Rabbits and the specious origins of domestication

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Abstract

Rabbits are commonly thought to have been domesticated in ~600 AD by French monks. Using historical and archaeological records, and genetic methods, we demonstrate that this is a misconception and the general inability to date domestication stems from both methodological biases and the lack of appreciation of domestication as a continuum.

Main Text

Traditional archaeological approaches for inferring the origins of domestic taxa have recently been complemented by the application of genetic methods, though the two techniques have often produced widely discordant estimates [1]. The lack of consilience between these approaches has frustrated efforts to understand the origins of domestic plants and animals. More generally, the wide variation in reported dates raises questions about what aspects of domestication are being dated.

Most efforts to establish the timing of domestication have focused on the late Pleistocene and early Holocene when the first animals were domesticated [1]. In order to better assess the lack of methodological consilience, we investigated European rabbits (*Oryctolagus cuniculus*). This species is ideal since they were domesticated in

historic times from a geographically restricted source population (on the Iberian Peninsula and southwest France), and are present in archaeological faunal records inside and outside their indigenous distribution. The well-resolved geographic origin and the presence of an extant wild progenitor population also allowed for the application of population genetic methods to model the timing of their domestication.

The Historical Record

The earliest documentary records of rabbits were authored by Romans who encountered the species in the Iberian Peninsula. Varro, writing in the 1st century BC, gave instructions to his wife to keep rabbits alongside hares in her *leporarium* (the Roman precursor to medieval warrens) and to fatten them in hutches before slaughter (*De Re Rustica*, 3.12). Nachstein, however, argued that this did not lead to domestication since the Roman practice of actively hunting rabbits within *leporaria* would select against tameness, and that because rabbits continued to breed underground they escaped direct animal husbandry [2].

A recent study [3] reported that rabbit domestication was initiated by French monks in ~600 AD as the result of an edict by Pope Gregory the Great that allowed Christians to consume newborn or fetal rabbits (*laurices*) during Lent, since they were not considered meat. The idea that rabbits were a popular source of protein during Lent can be traced to Nachtsheim [2] and Zeuner [4] both of whom miscited a late 6th century latin manuscript by St Gregory of Tours [5]. Though laurices were first described by Pliny the Elder in the 1st century AD as a most delicate food (*Naturalis Historia*, 8.55), there is no evidence that they were not considered meat. This fallacy, along with their wrongly assumed popularity during Lent resulted directly from the miscitation (Supplementary Material). Lastly, this popular narrative also mistakenly conflates Pope Gregory the Great and Saint Gregory of Tours, two contemporaneous but unrelated individuals.

The Archaeological Record

Archaeological evidence demonstrates that rabbits were extensively exploited during the Epipaleolithic, Mesolithic, and early Neolithic in the Iberian Peninsula and southwest France [e.g. 6]. Besides a few isolated cases of rabbits appearing on Mediterranean islands ~2,500 years ago [7], rabbits were intentionally transported across Europe only during the Middle Ages when they were considered a high-status food (Figure 1) [8]. Though the expansion is historically well-attested, identifying and dating it archaeologically has been difficult owing to site recovery biases and the intrusion of rabbits into archaeological stratigraphies [8].

In addition, transported rabbits were largely indistinguishable from their wild counterparts. In fact, skeletal changes do not appear until the 18th century [8], almost two thousand years after the earliest historical account of their exploitation in captivity. The first appearance of skeletal morphological changes distinguishing wild from domestic populations instead coincides with the earliest evidence for rabbits as pets [8].

The Genetic Perspective

Genetic approaches to domestication can reveal the time depth of the most recent common ancestor of wild and domestic taxa. The conversion of molecular time estimates into calendar years requires a robust mutation rate, and for rabbits, four separate published rates vary by up to 45% (1.62×10^{-9} – 2.35×10^{-9}). As a result, analyses of rabbit genomic data suggest that wild French and domestic rabbit possibly split between 12,200 years and 17,700 years ago (Figure 2; Supplementary Material), though these estimated mutation rates are derived from imprecise fossil calibrations. When compared to estimates derived from more sophisticated methods, these rates are an order of magnitude faster than human rate estimates and up to 3 times slower than rates in domestic mice (Supplementary Material).

Notwithstanding the uncertainty in the mutation rates and divergence estimates, the calculated rabbit split times are more consistent with population fragmentation associated with the Last Glacial Maximum than with domestication. Because population substructure is common (and is a feature of rabbit evolutionary history [3]), accurately dating domestication requires sampling the wild population most closely related to the population that was domesticated. Dating analyses that make use of modern wild populations that are not descended from those involved in the domestication process results in split times that can significantly predate the origins of domestication (Figure 2).

Domestication as a Process, not an Event

Rabbits are amongst the most recently domesticated animals, yet none of the three methods described above can satisfactorily identify the rabbit's temporal origins. The historical record does not support the narrative built upon it since there was no papal edict, no dispensation to eat *laurices*, and no historical or archaeological evidence that the practice was commonplace. The archaeological evidence records skeletal morphological changes coinciding with modern pet-keeping, and the shifts in distribution sometimes post-date the historical evidence. Lastly, genetic approaches are complicated by both large mutation rate uncertainty and population substructure.

Discrepancies also result from *a priori* definitions of domestication. For instance, rabbit domestication may be concomitant with the earliest record of penning in Roman *leporaria* in the 1st century BC, with *laurice* consumption in the Middle Ages [2], or with the appearance of morphological changes distinguishing wild from domestic in the 18th century [8] (Figure 2). Archaeologists also commonly use the translocation of a species outside its native range as circumstantial evidence for the process of domestication. For rabbits, this is complicated by the fact that there is no evidence that the rabbits dispersed across Europe in the Middle Ages were domestic.

The willingness of scholars across broad disciplinary boundaries to accept the erroneous story of *laurices* in 600 AD reveals how frequently the domestication process is misconstrued as a discrete event. Instead, the combination of the methodological and semantic factors highlighted in this study suggest that a precise domestication date does not exist. The domestication of rabbits, like most other animals, was the result of a continuous, dynamic process that reflects gradual shifts in the nature and intensity of the relationship between humans and other species [9].

To obtain a satisfying rabbit domestication narrative we need to view domestication and its associated biological changes as a process that occurs along a continuum [9,10]. Timing domestication should therefore focus on questions related to the numerous changes in the way humans interacted with domesticates, how those relationships varied in time and space, the relative intentionality of human actions, and the genetic and morphological effects on the taxa in question. For example, rabbits were hunted during the Paleolithic, deliberately transported to Mediterranean islands, consumed as fetuses, housed in Roman *leporaria*, kept in Medieval pillow mounds and warrens, forced to reproduce in hutches, and only recently bred for morphological novelties as pets. No single one of these activities can be classified as the domestication threshold but collectively, they formed the processes by which rabbits became domesticated. Investigating domestication from a perspective that makes systematic use of multiple lines of evidence and emphasises the entirety of the process will result in a far more sophisticated appreciation of the origins of our pets and livestock.

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Figure Legends

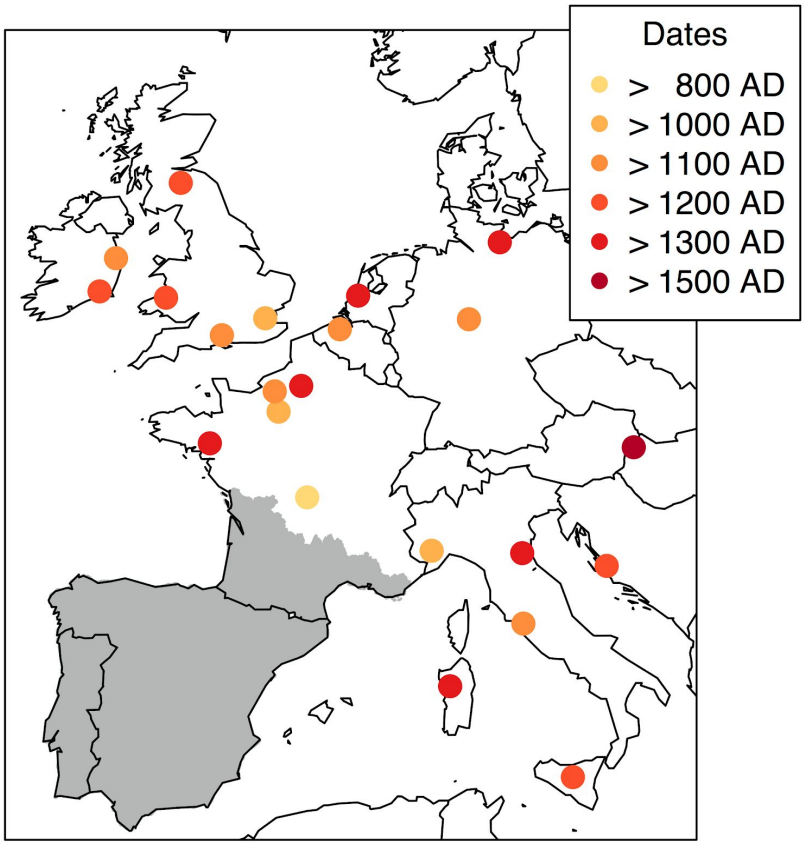

Figure 1. Map of the Medieval dispersal of rabbits across Western Europe. The grey region depicts the approximate natural range of the European rabbit. Coloured dots indicate the earliest historically or archaeologically documented appearance of rabbits in those regions. Figure adapted from [8].

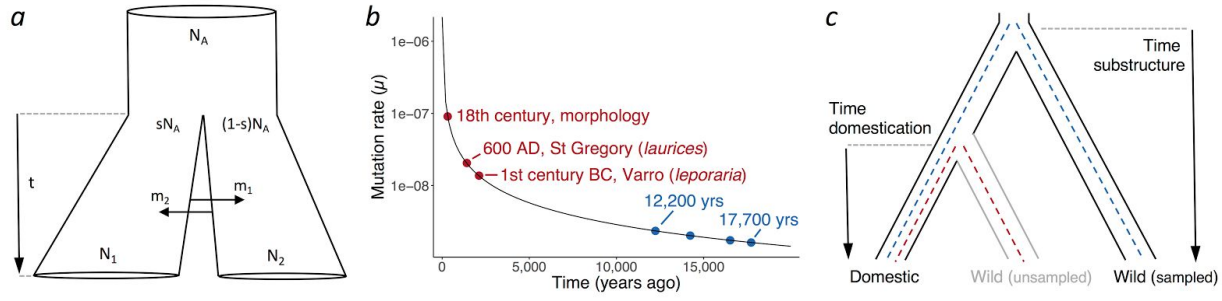

Figure 2. Demographic modelling of rabbit domestication. An illustration of modelling results of the evolutionary history of rabbits based on genomic data from wild

French and domestic rabbits [11], using ∂a∂i [12] with an Isolation–Migration (IM) model (Supplementary Material). Panel (a) depicts a schematic of the IM model where t is the time elapsed since the two populations separated, s is the bottleneck ratio (the proportion of the wild population that underwent domestication), m_1 and m_2 are migration rates (i.e. the amount of gene flow between the two populations) and N_1 and N_2 are effective population sizes. Inferring split times requires a mutation rate (μ) and a generation time in order to convert results into calendar years. In panel (b) blue dots represent inferred calendar year split times using five published estimates for μ. Red dots represent suggested rabbit domestication dates based on different criteria. Even armed with an accurate mutation rate, estimating the time of domestication would require sampling the wild population from which domestic rabbits arose (see panel (c)). The dates obtained by sampling other wild populations are consistent with events (e.g. deglaciation) that induced the substructure in wild rabbits.

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