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Milk as a pivotal medium in the domestication of cattle, sheep and goat.

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Abstract

The ability to lactate connects us with all mammals big and small, indeed it was the key characteristic used by Linnaeus to determine the taxonomic class *Mammalia*. The milk of domesticated animals is a rich resource that can be transformed by humans into a myriad of dairy products with long and short shelf-lives. Archaeozoological evidence suggests that perhaps milk was a principal catalyst in the domestication of cattle, sheep and goats starting from 10.5 kyBP. Direct evidence for the processing of milk is found in the first ceramic vessels excavated at early farming communities in Near East and Europe dating from the 9 kyBP indicating that human populations largely intolerant to lactose, the main sugar in milk, were processing milk in ceramic vessels. Innovation in techniques to process milk through cooking and other methods, such as fermentation, to enable milk consumption without adverse side effects, appears to have been a component of the European Neolithic package. For the pioneer farmers of Europe, milk would have offered a renewable food resource as husbandry practices where meat is secondary to milk production ensure the growth of the herd and are more sustainable. The consumption and production of milk has led to significant changes in the genetic structures of humans and dairy species. Here we discuss the role of milk played in the domestication of cattle, sheep and goats, the spread of the Neolithic way of life into Europe, and its lasting effect on food culture and human and animal genetics.

Introduction

Milking and man's relationship with domestic animals

The domestication of animals and the development of food-producing economies facilitated the introduction of new foods into the human diet. Moreover, the introduction of animal milks completely reshaped the human culture, biology and economy. The multi-billion Euro modern dairy economy is the direct consequence of the both human's ability to tame ruminant species and their genetic adaptation to animal's milk, namely lactase persistence (LP), with most people in Europe being tolerant to lactose. Milk links man with animals, and indeed, breastfeeding pets, such as dogs, pigs, bears and monkeys, has been reported in hunter-gatherer societies ranging from Australian aborigines to South American Indians (Milliet, 2007). This form of positive care is believed to ensure the survival of the young animal, for example for economic gain, such as for the valuable sleigh dogs among the Inuit (Gray and Young, 2011). Seasonal observations of dams suckling young would have resonated within hunter-gatherer populations familiarising them with animal milk as a food source (Fischler, 1988). The capture of dams with their offspring would have been easier than a buck and likely aided the domestication process, with young being hand reared by humans, thereby reducing the flight instinct (Hemmer, 1990). Once in settlements, tamed animals could have been exploited for their milk. Archaeozoological evidence shows clearly that domesticated ruminants from the Near East at some of the earliest farming sites were exploited for their milk (Helmer, 1994; Helmer *et al.*, 2007). Those captive animals would have been valued as living animals, rather than as a source of meat. In the archaeological record, direct evidence of positive care have been observed in early managed goats with broken hind limbs at the pre-pottery Neolithic B (PPNB) site of Jarmo (Central Zagros) being treated instead of, as one would expect, slaughtered for their meat (Bendrey, 2014). Studies have shown that a strong relationship of mutual trust develops between the farmer and each dairy animal (Porcher and Schmitt, 2012). This attachment relates both to affection, partly because milking requires a physical proximity between the dairyperson and the animal, and utility. In contrast, cattle raised for meat are often seen as a "tool of production" and considered as part of a larger entity, the herd, rather than individual animals (Bock *et al.*, 2007). This invokes a situation where domesticated animals were chosen for their capacity to produce milk and where the developing

relationship between prehistoric humans and early domesticated animals was cemented by the act of milking.

Milk as a nutritious food

Milk is a rich nutritional food source, made up of water, sugars (mainly lactose), proteins, lipids and minerals. At present, it is a major source of dietary energy, protein and fat as well as containing numerous nutrients providing a significant contribution to the body's daily requirements (McClellan *et al.*, 2008). In 2007, 84.9 kg of milk and dairy products per capita were consumed globally (Gerosa and Skoet, 2013). The composition of milk varies between species and is a reflection of the long-term nutritional needs of the offspring. Lactose is important in the intestinal absorption of calcium, magnesium, phosphate and the utilisation of vitamin D (Wijesinha-Bettoni and Burlingame, 2013). Human milk is high in lactose but low in protein in comparison with the other species (Table 1). This variation in milk composition between humans and ruminants is a reflection of the semi-altricial state that babies are born in compared to cattle, sheep and goats' offspring (McClellan *et al.*, 2008). Calves, lambs and kids are able to stand within hours of their birth and grow quickly so require high-quality protein to support maximal growth. Milk composition also changes over the lactation period to meet the need of the infant and as a result of foddering practices (Wijesinha-Bettoni and Burlingame, 2013). Animal milks, pure or mixed with cereals and pulses, are often used as a weaning food for human infants. Due to nutritional differences in composition between human milk and ruminant milk, such as the lack of iron in ruminant milk, it is recommended that infants should not be given untreated non-human milk before 12 months old, particularly cow's milk (Leung and Sauve, 2003). However, after 12 months, the consumption of milk and dairy products has noticeable positive effects on child health and development (Wijesinha-Bettoni and Burlingame, 2013).

Table 1. Composition of cow, sheep, goat and human milk (after Table 3.3; Wijesinha-Bettoni and Burlingame, 2013).

Species	Water (g/100g)		Fat (g/100g)		Protein (g/100g)		Lactose (g/100g)		Ash/Minerals (g/100g)	
	Average	Range	Average	Range	Average	Range	Average	Range	Average	Range
Cow	87.8	87.3-88.1	3.3	3.1-3.3	3.3	3.2-3.4	4.7	4.5-5.1	0.7	0.7-0.7
Sheep	82.1	80.7-83.0	6.4	5.8-5.7	5.6	5.4-6.0	5.1	4.5-5.4	0.9	0.8-1.0
Goat	87.7	86.4-89.0	3.9	3.3-4.5	3.4	2.9-3.8	4.4	4.2-4.5	0.8	0.8-0.8
Human	87.5	-	4.4	-	1.0	-	6.9	-	0.2	-

Livestock domestication and the role of milk

Animal remains can provide evidence for a species being domesticated, as archaeozoological analyses allow the detection of an animal translocated outside its normal ecological range; morphological changes (e.g. decrease in bone size; changes in teeth shape) and/or changes in slaughtering profiles and/or herd composition (e.g. increase in females) usually implying an anthropogenic impact on the species in question (Vigne, 2011). Evidence for intensive cattle, sheep and goat management appeared around 10.5 kyBP in the middle and upper Euphrates valley and the Zagros mountains within PPNB communities (Helmer *et al.*, 2005a; Peters *et al.*, 2005; Zeder, 2005). By 10.4-10.2 kyBP, these intensive practices appeared in the South Levant (Horwitz *et al.*, 1999) and Cyprus (Vigne *et al.*, 2011). This intensification appeared to have little effect on hunting practices with large game, such as gazelle and ibex, continuing to be exploited and were probably the principle source of meat (Peters *et al.*, 2005). Indeed in many societies worldwide meat is laden with social meaning and is often reserved for formal occasions or special ceremonies. The symbolic value of meat from domesticates compared to wild animals varies across populations, with evidence that in some foraging communities meat makes up a small proportion of overall diet (Marciniak, 2005).

Full scale widespread herding did not establish itself until 9.5 kyBP in Anatolia and the Near East (Vigne, 2011), which begs the question of the role of these animals prior to the establishment of domesticate husbandry. The hypothesis of milk as a catalyst for domestication contrasts with the long-held *Secondary Products Revolution* hypothesis, where dairy husbandry evolved later perhaps during the 4th-3rd millennium BC in Mesopotamia and then spread through either transmission of ideas or by physical

migration of populations into Europe (Sherratt, 1981). The original hypothesis was based on three lines of evidence: (i) humans' natural predisposition of lactose intolerance (human genetics); (ii) adoption of pottery shapes appropriate for the manipulation of liquids from the Bronze Age in Europe (material evidence); (iii) early domesticates' let-down ability and production capacity (ruminant genetics);

Humans and lactose intolerance

The latin word “*lac*” for milk was chosen to name the sugar contained in milk: *lactose*. Indeed, most mammalian milks contain lactose, with the exceptions of the monotremes (platypus and echidnas) and the pinnipedia (seals, walruses and allies; Fuquay *et al.*, 2011). Lactose is the primary source of energy in milk. This disaccharide sugar is broken down into glucose and galactose by the enzyme lactase present in the consumer's small intestine. This enzyme is crucial for the young as it enables them to obtain the nutritious simple sugars from the disaccharide lactose. However, in mammals, including most humans, the enzyme activity is down-regulated after weaning, leading to *lactase non-persistence* or *lactose intolerance*. The consumption of lactose-rich foodstuffs by lactose intolerant individuals can induce abdominal discomfort, flatulence and diarrhoea (Flatz and Rotthauwe, 1977). More than two thirds of the population worldwide do not express the enzyme lactase in adulthood and are thus unable to digest lactose (Itan *et al.*, 2010). The rest of the human population is able to express the enzyme lactase in adulthood, making them *lactase persistent* (LP) or *lactose tolerant*. In Europe, the ability to digest lactose in adulthood is related to a single mutation (-13,910*T) on one gene (LCT). In contrast, five different alleles (-13,907*G, 13,910*T, -13,915*G, -14,009*G and -14,010*C), including the one observed in Europe, are detected in lactase-persistent Africans. Genetic studies have demonstrated that the European LP allele (-13,910*T) only appeared in European populations very recently in the last 2-7 to 12-20 ky. Current frequency of the LP allele in modern populations is extremely high (Gerbault *et al.*, 2013 for a review) and genetic drift alone is unlikely to explain the rapid increase in frequency of this allele in few millennia. A high natural selection must thus be invoked with genetic studies showing that a selection strength between 0.8 and up to 19% is needed to explain the distribution of the -13,910*T allele. Such positive

natural selection is one of the highest ever seen in the human genome in the last 30,000 years, and may even have fluctuated over time and space.

LP is distributed unevenly worldwide (Itan *et al.*, 2010) with populations with a history of dairying having higher frequencies of LP (Simoons, 1970; Holden and Mace, 1997). The human genome has thus been shaped by the introduction of milk and dairy foods into the diet. This genetic adaptation to a dietary shift is described as *gene-culture co-evolution* (Holden and Mace, 1997). The consumption of lactose-rich products must have exerted a high selective advantage since the appearance of the -13,910*T allele in the human genome. Several hypotheses have been formulated to explain the evolution of lactose tolerance (McCracken, 1971; Holden and Mace, 1997), with the *calcium assimilation hypothesis* being often invoked for the European populations. Calcium assimilation in the gut is promoted by vitamin D sourced from the diet or synthesised in the skin from its precursor 7-dehydrocholesterol and UV-B light (Engelsen, 2010). Communities in the high latitudes may have been deficient in vitamin D and therefore milk would have provided a source of calcium and vitamin D, preventing farmers from developing rickets induced by high cereal consumption (Cordain 1999). This is evident when Mesolithic hunter-gatherer communities in high latitudes shifted from aquatic resources (particularly rich in vitamin D) to resources obtained from domesticated plants and animals in the Neolithic (Cramp *et al.*, 2014 for the UK). Individuals living in farming communities with an access to milk would have benefitted from its many advantages, such as its high nutritional value (Simoons, 1970; McCracken, 1971) and non-LP individuals could have avoided the lactose intolerance symptoms by milk processing techniques.

Indeed, although fresh milk from cattle, sheep and goat contains high levels of lactose (up to 5 g per 100 g; Table 1), the manufacture of dairy products can lower the lactose content, making them more digestible by lactose-intolerant individuals. Curdling the milk and straining the whey from the curds separates the lactose-rich whey (lactose is water-soluble) from the lactose-poor curds. Consequently, cheeses such as camembert, roquefort or cheddar contain only traces of lactose, and parmesan <1 g per 100 g (Food Standards Agency, 2002). Cream also has a lower concentration of lactose than milk (2.2 g per 100 g of cream vs. up to 5 g per 100 g of milk; Food Standards Agency, 2002) as it is obtained by letting milk

stand for a few days to allow the fat-rich cream to float on the surface of skimmed milk containing the water-soluble lactose. The manufacture of butter from cream by churning also reduces the lactose content (0.6 g per 100 g) by removing the buttermilk (5.0 g per 100 g; Food Standards Agency, 2002). The manufacture of yoghurt from milk involves the fermentative conversion of lactose into lactic acid by bacteria, thereby reducing the lactose concentration of yoghurt compared to milk. However, yoghurt still contains relatively high concentration of lactose (<5 g per 100 g; Food Standards Agency, 2002).

Milk and dairy products from sheep, goats, cattle and horses form the cornerstone of modern pastoral societies subsistence practices, such as those of the Eurasian steppe. Those populations practice extensive pastoral systems and raise animals primarily for their milk and meat with little or no supplementary agricultural activity. Milk is commonly processed into fermented liquids, i.e. *kumys* or *airag* (fermented mare milk), and dried products, particularly *aaruul* (dried milk curd). Winter and spring can be harsh on the steppe and these products, produced throughout the lactation period, are stored for the demanding coming months, extending the shelf-life of milk (Sadler *et al.*, 2010).

Detecting milk use in Prehistory: organic residues in pottery vessels

Ceramic containers appear in the Near East after c. 9 kyBP, in a region spanning from Central Anatolia and Upper Mesopotamia (Le Mière and Picon, 1998). The introduction of ceramics allowed the newly settled agricultural communities to improve their storage facilities and provide more efficient ways of processing food (Redman, 1978; Moore, 1995). Cooking increases the palatability and digestibility of otherwise toxic and/or inedible foodstuffs (Dunne *et al.*, 2016).

A portion of lipids (= fats) contained in foodstuffs are readily absorbed in the clay pores within the vessel walls and preserved from microbial degradation for thousands of years (Evershed, 2008b). Ceramic sherds excavated at archaeological sites and the lipids preserved therein are, thus, considered to reflect the variety of foodstuffs processed in the pots, recording the subsistence strategies as practiced by early

farmers (Roffet-Salque *et al.*, in press). Lipids trapped in the clay pores of pottery sherds are extracted using organic solvents and characterised using state-of-the-art analytical methods (Evershed *et al.*, 1990; Charters *et al.*, 1993; Dudd and Evershed, 1998; Correa-Ascencio and Evershed, 2014). Compounds are separated using chromatography, identified using mass spectrometry and further characterised using isotope ratio mass spectrometry. These analytical methods allow both culinary and technical uses of organic materials to be investigated (Roffet-Salque *et al.*, in press). Beeswax (e.g. Roffet-Salque *et al.*, 2015), resins and tars (e.g. Regert *et al.*, 2008), plant waxes (e.g. Dunne *et al.*, 2016) and animal fats (e.g. Dudd and Evershed, 1998) have characteristic molecular composition, and thus can be identified based on the detection of “biomarkers”, biomolecular proxies, for the processing a wide range of animal and plant products (Evershed, 2008b). Animal fats are usually too degraded to identify their source using their molecular composition only, and thus compound-specific isotopic analyses are performed on fatty acids to identify whether the fats originate from non-ruminant or ruminant animals, and carcass or milk (Dudd and Evershed, 1998; Copley *et al.*, 2003).

The advent of organic residue analyses of lipids preserved in archaeological pottery vessels and the possibility of identifying dairy fats, have provided new avenues of investigation regarding the use of early pottery vessels and the emergence of dairying in early farming communities. The extensive study of >2,200 pottery sherds from SE Europe, the Near East and the Levant provided direct evidence for early milk use. Archaeological sites around the Sea of Marmara showed intensive dairy practices from 8.5 kyBP, with >70% of the residues detected in the sherds investigated in the study revealing traces of milk residues, with the faunal remains pointing to a dominance of cattle herding (Evershed *et al.*, 2008). Investigations of pottery containers coupled with osteological analyses of domesticates demonstrated that dairying was part of the subsistence economy at early farming sites along the Northern Mediterranean coast (Debono Spiteri *et al.*, 2016). Finally, the onset of the Neolithic in the UK was characterised by a dramatic shift in subsistence practices, with the abandonment of aquatic resources for animal products obtained from domesticated animals, particularly milk (Richards *et al.*, 2003; Cramp *et al.*, 2014). The nutritional quality of milk clearly contributed to the success of the farming communities living in such

marginal extreme environments (Cramp *et al.*, 2014). Milk was also adopted in the Baltic region at the same time as farming practices, although fishing, hunting and gathering activities continued alongside agriculture (Craig *et al.*, 2011). In this region, milk thus complemented existing staple foods rather than replacing them.

The adoption of milk in the Neolithic as seen through the lens of ceramic vessels is widespread across Europe (Fig. 1). The detection of dairy lipids in pots is usually interpreted as evidence for milk processing, as heating up foodstuffs promotes the absorption of lipids in the clay walls of vessels (Evershed, 2008a). However, the detection of milk residues in ceramic containers, such as pots, pans and dishes, rarely allow explicit definition of the exact processing practices, except when typological similarities between modern-day dairy utensils and archaeological vessels provide credence for the use of such ceramic vessels in milk processing. Indeed, Copper Age vessels from Hungary were suggested to be “milk jugs” although lipid residue analyses on eight such vessels failed to prove that they were used for storing, processing or serving milk (Craig *et al.*, 2003). Perforated vessels excavated in Neolithic Central Europe were hypothesised to be cheese-strainers due to their similarity to modern-day and ethnographic cheese-strainers (Bogucki, 1984). These bowl- and funnel-like perforated vessels are found in sites from the Neolithic Linear Pottery culture (LBK) in Central Europe. Bogucki (1984) also noticed that cattle herding strategies at these sites reflect dairy subsistence practices. Recent analyses of 50 sieve fragments from the region of Kuyavia (north-central Poland) showed that milk lipids were present in most of the sieves (Salque *et al.*, 2013), supporting Bogucki’s hypothesis. The idea is that the sieves were used to separate the curds from the whey to make (cow’s-milk) cheese as early as 7.2 kyBP, although the geographical and chronological extent of this practice is still largely unknown. Cheese-making provides digestible dairy products for lactose intolerant early farming communities and extends the shelf-life of milk, allowing the nutritional benefits of milk to be available outside of the milking season (Salque *et al.*, 2013).

Detecting the evolution of dairy husbandry in the faunal record

Understanding the mechanisms behind milk production, different modes of dairy husbandry and the factors that influence the decisions of farmers, are crucial in tracking dairy husbandry amongst early European Neolithic farmers (Gillis, 2017). A longstanding method for identifying dairy husbandry in archaeozoological assemblages is by examining the animal remains (mainly dental remains) and determining the age-at-death for individuals. These data can be used to construct mortality profiles, which are compared with hypothetical models of production (Payne, 1973; Helmer *et al.*, 2005b). The production of milk is dictated by the ability of animals to let-down their milk and this varies between species and breed types. Indeed, the ejection of milk to the teat cisterns is stimulated by the hormone oxytocin, and the production of the hormone by the sensory and tactile stimulus of the young or by artificial means. Milk is stored temporarily in the alveolar units and then actively transferred in the teat cisterns by the ejection reflex induced by oxytocin. The proportion of *cisternal* milk (available without ejection reflex) is higher in caprines than cattle, particularly in goats. Consequently, the need for the offspring to stimulate the production of oxytocin is less important for small stock (review by Balasse, 2003). Ethnographic examples have unsurprisingly shown that lambs and kids can be removed without affecting the flow of milk (Halstead, 1998). The goat's long lactation and high milk production, together with their tolerance to harsh conditions, ideal in marginal environments, make them known as the "poor man's cow" (Haenlein, 2007). The age of slaughter is also related to the demands of market or family consumption, regional traditions, and the replacement needs of the herd (Halstead, 1998; Boyazoglu and Morand-Fehr, 2001). For example, for caprines, the young tender meat (0-3 months) is a delicacy in the modern-day Mediterranean, whereas in Middle Eastern and African societies older heavier lambs are prized (Boyazoglu and Morand-Fehr, 2001). If sheep milk is highly valued then the lamb will be removed early to ensure maximum production for human consumption and not shared with the infant.

In contrast, for cattle, the let-down milk without the infant can inhibit milk production, which is particularly evident in traditional breeds of cattle (Clutton-Brock, 1981). This was one of the lines of evidence used to support Sherratt's Secondary Products Revolution hypothesis (Sherratt, 1981). However, many traditional societies practice milk sharing where the infant animal is allowed to suckle prior to removing the milk for human consumption. These practices, beautifully represented on Saharan

rock art iconography (Le Quellec, 2011; Fig. 2), are applied to all dairy ruminant and non-ruminant species, including horses. Milk sharing between the young and the herder has been proposed as being distinctive for cattle dairy husbandry in archaeological contexts, where such practices would be translated into high proportion of calves being slaughtered at the end of the lactation period (Peske, 1994; Fig. 3a). When milk is the primary objective (“intensive cattle dairy model”), an increased infant slaughter prior to 6 months is expected, particularly of unwanted male calves (Legge, 1981; Fig. 3b). Such a slaughter strategy may inhibit milk let-down (Balasse, 2003), however, there is extensive historical and prehistoric evidence for the stimulation of cattle milk let-down when the calf is absent (Ireland: Lucas, 1989; Sub-Saharan Africa: Le Quellec, 2011). Therefore, it is conceivable that ingenuous tactics, such as blowing into cows’ vagina and replacement of the calf with a dummy, could have been employed by early prehistoric farmers. Cows are also less likely to need to the calf to stimulate milk ejection after the first parturition. Furthermore, allomaternal nursing, where the cow will allow foreign calves to suckle, is more common after the first parturition (Le Neindre, 1989). This ability to adopt calves to free younger lactating females was recognised by Columella (VI: XXIV), where he describes the small Altinian cattle from the land of Cevals (region now Switzerland) as having great quantities of milk and had the disposition to allow foreign calves to suckle.

The evolution of dairying in Europe

Both lipid residue analyses of ceramic containers for demonstrating milk use, and archaeozoological studies for reconstructing herding practices, have been used extensively to detect dairying practices in the past. Study of early archaeozoological assemblages indicate that shared milking and intensive slaughtering was practiced during the Neolithic. This selection of animals for specific roles was probably based on their individual productive capacities and physiologies. The choice of dairy animal appears to be governed in-part by environmental constraints. Studies have shown that cattle prefer water-rich environments (Gander *et al.*, 2003), whereas caprines can survive in areas of aridity like the Mediterranean and the Balkans (Boyazoglu and Morand-Fehr, 2001). Milk exploitation was a component of early Neolithic farming across most regions of Europe (Helmer and Vigne, 2004; Helmer *et al.*, 2007;

Vigne and Helmer, 2007; Evershed *et al.*, 2008; Debono Spiteri *et al.*, 2016; Ethier *et al.*, 2017) with caprines and cattle being the main milk producers along the Mediterranean and in Central Europe, respectively. There is little evidence for dairying in areas of the initial expansion of Neolithic cultures in Greece and South-East Europe, although by the time Neolithic culture have spread to the Cycladic islands caprines appear to be managed for milk (Debono Spiteri *et al.*, 2016). There are differences in the way sheep and goats were managed during the Neolithic, with the latter perhaps being used for dairy with evidence of early slaughter of infants, and the former as a source of fast growing meat in Southern Europe (Helmer and Vigne, 2004; Greenfield and Arnold, 2015). By 7kyBP, there is evidence from stable isotopic analysis of age-specific mandible samples for post-lactation slaughter of cattle in France and Romania (Balasse and Tresset, 2002; Gillis *et al.*, 2013), which may have developed due to increasing herds sizes. Large herds of cattle are observed in Central Europe, with milk being transformed in cheese using sieves in the LBK site of Ludwinowo (Salque *et al.*, 2013). Intensive slaughtering of calves has been proposed at some early Neolithic sites in Spain (Gillis *et al.*, 2016) and Southern Europe (Vigne and Helmer, 2007), which may be a deliberate strategy to increase milk supply but may also be a way to alleviate stocking pressures caused by extreme weather. Mediterranean livestock were introduced beyond their natural climatic range by farming groups dispersing into the interior of the Balkans by 7.6 kyBP. Climate-driven selective pressures led to a better adaptation of the livestock to their new environment (Ethier *et al.*, 2017). Husbandry practices had a role in shaping the breeds that exist today, through natural selection of animals adapted to feed scarcity or ability to reduce metabolism in winter (Ethier *et al.*, 2017) and artificial selection of phenotypes with advantageous traits, such as milk production and ability to let-down milk with little intervention. Genetic changes linked to milk production were actively selected for in the last century. Indeed, dairy management practices and dairy breeding rapidly evolved after the Second World War to maximize dairy species' production capacities (Labussière, 1999; Orland, 2003). Specialised sheep breeds now produce double the milk of traditional breeds, whereas dairy goat breeds can produce five times as much milk as traditional breeds (Haenlein, 2007). The most dramatic change in production

is seen in cattle where specialised breeds, such as Friesian, produce ten times as much as traditional breeds for twice as long¹.

Final comments

The exploitation of milk from domesticates played an important role in feeding entire communities across Europe, with infants and adults benefitting from the introduction of animal milk into their diet. Milk provided a new range of weaning foods and the majority of today's infant formulas are still based on cow's milk. Cow's milk was given to infants in Greco-Roman Egypt, as reported in a wet-nursing contract from the period (Fildes, 1986). Ethnographic studies suggest that weaning liquids and solids are generally introduced earlier in food-producing communities compared to hunter-gatherer societies (Sellen and Smay, 2001), although it seems that early weaning is not entirely a consequence of using animal milk as a weaning food, as a range of weaning foods is also available for hunter-gatherers (Sellen and Smay, 2001). The reduction in breastfeeding duration in farming communities is suggested to be related to the working patterns of women and the constraints of carrying a toddler to distant arable fields (Fouts *et al.*, 2005; Ghosh *et al.*, 2006). The possible early weaning of babies at the start of the Neolithic would have shortened the period of breastfeeding, thereby reducing intervals between births. Indeed, the Neolithic is well-known to have been a period of increased population growth, attributed to an increased fertility rate followed by an increased mortality rate (Bocquet-Appel and Bar Yosef, 2008). Milk must have provided a stable seasonal resource to early farming communities and increased the quality of the overall diet, probably increasing the life expectancy of Neolithic people (Vigne, 2008).

The exploitation of domesticated animals for milk has had an impact on the human genome, with a third of the world's population being able to digest the lactose in milk in adulthood. Nowadays, cattle dominate dairy production particularly in Northern Europe, while sheep and goat play important roles in providing milk and meat for pastoral communities across the Mediterranean basin and the Balkan region. This

¹ www.dad.fao.org

distribution of dairy species in modern-day Europe was initiated in the Neolithic, where caprines and cattle were already exploited in the geographical areas we see today. The advances of analytical methods are now allowing us to study at least some of the mechanisms underlying the emergence of dairying in prehistory, in particular subsistence and herding practices at the household, site and regional levels, which are shedding light on patterns we see today. Over the last 20 years, the increasing integration of multiple strands of evidence has worked towards drawing a picture of the processes at play for the domestication of ungulates, the emergence of LP in Europe and the role of milk in those processes.

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Figure captions

Figure 1: Proportion of animal fat residues identified as milk fats (yellow, $\Delta^{13}\text{C} \leq -3.1\text{‰}$), ruminant and non-ruminant adipose fats (purple, $\Delta^{13}\text{C} > -3.1\text{‰}$) and aquatic fats (blue, aquatic biomarkers detected) in archaeological sherds from the Neolithic in Europe and the Near East. n Numbers represent the number of residues identified as animal fats for each group of sites.

a. Copley *et al.* (2003); b. Craig *et al.* (2011); c. Cramp *et al.* (2014); d. Debono Spiteri *et al.* (2016); e. Evershed *et al.* (2008); f. Gregg *et al.* (2009); g. Matlova *et al.* (2017); h. Salque *et al.* (2013); i. Smyth and Evershed (2016); j. Šoberl *et al.* (2008).

Figure 2: Detail of a milking scene from rock art in a rockshelter at Tasigmet, Oued Djerrat (Tassili-n-Ajjer). Note that the calf is present during milking and probably tied beside its dam. Drawing from Balasse *et al.* (2000)

Figure 3: Hypothetical cattle kill-off profiles showing (a) a post-lactation slaughtering and (b) an increased calf slaughter before 6 months, where milk production could have been maintained using artificial means or sharing of calves between multiple females. Method based on Gerbault *et al.* (2016).

Figure 1

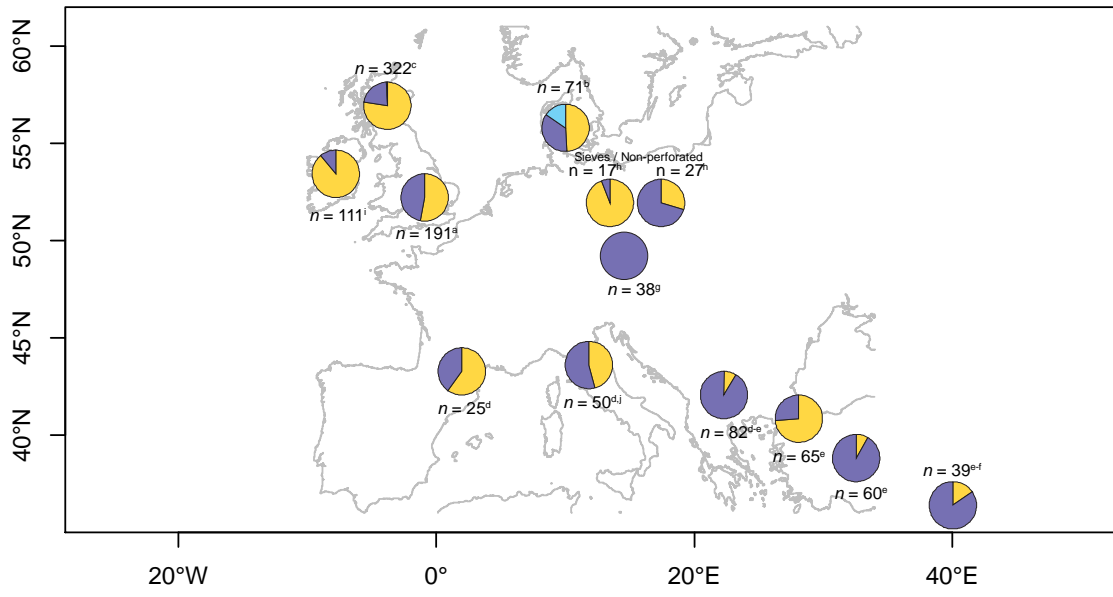


Figure 2

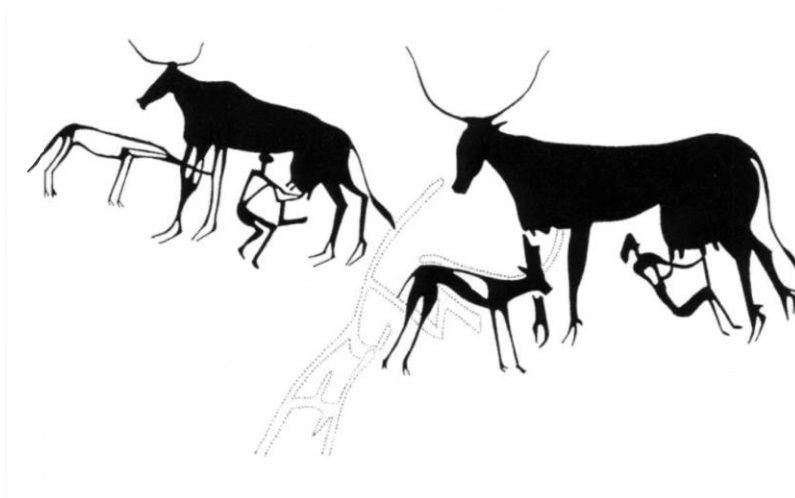


Figure 3

