

Part 3

What If? Exploring Different Human Pathways

In this part, we consider alternative pathways in human evolution, and how we might better understand the different humans we might have been. We focus on different adaptive pathways in emotional dispositions, and open up new possibilities, such as situating Neanderthals as *different* but *equal* within our evolutionary story. We also consider how the concept of branching pathways may help us to move away from progressive narratives and better understand human origins as a pattern of compromises and vulnerabilities as well as strengths.

CHAPTER 8

What If? The Evolutionary Basis for Different Pathways

Abstract

All too often, we see our evolutionary past as some inevitable ladder of progression. In considering our emotional connections, it is easy to imagine that the increased external friendliness and sensitivity seen in 'modern' humans represents some progressive or superior development from a more aggressive past. However, a close consideration of how external friendliness changes in closely related species reveals a far more complex picture, with advantages and disadvantages to different evolutionary pathways, each displaying a different type of prosocial or collaborative behaviour.

There are always many possible evolutionary pathways, affecting brains, bodies and behaviours. Here, however, we focus on simple contrasts in the adaptive routes followed within our nearest living relatives, chimpanzees and bonobos, and those within our closest friends, wolves and dogs. This brings some insights into how an increased openness, and the capacities to develop new external bonds, may have evolved. We reveal that each evolutionary pathway

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brought both advantages and disadvantages, depending on context, rather than any specific pathway being a progression. Our similar physiological and behavioural adaptations under pressures to be more *tolerant* (discussed in Part 2) suggest that the same processes that occurred in these species also affected humans. An understanding of our evolutionary past as one of different alternative trajectories, and of possibilities and constraints along these, helps to frame our understanding of the process of human evolution, and the story of our origins.



Figure 8.1: Paths diverge in a wood. Photo by Beth Macdonald on Unsplash: https://unsplash.com/photos/P3rS8J1THi4?utm_source=unsplash&utm_medium=referral&utm_content=creditShareLink, with unrestricted use.

Introduction

The Road Not Taken

Two roads diverged in a yellow wood,
And sorry I could not travel both
And be one traveler, long I stood
And looked down one as far as I could

...

Two roads diverged in a wood, and I—
I took the one less travelled by,
And that has made all the difference

Robert Frost, 1916

If we look back on our lives, we can all think of key points at which there were different pathways to take, neither of which at the time seemed better or worse than the other but from which our choice made a significant difference to the rest of our lives. Robert Frost's poem 'The Road Not Taken'

epitomises some of these moments, in which we stand as if at a forked point on a path (Figure 8.1), and wonder what each alternative entails. We often later create a story of why our particular choice was the better one (Orr 2015).

It would be easy to consider changes that take place along our evolutionary journey, and particularly with the emergence of modern humans, as a simple progression towards humans becoming increasingly better, more social, more sensitive and more collaborative. As we have seen in the introduction to this volume, we tend to prefer to think of our evolutionary past as a natural progression towards a better human being (Anderson 2019; Porr and Matthews 2017; Porr and Matthews 2019). The reality, however, is quite otherwise: our evolution has been a series of alternative pathways, each with different advantages and disadvantages – a far more complex and more interesting story.

Different versions of human, living alongside each other, seem like something that should be part of science fiction. However, we know that our single existence as the only human species stands out as unusual in our evolutionary past. Before the last 50,000 years, various different humans were around at the same time, and often in the same regions. Each had followed a different pathway, with each equally viable at the time.

Often, differences between species were driven by adaptations to different ecological conditions. The separation of distinct evolutionary pathways at times of intense environmental unpredictability mark many of the major changes in human evolution. Moreover, extinctions of human species closely match climate changes (Raia et al. 2020). As we have discussed in Part 1, around 2 million years ago members of the genus *Homo* took a path towards increasing reliance on hunted meat, and so intense collaboration and interdependence. However, other hominins, the paranthropines, specialised more on a plant-based diet, followed a different evolutionary pathway and lived successfully alongside members of the genus *Homo* for at least 1 million years. Other, equally viable alternatives clearly existed throughout human evolution. Their brains, bodies and social lives were probably *even stranger than fiction*. Often, the circumstances that drove different adaptations are difficult to determine. The small-brained *Homo naledi*, for example, managed to survive perfectly well amongst much larger-brained members

of the genus *Homo*, around 250,000 years ago. Areas of their frontal cortex promoting a complex social understanding may have promoted collaborative behaviours (Holloway et al. 2018), whilst a smaller overall brain than other species would have been less energetically costly. Under different conditions, it might have been the descendants of these diminutive and small-brained humans, rather than larger-brained species of *Homo*, that took our place today. In short, there have been many different pathways in our evolutionary history. Both our tendencies to want to see our origins as a single story of progression and a lack of evidence tend to obscure their existence.

The differences between other closely related species of highly social animals can sometimes provide clues as to the differences between alternative species of human, not only physically but also in their minds, feelings and behaviours. Considering non-human animals can also be helpful because, whilst we find it hard not to impose a ladder of progression on humans, we readily understand that the differing adaptations that different animals show to their circumstances are comparatively neither better nor worse. The primate order is full of such examples. Closely related species can adapt to behave in quite notably different ways in response to subtle changes in their environments working with their existing evolutionary history. Fat-tailed dwarf lemurs (*Cheirogaleus medius*) in Madagascar hibernate to survive resource shortages, for example, whilst other lemurs live in different environments or adapt to resource shortages in different ways. These paths can also sometimes converge, not only genetically, when species interbreed, but also behaviourally. Similar challenges often provoke similar responses in different species, or at least responses that do the same job but in different ways. Differing hormonal changes seems to underlie monogamous relationships in differing species of lemur as a result of different evolutionary trajectories, for example (Grebe et al. 2021).

Other examples come from social mammals much more distantly related to us, as we have seen in Chapters 1, 4 and 5. A fascinating example of subtly differing pathways is provided by African wild dogs (*Lycaon pictus*) and grey wolves (*Canis lupus*). These closely related social canids are both highly collaborative and share very similar social structures. They hunt together, raise offspring collaboratively, take risks to defend each other, and share food. Nonetheless, these two different species show subtle differences that

reflect slightly different ecological conditions, existing adaptations, or even just chance. African wild dogs' social communication focuses particularly on vocalisations, notably coughs, and on ear movements, whereas wolves are somewhat more dependent on facial expressions. African wild dogs (as discussed in Chapter 1) are the most internally socially cohesive of all canids, supporting the ill and injured. It might be easy to decide that they are the most social, and most collaborative. However, they are also more territorial and defensive towards outsiders than wolves can be. Neither one nor the other is 'better', or even more social, but these apparently very similar species are simply collaborative in a different way. Whilst we might prefer a simple story of one species being *better* than another, other highly social animals demonstrate that the reality is far more complex.

We particularly struggle to apply these understandings to humans. Often, we seem only able to think about ladders of progression, and see all humans that show differences from ourselves as inferior. Moreover, even though we know that different branches of recent humans have converged, blurring the distinction between what we think of as our own species and other contemporaries, we prefer to focus our attention on 'our' ancestors, and elevate these people above others. Even using the term 'modern humans' for people alive today, and their ancestors evolving in Africa from 300,000 years ago, is problematic, implying some sense of betterness or progression. *Homo sapiens* is no better than other, now extinct species of humans (what makes our species more wise?). We just do not have a widely understood and accepted term for ourselves that does not imply superiority.

Finds evidencing the increasingly diverse species of humans living after 300,000 years ago, and contemporary with the ancestors of modern humans, have pushed the beginnings of a reappraisal. One suggestion has been to see human evolution not as a ladder but as a braided stream (in which all humans flow or evolve in the same direction along parallel paths). This may be an improvement on a simple ladder but it is far from without problems. The reality is that different species of humans, like other animals, often adapt in *different* directions. One fascinating example is the possibility that Neanderthals hibernated (Bartsiakas and Arsuaga 2020). This is far from a ridiculous suggestion as Neanderthals may have adapted to resource shortfalls much like the fat-tailed dwarf lemur. It would, however, be an adaptation that meant Neanderthals travelled along a notably different direction than

modern humans did, not only in physiology but also, in turn, in its effects on social behaviour. The possibility raises all kinds of questions around how hibernation might have been managed within an essentially human society. It seems more like science fiction, yet these very 'what if' questions around adaptations that seem radically unfamiliar are important to ask. Of course, the idea of branching pathways proposed here, which may sometimes coalesce, and sometimes lead in very different but equally viable directions, still oversimplifies what might be better thought of as a multidimensional set of pathways in which there are different domains of adaptation.

However we choose to represent our recent evolutionary trajectory, and here we think in terms of different pathways, the key issue is that of understanding differences without imposing value judgements. This seems to be a particular challenge with mind or emotion. As we have seen in Chapter 3, there are real differences in mind within our populations, all too often seen as inferiorities, making the challenge of understanding differences without a value judgement all the more important. Developing our understanding of how the emotional dispositions of closely related species can be different, with advantages and disadvantages according to context, and even equally social or collaborative, albeit in different ways, may be one way to help us rise to these challenges.

Here we draw on our knowledge of different branches of emotional dispositions taken by closely related species to better understand the different pathways that may have been taken by humans in the past. In the case of non-human animals, it can be easier to acknowledge that subtly different branches may be neither better nor worse, more nor less social, and nor more or less collaborative than either other, but are rather differently social or differently collaborative. Understanding the emotional and behavioural changes occurring in recent human evolution as being alternative pathways affecting emotional connections may help us understand many of the differences between archaic humans, such as Neanderthals, and modern humans.

Each point of divergence along the different evolutionary paths offers many different possible directions of travel, which may result in different divergent aspects of brain, biology or behaviour. Here we focus particularly on the different pathways in emotional connections brought about by changes in

tolerance (discussed in Part 2) and their implications for our understanding of human origins. In Chapter 9, we then apply this understanding to interpretations of our close cousins, Neanderthals.

Alternative evolutionary pathways in other species

How different pathways towards or away from external tolerance or ‘friendliness’ play out in closely related species can provide us with useful insights into the advantages and costs of these alternatives in our own evolution, and the ecological and social context from which increasing externally social humans emerged.

In particular, the changes we see in bonobos, in contrast to their close relatives chimpanzees, and dogs, in contrast to their close relatives wolves, provide us with potential analogies for similar pathways in our own evolution. In both cases, we see how, in closely related species, changes in ecology and demography have driven changes in neuroendocrine function. In each case, particular social and ecological contexts have driven changes in emotional preferences, capacities and vulnerabilities and enabled new types of relationships to emerge. Whilst, typically, dogs and bonobos are seen as ‘friendlier’, we argue that neither pathway can easily be identified as better or worse, or more or less social or collaborative, but, in contrast, demonstrate subtly different adaptations and subtly different types of collaboration.

Contrasts in tolerance between chimpanzees and bonobos

Chimpanzees and bonobos are closely related and share many common characteristics. In fact, many people might struggle to tell them apart. Both chimpanzees and bonobos share cognitive and emotional capacities to build strong reciprocal alliances within their group, including to non-kin, and, in both, there is a certain amount of mobility between groups, mostly by females. However, there are notable differences in the levels of aggression, both within and between groups, as discussed in Chapter 4. Only bonobos can *feel comfortable* enough, when meeting other groups, to be generous to unfamiliar individuals and to share food (Lucchesi et al. 2020).

Differences in social behaviours between these two species may relate not only to random genetic drift through the geographic isolation of bonobos

but also to how their distinctive ecological circumstances influence the advantages and disadvantages of different social behaviours (Gruber and Clay 2016). Bonobos benefit from living in environments with more stable and reliable resources than those occupied by most chimpanzees. This has several implications. Firstly, female bonobos carrying young do not have to travel as far to find enough food, and so have more energy to spend in alliance formation, which in turn affects the ability of males to form aggressive alliances. Secondly, more stable and reliable resources lead to reduced female competition (Clay, Furuichi, and de Waal 2016). Furthermore, less widely distributed resources also mean that bonobos travel in larger groups, making it much less likely that any individuals or small groups would be vulnerable to attack (Furuichi 2009; Wilson et al. 2014). In effect, these subtle differences mean that female bonobos gain less from competition and more from collaboration than do female chimpanzees, and that intergroup aggression is less potentially advantageous. Effectively, larger subgroups made up of several individuals are not 'worth' attacking, given little probability of success, and stronger female coalitions would also be more likely to defend against attacks. Both of these factors significantly reduce the potential advantages of entering into intergroup conflict (Furuichi 2009; Pandit et al. 2016). Being better at collaboration was more likely to pay off, in evolutionary terms, for bonobos than it was for chimpanzees. More tolerant and collaborative encounters also occur where resources are most plentiful (Lucchesi et al. 2020).

At least partly as a result of different ecological contexts, bonobos and chimpanzees thus followed different evolutionary pathways in relation to the levels of tolerance after their split 1.7 million years ago (Figures 8.2 and 8.3).

As selective pressures to collaborate increase, and pressures to compete aggressively are reduced, testosterone production in bonobos, in contrast to chimpanzees, also begins to decline. As discussed in Chapter 4, the effect of these variations is seen in differences in androgen pathways, and so in reduced aggression and greater potential for intergroup interaction in bonobos (Hare, Wobber, and Wrangham 2012). However, as we have seen in Chapter 2, selection pressures acting to change hormone systems tend to have broad effects. Differences in testosterone thus also have wide effects beyond the specific behaviours being selected for (Hare, Wobber, and Wrangham 2012). Reduced testosterone not only leads to bonobos

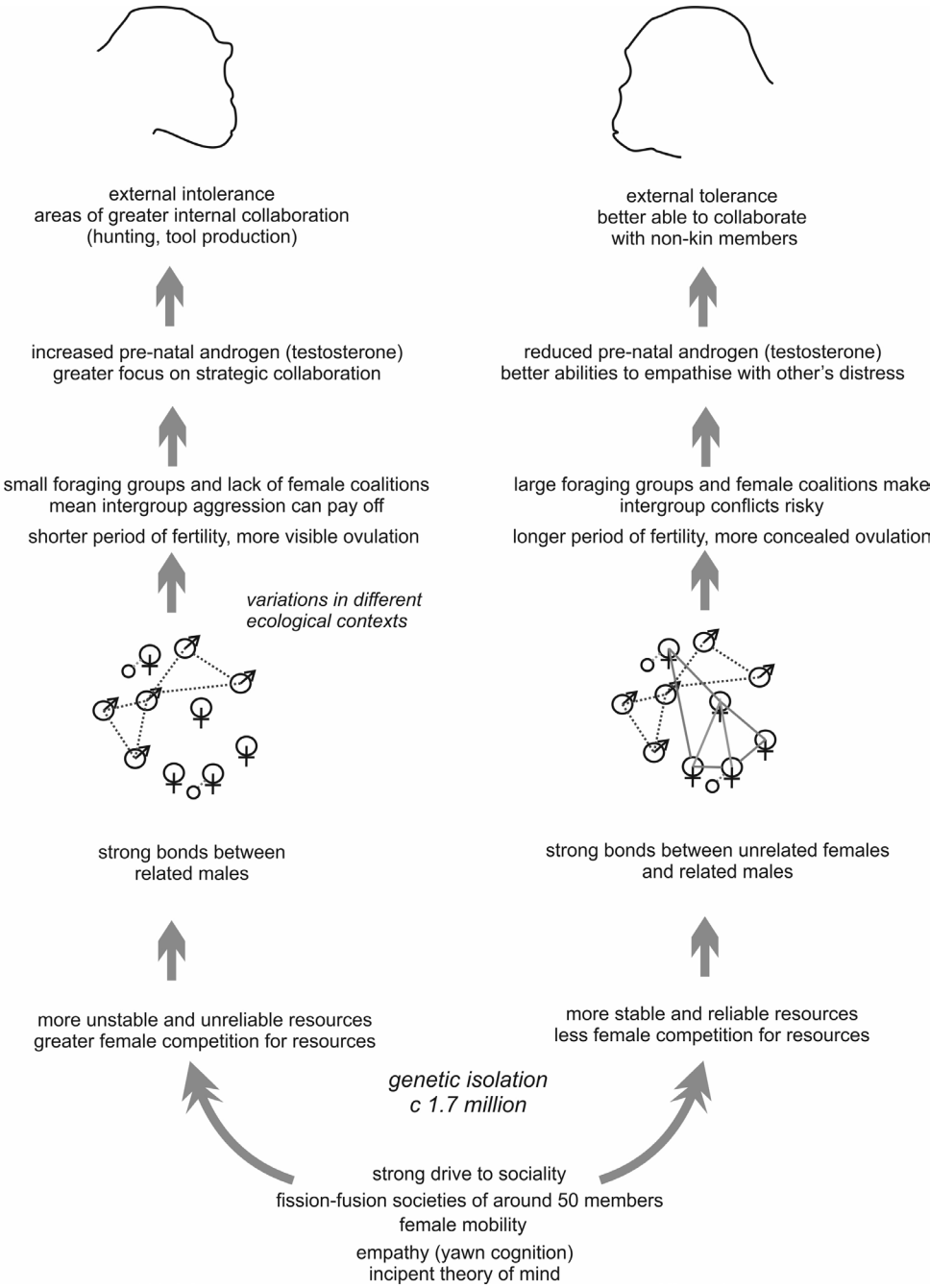


Figure 8.2: Ecological contexts influencing differences in social behaviour between chimpanzees and bonobos. Penny Spikins, CC BY-NC 4.0.



Figure 8.3: Male chimpanzee (left), showing marked brow ridge, and male bonobo (right). Rennett Stowe (chimpanzee image) and natataek (bonobo image), respectively, CC BY-SA 3.0, via Wikimedia Commons: [https://commons.wikimedia.org/wiki/File:Composite_image_of_male_chimpanzee_\(left\)_and_male_bonobo_\(right\).jpg](https://commons.wikimedia.org/wiki/File:Composite_image_of_male_chimpanzee_(left)_and_male_bonobo_(right).jpg).

retaining aspects of juvenile behaviour but also affects wider elements of behaviour, physiology and physical appearance. Bonobos have flatter faces, with reduced brow ridges in comparison to chimpanzees, as well as a more juvenile face shape. They also have reduced cranial capacity and depigmentation of their lips and tail tuft (Hare 2017). Bonobos are also less aggressive and more prosocial to non-kin within their group than chimpanzees are (Tan and Hare 2017), and in a wider range of different contexts. Laboratory experiments have even demonstrated that bonobos are simply more willing to be altruistic to strangers and to give food away accordingly (Tan and Hare 2013).

Research into bonobo and chimpanzee physiology, neurology and behaviour continues to reveal potentially important differences. There are also some suggestions that changes in other hormones may have had a role to play in the differences between chimpanzees and bonobos. Bonobos show a greater socio-emotional competence, and are more ready to provide consolation to others in distress (Clay and de Waal 2013), and to offer to help without it being solicited (Tan, Ariely, and Hare 2017), suggesting that oxytocin-related empathetic responses to others are more prominent than in common chimpanzees. That they are more focused on eye contact

than chimpanzees provides further evidence of a more empathetic orientation to their interactions (Hare, Wobber, and Wrangham 2012; Kano, Hirata, and Call 2015; Stimpson et al. 2016). Indeed, bonobos are so socially focused that they will even sometimes prefer social interaction and play rather than a food reward (Warneken 2018). Getting on peacefully with others seems to have been so important to their survival that motivations to be sociable and to play can even override more basic motivations to eat. As research continues, further subtle but important differences are likely to come to light.

Different evolutionary pathways bring both advantages and disadvantages, and the levels of social tolerance seen in bonobos seems to come with certain costs. In fact, rather than see bonobos as simply more 'prosocial' than chimpanzees, it may be more appropriate to view them as social in different ways. They may be more focused on empathy and reduced competition, though perhaps less focused on technology and strategic collaboration. Though bonobos are as able to make tools in a laboratory setting, their use of tools in the wild is far more restricted than that of chimpanzees, for example. They seem to be too socially focused to be able to find technological solutions to problems. Not only is tool making less evident in bonobos but collaborative hunting is also much rarer, and much less of their diet is based on hunted meat than that of chimpanzees (Layton, O'Hara, and Bilsborough 2012). This may be because collaborative hunting often involves rather more strategic collaboration than empathetic collaboration. Likewise, whilst chimpanzees are far more reluctant to give away food than bonobos are, they are *more* willing to help with tools (Krupenye, Tan, and Hare 2018). For bonobos, interactions with tools seem to turn into a social game. Rather than hand the experimenter a tool that is needed, bonobos are more likely to tease them (Krupenye, Tan, and Hare 2018).

Increased juvenile behaviour, and increased playfulness, is a common element of changes associated with increasing tolerance (Wrangham 2014). Whilst play behaviour is important in imagination and social bonding, it can come at the cost of achieving a goal for which technology is required.

Contrasts between two other closely related species, this time not *our closest relatives* but *our closest friends*, wolves and dogs, provide us with a further significant glimpse into how increasing tolerance may have emerged.

Whilst we look like other apes, and share many social and cognitive features, there are many emotional similarities we share with social carnivores (as discussed in Chapter 1).

Differences in out-group tolerance
<ul style="list-style-type: none"> – Intergroup encounters are often aggressive in chimpanzees, and are more passive in bonobos (Sakamaki et al. 2018; Sakamaki et al. 2015). – Bonobos are known to share food at borders (Fruth and Hohmann 2018). – Bonobos can be altruistic to strangers (Jingzhi Tan and Hare 2013).
Key ecological/structural differences
<ul style="list-style-type: none"> – More stable and reliable resources imply less female competition for resources in bonobos, added to which, females carrying young have less far to travel and more time to socialise (Clay, Furuichi, and de Waal 2016). – Bonobos travel in larger parties. Intergroup conflict is thus less effective, as there are fewer opportunities for picking off individuals or small groups (Furuichi 2009; Wilson et al. 2014).
Differences in social structure
<ul style="list-style-type: none"> – Bonobos have stronger female associations (Furuichi 2011). – Immigrant females bond first with females in bonobos (Sakamaki et al. 2015) but with males in chimpanzees (Boesch et al. 2008). – Bonobos have longer periods of sexual swelling, ovulation is more hidden, and paternity is more disguised (Gruber, Clay, and Zuberbühler 2010). – Bonobos respond more readily to the distress of others within their group (Clay and de Waal 2013).
Physiological differences
<ul style="list-style-type: none"> – In bonobos, testosterone stays at similar levels through development, but it rises in chimpanzees (Hare, Wobber, and Wrangham 2012; Stimpson et al. 2016; Wobber et al. 2010; Wobber et al. 2013). – Prenatal androgen in bonobos affects the balance of empathising-systemising (MacLean 2016; MacLean et al. 2017). – Bonobos show differences in vasopressin receptor genes, which may be implicated in differences in social bonding (Hopkins, Stimpson, and Sherwood 2017). – Possible differences in bonobos related to oxytocin production (Hare and Woods 2017).

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Social cognitive differences
<p>Social interactions</p> <ul style="list-style-type: none">– Bonobos show a greater socio-emotional competence (Clay and de Waal 2013).– Bonobos are prosocial in wider range of different contexts than are chimpanzees (Krupenye, Tan, and Hare 2018).– Bonobos voluntarily hand over food to an experimenter more readily than chimpanzees; chimpanzees more readily help with tool use (Krupenye, Tan, and Hare 2018).– Bonobos make more eye contact than chimpanzees and their gaze attention is more drawn to faces compared to the rest of the body than that of chimpanzees (Kano, Hirata, and Call 2015).– Bonobos are more motivated (and able) to collaborate than chimpanzees (Hare et al. 2007).– There are differences in neuroanatomical structures between the two species (Staes et al. 2019) and differences in socio-emotional circuits (Issa et al. 2018). <p>Juvenile behaviour and play</p> <ul style="list-style-type: none">– Bonobos show delay in social inhibition and no reduced tolerance to others with age, whilst chimpanzees do not (Wobber, Wrangham, and Hare 2010).– Bonobos use tools in a play context more readily than chimpanzees (Gruber, Clay, and Zuberbühler 2010).– Bonobos will also sometimes prefer social interaction and play rather than a food reward (Warneken 2018).

Table 8.1: Contrasting behavioural ecology of chimpanzees and bonobos.

Contrasts in tolerance between wolves and dogs

In the transition towards becoming dogs, descendants of wolves took a step further in tolerance than bonobos. They not only became comfortable with forming bonds with outsiders, even other species (ourselves), but, more than this, they are *driven to do so*, and are particularly adept at forming new emotional bonds.

As discussed in Chapter 7, wolves and dogs are close relatives. Modern dogs are relatives of the grey wolf, whose ancestors' ranges overlapped with early human populations in Eurasia. Humans will certainly have come into contact with wolves well before 'domestication', at the very least as competitors for hunted prey. Carnivore gnawing is common on archaeological sites where human remains are found, and wolf bones themselves are found on archaeological sites such as at Boxgrove, England, around 400,000 years ago; Zhoukoudian in China, dated to 300,000 years ago; and La Lazaret, France, dated to 150,000 years ago, for example (Serpell 2016). However, evidence for an unusually close relationship between humans and wolves dates to after 40,000 years ago, and postdates the arrival of modern humans into Europe and Asia. At this point, interactions with humans led the ancestors of grey wolves along two different contrasting pathways. Whilst we tend to focus on the wolf ancestors of modern dogs, it is easy to forget that 'wild' wolves did not remain the same but also followed their own path. Whilst wolves who were attracted to the opportunities provided by human occupation ultimately became the ancestors of domestic dogs, other wolves, those who avoided humans, led to modern grey wolves.

The close, social interactions that began to emerge between ancestral dogs and humans were aided by a similarly complex social cognition (see Chapter 7). Like humans, wolves have complex rules about social behaviour and have a sense of 'fair play', with certain gestures such as play bows, which are honest signals that they will not harm others (Allen and Bekoff 2005; Palagi et al. 2016). Like non-human apes, and humans, wolves seem to have the rudiments of a theory of mind (Horowitz 2011; Udell, Dorey, and Wynne 2008; Udell, Dorey, and Wynne 2011). Wolves show yawn contagion (one wolf yawning prompts others to do the same), a sign of empathy (Romero et al. 2014), and communicate emotions through facial expression. Moreover, as we have seen in Chapter 1, wolves have high levels of within-group altruism (Jouventin, Christen, and Dobson 2016).

Once again, differing resource availability may have played an important role in influencing changes in social behaviours between wild wolves and ancestral dogs. Wild wolves exploit animal prey that is unpredictable and concentrated, making them dependent on collaborative hunting to survive. Wolves living near human settlements, in contrast, will have been

exploiting a more predictable and widely dispersed resource. This favoured individual exploitation (Marshall-Pescini, Cafazzo, et al. 2017), whether it took the form of food scavenged from humans, food given to puppies or favourite adults by humans, or simply that a different suite of smaller prey was found near human settlements.

As a consequence of different resource characteristics, wolves living near human settlements seem to have become much less internally cohesive and more independent, even before any sustained interaction with humans (see Figure 8.4).

Typically, we compare wolves to dogs that are domestic pets. However, the contrast between wolves and modern free-ranging dogs, rather than with pet dogs (Figure 8.5), provides us with a useful comparison in natural social behaviour. Whilst wolves share the proceeds of a hunt fairly, provisioning others such as pups and lactating females, dogs only rarely share food. Although pack dogs sometimes hunt, they usually do so individually. Similar contrasts are seen in raising offspring. Wolves form often lifelong pair bonds, and also parent collaboratively, with other family members looking after the young whilst others hunt, and with pups dependent on adults for many months. Free-ranging dogs, on the other hand, tend to exhibit a very varied mating system, in which pair bonds are rare. They typically parent their offspring alone, are not provisioned, and pups have to be independent at a much earlier age (Marshall-Pescini, Cafazzo, et al. 2017). Free-ranging dogs even exhibit a novel genetic adaptation to digest starch which is not shared by wolves (Axelsson et al. 2013). The nature of emotional connections and social behaviour in wolves and free-ranging dogs has adapted, along each different pathway, to the distinctive constraints and opportunities each faced.

We might be forgiven for thinking of free-ranging dogs as less social, or less collaborative, than wolves since they are far less supportive of others in their pack. However, this would be far too simple a characterisation. Free-ranging dogs are much more outwardly tolerant than wolves. A need to tolerate proximity to humans may partly influence changes in pack dynamics in dogs. Wolves tend to be defensive or, even, aggressive towards other packs. However, free-ranging dogs are much more tolerant of outsiders. In some regions, previously pet dogs even commonly join free-ranging packs (Miklosi 2014). Packs themselves are also different in character. Wolf packs typically comprise a 'family' with a breeding pair and their relatives,

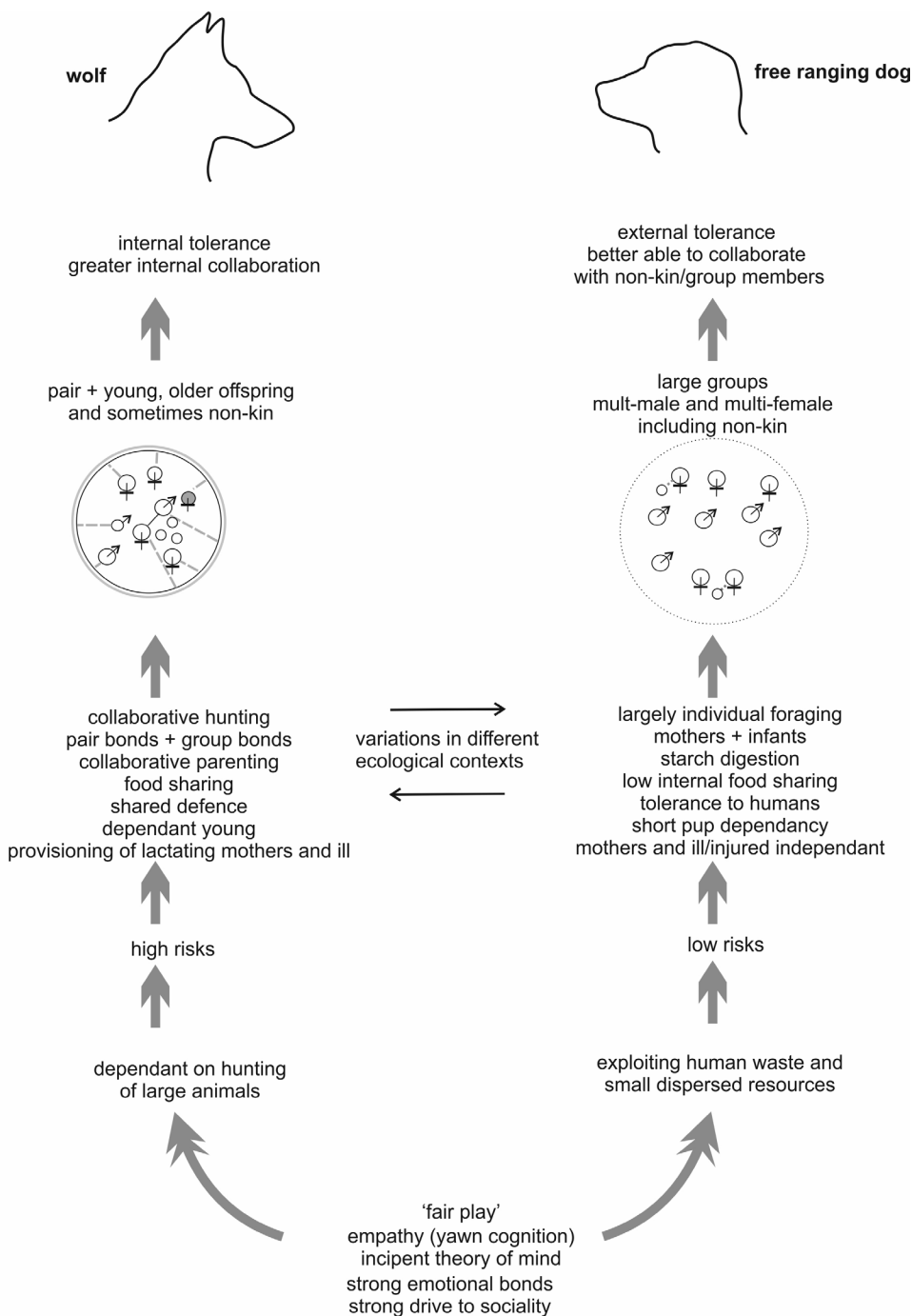


Figure 8.4: Ecological contexts influencing differences in social behaviour between wolves and free-ranging dogs. Penny Spikins, CC BY-NC 4.0.



Figure 8.5: Left: Eurasian Wolf showing long muzzle and short ears. Mas3cf, CC BY-SA 4.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/Canis_lupus#/media/File:Eurasian_wolf.JPG. Right: Free-ranging street dogs, showing shorter muzzle, flatter face and more pronounced ears, as well as changes in coat colouring. Andrew Currie from Toronto, Canada, CC BY-SA 2.0, via Wikimedia Commons: https://en.wikipedia.org/wiki/Free-ranging_dog#/media/File:Street_Dogs.jpg.

and non-kin only join packs when important members have been lost. Free-ranging dogs, on the other hand, maintain much larger pack sizes, and have a very fluid composition, made up predominantly of non-related animals. Free-ranging dogs can often form bonds with certain particular humans, and do so much more frequently and with greater ease than wolves.

Like the changes we have discussed above between chimpanzees and bonobos, these changes have been brought about by selective pressures acting on key genes affecting many aspects of biology and behaviour, and particularly on hormone systems (Dobney and Larson 2006; Trut, Oskina, and Kharlamova 2009; Wilkins, Wrangham, and Tecumseh Fitch 2014). Firstly, dogs have experienced a reduction in stress reactivity in comparison to wolves through changes in the hypothalamic–pituitary–adrenal (HPA) axis, adrenal glands and cortisol. In effect, unfamiliar dogs or people are simply less scary. Secondly, their abilities to form strong emotional bonds have changed, with changes in eye gaze-based bonding and oxytocin release (Buttner 2016). Close relationships with people can provoke a similar response in dogs themselves similar to that ‘warm fuzzy feeling’ we feel in our own human-to-human attachments (Nagasawa et al. 2015). A further effect of hormonal and wider genetic changes has been on the physical differences between wolves and dogs, which are more pronounced than those seen between chimpanzees and bonobos. Modern dog

'breeds' have been selected for certain physical and behavioural features. However, ancestral dogs, and certain 'wild' dogs, show common features in response to selection for increasing tolerance, notably shorter, flatter faces, reduced teeth size and reduced cranial capacity. Dogs' greater compliance/eagerness to please, lower aggression, and heightened social sensitivity may be brought about through changes in the ventral striatum, with changes in facial musculature allowing them to be more expressive, particularly when it comes to expressing vulnerability (Raghanti 2019).

A potentially interesting insight into the social behaviours of incipiently domesticated dogs comes from dingoes (Figure 8.6), discussed in relation to domestication in Chapter 7. Dingoes were separated from incipiently domesticated dogs around 6,000–8,000 years ago, and their group social behaviour seems to reflect that of incipient, rather than fully domesticated, dogs. In effect, they seem to represent some kind of middle ground between the outward-focused emotional connections of dogs and the inward-focused emotional connections of wolves. Rather than the disorganised group social



Figure 8.6: The Australian dingo has affinities with both wolves and free-ranging dogs, and is significant in sharing some elements of social behaviour with both. Jarrod Amore from Sydney, Australia, derivative work: Mark Marathon, CC BY 2.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Dingo_walking.jpg.

behaviour seen in free-ranging dog packs, dingoes have a monogamous mating system, and hunt and parent collaboratively, sharing food resources between themselves in a more wolf-like social manner (Miklosi 2014). They also tend to defend their territory and their groups, in contrast to the more flexible social group patterns seen in free-ranging dogs. Dingoes are also far more tolerant of humans than wolves. They maintain eye contact more than wolves, though less than dogs (Johnston et al. 2017). Whilst showing a more cohesive internal social structure, dingoes are still able to form close relationships with humans, albeit being less biddable than fully domesticated dogs. Whilst we may make simple contrasts between chimpanzees and bonobos, or wolves and dogs, in terms of inward or outward focus of emotional connections there are clearly shades of adaptation in between, as well as other possibilities we may not have considered.

As with bonobos, the greater tolerance seen in dogs does appear to have come at a price, or at least as a *compromise* (see Table 8.2).

Dogs have also become more socially sensitive and, in turn, more emotionally vulnerable than wolves, largely as a side effect of the neuroendocrine changes promoting their enhanced tolerance (Miklosi 2014). A narrow window of reduced fear reactions in wolf pups allows them to orientate themselves to features of their social and physical environment that are not dangerous and can be trusted, such as other members of the wolf pack, though this window closes after two to three weeks. However, in dogs, this window is expanded by several weeks, providing an opportunity to 'socialise' with humans and thereafter view them as potential allies. This downside of this increasingly behavioural plasticity is that it also brings with it a vulnerability to the effects of an unsupportive emotional context. Dogs suffer in isolation and crave social contact far more than wolves (Bradshaw 2011; Serpell 2016). As discussed in Chapter 7, it is not difficult to see how our human social sensitivities and emotional vulnerabilities share many similarities with those of dogs.

In both chimpanzees/bonobos and wolves/dogs, we can see how subtle changes in ecology, combined with existing social patterns, can be related to different pathways in emotional connections – towards or away family or external connections. The different pathways may give us unique insights into differing human emotional connections and social systems in the past.

<p>Interactions with non-kin and outsiders</p> <ul style="list-style-type: none"> – Aggression towards strangers is typical in wolves, although, occasionally, in exceptional circumstances, non-kin also join packs, such as when packs are missing key members (Miklosi 2014). Free-ranging dogs have a fluid group membership. The pack may defend itself from other packs. However, outsiders are often incorporated within packs, and dogs which have previously been ‘pets’ join free-ranging dog packs (Miklosi 2014). – Wolf packs are typically made up of a breeding pair and their offspring (a ‘family’), whilst free-ranging dog packs are typically made up of a large group of non-relatives.
<p>Ecology</p> <ul style="list-style-type: none"> – Wolves largely depend on high-risk and unpredictable food resources (hunted animals), which requires collaboration, whilst free-ranging dogs depend on widely distributed but more dependable resources from human settlements, which they typically exploit as individuals. Feral dogs have been known to kill larger prey. However, they also typically do this as individuals (Miklosi 2014). – Dogs have evolved an adaptation to digest starch (Axelsson et al. 2013). – Wolves have a single breeding season, whilst dogs typically breed twice a year (Miklosi 2014).
<p>Social structure</p> <ul style="list-style-type: none"> – Free-ranging dogs tend to live in larger groups than wolves, of varying size and in multi-male, multi-female communities. Wolves, in contrast, typically live in groups of around eight individuals, though there can be as many as 40 individuals in a pack. In some ecological conditions, wolves are mostly lone animals (Miklosi 2014). – Free-ranging dogs have a fluid group membership, made up of non-kin, whilst wolves’ packs are typically a ‘family’. – Free-ranging dogs match a linear hierarchy more clearly than wolf family structures. Whilst aggression is low when food is absent, aggression over food resources is common in free-ranging dogs (Miklosi 2014). Affiliative behaviours are common in wolves, which also display tactics to reduce tension through appeasing behaviour (such as looking away from a threatening approach). – Wolves develop long-term pair bonds, whilst free-ranging dogs have a very flexible mating system and can display monogamy, polygyny, polyandry and promiscuity (Pal 2003).

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Social structure
<ul style="list-style-type: none">– Wolf pups are reliant on adults of their species for seven to eight months, dog pups for only up to three months (Miklosi 2014).
Differences in within-group collaboration
<ul style="list-style-type: none">– Wolves share food, parent collaboratively, hunt collaboratively (often taking risks on behalf of the group), risk injury to defend the pack, provision pregnant and lactating females, and can provision the ill and injured. However, these behaviours are typically not seen in free-ranging dog packs (Miklosi 2014).– Dingoes, separated from incipiently domesticated dogs around 6,000–8,000 years ago, have a monogamous mating system, defend territories, hunt and parent collaboratively, and share food, possibly deriving from an ancestral wolf-like pattern (Miklosi 2014).– Conflict is observed more frequently in wolves than in free-ranging dogs. However, conflict is more likely to escalate to serious fighting in dogs (Marshall-Pescini, Cafazzo, et al. 2017).– Wolves outperform dogs in conspecific cooperation tasks (Marshall-Pescini, Schwarz, et al. 2017).– Wolves are more tolerant of proximity during feeding and do not monopolise food (Marshall-Pescini, Cafazzo, et al. 2017).
Neurophysiology
<ul style="list-style-type: none">– Dogs show a delay in the fear-mediating responses as puppies, creating a longer period when fear responses to novelty are reduced (about three to 12 weeks), and during which socialisation with humans occurs (Buttner 2016; Topál et al. 2005).– Dogs show reduced stress reactivity through changes in the SAM (sympathetic–adrenomedullary) system affecting ‘flight or fight responses’, and HPA axis affecting adrenal glands and so influencing the action of hormones such as glucocorticoids (e.g. cortisol) (Buttner 2016; Saetre et al. 2004).– Dogs show an oxytocin-mediated attachment pathway with humans, engaging in mutual eye gaze from an early age (Buttner 2016; Kaminski et al. 2009), which stimulates oxytocin responses (Kis, Ciobica, and Topál 2017; Kis et al. 2014; Kis et al. 2017).– Dogs’ social focus on humans means that they commonly prefer praise to a food reward (Cook et al. 2016).

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Forms of collaboration with humans
<p>Emotional connection</p> <ul style="list-style-type: none"> – Dogs (but not wolves) have a long period of potential socialisation with humans during development, in which their fear response is much reduced in comparison to similar aged wolf puppies. – Dogs (but not wolves) can develop a secure attachment to humans, acting emotionally like an attachment figure (Kurdek 2008), or better understood as close friend (Miklosi 2014), and providing emotional support (Miller et al. 2009). Humans, likewise, provide emotional support for dogs. – Wolves take longer to be socialised with humans (though this can be achieved). – Dogs have an oxytocin-based response to the human gaze (Kis, Ciobica, and Topál 2017; Kis et al. 2014; Kis et al. 2017; Thielke and Udell 2017). Din-goes establish eye contact more than wolves, but less than dogs (Johnston et al. 2017). – Dogs approach a novel object in a shorter time than wolves (Marshall-Pescini, Cafazzo, et al. 2017). <p>Strategic collaboration</p> <ul style="list-style-type: none"> – Wolves and dogs can collaborate with humans by indicating where food is, and adapting to a more collaborative or competitive human (Heberlein et al. 2016). – Dogs are more dependent/pay more attention to humans when moving together (dogs 'look back', whilst wolves do not) (Miklósi et al. 2003). – Once socialised, wolves are even better at strategic collaboration, and better able to interpret human social clues (Udell, Dorey, and Wynne 2008). – Wolves are better able to solve problems independently (Udell 2015).

Table 8.2: Contrasting behavioural ecology of wolves and free-ranging dogs.

Of course, it is easy to oversimplify. There are subtle but important differences, nonetheless, between changes occurring in wolves/dogs and those in chimpanzees/bonobos, and this will also have been the case with similar changes in different species of human. Whilst bonobos are principally less aggressive in both within-group and out-group contexts, dogs have taken tolerance much further, with a marked openness to new relationships including with ourselves. They also display more notable novel social and

emotional competences. Clearly, there are common directions in changes in behaviour as a result of pressures towards increasing tolerance and common genetic changes as a result, but, nonetheless, each species also follows its own trajectory.

Different but equal human evolutionary pathways?

How do contrasts between different emotional connections in closely related chimpanzees/bonobos and wolves/dogs help us to understand different pathways in past humans?

As we have seen in Part 1, humans have been under strong selection pressures to be more internally prosocial from at least 2 million years ago. These pressures affected the strength of emotional bonds in close-knit groups, emotionally motivated to care for each other. However, selection pressures towards wider emotional connections outside the local group, and even beyond that to imagined beings (Chapter 5), other species (Chapter 7) or even objects (Chapter 6), appear to have come to the fore in much more recent human evolution, and most particularly in changes we see occurring after 300,000 years ago. As with chimpanzees/bonobos and wolves/dogs there are plausible ecological explanations for the different pathways (Spikins et al. 2021). These latter changes share many similarities with those seen in bonobos and in dogs. Rather than a case of one superior, more intelligent or even more 'social' route, different pathways are taken by different species under various selection pressures, with each pathway bringing both advantages and disadvantages. In each contrasting set of pathways we also see a move towards more infant-like (paedomorphic) features in the bonobo/dog/modern human sister species, associated with increased tolerance, greater intergroup interaction and increased social sensitivity.

These similarities have a genetic component in humans, much as they do in chimpanzees/bonobos and wolves/dogs (discussed in Chapter 5). There is some evidence for certain levels of convergent genetic evolution between humans and bonobos, for example. Genetic changes associated with increased prosociality are seen in both these species which are absent from the chimpanzee genome (Theofanopoulou, Andirko, and Boeckx 2018). These changes have been seen in terms of shared adaptive shifts towards 'tameness', 'friendliness', 'domestication' or 'self-domestication' (Hare 2017; Hare, Wobber, and Wrangham 2012; Hare and Woods 2017;

Theofanopoulou et al. 2017). Similarities to changes occurring in dogs are even more pronounced. In both humans and dogs, selection for ‘tameness’ has led to reduced stress reactivity brought about through changes in the HPA axis and reduction in production of stress hormones such as cortisol (Buttner 2016), whilst novel types of emotional bonding are the result of changes in oxytocin pathways (Herbeck et al. 2017; Theofanopoulou et al. 2017). This reduced stress reactivity may well play a more important role in encouraging friendly approach behaviour than any changes in androgens, particularly since social aggression in humans is more clearly related, in terms of hormonal reactions, to a complex relationship between testosterone and cortisol, rather than to testosterone alone (Montoya et al. 2012).

There are other significant changes. A willingness to explore new situations and openness to new relationships, mediated through dopamine, is also common to both dogs and humans. In both species, this openness is achieved through an increased sensitivity to social environment, with changes in similar genes affecting this new ‘hypersociality’ of both species (Shuldiner et al. 2017). An increase in juvenile-like behaviour in both species, associated with more paedomorphic (infant-like) facial anatomy, may also have led to increased playfulness and, perhaps, imagination (Fuentes 2017; Nowell 2016). These changes also affect eye gaze. Bonobos, for example, are more focused on eye contact than chimpanzees are (Kano, Hirata, and Call 2015), and similar changes may be happening in modern humans, given our extraordinary sensitivity to facial expressions round the eye area and the significance of our movable eyebrows (Godinho, Spikins, and O’Higgins 2018). In both humans and dogs, changes related to social bonding hormones such as oxytocin may have a particular effect on eye gaze (Decety 2015; Decety et al. 2012; Kis et al. 2017). Contrasts *within* human populations, between individuals with different alleles of oxytocin receptor genes, for example, illustrate that higher effective levels of oxytocin are associated with better abilities to read emotions in others (Dannlowski et al. 2016). These same alleles are also associated with lower stress in socially supportive contexts (Chen et al. 2011), and greater tendencies to make relationships, trust others and form strong bonds, all of which are likely to be selected for under conditions in which friendliness is selectively advantageous. As we have seen in Chapter 1, oxytocin is important in our close relationships, creating a sense of warmth, comfort and security (Gilbert 2015a; Gilbert 2015b). These stronger emotional bonds not only functionally cement social networks but also buffer us from other stresses.

For both humans and dogs, their elevated sensitivity to social environment, coupled with a greater capacity to form new social bonds, brings both new vulnerabilities as well as new ways to counteract them. Dogs are extraordinarily socially sensitive and have a long period of sensitivity to surrounding social cues, accompanied by increased emotional vulnerability to any lack of socially supported interaction (Miklósi 2014). In humans, as in dogs, a greater developmental (behavioural) plasticity has led to an enhanced ability to learn, and an increasing openness (Miklosi 2014). Recent evolution leading to modern humans, and along a separate pathway to other archaic species such as Neanderthals or Denisovans, has also contributed to our heightened neuroplasticity (Sherwood and Gómez-Robles 2017). Both species thus benefit from an increasingly sensitive and plastic brain, with an elevated capacity to adapt after birth and outside of that which is under direct genetic control. These changes bring elevated capacities to learn from our environment, particularly during development, such as, in the case of humans, potentially aiding in the acquisition of complex language and complex cultural norms.

Comparisons with the contrasting pathways taken by chimpanzees and bonobos, and by wolves and dogs, give us an opportunity to bring into focus contrasting pathways in humans. It is not difficult to see that, in many ways, modern humans have taken the more externally tolerant pathway, much like that taken by bonobos or dogs, whilst other human species followed a different direction (Figure 8.7). Similar changes in emotional dispositions in modern humans share many similarities with the different pathways recorded in chimpanzees and bonobos, and in wolves and dogs.

To think only of two contrasting pathways is, of course, an oversimplification. Like the example of dingoes, who share some characteristics with dogs and others with wolves, there will be pathways in between. Moreover, other pathways will have led in entirely different directions. Nonetheless, the concept of equal but different pathways in emotional connections can help us move beyond ideas of superiority or sameness in interpreting the social lives and behaviours of our close relatives such as Neanderthals, discussed in Chapter 9.

Changes in emotional capacities and dispositions at this point of divergence need only to have been subtle to have far-reaching effects on human

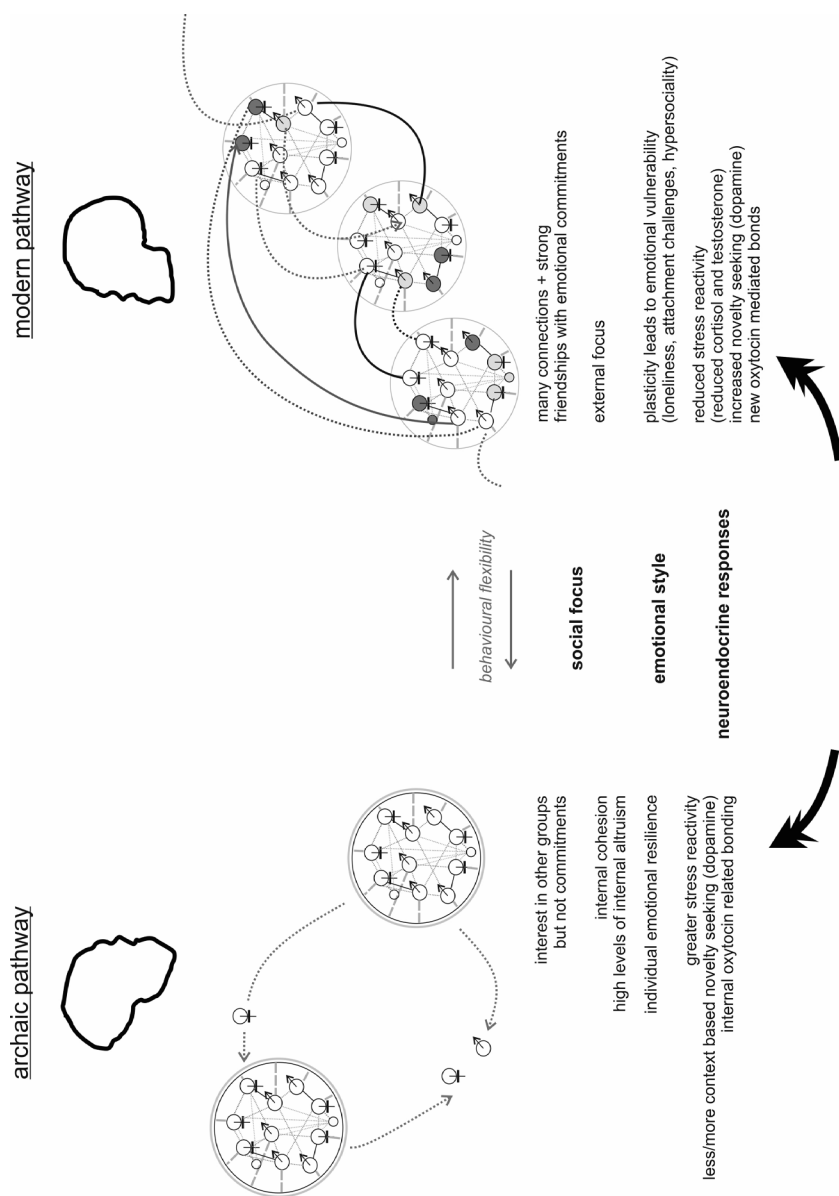


Figure 8.7: Potential changes in emotional dispositions along different pathways in human evolution 300,000 to 30,000 years ago. Penny Spikins, CC BY-NC 4.0.

social relationships. Extending our social network has far-reaching effects, for example. The number of people you might know and learn from, and who might be your potentially significant friends, increases dramatically if you are able to tolerate and approach unfamiliar individuals. Hill notes that, in recent hunting and gathering populations, individuals might reasonably expect to meet a thousand other people in their lifetime, compared to around 20 individuals in the lifetime of the chimpanzee (Hill et al. 2014). New types of mutually generous bonds with distant allies, maintained despite a gap of time and distance, also provide a remarkable degree of social buffering in times of shortfalls (as discussed in Chapter 5). These alliances can make a difference between death and survival. An elevated social sensitivity also allows cultural and social norms to become easily adopted, and for cultural ideas to spread, potentially helping innovations to buffer the effects of environmental changes and contributing to a large-scale social harmony. This elevated sensitivity may even have been instrumental in complex language abilities (Thomas and Kirby 2018). There is little doubt that this path, in the words of Robert Frost, '*made all the difference*'.

Though we should be wary of making comparisons which are too simplistic, there is much to learn from these differing pathways in *our closest living relatives* and *our closest friends* about our own evolutionary past.

As we have seen in wolves/dogs and in chimpanzees/bonobos, advantages brought by expanding the scope of social connectivity come with costs and compromises. The same evolved sensitivities that bring possibilities for high levels of cultural dynamism, extensive social connection and greater community resilience, come with elevated emotional needs and sensitivities. We all feel the costs of these evolved vulnerabilities in various ways.

At an individual level, as we have seen, we need close social support and emotional connection to thrive, and easily suffer in profound ways from loneliness or social isolation. We are liable to attachment disorders where genuinely caring relationships are lacking (discussed in Chapter 5) and, though we may have adapted new types of compensatory attachments (discussed in Chapters 6 and 7), even as adults we are easily weighed down by the fears, anxieties and even health effects that a lack of secure attachments bring. We want to belong, to help people, to feel significant and cared for. In emotionally supportive contexts, we reach out to help others and are

sensitive to their feelings. When the structures we need to support our emotional capacities and needs are not there, however, not only do we easily slip into anxiety or depression but we often take what we can get in terms of human connection, even if what we turn to hurts ourselves or others. Sometimes a lack of connection leads us to damage ourselves if we sink into addictions and, at other times, it can harm others if we lose a sense of reality and sacrifice principles to belong to any group that gives any sense of connection, however unhealthy.

At the level of our societies, our capacity to connect with people who are unfamiliar can unravel, particularly when we are anxious or fearful. It has been argued that changes in oxytocin and, with them, propensities not only to *tend* but also to *defend*, might have elevated tendencies to dehumanisation (Hare and Woods 2021). However, much of our shared biological responses to the differences that can fuel racism or other negative attitudes are ones which we share with other apes (Sapolsky 2017), as discussed in Chapter 4. Furthermore, again as seen in Chapter 4, oxytocin can also prompt *befriending*, and changes in hormonal responses can have complex behavioural implications within a cultural context. Rather, tolerance itself, in bringing with it large-scale connected societies, may be laying the basis for the level of social interaction that makes dehumanisation an issue, where previously interactions with others were rare. Simply being prone to a range of social anxiety, fears and feelings of helplessness and isolation is quite enough to fuel hatreds. Moreover, our acute social sensitivity means we are highly liable to ‘follow the crowd’, and our need to belong can make us override our sensibilities about others’ welfare. As the now-famous experiments of Stanley Milgram and Phillip Zimbardo have demonstrated, compliance with authority, rather than widespread individual evil, can make us cruel (Zimbardo 2011). Our modern industrialised societies seem some of the most alienating (Gilbert 2021). All too often, our emotionally vulnerable brains can be pushed too much to their limits by a lack of connection, and be so overwhelmed by the challenges of surviving without the right kinds of connection that there is little space for caring about other people or nature.

We can identify how our emotional vulnerabilities and needs for emotional connection were adaptive in the past. The evolutionary pathway our species followed can be judged a ‘successful’ one in terms of survival, expansion and population numbers. Amongst other changes, elevated tolerance and social

connection provided a buffer to resource shortfalls, a means of sustaining social relationships in the absence of loved ones, and an ability to find close friendships outside of human relationships to bolster losses or make us better people. That this pathway was 'successful' in these terms does not take away the emotional suffering that human sensitivities, needs for connection and emotional vulnerability sometimes brings, or the potential damage that humans can inflict on themselves or nature. We are, after all, just one species of many, with emotional responses and behaviours that have been cobbled together from existing structures along adaptive pathways entailing many compromises.

Implications

A closer look at our evolutionary past reveals a rather different story from the one we are used to in which our species is portrayed as being better than any others, and perfectly adapted.

We have already seen from Chapter 4 that evolution is far less ordered and predictable than we might imagine. Species adapt according to immediate circumstances, regardless of which better options might exist elsewhere in the longer term. We are lumbered with the back problems that our ancestral bipedal locomotion brings, for example, as we are too far along this track to move to something that might place less stress on our lower back, such as four-legged locomotion. Painful emotions such as shame evolved to motivate us to do what is needed to belong to a group, but they are far from an ideal means to do so, bringing not only great unhappiness but tendencies to follow group behaviours no matter the cost, and propensities to depression (Gilbert 2021). We would not have designed ourselves this way. Added to which, even when there is selection for one gene that might bring advantageous traits, since many genes are associated with each other, many other traits come along with the ride. Moreover, the very mutations on which adaptations depend occur by chance and there are also all kinds of complex epigenetic factors that influence which genes are expressed in which particular contexts. The more deeply we look, the clearer it becomes that we are far from perfect, or even perfectly adapted. It can seem remarkable that we manage to negotiate life with our evolved minds, bodies and feelings as well as we do.

A new perspective on differing adaptive pathways in tolerance, explored in this chapter, adds to this picture by bringing into focus not only the advantages but also the compromises that have been brought by changes in emotional responses.

There are several implications.

Firstly, an understanding that each evolutionary pathway brings compromises affects our interpretations of the archaeological and human evolutionary record. Most obviously, we might revise some of our interpretations of our closest fossil relatives. An understanding of differing but equal pathways in tolerance provides explanations for previously enigmatic aspects of Neanderthal behaviour, for example. Rather than being inferior, or simply the same, as our own species, Neanderthals may have had different types of emotional connections, and a different focus to collaboration (explored in Chapter 9). We might also consider some of the many other species of human from which our pathway has diverged in the past, or who have been contemporaries. Diminutive species such as *Homo naledi*, which had small brains that nonetheless had enlargements in areas associated with social and emotional processing, might be considered to be following a pathway with a particular focus on strong emotional connections, for example. We can and should widen the scope of our interpretations to consider different ways of being emotionally human.

Perhaps even more importantly, there are implications for our understanding of ourselves. We are naturally able to care about others and to collaborate to make things better, not only for our kin and friends but also contributing to the wellbeing of our wider communities or people more generally. Yet there is a price to pay for these capacities in terms of emotional vulnerabilities and sensitivities, and this price is something that can be obscured by a reassuring narrative of superiority. It is all too easy to plan our lives and societies around an idea of ourselves as independent, and emotionally invulnerable, beings. An understanding that our evolutionary history has been one of compromises, in contrast, highlights the significance and challenges of our emotional vulnerabilities. We may be far more willing to give things up for others than a traditional view of ourselves as independent and self-oriented beings would suggest, as we have seen through widespread

adherence to constraints on freedoms during the COVID-19 pandemic across the world. Yet recent times have also demonstrated that we are far more emotionally vulnerable, profoundly affected by our social and natural surroundings, prone to depression or anxiety through loneliness and a lack of belonging, or liable to be influenced by others, than we like to imagine.

Has our evolutionary story of superiority itself contributed to a disregard for the emotional costs that come with a lack of connection, perhaps even in this way adding to a sense of alienation in modern societies? It is difficult to know for sure. Nonetheless, perhaps a better understanding of our evolutionary history may help us to be more humble about our place in nature, and to recognise that we are vulnerable to the effects of social isolation or a lack of social safety. Only by creating supportive emotional connections can we be what we want to be.

Conclusions

We often think of human evolution as a progressive development of ever better forms of human, moving towards ourselves as some kind of pinnacle of evolutionary processes. There were, however, different pathways, and different types of human, many of which lie at the limits of our imagination.

Changes in tolerance and emotional connections in recent human evolution can easily be seen as advancements. However, when we consider how similar changes in tolerance play out within closely related species, those most closely related to us (chimpanzees and bonobos) and those most closely connected to our past ecological niche and present lives (wolves and dogs), it becomes clear that such changes present both potentials and pitfalls.

Studies of evolutionary changes in external social tolerance in closely related species cast insight into the types of changes that may have been taking place within recent human species. Particular ecological and social contexts may have allowed adaptations leading to external social alliances to become adaptive. As a result, one evolutionary pathway led to modern humans with new types of relationships and more extensive social networks. It would be too simplistic to see this as simply as an advancement or, even, as a more *prosocial* adaptation. Different evolutionary directions have

both advantages and disadvantages, and it may, perhaps, be more appropriate to see the alternative pathways lying between early modern humans and other archaic humans as different types of sociality.

By following our particular evolutionary path, we have benefited from an increased openness to new relationships, reduced stress reactivity in the presence of unfamiliar others, reduced aggression, and capacities to build new bonds. However, these adaptations also brought costs in terms of individual emotional vulnerabilities and needs for supportive and caring social contexts. We can easily feel isolated and lack the right kind of emotional connection, making us prone to depression or anxiety. In modern industrialised contexts, where social isolation seems to be particularly widespread, and where we all too often lack a sense of social safety or relationships based on trust, these responses are particularly common. Perhaps, if we recognise that we are not some pinnacle of a process of increasing perfection, but rather the product of alternative paths, all with compromises, we might find it easier to understand why we have both the emotional capacities and the needs that we do.

If we are honest with ourselves, we would probably admit that our traditional story of human origins gives us a reassuring sense of entitlement, or at least a reassurance of things falling into place. A closer consideration of our evolutionary past reveals far less of a sense of direction, and far more of a story of the influence of chance, compromise and vulnerabilities. This may be a good point in human history to pause and reconsider our place in the world around this somewhat different story.

Key points

- Different species of human in the past did not follow a ladder of progression towards ourselves but travelled along different evolutionary pathways. For humans, as for other highly social animals, subtle changes in ecology can create different selective pressures affecting tolerance and the focus of emotional connections.
- Although changes taking place in modern humans, in contrast to archaic humans, after 300,000 years ago cannot be seen as simply a contrast

between 'wild' and 'tame', there are, nonetheless, important parallels with similar changes taking place between both wolves and dogs, and chimpanzees and bonobos.

- A process of becoming more tolerant is not as simple as that of becoming more social or more collaborative, but rather one of greater social and emotional sensitivities, greater motivations to explore and to be playful, and social relationships with a more outward social focus at the potential expense of within-group collaboration.

References

- Allen, Colin, and Marc Bekoff. 2005. 'Animal Play and the Evolution of Morality: An Ethological Approach.' *Topoi. An International Review of Philosophy* 24 (2): 125–35.
- Anderson, Kay J. 2019. 'Modern Ontologies of the "More-than-Animal" Human: Provincialising Humanism for the Present Day.' In: Martin Porr and Jacqueline Matthews (eds.) *Interrogating Human Origins: Decolonisation and the Deep Human Past*: 56–71. Routledge.
- Axelsson, Erik, Abhirami Ratnakumar, Maja-Louise Arendt, Khurram Maqbool, Matthew T. Webster, Michele Perloski, Olof Liberg, Jon M. Arnemo, Ake Hedhammar, and Kerstin Lindblad-Toh. 2013. 'The Genomic Signature of Dog Domestication Reveals Adaptation to a Starch-Rich Diet.' *Nature* 495 (7441): 360–64.
- Bartsiokas, Antonis, and Juan Luis Arsuaga. 2020. 'Hibernation in Hominins from Atapuerca, Spain Half a Million Years Ago.' *L'Anthropologie* 124 (5): 102797.
- Boesch, Christophe, Catherine Crockford, Ilka Herbinger, Roman Wittig, Yasmin Moebius, and Emmanuelle Normand. 2008. 'Intergroup Conflicts among Chimpanzees in Taï National Park: Lethal Violence and the Female Perspective.' *American Journal of Primatology* 70 (6): 519–32.
- Bradshaw, John. 2011. *In Defence of Dogs*. Penguin.
- Buttner, Alicia Phillips. 2016. 'Neurobiological Underpinnings of Dogs' Human-Like Social Competence: How Interactions between Stress Response Systems and Oxytocin Mediate Dogs' Social Skills.' *Neuroscience and Biobehavioral Reviews* 71 (December): 198–214.
- Chen, Frances S., Robert Kumsta, Bernadette von Dawans, Mikhail Monakhov, Richard P. Ebstein, and Markus Heinrichs. 2011. 'Common Oxytocin Receptor Gene (OXTR) Polymorphism and Social Support Interact to Reduce Stress in Humans.' *Proceedings of the National Academy of Sciences of the United States of America* 108 (50): 19937–42.
- Clay, Zanna, Takeshi Furuichi, and Frans B. M. de Waal. 2016. 'Obstacles and Catalysts to Peaceful Coexistence in Chimpanzees and Bonobos.' *Behaviour* 153 (9–11): 1293–330.
- Clay, Zanna, and Frans B. M. de Waal. 2013. 'Development of Socio-Emotional Competence in Bonobos.' *Proceedings of the National Academy of Sciences of the United States of America* 110 (45): 18121–26.

- Cook, Peter F., Ashley Prichard, Mark Spivak, and Gregory S. Berns. 2016. 'Awake Canine fMRI Predicts Dogs' Preference for Praise vs Food.' *Social Cognitive and Affective Neuroscience* 11 (12): 1853–62.
- Dannlowski, Udo, Harald Kugel, Dominik Grotegerd, Ronny Redlich, Nils Opel, Katharina Dohm, Dario Zaremba, et al. 2016. 'Disadvantage of Social Sensitivity: Interaction of Oxytocin Receptor Genotype and Child Maltreatment on Brain Structure.' *Biological Psychiatry* 80 (5): 398–405.
- Decety, Jean. 2015. 'The Neural Pathways, Development and Functions of Empathy.' *Current Opinion in Behavioral Sciences* 3 (Supplement C): 1–6.
- Decety, Jean, Greg J. Norman, Gary G. Berntson, and John T. Cacioppo. 2012. 'A Neurobehavioral Evolutionary Perspective on the Mechanisms Underlying Empathy.' *Progress in Neurobiology* 98 (1): 38–48.
- Dobney, K., and G. Larson. 2006. 'Genetics and Animal Domestication: New Windows on an Elusive Process.' *Journal of Zoology* 269 (2): 261–71.
- Fruth, Barbara, and Gottfried Hohmann. 2018. 'Food Sharing across Borders.' *Human Nature* 29 (2): 91–103.
- Fuentes, Agustín. 2017. *The Creative Spark: How Imagination Made Humans Exceptional*. Penguin.
- Furuichi, Takeshi. 2009. 'Factors Underlying Party Size Differences between Chimpanzees and Bonobos: A Review and Hypotheses for Future Study.' *Primates; Journal of Primatology* 50 (3): 197–209.
- Furuichi, Takeshi. 2011. 'Female Contributions to the Peaceful Nature of Bonobo Society.' *Evolutionary Anthropology* 20 (4): 131–42.
- Gilbert, Paul. 2015a. 'The Evolution and Social Dynamics of Compassion.' *Social and Personality Psychology Compass* 9 (6): 239–54.
- Gilbert, Paul. 2015b. 'An Evolutionary Approach to Emotion in Mental Health With a Focus on Affiliative Emotions.' *Emotion Review: Journal of the International Society for Research on Emotion* 7 (3): 230–37.
- Gilbert, Paul. 2021. 'Creating a Compassionate World: Addressing the Conflicts Between Sharing and Caring Versus Controlling and Holding Evolved Strategies.' *Frontiers in Psychology* 11: 3572. DOI: <https://doi.org/10.3389/fpsyg.2020.582090>.
- Godinho, Ricardo Miguel, Penny Spikins, and Paul O'Higgins. 2018. 'Supraorbital Morphology and Social Dynamics in Human Evolution.' *Nature Ecology & Evolution* 2 (April): 956–61.
- Grebe, Nicholas M., Annika Sharma, Sara M. Freeman, Michelle C. Palumbo, Heather B. Patisaul, Karen L. Bales, and Christine M. Drea. 2021. 'Neural

- Correlates of Mating System Diversity: Oxytocin and Vasopressin Receptor Distributions in Monogamous and Non-Monogamous Eulemur.' *Scientific Reports* 11 (1): 3746.
- Gruber, Thibaud, and Zanna Clay. 2016. 'A Comparison Between Bonobos and Chimpanzees: A Review and Update.' *Evolutionary Anthropology* 25 (5): 239–52.
- Gruber, Thibaud, Zanna Clay, and Klaus Zuberbühler. 2010. 'A Comparison of Bonobo and Chimpanzee Tool Use: Evidence for a Female Bias in the Pan Lineage.' *Animal Behaviour* 80 (6): 1023–33.
- Hare, Brian. 2017. 'Survival of the Friendliest: Homo Sapiens Evolved via Selection for Prosociality.' *Annual Review of Psychology* 68 (January): 155–86.
- Hare, Brian, Alicia P. Melis, Vanessa Woods, Sara Hastings, and Richard Wrangham. 2007. 'Tolerance Allows Bonobos to Outperform Chimpanzees on a Cooperative Task.' *Current Biology: CB* 17 (7): 619–23.
- Hare, Brian, Victoria Wobber, and Richard Wrangham. 2012. 'The Self-Domestication Hypothesis: Evolution of Bonobo Psychology Is Due to Selection against Aggression.' *Animal Behaviour* 83 (3): 573–85.
- Hare, Brian, and Vanessa Woods. 2017. 'Cognitive Comparisons of Genus Pan Support Bonobo Self-Domestication.' In: Brian Hare and Shinya Yamamoto (eds.) *Bonobos: Unique in Mind, Brain and Behaviour*. Oxford: Oxford University Press.
- Hare, Brian, and Vanessa Woods. 2021. *Survival of the Friendliest: Understanding Our Origins and Rediscovering Our Common Humanity*. Random House.
- Heberlein, Marianne T. E., Dennis C. Turner, Friederike Range, and Zsófia Virányi. 2016. 'A Comparison between Wolves, Canis Lupus, and Dogs, Canis Familiaris, in Showing Behaviour towards Humans.' *Animal Behaviour* 122 (December): 59–66.
- Herbeck, Yu E., R. G. Gulevich, D. V. Shepeleva, and V. V. Grinevich. 2017. 'Oxytocin: Coevolution of Human and Domesticated Animals.' *Russian Journal of Genetics: Applied Research* 7 (3): 235–42.
- Hill, Kim R., Brian M. Wood, Jacopo Baggio, A. Magdalena Hurtado, and Robert T. Boyd. 2014. 'Hunter-Gatherer Inter-Band Interaction Rates: Implications for Cumulative Culture.' *PLoS One* 9 (7): e102806.
- Holloway, Ralph L., Shawn D. Hurst, Heather M. Garvin, P. Thomas Schoenemann, William B. Vanti, Lee R. Berger, and John Hawks. 2018. 'Endocast Morphology of Homo Naledi from the Dinaledi Chamber, South Africa.' *Proceedings of the National Academy of Sciences of the United States of America* 115 (22): 5738–43.

- Hopkins, William D., Cheryl D. Stimpson, and Chet C. Sherwood. 2017. 'Social Cognition and Brain Organization in Chimpanzees (Pan Troglodytes) and Bonobos (Pan Paniscus).' In: Brian Hare and Shinya Yamamoto (eds.) *Bonobos: Unique in Mind, Brain and Behaviour*. Oxford: Oxford University Press.
- Horowitz, Alexandra. 2011. 'Theory of Mind in Dogs? Examining Method and Concept.' *Learning & Behavior* 39 (4): 314–17.
- Issa, Habon A., Nicky Staes, Sophia Diggs-Galligan, Cheryl D. Stimpson, Annette Gendron-Fitzpatrick, Jared P. Taglialatela, Patrick R. Hof, William D. Hopkins, and Chet C. Sherwood. 2018. 'Comparison of Bonobo and Chimpanzee Brain Microstructure Reveals Differences in Socio-Emotional Circuits.' *Brain Structure & Function* 224 (1): 239–51.
- Johnston, Angie M., Courtney Turrin, Lyn Watson, Alyssa M. Arre, and Laurie R. Santos. 2017. 'Uncovering the Origins of Dog–Human Eye Contact: Dingoes Establish Eye Contact More than Wolves, but Less than Dogs.' *Animal Behaviour* 133 (November): 123–29.
- Jouventin, Pierre, Yves Christen, and F. Stephen Dobson. 2016. 'Altruism in Wolves Explains the Coevolution of Dogs and Humans.' *Ideas in Ecology and Evolution* 9 (1). DOI: <https://doi.org/10.4033/iee.2016.9.2.n>.
- Kaminski, Juliane, Michael Tomasello, Josep Call, and Juliane Bräuer. 2009. 'Domestic Dogs Are Sensitive to a Human's Perspective.' *Behaviour* 146 (7): 979–98.
- Kano, Fumihiko, Satoshi Hirata, and Josep Call. 2015. 'Social Attention in the Two Species of Pan: Bonobos Make More Eye Contact than Chimpanzees.' *PLoS One* 10 (6): e0129684.
- Kis, Anna, Melinda Bence, Gabriella Lakatos, Enikő Pergel, Borbála Turcsán, Jolanda Pluijmakers, Judit Vas, et al. 2014. 'Oxytocin Receptor Gene Polymorphisms Are Associated with Human Directed Social Behavior in Dogs (Canis Familiaris).' *PLoS One* 9 (1): e83993.
- Kis, Anna, Alin Ciobica, and József Topál. 2017. 'The Effect of Oxytocin on Human-Directed Social Behaviour in Dogs (Canis Familiaris).' *Hormones and Behavior* 94 (August): 40–52.
- Kis, Anna, Anna Hernádi, Bernadett Miklósi, Orsolya Kanizsár, and József Topál. 2017. 'The Way Dogs (Canis Familiaris) Look at Human Emotional Faces Is Modulated by Oxytocin. An Eye-Tracking Study.' *Frontiers in Behavioral Neuroscience* 11 (October): 210.
- Krupenye, Christopher, Jingzhi Tan, and Brian Hare. 2018. 'Bonobos Voluntarily Hand Food to Others but Not Toys or Tools.' *Proceedings. Biological*

- Sciences/The Royal Society* 285 (1886): 20181536. DOI: <https://doi.org/10.1098/rspb.2018.1536>.
- Kurdek, Lawrence A. 2008. 'Pet Dogs as Attachment Figures.' *Journal of Social and Personal Relationships* 25 (2): 247–66.
- Layton, Robert, Sean O'Hara, and Alan Bilsborough. 2012. 'Antiquity and Social Functions of Multilevel Social Organization Among Human Hunter-Gatherers.' *International Journal of Primatology* 33 (5): 1215–45.
- Lucchesi, Stefano, Leveda Cheng, Karline Janmaat, Roger Mundry, Anne Pisor, and Martin Surbeck. 2020. 'Beyond the Group: How Food, Mates, and Group Size Influence Intergroup Encounters in Wild Bonobos.' *Behavioral Ecology: Official Journal of the International Society for Behavioral Ecology* 31 (2): 519–32.
- MacLean, Evan L. 2016. 'Unraveling the Evolution of Uniquely Human Cognition.' *Proceedings of the National Academy of Sciences of the United States of America* 113 (23): 6348–54.
- MacLean, Evan L., Esther Herrmann, Sunil Suchindran, and Brian Hare. 2017. 'Individual Differences in Cooperative Communicative Skills Are More Similar between Dogs and Humans than Chimpanzees.' *Animal Behaviour* 126 (Supplement C): 41–51.
- Marshall-Pescini, Sarah, Simona Cafazzo, Zsófia Virányi, and Friederike Range. 2017. 'Integrating Social Ecology in Explanations of Wolf–Dog Behavioral Differences.' *Current Opinion in Behavioral Sciences* 16 (August): 80–86.
- Marshall-Pescini, Sarah, Jonas F. L. Schwarz, Inga Kostelnik, Zsófia Virányi, and Friederike Range. 2017. 'Importance of a Species' Socioecology: Wolves Outperform Dogs in a Conspecific Cooperation Task.' *Proceedings of the National Academy of Sciences of the United States of America* 114 (44): 11793–98.
- Miklósi, Ádam. 2014. *Dog Behaviour, Evolution, and Cognition*. Oxford: Oxford University Press.
- Miklósi, Ádam, Enikő Kubinyi, József Topál, Márta Gácsi, Zsófia Virányi, and Vilmos Csányi. 2003. 'A Simple Reason for a Big Difference: Wolves Do Not Look Back at Humans, but Dogs Do.' *Current Biology: CB* 13 (9): 763–66.
- Miller, Suzanne C., Cathy C. Kennedy, Dale C. DeVoe, Matthew Hickey, Tracy Nelson, and Lori Kogan. 2009. 'An Examination of Changes in Oxytocin Levels in Men and Women Before and After Interaction With a Bonded Dog.' *Anthrozoös* 22 (1): 31–42.
- Montoya, Estrella R., David Terburg, Peter A. Bos, and Jack van Honk. 2012. 'Testosterone, Cortisol, and Serotonin as Key Regulators of Social

- Aggression: A Review and Theoretical Perspective.' *Motivation and Emotion* 36 (1): 65–73.
- Nagasawa, Miho, Shouhei Mitsui, Shiori En, Nobuyo Ohtani, Mitsuaki Ohta, Yasuo Sakuma, Tatsushi Onaka, Kazutaka Mogi, and Takefumi Kikusui. 2015. 'Social Evolution. Oxytocin-Gaze Positive Loop and the Coevolution of Human-Dog Bonds.' *Science* 348 (6232): 333–36.
- Nowell, April. 2016. 'Childhood, Play and the Evolution of Cultural Capacity in Neanderthals and Modern Humans.' In: Miriam N. Haidle, Nicholas J. Conard, and Michael Bolus (eds.) *The Nature of Culture. Vertebrate Paleobiology and Paleoanthropology*: 87–97. Springer. DOI: https://doi.org/10.1007/978-94-017-7426-0_9.
- Orr, David. 2015. 'The Most Misread Poem in America.' *The Paris Review*, 11 September. Available at: <https://www.theparisreview.org/blog/2015/09/11/the-most-misread-poem-in-america>. Accessed 01/06/21.
- Palagi, Elisabetta, Giada Cordoni, Elisa Demuru, and Marc Bekoff. 2016. 'Fair Play and Its Connection with Social Tolerance, Reciprocity and the Ethology of Peace.' *Behaviour* 153 (9–11): 1195–216.
- Pal, Sunil Kumar. 2003. 'Reproductive Behaviour of Free-Ranging Rural Dogs in West Bengal, India.' *Acta Theriologica* 48 (2): 271–81.
- Pandit, Sagar A., Gauri R. Pradhan, Hennadii Balashov, and Carel P. Van Schaik. 2016. 'The Conditions Favoring Between-Community Raiding in Chimpanzees, Bonobos, and Human Foragers.' *Human Nature* 27 (2): 141–59.
- Ponce de León, M. S., and C. P. E. Zollikofer. 2006. 'Neanderthals and Modern Humans — Chimps and Bonobos: Similarities and Differences in Development and Evolution.' In: Jean-Jacques Hublin, Katerina Harvati, and Terry Harrison (eds.) *Neanderthals Revisited: New Approaches and Perspectives*: 71–88. Dordrecht: Springer.
- Porr, Martin, and Jacqueline M. Matthews. 2017. 'Post-Colonialism, Human Origins and the Paradox of Modernity.' *Antiquity* 91 (358): 1058–68.
- Porr, Martin, and Jacqueline M. Matthews. 2019. 'Interrogating and Decolonising the Deep Human Past.' In: Martin Porr and Jacqueline Matthews (eds.) *Interrogating Human Origins Decolonisation and the Deep Human Past*: 3–32. Routledge.
- Raia, Pasquale, Alessandro Mondanaro, Marina Melchionna, Mirko Di Febbraro, José A. F. Diniz-Filho, Thiago F. Rangel, Philip B. Holden, et al. 2020. 'Past Extinctions of Homo Species Coincided with Increased Vulnerability to Climatic Change.' *One Earth* 3 (4): 480–90.

- Raghanti, Mary Ann. 2019. 'Domesticated Species: It Takes One to Know One.' *Proceedings of the National Academy of Sciences of the United States of America* 116 (29): 14401–403.
- Romero, Teresa, Marie Ito, Atsuko Saito, and Toshikazu Hasegawa. 2014. 'Social Modulation of Contagious Yawning in Wolves.' *PLoS One* 9 (8): e105963.
- Saetre, Peter, Julia Lindberg, Jennifer A. Leonard, Kerstin Olsson, Ulf Pettersson, Hans Ellegren, Tomas F. Bergström, Carles Vilà, and Elena Jazin. 2004. 'From Wild Wolf to Domestic Dog: Gene Expression Changes in the Brain.' *Brain Research. Molecular Brain Research* 126 (2): 198–206.
- Sakamaki, Tetsuya, Isabel Behncke, Marion Laporte, Mbangi Mulavwa, Heungjin Ryu, Hiroyuki Takemoto, Nahoko Tokuyama, Shinya Yamamoto, and Takeshi Furuichi. 2015. 'Intergroup Transfer of Females and Social Relationships Between Immigrants and Residents in Bonobo (*Pan Paniscus*) Societies.' In: Takeshi Furuichi, Juichi Yamagiwa, and Filippo Aureli (eds.) *Dispersing Primate Females: Life History and Social Strategies in Male-Philopatric Species*: 127–64. Tokyo: Springer.
- Sakamaki, Tetsuya, Heungjin Ryu, Kazuya Toda, Nahoko Tokuyama, and Takeshi Furuichi. 2018. 'Increased Frequency of Intergroup Encounters in Wild Bonobos (*Pan Paniscus*) Around the Yearly Peak in Fruit Abundance at Wamba.' *International Journal of Primatology* 39 (4): 685–704.
- Sapolsky, Robert M. 2017. *Behave: The Biology of Humans at Our Best and Worst*. New York: Penguin.
- Serpell, James. 2016. *The Domestic Dog*. Cambridge University Press.
- Sherwood, Chet C., and Aida Gómez-Robles. 2017. 'Brain Plasticity and Human Evolution.' *Annual Review of Anthropology* 46: 399–419.
- Shuldiner, Emily, Ilana Janowitz Koch, Rebecca Y. Kartzinell, Andrew Hogan, Lauren Brubaker, Shelby Wanser, Daniel Stahler, et al. 2017. 'Structural Variants in Genes Associated with Human Williams-Beuren Syndrome Underlie Stereotypical Hypersociability in Domestic Dogs.' *Science Advances* 3 (7): e1700398.
- Spikins, Penny, Jennifer French, Seren John-Wood and Calvin Dytham. 2021. 'Theoretical and Methodological Approaches to Ecological Changes, Social Behaviour and Human Intergroup Tolerance 300,000 to 30,000 Bp.' *Journal of Archaeological Method and Theory* 28: 53–75.
- Staes, Nicky, Jeroen B. Smaers, Amanda E. Kunkle, William D. Hopkins, Brenda J. Bradley, and Chet C. Sherwood. 2019. 'Evolutionary Divergence

- of Neuroanatomical Organization and Related Genes in Chimpanzees and Bonobos.' *Cortex* 118: 154–64.
- Stimpson, Cheryl D., Nicole Barger, Jared P. Tagliabata, Annette Gendron-Fitzpatrick, Patrick R. Hof, William D. Hopkins, and Chet C. Sherwood. 2016. 'Differential Serotonergic Innervation of the Amygdala in Bonobos and Chimpanzees.' *Social Cognitive and Affective Neuroscience* 11 (3): 413–22.
- Tan, J., and B. Hare. 2017. 'Prosociality among Non-Kin in Bonobos and Chimpanzees Compared.' In: Brian Hare and Shinya Yamamoto (eds.) *Bonobos: Unique in Mind, Brain and Behaviour*. Oxford: Oxford University Press.
- Tan, Jingzhi, Dan Ariely, and Brian Hare. 2017. 'Bonobos Respond Prosocially toward Members of Other Groups.' *Scientific Reports* 7 (1): 14733.
- Tan, Jingzhi, and Brian Hare. 2013. 'Bonobos Share with Strangers.' *PLoS One* 8 (1): e51922.
- Theofanopoulou, Constantina, Alejandro Andirko, Cedric Boeckx and Eric D. Jarvis. 2018. 'Oxytocin and Vasopressin Receptor Variants as a Window onto the Evolution of Human Prosociality.' *bioRxiv*. DOI: <http://dx.doi.org/10.1101/460584>.
- Theofanopoulou, Constantina, Simone Gastaldon, Thomas O'Rourke, Bridget D. Samuels, Pedro Tiago Martins, Francesco Delogu, Saleh Alamri, and Cedric Boeckx. 2017. 'Self-Domestication in Homo Sapiens: Insights from Comparative Genomics.' *PLoS One* 12 (10): e0185306.
- Thielke, Lauren E., and Monique A. R. Udell. 2017. 'The Role of Oxytocin in Relationships between Dogs and Humans and Potential Applications for the Treatment of Separation Anxiety in Dogs.' *Biological Reviews of the Cambridge Philosophical Society* 92 (1): 378–88.
- Thomas, James, and Simon Kirby. 2018. 'Self Domestication and the Evolution of Language.' *Biology & Philosophy* 33 (9). <https://doi.org/10.1007/s10539-018-9612-8>.
- Topál, József, Márta Gácsi, Ádám Miklósi, Zsófia Virányi, Enikő Kubinyi, and Vilmos Csányi. 2005. 'Attachment to Humans: A Comparative Study on Hand-Reared Wolves and Differently Socialized Dog Puppies.' *Animal Behaviour* 70 (6): 1367–75.
- Trut, Lyudmila, Irina Oskina, and Anastasiya Kharlamova. 2009. 'Animal Evolution during Domestication: The Domesticated Fox as a Model.' *BioEssays: News and Reviews in Molecular, Cellular and Developmental Biology* 31 (3): 349–60.

- Udell, Monique A. R. 2015. 'When Dogs Look Back: Inhibition of Independent Problem-Solving Behaviour in Domestic Dogs (*Canis Lupus Familiaris*) Compared with Wolves (*Canis Lupus*).' *Biology Letters* 11 (9): 20150489.
- Udell, Monique A. R., Nicole R. Dorey, and Clive D. L. Wynne. 2008. 'Wolves Outperform Dogs in Following Human Social Cues.' *Animal Behaviour* 76 (6): 1767–73.
- Udell, Monique A. R., Nicole R. Dorey, and Clive D. L. Wynne. 2011. 'Can Your Dog Read Your Mind? Understanding the Causes of Canine Perspective Taking.' *Learning & Behavior* 39 (4): 289–302.
- Warneken, Felix. 2018. 'How Children Solve the Two Challenges of Cooperation.' *Annual Review of Psychology* 69: 205–29.
- Wilkins, Adam S., Richard W. Wrangham, and W. Tecumseh Fitch. 2014. 'The "Domestication Syndrome" in Mammals: A Unified Explanation Based on Neural Crest Cell Behavior and Genetics.' *Genetics* 197 (3): 795–808.
- Wilson, Michael L., Christophe Boesch, Barbara Fruth, Takeshi Furuichi, Ian C. Gilby, Chie Hashimoto, Catherine L. Hobaiter, et al. 2014. 'Lethal Aggression in Pan Is Better Explained by Adaptive Strategies than Human Impacts.' *Nature* 513 (7518): 414–17.
- Wobber, Victoria, Brian Hare, Susan Lipson, Richard Wrangham, and Peter Ellison. 2013. 'Different Ontogenetic Patterns of Testosterone Production Reflect Divergent Male Reproductive Strategies in Chimpanzees and Bonobos.' *Physiology & Behavior* 116–117 (May): 44–53.
- Wobber, Victoria, Brian Hare, Jean Maboto, Susan Lipson, Richard Wrangham, and Peter T. Ellison. 2010. 'Differential Changes in Steroid Hormones before Competition in Bonobos and Chimpanzees.' *Proceedings of the National Academy of Sciences of the United States of America* 107 (28): 12457–62.
- Wobber, Victoria, Richard Wrangham, and Brian Hare. 2010. 'Bonobos Exhibit Delayed Development of Social Behavior and Cognition Relative to Chimpanzees.' *Current Biology: CB* 20 (3): 226–30.
- Wrangham, Richard. 2019. *The Goodness Paradox: The Strange Relationship Between Virtue and Violence in Human Evolution*. Pantheon.
- Zimbardo, P. 2011. *The Lucifer Effect: How Good People Turn Evil*. Random House.