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Perspective: ILLUMINATING THE MYSTERIES OF WOLF HISTORY

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One of the most enduring surprises about the genetic history of Late Pleistocene populations is that continuity is often disturbed by upheaval. In fact, studies that support population continuity are increasingly rare in humans, a variety of vertebrate taxa, and vascular plants (Hofreiter & Stewart, 2009; Burbrink et al., 2016). Perhaps such continuity should not be expected as the Pleistocene is marked by episodes of climate change, glaciation and the invasions of humans into previously isolated areas. Although fossils are one of the primary sources for inferring population continuity, a problem with fossil material is that although similar morphological forms might exist in a place over time, they may not be from the

same genetic lineage. There are now readily available methods to assess genetic continuity solely from DNA found in fossil material, provided the record is fairly continuous. In a From the Cover article in this issue of Molecular Ecology, Loog et al. (2020) apply some of these readily available methods to analyze mitochondrial genomes and model the demography of wolves over the last 50,000 years.

A prime example of the uncertainty generated by morphologic data is apparent in the fossil record of wolves. There is evidence for distinct changes in body size and morphology of wolves over the Late Pleistocene, however, these changes may be driven in part by differences in prey size and composition; more robust prey may generate more robust wolves through skeletal developmental processes alone. Nonetheless, on the whole, the record of Holarctic wolves seems to argue for continuity. Gray wolves have a fossil record dating to as much as one million years ago in Eurasia, and several thousand years ago in North America (Wang and Tedford, 2008, p52; Kurten, 1976, pg. 109). An early genetic study questioned this continuity by showing that High Arctic North American wolves defined a separate, now extinct clade of control region haplotypes (Leonard et al., 2007), as well as having differences in morphology and isotope values that suggested a prey base of megafauna species. This megafauna wolf lineage went extinct sometime before the Holocene, and presumably left no descendants. This mystery of turnover deepened with genome-based evidence of a population bottleneck in wolves just prior to their divergence from the dog lineage (see Figure 3 in Freedman et al., 2014, 2016). However, because this first comparison of genomic variation between dogs and wolves (Freedman et al., 2014) used previously bottlenecked, modern wolves for comparison, aspects such as effective population size and the date of dog domestication were underestimated. A demographically corrected history suggested a decreased to 10% of their effective size rather than half (Freedman et al., 2014).

In general, demographic inferences based on genomic data from extant populations are often open to question because they depend on simplifying assumptions about population history, structure and composition (reviewed in Schraiber & Akey 2015). The only direct test of inferences based on modern samples is by use of ancient DNA from past populations; these ancient DNA sequences can be used to assess the temporal pattern of population continuity and admixture between geographically structured populations that may be common in species' histories. The first such comprehensive study of wolves and dogs found that mitochondrial genomes of ancient wolves assort to five discrete clades within the larger phylogeny of wolf mitogenomes. However, most modern dog haplotypes derive ancestry from only one of these clades (Thalmann et al., 2013). This finding was consistent with a domestication bottleneck event that greatly reduced mtDNA diversity, but the study used only 10 ancient wolf genomes with limited geographic coverage. In this issue, Loog et al., undertake a more comprehensive mtDNA genome sequencing of 45 ancient wolves spanning the last 50,000 years and 95 modern wolves, worldwide. By testing 16 different spatially and temporally explicit demographic scenarios, the authors find support for an expansion from the geographic region spanning Beringia, Northeast of Siberia. This suggests that the Beringia region was the likely source population from which other populations in North America and Eurasia were derived (Fig. 1). Loog et al. find that gray wolves suffered a species-wide bottleneck, approximately 25,000 years ago, and expanded from the Northeast of Siberia to repopulate their former range. Modern wolves therefore represent a large scale replacement of Late Pleistocene wolf populations outside of Beringia. This recent common ancestry has important implications. First, it suggests the genetic structure of dogs, such as the large divergence between European and East Asian populations (Frantz et al., 2016), might in part derive from post-LGM admixture with substructured wolf populations. As demonstrated previously (Freedman et al., 2014), modern dogs appear to show signals of ancestry from ancient wolf populations, some of which may now be extinct. Secondly, the refugial population was likely in Beringia, Northeast of Siberia, highlighting a demographic event of unknown cause that greatly reduced wolf numbers prior to the most recent glaciation. Although the authors do not speculate on the cause of this event, it may conceivably be related to the entrance of the first modern humans into Northern Eurasia. Humans may have directly eliminated or excluded wolves or reduced their prey base (see discussion in Larson & Fuller, 2014). Thirdly, the inferred recent common ancestry of North American wolf-like canids suggests that they colonized North America tens rather than hundreds of thousands of years ago. If other related North America canids, such as the modern coyote and red wolf, were derived from this recent invasion, then their origin is very recent, a conclusion generally consistent with genomic data (vonHoldt et al. 2016, Sinding et al., 2018). The ancient wolves of the Holarctic that existed prior to the bottleneck are poorly characterized genetically (Skoglund et al., 2015), but one or more of these ancient populations were more directly ancestral to dogs, and conceivably more prone to domestication by the first humans who invaded Eurasia.

Although the ancient DNA history of wolves is still very incomplete, a more satisfying picture of the evolution of wolves and dogs is emerging. Modern wolves likely resulted from a recent population expansion from a population Northeast of Siberia that replaced other ancient wolf populations worldwide. This source population was probably not the one from which dogs were derived, but interacted with dogs through admixture, obtaining coat color genes related to immunity (Anderson et al., 2009; Schweizer et al., 2018) and providing genes to dogs allowing adaptation to high-altitude environments (vonHoldt et al. 2017; Miao et al. 2016). Nonetheless, identifying the exact location of the bottleneck requires additional sampling, especially in North America. Moreover, as with any mtDNA study, inferences need to be better explored with nuclear genomic data. Nuclear genomes exist for a few ancient wolves and dogs (e.g. Skoglund et al., 2015; Botigué et al., 2017; Frantz et al., 2016), but the financial support for genome sequencing ancient samples for population level characterization and composition is still beyond the resources of even the best funded non-human oriented labs. However, the future is very promising, for example, for species such as horses and cattle, we are approaching large scale characterization of ancient genomes from which the complexity of ancestry across the Late Pleistocene may be resolved and demographic models based on recent samples better tested (MacHugh et al. 2017; McHugo et al., 2019). Ancient DNA population levels studies such as Loog et al. shine a light on history that genomic models based on recent genomes alone do not well illuminate.

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Figure

Figure 1. Revised wolf demography as inferred from Bayesian analysis of mitochondrial genome sequences suggests that Siberia was the likely source population from which other populations in North America and Eurasia were derived. Map shows the scenario for an out-of-Beringia expansion of six derivative wolf populations, with dates for population replacement for each deme shown in the boxes (median and 95% confidence intervals). Redrawn from Figure 5a of Loog et al., this issue.