Z., & Range, F. (2015). The effect of domestication on inhibitory control: Wolves and dogs compared. *PLoS ONE*, 10, e0118469. doi:10.1371/journal.pone.0118469
- Mech, L. D. (2012). *The wolf: The ecology and behaviour of an endangered species*. New York: Doubleday.
- Miklósi, A. (2015). *Dog behaviour, evolution, and cognition* (2nd ed.). Oxford: Oxford University Press.
- Miklósi, A., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csanyi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*, 13, 763–766.
- Miklósi, Á., & Topál, J. (2013). What does it take to become 'best friends'? Evolutionary changes in canine social competence. *Trends in Cognitive Sciences*, 17, 287–294. <https://doi.org/10.1016/j.tics.2013.04.005>
- Min Hooi Yong & Ruffman, T. (2014). Emotional contagion: Dogs and humans show a similar physiological response to human infant crying. *Behavioural Processes*, 108, 155–165.
- Mitchell, R. W. (2001). Americans' talk to dogs: Similarities and differences with talk to infants. *Research on Language and Social Interaction*, 34, 183–210.
- Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A. H., & Howerter, A. (2000). The unity and diversity of executive functions and their contributions to complex "frontal lobe" tasks: A latent variable analysis. *Cognitive Psychology*, 41, 49–10. <https://doi.org/10.1006/cogp.1999.0734>
- Molnar, C., Pongracz, P., Farago, T., Doka, A., & Miklósi, A. (2009). Dogs discriminate between barks: The effect of context and identity of the caller. *Behavioural Processes*, 82, 198–201.
- Moretti, L., Hentrup, M., Kotrschal, K., & Range, F. (2015). The influence of relationships on neophobia and exploration in wolves and dogs. *Animal Behaviour*, 107, 159–173.
- Müller, C. A., Riemer, S., Virányi, Z., Huber, L., & Range, F. (2016). Inhibitory control, but not prolonged object-related experience appears to affect physical problem-solving performance of pet dogs. *PLoS ONE*, 11, e0147753. <https://doi.org/10.1371/journal.pone.0147753>
- Müller, C. A., Schmitt, K., Barber, A. L., & Huber, L. (2015). Dogs can discriminate emotional expressions of human faces. *Current Biology*. <https://doi.org/10.1016/j.cub.2014.12.055>
- Musiani, M., et al. (2007). Differentiation of tundra/taiga and boreal coniferous forest wolves: Genetics, coat

- colour and association with migratory caribou. *Molecular Ecology*, *16*, 4149–4170. <https://doi.org/10.1111/j.1365-294X.2007.03458.x>
- Naderi, S. Z., Miklósi, A., Dóka, A., & Csányi, V. (2001). Co-operative interactions of blind persons and their dogs. *Applied Animal Behaviour*, *74*, 59–80.
- Naderi, S. Z., Miklósi, A., Doka, A., & Csanyi, V. (2002). Does human-dog attachment affect their interspecific cooperation? *Acta Biologica Hungarica*, *53*, 537–550.
- Nagasawa, M., Mitsui, S., En, S., Ohtani, N., Ohta, M., Sakuma, Y., . . . Kikusui, T. (2015). Oxytocin-gaze positive loop and the coevolution of human-dog bonds. *Science*, *348*, 333–336. <https://doi.org/10.1126/science.1261022>
- Newsome, T. M., Fleming, P. J. S., Dickman, C. R., Doherty, T. S., Ripple, W. J., Ritchie, E. G., & Wirsing, A. J. (2017). Making a new dog? *BioScience*, *67*, 374–381. <https://doi.org/10.1093/biosci/bix022>
- Parker, H. G., et al. (2004). Genetic structure of the purebred domestic dog. *Science*, *304*, 1160–1164. <https://doi.org/10.1126/science.1097406>
- Parker, H. G., Shearin, A. L., & Ostrander, E. A. (2010). Man's best friend becomes biology's best in show: Genome analyses in the domestic dog. *Annual Reviews of Genetics*, *44*, 309–336. <https://doi.org/10.1146/annurev-genet-102808-115200>
- Peterson, R. O. (1995). *The wolves of Isle Royale: A broken balance*. Minocqua, WI: Willow Creek Press.
- Pongrácz, P., Molnár, C., Dóka, A., & Miklósi, A. (2011). Do children understand man's best friend? Classification of dog barks by pre-adolescents and adults. *Applied Animal Behaviour Science*, *135*, 95–102.
- Pongrácz, P., Molnár, C., & Miklósi, A. (2010). Barking in family dogs: An ethological approach. *Veterinary Journal*, *183*, 141–147.
- Ragatz, L., Fremouw, W., Thomas, T., & McCoy, K. (2009). Vicious dogs: The antisocial behaviors and psychological characteristics of owners. *Journal of Forensic Science*, *54*. <https://doi.org/10.1111/j.1556-4029.2009.01001.x>
- Randi, E., Hulva, P., Fabbri, E., Galaverni, M., Galov, A., Kusak, J., . . . Caniglia, R. (2014). Multilocus detection of wolf x dog hybridization in Italy, and guidelines for marker selection. *PLoS ONE*, *9*, e86409. <https://doi.org/10.1371/journal.pone.0086409>
- Range, F., Horn, L., Virányi, Z., & Huber, L. (2008). The absence of reward induces inequity aversion in dogs. <https://doi.org/10.1073/pnas.0810957105>
- Range, F., Jenikejew, J., Schröder, I., & Virányi, Z. (2014). Difference in quantity discrimination in dogs and wolves. *Frontiers in Psychology*, *18*. <https://doi.org/10.3389/fpsyg.2014.01299>
- Range, F., Ritter, C., & Virányi, Z. (2015). Testing the myth: Tolerant dogs and aggressive wolves. *Proceedings Royal Society B*, *282*, 215–220. <https://doi.org/10.1098/rspb.2015.0220>
- Range, F., & Virányi, Z. (2011). Development of gaze following abilities in wolves (*Canis lupus*). *PLoS ONE*, *6*, e16888. <https://doi.org/10.1371/journal.pone.0016888>
- Range, F., & Virányi, Z. (2013). Social learning from humans or conspecifics: Differences and similarities between wolves and dogs. *Frontiers in Psychology*. <https://doi.org/10.3389/fpsyg.2013.00868>
- Range, F., & Virányi, Z. (2014). Wolves are better imitators of conspecifics than dogs. *PLoS ONE*, *9*, e86559. <https://doi.org/10.1371/journal.pone.0086559>
- Range, F., & Virányi, Z. (2015). Tracking the evolutionary origins of dog-human cooperation: The “canine cooperation hypothesis.” *Frontiers in Psychology*. <https://doi.org/10.3389/fpsyg.2014.01582>
- Ripple, J., et al. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*, 151, 1241484. <https://doi.org/10.1126/science.1241484>
- Russow, L.-M. (2002). Ethical implications of the human-animal bond in the laboratory. *ILAR Journal*, *43*, 33–37. <https://doi.org/10.1093/ilar.43.1.33>
- Schleidt, W. M., & Shalter, M. D. (2003). Co-evolution of humans and canids: An alternative view of dog domestication: *Homo homini lupus? Evolution and Cognition*, *9*, 57–72.
- Schneider, W. (2014). *Der Soldat. Ein Nachruf. Eine Weltgeschichte von Helden, Opfern und Bestien*. Berlin: Rowohlt.
- Schöberl, I., Wedl, M., Beetz, A., & Kotrschal, K. (2017). Psychobiological factors affecting cortisol variability in human-dog dyads. *PLoS ONE*, e0170707. <https://doi.org/10.1371/journal.pone.0170707>
- Scott, J. P., & Fuller, J. L. (1965). *Genetics and the social behavior of the dog*. Chicago: University of Chicago Press.
- Se Jin Song et al. (2013). *Cohabiting family members share microbiota with one another and with their dogs*. *eLife*, *2*, e00458. <https://doi.org/10.7554/eLife.00458>
- Serpell, J. (1990). Pet keeping and animal domestication—a re-appraisal. In J. Clutton-Brock (Ed.), *The walking ladder: Patterns of domestication, pastoralism, and predation* (pp. 10–21). London: Unwin & Hyman.

- Serpell, J. (Ed.). (2016). *The domestic dog: Its evolution, behavior and interactions with people*. Cambridge: Cambridge University Press.
- Shipman, P. (2015). *The invaders. How humans and their dogs drove Neanderthals to extinction*. Cambridge, MA: Harvard University Press.
- Solomon, J., Beetz, A., Schöberl, I., Gee, N., & Kotrschal, K. (2018). Attachment security in companion dogs: Adaptation of Ainsworth's Strange Situation and classification procedures to dogs and their human caregivers. *Attachment and Human Development*, in Press.
- Stoeckel, L. E., Palley, L. S., Gollub, R. L., Niemi, S. M., & Evins, A. E. (2014). Patterns of brain activation when mothers view their own child and dog: An fMRI study. *PLoS ONE*, *9*, e107205. <https://doi.org/10.1371/journal.pone.010720>
- Svartberg, K., & Forkman, B. (2002). Personality traits in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science*, *79*, 133–155.
- Svartberg, K., Tapper, I., Temrin, H., Radesaeter, T., & Thorman, S. (2005). Consistency of personality traits in dogs. *Animal Behaviour*, *69*, 283–291. <https://doi.org/10.1016/j.anbehav.2004.04.011>
- Thalmann, O., et al. (2013). Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science*, *342*. <https://doi.org/10.1126/science.1243650>
- Topál, J., Byrne, R. W., Miklósi, A., & Csányi, V. (2006). Reproducing human actions and action sequences: “Do as I do!” in a dog. *Animal Cognition*, *9*, 355–367. <https://doi.org/10.1007/s10071-006-0051-6>
- Topál, J., Miklósi, A., & Csányi, V. (1997). Dog-human relationship affects problem solving behaviour in the dog. *Anthrozoös*, *10*, 214–224.
- Topál, J., Miklósi, A., Csányi, V., & Dóka, A. (1998). Attachment behavior in dogs (*Canis familiaris*): A new application of Ainsworth's (1969) Strange Situation test. *Journal of Comparative Psychology*, *112*, 219–229.
- Udell, M. A. R., Dorey, N. R., & Wynn, C. D. L. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour*, *76*, 1767–1773. <https://doi.org/10.1016/j.anbehav.2008.07.028>
- Ulmer, T. (2010). *Der Hund in den Kulturen der Plains-Indianer*. Marburg: Tectum.
- Urbigkit, C. (2008). *Yellowstone wolves: A chronicle of the animal, the people, and the politics*. Newark, NJ: McDonald and Woodward.
- Urquiza Haas, E. G., & Kotrschal, K. (2015). The mind behind anthropomorphic thinking: Attribution of mental states to other species. *Animal Behaviour*, *109*, 167–176. <https://doi.org/10.1016/j.anbehav.2015.08.011>
- Viranta, S., Atickem, A., Werdelin, L., & Stenseth, N. C. (2017). Rediscovering a forgotten canid species. *BMC Zoology*, *2*, 6. <https://doi.org/10.1186/s40850-017-0015-0>
- Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., & Miklósi, A. (2008). Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition*, *11*, 373–387. <https://doi.org/10.1007/s10071-007-0127-y>
- Wedl, M., & Kotrschal, K. (2009). Social and individual components of animal contact in preschool children. *Anthrozoös*, *22*, 383–396.
- Wells, D. L. (2004). The facilitation of social interactions by domestic dogs. *Anthrozoös*, *17*, 340–352.
- Wilkins, A., Wrangham, R. W., & Fitch, T. W. (2014). The “Domestication syndrome” in mammals: A unified explanation based on neural crest cell behavior and genetics. *Genetics*, *197*, 795–808. <https://doi.org/10.1534/genetics.114.165423>
- Wilson, E. O. (1984). *Biophilia*. Cambridge, MA: Harvard University Press.
- Wilson, E. O. (2012). *The social conquest of earth*. New York: W. W. Norton.
- Xenophon. (400 BCE). *Kynegeticon*.
- Zimen, E. (1980). *Der Wolf: Mythos und Verhalten*. Wien, München: Meyster.
- Zimen, E. (1988). *Der Hund. Abstammung—Verhalten—Mensch und Hund*. München: C. Bertelsmann.