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Wolf (*Canis lupus* Linnaeus, 1758) domestication: why did it occur so late and at such high latitude? A hypothesis

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ABSTRACT

Wolf (*Canis lupus* Linnaeus, 1758) domestication has been the subject of many studies the last decades. All agree to consider that the dog (*Canis familiaris* Linnaeus, 1758) is the product of wolf domestication, and that this process occurred in Eurasia. Many divergences remain however on the geographic origin(s) of the process, whether domestication was a single event or multiple independent events, the earliest occurrences (roughly between 37 000 and 15 000 cal years ago), and the modalities of this process. A rarely debated question is why wolf domestication occurred so late and at such high latitudes, and not in Africa or Middle East, where humans and wolves have coexisted much longer. We hypothesize that domestication was triggered by one of the five extreme cold events (so-called Heinrich events) which occurred in Eurasia in the range of time between 37 000 and 12 000 cal years, which correspond to the range of wolf domestication. Use of a large-sized wolf/dog was probably an unprecedented way for first societies of Eurasia to survive in such extreme conditions.

KEY WORDS

Wolf,
domestication,
Upper Palaeolithic,
Heinrich events,
aggression,
high latitudes.

RÉSUMÉ

Domestication du loup (Canis lupus Linnaeus, 1758) : pourquoi si tardivement et à des latitudes si élevées ? Une hypothèse.

De nombreux travaux ont été effectués sur l'émergence du chien (*Canis familiaris* Linnaeus, 1758) au cours des dernières décennies. Tous s'accordent à considérer que le chien est une forme domestiquée du loup (*Canis lupus* Linnaeus, 1758) et que ce processus s'est enclenché en Eurasie. Des points de divergence subsistent cependant sur le (ou les) lieux de domestication (Europe vs Asie), sur la répétition du processus au cours du temps, sur les périodes du Pléistocène supérieur au cours desquelles se sont produits ces événements entre 37 000 et 15 000 ans AP, selon les hypothèses en cours, et sur les objectifs et les modalités de la domestication. Nous nous penchons ici sur un autre débat : les raisons pour lesquelles la domestication s'est produite aussi tard dans l'histoire humaine et aux hautes latitudes, alors que la coexistence homme-loup est bien plus ancienne en Afrique centrale et au Moyen Orient. Une hypothèse développée dans ce travail est que la domestication aurait pu être initiée au cours d'un des cinq événements climatiques de froid extrême (dénommés événements de Heinrich), qui se sont produits en Eurasie entre 37 000 et 12 000 ans AP et qui entrent dans la fourchette admise pour la domestication du loup. La domestication d'une grande espèce carnivore telle qu'était le loup pléistocène pouvait avoir de multiples avantages pour la survie des premiers peuples de l'Eurasie confrontés à des situations extrêmes.

MOTS CLÉS
Loup,
domestication,
Paléolithique supérieur,
événements de Heinrich,
agression,
hautes latitudes.

INTRODUCTION

Wolf (*Canis lupus* Linnaeus, 1758) domestication has been the subject of many studies, most of which have focused on geographic origins, the earliest occurrences, and the modalities of the process. Agreement is widespread that the only ancestor of the dog (*Canis familiaris* Linnaeus, 1758) is the wolf (Benecke 1987; Vilà *et al.* 1997, among many) – and more precisely, a large-sized (now extinct) wolf morphotype (Pilot *et al.* 2010; Freedman *et al.* 2014) – and that the origin of the dog is Eurasia. Yet considerable debate continues to surround four main questions: Did domestication occur before the Last Glacial Maximum or later? Did it occur in East or West Eurasia? Was domestication a single event or were there multiple independent events? And what were the modalities of the domestication process with regard to the ecological context of the Upper Palaeolithic and the sociopsychology of modern humans?

WOLF DOMESTICATION: A SUBJECT OF MANY STUDIES THAT MAINLY FOCUSED ON THE ORIGINS AND PROCESSES OF DOMESTICATION

For a few authors, the first dogs appeared 31 700 years ago in Western Europe (Germonpré *et al.* 2009, 2012). For Ovodov *et al.* (2011) and Ding *et al.* (2012), domestication occurred earlier (33 000 years ago) in East Asia. These earlier ages have been challenged by several authors. Boudadi-Maligne & Escarguel (2014), for example, argue that the substantial variability of both modern and Pleistocene wolf populations makes it difficult to accept (or reject, Perri 2016) these dates. There is much less debate about assigning the presence of Upper Paleolithic dogs from at least the Middle Magdalenian to

the end of the Epipaleolithic (i.e. 15 000–11 500 cal BP) (Vigne *et al.* 2005; Holdt *et al.* 2010; Pionnier-Capitan *et al.* 2011; Larson *et al.* 2012; Wang *et al.* 2013; Freedman *et al.* 2014; Skoglund *et al.* 2015).

The question of the geographic origins (East and/or West Eurasia) has also remained unresolved. Some authors argue for Southern Asia (Savolainen *et al.* 2002; Pang *et al.* 2009; Ardan *et al.* 2011; Ding *et al.* 2012; Shannon *et al.* 2015) or the Middle East and Europe (Holdt *et al.* 2010; Thalmann *et al.* 2013). Pang *et al.* (2009) developed the idea that the wolf was domesticated in a single part of Eurasia, while others explain the process by multiple independent events in both Asia and Europe (Clutton-Brock 1995; Vilà *et al.* 1997; Holdt *et al.* 2010; Pionnier-Capitan *et al.* 2011; Skoglund *et al.* 2015). A recent model proposes another “mixed” theory: the wolf was domesticated from distinct populations in both East and West Eurasia, with East Eurasian dogs later (at least 6400 years ago) partially replacing European Palaeolithic dogs through human translocation (Frantz *et al.* 2016).

Other questions persist concerning the modalities of domestication. From a socio-ecological perspective, the process of domestication can be understood as the intensification of the relationship between human and wolf populations through multigenerational goal-oriented behavior (Horard-Herbin *et al.* 2014). Generally, the authors assume that the first dogs were employed for many tasks, depending on the society and the ecological context: as auxiliary hunters of large mammals, barking sentinels against other scavenging carnivores around campsites, and auxiliaries in transporting equipment, supplies and lithics (Serpell 1989; Turner 2002). They may also have had a role in accomplishing rituals (Shipman 2010). The impressive size of wolves was probably a determining factor for most of these uses.

Whatever the uses of these tamed wolves, the first concrete step was to integrate individuals into human society by adopting very young pups just before the beginning of socialization (Galton 1865; Schenkel 1967; Woolpy & Ginsburg 1967; Clutton-Brock 1999; Topál *et al.* 2005). Adoption of young animals by other species is a very rare phenomenon in nature, but here it can be explained by the innate traits of modern humans that facilitate attachment to members of other species (so-called empathy; Shipman 2010; Herzog 2014). The affective links that were woven between wolves and humans may have been helped by oxytocin, a molecule present in both species and known to support social behaviour and cooperation (Nagasawa *et al.* 2015).

WHY OCCURRED SO LATE AND AT SUCH HIGH LATITUDES?

An interesting but still little debated question is why wolf domestication occurred so late and at such high latitudes. The coexistence of *Homo sapiens* and *Canis lupus* had lasted tens of thousands of years in Africa, where an endemic relatively ancient gray wolf lineage (*Canis lupus lupaster* Hemprich & Ehrenberg, 1833) was recently discovered in a large area between Senegal and Ethiopia with a fairly large, past effective population size (Gaubert *et al.* 2012). In the Middle East, which is at the southern limit of *Canis lupus* sensu largo (Boudadi-Maligne 2011), humans have coexisted with the wolf much longer than at upper latitudes, at least for 75 000 years (Bar & Vandermeersch 1991; Shea 2008).

A reasonable assumption is that domestication was a late cultural innovation triggered by the constraints of a prolonged and stressful event. Humans respond in a variety of ways to climate and environmental change: they can move and shift habitat, adapt by experiencing breakdowns in their social-cultures, and adopt innovating approaches. In fact, climate change is often considered a key factor in the cultural and biological events of the Middle and Early Upper Palaeolithic (among many: Keeley 1988; D'Errico & Sánchez-Goni 2003; Mellars 2006; Bradtmöller *et al.* 2012; Banks *et al.* 2013; Discamp 2014; Birks *et al.* 2014). Interestingly, Descola (2005) hypothesized that the domestication of reindeer, which only occurred in Eurasia and not in Alaska, was the result of changes in cosmological belief.

The Greenland ice cores have revealed that the North Atlantic region experienced six abrupt climatic changes during the last glacial period, with extreme coldness and instability and iceberg discharges (e.g. Heinrich stadial) (Broecker 1994; Genty *et al.* 2003). During these cold events, the landscape was sparsely vegetated (steppe-tundra) with episodic development of woody vegetation and was subjected to intense geomorphologic processes (Fletcher *et al.* 2010). Fluctuations in ungulate biomass were noticeable above 50° latitude, with a general drop when the carrying capacity of the ecosystems decreased.

CONCLUSIONS

Five Heinrich events occurred after the arrival of humans in West Europe 37 000, 29 000, 23 000, 16 500 and 12 000 cal years ago (Broecker 1994), within the time period when domestication of large-sized wolves occurred. Perhaps the tamed wolves were useful for herding large herbivore prey when their densities became more fluctuating. Perhaps also wolves helped humans to fight off other predators or aggressive conspecifics, thanks to an innate altruistic behaviour here enlarged to the human families who have adopted them, as hypothesized by Jouventin *et al.* (2016). Use of a large-sized wolf/dog was probably an unprecedented way to survive in a cold, open and dangerous land.

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