

DOMESTICATED MEGAFUNA OF AMERICAS: NEEDS, POSSIBILITIES AND RESULTS

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ABSTRACT

The article aims to determine why so few domestic animals originated in American domestication centres. The knowledge has been gathered from interdisciplinary sources taking into account recent archaeogenomic and spatial analysis research. The process of domestication is described, and different domestication centres are compared to the domestication needs and opportunities on the American continents. Human colonization of the American continent is considered. Important domestication centres on the North and South American continent are described. Dogs that colonized the American continents together with people and horses that arrived during the European colonization are also considered. The analysis of the American megafauna that lived on the continent during the first colonization of *Homo sapiens* showed that the big extinction occurred due to climate change and overhunting. Comparing the evolutionary process of domestication between Afro-Eurasia and America we found that there was no intentional domestication in areas peripheral to the original domestication centres in the Americas. Also, diversification of the domesticated animal purpose in the Americas is limited to dogs.

KEY WORDS

North America, South America, domestication, animals, megafauna

CLASSIFICATION

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INTRODUCTION

Anatomically modern human (*Homo sapiens*) evolved in Africa around 300 000 years ago [1]. Approximately 60 000 years ago some groups started leaving Africa and ‘conquering’ the rest of the world [2]. At that time humans used primitive tools against much larger predators than those we know today, expanding from the original habitat due to climate changes and the population growth in search for prey animals and gathering food. Pleistocene, known as ‘The Ice Age’, lasted from around 2 588 000 to 11 700 years ago. During that time Earth endured some of the biggest changes since its formation, which defined the world we know today. Looking at all the challenges an early human had to face we could say that it is an impressive achievement that in less than 50 000 years he managed to spread all over the world, even reaching America at earliest around 14 600 years ago [3, 4]. There are indications for dog assisted mammoth hunt as far as 16 200 years ago in Yakutia during the settling of northeast Asia [5]. When raw strength was not enough, early humans depended on their brain and intelligence, unknowingly changing the world around them, making better use of their environment. Today, it is known that people settled America using the ‘Bering Strait’, a narrow sea passage that connects Siberia with Alaska, which was covered with ice, therefore walkable during Pleistocene [4, 6]. However, people did not manage that feat on their own: they were followed by early domesticated dogs over the harsh cold Arctic, where hunting of the large prey such as mammoth, bison, woolly rhinoceros, musk-ox or wild horse, was the only feeding option with no gathering possible because of the climate [5, 7, 8]. Looking through all of the human history, domestication was one of the first things that really separated anatomically modern man from other animals and other Hominidae species, and was crucial for development of material culture (for example: horse and crops) through the development of agriculture [9-11]. Today we still do not know if the early human managed to tame a wolf and create, from this predator species, what is today known as ‘man’s best friend’ on his own; or if the wolf basically domesticated himself with cohabitation and later commensalism and/or friendship with humans [12, 13].

The aim of this article is answering the question why the two American continents contributed so little to megafaunal domestication in comparison with Afro-Eurasia. To provide this answer (i) overview of domestication needs, capabilities and opportunities in North and South America is given from the start of human colonization of the continents to the time of the European invasion; (ii) animal species domesticated in America are examined; and (iii) the possibilities for domestication that America possessed are critically reviewed.

DISCUSSION

DOMESTICATION

The definitions and comparative timelines are provided in this section in order to provide an overview of domestication process in North and South America and discuss the results of historical megafaunal domestication in comparison with Afro-Eurasian domestication centers. In the Encyclopedia Britannica [14] domestication was defined: “Domestication is the process of hereditary reorganization of wild animals and plants into domestic and cultivated forms according to the interests of people.” Martin and Sauerborn [15] elaborated that not every animal or plant can be domesticated [16]. To endure domestication an animal must abide by certain principles: (i) feed easy to obtain; (ii) short generation interval; (iii) no nasty disposition; (iv) willing to breed in captivity; (v) willing to follow hierarchy; (vi) does not panic in captivity.

The first and haphazard domestication of the dog in north Asia and the first crop domestication in the Fertile Crescent are at least 2 000 years apart, and even more time separates the second domesticated animal (sheep), from the domesticated dog. However, all

three of these cases share the same unintentional process of the domestication according to Zeder [17]. If we focus on animal domestication as an authentic evolutionary process in its own right, it can be said that the commensal way and the way of domestication of the prey were important initial pathways of domestication starting in the Neolithic, but the most of the animal species were domesticated intentionally in the period starting from the Iron Age until the recent few centuries [10]. Aimed and intentional domestication of animals geographically happened peripherally to the first domestication centers (*Equus africanus asinus* (Linnaeus, 1758), *Camelus dromedarius* (Linnaeus, 1758), *Camelus bactrianus* (Linnaeus, 1758), *Numida meleagris* (Linnaeus, 1758)) and is contemporary with the first intentional introgressive capture cases during the Iron Age that can be the cause of the artificial inflation of the count of independent domestication cases in certain species [18]. Providing animals for efficient transport coincides with the times of the expansion of agriculture into new areas starting at the end of the Bronze Age with domestication of the dromedary [10].

Besides for cats and dogs, and perhaps pig, the unintentional and initial commensal way could have been the domestication pathway for the guinea pigs in southern Peru and Bolivia [17]. The pathway of the domestication of the prey animals includes the motive of more reasonable resource management and starts with the sheep, goat and cow about 10 500 BCE in the sedentary societies and somewhat later for other bovine species further south and in the nomadic cultures of the European and Asian north (*Rangifer tarandus* (Linnaeus, 1758) and *Equus f. caballus* (Linnaeus, 1758)) [10, 19]. Starting with 6 000 – 5 000 BCE the same pathway of domestication was used for llama (*Lama glama* (Linnaeus, 1758)), alpaca (*Vicugna pacos* (Linnaeus, 1758)), turkey (*Meleagris gallopavo* (Linnaeus, 1758)) and muscovy duck (*Cairina moschata* (Linnaeus, 1758)) [10, 20, 21]. Little research is available on the insects and fish domestication on the American continents [22, 23].

Later onset of domestication is the characteristic of the American domestication centers, due to the timing of the first settlement of the continents. In the light of the global pattern of the domestication the characteristics of the domestication process of large animals in the Americas never reached beyond the prey pathway of domestication. Domestication of animals in Americas remained geographically limited to domestication centers with no diversification of purpose or aimed domestication typical for domestication of the end of Bronze Age and the Iron Age in Afro-Eurasia. It is important to notice that exactly this characteristic of domestication peripheral to early domestication centers at the end of Bronze Age in Afro-Eurasia enabled more of the wild species to be domesticated (donkeys, dromedary and Bactrian camels). Coincidentally, the American cultures and civilizations did not reach the iron smelting technologies that are contemporary with the aimed domestication in Afro-Eurasia, until the contact with the European civilizations.

GEOGRAPHICAL SETTING

In this section we assess the possibilities for domestication that America possessed geographically in comparison with Afro-Eurasia. Animal domestication happened in almost every part of the world (Table 1.) and changed the world biosphere in the recent 11 500 years, the size of human populations and the human evolution [10]. Due to the geography North America and eastern Brazil did not have any domesticated animals, as was the case with the Mediterranean and the North-central China domestication centers [24]. The Afro-Eurasian domestication centers were better connected, therefore the trading of cultures and knowledge was made possible. Migrations and sharing of information happened through all human history over Afro-Eurasia. It can be seen that in the Iron Age in Afro-Eurasia a lot of domesticated large species were used for migrations, trading, and war over far distances, which in turn helped spreading cultures and other domesticated species over the continents [9, 10, 17, 25]. Although the horse was domesticated before this period [26] probably as a mean of control of the wild herds of horses, morphologically this domestic species has changed notably between 5 500 BCE and 4 000 BCE, and after that

period it is notably used for trade transport, warfare (with the development of a cart) and milking [27]. In the Americas the only beasts of burden at that time are widespread dogs, and the llama in the limited geographical area. Moreover, llama was never used as a plough animal.

Geographical feature of the continents enables the trade and the transfer of the domesticated species over the temperate zone. The temperate zone spans over the east-west direction of the Afro-Eurasian setting of the domestication centers and enables additionally for the tamed animals to change the culture where they were used, and therefore the invention of new purposes and techniques of their use [28]. On the other hand, north-south span of the American continents forces the humans to adapt to different climate and biotic zones traveling over that direction. The Inca, versed in agriculture, did manage the giant feat of gaining reign and control of the vast area of the western south-American coast, with colonies in the Mesoamerica, while the non-agricultural cultures of the North America (such as the Inuit or the Kickapoo) did not. There was exchange of some of the animals over different American cultures, the dog was present almost everywhere, however, the llama and alpaca were not. Most American cultures did not really know of each other's existence, or they did not exist at the same time. By the time Aztecs appeared Mayan civilization was already gone or falling apart, having collapsed somewhere between 750 AD and 900 AD. Inca and Aztec civilization did exist at the same time but it seems they never shared any information or even knew of each other's existence [29]. Additionally, the conquering dominating cultures treasured their domesticated food sources and did not provide them freely for their conquered subordinates.

Table 1. Animals domesticated in different domestication centers. Numbers represent thousands of years before present as the latest time by which domestication occurred [10, 34].

American continents	Africa	Europe	Asia		
Mesoamerica and South America	East Africa, South Arabia	Mediterranean	East Asia	South Asia	Southwest Asia (Middle east and Egypt)
Llama 6-4	Cattle – cow (taurine) 8,5-6,5		Dog 15	Cattle – zebu (indicine) 8-6,5	Pig 10,3-9
Alpaca 5-3	Donkey 5,5-3,5		Pig 8,5-6	Water buffalo 6-4,5	Sheep 11
Guinea pig 5-4	Honey Bee 3,5 [30]	Rabbit 2 [31]	Horse 5,5-4		Goat 10,5-8
Muscovy duck 4-2	Camel (Dromedary) 3		Silkworm 5,5		Cattle – cow (taurine) 10,3-8
Turkey 2	Guineafowl 1,5		Yak 10-7		Cat 9,5-4
Ni-in? <i>Llaveia axin axin</i> [23]			Camel (Bactrian) 4,5		Pigeon 5-3 [32]
Stingless bee 2 [22]			Chicken 4		Goose 3 [33]
			Duck 1		

AMERICAN MEGAFUNA

It is disputable that the places that were more abundant in animal species naturally had more domesticated animals. Besides the abundance of animal species, the type of the animals must be taken into consideration together with the general geography and human needs and capabilities at that time. To provide an overview of biological domestication opportunities in this section we discuss the wild American megafauna.

Although there are different definitions [35], terrestrial zoology considers megafauna to be any animal weighting more than 45,3 kilograms [36]. The biggest North American terrestrial megafauna specimen today is bison, weighting up to 1 ton [37]. South America today is more abundant in small land animals, biggest land mammal is tapir, which weighs up to 250 kilograms [38]. The biggest American mammals alive today are dwarfed in size by the extinct species. Approximately 97 out of 150 American megafauna species went extinct at the end of Pleistocene, about 10 000 years ago [39].

Apparently, during the time of domestication on American continents not many animals could meet the required predispositions for domestication. Since the wild megafauna of European continent was shared with North American to a certain extent, and North American with South America, we would expect that there were some animal species able to endure the domestication process present at all these spaces. Four main theories are used to explain the first human related American extinction of megafauna: (i) humans hunted them to extinction; (ii) climate change; (iii) spread of new diseases; (iv) asteroid hit. It is important to note that these theories are not mutually exclusive [40]. American continent was not an isolated case of big animal extinction, in general, closely followed by the appearance of *Homo sapiens* [11], for instance: Australian extinction 50 000 BCE, Solomon Islands 30 000 BCE, Cyprus 9 000 BCE, Antilles 6 000 BCE, Madagascar 2 000 BCE, New Zealand 800 BCE, Commander Islands 250 BCE.

The Pleistocene is characterized by a succession of colder and warmer periods, the glacial–interglacial cycles. Before the end of Pleistocene ice sheets spread and covered up to 30 % of total Earth surface, making the migrations possible. Before the temperature change, at the end of Pleistocene, yearly temperatures were 5–10 °C lower on average than they are nowadays. Because of the lower temperatures, the air was drier and precipitation much less frequent. Animals living at the time adapted and thrived up until about 11 000 years ago when the climate started changing and when humans arrived at the continent. Temporal proximity of the initial human immigration to North America and the rapid climate change of Younger Dryas cover the same 5 000-year window. Due to inefficient statistical methods used up until the Emery-Wetherell, McHorse, and Davis [41], who used a fine-scale geospatial approach in combination with meticulously pruned dataset of 95 megafaunal last-appearance and 75 human first-appearance radiocarbon dates to evaluate the North American megafaunal extinction, the efforts to identify the ultimate extinction cause gave contradictory results among researchers. Their spatially explicit approach resulted in rejecting the hypotheses of continent-wide extinction considering the blitzkrieg hypotheses, man carried disease, Clovis technology, and uniform climate change. However, the blitzkrieg or intensification hypotheses, a combination of climate and human influences, or a climatically driven extinction with large-scale refugia and environmental buffers that delayed extinction in several areas were not rejected. Emery-Wetherell et al. [41] found that the last appearances of megafauna in North America and their overlap with human populations were highly regional in nature. Megafauna had last appearances in Alaska before humans first appeared, consistent with climate as a primary driver, but human influence cannot be excluded from all regions. The Great Lakes regions and Mexico have a delayed last-appearance events with long overlap, but the reason for this refugia is not explained.

Emery-Wetherell et al. [41] incorporated an abundance of proboscidean fossils (*Mammuthus* (Brookes, 1828) and *Mammut* (Blumenbach, 1799)) in the last-appearance data. Three elephant species (mastodons) lived on the continent [42] best known is the wholly mammoth. This situation may have arisen because of their easy identification or possibly reflect the predicted staying power [43] of proboscideans against overhunting. Species of the genus *Equus* (Linnaeus, 1758), and order Artiodactyla (Owen, 1848) were grouped in their work to assess possible differences of the extinction trends. North America was also home to different Camelid species-*Camelops* (Leidy, 1854), close relative of the domesticated camelids of South America and the 'Old world' Bactrian camel, which were domesticated 2 500 BC in Northeast Afghanistan or southwestern Turkestan and were most important as animals of burden, but also as a source of milk and meat in Eastern Asia. Other animals that could have possibly endured domestication are few extinct Bovidae species: *Bison antiquus* (Leidy, 1854) and *Bison occidentalis* (Lucas, 1898), *Bootherium bombifrons* (Harlan, 1825), *Euceratherium* (Furlong & Sinclair, 1904), and were not included in the research of Emery-Wetherell et al. [41] since they had later extinction dates [44]. American wild bison has never been domesticated, due to wild and ungovernable temper [16].

South America was home to the giant sloth, who fed on avocado fruit with the seed which enabled the plants reproduction [45]. Besides the only domesticated megafauna of America lama (*Lama glama* (Linnaeus, 1758)) derived from guanaco (*Lama guanicoe* (Müller, 1776)) and alpaca (*Vicugna pacos* (Linnaeus, 1758)) derived from vicuna (*Vicugna vicugna* (Molina, 1782)), South America was home to specific animals such as *Macrauchenia* (Owen, 1838), *Doedicurus* (Burmeister 1874), *Glyptodon* (Owen, 1839), and *Toxodon* (Owen, 1839). Elephants also lived here, most notably the *Stegomastodon* (Pohlig, 1912) and *Cuvieronius* (Osborn, 1923). Horse genus *Hippidion* (Owen, 1869) was present until approximately 8 000 years ago.

THE NEED FOR ANIMALS OF DIFFERENT PURPOSE

The need for domestication, intention and purpose are demonstrated in this section taking account of North and South America, sedentary and nomadic cultures.

The only domesticated animals that North American Indians kept were dogs. Dogs were not originally domesticated in America (even though the precise origin of dog is still unknown) [46-48]. The first dog breeds made the life in northernmost parts of America possible by hunting, carrying cargo, dragging sleds, which made migration possible, providing warmth, medicine (dog urine), and sometimes food for people [49]. Dogs were so important to the Inuit that they only ate them in time of the greatest starvation, when dogs and people would die anyways [50]. As was the case in the Siberian Arctic, cold environment provided mostly prey, with short period during the year for gathering berries or plant material for making fire, which is indicative in the Abenaki word 'Esquimantsic' denoting the ones eating raw meat.

North America with temperate climate, further south (along the Wabash River), was area where dogs were much more often used as food. This was the area of the hunter-gatherer and fishing tribes with far more opportunity for gathering, and the area where nomadic life was not burdened by domestication or agriculture. Noteworthy are the Kickapoo Indians of the American southwest, who reared dogs in a ceremonial way, aside from the "regular" way for the company and dogs used for migrations and ate dog meat for ceremonial purposes [51]. One of the more interesting dog breeds that originated in North America is the 'Salish wool dog'. These dogs were selected for white hair that was used for clothes and was sheared. With arrival of Europeans and introduction of sheep to America these dogs went extinct [52].

Despite the fact it was colonized the last, South America was also home to some of the most important American civilizations. Like Central American Olmec and Maya civilizations, South America was also home to arguably the oldest (Norte Chico) and the biggest (Inca) civilizations [53].

Southern American Indians were well versed in agriculture and animal domestication. They kept dogs, mostly used as a food source or just for general company. Well known today is 'Inca Orchid' breed which despite the name is older than the Inca civilization. Poultry was also an important aspect of their life. 'Mocha' culture of the Meso-America domesticated muscovy duck (*Cairina moschata* (Linnaeus, 1758)) and used it as early as 50 BCE. Apart from the obvious food source aspect, Muscovy ducks were kept as 'pest control'. They love feeding on fly and mosquito larva, which is very useful in the jungles where these animals are abundant [17]. Aside from ducks, guinea pigs (*Cavia porcellus* (Linnaeus, 1758)) were also a useful domesticated food source. Used in settlements at the earliest at around 900 BCE in the Altiplano region of Bolivia and south Peru [54], guinea pigs proved to be very easy to keep and they reproduced rapidly. Unfortunately, due to their small and fragile remains in the zone where dogs were also kept it is possible that more detailed archaeological and genetic investigation of their early domestication in the period long before the Inca is impaired. Due to their nutritional value they remained one of the most important South American food sources even today. Only after spreading to Europe guinea pigs gained the 'pet' status that we are familiar with today [54].

The biggest domesticated animals of American continents are llama and alpaca, domesticated by the Inca civilization around 4 000 BCE. Since the American civilization did not use the wheel (besides for children toys) llamas, being bigger than alpacas, were very useful for carrying burden. Alpacas were mostly used for clothes production; their soft fleece is still regarded as a premium clothes material [55, 56].

DOMESTICATION CAPABILITIES – HORSES ON THE AMERICAN CONTINENT

In order to further assess human capabilities and opportunities for domestication, in this section we discuss the case of horses on the American continents.

Long before human migrations, American continent was home to two horse species, wild horse *Equus ferus* (Boddaert, 1785) [26] and, somewhat newly discovered genus *Haringtonhippus* (Heintzman et al., 2017) that lived contemporary with the wild horse [57]. Together with most of the megafauna' species, *E. ferus* (Boddaert, 1785) went extinct in America at the end of Pleistocene, around 11 000 years ago, while in Europe it survived until the 19th century. *E. ferus* (Boddaert, 1785) originated in North America around 4 million years ago, 2 million years ago some specimens crossed the Bering Strait and rapidly colonized Eurasia [58], where it was domesticated. Domestic horses proved to be very important for the development of the old world. Some of the great ancient civilizations began and ended on horseback, for instance, the Scythians defeated the Egyptians because of the horses. Horses made intercontinental migrations and trade possible. It is said that during the Mongolian rule in the 13th - 14th century, with the clever use of a horse, messages could be carried up to 300 km in a single day [59], feat which was not repeated until the construction of Trans-Siberian railway in 1904 [60]. Without the horse American Indian tribes were almost isolated from one another. Trade was very hard, routes had to be traveled on foot and burden carried on back or with use of dog sleds.

Reintroduction of horse to American continent occurred during the 16th century with the arrival of conquistadores. First were brought to Cuba by Christopher Columbus on his second voyage to the 'New world'. First sighting of horse riders must have been terrifying, horse riders seemed to blend with their horse, and they wore bells on their armor which aided the confusion [61]. Real spread of horses in America happened after the 1680 Pueblo Revolt in New Mexico. All

of the Spanish conquistadores were pushed out of New Mexico by the revolting tribes. They were forced to escape without their livestock, leaving behind around 1500 horses. Pueblo people (aided by nomad tribes: Utes, Navajo, Apache and Comanche) quickly adopted horses in their culture. With trading, raids and escape, horses were quickly reintroduced to the continent [62]. The Great American Plains proved to be perfect habitat for the horses. Escapees from the Mesoamerican tribes and the invading Europeans quickly spread and became feral. Indian tribes adapted new ways of horse taming, bareback riding and even horseback warfare. In addition to that, horses soon became the measure of wealth and power, the more horses a tribe had the better it was of. In that way Indian cultures of the 17th century soon resembled Asian steppe bronze-age tribes, where the horse was originally domesticated [63].

CONCLUSION

Recent interdisciplinary research enables deeper comprehension of history of both man and fauna surrounding us, elucidating processes and motivation. Archaeogenomics and spatial methods in research are the two most prominent areas contributing insight in times and spaces where historiography is missing. Interdisciplinary overview of times and spaces without historiography is valuable in forming broader comprehension of the human history.

Animal domestication is one of the most important moments in the entire human history, it completely changed our cultures. The need and the possibility of domestication were present in sedentary and nomadic cultures all over the globe, however, not all of them had the same geographical or biological setting, or arose at the same time in the history. This led to differences in the accumulation of material wealth and differences in freely available time during their lifetime for the development of cognitive technologies such as writing, spying, or trade communication with different cultures. Late onset of human history in comparison to Afro-Eurasia and north to south orientation of the American continents in comparison with east to west orientation of Afro-Eurasia were the main characteristics of the global domestication opportunities.

The need for domestication, intention and purpose are demonstrated all over American continents in both sedentary and nomadic cultures on the examples of dog selection and crop domestication. Capability of people to domesticate megafauna is demonstrated in secondary domestication of horses. The two camelid species, llama and alpaca remain the only domesticated megafauna of the Americas. Both overhunting and climate related megafaunal extinction explain the nature of megafaunal domestication in the Americas more than the human factor. The pattern of animal domestication from the north towards the south of Americas showing no animal domesticates in North America (despite the need for large animals of different purpose that was satisfied mostly with dog breeding), followed by the small fauna domesticated in the Meso-America, and finally the two camelid species of the South America leads towards the idea that this event of history was at least partially caused with overhunting during the first human settling of the continents.

The most pronounced differences of the people of the Americas and civilizations of Afro-Eurasia accumulated due to three main animal domestication issues: (i) the lack of horse for domestication on the American continents; (ii) the lack of intentional domestication typical for the Iron Age; (iii) the lack of diversification of the domestic animal purpose in contact with different cultures. The lack of wild horse for domestication, to use as herd control, for warfare and trade, was the first step in making the timing and the biological and geographical setting more pronounced. The lack of intentional domestication typical for the Iron Age and beasts for long trade routes and as ploughing animals was a cultural and civilizational achievement which never occurred in the Americas, as was the lack of diversification of the domestic animal purpose in contact with different cultures.

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