DOGS AND MANKIND: COEVOLUTION ON THE MOVE - AN UPDATE

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ABSTRACT

As an alternative to the domestication hypothesis, it has been proposed that "Wolves met humans in a phase of human apprenticeship to wolf pastoralism and, in a subsequent process of coevolution, wolves turned into dogs." (Schleidt, 1998, p. 4).
Here we provide an update in the context of new information, notably on Pleistocene climate and ecology, and new insights from canid and human genetics and genomics.

Keywords: *Human, wolf, dog, evolution, coevolution, domestication, pastoralism*

Pleistocene climate of northern Eurasia was not, as previously assumed, continuous ice and cold but rather extremely seasonal, characterized by an annual alternation between lean times and plenty during the growing season. Even during glacial periods, brief warm episodes occurred frequently. This understanding opens a new view on coexistence and coevolution of life in northern Eurasia during the Glacials that is very different from original assumptions. In the environment at that time, any animal that was able to move some distance migrated in an annual rhythm back and forth across the tree line. Only a few species hibernated or eked out a living under the snow cover.

New studies of the genetics and genomics of canids emerging from an increasing data set indicate that wolves exist in several clades varying in morphology and behavior. As the particular clades of wolves that adapted as dogs to a great variety of specific tasks within human societies, we must not forget the specific adaptations of other wolf clades, as for example the different traits of tundra wolves vs. forest wolves. (Musiani, M., et al., 2007). Furthermore, as dogs adapted to live in close association with humans, wolves

must have adapted over the past 20 000 years to humans carrying lethal armament. Thus, the wolves of Yellowstone Park, today, we accept as typical for Canis lupus, most likely are very different in behaviour and genetic makeup from the wolves who first immigrated into this area after the Laurentide Ice Sheet receded, or those, described by early explorers (Pierotti & Fogg, 2017). Times and regions of the origins of dogs remain uncertain because of continuous interbreeding among different clades of wolves and even with other canids.

During the last glacial period, when some wolves became dogs, humans were not yet a big success, but existed as humble foragers at extremely low densities. Not "man the hunter", but rather "woman the gatheress" fed the family and befriended the wolves during the last ice age, while men contributed meat and served as protectors of their families. Humans became top predator and a key species only after the Last Glacial Maximum (LGM), when new armament, i.e. the atlatl and bow and arrow, made it possible for the hunter to kill his game at minimal personal risk of retaliation. The ability to kill at minimal risk ended the balance between predator and prey and turned man the hunter into the "natural disaster" (Schaller, 1991) of our times.

To what extent and in which respect the behavior of wolves influenced human behavior, and vice versa, remains in the dark. Among primates, human sociality and parental behavior are amazingly similar to that of social canids. Dogs as companions have found their place in the human social network like no other species. Details are still lacking.

INTRODUCTION

The most important progress since the proposal of the coevolution hypothesis of humans and canids (Schleidt, 1998; Schleidt & Shalter, 2003) is in the area of climatology in the wider context of the impact of burning fossil fuel to obtain energy for our industrial advancements, global warming, and the greenhouse effect. New data about past climates have become available and have revolutionized our views of the climate during the last glacial period when humans settled Eurasia and wolves became dogs.

The ice ages, until recently, were depicted as catastrophic eras of the distant past when the globe froze over. During "Glacial Periods", glaciers covered the poles and surroundings far into the latitudes we now call the temperate zone. The region around the North Pole's ice cap covered by year-round "permafrost" supported a meager vegetation of lichens, mosses, and a few grasses. Hardy mammoths, woolly rhinos, and reindeer were braving the ice and snow of a treeless, windswept "Mammoth Steppe", a biome like that we find today north of the tree line in Canada and Siberia, where reindeer thrive to this day (Guthrie, 1982, 2001).

The fact that during Pleistocene summers in central Europe the sun stood high in the sky above the woolly rhinos, mammoth, and reindeer, and must have supported a rich flora, has been ignored. The striking seasonality of the climate of northern Eurasia, the change between warm summers and icy winters, is the key to understanding the high mobility of megafauna in the tundra steppe and adjoining boreal forest.

Recent analyses of the record preserved in ice cores, pollen profiles, and remnants of the megafauna's fodder preserved in permafrost have revealed a very different climate and life at the southern fringes of the Mammoth steppe. Winters with hard frost and

snow blanketing the earth were rather hostile to life, but over the past 2.5 million years flora and fauna adjusted to winter cold. Within the "temperate" latitudes spring and summer were highly productive, and fall brought a rich harvest that allowed animals to fatten up or stock supplies for the lean period of winter. The flora responded by evolving perennials with underground storage organs (roots, tubers, bulbs, etc.) for a head start the following year. These underground storage organs became an important resource for animals and humans during the lean periods of winter. Some animals hibernated, as for example bears, groundhogs, and dormice, while others moved to sheltered winter pastures, as reindeer still do today.

Homo erectus ventured from Africa into northern Eurasia several hundred thousand years ago. Pleistocene humans became permanent residents at extremely low densities, not as the fierce hunters able to kill any animal in sight, as proposed occasionally (e.g. Bocherens et al., 2015, Richards & Trinkaus, 2009, Shipman, 2015), but as humble omnivorous foragers (e.g., Perri, Smith & Bosch, 2015), competing with the more numerous brown bears and wild boar. Early humans were predators of small game and prey of the big cats, like foragers of Africa and India still today:

> "Lions were seen as social superiors with the power of gods and spirits of the dead with whom the people were socially engaged. Therefore lions needed to be treated as social actors – their needs and intentions understood in order to navigate the tense set of relations between humans and lions." Baynes-Rock & Thomas, 2017, p. 118.

Neandertals and later the more numerous "Anatomically Modern Humans" (AMHs) excelled because of their manual dexterity and cognitive superiority (Mellars & French, 2011; Trinkaus, 2014). They developed craftsmanship in making wooden lances and spears for defense against dangerous predators like the European saber-toothed cat (Homotherium latidens), and for ambush hunting of horses, 300 000 years BP (Thieme, 1997; Schoch et al., 2015; Serangeli et. al., 2015; Hussain & Floss, 2015).

In view of the striking seasonality of the northern Eurasia climate during the late Pleistocene, the change between warm summers and icy winters, and the high mobility of megafauna of the tundra steppe and adjoining boreal forest, we can safely assume that Pleistocene humans were reasonable and doing alike:

> "Since the data from N. Germany, the Alps and the Pyrenees show unequivocal evidence for seasonal movement in reindeer economies it is difficult to understand how man and beast in the Perigord could be so totally aberrant during the same period." (Bahn, 1977, p. 250, referring to Magdalenian sites, 17 to 12 ka ago)

So, the seasonal migration of hoofed animals, their predators, and humans provided plenty of opportunity for interactions among them.

CLIMATE AND VEGETATION DURING THE LAST GLACIAL PERIOD IN NORTHERN EURASIA

"Ice Age", the popular term, or "Glacial" as the scientific concept, unusually implies low global temperatures, with polar ice caps surrounded by a belt of permafrost, an environment inhospitable to life. Only the hardiest Pleistocene megafauna, like woolly

mammoth, woolly rhinoceroses, bison, cave bears, and a few Neandertals were able to survive under such cruel conditions

The polar ice cap itself, which included the Laurentide Ice Sheet and the Scandinavian Ice Sheet, covering today's Canada, the northern USA, and most of northern Europe was unsuitable even for the megafauna. But the area blanketed by permafrost was not that inhospitable. In the tundra's southern parts during summer months the sun shone high above the megafauna and supported a nutritious vegetation, comparable to the lush meadows of our alpine high pastures and summer resorts. During the Last Glacial Maximum (LGM, 24 – 18 kyr BP) temperatures in central Europe were cooler by ca. 8° C – 12° C (Annan & Hargreaves, 2013), and around the equator, they were still "tropical". Because so much water was bound in polar ice caps, the sea level was about 125 m lower than it is today, and the climate was much dryer.

Currently, the mean annual temperature between the Tropic of Cancer and the Arctic Circle decreases roughly 1° C for every 154 km (De Frenne et al., 2013). Similarly, as one goes up a mountain, an increase in altitude by roughly 166 m lowers the air temperature 1° C (Kaiser& Scheifinger, 2014). There are several other important variables defining the local climate, notably precipitation, cloud cover, latitude, snow on the ground, etc. Temperature, however, is definitely a key variable for plant life.

The ultimate icon of the Pleistocene in the northern hemisphere is the mammoth, and the biome within which the Pleistocene megafauna was thriving was named appropriately "mammoth steppe" (Guthrie, 1982; 2001). The geographical extent of this biome is best visualized as the area between the current +10° C July isotherm, which corresponds roughly to the northern tree line, as well as to the arctic circle, and the current +18° C isotherm which corresponds roughly to the northern tree line during the LGM and thus the southern edge of the mammoth steppe during its maximal extent (Fig. 1)

One of the most misleading assumptions about the ice ages is that in a broad zone around the polar ice cap freezing temperatures were year round and throughout the "last glacial period" (ca. 110,000 to 11,700 years ago). Even though the ground of the boreal tundra-steppe biome (indicated in grey in Fig. 1) was frozen in "permafrost", the top layers thawed each summer to some degree – depending on the latitude – and seasonally vegetation "green-up" and provided fodder for the Pleistocene megafauna. Thus, climate, vegetation, and fauna within the Mammoth Steppe were quite different, depending on the latitude.

The recent ice core data (NGRIP was drilled in 2003, and data analysis is still in process) have revealed striking seasonal bands, like tree rings. Even though, throughout the Pleistocene, winters were harsh, during the summers, when the sun stood high over the temperate latitudes, the permafrost thawed and supported a lush vegetation, comparable to what we find in alpine pastures today. The ultimate surprise concerning the high productivity of this annual green-up of permafrost came with the documentation of fodder of Pleistocene megafauna, as preserved in permafrost (Zimov, 2012). In the intestines of four woolly mammoths, two woolly rhinos, one bison, and one horse, a variety of forbs and grasses was found (Willerslev et al., 2014) that are still common in alpine pastures and in the Canadian and Siberian tundra. (For details see Supporting Information: Table1).
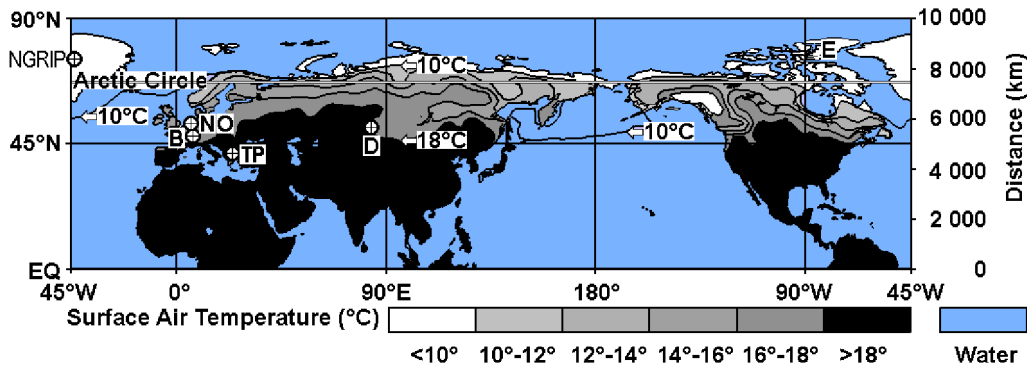.

Figure 1: The Pleistocene boreal tundra-steppe biome, indicated by grey shades, as inferred from recent July isotherms of surface air temperature in the northern hemisphere (composite mean July 1950 to 1969). The 10° C July isotherm delineates the current border between the Arctic and the Boreal Forest (the northern tree line, coinciding roughly with the Arctic Circle). This 10° C July isotherm can serve as indicator of the northernmost extent of the tundra steppe. The 18° C isotherm, depicted in Fig. 1, can serve as a useful indicator of the southernmost extent of the tundra-steppe during the coldest episodes of Pleistocene, estimated 8° C lower than at present (see Fig. 2). Source: NOAA/ESRL Physical Science Division. Image provided by the NOAA/ ESRL Physical Sciences Division, Boulder Colorado from their Web site at http:// www.esrl.noaa.gov/psd/, based on Kalnay & al. 1996. Several significant locations, mentioned in this paper, were also entered in this map (NGRIP members, 2004) **NGRIP**: ice-core drilling site in Greenland. **B**: Berne, Switzerland (as reference location for converting the NGRIP temperature estimates to central Europe. **N:** Neandertal cave, where the first Neandertal skeleton had been found. **O**: Oberkassel of the burial of two humans and a dog. **TP**: Tenaghi Philippon pollen-core drilling site in Greece. **D**: Denisova cave, where the first Denisovan and the Altai Neandertal were found. **E**: Ellesmere Island, now the northernmost refugium of the Mammoth Steppe.

Furthermore, ice core data reveal that throughout the last glacial period temperatures were not continuously low, but varied considerably and rose unexpectedly quickly during the so-called Dansgaard–Oeschger events (Dansgaard et al., 1993; see Figure 2). It is remarkable how quickly the vegetation responded to the global temperature changes, as revealed in the pollen record of the Tenaghi Philippon pollen-core drilling site in Greece, at the southern edge of the boreal tundra-steppe biome (Müller, 2011, Figure 2). These new discoveries raise severe doubts about current assumptions concerning the complete "disappearance" of a variety of species into a few refuge areas at the southern edge (as assumed by Hewitt, 1999) and suggest a multitude of small refuges from where previously inhabited areas were reclaimed relatively quickly. Considering the various mountain ranges, river valleys, and the relief of the landscape throughout Eurasia, the Pleistocene boreal tundra-steppe biome must be viewed as a patchwork of a variety of vegetation types, waxing and waning with the change of temperature.

In this context of waxing and waning of distribution ranges, we must point out that the conventional thinking in terms of two-dimensional parcels, like home ranges, is misleading. Land-dwelling mammals move along trails, not in a plane, as commonly assumed, and home ranges are not areas in a geometrical sense, but rather networks of trails.

Summing up the new insight about the climate during the last glacial period in northern Eurasia where wolves became dogs: This biome was not a year-round icy desert that supported only a meager vegetation of lichens, mosses, and a few grasses. Mammoths, woolly rhinos, bison, and horses filled their stomachs with nutritious forbs and grasses, as did reindeer, ever-present in the archeological record (Sommer et al., 2014), the only species that still thrives today in some areas (e.g. the Porcupine herd in Yukon: Hayes et al., 2013; Anonymous 1, no date; Anonymous 2, no date). The "Mammoth Steppe" was not a wide, homogenous plain, but more like a sequence of belts between polar ice caps and boreal forest. Each belt had a temperature gradient, as depicted in Fig. 1. that determined vegetation and fauna. The northern belt dominated by Muskox, the southern belt by horses, and in-between reindeer, geese, and mammoths migrating with the seasons and feasting on a rich vegetation of forbs and grasses, comparable to those growing in the high pastures of the European Alps during summer.

A second thought about mammoth steppe in winter: It was not always inhospitable, freezing, and windswept. On a sunny day, it was more like today's alpine high pastures in winter with skiing resorts for affluent urbanites.
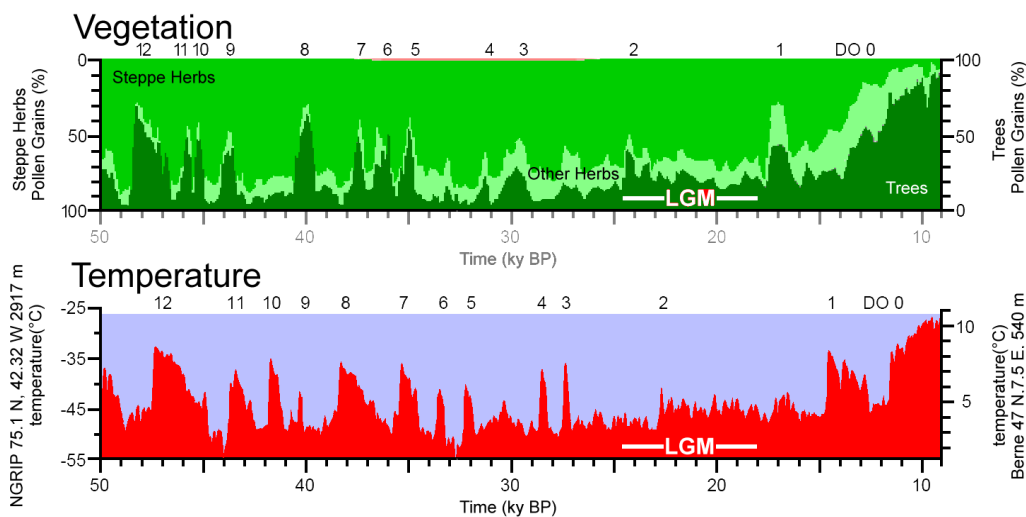

Figure 2: Temperature and vegetation in northern Eurasia, when some "dog-wolves" became dogs. Temperatures were less frigid, and overall climate was very different from what had been assumed previously. Rapid changes in temperatures caused an unexpectedly rapid change in vegetation cover. Seasonal frost and snow cover resulted in an annual cycle of productivity. Animals adapted by hibernation or extensive seasonal migrations. Lower half of the figure: **"Temperature"** is approximated by the: NGRIP temperature reconstruction from 9 to 50 kyr BP. Most striking are the abrupt temperature rises of up to 5° C within a few hundred years at the beginning of each Dansgaard–Oeschger event (DO 0 – 12). This graph is based on Kindler et al. 2014, Fig. 3 a, modified and temperature estimate in °C for central Europe – Berne, Switzerland, scale on the right side of the graph – added (all courtesy Markus Leuenberger). Upper half of the figure: **"Vegetation"** is based on the pollen record from the new Tenaghi Philippon core. The time scale has not been adjusted to calendar time, and therefore has been indicated in grey, and the Dansgaard–Oeschger events are currently the best time marks available. It is remarkable how quickly vegetation adjusted to the changes in temperature during Dansgaard–Oeschger events. All based on Müller et al. 2011, Figure 4.

HUMANS AND FAUNA IN THE SOUTHERN FRINGES OF THE MAMMOTH STEPPE

New insights into the genetics of organisms have revealed a much more complicated history of both mankind and canids than we were led to believe when the coevolution idea of humans and canids was first proposed. Although we poked fun at the "Neandertal-bashing" at that time and at the celebration of "African Eve" as the mother of real mankind, we endorsed the claims of a purely wolf ancestry of dogs.

Now we accept that western Eurasians carry a significant percentage of Neandertal genes, and in the Far East, Denisovan genes indicate the importance of regional adaptations (e.g., Pagani et al., 2016). Our dogs' ancestry is no longer that ideal pedigree, fit to be endorsed by the American Kennel Club, but more like a brushwood, lines of decent changing with every new study (e.g., Vilà et al., 1997; Freedman et al. 2014; Frantz et al. 2016; Fan et al. 2016). The exchange of genes between dogs and wolves continues till today, and wolves are split into numerous clades, with specific traits (e.g., tundra wolves vs. forest wolves. Musiani, M., et al., 2007) but also mixing with other canids forming stable hybrids (e.g., Canis rufus. vonHoldt et al., 2016) which makes one wonder about the "academic" concept of what constitutes a species.

One of the fringe benefits of accumulating a mind-boggling amount of genomic data is the possibility of reconstructing the effective population size of individual gene pools, and compare – over time – human populations that moved into Eurasia and no longer interbred with the populations which stayed behind in Africa: see Fig. 3.
Similar to the human case, it is possible to estimate the changes of the total populations of reindeer, wolves, and the wolf-ancestors of East Asian dogs, West Eurasia dogs, dingo, or basenji. It must be emphasized that these estimates are made under numerous assumptions subject to variability, and concern only the breeding population. Thus, the actual "census populations" are likely to be more numerous, by a factor estimated to be between 3 and 10. For example: while the estimates for reindeer in Fig. 3 range between 300 000 and 900 000, the current population of reindeer in the Old World is approximately 3,000,000 (Røed et al., 2014), even though the climate during Pleistocene may have been more favorable for this species.

Within the Pleistocene megafauna of northern Eurasia, at the southernmost fringes of the mammoth steppe, the human populations, because of their low numbers and their negligible effect on Pleistocene ecosystems as a whole, played only a minor role. As for the density estimates, however, a few more words of caution must be inserted here: the remarkable feat (Mazet et al., 2016) of the Li and Durbin landmark study in 2011 (Li & Durbin, 2011), rests on several assumptions that may be questionable, especially in the case of Pleistocene populations of humans at extremely low densities: panmixia, or the spread in a two-dimensional diffusion process, and a comparison of data sets obtained with different methods under varying assumptions from very different populations, even from different species (e.g., Lorenzen et al., 2011). However, the extremely small human population size estimates for Pleistocene Eurasia, as calculated by the "genetic" N_e, and here used as substitute for N_c – the census population size – are well supported by recent estimates based on the archeological evidence from Pleistocene camp sites in Europe (French, 2015; French & Collins, 2015; Maier et al., 2016).
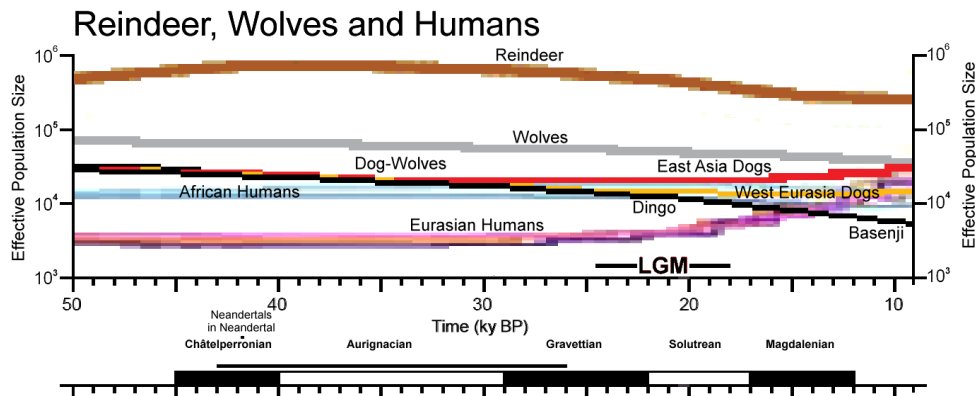
Figure 3: Fauna and human population during the Last Ice Age in northern Eurasia, when some "dog-wolves" became dogs. High population sizes of reindeer indicate high availability of fodder, and high population size of wolves, as a top predator, indicates an abundance of prey. The human population, in sharp contrast, numbering all over Eurasia only a few thousand individuals, narrowly had escaped extinction during the Pleistocene bottleneck, remained on a level of ecological insignificance for thousands of years, and started its rise only after the LGM to become the ultimate keystone species and "natural catastrophe" (Schaller, 1991). "**Reindeer, Wolves, and Humans**" shows estimated effective sizes of human populations (Ne) of Africa and Eurasia from multiple genome sequences (Schiffels & Durbin, 2014, Figure 3b) as compared to that of wolves (Frantz et al., 2016), "Dog-wolves" and their descendants (East Asia dogs and West Eurasia dogs: Frantz et al. 2016, Dingo and Basenji: Freedman et al., 2014), and reindeer (Lorenzen et al., 2011). Note that, in contrast to the response of vegetation (Fig. 2.), there are no striking changes in the population sizes of the animal species selected here that can be attributed to climate (or human interference), except at the very end, starting around 15 kyr BP, at the transition into the Holocene. While plant populations changed with the climate, animals either moved with the climate seasonally and also followed climate changes during Dansgaard–Oeschger events by migrating into their optimal environment, or endured lean times by hibernating or estivating.

One of the most striking and unexpected results of such population size estimates for the second half of the Last Glacial Period for all these species is that there is no noticeable effect of the changes in climate and vegetation on the size of those populations, not even during the LGM   (see Figure 3). In fact, the human population of Eurasia started its upswing before LGM, and continued at a time when climate was most hostile to all life in northern Eurasia.

Another interesting observation is the extremely low population density of the new wave of AMHs, as estimated by Timmermann & Friedrich (2016; e.g. Fig. 4).

This amazingly low density of AMHs could be interpreted, of course, in support of the traditional view of Homo sapiens as a "top-level carnivore" (e.g., Richards & Trinkaus, 2009) and keystone species. However, recent studies have debunked the myth of carnivorous nutrition (Speth & Spielmann, 1983 Speth, 2010; Henry, Brooks & Piperno 2014; Hardy et al., 2015; Fiorenza et al., 2015; Melamed et al. 2016) and indicate an omnivorous diet based on foraging. The recovery of Eurasia mankind from the bottleneck is most likely unrelated to changes in climate or vegetation but rather to

the invention of new armament, i.e. bow and arrow and the atlatl; hunting weapons that allowed for the first time to hit a target accurately and kill at a distance, involving little risk to the hunter.
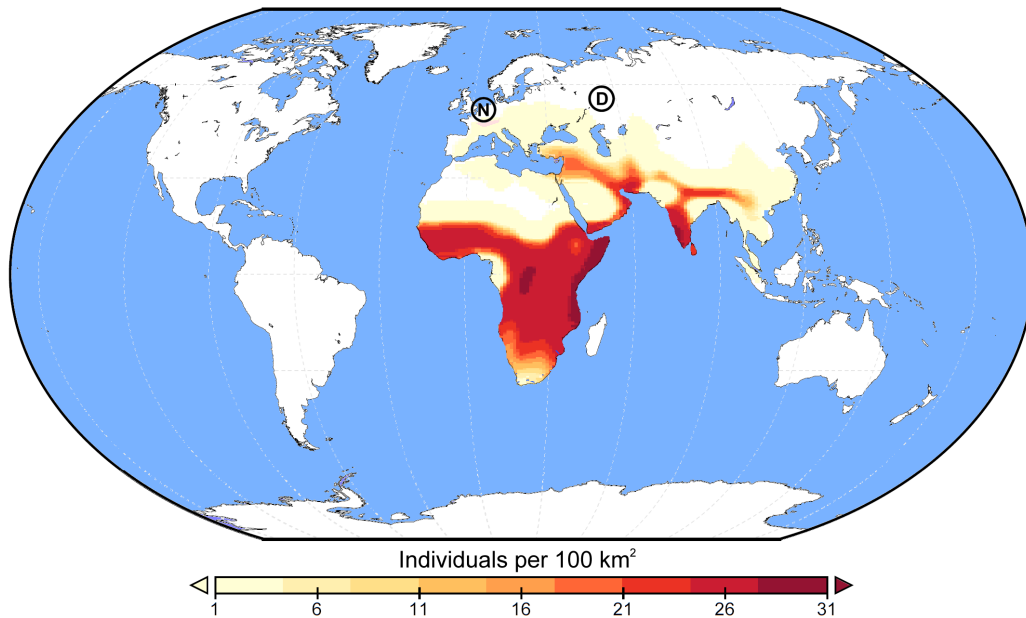

Individuals per 100 km²

Figure 4: State of Pleistocene dispersal of Anatomically Modern Humans 90 ka BP. Snapshot of the simulated evolution of density of AMHs (individuals per 100 km²) 90 thousand years BP, using the parameters of scenario A (early exit) experiment of Timmermann & Friedrich, 2016, as depicted in Figure 2. ; N: Neandertal cave, where the first Neandertal had been found; D: Denisova cave, where the first Denisovan and the Altai Neandertal were found. With special thanks to Axel Timmermann for his permission to use his data and especially for providing the basic information for this new version of the 90 ka Snapshot of Figure 2 of Timmermann & Friedrich, 2016.

The proposal of a pronounced and enduring bottleneck in the human population of Eurasia during the second half of the Last Glacial Period (Li & Durbin, 2011), reducing the total population of AMHs to a few thousand, was met with disbelief at first. Meanwhile the geneticists' estimates have been confirmed, and recent numerical estimates of census populations are on the same order of magnitude: "... *the largest population can be identified in Franco-Cantabria, comprising between 750 and 3600 people...*" and "*The estimated absolute number of people in the East*" (of Central Europe) "*ranges between 60 and 100 people*" (Maier et al., 2016, p. 59). Thus, the well documented fluctuations in population levels across the Upper Palaeolithic in Southwestern France reflect migration events when this area became a refuge during cold stages (French & Collins, 2015). These recent discoveries match well with the summary statement of Paul Bahn, forty years ago:

> *A reappraisal of all pertinent evidence leads to the hypothesis that the human groups for whom the reindeer was a staple resource during the late glacial period in SW France were compelled to follow the herds in seasonal migrations; that the "classic" cave-sites and shelters of the Perigord and the Pyrenees constituted agglomerations of seasonal bases; and that the reindeer followers were relatively few in number but highly mobile.* (Bahn, 1977, p. 255).

All this fits well with the ancient connection between the early Europeans and reindeer, which continues today in the high north. Recent estimates indicate that reindeer in today's Norway are descendants of those roaming Palaeolithic Southwestern France (Sommer et al., 2014; Røed et al., 2014). The descendants of the humans who followed their herds during Upper Palaeolithic apparently still survive in the Pyrenees as Basque, while the reindeer in the north are now followed by Sami people whose ancestors came from the east.

It would be interesting to check whether the reindeer of Norway today carry genes from the Pleistocene population of Franco-Cantabria, and whether Sami people share genes with the Basque.

WOLVES AS PASTORALISTS - HERD FOLLOWING AS A RESULT OF SEASONAL MIGRATION

Ever since the observation of wolves following herds of ungulates and thus the idea that wolves act as if they were pastoralists (for a profound discussion see Ingold, 1980), a confusion concerning the concept of herd taints the discussion of this topic. In everyday language "herd" refers to certain domestic ungulates, owned, assembled and controlled by humans, with the prototypical image of a shepherd and his dogs in control of a closely assembled flock of sheep, moving through a pasture, grazing….a shepherd in the highland giving commands to a border collie that herds, circles a tight flock of sheep.

Here we are talking about herds of wild animals, such as a social grouping of ungulates, as members of the Eurasian megafauna, ranging in size from a herd of red deer – one stag and a few hinds to the Bathurst herd (see Fig. 4 A) of a few ten thousand caribou to the porcupine herd of 150 000 head or more.

Far from being bloodthirsty beasts killing for killing's sake, wolves are apparently very careful observers of their potential prey, attacking mostly what they can get without much risk to themselves—the young, the old, and the infirm—behaviors that have led some observers to compare them with pastoralists, caring for their herds (Derr, 2011): e.g.: "…*we scarcely see a gang of buffaloe without observing a parsel of those faithfull shepherds on their skirts in readiness to take care of the mamed & wounded.*" (Lewis, 1805, original spelling). This view of wolves taking care of their herds and not having a detrimental effect is supported by recent studies that found wolves were not a primary factor limiting the size of the porcupine caribou herd (Hayes, Baer & Clarkson, 2013).

So, how do the wolves enter the story of small bands of humans following the seasonal tide of plenty and dearth? Presumably, some wolves were following the herds of reindeer, as today's "tundra wolves" wandering with the caribou in North America.

These wolves are not, contrary to popular belief, the vicious predators that can take any prey they desire, but highly specialized in selecting those sick or aged individuals that can be subdued with minimal risk. These wolves act in a very similar way as "a good shepherd", with one significant difference: their "natural selection" is better for the prey than the common "artificial selection". As Friederich E Zeuner wrote: "the wolf and the pastoralists might be seen to have much in common" (Zeuner, 1963, p. 124); for a more detailed discussion see Schleidt, 1998, footnote 10 and the chapters „Wolf: The Pastoralist" and "Man: The Reindeer Hunter"(Schleidt & Shalter, 2003, pp. 66-68). A "good shepherd" may be able to protect his herd from some predators and competing herders who try stealing livestock, but for his own consumption he selects only the best: the biggest, fattest, meatiest individuals. This "artificial selection" results in the common effect of domestication; namely that, in the archeological record, the first indication of human control is the reduction in body size of domesticated animals.

As for the association between wolves and reindeer, it has been well established that in Canada wolves and caribou follow the same routes during their seasonal migration (Walton et al., 2001, Musiani et al., 2007; see also Fig. 3 A). Even though wolves are the main predator of caribou, they are in equilibrium with their prey; a predation rate model found wolves are not a primary factor limiting the size of the Porcupine Caribou Herd. (Hayes & al., 2013), supporting the hypothesis that wolves "manage" the herd as a responsible shepherd would do.

In northern Russia during the recent past, wolves had been severely persecuted, and, unfortunately, no data on the seasonal migration of reindeer and wolves, comparable to those available from the Canadian Porcupine or Bathurst Herd, are available. But in a recent and extensive study by Dallmann, Peskov and Murashko, 2010, at least the seasonal migration of reindeer under the supervision of their Nenet herders was documented in unprecedented detail (see Fig. 3B and Figure SI-1.png, Dallmann, Peskov & Murashko, 2010). And the camp sites of such migrant reindeer herders are excellent sources for comparative studies with Paleolithic sites of Late Pleistocene camps, especially when archeologists like Jiří Svoboda with many years of excavations at famous locations such as Dolní Věstonice take a close look at the life of comparable camp sites of Nenet herders (Svoboda, Péan & Wojtal, 2005; Svoboda et al., 2010).

In passing it should be mentioned that many cases of bird migration observed today have evolved presumably in adaptation to the seasonal seesaw between summer and winter of the Pleistocene. And, in mountainous regions of Sweden, wild reindeer and domestic herds migrate seasonally east-west, up and down the mountain slopes (Beach 1990, Fig. 9.2 see Figure SI-2). In the Austrian Alps red deer show a striking seasonal migration (e.g. Reimoser, 2007). The Alpine transhumance as practiced as "*Almwirtschaft*" can be viewed as a continuation of Pleistocene migrations.

DOGS ARE WOLVES

"Dogs are gray wolves, despite their diversity in size and proportion; the wide variation in their adult morphology probably results from simple changes in developmental rate and timing." (Wayne 1986; 1993; Vilà et al., 1997; Fan et al., 2016). Thirty years research, with unbelievable progress in methods, and broadening of the database have confirmed this statement in many ways. Comparable studies of changes in wolves are wanting.
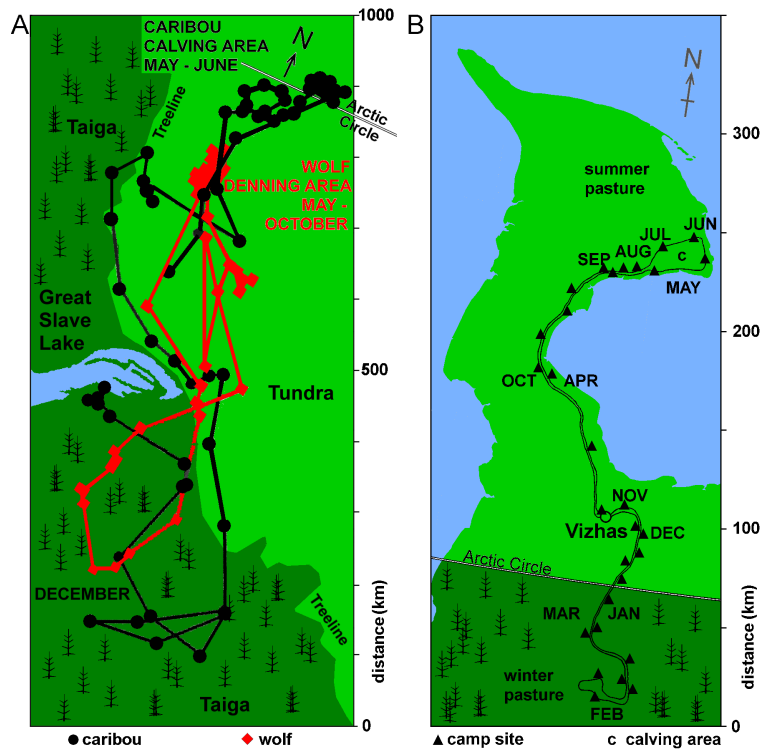
Figure 5: Reindeer migration. A. The annual migration of caribou and tundra wolf in the Northwest Territories, Canada. Straight-line distances between consecutive locations of a collared caribou of the Bathurst herd (black circles connected by black lines) and a collared tundra wolf (red squares connected by red lines) during the period June 1997–June 1998. Caribou locations form a distinctive cluster during the months of May and June, corresponding to the calving ground, just above the Arctic Circle, whereas wolf locations form a distinctive cluster throughout the period from May to October, around the denning area. Locations of the caribou and tundra wolves coincided in mid-December. (Musiani et al., 2007, Fig 3, with permission of the Authors). B. The annual migration of the reindeer herd of SPK Voskhod along the east coast of Kanin peninsula, between winter pasture and summer pasture with calving area (Dallmann et al., 2010). With special thanks to Winfried K. Dallmann for providing the basic information for this map. For a more detailed map see SI Fig. 1.

As for our coevolution hypothesis, two paradoxical points deserve consideration: The search for a particular location and moment in space and time where and when our dog clade separated from the rest of "wolfkind" is likely to be futile, because there was no complete isolation of the populations involved, and exchange of genes between them has continued to this very day in both directions (Anderson, 2009; Kopaliani et al., 2014; Perri, 2016; vonHoldt et al., 2016).

The dog clade separated from the rest of wolfkind in the distant past, at a time when the human population in the area was so minute that it is very unlikely it had an influence on this separation. Interestingly, no "wild wolves" of this "dog-clade" have survived: "*dogs were derived from an extinct wolf population.*" (Fan et al., 2016 Abstract).

Freedman et al. (2014) suggested that "*dogs and wolves diverged 11,000–16,000 years ago.*" (Author Summary). Others have suggested 20,000 to 60,000 (Frantz et al., 2016) and ~50,000 (Fan et al., 2016). In all these estimates, a generation time of 3 years was assumed, while we now know that 4.5 years is a more realistic value (Mech et al., 2016). This lengthens all these estimates by the factor of 1.5. If one accepts the various curves of "effective population size" at face value, ALL wolves including the dog ancestors) reach their maximum population size around or during the Eemian interglacial period, and the wolfish ancestors of dogs diverged from the rest of wolfkind contemporary with Neandertals and Denisovans, and before AMHs entered Europe (Fig. 6.).
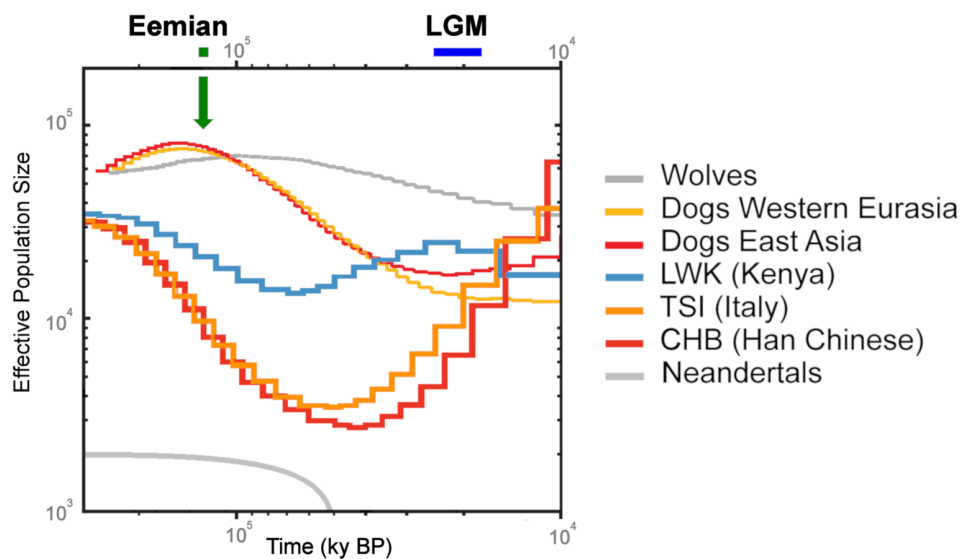

Figure 6. Wolves and Humans during Late Pleistocene shows estimated effective population sizes (Ne) of human populations   in Africa and Eurasia from multiple genome sequences (Schiffels & Durbin, 2014, Figure 3b) in contrast to those of wolves, ancestors of dogs, "Dog-wolves" and their descendants (East Asia dogs and West Eurasia dogs: Frantz et. al., 2016). Parts of these datasets are contained in Figure 3, but here the time window is extended to 300 ky B.P., before the Eemian Interglacial. Here we added a rough estimate of the Ne of Neandertals, based on the estimates of the Neandertal from the Altai Mountains of Prüfer et al., 2014, Figure 4, and adjusted it to a lower, more realistic mutation rate and a later decline toward extinction. Remember, however, that parts of their DNA has survived in AMHs Neandertals had interbred with (e.g. Geher et al., 2017). Thus in the long run Neandertals DNA continues to multiply and supports the livelihood of AMHs outside Africa to our days.

According to the estimates of the effective population size, depicted by Frantz et al., 2016 in their Fig. 2 A. the population of the dog ancestors was a clade of wolves that was in the Eemian interglacial more numerous than the rest of wolfkind before it decreased in numbers, as compared to other wolves. Such a decrease in numbers is commonly interpreted as a loss of fitness, but it also could be attributed to an increase in efficiency in managing the herds of prey – a vital task that may require smaller group sizes. Following the hypothesis that wolves invented an early form of pastoralism, the initial

invention of this form of herd management, as an alternative to conventional predation, could initially result in an increase in the carriers of the new trait, until they reached a level of control of "their herds" that required fewer pack members and thus led to a shrinking of the over-all population of "wolves to become dogs".

Or, if wolves and human foragers were at that time already in loose contact, the presence of humans within this system as the "apprentices" of the pastoralist wolves would diminish the number of pack members necessary to take care of the herd ("Wolves meeting humans in a phase of human´s apprenticeship to wolf pastoralism" Schleidt, 1998).

If the hypothesis of a coevolution of wolves/dogs and humans is applied evenhandedly, forming "mixed packs" could also reduce the optimal human group size, and may be one of the relevant variables contributing to the mysterious bottleneck. Even though the stress of physiological adjustments (temperature regulation, nutrition, immune system, and the like) as adaptations to the different climate and resources are most likely and important factors causing the bottleneck, the early decline of the populations of AMHs following their move into Eurasia, the assistance they received from wolves and dogs as mutual helpers may have been essential for their survival in the hostile, cold north.

Most recently, the hypersociability in domestic dogs, as compared to wolves that have adapted to the coexistence with most dangerous humans, has been attributed to a genetic variant, akin to a human form of "pathological" hypersociability, known as Williams-Beuren Syndrome (vonHoldt et al., 2017). "This finding suggests that there are commonalities in the genetic architecture of WBS and canine tameness and that directional selection may have targeted a unique set of linked behavioral genes of large phenotypic effect, allowing for rapid behavioral divergence of dogs and wolves, facilitating coexistence with humans." (vonHoldt et al., 2017, p. 1).

The best-known case of "commonalities in the genetic architecture" in humans and canids so far is that the copy number variation of amylase gene (AMY1) in humans is correlated positively with salivary amylase (Perry et al., 2007). This increase in copy number is apparently a rather recent adaptation to the invention of agriculture roughly 9 500 B.P. and a diet rich in starch. Dogs, as members of human households, coevolved a higher efficiency for digesting starch by increasing their copy number of the pancreatic amylase gene AMY2B (Freedman et al., 2014 Figure 6.).

Similar commonalities in the genetic architecture of humans and canids have been found in the hormonal control of sociality, and it was found, for example that "exogenous oxytocin promotes positive social behaviors in the domestic dog toward not only conspecifics but also human partners. " (Romero et al., 2014, p. 9085). A follow-up study provides the first evidence that oxytocin promotes social play in dogs (Romero et al., 2015). Playfulness of both wolves and humans could be an important feature in their union within mixed packs. Thus, a mutant in the genetic architecture controlling social behavior – not necessarily to the extreme of a Williams-Beuren Syndrome, but e.g. in the oxytocin system – could explain the split between the mainstream of wolfkind and the wolves that became dogs within the range of the Eemian interglacial (Figure 5).

Another candidate for the behavioral advancement that led to a more efficient herding ability of wolves-to-become-dogs during the Eemian (?) and ultimately to the separation from the mainstream of wolfkind is an increase in the cognitive domain of recognizing

objects or individuals. Rico (1994-2008), a well-trained border collie, was the first dog who was shown to distinguish the labels of over 200 different objects (Kaminski, Call & Fischer, 2004), an ability that meanwhile was well confirmed, and the number of items was exceeded by far. Isa (1995-2008), a golden retriever, was not well trained, had a mind of her own and preferred to suggest to us, as to what she wanted us to do for her. At times she decided to select a particular toy from her collection and to bring it to a person of her choice. We turned this into a game and at our suggestion, e.g. "bring Henrike den Bär" Isa found delight in selecting toy "x" from a set of ten and bring it to the specific person "y" she knew by name, once again, from a set of about ten (Wolfgang & Monika Schleidt, unpublished personal observation). In a pack of wolves or in an experienced team of human workers such acts of cooperation do not require verbal commands, and it is obvious that dealing with a greater number of items and individual pack members could be an important ability that would increase the skills of a herder, and the fitness of pack members.

Throughout the Late Pleistocene wolves were much more numerous than humans (see Fig. 3. once again). The population size of then already "real dogs" declined to the level of Eurasian humans, who were just slowly rising from their Late Pleistocene bottleneck around 12,000 years ago. The two curves intersected around the time of the first fossil record of a verified true dog, the find at Bonn-Oberkassel (Street, 2002; Thalmann et al., 2013)

Wolves and humans forming "mixed packs" of about equal proportions fit well with estimates from Indigenous American tribes before the introduction of horses (e.g., Fogg, Hernandez-Howe & Pierotti 2015, citing Russell 1914: "six men, seven women, and ten children, accompanied by thirty dogs, was described in Yellowstone in 1835"). In such associations, wolves, dogs and humans interacted at eye level: *Although it is clear that attitudes concerning wolves vary among tribes, many shared themes are present, and all credit the wolf with being a figure from which the human can learn.*" (Fogg, Howe & Pierotti 2015, p. 278; Pierotti & Fogg, 2017).

CONCLUDING REMARKS

Humans and wolves were parts of the Pleistocene megafauna and bound together in a "web of complex relations" (Darwin, 1859, p. 73). Since we first proposed our coevolution hypothesis of humans and canids, the view of this complex system has been revolutionized. This web of relationships is an excellent example of a "system" in which each part has an effect, and is affected by all the other parts. Nevertheless there were "keystone species" (Paine, 1999), such as mammoths, reindeer, cave lions, and wolves. Humans, too, were traditionally assumed to have been high up on the list of keystone species and even held responsible for the extinction of Pleistocene megafauna. Such extinctions are now best understood NOT due to frigid climate during LGM or human predation, but rather the result of abrupt temperature rises during the various Dansgaard-Oeschger events, and finally, the beginning of our current interglacial period (Cooper et al., 2015).

The traditional myth of man the Ice age hunter as "the mighty top carnivore" and keystone species has been eroded by mounting evidence of the importance of plant food in human nutrition (Hardy et al., 2015; Fiorenza et al., 2015). A more probable

depiction of AMHs during the second half of the last ice age is that of small bands of foragers who supplemented a mainly vegetarian diet with small game and leftover megafauna carcasses, surviving on the southern fringes of the mammoth steppe due to the association with their dogs.

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REFERENCES

Anderson, T.M., vonHoldt, B.M., Candille, S.I., Musiani, M., Greco, C., et al. (2009). Molecular and Evolutionary History of Melanism in North American Gray Wolves. *Science, 323*, 339-1343. DOI

Annan, J. D., & Hargreaves, J. C. (2013). A new global reconstruction of temperature changes at the Last Glacial Maximum. *Climate of the Past, 9*(1), 367-376. DOI

Anonymous 1 (no date). Animated map of seasonal movement of the porcupine caribou herd. CARMA – Circum Arctic Rangifer Monitoring and Assessment Network http://caff.is/images/_Organized/CARMA/Herds/Porcupine/PCH.mov

Anonymous 2 (no date). Alaska Caribou herds. CARMA – Circum Arctic Rangifer Monitoring and Assessment Network. https://vimeo.com/148136817

Bahn, P. (1977). Seasonal migration in South-west France during the Late Glacial period. *Journal of Archaeological Science, 4*, 245-257. DOI

Baynes-Rock, M., & Thomas, E.M. (2017). We Are Not Equals: Socio-Cognitive Dimensions of Lion/Human Relationships, *Animal Studies Journal, 6*(1), 104-128.

Beach, H. (1990). *Comparative systems of reindeer herding. In: The world of pastoralism: Herding systems in comparative perspective* (Galaty, J. G. & Johnson, D. L., Eds.). New York/London: The Guilford Press. 255-298.

Bocherens, H., Drucker, D.G., Germonpré, M., Láznicková-Galetová, M., Naito, Y.I., et al. (2015). Reconstruction of the Gravettian food-web at Předmostí I using multi-isotopic tracking (13C, 15N, 34S) of bone collagen. *Quaternary International*, 359-360, 211-228.. DOI

Cooper, A., Turney, C., Hughen, K.A., Brook, B.W., McDonald, H.G., et al. (2015). Abrupt warming events drove Late Pleistocene Holarctic megafaunal turnover. *Science, 349*(6248), 602-606. DOI

Dallmann, W.K., Peskov, V.V., & Murashko, O.A. (2010). Monitoring of development of traditional land use areas in the Nenets Autonomous Okrug, Northwest Russia. *Norwegian Polar Institute Report Series 138*. Tromsø, Norway: Norwegian Polar Institute. http://ipy-nenets.npolar.no/main%20pages/frame.html

Dansgaard, W., Johnsen, S. J., Clausen, H. B., Dahl-Jensen, D., Gundestrup, N. S., et al. (1993).. Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature, 364*, 218–220. DOI

Darwin, C. (1859). *The origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. London: Murray

De Frenne, P., Graae, B. J., Rodriguez-Sanchez, F., Kolb, A., Chabrerie, O., et al. (2013)… Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology, 101*(3), 784–795. DOI

Derr, M. (2012). *How the dog became the dog: From wolves to our best friends.* London: Duckworth Overlook.

Fan, Z., Silva, P., Gronau, I., Wang, S., Armero, A.S., et al. (2016). Worldwide patterns of genomic variation and admixture in gray wolves. *Genome Research. 26,* 163-173. DOI

Fiorenza, L., Benazzi, S., Henry, A.G., Salazar-Garcia, D.C., Blasco, R., et al. (2015). To meat or not to meat? New perspectives on Neanderthal ecology. *American Journal of Physical Anthropology, 156*(S59), 43–71. DOI

Fogg, B.R., Howe, N. & Pierotti, R. (2015). Relationships between Indigenous American peoples and wolves 1: Wolves as Teachers and Guides. *Journal of Ethnobiology, 35,* 262-285. DOI

Frantz L.A., Mullin, V.E., Pionnier-Capitan, M., Lebrasseur, O., Ollivier, M., et al. (2016).. Genomic and archaeological evidence suggests a dual origin of domestic dogs. *Science 352*(6290), 1228-1231. DOI

Freedman, A.H., Gronau, I., Schweizer, R.M., Ortega-Del Vecchyo, D., Han, E., et al. (2014). Genome Sequencing Highlights the Dynamic Early History of Dogs. *PLoS Genetics, 10*(1): e1004016. DOI

French, J.C., (2015). Demography and the palaeolithic archaeological record. *Journal of Archaeological Method Theory, 23,* 150-199. DOI

French, J.C. & Collins C. (2015). Upper Palaeolithic population histories of Southwestern France: a comparison of the demographic signatures of 14C date distributions and archaeological site counts. J*ournal of Archaeological Science 55,* 122-134. DOI

Geher, G., Holler, R., Chapleau, D., Fell, J., Gangemi, B., et al. (2017). Using Personal Genome Technology and Psychometrics to Study the Personality of the Neanderthals. *Human Ethology Bulletin, 3,* 34-46. DOI

Guthrie R.D. (1982). Mammals of the mammoth steppe as paleoloenvironmental indicators. In: *Paleoecology of Beringia. Wenner-Gren Foundation for Anthropological Research Symposium* (81st: Burg Wartenstein, Austria) David M. Hopkins, John V. Matthews, Charles E. Schweger (Eds.). New York: Academic Press, INC. PP. 307-326.

Guthrie, R.D., (2001). Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews, 20,* 549-574. DOI

Hardy, K., Brand-Miller, J., Brown, K.J., Thomas, M.G., & Copeland, L. (2015). The importance of dietary carbohydrate in human evolution. *The Quarterly Review of Biology, 90*(3), 251–268. DOI

Hayes, R.D., Baer A.M., & Clarkson P. (2013). *Ecology and Management of Wolves in the Porcupine Caribou Range, Canada – 1987 to 1993.* Yukon Department of Renewable Resources. Haines Junction, Yukon, Canada.

Henry, A.G., Brooks A.S. & Piperno, D.R. (2014). Plant Foods and the Dietary Ecology of Neanderthals and Early Modern Humans. *Journal of Human Evolution, 69,* 44-54. DOI

Hewitt, G. (1999). Postglacial recolonization of European Biota. *Biological Journal of the Linnean Society. 68,* 87–112. DOI

Hussain, S.T. & Floss, H. (2015). Sharing the world with mammoths, cave lions and other beings: linking animal-human interactions and the Aurignacian "belief world". *Quartär, 62,* 85-120. DOI

Ingold, T. (1980). *Hunters, pastoralists and ranchers. Reindeer economics and their transformations.* Cambridge: Cambridge University Press. DOI

Kaiser, A., & Scheifinger, H. (2014): *Meteorologische Analyse des großräumigen Ozontrends im Alpenraum. Ein Beitrag zum Global Atmosphere Watch Programm der World Meteorological Organization.* Wien: ZAMG.

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., et al. (1996). The NCEP/NCAR Reanalysis 40-year Project. *Bulletin of the American Meteorology Society., 77,* 437-471. DOI

Kaminski, J., Call, J. & Fischer, J. (2004). Word Learning in a domestic dog: Evidence for 'fast mapping'. *Science, 304* (5677), 1682–1683. DOI

Kindler, P., Guillevic, M., Baumgartner, M., Schwander, J., Landais, A., & Leuenberger, M. (2014). Temperature reconstruction from 10 to 120 kyr b2k from the NGRIP ice core, *Climate of the Past, 10,* 887-902. DOI

Kopaliani, N., Shakarashvili, M., Gurielidze, Z., Qurkhuli, T. & Tarkhnishvili, D. (2014). Gene Flow Between Wolf and Shepherd Dog Populations in Georgia (Caucasus). *Journal of Heredity, 105* (3), 345-353. DOI

Lewis, M., (1805). in Lewis, Meriwether, Clark, William, et al. May 5, 1805 entry in *The Journals of the Lewis and Clark Expedition*, ed. Gary Moulton. Lincoln, NE: University of Nebraska Press / University of Nebraska-Lincoln Libraries-Electronic Text Center, 2005. http://lewisandclarkjournals.unl.edu/journals.php?id=1806-09-04.

Li, H., & Durbin, R. (2011). Inference of human population history from individual whole-genome sequences. *Nature 475*(7357), 493-6. DOI

Lorenzen, E.D., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., et al. (2011). Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature 479,* 359-365. DOI

Maier, A., Lehmkuhl, F., Ludwig, P., Melles, M., Schmidt, I., et. al. (2016). Demographic estimates of hunter-gatherers during the Last Glacial Maximum in Europe against the background of palaeoenvironmental data. *Quaternary International 425,* 49-61. .DOI

Mazet, O., Rodríguez, W., Grusea, S.,Boitard, S., & Chikhi, L. (2016). On the importance of being structured: instantaneous coalescence rates and human evolution—lessons for ancestral population size inference? *Heredity, 116,* 362–371; DOI

Mech, L.D., Barber-Meyer, S.M.& Erb, J. (2016). Wolf (Canis lupus) Generation Time and Proportion of Current Breeding Females by Age. *PLoS ONE, 11* (6): e0156682. DOI

Melamed, Y., Kislev, M.E., Geffen, E., Lev-Yadun, S., & Goren-Inbar, N. (2016). The plant component of an Acheulian diet at Gesher Benot Yaʻaqov, Israel. *PNAS, 113 (51).* DOI

Mellars P. & French J.C. (2011). Tenfold Population Increase in Western Europe at the Neandertal–to–Modern Human Transition. *Science, 333*(6042), 623-627. DOI

Müller, U.C., Pross, J., Tzedakis, P.C., Gamble, C., Kotthoff, U., et al. (2011). The role of climate in the spread of modern humans into Europe. *Quaternary Science Reviews, 30,* 273-279. DOI

Musiani, M., Leonard, J.A., Cluff, H.D., Gates, C.C., Mariani, S., et al. (2007). Differentiation of tundra and boreal coniferous forest wolves: genetics, coat color and foraging ecology. *Molecular Ecology 16,* 4149–4170. DOI

NGRIP - North Greenland Ice Core Project members, (2004). High-resolution record of northern hemisphere climate extending into the last interglacial period. *Nature, 431,* 147-151. DOI

Pagani, L., Lawson, D.J., Jagoda, E., Mörseburg, A., Eriksson, A., et al (2016). Genomic analyses inform on migration events during the peopling of Eurasia. *Nature, 538*(7624), 238-242. DOI

Paine, R.T. (1995). "A Conversation on Refining the Concept of Keystone Species". *Conservation Biology, 9* (4), 962–964. DOI

Perri, A. (2016). A wolf in dog's clothing: Initial dog domestication and Pleistocene wolf variation. *Journal of Archaeological Science, 68,* 1-4. DOI

Perri, A.R., Smith, G.M., Bosch, M.D., (2015). Comment on "How do you kill 86 mammoths? Taphonomic investigations of mammoth megasites" by Pat Shipman. *Quat. Int. 368* (11), 112-115. DOI

Perry, G.H., Dominy, N.J., Claw, K.G., Lee, A.S., Fiegler, H., et al. (2007). Diet and the evolution of human amylase gene copy number variation. *Nat Genet. 39*(10), 1256–1260. DOI

Pierotti, R., & Fogg, B.R. (2017). *The First Domestication: How Wolves and Humans Coevolved.* New Haven, CT: Yale University Press. DOI

Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., et al. (2014). The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature, 505,* 43–49. DOI

Reimoser, F., (2007). *Begleitforschung und Telemetriestudie im Bereich der Nationalpark-Reviere im Gasteinertal.* Bericht, Oktober 2007. Wien: Forschungsinstitut für Wildtierkunde und Ökologie, Veterinärmedizinische Universität

Richards, M.P. & Trinkaus, E. (2009). Isotopic evidence for the diets of European Neanderthals and early modern humans. *PNAS, 106,* 16034–16039. DOI

Røed, K.H., Bjørnstad, G., Flagstad, Ø. et al. (2014). Ancient DNA reveals prehistoric habitat fragmentation and recent domestic introgression into native wild reindeer. *Conservation Genetics, 15,* 1137–1149. DOI

Romero, T., Nagasawa, M., Mogi, K., Hasegawa, & T., Kikusui, T.. (2014). Oxytocin promotes social bonding in dogs. *PNAS, 111(25),* 9085-90. DOI

Romero T, Nagasawa M, Mogi K, Hasegawa T, Kikusui T. (2015). Intranasal administration of oxytocin promotes social play in domestic dogs. C*ommun Integr Biology,* 23:8(3):e1017157. DOI

Russell, O. (1914). *Journal of a Trapper, or Nine Years in the Rocky Mountains, 1834-1843.* Syms York, Boise, ID.

Schaller F. (1991). Der Mensch einmal als Naturkatastrophe betrachtet. – *Schriften des Vereins zur Verbreitung naturwissenschaftlicher Kenntnisse Wien, 129*: 55–69.

Schiffels, S. & Durbin, R. (2014). Inferring human population size and separation history from multiple genome sequences. *Nature Genetics 46*(8), 919-925 DOI

Schleidt, W.M. (1998).. Is humaneness canine? *Human Ethology Bulletin, 13*(4), 1-4.

Schleidt, W.M., & Shalter, M.D. (2003). Co-evolution of humans and canids: An alternative view of dog domestication: HOMO HOMINI LUPUS? *Evolution and Cognition, 9*(1), 57-72.

Schoch, W.H., Bigga, G., Böhner, U., Richter, P., & Terberger, T. (2015). New insights on the wooden weapons from the Paleolithic site of Schöningen. J*ournal of Human Evolution 89,* 214-225. DOI

Serangeli, J., Van Kolfschoten T., Starkovich, B.M., & Verheijen, I. (2015). The European saber-toothed cat (Homotherium latidens) found in the "Spear Horizon" at Schöningen (Germany). *Journal of Human Evolution, 89,* 172-180. DOI

Shipman, P., (2015). How do you kill 86 mammoths? Taphonomic investigations of mammoth megasites. *Quaternary International* 359–360, 38-46. http://dx.doi.org/10.1016/j.quaint.2014.

Sommer, R.S., Kalbe, J., Ekström, J., Benecke, N., & Liljegren, R. (2014) Range dynamics of the reindeer in Europe during the last 25,000 years. J*ournal of Biogeography, 41,* 298–306. DOI

Speth, J.D. (2010) *Paleoanthropology and Archaeology of Big-Game Hunting: Protein Fat or Politics?* New York, Dordrecht, Heidelberg, London: Springer. DOI

Speth J.D. & Spielmann, K.A. (1983). Energy source, protein metabolism, and hunter–gatherer subsistence strategies. J*ournal of. Anthropological Archaeology, 2,* 1–31. DOI

Street, M. (2002) Ein Wiedersehen mit dem Hund von Bonn-Oberkassel. *Bonner zoologische Beiträge 50*(3), 269-290.

Svoboda, J., Kosincev, P.A., Sázelová, S., Jankovská, V. &Holub, M. (2010). Ethnoarchaeology of Nenets Campsites, Case of Yangana Pe and Oktyaberskaya (Polar Ural Mts., Northwest Siberia.*Přehled výzkumů 51* (1-2), 31-53.

Svoboda, J., Péan, S. & Wojtal, P. (2005). Mammoth bone deposits and subsistence practices during Mid-Upper Palaeolithic in Central Europe: three cases from Moravia and Poland. *Quaternary International, 126–128,* 209–221. DOI

Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V.J., Sawyer, S.K., et. al.. (2013). Complete Mitochondrial Genomes of Ancient Canids Suggest a European Origin of Domestic Dogs. *Science 342*(6160), 871-874. DOI

Thieme, H (1997). Lower Palaeolithic hunting spears from Germany. *Nature, 385,* 807–810.. DOI

Timmermann, A. & Friedrich, T. (2016). Late Pleistocene climate drivers of early human migration. *Nature 538*(7623), 92–95. DOI

Trinkaus, E., Buzhilova, A.P., Mednikova, M.B. & Dobrovolskaya, M.V. (2014). *The People of Sunghir. Burials, Bodies, and Behavior in the Earlier Upper Paleolithic.* Oxford University Press, New York 2014, 420 S. ISBN 9780199381050.

Vilà C., Savolainen P., Maldonado J. W., Amorim, I. R., Rice, J. E., et al., (1997). Multiple and ancient origins of the domestic dog. *Science, 276* (5319), 1687-1689. DOI

vonHoldt, B.M., Cahill, J.A., Fan, Z., Gronau, I., Robinson, J, et al. (2016). "Whole-genome sequence analysis shows that two endemic species of North American wolf are admixtures of the coyote and gray wolf". *Science Advances, 2*(7): e1501714. DOI

vonHoldt, B.M., Shuldiner, E., Koch, I.J., Kartzinel, R.Y., Hogan, A., et al. (2017). Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. *Science Advances, 3*(7): e1700398. DOI

Walton, L.R., Cluff, H.D, Paquet, P.C. & Ramsay, M.A. (2001) Movement Patterns of Barren-Ground Wolves in the Central Canadian Arctic. J*ournal of Mammalogy, 8*(3), 867-876. DOI

Wayne, R.K. (1986). Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution, 40,* 243-261. DOI

Wayne, R.K. (1993). Molecular evolution of the dog family. *Trends in Genetics, 9,* 218-224. DOI

Willerslev, E., Davison, J., Moora, M., Zobel, M., Coissac, E. et al. (2014). Fifty thousand years of arctic vegetation and megafaunal diet. *Nature, 506*(7486), 47–51. DOI

Zeuner, F.E. (1963). *A history of domesticated animals.* Harper & Row, New York/ Evanston.

Zimov S.A., Zimov, N.S., Tikhonov, A.N. & Chapin III, F.S. (2012) Mammoth steppe: a high-productivity phenomenon. *Quaternary Science Reviews, 57,* 26-45. DOI

SUPPORTING INFORMATION

Table 1. The Fodder of Pleistocene Megafauna – a selected Menu of Forbs and Grasses.
Molecular operational taxonomic unit Identification and counts of sequences of DNA-based diet analysis of coprolite/gut content from one each: wholly mammoth (H, tag 11, Finish Creek Valley Mammoth, Kolyma, Russia), wholly rhinoceros (D, tag 10, Kolyma, Russia), bison (B, tag 13, Kolyma, Russia), and horse (E, tag 22 Last Chance Creek Horse, Yukon). Data selected from Supplementary Data Willerslev_nature12921-s6.xlsx from Willerslev et al., 2014.

| Species	Woolly mammoth	Woolly rhinoceros	Bison	Horse	Total count
Sample Type	Coprolite	Stomach	Coprolite	Gut	
Calendar Age	21,819	44,120	>52,00	31,225	
Alpine Forget-me-not (*Myosotis alpestris*)	709	0	53	0	762
Cinquefoil (*Potentilla* sp.)	164	301	137	0	602
Willow (*Salix* sp.)	50	89	64	320	523
Arctic Alpine Forget-me-not (*Eritrichium* sp.)	85	0	327	0	412
Buttercups (*Ranunculus acris*; *R. turneri*; *R. subborealis*)	12	4	0	359	375
Plantain, (*Plantago media*; etc.)	225	127	0	0	352
Eastern Pasqueflower (*Anemone patens*)	138	0	23	0	161
Mugwort, etc. (*Artemisia*; *Achillea*; *Chrysanthem*, etc.)	12	18	14	36	80
Great Burnet (*Sanguisorba officinalis*)	7	40	0	11	58
Marsh-marigold (*Caltha palustris*; *C. arctica*)	0	52	0	0	52
Forbs (total)	**1402**	**631**	**618**	**726**	**3377**
Grasses (*Stipeae* sp. *Poeae* sp.)	59	132	114	32	337
Grass (*Festuca* sp.)	55	69	54	3	181
Grasses (*Koeleria* sp.,*Trisetum* sp.)	28	96	0	0	124
Grasses (*Agrostis* sp., *Calamagrostis* sp.)	0	63	0	0	63
Grass (*Deschampsia* sp.).	0	13	0	24	37
Grasses (*Arctophila* sp., *Dupontia* sp.)	0	0	19	0	19
Grass (*Puccinellia* sp.)	0	16	0	0	16
Grasses (total)	**142**	**389**	**187**	**59**	**777**
Total counts	**1544**	**1020**	**805**	**785**	**4154**
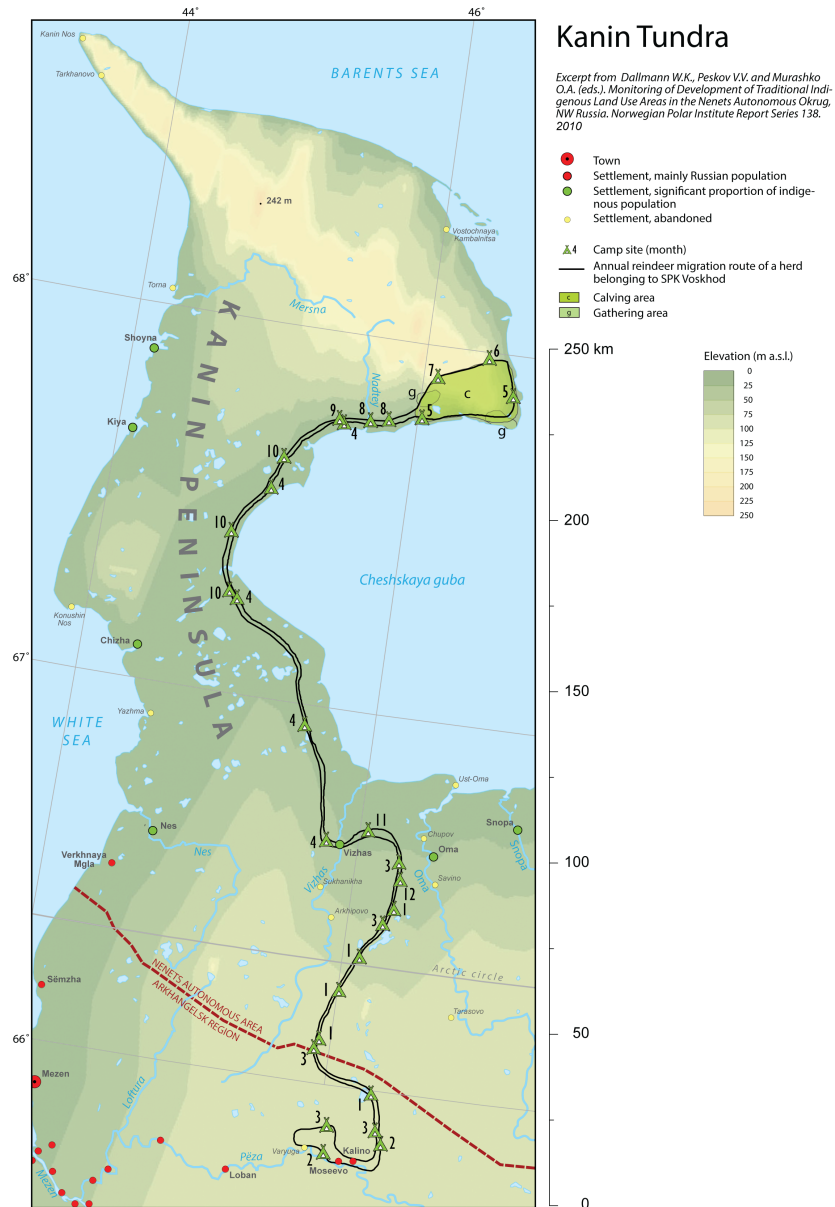
Figure SI-1. The annual migration of the reindeer herd of SPK Voskhod along the east coast of Kanin peninsula (Dallmann, Peskov, Murashko, 2010): The herd of 5,5000 reindeer attended by 55 Nenet herders, spending 4 months on winter pasture in the taiga below the arctic circle and near a village, 2 months going north, 4 months summer pasture at Barents Sea, with calving grounds at the slope of a hill reaching up to 242 m above sea level (insuring a nice breeze, presumably few insects), 2 months going south with a half way stop at Vizhas (administrative base of SPK Voskhod, slaughter house, health check, shopping and refueling) .With special thanks to Winfried K. Dallmann for providing this map.
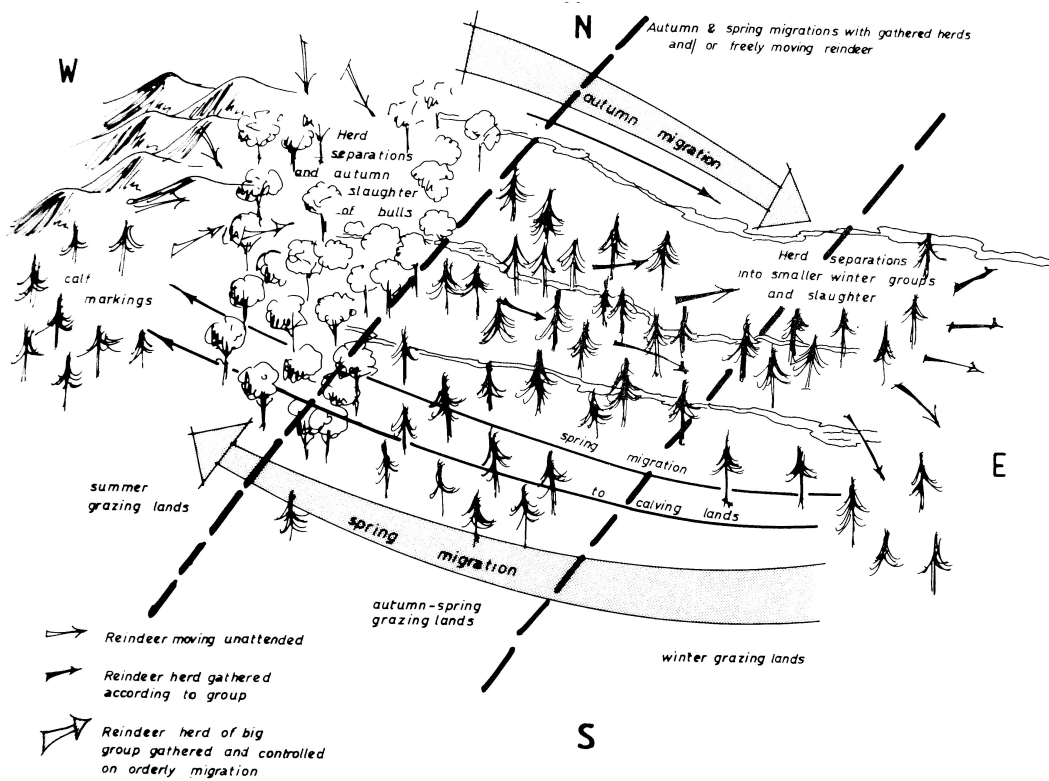
Figure SI-2. Typical seasonal herding pattern of a Swedish mountain herding collective (Hugh Beach, Fig. 9.2 in Comparative systems of reindeer herding. In: The world of pastoralism: Herding systems in comparative perspective (Galaty, J. G. & Johnson, D. L., Eds.). 1990, New York/ London: The Guilford Press. Reprinted with permission of Guilford Press.