

Review Article

Does Palaeolithic Resource Management Leading to Domestication Explain Human “Modernity”?

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Domestication involves the close co-existence of two different organisms, with at least one subjected to artificial selection. Humans domesticated numerous plants and animals. It is said that domestication by humans is a gradual process, starting with managing some aspects of other organisms' existence and ending with control over their reproduction through selecting traits that meet human needs. This selection results in a “domestication syndrome” that produces altered behaviour, anatomy, and physiology in domesticates (e.g., tameness, smaller brains, longer lactation in animals, and differing size and properties of fruits and whole organisms in plants). Archaeologically documented human domesticates date back to the transition from the Pleistocene to the Holocene (around 12,000 years ago). However, signs of changes in human populations indicating changing methods of exploiting environmental resources date back to the transition from the Middle Palaeolithic to the Upper Palaeolithic (about 50–40 thousand years ago). At this time, there is also a shift in human characteristics, indicating self-domestication (reduction in cranial capacity, gracilisation of the body, neoteny). This paper discusses the possibility that human self-domestication was linked to the management of large mammals during the Late Pleistocene, being an initial step towards domestication. However, this idea lacks firm support based on the available archaeological evidence.

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What is clear is that people could not begin intentionally domesticating animals until they had procured them through entirely unintentional means. (Lawson and Fuller 2014: 127)

... the term “management,” ... can be defined as: the manipulation of the conditions of growth of an organism, or the environment that sustains it, in order to increase its relative abundance and predictability and to reduce the time and energy required to harvest it.^[1]

Introduction

Hominins, from the outset of their existence in the Pliocene, exhibited behaviours aimed at managing their environments^[2] more than other species did. Initially, these included the use of objects (stones, sticks, straws...) to procure food, to construct shelters by rearranging vegetation and rocks, and to satisfy emotional needs (e.g. early music in Lomekwi^[3]). These behaviours did not differ much from great ape behaviours. Hominins, as early as the times of *Ardipithecus ramidus*, displayed adaptations to cooperative parenting and alloparenting^[4]. With the advent of regular exploitation of sources of animal protein and extrasomatic production of energy by fire in the Early Pleistocene^[5], hominin management of their environments probably started changing the effects of the basic ecological rule of survival, $C * E > S$, [C – carrying capacity of the environment, E – extractive efficiency of individuals or groups, S – sum of needs]^{[6][7]} by expanding the extractive efficiency (E) through the use of improved technologies and complex multi-person organisation of food acquisition, food transformation (cooking, smoking, drying, fermentation) and food sharing^[8]. At the same time, the carrying capacity of the environment (C) was altered by the construction of shelters, the use of body coverings (“clothing”), and the use of fire for warmth, which all limited the passive radiation of energy from bodies. Thus, the energy balance changed. The quantity of energy hominins could use was increased by both their better extraction from the environment (E) and re-shaping of the environment (C). This surplus energy allowed an increase in the size of local groups and in the size of individual bodies. The increase in population size created demographic pressure necessitating further modifications to environmental management methods that could include alteration of flora and fauna. The system of autocatalytic feedback loops driving hominin evolution^[9] (Henneberg and Eckhardt 2021), into which greater energy input was introduced, could have enabled evolutionary changes in human social organisation, improved technology, extended childhood, reproductive behaviours, mental capacities and the structure and function of human bodies in response to changing energy balance.

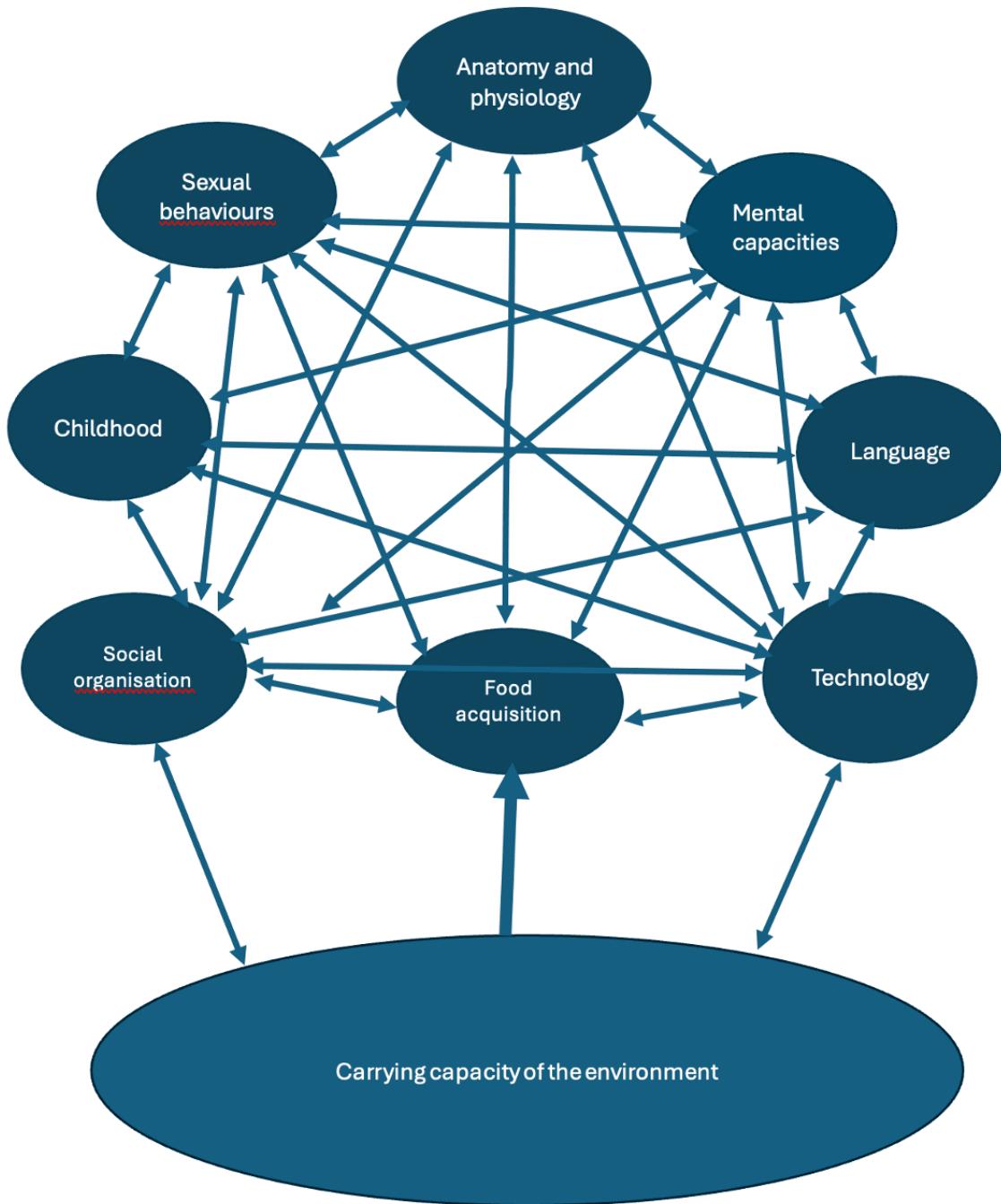


Figure 1. A set of positive, autocatalytic feedbacks guiding hominin evolution. Modified from Henneberg and Eckhardt^[10] and Henneberg^[9].

Foraging human populations do not have decisive control over the carrying capacity of their environments. They extract food from the natural environment by using the extractive efficiency of their technologies and social organisation. Human control over the carrying capacity of their environment

necessitates intervention in its structure and natural processes. It is difficult to point out exactly when such interventions started at a scale large enough to qualitatively alter the acquisition of energy to the extent that would alter the set of autocatalytic feedback loops influencing hominin evolution (Figure 1). However, the improvement of many observable elements of the human system (e.g. technology, bodily characteristics) during the Palaeolithic indicates that humans must have started gradually improving the management of their environment very early in their history as a genus. The direct evidence of human-caused environmental changes is difficult to obtain for periods before the time when food production, evidenced by archaeological finds of categorically new qualities of “agriculture” and “animal husbandry” dating to the early Holocene, significantly changed technology, social organisation and human anatomy (e.g. intensifying gracilisation and reduction in cranial capacity initiated in the Late Pleistocene;^[11]). This change was so profound that it provided humans with surplus energy, time and means to produce durable shelters, abundant figurative art and, ultimately, written records and science.

The underlying force of these changes was human management of plants and animals. It eventually altered their reproductive cycles, resulting in the phenomenon of domestication. Generally, the domestication of animals, plants and fungi results in the collective genetic alteration of their physiology, behaviour (where applicable), appearance or life cycle through selective breeding. However, its most effective expressions derive through the introduction of the domestication syndrome (^{[12][13][14][15][16][17]}, cf. ‘domesticated phenotype’, ^{[18][19]}). This syndrome is activated when a pleiotropic reaction to a sustained selection of specific phenotypic traits consequently introduces changes to the domesticated that seem unrelated to the domesticator’s intent. For instance, selection for a reduction in flight response (‘tameness’ or docility) might cause incidental shortening of the face, floppy ears, relative brain-size reduction or change of coat colour, among other changes. Artificial intentional selection by domesticators tends to involve only a single character or a few characteristics, but may be expressed in more numerous pleiotropic consequences that seem unconnected to the selection criterion. This may be due to the linkage of genes or other mechanisms of pleiotropic action of genes (e.g. epistatic effects). Additionally, the neural crest hypothesis proposes that pleiotropic genes affecting neural crest cell development are responsible for the domestication syndrome (^{[16][17]}, cf. ^[20]), at least in mammals.

Bearing in mind that domestication processes are almost innumerable in nature, it is not surprising that they involve many complexities. Thousands exist in the natural world, laying to rest the view that humans are the only domesticators, shared even by Charles Darwin. Another complicating factor is that symbiotic relationships often accompany domestication: wheat would not have become one of the

world's most common plant species had it not been domesticated. Dogs and humans exchanged mutual benefits of protection, feeding, hunting assistance and companionship. Also, the domestication process comprises two phases: an initial state of increased habituation followed by a much longer 'breed formation' stage^[17]. Humanly initiated domestications occurred at different times, and for different purposes, starting with the Final Pleistocene and up to recent times, which means that each of them must be at a unique stage of development at present. To add further to the diversity, these stages can be assumed to unfold at different rates in each species. Is the domestication of the reindeer, with its relatively minimal human control over the animal, a practice introduced relatively recently? Or is the rate of development a function of species- or environment-specific conditions? Some organisms appear more "domesticable" than others. For instance, vertebrates with a strong "flight response" to humans, e.g. deer or zebras, could not be domesticated. In each domestication history's progress, these and other factors need to be fully engaged to determine the significance of the current state. The only factor that effectively links domestication events is the domestication syndrome, first considered in plants^[13] and best explored in vertebrates, particularly mammals. Somatic changes include those in cranial and facial morphology (such as shortening of the snout), reductions of tooth size (notably the canines), reductions in brain volume and in specific brain regions, shortening of the spine, shape changes to body parts (e.g. ear and tail forms) and depigmentation (coat colour changes). Non-somatic effects of the domestication syndrome include more frequent and non-seasonal oestrus cycles that can range to their complete elimination, changed concentrations of several neurotransmitters, alterations in adrenocorticotrophic hormone levels, increased docility, prolongation of juvenile behaviour and various other neotenous effects.

In humanly initiated domestication, consistent long-term selection probably only occurred for one of these features: increased docility. This implies that the uniformity of the remaining characteristics derives from the pleiotropy inherent in the domestication syndrome. These other traits are not advantageous to domestication, so they would not have been selected deliberately. They are a random collection, rendered even more diffuse by the idiosyncratic trajectory of each domestication process and by its present-day status. Yet the traits affected are consistent across the domestication of numerous species. It does, however, raise a big question. Just as the change in one characteristic in domestication causes the alteration of several unrelated others by the agency of pleiotropy, general evolution also selects in favour of specific traits. Have such pleiotropic consequences been detected in evolution? This observation raises the possibility that evolution is a considerably more complex process than thought.

Domestication by humans resulted in a reduction in brain size in nearly all domesticated mammalian species. The progenitor species with the largest brain volume experienced the maximal degree of folding^{[21][22][23][24]}. The reduction has been determined to range from 6% to 40% in mammals. However, each conversion process has been operational for a different duration and mutation rate and would have been subjected to unique circumstances. Where the selection was for greater meat production, it involved considerable body augmentation^[25], affecting the brain/body size ratio (encephalisation). Domestication-derived brain atrophy seems not limited to mammals; it has also been reported in birds and the rainbow trout^[26]. The domestication traits seem irreversible because when domesticates revert to a wild state (becoming feral), they retain their smaller brains and other modified traits^{[27][24]}. For instance, when the Australian dog, the dingo, was imported by human mariners in mid-Holocene times, it must have been in domestic form. Since then, it became feral without relinquishing its domestication characteristics^{[28][29][30]}.

There is some evidence of pre-Holocene human intervention in nature. Aboriginal Australians' use of fire to restructure vegetation and fauna is but one example that may extend back into the Pleistocene. The development of human commensal relations with canids is another one. Human symbiotic relations with wolves started in the Pleistocene; whether it was at just 15 ka or at 100 ka is still debatable^{[31][32]}, but it clearly preceded the visible Holocene domestication of plants and other animals.

There is specific evidence of pre-Neolithic management of ungulates. It comes from the Mediterranean oceanic islands (not connected to the mainland during the Pleistocene). In Cyprus, wild boars and Mesopotamian fallow deer had been present and hunted nearly 12 ka ago, several thousand years before the earliest Neolithic (agricultural) settlements^{[33][34]}. There were no native ungulates on the Mediterranean oceanic islands until seafaring humans^[35] introduced them. The introduction had occurred before any traits of the domestication syndrome developed in these animals. It is confirmed by the simple fact that Mesopotamian fallow deer are not domesticable and were never domesticated on the mainland. The boars and the deer were purposely transported by Palaeolithic humans to the island at great effort for the purpose of them reproducing there and being available for hunting. Transporting large mammals on early watercraft involved a substantial organisation in making craft large enough to transport not only animals but also fodder and water for their use during the passage and bringing in a sufficient number of mates of both sexes to avoid inbreeding. Clearly, substantial numbers of animals were transported so that herds remained viable for several thousand years without the effects of inbreeding. All this happened without the domestication syndrome being observable. This management

required understanding of animal physiological needs during the voyage and at least of basic notions of breeding. Such understanding had to develop over a long period of observations and interactions between humans and animals before the first voyage.

The Cyprus example proves that humans managed animals in their environments a long time before the management progressed to the stage at which breeding became controlled to the extent that it produced the domestication syndrome. It can be speculated that in mainland situations, large herbivores were managed by humans for significant periods well before they developed signs of the domestication syndrome recognisable in skeletal material.

Archaeological evidence of plant domestication is persuasive because agricultural production requires tilling the soil with specialised tools, harvesting useful plant parts, storing harvested products in pits or containers, and processing plant matter into edible forms (grinding, pounding, baking, boiling, fermenting). All these activities require the use of specific implements or constructions that, in large part, are durable enough to persist for millennia. Agricultural production of food quantities required to support local populations of high density is relatively easy, removing the need for nomadism and allowing people to invest energy in the construction of permanent settlements (villages, towns, cities) from durable materials.

Food production through animal husbandry is efficient, but its archaeological evidence is less abundant due to the nature of this type of production. When and where animal husbandry was linked to agricultural production, such as in domesticating pigs or fowl, it is visible archaeologically as a part of permanent constructions to hold animals and implements used to process animal produce: corrals, barns, dairy, meat, wool, hides and horns. However, for populations of pastoralists and herders, the long-lasting material evidence is harder to find archaeologically. Herders follow the herds, so they have no permanent settlements. Their dwellings and other constructions are either transportable (e.g. yurts, tents) or temporary and made of perishable materials (pit houses, lean-tos, shacks, kraals for cattle). Specific implements related to herding are either perishable (whips, clubs, ropes, sticks) or of non-specific application (knives, spears, axes). Processing and storage of products of butchery can be carried out without containers; meat is either roasted, smoked, dried, or even fermented, while fresh animal fat is solid in temperate climate temperatures, not requiring special containers. Dairy processing requires the use of containers, which can, however, be made of animal hides or plant gourds that are perishable. Therefore, archaeological evidence of pastoralism and animal husbandry is less abundant.

The evidence of animal domestication can be found in non-perishable animal remains. Shapes and sizes of bones and teeth of domesticates may have differed from those of their wild counterparts — we have mentioned already smaller brains and the whole suite of characters changed by the domestication syndrome. Selective breeding clearly produces genetic differences now detectable by ancient DNA and proteomics analyses^{[36][37]}. The need to recover energy invested into care for domesticated animals makes people who exploit them use practically all parts of animal bodies, rather than just butcher the most valuable parts of the carcass. Careful study of faunal remains, especially those related to human settlements, may indicate early stages of management leading to domestication^[38].

Animal husbandry can develop gradually as people initially follow wild herds of animals and harvest them occasionally, slowly increasing their coexistence with herds and intervening in their biological dynamics^[1]. Coexistence of humans with herds or flocks of animals is beneficial for human food acquisition compared to occasional hunting, as animals become used to human presence while humans learn how to influence herd composition and what prey to kill, to better suit their needs. An example is animal tolerance of human presence (tameness, lack of flight response). They are then easier to exploit than when an unfamiliar hunter approaches an animal. Furthermore, herders can protect animals from predator attacks, thus preventing a reduction of herd sizes. All these activities are archaeologically invisible because they leave no durable objects of material culture. However, by increasing the useful human carrying capacity of the environment, they contribute to all elements of the set of feedback loops running human evolution (Figure 1). Thus, with herding or pastoral care of animals, human anatomy and physiology, technologies (kinds of artefacts, their shapes and sizes, decorations, materials used), social organisation, population densities, mental capacities, language and even sexual behaviours, can all change.

There is abundant evidence of changed technologies (lithic “cultures” or industries, sewing needles, jewellery, artistic expressions) in the Upper Palaeolithic. Human anatomy shifts from a robust to a more gracile appearance, with a clear reduction in the size of the masticatory apparatus and other robust features. These latter changes can be attributed to human self-domestication^{[15][39][40]}. There is also fossil and genetic evidence of commensal domestication of canids, predators who feed, among others, on large herbivores, reaching back well in time. Why could human and canine domestications occur without this phenomenon already spreading to many herding or flocking animals?

It is, however, the process of artificial selection of breeding animals that introduces the domestication syndrome^{[13][19][16]}. It is not clear at what stage of human-animal coexistence the management of

breeding took place. With human ability to provide alloparenting, the ability to see some mammal or a bird as an individual deserving care is thinkable. One of many possible interpretations of representations of individual animals in cave art is that they were actual or desired ‘pets’ of artists who painted them, individuals having a special meaning for the human-animal relationship. Some of the depictions of carnivores, e.g. lions, show them not as attacking predators, but as quiet individuals, either potential competitors or perhaps commensals. Heads and faces of some animals in both rock and mobile art are given more attention than their entire bodies. Perhaps a sign of an impersonation rather than just an objective depiction? True enough, more recent rock art contains apparent scenes of people with ‘weapons’ approaching animals. Those using bows and arrows were most likely hunting, but users of spears or knives could be slaughtering tame individuals. Moreover, some scenes do not show people intent on killing animals depicted next to them.

A large portion of the evidence of Upper Palaeolithic human activities comes from the temperate zone of Eurasia. In the Earth’s temperate terrestrial zones, the carrying capacity of the environment usable for pre-industrial humans consists of forests and grasslands. These do not contain enough wild food sources extractable by foragers throughout all seasons of the year, if large mammals are excluded. The almost countless mass extinctions of large mammals and birds marking the Final Pleistocene seem to reflect either the impoverishment of the carrying capacity of the human environment by natural forces or the environmental stress introduced by growing human populations overexploiting available resources. Managed to some extent flocks/herds of large mammals may have allowed the growth of Upper Palaeolithic human populations that enabled the whole set of feedback loops acting in human evolution to reach the level of greater technological and social complexity. With the Terminal Pleistocene climate change, management of herds became insufficient to sustain their existence, resulting in depopulation. The oldest evidence of animal husbandry recognised by students of human history comes from the terminal Upper Palaeolithic, just before the early Holocene, more than 12 ka before present, likely before the dates of the solid evidence of agricultural activities^[1]. Most of the early archaeological evidence of animal husbandry, however, is linked to that of agriculture. This is probably the result of the earlier-mentioned lack of non-perishable objects related to early animal husbandry, which may date back to the mid-Upper-Pleistocene, if not even earlier, to the origin of anatomical evidence for the “modern” humans.

In the caves of Bacho Kiro, Les Cottes and La Ferrassie, spanning the transition from the Middle to the Upper Palaeolithic, faunal assemblages undergo a transition from being partly accumulated by carnivores

in the MP to being exploited almost exclusively by humans in UP, who changed their selection of fauna towards reindeer and equids^[41]. There is no direct evidence that such selection was some initial form of herding, but changes in the most often consumed animal carcasses may indicate deliberate choice. It so happens that reindeer are amenable to interactions with humans, while horses seem to be similarly disposed.

The case of the reindeer

Here, we will consider the complexities and potential pitfalls of contrasting the domestication histories and effects on some different species by comparing what we know about significantly different scenarios and their outcomes. We illustrate this with the impact of endeavours to control populations of reindeer, a species that has experienced only partial domestication, which led to a seemingly stable symbiosis with humans^[42]. This will then be contrasted with much more intensively domesticated species and with the self-domestication of hominins, effectively in the absence of a domesticator. We intend to avoid anthropocentric perspectives as much as possible.

The reindeer (*Rangifer tarandus*) ranges widely in the circumpolar region of both Eurasia and North America and has been extensively ‘semi-domesticated’ from northern Scandinavia to eastern Siberia. It is the only species of its genus but has been divided into eight subspecies^[43]. About one-half of the five million reindeer now living are domestic herds, but they continue to interbreed with wild herds. Studies of reindeer mtDNA suggest that domestication occurred in at least two widely separated regions, perhaps 2–3 ka ago in eastern Siberia and then in Fennoscandia, possibly in Medieval times^[44]. Further independent establishment of the practice elsewhere is possible. The most likely trigger of domestication is that human groups followed wild herds for prolonged periods, culling animals as needed while protecting herds against wolf attacks. However, some reindeer still fear humans today, and the habituation process is incomplete, relative to the principal mammalian domesticates.

Stépanoff^[45], who studied the small herding system of the Tozhu people of eastern Tuva, Siberia, provides much insight into the domestication practices. The herders depend significantly on their animals to support them, providing them with milk and labour in the form of transport of people and goods, and occasionally with meat, skins and antlers. When an animal is to be killed, an ill, wounded, old or rebellious individual is chosen. The latter trait contributes to artificial selection, changing the genome towards docility. The practice of castrating most of the males, keeping just one carefully chosen buck per

thirty females, increases docility, too. Castrated males are destined to become pack animals. Similarly, female leaders in the herd that prompt others to flee from humans are preferentially slaughtered. The reindeer are free to wander into the taiga, even join a wild herd, and one factor bringing them back to the camp is the promise of salt or human urine to lick. For the latter, the Tozhu construct wooden urinals at a convenient height. Young fawns receive salt, even sugar, while they are tied up without their mothers. Importantly, it is the reindeer's prerogative to choose the timing and route of the annual migration (cf. [46]). The herders also respect the reindeer's aversion to human infrastructures such as fences and buildings^[47]. As Stépanoff^[45] poignantly observes, paradoxically, humans can domesticate reindeer only if they keep them relatively wild. Unlike most other human domesticates, reindeer are domesticated by (partly) nomadic people rather than by settled agriculturists.

The reindeer is one of the most recently domesticated mammal species, considering that the popular meme of the domestication of the rabbit by French monks in Medieval times (as a result of a Papal decree that rabbits are fish, permitting their consumption during Lent) is a falsity^[48]. This may explain the 'incomplete' state of domestication of reindeer, although peculiarities specific to it may also be implicated. These could include the logistical difficulties of migrating herds in forest and mountain regions, the impracticalities of corralling them in holding pens and the reindeer's reluctance to abandon flight responses entirely. The resulting symbiosis with humans remains underdeveloped, with some populations (the Fennoscandian breed) having been subjected to domestication only for several centuries. Therefore, the case of the reindeer provides an example of a domestication process that still has to run much of its course.

The case of the horse

Homo heidelbergensis and *H. sapiens neanderthalensis* have been hunting horses for several hundred millennia (e.g. at Boxgrove, Schöningen and Bilzingsleben), apparently by driving them over cliffs or spearing them at water sources. During the Upper Palaeolithic, *Equus ferus ferus* and *Equus ferus przewalski* were so widely hunted by humans that horses became extinct in much of Europe towards the end of that period, i.e. ~12 ka ago. The rich record of equid fossils from Eurasia and the Americas exemplifies evolutionary processes better than for most other clades^[49]. However, difficulties in distinguishing wild from domesticated horses hamper reliable interpretation^[50]. Subtle differences occur in tooth morphology, cranial shape and overall bone size. Nevertheless, no single feature is definitive. The intricate folds of tooth enamel provide some differentiation^[51], and wild animals tend to have larger,

broader skulls with rounder braincases and less developed occipital condyles. The differences between wild and domestic specimens are more pronounced than in reindeer, but they are significantly less developed than in dogs, for example.

Concerning horse domestication, Bogaard et al.^[52] observed that “[t]he more extended in time a process unfolds, the greater the likelihood that the causal elements were diffuse and complex”. We suggest that this applies to all domestications. The complexities are well illustrated by the intricate difficulties relating to determining where horse domestication began, and the controversial status of the tarpan. It remains unclear whether this free-ranging horse (*E. ferus ferus*), which became extinct in 1909, was wild, feral domesticated horse or a hybrid of Przewalski's and domestic horses^[53]. It has been assumed that the only surviving wild horse is *E. ferus przewalskii*, once occurring widely across Eurasia, but now limited to five protected herds in China and Mongolia (Figure 2). This view has been challenged by Chalcolithic finds of the Botai, a horse-reliant culture of northern Kazakhstan^[54] (5500–5000 years BP). The gracility of the metacarpals of the Botai horses and other factors suggest that they experienced domestication, but they are thought to be of Przewalski's horse. After this was confirmed by DNA analysis, it was challenged by rejecting the idea that this subspecies was ever domesticated^[55].



Figure 2. Przewalski's horses, Hustai Nuruu National Park, Mongolia. Photo by RGB.

Since the skeletal evidence of distinguishing domestic from wild horses remained so ambiguous, archaeological indicators have also been consulted^[56]. They include fat residues from the insides of ceramic vessels believed to be from horse milk and found among remains of the Botai culture, and dental

evidence of bit wear from the same context^[57]. The Khvalynsk culture on the Middle Volga, west of the Ural Mountains, has been suggested to be even earlier (up to 6800 years BP) and is credited with having domestic horses^{[58][59][60]}. The evidence for this includes post-moulds of presumed animal pens containing horse dung, and the skeletal remains of 16 horses, believed to be sacrificial, from the Eneolithic cemetery of the type site. The Samara tradition, which predates the Khvalynsk culture, dates to the early fifth millennium BCE and has produced horse bones from human graves. However, it is unclear if these horses were domesticated or simply part of grave goods. The most reliable evidence for equine domestication has been provided by the Sintashta culture, a Middle Bronze Age archaeological tradition of the southern Urals, dated to the period 4200–3900 years BP. It has provided chariots that were buried with horses. Chariots appear in the southern Trans-Urals region in the middle and late phases of the culture, c. 4050–3750 years BP^{[61][62]}.

The credible proposals for the beginning of horse domestication are thus from the steppes of southern Russia and Kazakhstan. Accordingly, it occurred between 7000 and 4000 years ago in that general region. However, the find of a buried horse in the Eneolithic site of Le Cerquete–Fianello near Rome narrows this estimate further^[63]. The Chalcolithic ends about 4200 years BP in Italy, so it is reasonable to suggest that the domestication of the horse occurred between 7000 and 4200 years ago, based on the present evidence. Proposals for alternative independent domestication of *E. caballus*, such as in the Arabian Peninsula, lack supporting evidence and conflict with available genetic evidence^[64].

The outlined archaeological chronology has been partially confirmed by genetics. Liu et al.^[65] detected positive selection of *ZFPM1* in samples about 5000 years old, leading to intensive selection of *GSDMC* (encoding the protein Gasdermin C) about 250 years later. The first gene is implicated in behavioural changes (e.g. towards docility), the second is associated with spinal stenosis, among other factors. This second change is attributed to the introduction of horse riding and the consequent strengthening of the spinal column. One of the concerns with riding on reindeer is that the rider must be careful not to damage the animal's spinal column. For instance, they use the support of a tree stump to mount "without harming the animal's back"^[45]. This confirms not only that the horse has been domesticated significantly earlier than the reindeer, but it also provides a rough timescale for specific developments.

The case of bovids

Sheep, goats and cattle were most likely domesticated following the “prey” route^[1], meaning that people who hunted them gradually developed ways to manage herds or flocks in which they tended to harvest specific age/sex groups (e.g. young males while protecting breeding females) and eventually limited herd mobility and controlled their reproduction. There is evidence of both human management strategies and morphological modifications of ungulates leading to the “domestication syndrome” from the Euphrates Basin at around 10.5 ka ago^{[66][67]}.

Goats were domesticated in the area of southwestern Asia (Turkey–Pakistan) from mountain goats (*Capra aegagrus*) as evidenced by zooarchaeological and genetic studies^{[68][69]}. However, nuclear DNA studies indicate numerous admixtures from other wild goat populations^[70], both at the time of domestication and later when domesticates were spread to all habitable continents.

Sheep followed a similar path to domestication. Their progenitor in SW Asia was likely the mouflon (*Ovis orientalis*), though other *Ovis* species of the same area are possible alternatives^[71]. Recent genetic studies^{[72][73]} confirmed this statement but also indicated a possible mosaic of domestic sheep ancestors. Due to the number of ways sheep were exploited — milk, wool, meat and even horns — morphologies of domesticates are varied depending on which aspect of economic utility was specifically desired by local domesticators. Initially, sheep were reared for meat; only later, their other products became of interest to domesticators^[74]. Wool production attracted most attention, leading to the creation of a number of breeds differing in the quality and colour of coats.

Cattle were domesticated from more than one wild ancestor. One of them was aurochs (*Bos primigenius*), a Eurasian wild cattle; another an African aurochs (*Bos taurus*) and yet another one from Asia (*Bos indicus*) known as zebu^{[75][76]}. Whether the domestication of each of these wild ancestors was an independent event or initially domesticated Eurasian cattle mixed with other wild aurochs, acquiring their genetic signatures, is still unclear. The independent African ancestry is unlikely^[77]. In terms of the antiquity of cattle’s domestication, it is interesting that cattle, together with other domesticates, were transferred to Cyprus at least 10 ka ago^[78]. Such transport necessitated covering a distance of tens of kilometres on the open sea with heavy animals, their fodder and water on board a large vessel. Sustained presence of domesticated bovids on the island proves that the maritime transport of large animals was not a single random event, but a planned, organised activity, since at the very least several animals of both sexes had

to be successfully transported to initiate a viable herd. The presence of cows in Cyprus proves not only the ability of their owners to build and operate large navigable vessels, but also their advanced skills of caring for domestic animals at least 10 ka ago. Such skills must have been developed and refined substantially earlier. Considered in the light of the taphonomic logic (see below), it indicates that significant management of cattle must have started some millennia before their first sea voyage.

The case of the wolf/dog

Canis lupus developed a commensal relationship with humans early on when the waste of human consumption of animals' bodies became abundant enough in camp areas to attract scavengers. Since wolves are animals living in social groups, they were likely to consider humans as members of their social relationships. Even today, domesticated dogs consider their human owners as pack leaders. This commensal relationship between canids and humans strengthened over time when canids expanded their symbiotic activities with humans beyond just consuming the refuse of human hunting and joined hunters as part of their hunting packs. There were suggestions, based on analyses of canid skeletal remains, that early domestication occurred as early as 36–31 ka ago^{[31][79][80]}. These findings were challenged^[81]. Therefore, it is difficult to establish when early changes leading to the formation of domestic dog lineages started to happen. The commonly accepted date of *post hoc* domestication has been suggested as about 15 ka based on both archeozoological and genetic studies^{[82][83][84][85][86]}. Around 12 ka, dogs were present at numerous archaeological sites across Eurasia^[87].

Hominin domestication

If it were possible to show that domestication of mammals began at least at the beginning of the Late Pleistocene, it would be easier to understand how humans could use principles of domestication in the organisation of the life of human societies — provided we assumed that auto-domestication was deliberate. Human self-domestication would not stand alone as an exceptional process but rather be a natural consequence of changing relations between humans and nature. However, hominin self-domestication was completely unintentional. Conversely, self-domestication has also been attributed to other species^[88] (dog, bonobo, possibly elephant).

The hypothesis that the introduction of human modernity is the result of the domestication of robust *Homo sapiens* populations occurring during the last third of the Late Pleistocene was a response to the

replacement hypothesis, also labelled African Eve theory. Unable to attribute that relatively sudden appearance of “modern” humans in Europe to evolution, that meme had ascribed the change from robust to gracile hominins to a speciation event in sub-Saharan Africa, leading to a cognitively superior species that replaced all human populations of the world by outcompeting or eradicating them. Initially based on a hoax by a German biological anthropology professor in the 1970s^[89], the replacement hypothesis has been contradicted by genetic evidence in recent years: Neanderthals, Denisovans and extant humans are one species. The inability of scholars to explain how the teleological ‘anatomically modern human’ could have evolved in a geological instant (a few tens of millennia) prompted them to propose the mass migration of a new species. However, there is no substantive evidence in favour of this notion, be it anthropological, archaeological, demographic or genetic. Moreover, the replacement theory provides no plausible explanation for any aspect of human modernity, be it somatic changes, susceptibility to countless detrimental conditions and maladaptations, brain atrophy, loss of oestrus, genetic impairments, or general neoteny. The domestication hypothesis, by contrast, explains all these factors exhaustively as the outcomes of a process capable of transforming an entire species within very few millennia: the pleiotropic effects of domestication^{[15][39][40]}.

Better acquisition of energy from animal sources at the beginning of the Upper Palaeolithic could have produced larger local human populations. Whether the total number of humans in the world or on some continent has increased is irrelevant here. It is the size of a local population of humans who interact with each other in economic and cultural activities and, inevitably, in sexual ones, that is important. Egalitarian local populations of foragers consist of a few hundred individuals^[90]. Increasing extractive efficiency by some form of management of large mammals could increase this size several times. Population size increase could lead to social stratification, which is suggested by the increasing use in the Upper Palaeolithic of body decoration, in some instances, grossly exaggerated^[91] (e.g. Sungir’ burials).

Taphonomic logic to the fore

Are these realistic speculations? How secure can archaeology’s interpretation of the evidence for domestications be regarded?

In the interpretation of all empirical evidence of the past, the concept of taphonomic logic is paramount. It derives from the principles of taphonomy, the discipline introduced by Efremov^[92] when he tried to counter actuopalaeontology, the explanation of the palaeontological record as a literal reflection of the

living system (see [93] for a superb discussion). It took archaeologists, forensic scientists, rock art researchers and others more than forty years to realise that the generic issues of taphonomy have significant applications in their fields as well. Bednarik^[94] formulated these underlying principles and proposed that the ‘ratio’ between the ‘quantified’ event or living system and the surviving evidence of it can be expressed as an integral fraction. Whilst the original concept of taphonomy addressed the decay, disarticulation, dispersal, accumulation, fossilisation and mechanical alteration of palaeontological evidence, taphonomic logic focused on the progressive loss with time of evidence deriving from events or phenomena of the past that need to inform their interpretation in the present. They might include the methods of recovery of evidence, its reporting and selective dissemination, its statistical treatment, or even the individual researcher’s own biases and limitations. These tendencies are likely to be systematic, and there should be no doubt that there is a very considerable gap between the reality of what happened in the distant past and the abstraction of it as perceived by the individual archaeologist interpreting a specific, subjectively selected and non-random sample of evidence truncated in various ways.

The most significant principle of taphonomic logic is the relationship between the surviving evidence of a phenomenon and its actual occurrence in the living system (Figure 3). In this graph, the alpha curve represents all examples of a specific phenomenon ever created, say, every bead made. Most of these may not have survived, so the beta curve represents those collected, correctly interpreted and disseminated. Assuming we experience a loss of 10% of beads in one time-unit (which may be a century or a millennium or whatever), the loss in two time-units should be in the order of twice that, and so on. After ten or so time-units, the bead population has largely vanished. However, a zero-probability of survival of any archaeological phenomenon is not possible. Therefore, while the “preservation bias” forces the beta curve away from the alpha curve as we proceed back in time, the “equilibrium bias” prevents it from touching the zero-population abscissa. So, as it approaches the abscissa, the beta curve forms a parabola at point D, the ‘taphonomic threshold’. From there on back in time, it hovers close to the abscissa, touching it only before point B, when beads were first made. The number of surviving specimens is so low that archaeology would be either incapable of detecting them, or if it did, it might reject them as stray occurrences, as intrusive, or as “running ahead of time”^[95]. The latter rationalisation is particularly detrimental to archaeology because it systematically dismisses the most relevant available evidence of hominin cognition or technical ability, when scientific access to the human past is contingent on the coherent identification of that part of the extant characteristics of the evidence that is *not* the result of taphonomic processes.

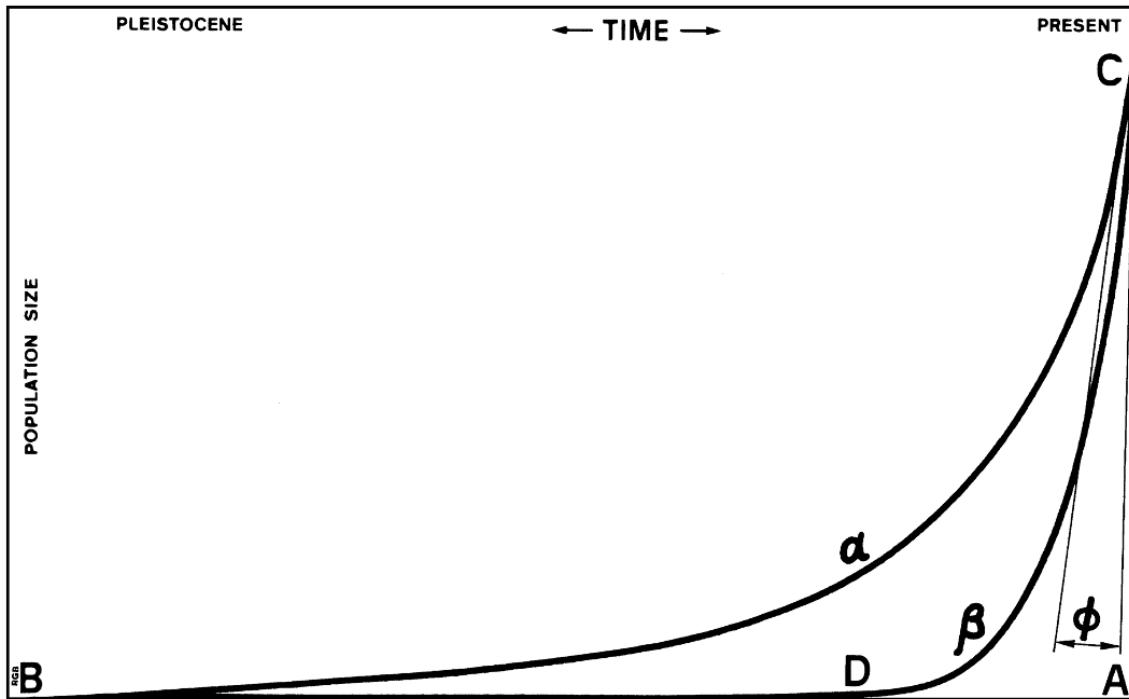


Figure 3. The principles of taphonomic logic: the relationship of total production of an archaeological phenomenon s_α to its surviving instances s_β as a function of angle ϕ .

Taphonomic logic demands that particular attention be paid to the taphonomic lag-time preceding the common occurrence of each archaeological phenomenon category. In many of these categories, the lag-time is likely to be in excess of 99% of the phenomenon's currency. Examples of very long lags have been documented, for instance, in the beginnings of presumed use of symbolism (including language), maritime colonisation (particularly affected by the taphonomy attributable to sea-level changes) or the use of perishable materials (wood, adhesives, string, clothing, etc.). All phenomenon categories strongly affected by taphonomic processes can only provide very conservative maximum ages, and it is expected that their historical duration extends much further back in time than commonly assumed in archaeology.

Discussion

Here, we are concerned with the extension of this generic principle to the question of when humans began to domesticate other animals. Most certainly, it was earlier than the times from which we have sound evidence of the origins of such practices. This evidence would show that the taxa in question had been eventually subjected to the domestication syndrome, physiologically or behaviourally. However,

domestication is a lengthy process rather than a definable moment, involving various stages, and it is, in most, if not all, cases, continuing. The case of the reindeer illustrates this. Although reindeer herders can distinguish between wild and domesticated individuals, there appear to be no skeletal differences between the two. Pleiotropic effects seem to be undetectable, and the animals' migrations continue to be determined by the herds rather than the herders. The current state can be defined as "incipient" domestication.

The appearance of cattle in Cyprus 10,000 years ago provides sound evidence that they were transported in adequate numbers on sea-going vessels. We can safely assume that would have only been possible with domesticated animals. Therefore, at present, it appears that the complex domestication of cattle followed the domestication of the wolf, the timing of which remains unresolved. It was accompanied by the domestication of the ovicaprids ~12,000 – 10,000 years ago. Of particular interest is the gradual spreading of these bovids from the Fertile Crescent across northern Africa from east to west^[96].

Evidence of human "anatomical modernity" began appearing in Europe about 40 ka ago and has been attributed to unintentional self-domestication of robust hominins. Does Palaeolithic resource management leading to domestication via taming or herding explain human "modernity"?

Most certainly, taphonomic logic decrees that animal husbandry of ungulates and other taxa must have begun earlier than the time of the first clear archaeological evidence of such practices. Such empirical evidence cannot be expected from the "lag-time" of the phenomenon category, which remains of unknown duration. An additional encumbrance is that it seems very hard to secure proof of taming or herding. Nevertheless, as the pleiotropic effects of the hominin auto-domestication begin appearing around 30 ka before those of ungulates, it is most unlikely that the question in this paper's title can be answered in the affirmative. In the case of the hominins, the pleiotropic consequences of domestication are amply manifest. For the domesticated animals, a realistic taphonomic lag-time needs to be ascertained.

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Data Availability

All data used for this paper have been already published and are available in the literature.

Author Contributions

Conceptualisation, M.H. and R.B. Methodology, M.H. and R.B. Writing – Original Draft Preparation, M.H. and R.B. Writing – Review & Editing, M.H. and R.B.

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