

Co-evolution of Humans and Canids

An Alternative View of Dog Domestication: Homo Homini Lupus?

Introduction

Why did our ancestors tame and domesticate wolves, of all creatures, and turn them into dogs to become man's best friend? Is man dog's best friend, as Mark DERR (DERR 1997) once dared to ask? Well, not according to Stephen BUDIANSKY's assertions in a new book, *The Truth About Dogs* (BUDIANSKY 2000). He claims that dogs are scavengers at heart "For all the myth and tales of dog's service to man, only a small fraction of dogs living off human society today earn their keep... the overwhelming majority of dogs were freeloaders" (p6), even though "in my role as brutally objective observer, I do love dogs" (p9). As scientists, we are skeptical about a successful journalist who claims to have found "the truth", especially in such a complex web of problems, connections, observations, opinions. And, his confession of his "love" for dogs has a strange contradictory ring.

Konrad LORENZ once stated: "Of all creatures the one nearest to man in the fineness of its perceptions and in its capacity to render true friendship is a bitch."

Abstract

Dogs and wolves are part of the rich palette of predators and scavengers that co-evolved with herding ungulates about 10 Ma BP (million years before present). During the Ice Age, the gray wolf, Canis lupus, became the top predator of Eurasia. Able to keep pace with herds of migratory ungulates wolves became the first mammalian "pastoralists".

Apes evolved as a small cluster of inconspicuous tree-dwelling and fruit-eating primates. Our own species separated from chimpanzee-like ancestors in Africa around 6 Ma BP and— apparently in the wider context of the global climate changes of the Ice Age—walked as true humans (Homo erectus) into the open savanna. Thus an agile tree climber transformed into a swift, cursorial running ape, with the potential for adopting the migratory life style that had become essential for the inhabitants of the savanna and steppe. In the absence of fruit trees, early humans turned into omnivorous gatherers and scavengers. They moved into the steppe of Eurasia and became skilled hunters.

Sometime during the last Ice Age, our ancestors teamed up with pastoralist wolves. First, presumably, some humans adopted the wolves' life style as herd followers and herders of reindeer and other hoofed animals. Wolves and humans had found their match. We propose that first contacts between wolves and humans were truly mutual, and that the subsequent changes in both wolves and humans are understood best as co-evolution.

Key words

Chimpanzee, co-evolution, cooperation, dog, Eurasia, human, hunter, Ice Age, pastoralist, Pleistocene, social, pack, wolf.

(LORENZ 1954, p85). Isn't it strange that, our being such an intelligent primate, we didn't domesticate chimpanzees as companions instead? Why did we choose wolves even though they are strong enough to maim or kill us? We do not claim to know "The Truth" but we offer in this paper a different view, with emphasis on companionship rather than human superiority.

Co-Evolution of Cooperation: An Alternative to Domestication?

The human species has refined sociality to a degree of complexity that remains unmatched in our world. The human capacity for cooperation starts at birth: even though a human mother is able to give birth and take care and full responsibility for the newborn, traditionally three women cooperate in the birth... the mother, the mother's mother and the

midwife. Growing up is sheltered by complex helper systems, staffed by siblings, babysitters, and teachers far beyond puberty, and group living within the family is well supplemented by socialization among

peers, from kindergarten, through school, kinship, work, and ending in funeral rites. But our communal life does not end there: We strive to join our ancestors in heaven, and meet our maker who made Adam in His likeness. Or, rather, humans created a god in their likeness who is their alter ego, and accepted by many as the ultimate judge of their moral behavior.

When we try looking back at the biological foundations of our moral behavior in a distant past, and, in the absence of any historical evidence turn to our closest relatives, the chimpanzees, we find ourselves in a strange conflict. The life of chimpanzees, especially their sociality, as revealed by the pioneering work of Jane GOODALL and others (GOODALL 1986; DE WAAL 1997) appears as a frightful caricature of human egoism. Even in their maternal behavior warmth and affection are apparently reduced to nursing and an occasional comforting hug; cooperation among group members is limited to occasional hunting episodes, or the persecution of a competitor, always aimed for one's own advantage and executed with MACHIAVELLIAN shrewdness. The first insight we get from chimpanzee society is: "We have come a long way". The high morality we claim as achievement of our species, however, is a very thin veneer on the old ape, and our newspapers are full of stories that reflect more chimpanzee than human ethics.

The closest approximation to human morality we can find in nature is that of the gray wolf, *Canis lupus*. This is especially odd in view of the bad reputation wolves have in our folklore, as expressed in the famous phrase, HOMO HOMINI LUPUS. In Thomas HOBBS' own words: „To speak impartially, both sayings are very true; That *Man to Man is a kind of God*; and that *Man to Man is an arrant Wolfe*.“ (HOBBS 1651). Since HOBBS' time, however, our understanding of wolves has changed considerably, even though for a rancher who leaves his livestock unsupervised and unprotected by a good shepherd, an "arrant Wolfe" is to this day a formidable threat (MECH 1970; FOX 1975, 1980; MECH/BOITANI 2003). Wolves' ability to cooperate in a variety of situations, not only in well coordinated drives in the context of attacking prey, carrying items too heavy for any one individual, provisioning not only their own young but also other pack members, baby sitting, etc., is rivaled only by that of human societies. In addition, similar forms of cooperation are observed in two other closely related canids, the African Cape hunting dog and the Asian dhole. Therefore it is reasonable to assume that canid sociality

and cooperativeness are old traits in terms of evolution, predating human sociality and cooperativeness by millions of years. Thus, we can give a new and very different meaning to HOMO HOMINI LUPUS: "*Man to Man is—or at least should be—a kind Wolfe.*"

This shift in our attitude toward wolves opens a new vista as to the origin of dogs. Instead of perpetuating our traditional attitude that our "domesticated animals" are intentional creations of human ingenuity, we propose that initial contacts between wolves and humans were truly mutual, and that various subsequent changes in both wolves and humans must be considered as a process of co-evolution. The impact of wolves' ethics on our own may well equal or even exceed that of our effect on wolves' changes in their becoming dogs in terms of their general appearance or specific behavioral traits.

The earliest suggestions that dogs do not fit the conventional paradigms of domestication, as proposed for hoofed animals and fowl, can be found in ZEUNER's pioneering work (ZEUNER 1963), but the gravity of the problem became apparent when the genetic relationship between wolves and dogs was elucidated by Robert WAYNE and Carles VILÀ (VILÀ et al. 1997), opening the possibility that the split between wolves and dogs may date back as far as 100 to 135 ka BP (135,000 years before present). Such a long common history of dogs and modern humans begs the question as to the dog's part in the endeavor of humans to take control of the world, and led to the formulation of a hypothetical "lupification" of human behavior, habits, and even ethics (SCHLEIDT 1998). Erhard OESER has pursued this lead and traced the contribution of dogs in the "humanization of the ape" in a wider context of human culture (OESER 2001, in press). Our own paper does not aspire to be a comprehensive review of the hypothetical co-evolution of cooperation between dogs and humans, but attempts merely to provide more details und pursue several collateral ideas emanating from the original proposal (SCHLEIDT 1998).

Primates and Canids: A Current View

Around 6 Ma BP humankind separated from chimpanzee-like tree dwelling and fruit-eating ancestors in Africa and moved as true human hunters and gatherers, *Homo sp.*, into the open savanna, conquered the plains of Eurasia, and became fierce hunters during the grueling conditions of the Ice Age.¹ There a new species emerged and dominated Europe and the Near East longer than any other

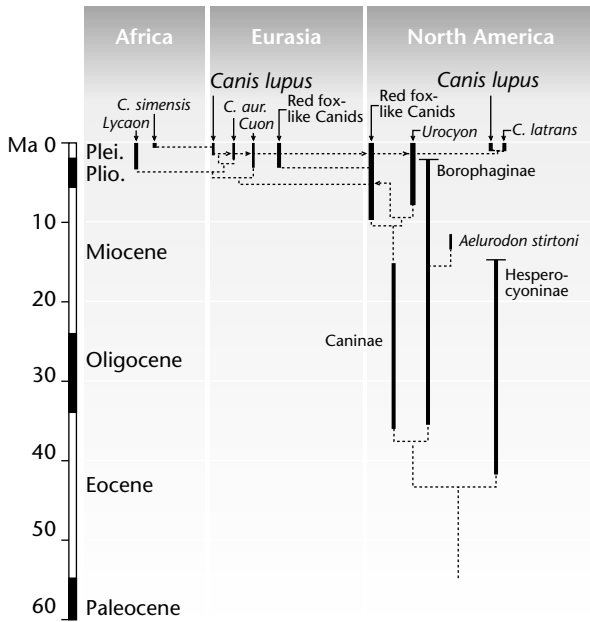


Figure 1: Cladogram indicating the phyletic relationship between *Canis lupus* and selected species and divisions of Canidae within their temporal and geographic ranges (after TEDFORD/TAYLOR/WANG 1995; MCKENNA/BELL 1997; WAYNE/VILÀ 2001, etc.).

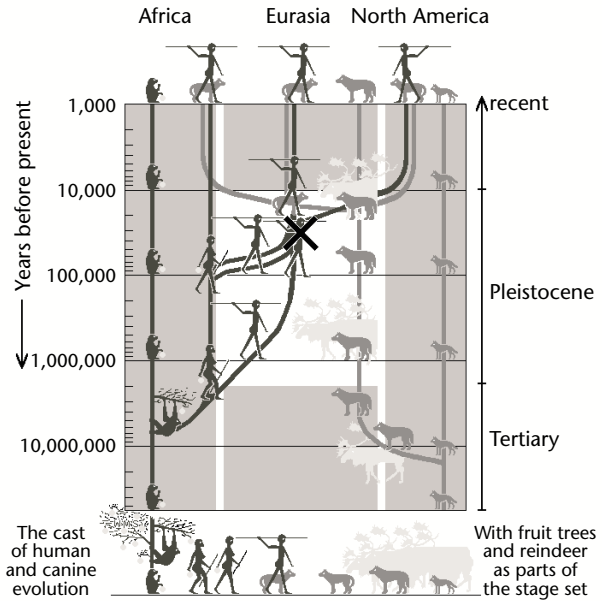


Figure 2: A schematic summary of the current teaching of human and canine evolution. Note the logarithmic time scale, and the simplistic view of Pleistocene as an epoch of inhospitable cold climate in circumpolar regions.

hominid: the clumsy, but successful Neanderthal man.² Meanwhile, around 150 ka BP—based on evidence from mtDNA—a superior woman, the legendary African Eve, had emerged. Her daughters moved into icy Europe and, thanks to their rich subcutaneous fat and superior intelligence, were able to out-compete Neanderthal women. Then, around 80 ka BP—based on evidence from nuclear DNA—the legendary African Adam emerged, the first man who really deserved the name “*Homo sapiens*”. He took to the daughters of African Eve who flourished in icy Eurasia, killed all the reindeer, mammoths and Neanderthals, and did beautiful art-work in the caves of Spain and France. So the story goes.

Back to serious science: The canids, also known as (wild) “dogs”, have their roots in North America.³ They, too, emerged from the forest and were originally about the size of a fox when grasslands opened and herds of grazing ungulates, notably horses and antelopes, began to dominate the open plains. A multitude of swift canid predators evolved, and around 10 Ma BP, they started to cross into Asia, Europe, Africa, and back into North America. Thus, they became part of the rich palette of canid predators and scavengers, coexisting and competing with the big cats and hyenas: the wolves, jackals, coyotes (the latter all members of the genus *Canis*), and the aberrant “wild dogs”; the African Cape hunting dog,

and the Asian dhole. The Genus *Canis* apparently evolved in Asia, and *Canis lupus*, the circumpolar big “wolf”, as a species distinct from the various jackals, appeared about one million years BP.

At the end of the ice age, man tamed wolves, which were scavenging among the rich refuse of human camp sites, and by artificial selection created the multitude of dog breeds we know today. Or as an alternative hypothesis, scavenging wolves took the initiative and conned the affluent hunting and gathering humans into sharing their plenty, by pretending to be their obedient servants and hunting companions.

Primates and Canids: A Different View

There is something in the bond among wolves and between dogs and humans that goes beyond that between us and our closest primate relatives, the chimpanzees. Here *we are not talking about intelligence*, but about what we may poetically associate with *kindness of heart*. Jane GOODALL, invited to comment on K. LORENZ’s statement quoted above, wrote in a letter to the first author:

“Dogs have been domesticated for a very long time. They have descended from wolves who were pack animals. They survive as a result of teamwork. They hunt together, den together, raise pups to-

gether. This ancient social order has been helpful in the domestication of the dog. Chimpanzees are individualists. They are boisterous and volatile in the wild. They are always on the lookout for opportunities to get the better of each other. They are not pack animals. If you watch wolves within a pack, nuzzling each other, wagging their tails in greeting, licking and protecting the pups, you see all the characteristics we love in dogs, including loyalty. If you watch wild chimps, you see the love between mother and offspring, and the bonds between siblings. Other relationships tend to be opportunistic. And even between family members, disputes often rise that may even lead to fights... even after hundreds of years of selective breeding, it would be hard if not impossible to produce a chimpanzee who could live with humans and have anything like such a good relationship as we have with our dogs. It is not related to intelligence, but the desire to help, to be obedient, to gain our approval." (GOODALL 1997).

Jane GOODALL's eloquent comparison is based not only on her own personal experience with dogs⁴ and many years of living with chimpanzees (GOODALL 1986), but also less well known to the general public on her familiarity with and research on the wild dog, also called the Cape hunting dog (*Lycaon pictus*), the African brother of our gray wolf. We not only value a dog's intelligence, but its warm affection, playfulness, and loyalty. Several species of canids show these special traits, and several other really outstanding behavior patterns related to harmonious life in a pack. They do superb teamwork, not only during the hunt, but in denning together and raising pups together. Although the core of the pack is usually one extended family, pack members can also accept strangers. Equally, when a stranger or even a close kin fails to comply, it can be attacked, driven off, or even killed.

E Pluribus Unum

From many, one. Many people, many peoples, one nation. But also, if two or more persons can agree to cooperate, they are stronger than a single person. As a rule, the bigger the group, the easier it can subdue a single person or a few, or force them to comply. That is the basis of majority-ruled democracy. There is a catch, however: the members of the group must cooperate, communicate, and agree on a common goal.

That is not as easy as it sounds, even for intelligent human beings. The old primate trait of selfish-

ness and MACHIAVELLIAN reasoning get in *the way of our* behaving communally. Let others take the risk and reap the gain for oneself and one's kin. Self interest first, and if there is a little surplus: practice nepotism. In theory, of course, we praise it as the highest expression of humaneness when, on rare occasion, a hero or saint can overcome temptations of selfishness. We preach love thy neighbor and ask our brave boys in uniform to be prepared to sacrifice their lives for the sake of their families, community, and nation; we admire the age-old saying, *Sweet it is to die for one's country*.

Strangely, there are indications that such humaneness, which many admire and hold, at least in theory, to be the highest achievement of humanity, was invented millions of years ago by early canids. It is practiced to this very day by some of their descendants and honed to perfection by members of the pack-hunting canid species: notably the gray wolf, but maybe even more so by the wild dog of Africa (*Lycaon pictus*), the dhole of India (*Cuon alpinus*) and, to a lesser extent, the bush dog of South America (*Spethos venaticus*). In fact, some of today's wolves may well be less social than their ancestors, as they have lost access to big herds of ungulates and now tend more toward a lifestyle similar to their "minor brothers:" coyotes, jackals, or even foxes.

The E PLURIBUS UNUM of the pack goes far beyond what makes UNUM, a unit, out of a herd or a gang of selfish fighters. As in the social insects (bees and ants), where the hive is only one of the units of selection (MORITZ 1993)⁵, the pack became one of many systems upon which natural selection acts.

Humane Canids

Among all the canids one species became the most successful mammalian predator ever: *Canis lupus*, the gray wolf. It roamed over all the northern hemisphere north of 15°N (Fig. 3) (HARRINGTON/PAQUET 1982). In some areas the gray wolf coexisted with less social members of the genus, and in India it was sympatric with the dhole. The ubiquity of the gray wolf is apparently due to its rich behavioral repertoire and the ability to adapt its life style opportunistically to local and temporal conditions: most successfully as a pack hunter of midsize ungulates, but able to squeeze by on the diet and life style of a fox: hunting mice and picking berries.⁶

What is it that makes the ancient pack social system so successful? Well, it is not a single life history trait, anatomical feature, or type of physiology or

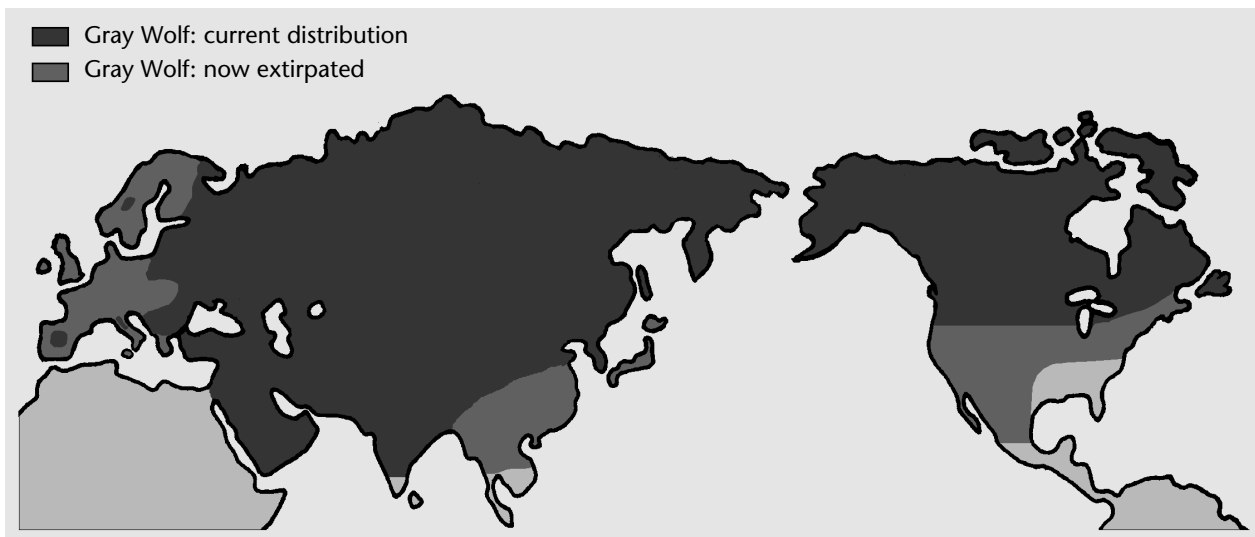


Figure 3: Grey wolf (*Canis lupus*) (after HARRINGTON/PAQUET 1982).

behavior. It is a whole array of specific adaptations which make communal life possible. Social pack-forming canids are essentially monogamous. Even though there may be several sexually mature adults in a pack, as a rule, only one pair breeds, but all members share food and parental care generously. Even siblings and friends share food and affection (unlike in chimps, lions, tigers, hyenas, where the strong tend to take from the meek).

The long-legged social canids are not only fast and long-distance runners, they are able to run as a single group, apparently well aware not only that another pack member is running where, but which individual. This awareness makes it possible for a team of dogs to pull a sled and run for hours without changing places, or for two dogs to race at full speed while holding onto a stick of wood.

Typically predators, when going for the kill, avoid the risk of disabling injury that would prevent them from hunting. The attacks on prey by lions, tigers, sharks, and the like conjure up images of bravery and fury. In reality, however, they are low-risk performances by smooth butchers. Only when they turn on each other, as, for example, in conspecific fighting over a limited resource (e.g. a female), do they incur high risk of getting seriously injured.

When canids hunt as a pack, they can, because of their focused attention and close cooperation, act much more as an integrated system than any group of chimps or lions, where the individual that makes the kill and can maintain possession of the carcass, or take it over by force, will get "the lion's share". In wolves each pack member can accept greater risks when attacking, because, when injured, the needy

will be fed by the other pack members.⁷ This cooperation and risk sharing not only among close relatives, but among individuals bonded as mated pairs or by lasting friendships among individuals of the same gender, is the central feature of canid pack living.

When wolves feed on a kill, there is growling and snarling, of course, and a low ranking pack member may have to wait, but compared to other predators there is little overt competition among pack members. All is tuned to swallow as much as possible as fast as possible (which is the basis for the story of Fenris-Wolf gulping down Odin, and for Grimm's fairy tale bad wolf swallowing grandmother and Little Red Ridinghood).

Wolfing down prey is apparently an ancient canid trait: Around 11 Ma BP a wolf-type canid (*Strebodon stirtoni*) roamed Nebraska, and a skeleton of this species on display in the Museum of Natural History of the Smithsonian Institution in Washington, D.C.⁸ reveals an amazing story: in the region of the ribcage one can see quantities of broken and etched bone representing at least two individuals of small antelope, leg bones articulated and neatly folded-up in the area where once the canid's stomach had been.

Wolfing down prey is but the first phase of feeding, which allows pack members to make maximal use of each kill and to leave little for others. By the time jackals, hyenas, and vultures arrive, there is usually not much left.

The second phase of feeding starts when the wolves have reached a cozy place for a rest some distance from the kill, or when they get home to the den. They then regurgitate the large chunks, sharing

with those that did not participate in the hunt, especially the pups and their babysitter, and carefully go over what they brought home in their stomach shopping bags. What had been carried communally, such as a leg of a prey, too large to swallow, is cut down to size, and pulled apart in a “tug of war”, with “real growls”, but actually quite playfully, and very different from the fighting over a kill, e.g., in hyenas. The pack at the den can process its loot in peace and spend time resting and digesting.

MACHIAVELLIANS, however, consider such doggish behavior—accommodating rather than fighting—as cowardly. Yet it is precisely what keeps canid pack members from incessant quarreling, as, for example, the way hyenas do, or from playing macho the way chimps or some humans cannot do without. The pack hunter’s social awareness is equally amazing. Contrary to the popular belief that canids are specialized in sniffing and have limited eyesight, they constantly watch each other; each member of the pack knows not only who is who but also who is where and who is doing what. For example, in spite of all the generous sharing of food, if they prefer, they keep pieces for themselves; when an individual buries its leftovers, it can behave very secretly, and start to dig only when nobody is in sight. The same applies to smart dogs: do not believe that opening the fridge or reaching for a can opener triggers a mere Pavlovian conditioned reflex in your dog. If you watch it carefully, you will see its eyes move, depending on who is going where. And if you cannot see its eyes, the movement of the eyebrow (the light spot above a Doberman’s eye or in the face mask of a husky) will tell you what it attends to, very much like you can determine what a dog listens to by observing its ears provided they are pointed like those of wild canids (SHALTER/FENTRESS/YOUNG 1977). If you question our claim and are hung up on your belief in Pavlovian conditioning, train your dog to bring specific items (toys you assign names to) and then give each to a different member of your family or deposit them at different locations. You will quickly realize that the conditioned reflex explanation for a dog’s awareness is a gross simplification.

Like wolves, dogs are also very much aware of who is who, who is where, and who is doing what. This awareness is an essential feature of both: enabling dogs to fit so well into our human social fabric and enabling the pack-hunting wolves to lead a communal life: moving and hunting together, sharing, etc.

There are other behavioral features of importance for the canid pack algorithm, e.g. dealing with hier-

archy with minimal bloodshed. Occasionally fights break out, and even close relatives can be killed, but only rarely does one observe strict rank orders and real macho behavior on the part of dominant pack members. Instead, enforcement of established rank can be a low-key affair, where serious threat by a high ranking member is rare compared to the gracious acceptance of a lower ranking individual’s signs of compliance or even submission. This is what in dogs makes it easy for wolfish families to form mixed, multi-species packs: humans, dogs, cats, goats, sheep, horses living in harmony.

Finally, we may ask: What about wolves at very low population densities as in most of Europe, where, for the past several centuries, just about every wolf was shot on sight? What about the lone wolf? Human wolf eradication programs go for the conspicuous individuals, and a pack raiding a sheep shed or bringing down a cow in a pasture is much more conspicuous than a single wolf that is forced to adopt the lifestyle of a fox. Thus, the wolves surviving at very low densities may well have lost their social competence, both in their genetically endowed propensities and in their social pack-living skills. Their social skills are practiced only toward their mates and young. When hunting, it appears they use the basic bag of canid tricks that foxes are known for: wandering around low profile, looking, listening and sniffing, then stalking, jumping, and chasing down whatever one can grab: a frog, a mouse, a rabbit, a hare—prey up to about one’s own body size—eating a few berries and a couple of mushrooms along the way. And, when two lone wolves meet, they can be so overwhelmed with joy that they bounce around and prance off together as if they were thinking: Let us prey!

Thus, the social systems of canids and their hunting strategies can be considered a continuum from fox to wolf, with the coyote and jackal somewhere in between. The African hunting dog and the dhole of India may be even a bit further out to the extreme of pack life, a life which only few, if any, of our wolves can indulge in today. But, the special success of the gray wolf may well be based on this species’ potential to live well like a dhole and still survive when forced to live like a coyote.

Lupification of Canids

When we talk about our own primate descent, about the hominization of Australopithecines, we are easily led to believe that our ancestors had nothing better to do than to leave their beastly existence

behind and let those not worthy of becoming “humans” die out (Neanderthals, bushmen, or the like). In spite of accepting the new creed of Darwinian natural selection, we find comfort in our cherished belief to *be fruitful, multiply, replenish the earth, and subdue it... to have dominion over the fish of the sea, and over the fowl of the air, and over every living thing that moveth upon the earth*. In other words, instead of seeing ourselves as part of the complex system of nature, we continue to pretend to be the very crown of creation.

If wolves could dig up the dens of their ancestors in Europe, Asia, and North America, sniffing at the old bones of their dead and the bones left of their meals, what would they find? How would wolves view the lupification of their canid ancestors?

As Africa is today considered to be the cradle of mankind, the origin of canids (as well as their old parasites, the fleas) is traceable to North America. When that continent became disconnected from the other land masses, some of its ancient predators specialized into fox-like carnivores, presumably living on small rodents, insectivores, and insects, with a degree of omnivorousness. When, possibly driven by changes in global climate, early horses and other ungulates changed from leaf eaters to grazers, grasses started to cover large areas of the earth, and an evolutionary arms race started between grazers and grasses. The predators latched onto this new and evolving ecosystem, preying on the smaller, slower grazers and especially on their young. As these herbivores responded by joining together in large herds, developing communal defense behaviors, and outgrowing their predators in size, the smart, fox-like early canids had to catch up with their prey. They grew larger and stronger, to the size of coyotes and larger. As a counter strategy to the herding of ungulates around 10 million BP, canids “invented” long legs for high speed running, the prerequisite for hunting in a fast moving pack.

When the land bridge united North America with the Asian continent in the area we call the Bering Strait, horses and canids poured into Asia. The horses, as fast runners, did exceedingly well in the open grassy plains of Asia and Africa, and the canids thrived on the native herbivores, which had adapted well to predation by felids, but were at the mercy of the new pack-hunting ancestors of wolves, hunting dogs, and dholes. Thus, when the pack hunters moved into Asia and Africa, they joined or even replaced the big cats at the top of the food pyramid. Not only did they compete for the resources formerly controlled by lions and tigers, but they

even attacked them and, if they failed to kill them, at least they killed their cubs. Only during the last few thousand years did humans propel themselves in mass to the top of the food pyramid, displacing the canid pack hunters.

The Ice Age as the geological epoch and the “Mammoth Steppe” as the biogeographical substrate (GUTHRIE 1990, Fig. 4) are most important variables in the evolutionary puzzle of the genus *Canis*, and, more recently, the genus *Homo* as well. Our understanding of these variables has changed dramatically in our lifetime. We are still far from a consensus about the causation and dynamics of Pleistocene geology, climate and ecology, however, but it has become obvious that many, if not most, of previous teachings were wrong, especially the image of northern Eurasia and America being covered by one gigantic ice shield that only temporarily gave way to a little green during the interglacials. The last interglacial, the Ipswichian of England, about 135 ka BP until about 70 ka BP, had a climate in Europe warmer than today, with hippopotamus wallowing in the Thames and Mediterranean vegetation flourishing in the valleys of the Austrian Alps. On the other hand, the grueling cold of the last phase of the Wisconsin (in America; Weichsel in northern Europe and Würm in the European Alps) peaked only 18,000 years ago.

Canine Humans?

So, what is the difference between a beloved golden retriever bitch, as a member of our household, and a shewolf as a member of a wolf pack? Let us look, point by point, at what we said above, under the heading *Humane Canids*: what made the ancient pack social system so successful was not a single life history trait, anatomical feature, or matter of physiology or behavior, but a whole array of specific adaptations that make communal action possible.

Humans, at least in Western cultures, live more or less monogamously, roughly as monogamously as most members of wolf packs. We share parental care generously, even among siblings and friends. Many humans behave the canine way, others still behave like chimps or lions, not necessarily humanely. In the human species we find a very wide range of family structures and a great variety of even more complex (“non-family”) social systems. Our spectrum includes the solitary existence of saintly hermits, family bands, villages to cities, nations, etc., with many niches for canine companions. A blind person may depend on a seeing-eye dog, a family dog

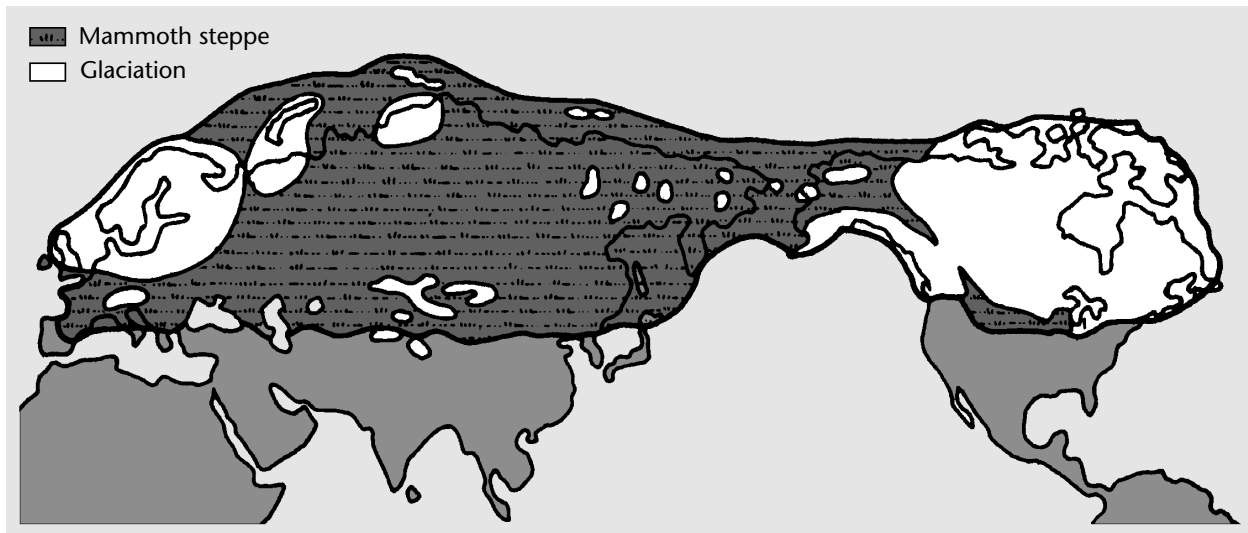


Figure 4: The “Mammoth Steppe” in the wider context of Pleistocene glaciation. The extent of the steppe varied over the last 2.5 million years and had been more extensive during glacial episodes and less so during interglacials, when varying parts of grassland were replaced by forests (after GUTHRIE 1990).

can be a great asset for a youngster, and a Dalmatian may not only serve as a fire department’s helper in situations where humans are bound to fail, but also a beloved mascot.

Humans run neither as fast nor with as much endurance as wolves, but they walk their dog around the block several times a day, or take it along jogging, biking, or hiking. They let it sniff fire hydrants, trees, and the strange air when riding along in a car with its nose stuck out the window. On the other hand, most dogs’ legs compared to those of wolves or working dogs are not suited for running and are even somewhat crippled. Not only dachshunds, bulldogs, Maltese, and Yorkshires act as if hobbled by their anatomy. Many a German shepherd champion is no match for a husky or greyhound on a long-distance run. Thus, many dogs prefer to lie on a windowsill and watch the world go by, having lost their wolfish striving for long-distance locomotion, as have most city dwellers, who no longer rely on their feet but on cars and elevators.

Joining dogs in communal hunting behavior was long reserved for pharaohs, royalty, and the upper class. Nowadays it is pretty much restricted to traditional Old English fox hunts with a pack of hounds, as sport for a few rich, to greyhound racing, as sport for the common man, and only exceptionally in the original, ancient mode: e.g., in the U.S., some still hunt with a pack of hounds—black bears and mountain lions, as well as squirrels. But today’s stereotypes are the American hunter with rifle rack in

his pickup truck and his retriever next to him, or the German forester with pipe and dachshund. But otherwise, hunting behavior by dogs is discouraged and subject to artificial selection: where local leash laws are not respected, strays are shot by game wardens or park police, or, at the very least, face an uncertain future in a pound. The only exceptions are a few breeds of so-called hunting dogs, (hounds, terriers), work/guard dogs (Dobermann, shepherds, St. Bernard, etc.), and the sporting group (beagles, fox terriers, golden retrievers, etc.), so long as they “work” under close human supervision.

Feeding on the kill? Well, what is in the food dish rarely involves much effort or opportunity to share or compete in a one-dog household. Although Fido still wolfs down his well-processed boneless meal, there is no need for him to regurgitate and look it over again. Once it’s down, it stays down, thanks to the grinding action of the dogfood industry. To ensure our dogs’ good teeth we buy special tartar-control treats, chewing toys, or a specially processed bone, piece of hide, dried pig’s ear or ox penis!

The dog’s social awareness is one of its greatest assets. Therefore, we remind you once again: contrary to the popular belief that canids are specialized in sniffing and have limited eyesight, they are constantly watching each other. A dog knows not only who is who but also who is where and who is doing what. This specific set of skills is a prerequisite for a dog’s ability to know and recognize many different people. Ulysses returning home in rags after many years away and being recognized and

greeted by his old dog has become the archetypical experience that repeats itself daily at many airports and train stations. And although dogs perform no obvious farewell ceremony, many show signs of sadness and depression after a beloved friend or any member of its family (its pack) has left.

A good family dog is well integrated into the social hierarchy and, provided there is a certain level of social competence among the human pack members, most dogs have no reason to even attempt to take over to become top dog and run the family.⁹

Domestication: Who Domesticated Whom?

The oldest remains of dogs, of a canid distinctly different from wolves, in the context of human activity are dated about 14,000 years BP, long before any trace of domesticated goats, sheep, and cattle (BENECHE 1995; SABLIN/KHLOPACHEV 2002). Thus, there is little argument that dogs are the oldest domesticated animal (ZEUNER 1963; SERPELL 1995). A word of caution, however; what do we mean by “domesticated”? In a most general sense: “no longer in its wild or natural state.” But, were our own ancestors back then, long before they built permanent houses for themselves, less “wild” than the wolves they associated with? While canids are known to dig their own dens, and some of such dens may have been used by many generations, even over hundreds of years (THOMAS 1993), humans are apparently the only primates to make use of caves, and their association with dogs predates the construction of permanent houses by thousands of years. Is it not absurd to talk about the “domestication” of dogs by humans who had not yet any permanent domiciles (“domus”)?

What are the signs of domestication in the archeological record? In mammals it is usually a reduction in overall size, a foreshortening and rounding of the skull, and faster sexual maturation. Once the ranges of variability of the assumed wild ancestors and those of the ancestors of our domesticated forms no longer overlap substantially, we assume that the exchange of genetic material between those two populations was reduced or interrupted by human interference and control.

Are such domesticated forms now members of a different new species? Let the professional taxonomists fight that out. It can get tricky, however, depending on whether you ask a morphologist, paleontologist, ethologist, or geneticist. The most

common criterion for belonging to one species is interbreeding and having fertile offspring. But where do we draw the line between ancestral species? Could we interbreed with Neanderthals? In canids, we have a different problem: apparently, all species of the genus *Canis* can interbreed, e.g., the red wolf, *C. niger*, has revealed itself as a stable hybrid between the gray wolf, *C. lupus*, and the coyote, *C. latrans* (WAYNE/JENKS 1991).

In recent years, geneticists have developed a number of tests as measures for the degree of relatedness by comparing differences in the DNA of individuals and populations. Genetic differences between wild and domesticated forms can be estimated in various ways, and genetic distance can give us some idea of the elapsed time since two forms separated. Based on such studies in humans, for example, it has been assumed that the common ancestors of chimpanzees and early man split about 6 Ma BP. There is less agreement concerning the first *Homo sapiens*, the mother common to all modern humans; some scientists believe that this hypothetical Eve lived 160 ka BP in Africa, and our hypothetical Adam lived there 70 ka BP, but it will take a while before we come close to reconciling the many contradictory “facts”; that is, particular observations of the fossil and genetic evidence.¹⁰

New results, even more controversial, although supported by considerably larger data sets than many estimates of our own ancestry, indicate that the split between the ancestors of wolves and jackals occurred about 1 Ma BP. This study, based on the analysis of mtDNA (mitochondrial DNA) from various canids, was performed by Carles VILÀ et al. (1997, 1999) at the laboratory of Robert WAYNE at UCLA. mtDNA from 67 breeds of dog showed a high degree of similarity to that of wolves (as represented by 27 wolf populations from Europe, Asia, and North America), clearly supporting the hypothesis that dogs are descendent from wolves (not from the golden jackal or other canids, as Darwin, and many others had assumed previously).

But the most spectacular of WAYNE’s results is that the first split between dogs and wolves dates back roughly 135 ka BP, nearly TEN times further back than indicated by any bones or any paleontological evidence found thus far! And, based on the same reasoning that traces our Eve and Adam back to Africa, WAYNE’s data indicate that dogs are related closest to wolves found today between France and western Russia, and not to those in the Near East, where many of our domesticated animals and plants are assumed to have originated.

There is also indication of later influxes of wolf genes into dog populations, and this process is still going on in our time. It appears to us especially significant that the first dogs separated from wolves in an area and at a time when Neanderthals were the only hominids within the distribution range of wolves, even long before the time the hypothetical children of African Eve started to spread into Eurasia. Thus, the fate of dogs and humans has been intertwined for a very long time indeed.

Hominization and Canization

We now are confronted with this startling temporal and geographical coincidence between the emergence of mankind and dogkind, between hominization and canization. Reconsideration of past and current concepts of domestication has become inescapable. Even the term domestication has the wrong ring, since the meeting of wolves and modern humans predates, by far, anything that could be considered a human habitation in the form of a *domus* (Latin for house). Canids' use of dens dates back further. Consequently, instead of domestication, we should talk about "cubiliation" (*cubile*, Latin for den¹¹) as suggested earlier (SCHLEIDT 1998) and wonder who cubiliated whom.

From a biologist's vantage point, the intertwining process of hominization and canization makes sense only if viewed as coevolution. Whereas the evolution of man, our primate heritage, has attracted attention ever since the publication of Darwin's *The Descent of Man*, the evolution of wolves and dogs has remained a particular topic for paleontologists specialized in Pleistocene carnivores. *The descent of dogs*, to the best of our knowledge, has not been integrated into the descent of modern hominids. Consequently, we may ask: What was the state of affairs among our ancestors when some wolves separated from their conspecifics and became the immediate precursors of dogs?

At that time, Neanderthals were wandering around Europe, apparently having some success in killing mammoths, horses, and reindeer. Few animals can live on meat alone, however, so it has been proposed that Neanderthals similar to present-day gatherer-hunters also collected other foodstuffs (fruits, greens, tubers, etc.). In addition, they may have raided bee hives and underground grain stores of hamsters and other rodents. Unfortunately, there are many more artifacts attributed to Neanderthals than bodily remains, and much of what is being taught one day by one school of thought is chal-

lenged by another the next. Every new find seems to raise more questions than it answers.

Well, what about the state of wolfkind when Neanderthals roamed the "Mammoth Steppe", the Eurasian tundra and grass steppe ecosystems which reached from Spain to the far east of Siberia, and at times continued into the continent of North America? Although the mammoth must have been an impressive sight, it was not the species that constituted the greatest amount of biomass in that ecosystem. Mammoth bio-mass presumably could have been equaled by tasty rodents: lemmings, voles, squirrels, etc. and by the most abundant species of wolf food, the reindeer. Nowadays, Western culture's Santa's team, a few specimens in various zoos, and occasional images provided by National Geographic are all that is left of a species that was once part of one of the largest ecosystems on earth. Wolf packs, very likely, were an important part of that ecosystem.

Wolf: The Pastoralist

In fact, in Siberia, before it became a national sport to shoot wolves from helicopters, human pastoralists of reindeer, basically living off the herds they followed in their annual cycle of migration, not only tolerated wolf packs following their herds, but even considered those wolves to contribute to the breeding of better reindeer. Humans select only the best specimens for slaughter, whereas wolves take only what herd owners would never touch and would not even feed their own dogs: placentas on calving grounds, weaklings, the sick and the aged. So, in the ancient form of reindeer management, prior to governmental control, taxation, and special funding, and before bounty hunting and fur trade, wolves could have played a similar pastoral role: eliminating the unfit and keeping away the big cats, bears, and hyenas. Very much like today, in shepherd-controlled sheep herds, where the shepherd eliminates the unfit and dogs guard their herd from attacks by wolves.

Thus, among mammals, Eurasian wolves can be viewed as the first true pastoralists, ahead of human pastoralists by tens of thousands, hundreds of thousands of years. Wolves ability to hunt as packs, to share risk fairly among pack members, and to cooperate, unsurpassed by any of the big cats, moved them to the top of the food pyramid on the Eurasian plains.

It is noteworthy, however, that those wolves never became specialized big game hunters like the large cats of Africa. Wolves retained their full reper-

toire and zeal for hunting small rodents, taking birds and eggs, and in addition berries of various kinds, tending toward a degree of omnivorousness to which many human steak fans would pale in comparison.

Reindeer, traveling in ancient times, over hundreds of thousands, maybe millions of years, seasonally in vast herds in the realm between what is now Spain and eastern Siberia, and at times crossing the Bering strait into the North American continent, could well have coevolved with wolves in the sense that prey and predator became interdependent, symbiotic, as for example aphids and ants.

Some ants keep aphids throughout the winter in their nests, and, in the spring, when the first leaves appear, they take their aphids out to pasture in the trees. There, the aphids thrive and multiply under the close supervision and even protection of their ants, and, in exchange, they repay the ants service with aphid honey.

F. E. ZEUNER, reasoning about the domestication of dogs in his famous 1963 *History of Domesticated Animal*, after a careful comparison between herding behavior of wolves to single out potential prey and the herding behavior of sheep dogs, stated that “*the wolf and the pastoralists might be seen to have much in common.*” (ZEUNER 1963).

Man: The Reindeer Hunter

Could Neanderthals around 135 ka BP, having made it successfully through several ice age climate changes, presumably mainly by scavenging and occasionally killing big game, also have entered into the hypothetical ecosystem of the large herds of reindeer, protected by wolves? Had Neanderthals already ganged up with canids, even supplanting the wolves at the top of the food pyramid?

A single Neanderthal, even armed with fire, spear and stone weapons and with all his strength, would have been no match for a pack of wolves out to have him for a meal.

As a group, however, Neanderthals undoubtedly could keep a pack of wolves at bay, wound and even kill several members of the pack, convincing them that attempts to obtain human meat were not worth the risk (also still the best argument against human cannibalism as a stable strategy). Thus, we can assume that early Eurasian hominids, e.g., *Homo erectus*, armed with fire and spears (THIEME 1997), at least since around 400 ka PB, had the same mutual relationship with wolves as exists today in comparable cultures and situations. A single wolf may occa-

sionally gulp down a little Red Ridinghood, but the hunter with his gun will surely get him. So, what would Neanderthals and wolves have gained from a cooperative coalition?

Since, at this moment, we lack evidence for the use of tamed wolves as hunting companions, let's look at other alternative uses. Pups could have been used as baby substitutes, hot water bottles, and toys or playmates for human children (GROVES 1999). Adult wolves, however, were probably a risky addition to a Neanderthal family. A single Neanderthal out alone would have been no match against his own wolf's jaws in a sudden flare-up dispute over rank, and it is hard to imagine that a man would take the risk of becoming outranked by his former companion much less his former servant. So, in the end, in the ensuing struggle, the bond between such a brave hunter and his wolf would have been broken: either the hunter loses his face, literally cut away by his former servant's fangs, or the wolf loses its skin.

In a fair comparison, Neanderthals were superior to wolves only in (1) having greater cognitive ability and foresight (reflected especially in their scouting and scavenging skills), (2) seeing better at longer distances (having an eye level twice that of wolves, able to cover four times an area in the steppe), and (3) being able to hit a distant target. The latter is especially significant in dealing with herds of ungulates, which tend not to run away from every little disturbance, but approach a serious predator with curiosity:

American Indians pulled over a wolves hide to get close to a herd of buffalos, and Bushman fooled African undulates using similar tricks. Even hiking on the Alpine high pastures with a dog can easily provoke such a mobbing response in cattle.

Another common behavior among herding ungulates is standing one's ground: When a single individual has been separated from its herd, it tends not to run from a small predator, apparently not to provoke pursuit. Standing still, however, it becomes an easy target for a skilled hunter's spear. Thus, a group of Neanderthals could have eased their way into the thriving business of wolf pastoralists, at first only as junior partners, and have shared the plenty of those large reindeer herds without raising the level of intra-pack social friction.¹²

How could all this have happened around 135 ka BP? The flow diagram at the very end of this paper (Fig. 6) stakes out the time-space continuum the past 60 Ma BP within three continents: North America, Africa, and Eurasia as centerfield where “Man

meets dog” in a coevolutionary process. Glaciers had receded around the middle of the Riss glaciation, coniferous trees had reappeared, and after another advance of the glaciers and loess steppe, deciduous trees thrived in Europe’s Riss-Würm interglacial period. All this must have resulted in major population changes, from the smallest plants and insects to the largest mammals. We are still far from understanding all the consequences of the dramatic changes of climate, and the interactions of even the most relevant biological variables in that complex ecosystem and its effect on evolution.

Especially our understanding of the climate of the past has dramatically changed during recent years, due to new insights into the effect of continental drift on ocean currents and air streams, and new records of the past climates from pollen analysis, and cores from drilling deep sea bottoms and ice caps. Thus, “Pleistocene” is not simply a past epoch of grueling freezes, subdivided by brief interstadial and interglacial warm spells; rather, “*we are*” in Pleistocene. What has been named “Holocene”—our current epoch in which humanity has begun to change the face of the earth—is just an interlude before the next cold phase (Fig. 5).

There are many more variables of fundamental importance for the evolutionary process: food plants: e.g., lichens and grasses, predators: notably the big cats, insect pests, infectious diseases, etc., not shown in this schema for reasons of clarity. But, at least, we constructed a basic framework for the coevolution of hominids and canids: depicting the global time-space continuum on a logarithmic time scale, coding basic climatic conditions and indicating the confines of the continental plates and narrow land bridges. Within this framework species can be added or deleted, as it best suits our needs to understand the weave of nature, where ultimately everything is connected to everything.

Unfortunately, the image of the ice age landscape as endless plains of inhospitable snow-covered permafrost, bordered by rolling blizzard swept steppe and glaciers is still deeply engrained in teaching and described in textbooks. Only slowly do we gain, by a more detailed, fine-grain analysis of local geography, climate, and vegetation, a more realistic picture of that important time span of human history. Yes, the winters, especially in areas covered by glaciers were long and hard, but in summer the temperature in the valleys and in the plains rose nearly as high as at present and supported vegetation similar to that of Central Europe today. And, in the interglacials, the temperatures

were much higher than today, and areas now famous as European ski resorts supported Mediterranean vegetation.

One more point about climate is commonly not even mentioned, namely that the remarkable Pleistocene fluctuations did not roast and chill our ancestors and their dogs in a 100 000 year rhythm. As the trees, grasses and flowering plants did not die out, but moved gradually to stay within their preferred ranges of temperature and humidity, so did the animals, only faster, because they move with legs and not by seeds and their selective survival. Considering for how long *Homo erectus* type hominids were residents of Eurasia as far as China and for how long Neanderthals did very well for an amazingly long time, it is hard to believe that they disappeared without leaving a trace within the human genome. We personally favor the idea that we are not the descendents of an African elite, but a mixture of “the best of all our ancestors”, wherever they were.

Another important aspect is that, by no stretch of the imagination, should we think that *all* wolves got attached to *all* reindeer, and that *all* Neanderthals lived off mammoths and cave bears at first and then suddenly switched to reindeer to become helpers to wolves. However, there was already some flint trade going on across Europe, and along such routes, tame wolves could have changed hands, or moved with humans, as human genes and customs spread from one group to the next.

Wolfkind Today

Once a few Neanderthals had learned to live with wolves and adopt the pack algorithm (going beyond the close ties of kinship, learning to cooperate closely, and sharing risks) many alternative ways to make a living became available. Within this process of coevolution, technology transfer and diversification began to thrive. Humans became better gatherers, better hunters, more successful fishermen, gardeners, astronauts, you name it. Wolves became hunting companions, guards, sled pulls, beasts of burden, baby substitutes, toys, food, human substitutes in experiments, and the first “astronauts” to circle our planet.

Today, man sits atop the food pyramid throughout the entire world. Reindeer are mostly out of sight, and of all the non-human mammalian species that roamed Eurasia 1 Ma BP, wolves were the most successful in increasing their numbers as dogs, that is, presumably followed by the aurochs

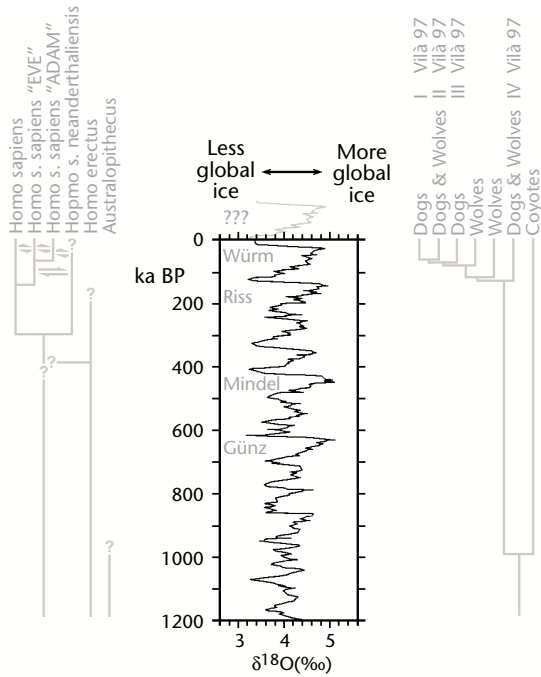


Figure 5: Climate and evolution of canids and hominids. In the center an estimate of global climate changes during the past 1.2 million years, effecting temperatures, ocean level, and subsequently, intercontinental faunal exchange (the extent of polar ice caps, based on oxygen isotope ratios in cores samples from the Ocean Drilling Program; van HUSEN 2000) Evolution of canids (left tree, estimates based on VILÀ et al. 1997) and of hominids.(right tree, based on various current sources). The labels Würm, Riss, Mindel and Gunz refer to the four major Alpine glaciations, where Würm corresponds to the North-west-European Weichsel and to the North-American Wisconsin glaciation. We could not resist extrapolating to the future glaciation (indicated by "???"), based on the familiar algorithm: "The sun will certainly rise tomorrow because it always did".

now represented by our cattle, or by sheep. In fact, wolves conquered Africa (e.g. as the Basenji infringed on the *Lycaon* range) and used humans as a vector to get to Australia (dingo), Polynesia, and Antarctica.

Wolves meeting humans in a phase of the latter's apprenticeship in wolf pastoralism and, in a subsequent process of coevolution, wolves becoming dogs and early humans becoming modern man, is a good alternative hypothesis to the current theories of domestication with man conquering beasts, including wolves, through cognitive superiority and to the bootstrapping theory of hominization with man domesticating himself (e.g., BUDIANSKY's idea that wolves weaseled their way into our hearts as scavengers).

Homo Homini Lupus?

"*Man to Man is an arrant Wolfe*" (HOBBS 1651). This pessimistic view that human nature is essentially brutish, antisocial and selfish led Thomas HOBBS (1588–1679) to recommend, in his treatise *Leviathan*, an all-powerful central government to impose order, ensure justice, and prevent men from destroying themselves in bestial fashion (HOBBS 1985). *Homo homini lupus* has been cited whenever humans turn on each other, attacking for no defensible reason, plundering, robbing, raping, or killing. Early accounts of our forefathers brutish behavior in the Bible and stories throughout history describe such atrocities, and have not ended today.

Are Wolves That Beastly?

The human is like a monkey to other humans. Is the wolf like a human to other humans? Well, there is some overlap, no doubt, and some dogs behave more humanely than some humans. Or, closer to the biological evidence, *Homo homini Pithecus—Lupus homini Homo?*

Final Remarks

This is not a POPPERIAN attempt to falsify any specific hypothesis concerning the evolution of humans or canids, but rather a proposal of an alternative that we find equally reasonable. We advocate the exploration of this alternative in the belief that within the complex process of co-evolution at different times and localities, a variety of interactions between humans and canids could have occurred that shaped their future interdependence.

The canids also known as (wild) "dogs" have their roots in North America. They were forest dwelling carnivores, originally about the size of a fox, with a leaning toward omnivorousness, akin to the feeding habits of the bears, their closest relatives. When grassland opened and herds of grazing ungulates, notably horses and antelopes began to dominate the open plains of North America, some early canids moved into this new habitat. A multitude of swift canid predators co-evolved with the herding ungulates, and around 10 Ma BP, they started to cross into Asia, Europe, Africa, and back into North America. Thus, the canids—the wolves, jackals, coyotes (all Members of the genus *Canis*), and the aberrant "wild dogs": the African Cape hunting dog, and the Asian dhole—became part of the rich palette of predators and scavengers, coex-

isting and competing with the cats, hyenas, bears and mustelids.

The advantage the canids had over their competitors was their special ability to deal with the herding strategies of the ungulates. While the big cats had become specialized for stalking and surprising their prey in a sudden, forceful attack, thus nipping away stragglers and individuals on the margins of a “selfish herd” (HAMILTON 1971), the “wolf-type canids” were able to keep pace with the herds, move fast and enduringly, and make most efficient use of every single kill by their ability to “wolf down” a large part of the quarry before the scavengers had detected the kill. Today’s “wolf-type canids” are considerably more social than any other predators; they generously share their loot with other pack members, a trait that dates back to around 5 Ma BP, to the common ancestor of the three social canids: wolf, cape hunting dog and dhole. The Genus *Canis* apparently evolved in Asia, and *Canis lupus*, the circumpolar big “wolf”, as a species distinct from the coyote, appeared 1 Ma BP. Thus, it appears that the big cats’ position on the very top of the food pyramid—with the lion as the “king” in the animal kingdom—had been relinquished to the social canids already several Ma BP. In fact, canids became herd followers, exploiting an ecological niche that anticipated early forms of pastoralism. And they never lost their omnivorous habits, their skills for hunting small prey, and at times of need their ability to survive by scavenging. With this wide range of abilities the social canids remained the dominant predator, until the invention of firearms propelled humankind to top of the food pyramid.

As noted above, humankind separated from chimpanzee-like tree-dwelling and fruit-eating ancestors in Africa around 6 Ma BP and moved as true humans (*Homo erectus*) into the open savanna. In the absence of fruit trees, early humans turned into omnivorous gatherers and scavengers. Thanks to their superior brain power, they learned to discriminate among a multitude of resources, to avoid peril, e.g., by carrying a big stick and speaking softly (at least, at first) and to bluff the fierce predators into deserting their quarry. As cunning scavengers, they moved into the plains of Eurasia during the mild interglacials of the Ice Age, culminating in the successful Neanderthal of Europe and adjoining Asia. Meanwhile, around 150 ka BP the tribe of the legendary African

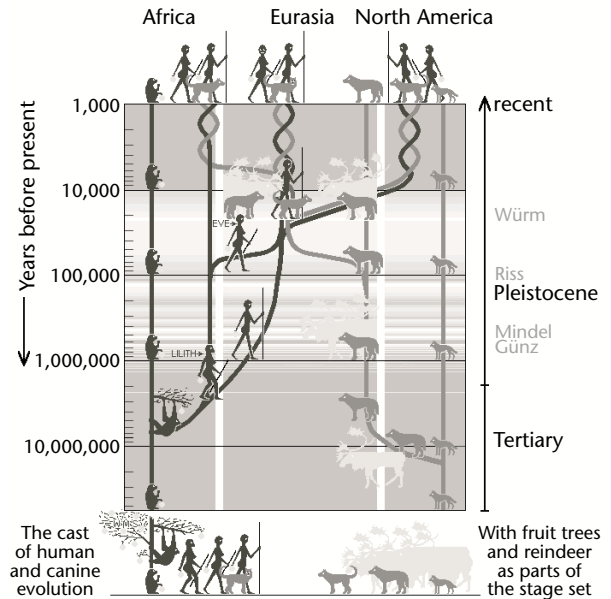


Figure 6: Graphic summary of the authors’ reading of the current state of the evidence concerning canid and human co-evolution.

Eve had emerged, and her daughters entered the Neanderthal domain. At this point, a strange coincidence occurred: at some time during the last ice age, our ancestors teamed up with pastoralist wolves (Figure 6). First, some humans adopted the wolves’ life style as herd followers and herders of reindeer, horses, and other hoofed animals. Wolves and humans had found their match, and “dogs” diversified and moved into other human cultures. Of course, not all wolves had become pastoralists, and neither had all humans. In the fringes of their range, humans remained gatherers and scavengers, or specialized as fish-hunters, hunter-gatherers, hunter-gardeners and, ultimately, became agriculturists. And dogs complemented human skills and satisfied human needs in many ways beyond herding and hunting: as beasts-of-burden, guards, hot-water-bottles, diaper service, and as true trusted companions, e.g. as seeing-eye dogs.

Authors’ address

Wolfgang M. Schleidt
 Email: wolfgang.schleidt@univie.ac.at
<http://www.schleidt.org/wolfgang/>
 Michael D. Shalter
 Email: retlash@aol.com

Acknowledgments

Special thanks especially to Dorothy W. GRACEY, Michael W. FOX, and Kurt KOTRSCHAL, but also to all the other friends, too numerous to mention, who helped us in developing our ideas.

Notes

- 1 Because of the hypothetical, and sometimes highly speculative nature of the interpretation of the paleontological record of human evolution, exaggerated claims, and frequently changing emphasis, we restrict our review to a few essentials and abstain from citing specific references for specific statements.
- 2 Following the common practice of balancing the paucity of the archeological record by generous interpretations in plain language, we take the liberty of borrowing for our brief digest of human evolution a few of those popular terms.
- 3 The paleontological record of canid evolution is quite rich, compared to human remains. Our review is based mainly on JANIS/SCOTT/JACOBS (1998) and MUNTHE (1998).
- 4 Jane GOODALL im Interview: „Ich hatte schon während meiner Kindheit einen wundervollen Lehrer: meinen Hund Rusty.“ (BAUR 2001).
- 5 Sociobiologists have tried to convince us for nearly a quarter century that individual success is the one and only basis of evolution—ignoring the wisdom of beekeepers, who knew of multiple matings of the queen all along.
- 6 Of course, many different subspecies have been described, and we can well assume that in addition to pelage and skeleton behavioral traits vary as well. In the other extreme, we face the puzzling fact that all member of the genus *Canis* apparently can interbreed, and one may wonder whether the “genus” *Canis* should be considered a single species.
- 7 More generally stated: social predators should have more healed injuries than solitary predators. Of course, in close association with humans, tamed wolves and dogs also have the potential to be subject to abuse by humans (e.g., BIRD/BIRD 1937), but also the benefit of being nursed back to full strength, as observed in the archeological record (e.g., PUCHER 1986).
- 8 Catalogued as USNM (US National Museum, S.I., Washington, D.C.) 215320; further details in MUNTHE (1989).
- 9 Of course, we all know of cases where especially males dominate their family by force or where bitches rule by superior social competence!
- 10 A more detailed discussion of the “Out Of Africa” hypothesis does not appear feasible, considering the scarcity of early *Homo* fossils (compared to the fossil record of *Canis*). Thus, the readings of the human record are still highly diverse and personal. For example, the recent discovery of modern human fossils in Ethiopia dated 160 ka (CLARK et al. 2003; WHITE et al. 2003) only supports a presence in that region at that time, but does not falsify the multi regional hypothesis (e.g., WOLPOFF/CASPARI 1997).
- 11 Same root as in cubicle and concubine.
- 12 The association between humans and reindeer in Pleistocene Europe had early on led to speculation that reindeer herding is an ancient form of subsistence (JARMAN/BAILEY/JARMAN 1982). Even though this view has been contested (e.g., BENECKE 1995), in our considered opinion, this issue is far from resolved.

References

- Baur, D. (2001) Jane Goodall im Interview: “Von den Schimpansen lernen, dass wir Tiere sind”. Spiegel Online 4. September 2001, <http://www.spiegel.de/wissenschaft/erde/0,1518,151707,00.html>
- Benecke, N. (1995) Mensch–Tier Beziehungen im Jung- und Spätpaläolithikum. In: Ulrich, H. (ed) Man and Environment in the Palaeolithic. E. R. A. U. L. 62: pp77–87.
- Bird, C. G./Bird, E. G. (1937) The management of sledge dogs. Polar Record 3: 180–184.
- Budiansky, S. (2000) The Truth about Dogs. Viking: New York.
- Clark, J. D./Beyene, Y./Woldegabriel, G./Hart, W. K./Renne, P. R./Gilbert, H./Defleur, A./Suwa, G./Kathoh, S./Ludwig, K. R./Boisserie, J.-R./Asfaw, B./White, T. D. (2003) Stratigraphic, chronological and behavioural contexts of Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. Nature 423: 747–751.
- Derr, M. (1997) Dog’s Best Friend: Annals of the Dog–Human Relationship. Henry Holt: New York.
- De Waal, F. B. M. (1997) Bonobo: The Forgotten Ape. University of California Press: Berkeley, CA
- Fox, M. W. (ed) (1975) The Wild Canids: Their Systematics, Behavioral Biology and Evolution. Van Nostrand Reinhold Company: New York.
- Fox, M. W. (1980) The Soul of the Wolf. Little, Brown: Boston.
- Goodall, J. (1986) The Chimpanzees of Gombe: Patterns of Behavior. Belknap: Cambridge MA.
- Goodall, J. (1997) Fax to Wolfgang M. Schleidt, Vienna on 25 September 1997. (Archive Wolfgang M. Schleidt, Vienna).
- Groves, C. P. (1999) The advantages and disadvantages of being domesticated. Perspectives in Human Biology 4: 1–12.
- Guthrie, R. D. (1990) Frozen Fauna of the Mammoth Steppe: The story of Blue Babe. University of Chicago Press: Chicago.
- Hamilton, W. D. (1971) Geometry for the selfish herd. Journal of Theoretical Biology 31: 295–311.
- Harrington, F. H./Paquet, P. C. (eds) (1982) Wolves of the World. Noyes Publications: Park Ridge NJ.
- Hobbes, T. (1651a) De Cive (The Citizen) Philosophical Rudiments Concerning Government and Society. R. Royston: London. Retrieved from the internet at <http://www.constitution.org/th/decive00.htm>.
- Hobbes, T. (1985) Leviathan, or the Matter, Forme, & Power of a Common-wealth Ecclesiasticall and Civill. Edited with an introduction by C. B. Macpherson. Penguin: Harmondsworth. Originally published in 1651.
- Janis, C. M./Scott, K. M./Jacobs, L. L. (eds) (1998) Evolution of Tertiary Mammals of North America. Volume 1. Cambridge University Press: Cambridge UK.
- Jarman, M. R./Bailey, G. N./Jarman, H. N. (eds). (1982) Early European Agriculture. Cambridge Univ. Press: Cambridge.
- Lorenz, K. Z. (1954) Man Meets Dog. Methuen: London.
- McKenna, M. C./Bell, S. K. (eds) (1997) Classification of Mammals Above the Species Level. Columbia University Press: New York.
- Mech, L. D. (1970) The wolf: The ecology and behavior of an endangered species. The Natural History Press: Garden City NY.
- Mech, L. D./Boitani, L. (eds) (2003) Wolves: Behavior, Ecology, and Conservation. University of Chicago Press: Chicago.

- Moritz, R. F. A. (1993)** Intracolony relationship in the honey bee colony (*Apis mellifera*): Molecular evidence and behavioral consequences. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 86(2): 151–158.
- Munthe, K. (1989)** Skeleton of the Borophaginae (Carnivora, Canidae): Morphology and Function. University of California Press: Berkeley.
- Munthe, K. (1998)** 7. Canidae. In: Janis, C. M./Scott, K. M./Jacobs, L. L. (eds) *Evolution of Tertiary Mammals of North America*, Volume 1. Cambridge University Press: Cambridge UK.
- Oeser, E. (2001)** Der Anteil des Hundes an der Menschwerdung des Affen: Von Platon zu Lorenz. In: Kotschal, K./Müller, G./Winkler, H. (eds) *Konrad Lorenz und seine verhaltensbiologischen Konzepte aus heutiger Sicht*. Filander Verlag: Fürth.
- Oeser, E. (in press)** Hund und Mensch. Die Geschichten einer Überlebensgemeinschaft. Wissenschaftliche Buchgemeinschaft: Darmstadt.
- Sablin M. V./Khlopachev G. A. (2002)** The earliest ice age primitive dogs are found at the Russian Upper Paleolithic site Eliseevichi. *Current Anthropology* 43: 795–799.
- Pucher, E. (1986)** Untersuchungen an Tierskeletten aus der Urnenfelderkultur von Stillfried an der March (Niederösterreich). *Forschungen in Stillfried* 7:23–116.
- Schleidt, W. M. (1998)** Is humaneness canine? *Human Ethology Bulletin* 13(4): 14.
- Serpell, J. (ed) (1995)** *The domestic dog: Its evolution, behaviour and interactions with people*. Cambridge University Press: Cambridge.
- Shalter, M. D./Fentress, J. C./Young, G. W. (1977)** Determinants of response of wolf pups to auditory signals. *Behaviour* 60: 98–114
- Tedford, R. H./Taylor, B. E./Wang, X. (1995)** Phylogeny of the Caninae (Carnivora: Canidae): The living taxa. *American Museum Novitates* 3146: 1–37.
- Thieme, H. (1997)** Lower palaeolithic hunting spears from Germany. *Nature* 385: 807–810.
- Thomas, E. M. (1993)** *The Hidden Life of Dogs*. Houghton Mifflin: Boston/New York.
- Vilà, C./Maldonado, J./Wayne, R. K. (1999)** Phylogenetic relationships, evolution and genetic diversity of the domestic dog. *Journal of Heredity* 90: 71–77.
- Vilà, C./Savolainen, P./Maldonado, J. W./Amorim, I. R./Rice, J. E./Honeycutt, R. L./Crandall, K. A./Lundeberg, J./Wayne, R. K. (1997)** Multiple and ancient origins of the domestic dog. *Science* 276(5319): 1687–1689.
- Wayne, R. K./Jenks, S. M. (1991)** Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf *Canis rufus*. *Nature* 351: 565–568.
- Wayne, R. K./Vilà, C. (2001)** Phylogeny and origin of the domestic dog. In: Ruvinsky, A./Sampson, J. (eds) *The Genetics of the Dog*. CABI international: Oxon, pp. 1–13.
- White, T. D./Asfaw, B./Degusta, D./Gilbert, H./Richards, G. D./Suwa, G./Howell, C. (2003)** Pleistocene homo sapiens from middle Awash, Ethiopia. *Nature* 423: 742–747.
- Wolpoff M./Caspary, R. (1997)** *Race and Human Evolution*. Simon & Schuster: New York.
- Zeuner, F. E. (1963)** *A History of Domesticated Animals*. Harper & Row: New York, Evanston.