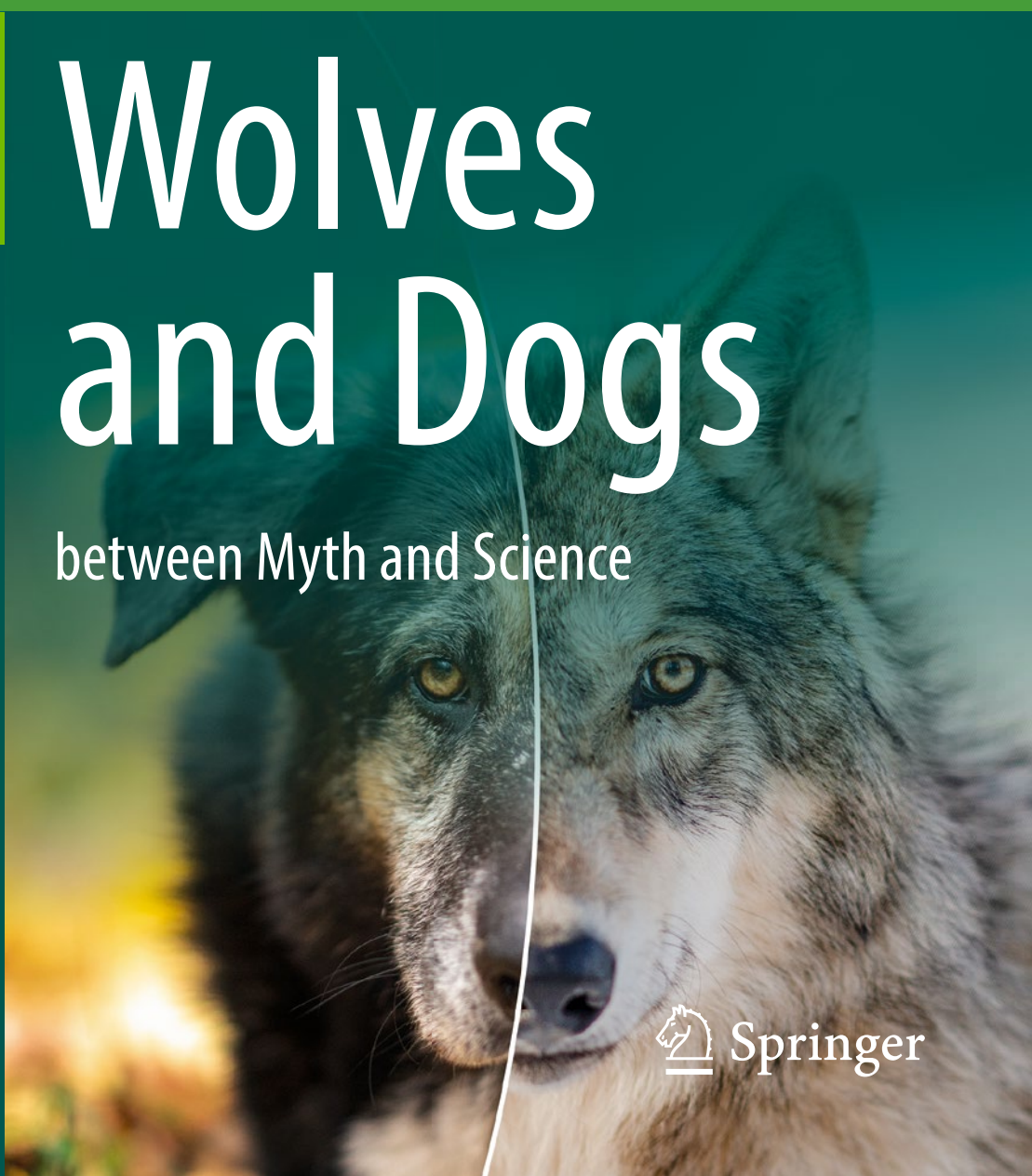
Fascinating Life Sciences

Friederike Range
Sarah Marshall-Pescini

Wolves and Dogs

between Myth and Science



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Dedicated to our families (the two- and four-legged ones)

Foreword

Wolves and dogs—what a pair of species! Everybody knows them—at least most people have an opinion about them. And they are described and referred to in so many different ways. One is the wild, the brave, the fearless, the clever, the selfish, or the greedy, while the other is rather tender, withdrawn, obedient, sharing, or kind, perhaps a friend of us. So something like yin and yang or black and white?

All this may sound familiar to people, especially those living in Europe, who grew up hearing the tales by the Grimm brothers, such as Little Red Riding Hood. But there is also another story to tell in which the same wolves are admired by people for their spirit and pure nature, and are regarded by many historic tribes as their ancestors. This culture of wolves was also resurrected by the Romans claiming that a she-wolf raised the two founders, Romulus and Remus, of the city Rome.

So, what could be a greater challenge than to write a book about wolves, probably one of the most mythical animals in human culture. Not to mention that there have been only a handful of scientists who dared to step on this road. Friederike Range and Sarah Marshall-Pescini are just at the right place at the right time to follow this tradition to update what one may call the "ethology and ecology of wolves". There is no place here to list all the books on wolves that have dealt with their life history, behaviour, and evolution. Many earlier works are mentioned in this book. However, thanks to the advancements of the last 20–30 years, and our growing knowledge about wolves, the content of this book is a very significant addition to the earlier published monographs, for example, by biologists Erik Zimen (1971), David Mech (1981), and Mech and Boitani (2010).

Wolves are always a topic for discussion. In a not too distant past, there was the worry that wolves would be pushed to the brink of extinction, at least in Europe and the Americas, but their populations were also decreasing elsewhere. But thanks to conservationists, their fate has changed during the last 20–30 years, and they are now re-colonising many previously abandoned habitats both in Europe and in North America. Although the re-introduction of wolves to Yellowstone was heatedly debated, their showing up in many regions had a positive effect on the ecosystem. Wolf populations recovered even in the absence of active human involvement; a ban on hunting and providing an area with little disturbance appears to be largely sufficient. International students who visited our department were always asked to give a short presentation about their work. Many years ago, a young Dutch student

talked about the measures that may be useful to introduce wolves in the Netherlands. We all listened to her very politely, but after the talk we could not resist commenting: "But there are no wolves in the Netherlands!" She was prepared for such a remark and replied very firmly: "Yes, but they will come." And she was right! In 2019 the media reported several sightings of wolves in this country.

So now we have achieved what we had wanted. Are we satisfied and happy? Well, the respected and sacred wolves can end up quickly on the negative end of the news, if we start to believe or actually find out that they are also killing our livestock. So now we all have to learn how to share the land. We should allow the wolves to establish stable populations which help to balance the ecosystem, but we also have to ensure that humans and their livestock are protected from attacks from this top predator.

Friederike Range and Sarah Marshall-Pescini are not afraid of describing and analysing at least 9 different domestication hypotheses. There is the rumour that at the end of the nineteenth century the French academy "banned" the publication of new hypotheses on the emergence of human language. It seems that many people in the community of wolf and dog research enjoy coming up with "THE" domestication hypothesis that explains "everything" about the history of our animal friends. However, if one appreciates the complexity of evolutionary processes, mechanisms of selection, and the interwoven nature of genetic and environmental factors, then it turns out that most such proposals can explain only a small part of the changes in the variation of traits that gave raise to modern dogs. So, although in most of those hypotheses there is likely some "truth", the problem is that we do not necessarily know where it actually is. The main issue is that we do not have the necessary tools to provide experimental evidence for a specific and unique series of events that occurred in the distant past. This situation can be traced in the scientific adventure towards the understanding of where and when dogs were domesticated. Since the first paper using genetic data to establish the time frame and the location of dog domestication (Vila et al 1997), the evidence for a specific time interval and location changed from key paper to key paper. And one important limitation of this approach (probably unlikely to be solved in the near future) is that it is impossible to save very ancient DNA. Moreover, most of these hypotheses are rather complementary than exclusive; they look at different levels of biological organisation. For example, possible selection for genes that may make dogs look so young (see Kinderschema, Lorenz) in the eyes of their human friends may not exclude earlier/parallel/later selection for more flexible agonistic behaviour at older age. Pleitropy and polygenetic effects are also likely to make the unveiling of an evolutionary process very difficult.

I, personally, totally agree with the authors' preference to regard wolves and dogs as two species, but talking about "wolves" and "dogs" in an evolutionary scenario, as it often happens, is a major oversimplification. "Putting things into boxes" is a typical human way of thinking, probably based on our bias to think in linguistic terms. But in reality there are (were?) at least 10–14 subspecies of wolves ranging from Saudi Arabia to Alaska, and there are more than 400 breeds of dogs dispersed

over the entire globe, not to mention the dingoes and the millions of stray and feral dogs. So when scientists seek to explain the emergence of differences in certain phenotypic traits, they often imagine the two species as extremes, corresponding to the adjectives above that typically characterise "wolves" and "dogs", but in reality there are many wolf-like dogs and also dog-like wolf populations. I think we should take both within and between phenotypic variation in these species seriously.

On the more positive side there is also some good news, when it comes to our much improved knowledge about the social life of wolves. Extensive field observations of wolf populations and individual groups are now complemented with observations on social structure, migration of individuals, and intra- and intergroup competition for resources. And the major discovery, attributed to Jane Packard, is also quite recent: typical wolves live in families; that is a father, a mother, and their offspring make up a group. So the old idea of the wolf pack, in which all individuals fight for being the leader, can be thrown into the garbage heap of outdated scientific ideas. Nevertheless, this discovery finds its place only slowly in the mind of people as many still refer to wolf packs instead of families. Somebody may ask, what is the difference? Well, a lot. If the family is the social unit in wolves, their cooperation at various tasks and challenges is less of a surprise. The parents can realise their fitness only if they are able to raise as many young animals as possible, and the offspring can also gain a lot from cooperating with their parents. The collaboration among siblings can be explained on similar grounds. If collaboration in wolves is based on kin selection, then actually the transition to a collaborative dog is actually not a straightforward evolutionary issue because those kin-related genetic factors do not operate when humans and dogs work together.

This book is packed with much knowledge on wolves most of which was established in the last 20 years. I think we all, who are fascinated by the evolution, ecology, and behaviour of wolves and dogs, have to thank those few enthusiastic scientists who dedicated a part of their careers to follow the lives of these amazing creatures. Friederike Range and Sarah Marshall-Pescini deserve a fine place among these brave researchers together with Zsófia Virányi, Enikő Kubinyi, and Márta Gácsi, to name only a few others. The science that is presented with great care in this book, taking into account different views, perspectives, and lack of knowledge, should invite any readers interested in biology to get a closer look at this species without actually getting cold or dirty, and they also do not need to stand the look of a wolf from a short distance.

Congratulations, Friederike and Sarah!

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31 October 2021

Ádám Miklósi

Foreword

Investigating the relationships between humans, wolves, and dogs provides a more important mirror to understand ourselves and our relationship with the world, than most people would appreciate. *Homo sapiens* is the most invasive species on earth, permanently inhabiting even the most unlikely habitats such as deserts and the high Arctic. Dogs arguably contributed a lot to this roaring success. Unplanned and unintended, our ancestors bumped into wolves on their way into the Eurasian continent. It is still a miracle that this happened—and why it happened remains enigmatic. Even more astonishing is that some of these palaeolithic human–wolf associations turned into permanent companionship with domesticated wolves we call dogs. This amazing story raises many questions, for example, how did humans and wolves get into contact in the first place? How come that such a great variety of dogs originated from a single wolf type? And in what way do modern dogs differ from wolves, i.e. what happened during adapting to live with, or close to, humans during the process of domestication?

One would assume that science has long provided most of the relevant answers, but this is not the case. First of all, the topic is so close (too close) to many people, including scientists, that even research was—and still is—an ideological minefield. Second, and most importantly, only the most recent developments in palaeogenetics, archaeology, experimental behavioural biology, and other disciplines provided the kind of firm ground needed to increasingly allow knowledge to compete with opinionation. This book is a milestone of knowledge, integrating more than a decade of experimental research at the Wolf Science Center (WSC) with the relevant results of colleagues worldwide. As an anchor of facts it will provide the ground for further thinking, discussing, and developing the field.

The contents of this book even radiate into experimental archaeology, enlightening educated guesses as to why wolves and humans may have gotten into contact. The most promising candidate factor is the close match between the ecology, lifestyles, and social organisation of hunter-gatherer humans and wolves. Within-clan and within-pack cooperative orientation of humans and wolves was probably key in both the initial match making and our closer-than-ever companionships with dogs. Our present knowledge even contributes arguments towards the early scenarios, making hand-rearing and a respectful non-dominating human interaction style much more likely than the still prominent idea of “self-domestication”, holding

that some wolves actively chose the company of humans. But who knows? The last witnesses of these remarkable initial events lived some 100 000 generations ago.

The three founders of the Wolf Science Center—Friederike Range, Zsofia Viranyi, and myself were brought together by their keen common interest in wolf and dog behaviour, in the principles of cooperation, cognitive mechanisms, domestication, and human–dog relationships. Given the complexity and novelty of our goals, as well as the effort it would require working long-term with a considerable number of wolves and dogs, we knew that we had to cooperate, not just over developing the concepts, but also in raising funds and in building the necessary research infrastructure. We hand-reared our first four wolf pups in 2008—with a lot of enthusiasm and excitement, but with no financial plan and pretty naïve about what it would mean to run and fund a private enterprise, with 20 employees on the pay list just a few years later. The WSC not only survived, but quickly became scientifically productive. We were extremely grateful when the University of Veterinary Medicine, Vienna, took over the WSC a few years ago; after all, we are scientists, not business administrators. It was certainly worth all the effort. The WSC not just grew into the biggest and one of the most productive basic experimental canid research units worldwide, it is unique in allowing "fair" comparisons between equally raised and kept wolves and dogs, key to fathom the behavioural consequences of dogification.

This book summarises the major WSC research results over more than a decade in perspective with what other workgroups found out and hypothesised. Often enough, the outcomes contradicted mainstream wisdom and surprised ourselves. Less surprising was that the "one, big, fundamental" difference between wolves and dogs does not exist. Rather, a mosaic of differences (and even more matches) between wolves and dogs emerged. Such patterns make sense in the light of domestication, i.e. the adaptation of dogs to live with people, which resulted in an altered socio-ecology as compared to their wolf ancestors—either as an epiphenomenon of the general selection for tameness, or as adaptations of dogs to their new lifestyle, or both. This includes that dogs mentally and physically live in much steeper dominance hierarchies than wolves, affecting the way they relate to, and cooperate with, each other and their human partners, their neophobia and exploration, and how they act out their cognitive skills and solve problems (or not), just to mention a few aspects of the emerging, pretty dog-specific expression of the domestication syndrome.

Through this book, an amazingly coherent story emerges. Many of the mosaic patterns of mentalities and behaviours, as well as their ultimate level explanations, are novel, or at least offer new perspectives and insights. Still, at least as important as the new knowledge featured in this book is its overarching message that even seemingly simple facts may have much more complex mechanistic causalities, than one would wish. Thereby, this book generates a wealth of novel research questions, many of them as unexpected as they are tantalising. I suggest that at present, this is the closest approximation to wolf–dog–human behavioural reality ever, but as typical for science in general, it is certainly not the final word.

I hope—no—I am sure that this book will be well received by scientists as well as by the interested public, as it has considerable potential to reduce the misconceptions, myths, and outright fake news about wolves and dogs, even science is still burdened with. Provided that the messages hit target, they have the potential to make the world a better place for humans and dogs, and not the least, for wolves. Because this is a sober and (self)critical science text, never claiming "the truth" and avoiding any guru positions, it will spark vivid, controversial, and productive discussions and will motivate substantially more research. As every piece of good science, this book provides answers, but raises even more questions.

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Kurt Kotrschal

Acknowledgements

Writing this book has been quite a journey, giving us the precious opportunity to take time to sit and read, walk, and talk, discussing ideas—basically enjoying the best part of science—and trying to critically put all our thoughts on paper. Just as precious is that we have the incredibly good fortune of working with a fantastically collaborative team of researchers, as well as many colleagues around the world who generously gave us great feedback on different parts of this book.

We particularly thank Kurt Kotrschal for taking the time to carefully read through the entire manuscript, chapter by chapter, giving us suggestions on how to improve the readability of the book and, importantly, many wonderful comments to the scientific content. Given we do not always agree, his comments were the most thought-provoking and challenging and therefore immensely useful!

Several other people also provided very valuable feedback to one or several chapters including Andreas Berghänel, Giulia Cimarelli, Rachel Dale, Martina Lazzaroni, Malgorzata Pilot, Sabine Tebbich, Gwen Wirobski, and Clive Wynne. The lively questions and sometimes challenging comments from many different perspectives enriched our thinking, and we hope this comes through in the book. Renate Hengsberger helped us sorting out the references in the various chapters.

We would also like to acknowledge all the researchers who have worked with us over the years, observing and conducting experiments with the animals, but also contributing to our thinking, in particular Zsófia Virányi and Simona Cafazzo. In a memorable trip to Rome the 4 of us laid the ground for much of the work that is summarised in this book.

We would also like to thank the entire trainer team at the Wolf Science Center that made the work at the Wolf Science Center possible over the last decade: Bea Belenyi, Lars Burkert, Charles Gent, Anna Griebler, Nadine Gross, Marianne Heberlein, Marleen Hentrup, Corinna Kratz, Katharina Kriegler, Christine Mayer, Lina Oberliessen, Caroline Ritter, Rita Takacs, Laura Stott, and Cindy Voigt. Their dedication to the animals and support to the students greatly contribute to the unique environment, which makes our science possible. Equally essential is the support of all the administration staff at the Vetmed University: Brigitte Pavlik, Sandra Sperlinger, and Christina Szaga-Doktor and at the Wolf Science Center Marlene Fusek, Tina Gunhold-de Oliveira, Aleksander Orlic, Esther Rudolph, Claudia

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Contents

Introduction

1

The most erroneous stories are those we think we know best—and therefore never scrutinize or question. Stephen Jay Gould

1.1 Why Study the Cognitive Abilities of Wolves?

Most importantly, they are very charismatic animals, and they are just fantastic to watch and work with. But of course, there are also good scientific reasons why it is exciting to study wolves and dogs from a theoretical but also practical perspective.

First, the quest to understand the evolution of the large primate brain—especially the human brain—has governed a lot of research in cognitive biology over the past decades. Based on the assumption that, similar to morphological features, cognitive abilities are shaped by natural selection (Byrne 1997), researchers have focused on studying key traits thought to be evolutionarily relevant in this selection process. For example, it has been proposed that the large neocortex of primates evolved as an adaptation to cope with social complexity such as kinship networks, dominance hierarchies, and alliance formation ('the social brain hypothesis'; Byrne and Whiten 1988; Dunbar 1998). Others have suggested that the development of tools to extract food (Foraging or Technical Intelligence Hypothesis; Clutton-Brock and Harvey 1980; Rosati 2017) played a major role in the evolution of the large primate brain. Finally, it has been argued that the motivational and cognitive consequences of cooperative breeding played a major role in the evolution of human cognition (Burkart et al. 2009).

To test the general validity of hypotheses regarding the evolution of intelligence, it is important to also investigate the cognitive abilities of non-primate species. Wolves are actually a fantastic model species, because in contrast to chimpanzees, wolves live in family packs that largely depend on cooperative hunting. Thus, the socio-ecological niche of wolves is rather similar to the one humans have lived deep

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in pre-history: small-scale societies of hunter–gatherers (Hall and Sharp 1978; Marlowe 2005). Like wolves, traditional human groups rely much on meat. Meat is a high-value resource, but it requires a lot of effort to obtain when hunting is involved and success rates are rather low (Kaplan et al. 2000). To acquire food, humans, like wolves, often need to travel relatively far on a daily basis since these resources are widely dispersed (Marlowe 2005). Moreover, humans usually bring the food back to a central place, and the males provide females and their offspring with food (Kaplan et al. 2000). Similarly, during the puppy-raising period, the breeding male and other non-reproductive members of the pack will bring back food to a den or rendezvous site to share both with the breeding female and the puppies (see Chap. 3). Also, in terms of their social organization and social skills, wolves resemble traditional human groups: they live in family groups and cooperate during territory defence, raising of the young, hunting, and sharing of the food afterwards. This lifestyle requires not just high mutual tolerance but likely also skills like social learning (to learn how to hunt cooperatively), attentiveness, and coordination—all aspects that characterize our own species. Thus, overall, the 'similar' social organization and social skills of wolves and traditional human hunter–gatherer societies might reflect convergent adaptations to similar ecological niches (Hall and Sharp 1978), suggesting wolves may be a good model to investigate the evolution of human social skills.

Second, according to genetic studies, wolves are the closest wild-living relatives of dogs (Savolainen et al. 2002; Scott and Fuller 1965). The latter have shared the human environment for the last thousands of years (Frantz et al. 2016; Thalmann et al. 2013; Wang et al. 2014) and in some ways have become human's 'best' friends, i.e. social and working companions. It has been argued that since they are living in such close proximity to us, it is likely that they will enjoy advantages if they are able to communicate and cooperate with people (Miklósi et al. 2004). As such, dogs are thought to have developed cognitive–emotional responses, analogous to the ones that differentiate humans from other primates, in comparison to other animal species (Lakatos et al. 2009; Soproni et al. 2001), including chimpanzees (Bräuer et al. 2006; Hare et al. 2002, but see Mulcahy and Hedge 2012). Assuming that today wolves still strongly resemble the common Paleolithic ancestor of dogs and wolves (Lindblad-Toh et al. 2005), comparing their behaviours and cognitive skills gives us the possibility to explore the changes brought about by the evolutionary process of domestication,[1] i.e. the adaptation to the human environment. To date, many different hypotheses have been proposed to explain how exactly dog cognition might have changed during this process (Hare et al. 2002; Hare and Tomasello 2005a, b; Miklósi et al. 2003). We will discuss these hypotheses in detail in the light of the data on wolf–dog comparisons in the last chapter of this book.

[1] Domestication can be generally considered a selection process for adaptation to human agro-ecological niches and, at some point in the process, human preferences (Larson et al. 2014).

Finally, understanding wolf cognition and behaviour in itself and in comparison to dogs has a high practical relevance. First, a better understanding of wolves may actually pave the way for their return into our daily lives in light of the fact that wolves are spreading all over Europe regaining their past distribution. The return of the wolf into populated areas, however, does posit many challenges in terms of the protection of livestock, and it will be important to find the means for an acceptable coexistence. Understanding the behaviour and motivation of wolves might help in that regard.

Moreover, understanding differences and similarities between wolves and dogs may contribute to the development of socialization and training techniques that can facilitate the life of dogs and on the other hand help debunk some problematic but still highly popular notions that owners should behave 'like alpha wolves' in order to naturally educate their dogs. A closer look at this notion reveals that it is often a supposed justification for the use of force, inhibition, and aggression to control dogs' behaviour. The assumption that owners should behave like 'alpha' wolves is wrong on so many levels. To start with, as we shall see, wolf packs are largely based on affiliative and cooperative relationships with high levels of tolerance; hence, using wolf social behaviour to justify any form of aggression is incorrect (as well as entirely unethical). Second, while wolves and dogs are closely related, their social interactions with each other and humans are not the same but an outcome of the domestication process. So yet again, using a wolf model—especially the wrong one—to inform training aspects is inaccurate. Finally, we humans are primates, and the challenge, joy, and uniqueness of a fruitful and positive relationship with dogs is to find a common language, which can engender a strong positive bond between us, since what is certain from behavioural research is that for both canids and primates, social bonds are massively important.

1.2 How Wolves Became Dogs . . . Maybe

The domestication process is associated with rapid and extensive changes in phenotypic traits, either under the direct pressure of artificial selection by humans or as a result of adaptation to new habitats created by humans (Larson and Fuller 2014). Actually, the first animal to turn domestic was the wolf. This is one of the most intriguing domestication processes as wolves are highly successful group-hunting predators and are potentially dangerous to man (Linnell et al. 2002); the more as Paleolithic wolves may have been much less shy of humans than present day wolves, due to the lack of any severe hunting pressure. Nevertheless, of all domesticated species, dogs are probably those that form the closest social relationship with us. Based on many recent publications of genetic studies, the domestication process started about 15,000 to max. 30,000 years ago (Frantz et al. 2016; Larson and Bradley 2014; Skoglund et al. 2015; Thalmann et al. 2013; Wang et al. 2015) and happened somewhere in the Old World, however, where exactly is less clear (Freedman et al. 2014; Pang et al. 2009; Shannon et al. 2015; Thalmann et al. 2013; Wang et al. 2013; Wang et al. 2015). It is also not quite clear how many

independent wolf populations were involved in how many founding events (Botigué et al. 2017; Thalmann and Perri 2018). There is, for example, growing evidence that the wolf ancestral branch of dogs is now extinct (Bergström et al. 2020; Freedman et al. 2014), which is not surprising as many species are dynamically changing over time.

Despite these debates, most researchers agree that dogs were well established across Eurasia by the late Pleistocene. While during the Mesolithic period, humans lived in nomadic hunter–gatherer societies with a geographical overlap with wolf populations, with the climate change from the glacial times to more agreeable weather, humans started to settle in many areas, slowly engaging more and more into agriculture rather than living as hunter–gatherers about 10,000 BP (Richerson et al. 2001). A recent study suggests that five lineages of dogs already existed in the late Pleistocene, prior to the transition to the Holocene, and that very little wolf introgression is evident in these early dogs (Bergström et al. 2020). This suggests that, by this time, dogs and wolves were already genetically quite distinct.

There are two major scenarios relating to dog domestication: the human-selection and the self-domestication scenario.

1.2.1 The 'Human-Selection' Scenario

The 'human-selection' scenario (or 'directed pathway'; see Zeder 2012; Larson and Fuller 2014) suggests that people actively adopted wolf pups, raised them, and then selected the most docile animals (likely killing the others), which then reproduced with each other (Clutton-Brock 1992; Clutton-Brock 1995; Galton 1865). Based on pioneering studies by Belyaev and colleagues on silver foxes (see Box 1.1 and Chap. 11 for a discussion of these studies hypothesis), direct selection for a reduced fear response towards humans could result in approximately 50% of the population showing dog-like friendly responses after around 30 generations (Trut et al. 2009; Trut et al. 2004). However, the sustained effort to maintain strict control over the animal's breeding choices for so many generations appears, intuitively, somewhat at odds with the capacity and lifestyle of early humans (or in fact even modern humans considering the little control we have of free-ranging dogs' mating behaviours).

Box 1.1 The Tame Foxes and the Pioneering Ideas of Belyaev

The distinguished Russian geneticist, Dmitry K. Belyaev, was the first researcher proposing that the key factor of domestication is selection for *tameness* producing strikingly similar results in many species (Belyaev 1979; Trut et al. 2009). He hypothesized that by selecting against aggression and fright to facilitate human–animal symbiosis, significant behavioural responses (i.e. tame animals) appeared through destabilizing selection (*Destabilizing Selection for Tameness Hypothesis*; Belyaev 1979). The basis

(continued)

Box 1.1 (continued)
for this idea is the close relationship between the nervous and endocrine systems. By selecting for behaviour, the hormonal status of an animal can be changed, which in turn may have consequences for the ontogenetic development of the animals—after all, hormones regulate gene functions. Belyaev thought that this process was brought about by destabilizing selection, which results in 'breaking up previously integrated ontogenetic systems and thus leads to multiple phenotypic effects that seem genetically unrelated to the selected character, namely tame behavior'. This destabilization of the neuroendocrine control of ontogenesis seems to occur when stress factors in the environment appear or increase in strength (cited from Belyaev 1979). Since mammals share similar regulatory hormonal and neurochemical mechanisms, similar effects are expected across domesticated mammals.

To test his ideas, in the 1960s, Belyaev (1969) together with several colleagues, in particular with his student Lyudmila Trut, started a now 'textbook famous' experiment to investigate the effect of domestication. He used silver foxes bred for the fur industry and always selected the top 3–5% of animals that readily approached the hands of humans standing in front of their cages for breeding. This selection for presumably reduced fear and aggression towards humans led to animals that showed no fear and aggression but rather showed tail-wagging, whining, and licking of the experimenters' hand and face when approached as well as following the experimenter when allowed out of the cage (Trut et al. 2004). Moreover, the domesticated foxes had lower stress hormone levels than the unselected foxes, suggesting that the mechanistic basis of the tame behaviour is a change in the hypothalamic–pituitary–adrenal system (Trut et al. 2009).

The programme is still running today at the Cytology and Genetics Department of the Russian Academy of Sciences in Novosibirsk (for a lovely popular science book narrating the story of this project, see *How to Tame a Fox*; Dugatkin et al. 2017). Thanks to a chance meeting with Anna Kukekova, a Russian geneticist based in America who has been working with the foxes for many years, we were lucky enough to be able to visit the fox farm in Novosibirsk (in December!, Fig. 1.1). We were blown away by the dedication, persistence, and commitment of the team of scientists and keepers taking care of the animals against so many odds. It is an extraordinary living testament to the passion that science and animals can inspire! From a scientific perspective, it is also the best available model to better understand whether 'selection for tameness' in domestic dogs is indeed the trait which is (alone?) responsible for the wolf–dog differences we observe.

Fig. 1.1 Two enthusiastic faces, paying homage to Belyaev and his foxes at the Cytology and Genetics Department of the Russian Academy of Sciences in Novosibirsk

1.2.2 The Self-Domestication Scenario

The other scenario of dog domestication is the 'self-domestication' or 'commensal pathway', which proposes a two-stage process. In the first stage, dogs' ancestors started exploiting a new feeding niche provided by humans (Coppinger and Coppinger 2001, 2016; Hulme-Beaman et al. 2016; Larson and Fuller 2014; Larson et al. 2012; Zeder 2012). The beginning of dogs' domestication appears to coincide with the late Pleistocene megafauna extinction (Cooper et al. 2015) and is associated with a dramatically reduced prey availability, which resulted in a drastic fall in wolves' population size (Pilot et al. 2014). This also coincided with the disappearance of a subspecies, which exhibited a more robust craniodental morphology (Baryshnikov et al. 2009; Kuzmina and Sablin 1994; Leonard et al. 2007) likely specialized in hunting of and scavenging on megafauna (Fox-Dobbs et al. 2008; Germonpré et al. 2017). This subspecies was replaced by a less robust wolf likely originating from the Beringia region, where more reduced climatic fluctuation may have reaped less havoc with their environment and predator–prey equilibrium (Loog et al. 2020).

In this rapidly changing environment, some wolves might have discovered and slowly started to rely upon what could be found around human encampments that, at

this time, were largely nomadic. While these were certainly not food waste dumps (see Jung and Pörtl 2018), which emerged only thousands of years after the start of domestication, it might have been human faeces or other leftovers that humans could not digest, which attracted the animals. A new 'excess protein' hypothesis suggests that humans might have shared certain meat types with wolves (Lahtinen et al. 2021). Since humans are not fully adapted to a carnivorous diet due to the limited capacity of the liver to metabolize protein, they might have shared surplus of animal-derived protein with wolves/proto dogs especially during harsh winters when game is lean. While the authors suggest that humans actively shared their excess meat, no good argumentation is provided for it. Instead, they might as well have just left it, attracting the animal's presence. In any case, from the wolves' perspective, a new source of food linked to humans might have become available at a time of food scarcity.

Wolves being a highly adaptable species might have exploited this new niche, which likely leads to new adaptations selected for to increase fitness in the new environment (Zohary 2004). Indeed, a change in diet is linked to rapid adaptions. One study has found that differences in habitat, specifically precipitation, temperature, vegetation, and prey specialization, strongly affect wolves' craniodental morphology (Flower and Schreve 2014; Geffen et al. 2004; O'Keefe et al. 2013; Pilot et al. 2006). Despite living side by side and without physical barriers to prevent gene flow between them, North American wolf populations (Larson and Fuller 2014; Musiani et al. 2007; Stronen et al. 2014), as well as European wolf populations that have specialized in different prey and habitat use, show distinct genetic and morphological differentiation. This suggests that even without direct human control on the breeding choices of wolves, adaptation to a novel ecological niche could have resulted in morphological and genetic changes in direction towards dogs. Importantly, this natural selection process continues during the entire domestication process and is independent from the behaviour of the domesticator (Alter 2007; Heiser 1988; Zohary 2004).

A further catalyst for changes in dogs' temperament and behaviour may have been the rise in refuse availability, which accompanied the development of sedentary human communities associated with the agricultural revolution (Newsome and van Eeden 2017). While humans might have actively shared some resources (Lahtinen et al. 2021), the huge majority of dog food likely consisted of human faeces, which are surprisingly nutritious (Butler et al. 2018; see also Chap. 4), and animal or plant parts, which humans do not usually eat. Indeed, numerous studies have suggested that the availability of anthropogenic foods might alter a series of behaviours including predator–prey relationships, hunting behaviour, trophic interactions, and bottom-up and top-down processes as well as sociality, pack size, breeding rates, dispersal, and group density (Butler et al. 2018).

The importance of starch, and evidence of a shift in feeding ecology from hunting to scavenging, emerges from dogs showing genetic adaptations for starch digestion, which are absent in wolves (Axelsson et al. 2013) but already present in the ancient Newgrange dog (4800 BP, Botigué et al. 2017; Frantz et al. 2016). Analyses of DNA from ancient canines suggest that the adaptation was present already in some dogs

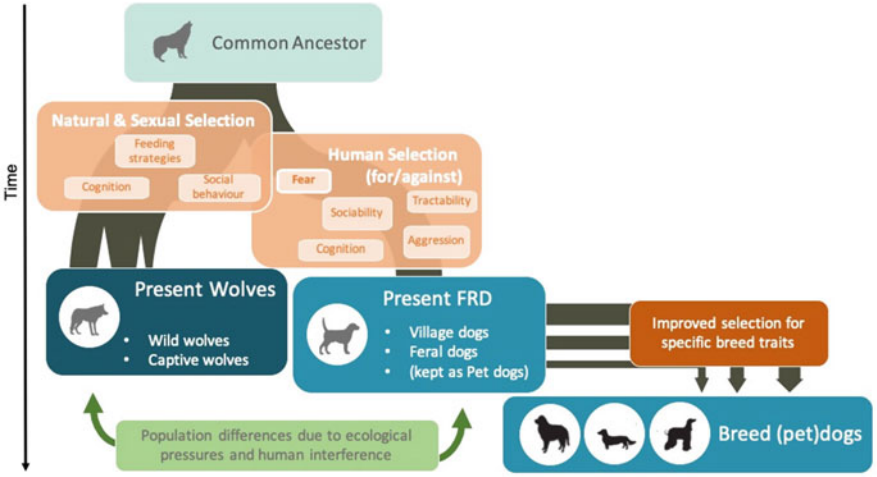

Fig. 1.2 Diagram of the dog domestication process. Figure reprinted from Trends in Cognitive Sciences, Range and Marshall-Pescini, Comparing wolves and dogs: current status and implications for human 'self-domestication, 2022, with permission from Elsevier (license number: 5297040356361)

living with hunter–gather human societies, but it emerged in full strength only after several thousands of years of living with humans, who had adopted an agricultural lifestyle (Bergström et al. 2020).

Overall, whereas it is likely that during the domestication process, from the very start, humans did put some selective pressure on the populations living in close proximity to them by removing unwanted animals (e.g. those that were too aggressive; see MacLean et al. 2019), it was only at a later stage of this domestication process, when the animals were likely already more amenable to being controlled, that humans directly selected for specific, desired traits (e.g. more attentive, responsive, cooperative, etc.) (Fig. 1.2).

However, this 'self-domestication' hypothesis that identifies a shift in wolves' niche as the initial stages of the domestication process is not without its critics. For example, as pointed out above, food waste dumps did not exist during the Pleistocene, and, if indeed food waste attracted wolves, it is unclear why other animals like foxes and jackals were not domesticated (Jung and Pörtl 2018). Moreover, wolves and humans likely encountered each other regularly since they were hunting the same prey, and there are some hints that they respected each other (Jung and Pörtl 2018). Ultimately, we will never know what happened, and most likely it was a combination of several factors leading wolves to being domesticated including that they are very social animals relying on cooperation with each other. Independent of the exact process, it is important to keep in mind that the domestication process involved initial stages, where humans lived as hunter–gatherers, then in small settlements, and finally in larger villages. Therefore, the change in the dogs' environment needs to be seriously considered, as well as the direct selection for certain traits by humans, when trying to understand the domestication process and the differences between wolves and dogs today.

Interestingly, a version of these two potential paths of domestication was already proposed by Darwin. He suggested that observed changes in domestic animals during domestication could occur either as methodical or unconscious selection (Darwin 1859). As implied by the names, Darwin saw the difference between the two selection processes as whether there was a purpose to improve the breed behind any selection or not. For example, if humans preserved the most valued and prevented the less valued individuals from reproducing, without any thought of altering the breed, he would term it unconscious selection. However, at the same time, humans would hope that the preserved animals would produce offspring with similar traits (see Bidau 2009 for a nice review on Darwin's ideas).

Building on Darwin's idea, we would argue that there are actually three types of selective pressures that formed and are still forming dogs. First, we often select animals for specific phenotypic traits that we would like to maintain and promote in the population (improved selection)—this is probably mostly, but not exclusively, conscious. Then there is selection 'against' a specific trait, which can be both conscious and unconscious. Unconscious selection likely defined many 100 s of years of cohabitation and still does in the free-ranging populations—e.g. too bold/aggressive/pushy animals get killed. And then, finally, there is likely also a selection process, which is not directly linked to human decisions (conscious and unconscious) but is rather determined by 'environmental/conspecific' selection. This was probably important during early domestication but still applies to FRDs today. It is what we usually refer to as natural and sexual selection in non-domesticated species and refers to the adaptation to the environment and the selection processes deriving from mate choice. This raises the question of how much the process of domestication is an intentional process based on human's deliberate decisions (Morey 1994). Or, at least in part, a 'self-domestication' process, where wild animals adapted to new, man-made ecological niches.

To sum up, while the self-domestication hypothesis suggests that dog behaviour evolved as a result of the combined pressures of natural and sexual selection that have enabled dog populations to adapt to a new niche that differs from those of grey wolves (see Fig. 1.2; Chaps. 3 and 4), as well as artificial selection imposed by humans, the human-selection hypothesis, as the name implies, focuses on the artificial selection.

1.3 Wolves and Dogs Today

Having outlined how the domestication *event* may have started, it is important to understand that domestication is in fact an *ongoing process*. Whereas it is perhaps easier to see how dogs continue to evolve today because it happens in front of our eyes, it is important to remember that also wolves did not 'stop evolving'. This is also why we should not refer to today's wolves as dogs' ancestors, but rather as their 'closest living relatives'.

The wolf population(s) giving rise to dogs during the early phases of domestication are likely extinct (Freedman et al. 2014; Thalmann et al. 2013). The wolves

living during the Pleistocene in Northern Eurasia and America represented a continuous population genetically and morphologically (e.g. a skull shape allowing for much greater bite force) distinct from the wolves living in this area today (Hofreiter 2007; Leonard et al. 2007). They were likely adapted to hunting and scavenging large ungulates such as bison (*Bison bison*) and horses (*Equus lambei*) and vanished with the extinction of the megafauna in the late Pleistocene (Leonard et al. 2007). Today's wolf populations all derive from a single wolf population from the Beringia areas, which successfully survived the megafauna extinction (Loog et al. 2020). In Europe, the haplogroup associated with the Beringian wolves also substantially decreased in frequency likely due to the same ecological processes (Pilot et al. 2010). The extinction of the megafauna and the resulting bottleneck in wolves soon after their divergence from dogs implies that at the onset of domestication, there was substantially more genetic diversity for selection to act upon than is present in our wolves today.

In the course of their history, wolves have undergone severe 'genetic bottlenecks', i.e. periods of their existence in which as a population they underwent drastic and significant reductions in numbers (Fan et al. 2016; Pilot et al. 2014). In recent centuries, these bottlenecks were caused by humans; however, for earlier cases, it is not as clear. In general, how severely humans affected wolf populations depends on location, which resulted in different degrees of genetic variability in populations across Eurasia as well as in America. For example, populations from Siberia and Mongolia show high genetic variability, whereas Italian and Iberian populations show low variability (Pilot et al. 2014), which probably reflects hunting pressure by humans. In North America, wolves originated (most likely) from a single expansion from Beringia, and as a result, their genetic variability has been low to start with, due to a process known as 'founder effect', which is similar to a population bottleneck.

Severe hunting pressures by humans on wolves may have effectively selected for 'shyer' animals, in that more elusive, fearful, maybe nocturnal animals may have succeeded in evading hunters more successfully than bolder ones. Interestingly, circumstantial support for the possibility that different hunting pressure between American and European wolves may have affected wolves on the shyness–boldness axis comes from the general perception of zookeepers that European wolves, compared to American ones, are more skittish, reactive, and shy, leading most centres to prefer either American or Arctic wolves that do not mind the presence of visitors as much as European wolves do. However, it is still possible that the inadvertent selection for shyer wolves might have also resulted in the selection for correlated traits such as higher aggression (Fadel et al. 2016; Wright et al. 2012).

The majority of the dogs we meet today at least in the Western world are modern breeds that originated from recent, stringent breeding efforts during the last 200 years (Lindblad-Toh et al. 2005; von Holdt et al. 2010). This strong artificial selection to breed dogs with specific characteristics to fulfil certain functions (e.g. herding, guarding, hunting) (Careau et al. 2010; Coppinger and Coppinger 2001; Svartberg 2006; Zapata et al. 2016) is responsible for the striking morphological differences among dog breeds (Ostrander et al. 2000; Spady and Ostrander

2008; Zapata et al. 2016) but also for a reduction in their genetic variability at least in pure-bred animals (Lindblad-Toh et al. 2005).

Another important aspect is that while wolves and dogs have clearly diverged in morphology, behaviour, physiology, and genetics, they can still produce fertile hybrid offspring. Thus, in terms of the biological species definition, they cannot be considered two different species, and, accordingly, dogs are often referred to as *Canis lupus familiaris*, i.e. as a subspecies of wolves. However, this is somewhat problematic, since there is also evidence that wolves mate with coyotes and produce fertile offspring (e.g. Bohling et al. 2016; Hinton et al. 2018; Mech et al. 2017) suggesting that maybe all *Canis* species can successfully interbreed and thus could be considered as a single species. On the other hand, it is clear that wolves and dogs differ in many aspects and are adapted to different ecological niches. Accordingly, and to facilitate terminology in this book, we will refer to wolves and dogs here as two species: *Canis lupus* and *Canis familiaris*.

However, the potential level of hybridization with dogs in any wolf population is an important point to keep in mind when comparing the two species, since 'hybrids' may well behave differently than both their original species. Studies so far have shown that dog introgression in North American wolf populations is much less of an issue compared with Eurasian wolves (Pilot et al. 2018, 2019).

In summary, while we can assume that the change from a common ancestor to today's wolves might not have been as profound as the change observed from Pleistocene wolf to modern dogs, it is also unlikely that wolves, as a species, have remained unchanged since the start of the domestication process. Indeed, at least old-world wolves and dogs might actually have been selected for opposite sides of a continuum: shyness towards humans versus affiliation and closeness to humans. So, in the end, what we can investigate is how wolves and dogs differ from each other at this current stage of the domestication process. We are unable to go back in time and understand every part of this journey, but based on the differences and similarities in the behaviour of wolves and dogs, we can propose likely scenarios about the possible selective pressures that shaped the domestic dog.

1.4 Book Overview

Having outlined the important steps in the domestication process (see Fig. 1.2; Boyko 2011), in the following chapters, we will first introduce the main (past and present) research programmes which have engaged in this comparison of wolves and dogs and then discuss results from studies investigating different topics. The aim of this book is not to review all literature on dog and wolf behaviour and cognition but rather to focus on studies where direct comparisons between the two species were conducted and then discuss what we can learn from such results about the domestication process.

We start the book by introducing the important aspects that need to be kept in mind when comparing wolf and dog behaviour and the main research groups (past and present) that focused on the wolf–dog comparison (Chap. 2). We then

summarize the social ecology of wolves (Chap. 3) and dogs (Chap. 4) to give the reader an idea of the environment and the potential challenges that the two species have adapted to. In the wolf chapter, we will review studies from many different researchers studying wolves in the wild and in captive settings, while in the dog chapter we highlight the distinction between pet dogs and free-ranging dogs and largely focus on studies of the latter.

In Chap. 5, we review studies comparing the social interactions of wolves and dogs with conspecifics focusing on dominance, affiliation, play, and conflict behaviours. In Chap. 6, we outline the social relationship both species can form with humans if they have received intensive socialization. These two chapters provide a good overview of the differences in the animals' social relationships and form the basis for the next two chapters, which focus on social cognition. In Chap. 7, after outlining what social cognition refers to, we review studies that investigate the abilities of wolves and dogs to use human communicative cues and how they themselves might use communicative behaviours to reach certain goals. In Chap. 8, we analyse the cooperative skills of wolves and dogs both with conspecifics and humans and try to understand the mechanism underlying such skills.

In Chap. 9, we will explore how motivational factors and low-level mechanisms such as persistence and inhibitory control might influence how wolves and dogs solve the problems that we reviewed in the previous chapters. Chapter 10 is dedicated to the few studies investigating how wolves and dogs perceive their non-social environment paying special attention to their ability to learn and make inferences. Finally, in the last chapter, we will consider the various domestication hypotheses that have been proposed and critically evaluate which are supported by the available data and where future researchers may need to focus in order to further our understanding of the two species.

While reviewing all the different literature on wolf and dog behaviour, we came across the following note from Erik Zimen (1981, page 5), which we wholeheartedly embrace both in reference to our own research and also to all the other studies reviewed here:

'Naturally I ***(we)*** will try to paint as true as possible a picture. But who can claim to paint a picture free of error? The acquisition of knowledge, even when carried out with scientific methods, is an ambiguous process, often the result of constructive misinterpretations, sometimes of chance, and always dependent on the inquirer himself (***themselves***) as well as on his (***their***) social and political consciousness and environmental conditions. So, I (***we***) invite the reader to keep an open mind about what I (***we***) have to say'.

We would also like to add that our results, both observational and experimental, are, strictly speaking, only valid for the specific contexts in which we raise, keep, and experiment with our animals. Consequently, the results can only be generalized to a certain degree and remain a matter of informed interpretation. While we can somewhat tackle the question of the context specifically in regard to experiments by using diverse paradigms to ask the same question, in the end, we will need verification of our results in other wolf and dog populations (which we are working on ☺) to pinpoint if and how results are specific to the dog and wolf populations studied so far.