examples, and the interspecific competition processes raised by Doherty and Driscoll, highlight the crucial role of biotic interactions in species recovery efforts.

Too often, conservation efforts are focused on species' abiotic requirements for persistence, and the complexities of the multiple interacting processes shaping species occurrence and responses to threats are underappreciated. The NRH provides a framework to consider species declines and conservation management in terms of the biotic and abiotic processes influencing the realized niche of declined species. The NRH aims to improve opportunities for drawing on ecological theory for applied conservation research and management. In the face of the emerging extinction crisis, the NRH can facilitate new insights into the causes of species decline, barriers to recovery, and options for innovative management solutions.

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https://doi.org/10.1016/j.tree.2017.12.001

References

1. Scheele, B.C. *et al.* (2017) Niche contractions in declining species: mechanisms and consequences. *Trends Ecol. Evol.* 32, 346–355
2. Doherty, T.S. and Driscoll, D.A. (2017) Competition in the historical niche: a response to Scheele *et al.*. *Trends Ecol. Evol.*
3. Fraser, C.I. *et al.* (2015) Priority effects can lead to underestimation of dispersal and invasion potential. *Biol. Invasions* 17, 1–8
4. Waters, J.M. *et al.* (2013) Founder takes all: density-dependent processes structure biodiversity. *Trends Ecol. Evol.* 28, 78–85
5. Hinton, J.W. *et al.* (2013) Red wolf (*Canis rufus*) recovery: a review with suggestions for future research. *Animals* 3, 722–744
6. Perring, M.P. *et al.* (2015) Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere* 6, 1–25
7. Thomas, J.A. *et al.* (2009) Successful conservation of a threatened *Maculinea* butterfly. *Science* 325, 80–83

Forum

Rabbits and the Specious Origins of Domestication

Evan K. Irving-Pease,[1] Laurent A.F. Frantz,[1,2] Naomi Sykes,[3] Cécile Callou,[4] and Greger Larson[1,*]

Rabbits are commonly thought to have been domesticated in ~AD600 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.

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]. 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 ~AD600 as the result of an edict by Pope Gregory the Great that allowed Christians to consume newborn or foetal 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

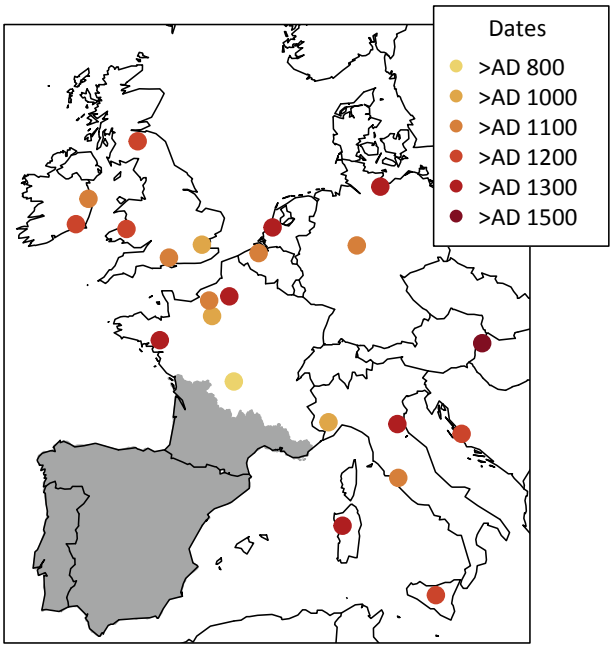

Figure 1. Map of the Medieval Dispersal of Rabbits across Western Europe. The grey region depicts the approximate natural range of the European rabbit. Coloured dots indicate the earliest historically or archaeologically documented appearance of rabbits in those regions. Adapted from [8].

from the miscitation (see Supplemental Information online). 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 ~2500 years ago [7], they 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 2000 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

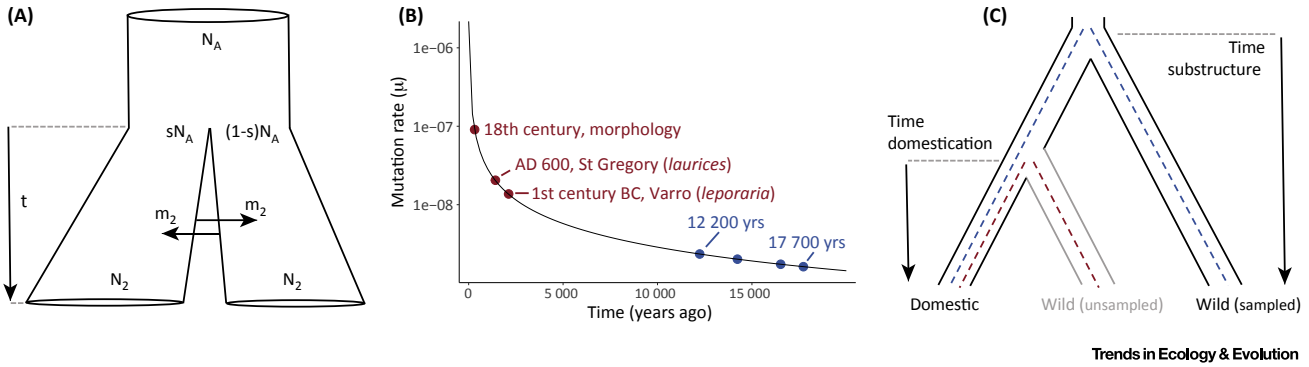

Figure 2. Demographic Modelling of Rabbit Domestication. An illustration of modelling results of the evolutionary history of rabbits based on genomic data from wild French and domestic rabbits [11], using diffusion approximations for demographic inference (∂a∂i) [12] with an isolation–migration (IM) model (see Supplemental Information online). (A) 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 to convert results into calendar years. (B) Time versus mutation rate. 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 when armed with an accurate mutation rate, estimating the time of domestication would require sampling the wild population from which domestic rabbits arose [see (C)]. The dates obtained by sampling other wild populations are consistent with events (e.g., deglaciation) that induced the substructure in wild rabbits.

requires a robust mutation rate, and for rabbits, four separate published rates vary by up to 45% (from 1.62×10^{-9} to 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; see Supplemental Information online), though these estimated mutation rates are derived from imprecise fossil calibrations. When compared with estimates derived from more sophisticated methods, these rates are an order of magnitude faster than human rate estimates and up to three times slower than rates in domestic mice (see Supplemental Information online).

By applying these mutation rates at face value, the divergence estimates are more consistent with the Last Glacial Maximum than with domestication (Figure 2). This could be the case since population substructure is a feature of rabbit evolutionary history [3], and it is possible that by making use of wild populations not descended from those involved in the domestication process, the resulting split times can significantly predate the origins of domestication (Figure 2). Regardless, the wide range of intraspecific variation in mutation rates generally (see Supplemental Information online) and the lack of clear population divergences during the domestication process suggest that molecular dating approaches to domestication should be treated with caution.

Domestication as a Process, Not an Event

Rabbits are amongst the most recently domesticated animals, yet none of the three aforementioned methods 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 large mutation rate uncertainty, population substructure, and the lack of clear separation between populations during domestication.

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 ~AD600 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 suggests that a precise domestication date does not exist. The domestication of rabbits, like 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 foetuses, 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.

Acknowledgements

L.A.F.F. and G.L. were supported by a European Research Council grant (ERC-2013-StG-337574-UNDEAD) and Natural Environmental Research Council grants (NE/K005243/1 and NE/K003259/1). L.A.F.F. was supported by a Junior Research Fellowship (Wolfson College, University of Oxford). E.K.I-P. was supported by a Clarendon Fund Scholarship, University of Oxford.

Supplemental Information

Supplemental information associated with this article can be found, in the online version, at https://doi.org/10.1016/j.tree.2017.12.009.

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https://doi.org/10.1016/j.tree.2017.12.009

References

1. Ho, S. and Larson, G. (2006) Molecular clocks: when times are a-changin'. *Trends Genet.* 22, 79–83
2. Nachtsheim, H. (1936) *Vom Wildtier zum Haustier,* Alfred Metzner (in German)
3. Carneiro, M. *et al.* (2011) The genetic structure of domestic rabbits. *Mol. Biol. Evol.* 28, 1801–1816
4. Zeuner, F.E. (1963) The small rodents. In *A History of Domesticated Animals*, pp. 409–416, Harper & Row
5. Gregory-Bishop of Tours (1969) *History of the Franks,* W.W Norton & Company
6. Sana, I. *et al.* (2013) Domestication of animals in the Iberian Peninsula. In *The Origins and Spread of Domestic Animals in Southwest Asia and Europe* (Colledge, S., ed.), Left Coast Press, pp. 195
7. Quintana, J. *et al.* (2016) Primera datació d'un mamífer no autòcton (*Oryctolagus cuniculus* [Linnaeus, 1758]) (Mammalia: Lagomorpha) del jaciment holocènic del Pas d'en Revull (barranc d'Algendar, Ferreries). *Rev. de Menorca. Tom* 95, 185–200 (in French)
8. Callou, C. (2003) *De la Garenne au Clapier: Étude Archéozoologique du Lapin en Europe Occidentale,* Publications scientifiques du Muséum Paris (in French)
9. Vigne, J.-D. (2011) The origins of animal domestication and husbandry: a major change in the history of humanity and the biosphere. *C. R. Biol.* 334, 171–181
10. Zeder, M.A. (2012) The domestication of animals. *J. Anthropol. Res.* 68, 161–190
11. Carneiro, M. *et al.* (2014) Rabbit genome analysis reveals a polygenic basis for phenotypic change during domestication. *Science* 345, 1074–1079
12. Gutenkunst, R.N. *et al.* (2009) Inferring the joint demographic history of multiple populations from multidimensional SNP frequency data. *PLoS Genet.* 5, e1000695