

Modern Taurine Cattle Descended from Small Number of Near-Eastern Founders

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Abstract

Archaeozoological and genetic data indicate that taurine cattle were first domesticated from local wild ox (aurochs) in the Near East some 10,500 years ago. However, while modern mitochondrial DNA (mtDNA) variation indicates early Holocene founding event(s), a lack of ancient DNA data from the region of origin, variation in mutation rate estimates, and limited application of appropriate inference methodologies have resulted in uncertainty on the number of animals first domesticated. A large number would be expected if cattle domestication was a technologically straightforward and unexacting region-wide phenomenon, while a smaller number would be consistent with a more complex and challenging process. We report mtDNA sequences from 15 Neolithic to Iron Age Iranian domestic cattle and, in conjunction with modern data, use serial coalescent simulation and approximate Bayesian computation to estimate that around 80 female aurochs were initially domesticated. Such a low number is consistent with archaeological data indicating that initial domestication took place in a restricted area and suggests the process was constrained by the difficulty of sustained managing and breeding of the wild progenitors of domestic cattle.

Key words: domestication, *Bos taurus*, coalescent simulation, ancient DNA, approximate Bayesian computation.

The earliest signs of wild aurochs domestication are seen at Dja'de in the Middle Euphrates Valley, dating to the Early Pre-Pottery Neolithic (EPPNB; 10,800–10,300 cal. BP, Helmer et al. 2005) and at Çayönü in the High Tigris Valley, between the Early and Middle PPNB (around 10,200 cal. BP, Hongo et al. 2009). After an initial breeding phase lasting some 1.5 millennia in an area between the Levant, central Anatolia and western Iran, domestic cattle started to appear in western Anatolia and southeastern Europe by 8,800 cal. BP, southern Italy by 8,500 cal. BP, and Central Europe by 8,000 cal. BP. Archaeozoological (Helmer and Vigne 2007; Vigne 2008) residual lipid (Craig et al. 2005; Evershed et al. 2008) and lactase persistence data (Itan et al. 2009) point to an increasing economic importance of cattle for meat and milk production.

Archaeozoological data provide substantial information on time, region, and duration of initial domestication, but reliable estimates of the number of wild progenitors that contributed to modern populations remain elusive. It is widely accepted that Eurasian taurine cattle have a single origin in the Near East and ancient and modern mitochondrial DNA (mtDNA) data reveal a limited number of lineages (Bollongino et al. 2006) and—with the possible exception of some Italian cattle (Mona et al. 2010)—indicate

little or no interbreeding with wild European aurochs. However, a lack of consensus on bovine mtDNA mutation rates and an absence of sequence data from early domesticates in the region where they were first identified, due to poor sample preservation (Edwards et al. 2004; Bollongino and Vigne 2008), as well as stochasticity in the genealogical process, mean that the number of founding individuals cannot be inferred directly from the number of surviving lineages in modern cattle populations that date to the domestication period. We report reliable mtDNA hypervariable region sequences (np. 15914–8) from 15 domestic cattle from several sites in Iran dating from between 8,000 and 1,900 BP (see [supplementary table S1, Supplementary Material](#) online). These sites are near the archaeological sites containing the earliest evidence of domestication (Hongo et al. 2009). These data, and an additional 26 modern cattle sequences from Anatolia and Iraq, were used to estimate the number of female aurochs that were initially involved in the domestication process (for sample details and accession numbers, see [supplementary tables S1 and S2, Supplementary Material](#) online). The modern data were restricted to the region of domestication in order to minimize any possible bias due to subsequent introgression from other aurochs populations outside the Near East and to allow

us to avoid modeling the bottleneck and range expansion processes associated with the movement of taurine cattle into Europe.

Coalescent simulations were performed assuming an intergeneration time of 6 years (published generation times vary between 5 and 7 years, MacEachern et al. 2009; Gautier et al. 2007) and an ancestral Near Eastern wild aurochs female effective population size (NA_{ef}) of 45,000 (MacEachern et al. 2009). A single domestication event of unknown size (ND_{ef}) was assumed, followed by exponential growth to a modern Near Eastern female domestic cattle effective population size (NM_{ef}) of 1,007,170 (for details, see [supplementary materials, Supplementary Material](#) online). We simulated with values of ND_{ef} drawn initially from a uniform prior of range 1–5,000, and later from a prior of range 1–1,000, and mutation rates (μ) drawn from a uniform prior of range 30–80 per million years, reflecting the range of previous estimates; 30.1% (Bradley et al. 1996) and 77.2% (Edwards et al. 2007) per million years.

To estimate values for these unknown parameters (ND_{ef} and μ), Near Eastern cattle sequences were grouped into two samples—“ancient” and “modern”—and approximate Bayesian computation (ABC) performed by conditioning simulations on 5 within and 4 between sample summary statistics (total = 14; for details, see [supplementary materials, Supplementary Material](#) online). For the ancient DNA sample, we took sequences from the serial coalescent simulations according to the medians of the calibrated radiocarbon ages, as described in [supplementary table 1 \(Supplementary Material](#) online). [Figure 1a](#) shows the joint posterior probability density for ND_{ef} and μ . The marginal mode for ND_{ef} was 80 (95% credible interval: 23–452) and for μ was 45% per million years (95% credible interval: 34–76), while the mode of the joint posterior distribution was found at $ND_{ef} = 84$, $\mu = 49\%$ ([fig. 1a](#)).

We recognize that our estimates may be biased by our assumed modern effective population size. To examine the sensitivity of our inferences to this assumption, we repeated our coalescent simulation and ABC analysis using values of NM_{ef} one order of magnitude higher (10,071,700) and one order of magnitude lower (100,717). The results of these analyses did not differ greatly from those presented above; for $NM_{ef} = 10,071,700$, the marginal mode for ND_{ef} was 66 (95% credible interval: 16–401) and for μ was 43% per million years (95% credible interval: 33–73), and for $NM_{ef} = 100,717$, the marginal mode for ND_{ef} was 128 (95% credible interval: 44–628) and for μ was 53% per million years (95% credible interval: 38–78). Plots showing the joint posterior distributions for both assumed NM_{ef} values are presented in [supplementary figures S1a and b \(Supplementary Material](#) online).

The domestication of wild cattle, with its associated changes in morphology and behavior, is likely to have been a protracted process. In this analysis, we have assumed a single domestication event for taurine cattle—which may have lasted for millennia—because 1) it is the simplest model, 2) it is consistent with linkage disequilibrium-based

estimates of predomestication ancestral effective population size being similar across a range of modern taurine breeds (Bovine HapMap Consortium 2009), and 3) there is no archaeological evidence of multiple independent domestication events in the Near East (Vigne 2008; Hongo et al. 2009). Nonetheless, it is possible that we have used a misspecified model—which would lead to misleading parameter estimates. To examine this possibility, we used Fisher’s method to combine two-tailed probabilities of the 14 observed conditioning statistics—obtained by comparison to simulations—across the same range of ND_{ef} and μ combinations as above (Voight et al. 2005). We then compared the resultant χ^2 values to those obtained by comparing each simulation against the set of all other simulations for each combination of ND_{ef} and μ (Voight et al. 2005). The resultant joint probability distribution ([fig. 1b](#)) is remarkably similar to joint parameter probability surface obtained by ABC ([fig. 1a](#)), with the maximum P value = 0.165 (for $ND_{ef} = 120$ and $\mu = 54\%$ per million years). We interpret this high P value as evidence that the model is a sufficient explanation for the combined summary statistics of the data.

We have modeled a single domestication event, but even if the first captive cattle were taken independently from a randomly mating wild population and interbred then the estimate we present should still represent the number of Near Eastern aurochs that contributed to the domestic stock. If the first captive populations were isolated from one another (e.g., in the case of multiple domestication events) then such structuring would preserve genetic variation and render the numbers presented here as overestimates. In any case, the low number of 80 (95% credible interval: 23–452) founding cattle points to a restricted number of initial captures. Considering the time span needed for domestication (it took up to 2,000 years from management of wild herds to the first unequivocal morphological signs of domestication; Zeder 2009; Conolly et al. 2011), an $ND_{ef} = 80$ is less than two females per generation and thus extremely low. The management and subsequent domestication of these few wild cattle over some centuries could have been carried out by a small-sized human group, like in a couple of small Neolithic villages (Bandy 2008).

Importantly, the two sites showing the earliest signs of wild aurochs domestication—Dja’de (Helmer et al. 2005) and Çayönü (Hongo et al. 2009)—are less than 250 km apart. The closeness of these sites permits local exchange of wild/early domestic cattle management skills, and possibly the cattle themselves, and adds support to the hypothesis of a restricted origin of taurine cattle in the Levant. Interestingly, archaeological signs of sedentism during the ninth millennium BC are restricted to the same region (Cauvin 1994). It is conceivable that the management of wild cattle was too challenging for the mobile population of the surrounding mountainous areas where goat was the preferred domestic species. Another possible explanation for the low number of domesticated females is that the management of large, aggressive, and territorial wild

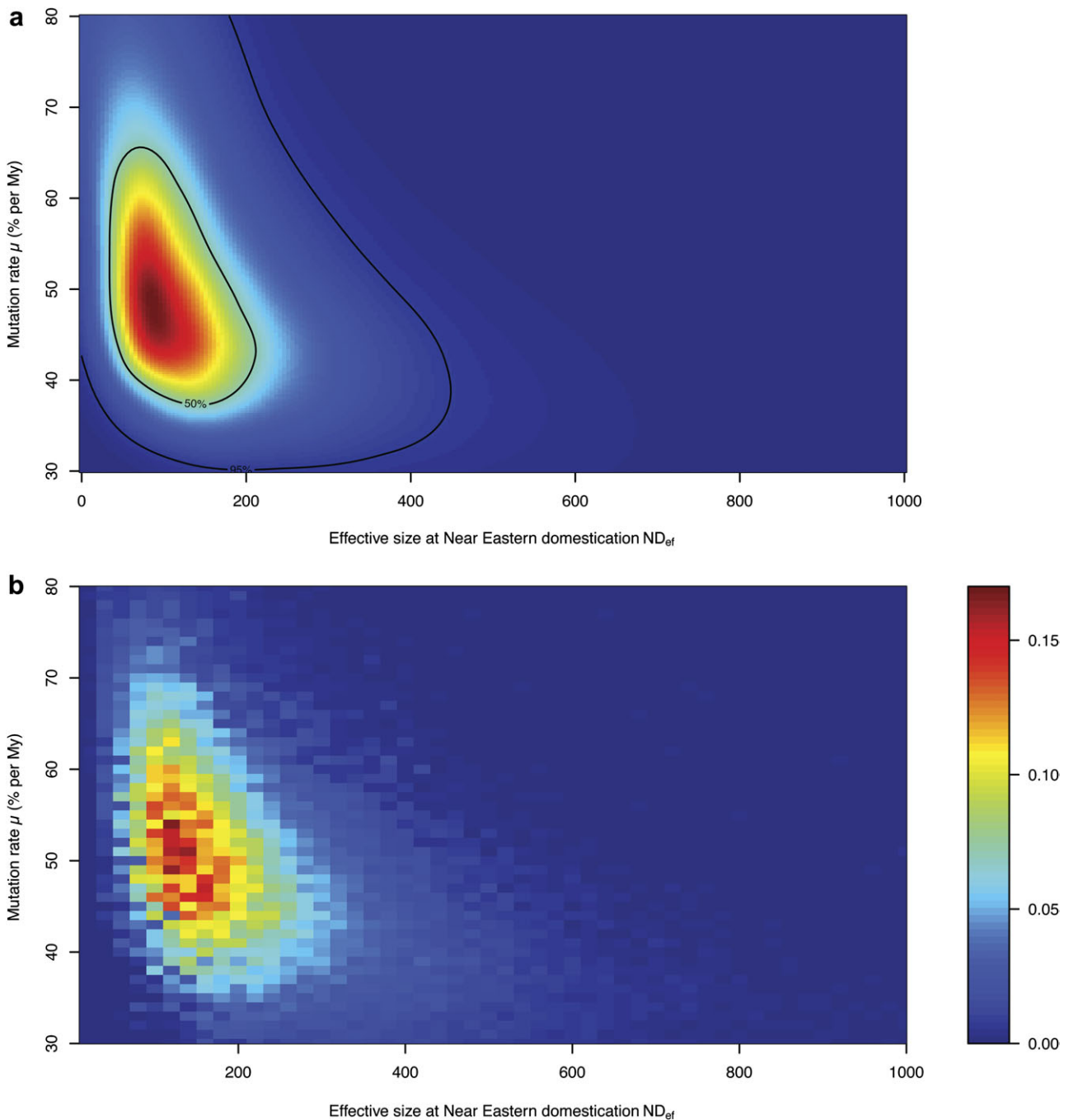


Fig. 1. Top panel: The approximate joint posterior probability density of the mutation rate per million years (μ) and the effective female population size at the time of the domestication event (ND_{ef}), given the data. The 50% and 95% credible intervals are overlaid as contours. Bottom panel: The confidence region for combinations of parameters μ and ND_{ef} on a 51×51 grid of values. P values are for the combined observed statistic C_{obs} and are calculated for each parameter combination by comparison with the empirical distribution C_{sims} produced from 10,000 coalescent simulations (for detail, see [supplementary materials, Supplementary Material online](#)).

aurochs was too complex to be disseminated more widely before breeding for docile characteristics. But evidence for a transportation of cattle by boat to Cyprus (Vigne et al. 2003, 2011) and their use to carry loads at an early stage of domestication (Helmer and Gourichon 2008) do not endorse this view. Alternatively, other attempts to domesticate cattle might simply not have been successful in the longer term. Either way, the low number of progenitors in-

dicates that successful cattle domestication was a limited phenomenon in the Near East.

Supplementary Material

Supplementary materials, figure S1, and tables S1 and S2 are available at *Molecular Biology and Evolution* online (<http://www.mbe.oxfordjournals.org/>).

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