

*New Idea***Altruism in wolves explains the coevolution of dogs and humans****Pierre Jouventin, Yves Christen, and F. Stephen Dobson***Pierre Jouventin, CEFE-UMR 5175 CNRS, Montellier, France**Yves Christen, Fondation Ipsen, Paris, France**F. Stephen Dobson (fsdobson@msn.com), Department of Biological Sciences, Auburn University, AL, USA***Abstract**

The date of historical domestication of dogs has been pushed back to between 15,000–30,000 years ago (estimates vary), a time when hunter-gatherer societies predominated in northern Europe and central Asia. We present insights from evolutionary behavioural ecology suggesting that wolves may have been “tricked” by their social evolution into contributing to the success of pre-historic human families or tribes. Four different wolves (one observed in great detail, as reported in recent book) that were raised by human families exhibited cooperative behaviours that protected their human “pack members.” Such hereditary altruistic behaviours may have been transferred by descent to the first dogs, which helped our ancestors hunt large animals and fight against other human tribes and wild carnivores. We hypothesize that the first need in domestication was for less aggressive wolf behaviour, within the wolf and human coevolution of the cooperative family or tribe that used wolves to increase their competitive fitness advantages.

Key words: wolf, dog, altruism, domestication

Introduction

The domestication puzzle of the evolutionary origin of dogs is a fascinating but complex subject, and has produced much speculation (Koler-Matznick 2002). Nevertheless, wolf biology, molecular paleontology (Grim 2015), and the molecular approach to social evolution (Nagasawa et al. 2015) have advanced recently

and have implications for this old problem. Due to the amazing variability among breeds of dogs, Charles Darwin (1868) and Konrad Lorenz (1954) supposed that dogs came from hybridization between canids, particularly jackals and wolves; but these giants of biological science were wrong. DNA studies have shown that the wolf is the dog’s only ancestor and is still closely related to it (Vila et al. 1997). Moreover, the age of this domestication has been increased more than threefold by recent discoveries of the first bones of dogs and ancient DNA of wolves, now estimated up to 36,000 years ago (Ovodov et al. 2001, Druzhkova et al. 2013, Thalmann et al. 2013, Skoglund et al. 2015). This very old dating is still debated. In fact, this field of research is highly contentious (Grim 2015), but the main finding that the dog appeared a long time before Neolithic settlements is generally accepted.

Thus, dogs were selected from wolves by prehistoric humans. This view is contrary to the accepted view that dogs were domesticated in similar fashion to other animals, in Neolithic villages of farmers and animal breeders. But dogs were derived from wolves much longer ago, in tribes of hunter-gatherers. Thus, the first steps of dog domestication seem to have occurred at a time when prehistoric humans were gradually moving in different parts of the northern hemisphere, suggesting that they were the first to domesticate dogs. Why was the wolf so crucial in the nomadic way of life of prehistoric man? It was not for herding other domesticated animals, since other animal breeding appears thousands of years later. So wolves were likely kept as a mutualistic aid with hunting and for camp safety. Wolves and then dogs have a special feature that pre-

adapted them for domestication: wolves will cooperate with humans as though they were their own species. Wolves exhibit altruistic behaviours within their packs (Schmidt & Mech 1997). We asked whether due to their social evolution, wolves might have been “tricked” into accepting humans as pack members during their domestication process. We further considered whether this could be due to the social subordination of the individual in wolf packs, a situation that would not have been possible in other wild predator groups (e.g., cave hyenas, cave lions) where more egalitarian groups lack this characteristic.

Methods

In developing our novel hypothesis, we considered literature sources about the origin of dogs from wolves via an early, prehistoric process of “natural” domestication. We combined these sources of information together with unique behavioral observations of a wolf that was raised by a human family.

Results and Discussion

Darwin (1859) showed that individual selection can provide a clear understanding of how evolution can occur. Peter Kropotkin, in his book ‘Mutual Aid’ (1902), complemented this picture by describing altruism in men and animals. Fifty years ago, William D. Hamilton (1964) provided the genetic and mathematical basis for kin selection, which can produce altruistic cooperation. Darwin briefly reflected on this sort of ‘family selection,’ and it is still the best explanation for the eusociality of complex insect societies of ants, bees and termites, as well as helping behaviours of a growing number of species including vertebrates. In mammals, the most sophisticated altruistic behaviours are found in species that live permanently in family groups. Because all members are kin, any altruistic behaviour in such groups is beneficial to other members, and through them the genetic basis of altruism is promoted. Indeed, altruism is not specific to our species, where it is considered a key to morality, but is found in many species (de Waal 1997).

Higher levels of mutual assistance are found in social carnivores, such as lions and killer whales. Field observations of African wild dogs, *Lycaon pictus* (probably the closest species to gray wolves in social behaviour), show that packs are strongly altruistic, with members assisting one another (Bussi re 2015). In pack hunters such as prehistoric humans, the ecological niche was also one of social hunting of large prey via cooperation of group members (Lee and deVore 1968). Thus humans, African wild dogs, and wolves were adapted to cooperative hunting, though with different characteristics according to their evolutionary origins.

According to Adriaan Kortlandt (1965), our species is alone among primates to have converged ecologically with social carnivores, such as the wolf.

Thirty-five years ago, Pierre Jouventin was early in his career as an ethologist of birds and mammals. He was also a consultant to the Director of the Zoo of Montpellier (France). Knowing that PJ’s wife was particularly fond of wolves, the Director called to propose that they adopt a wolf cub (a female, one week from birth) that the zoo otherwise had to kill. PJ inhabited the city centre, but was building an outlying home with a fenced park. So he accepted. Unfortunately, construction of his home was delayed for four years; so he reared the wolf in his family, and in their flat; probably a unique experience because rearing of wolves is common, but is usually effected in outdoor enclosures. Several behaviours of the wolf were difficult to understand: when the wolf became mature (at two years old), it pulled the Jouventins by the trousers when they were on their balcony, or by the shirt when leaning over the window (Figure 1), or by an arm from the bath (Figure 2). The explanation became obvious six months



Figure 1. Wolf restrains pack member that is trying to descend through a window.



Figure 2. Wolf “rescues” pack member from the bath.

later: when swimming in a river, the wolf came ten times to seize members of the family to bring them back to the bank (Figure 3 and moreover, movies <http://pierrejouventin.fr/>). The occurrence of these behavioural traits in a captive wolf in such a close relationship with humans suggests that a wolf can be altruistic with the relatives in its perceived pack (where kin selection occurs), and explains why some dogs have retained this feature. Our observations suggest that wolves can be altruistic towards humans, but further behavioural evidence is needed to test this conclusion for generality. The key to the altruistic behaviour that the Jouventin family observed is that young wolves have always developed in association with other wolves. When faced with both food and social reinforcement, young wolves accept humans as pack members due to their social evolutionary history (reviewed in detail by Jouventin 2012).

Why haven't wolf specialists previously documented the interspecific altruistic behaviour of this species that we found in artificial conditions? It is difficult to see such things in the wild. Also, living for several years in a flat provided a closer relationship than rearing wolves in outdoor enclosures. Another difficulty observing the altruism in wolves is that it appears only when the wolf becomes an adult at two-three years of age, and it is modulated according to the relationships with each pack member. The same wolf was completely altruistic with PJ's spouse, not always with his son, and sometimes aggressive with PJ, especially when he returned from a long absence. Altruistic tendencies were not restricted to this single wolf alone. In 2015, to ensure that the altruistic behaviours observed were not confined to the Jouventin's wolf, three other domesticated wolves (reared from pups by a human family) were tested with a “mock attack” on their owner (the head of the family

pack) (P. Jouventin, G. Richard, J. Pierronne, and F. Estrad, un-published results). These trials showed that the wolves aggressively protected their owner against an “outsider.” We suggest that this cooperative behaviour is likely a social adaptation common to wolves that have developed within human families; the human family functioning as a substitute for their natural pack. Many breeds of dogs have retained the protective aggressive behaviour toward their owner or their child against strangers; the same behaviours that one sees in wild wolves, originally an adaptation for defending the young in wolf packs.

The observation of such altruism in modern wolves can help us to understand why early wolves were so advantageous to humans, to fight against other men or animals and to hunt game. Two main theories potentially explain the domestication of the wolf (see Miklosi 2015: 125, for theories of dog domestication). The first is commensalism, where wild animals follow human hunters as scavengers, followed by adoption, where cubs are captured in dens to be reared among humans. Commensalism seems more likely to specialists, because it is observed in poor Arabic countries where Paria dogs, living with humans, but without domestication, provide a supposed first step toward domestication.



Figure 3. Wolf enters river, “rescues” pack member from the water.

According to our unusual and original observations, we suggest a second idea that relies on social cooperation of wolves and man. In this scenario, social canids were of substantial help to prehistoric humans. Wolves have a better sense of smell, run twice as fast, and can run farther than humans. These qualities were likely useful for humans. Prehistoric man lacked fangs and claws, but rather used weapons for group hunting. Wolves may have been another weapon in their hunting tactics. With wolves, it was easier to bring down large herbivores, as well as to defend the home camp or clan members against large carnivores or even to fight against hostile human tribes. Our hypothesis could help to explain one of the critical issues about the beginning of canine domestication: how to prevent the “wolf-like populations (...) from mixing?” (Miklosi 2015: 126). If these first ancestors of dogs were bred and raised within human families or clans, this behaviour might provide an efficacious barrier against genetic admixture (for evidence of reverse admixture, see Fan et al. 2016). A scavenging habit adjacent to human groups would not have provided this sort of separation of domestic and wild stocks. Such domestication might also have contributed to the later establishment of human permanent settlements (Coppinger and Coppinger 2001). Moreover, the first dogs (breeds that were close to wolves) were all found in very high latitudes (Germonpré et al. 2009, Ovodov et al. 2011, Skoglund et al. 2015). At these latitudes, canid help may have been essential in open fields for driving large herbivores to the slaughter. Early human settlements were likely isolated, thus facilitating the genetic differentiation of dogs.

But how were these two species, wolf and humans, able to cooperate? First, altruistic behaviour was particularly adaptive in a cooperative hunter such as the wolf, a pack being an enlarged family where most members are kin. Secondly, a cub learns adult behaviours socially, usually interacting only with congeners. This is the well-known ‘social imprinting’ popularized by Lorenz in his study of geese (Lorenz 1935). But the cub does not recognize its own species innately as a social interactant, because over evolutionary time, social interactions have always been with its own species. So when a cub is reared in a human family instead a wolf pack, it continues defending “relatives,” accepting human leadership and cooperating with family members as though it was kin-related, even though the cooperation is “misplaced” onto another species.

It is well known that a primitive hunter (Bushmen in the Kalahari desert or pygmies in Central Africa) brings in much more meat when a dog helps him (Lee and DeVore 1968). Before the dog, the wolf, able as we saw to live in a human family before domestication, was able to increase considerably the power of prehistoric humans, helping hunters, protecting the camp and clan,

bringing speed, and above all bringing olfaction to the skill set of the group (Schleidt and Shalter 2003). But the positives of the wolf were balanced by negative behavioural traits. When they are adults, wolves are not so tame, obedient, or cooperative, and are often even dangerous due to dominance competition inside the pack.

Socialization of wolf pups, however, is highly variable, with some pups developing heightened fear of humans from unfamiliarity, and others becoming co-socialized through living in close contact with humans and developing familiarity and even friendliness (Woolfy and Ginsburg 1967). Some pups are high in attraction to humans, though also high in fear; while other pups are high in fear and not attracted to humans. As fear develops after attraction, some individuals can be quite friendly to humans at first but gradually become more fearful. Others become relatively aggressive to humans (MacDonald 1987, Fox 1987). In the Upper Palaeolithic, we can suppose that aggressive and too fearful wolves were killed or returned to the wild, while more tamed wolves remained within short distances from humans, scavenging or even being fed.

The rearing of the wolf is so easy (as PJ and family found) and useful for hunting and protection, that we assume that the wolf coevolved behaviourally with man, facilitated by the earlier development of altruism within wolf packs (Lescureux 2009, Zink 2015). Such selection for behavioural domestication probably occurred in several places and over a long period of time, before further selection occurred. We suggest, differently from previous explanations of dog evolution, that wolves were the original domestic species, amicable behaviours being selected long before morphology. From a basic intuitive understanding of heredity, our ancestors prevented backcrosses with wolves. As demonstrated by the Russian geneticist Dimitri Belyaev in the 1960s, canids that are friendly to humans can be bred from wild Siberian foxes in only eight generations (Trut 1999). Anatomical traits of dogs such as drooping ears, turned-up tail and spotted coat were obtained from the fox breeding program, but not a close relationship with humans. We suggest that this is because foxes live in pairs and are not as social as wolf packs under natural conditions. Just as modern breeders choose among pups for the strongest or the most aggressive offspring, our ancestors probably selected only quiet cubs that retained neotenus (viz., juvenile) social aggression as adults. These wolves may have consequently been less competitive, more obedient, and peaceful as adults. If such individuals were reproductively isolated from wild stock, they could have developed into the first dogs.

For many authors, the earliest undisputable dogs were found in Eurasia about 18,000 years ago, during the hunter-gatherer nomadic period of the Magdalenian culture (Pionnier-Capitan 2011). Recently however,

doglike fossils, significantly larger than more recent dogs, were found at relatively high latitudes (around 50°N) in Europe (Belgium; Germonpre et al. 2009) and Eurasia (Siberia; Ovodov et al. 2011), and dated at least 30,000 years ago (Thalmann et al. 2013; Skoglund et al. 2015).

At northern latitudes landscapes were treeless, even during warm intervals (d’Enricco and Goni 2003), and consequently it was difficult in these open landscapes to approach prey closely enough to use spears, to herd or stampede large herbivores, and to perhaps defend against large carnivorous or other human tribes, without canid help. These results come together with the altruism of wolves to suggest a new hypothesis: the harsh conditions of the full glacial period led prehistoric humans to develop new subsistence strategies. To kill large-sized herbivores, in particular during cold periods where ungulate biomass was highly fluctuating, use of a large-sized wolf/dog was an ideal way to herd prey into open land and to stampede them toward hunters with spears.

A current emerging hypothesis suggests that extreme climate variability shaped human nature, allowing us to survive in all sorts of environments (Gibbons 2013). The wolf/dog and then the true dog may have helped humans thrive, increasing human fecundity through more and better food, and consequently moving *Homo sapiens* demography from a K-strategy (low fecundity) to a r-strategy (high fecundity) (Pianka 1971). Thus, in some thousands of years, tribes with dogs could replace not only Neandertals, but also other human populations that lacked the method of wolf taming (Shipman 2012, 2015b, Jouventin 2013). According to Shipman (2015b), dogs were “living weapons” used by modern humans to force Neanderthals into extinction.

Conclusions

If the domestication from the wolf is really linked to the altruism of the wolf, transmitted by heredity to the first dogs as we have suggested, this coevolution became essential in the harsh way of life of modern humans in the harsh environments of 15–30 thousand ybp. That is, cooperative hunting on large-sized herbivores and the protection against large social carnivores or other tribes may constitute a trigger threshold for selection of the dog. Besides predicting altruistic behaviour of the wolf in captivity as we have already observed, we also predict that such altruism will be found in the wild under natural pack conditions. We also predict that it will be difficult for palaeontologists to find primitive dogs much older than the first modern human settlements at high latitudes. But wolf (i.e., “wolf/dog”) material should be fairly common in the remains of nomadic hunter-gatherer clans and tribes.

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Referees

Sylvain Fiset – sylvain.fiset@umoncton.ca
Université de Moncton

Mietje Germonpré
– mietje.germonpre@naturalsciences.be
Koninklijk Belgisch Instituut voor
Natuurwetenschappen

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Response to Referee

The first goal of our study was to stimulate further research and to attract attention to the helping behaviours of wild or captive wolves to test for actual or misplaced altruistic behaviours. It is obviously difficult to see these mutual assistance behaviours, because they occur only between members of a wolf family (for genetic reasons that we gave in our article): it was a

chance to observe them in some human families through social imprinting and the rearing of a wolf at home. These altruistic behaviours were rare, and were given only when the wolf was an adult. But it was also necessary to recognize these behaviours. Proto-culture in monkeys was observed and confirmed by scientists only after the publishing in the 1970s of articles by Japanese scientists, because it was not considered possible that such cultural behaviours occurred in animals, even though we now consider them as common.

Our second goal was to point to the social convergence between the cooperation found in wolves and humans. This new point of view emphasizes the early domestication of the dog, an event that occurred in prehistoric man and consequently early during the process of hominization (as defined by anthropologists). We gave only a few details in this article on the behaviours observed because PJ wrote a book that gives many specific details, and only one wolf was carefully studied. But these altruistic observations, previously undescribed in this species, were commonly observed and are difficult to explain by alternative hypotheses. It was easy to activate the help of the wolf for its human members of the 'pack' in the bath, in a swimming pool, or by opening the window to simulate falling out of the window (Figure 1). The sequence in the movie where Line Jouventin is 'saved' by the wolf Kamala, that we show on the internet (and in Figures 2 and 3), could easily be triggered ten times in succession. It was obviously not a Pavlovian conditioning, and it is well known that some dogs such as the Newfoundland retriever do the same sort of saving of traditional fishermen. These dogs may have inherited this innate altruistic behaviour from the wolf, and the behaviour can be increased by training. As assumed by Klinghammer and Goodmann (1987), rearing a wolf is a 24-hour job for a modern trainer. But the same is not so for a hunter-gatherer, because preferred behaviours could be easily obtained in the family context. As the Jouventin family saw in a downtown flat, a wolf pup tries to integrate with a human family automatically, as it will with a pack in the wild. Moreover, wolves follow human hunters and learn to participate in collective hunting. Prehistoric men occupied a similar ecological niche as wolves; for example, cooperative hunting of big mammals. Both humans and wolves were top predators in the same ecosystem.

Since the inception of this article, we tested a new type of interaction with wolves reared by humans. We asked the owner of a family-raised wolf to simulate an attack by a stranger. At the first test, the wolf clicked its teeth close to the ears of the aggressor (for a wolf, an advertisement before biting). In the second test, the wolf took the skull of the aggressor in its jaws but it stopped when its owner gave a shouted command. Two other

wolves handled by humans were tested and also protected their owner. The referees asked how one might test our hypothesis: as you see, it is easy to test experimentally, but dangerous! We suggest from these new experiments (on three wolves, different from our previous reports above) that our wolf (Kamala) was not exceptional or trained. This altruistic behaviour likely occurs in any wolf because it is adaptive as a highly efficient way to hunt and to live cooperatively. We can also conclude that some breeds of dogs have inherited this altruistic behaviour from their ancestors. The altruism helps their relatives, even if it is not a canid of the same family, that is genetically kin, but a human "family member" learned through social imprinting.

Fiset (2016) points to the dating of dog domestication, arguing the Miklosi (2015) conclusions of around 15,000 years ago. Our main interest was not to decide if dog domestication occurs around 15,000 years ago or 30,000 years as Germonpre et al. (2009) and Thalmann et al. (2013) proposed. It was to point out that it occurred before the Neolithic period, that is before 10,000 years BC, and thus at a different time from all other domesticated animals, domesticated in villages. When men were still hunter-gatherers, they needed absolutely to kill big game; and the help of a wolf or early dog was useful for finding game and driving it to hunters with spears. Each prehistoric hunting group may have seen the cooperation of socially imprinted wolves and learned the use of this new technology for hunting (smelling and running), protection from conflicts between clans (noise and threat), and protection from predators (teeth and claws). A wolf in a human group was likely more useful than a supplementary hunter or warrior. Probably humans cooperated with wolves, taken at a wild den, several centuries or thousands years before artificial selection produced dogs, keeping docile cubs and preventing backcrosses with wild wolves. Sub-fossil bones found by Germonpre et al. (2009) are indeed from primitive dogs close to wolves. Miklosi (2015) concluded that archaeological evidence does not support the domestication of dogs before 15,000 years because cave prehistoric paintings represent no dogs or



Figure 4. Prehistoric painting of a wolf (or a primitive dog) in the Font-de-Gaume cave (Dordogne, France)

wolves. It is true that our ancestors showed rarely canids (see nevertheless the cave painting of Figure 4) but almost always big mammals. Also they rarely show humans, not because they were absent but perhaps because hunters were more interested in their prey. On the other hand, Shipman (2012; 2015a,b) concluded that the amount of big game killed by humans between 15,000 and 45,000 years ago can be explained only with the help of the first dogs.

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