

NEWS AND COMMENTARY

Conservation genetics

What ancient DNA tells us

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New analyses of ancient mitochondrial DNA (mtDNA) provide fuel for provocative ideas about the development of population structure within species. Hofreiter *et al.*'s (2004) new study supports the idea that current population structure in many species is due to recent (<10 000 years before present, 10 kbp) events and not long-term population structure. The authors extracted ancient mtDNA from cave bones of four European species to examine their past population structure: cave bears, cave hyenas, and Neanderthals – all now extinct – as well as the brown bear, *Ursus arctos*, which is still present in Europe today. The overall results from these four species led the authors to conclude that 10 000 years ago many European mammals lacked the population structure seen today.

Existing literature on contemporary and ancient samples in North American brown bears provides the context for these new findings. Waits *et al.* in 1998 examined mtDNA from 317 contemporary brown bears and found extensive genetic variation, primarily between different geographic areas. As a result, they suggested that the three phylogeographic groups they identified, clade II (from the ABC Islands), clade IV (south-

ern Canada and most of the USA), and clade III (Alaska and the rest of Canada) (Figure 1a), might represent three different evolutionary significant units (ESUs) and should be conserved and managed separately until nuclear DNA (nDNA) data were collected to evaluate male-mediated gene flow.

Subsequently, Leonard *et al.* (2000) examined seven brown bear samples preserved in the permafrost from eastern Alaska and northwestern Canada. Surprisingly, mtDNA sequences from all of the putative contemporary ESUs were found in permafrost samples dated 34–43 kbp and taken from a relatively small area (Figure 1b). Based on these results, Leonard *et al.* hypothesized that the founding bear population in that area included a mixture of haplotypes of the current clades and that current structure was likely due to lineage sorting and founder events. More recent studies of permafrost brown bear samples of different ages from a variety of locations in North America have also documented different patterns of population structure from those that have been observed in contemporary samples (Barnes *et al.*, 2002; Matheus *et al.*, 2004). It is obvious from these studies that it is not only

difficult to extrapolate past population structure from contemporary samples but ancient samples from different time periods might also have different structure. In addition, it seems apparent that to understand past structure, it is essential to have both samples throughout the time period and to ensure that sample size is adequate to evaluate population structure at different time periods, as would be required in contemporary samples.

In light of what we have learned from the North American brown bear example, how should conservation geneticists interpret the conclusion by Hofreiter *et al.* (2004) that there was a lack of phylogeographic structure in many European mammals 10 kbp ago? Does it provide any new and useful information for current management? Let us first examine the contemporary European brown bear data, which have two forms of clade I – the Western and Eastern clades – which are phylogeographically separated (Figure 2). Hofreiter *et al.* (2004) examined two ancient individual brown bear samples: the one from Ramesch, dated at 47 kbp, was from the Eastern clade, and the one from Winden (200 km east of Ramesch), dated at 40 kbp, was from the Western clade. Although this is not the site of the present day boundary between the Western and Eastern clades, the dynamic situation observed in ancient North American brown bears suggests that great caution should be exercised in interpreting population structure from these two ancient samples.

The largest ancient data set Hofreiter *et al.* (2004) examined is of 83 extinct cave bears (*Ursus spelaeus*), dating from

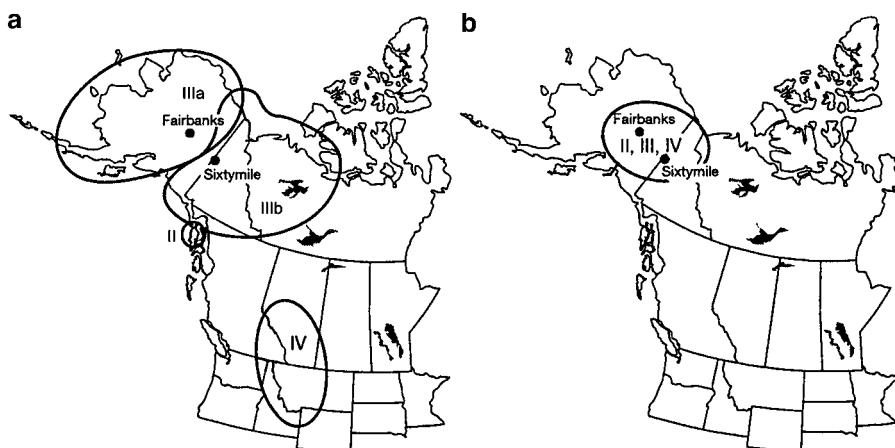


Figure 1 (a) The current (Waits *et al.*, 1998) and (b) past (36–43 kbp) geographic distributions of mtDNA clades II, III, and IV in the North American brown bear (Leonard *et al.*, 2000; Barnes *et al.*, 2002).

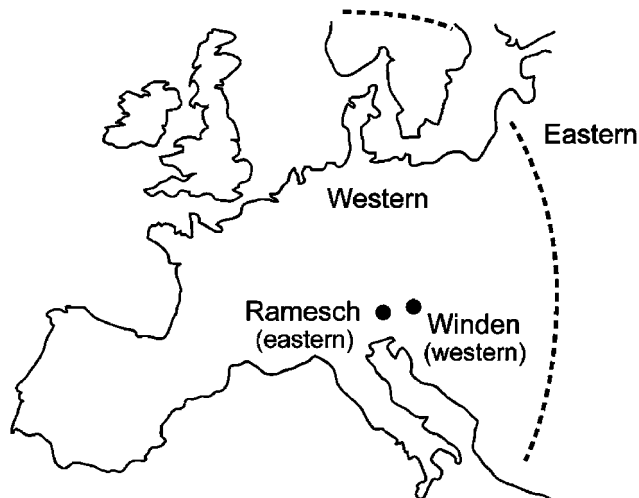


Figure 2 The current European distribution of the Eastern and Western clades of clade I of European brown bears and the location of the two ancient samples at Ramesch and Winden (Hofreiter *et al.*, 2004).

22 to 72 kbp. The 26 haplotypes represented in this sample fall into two major clades, the geographic distribution of which was largely overlapping. Hofreiter *et al.* (2004) also examined 18 ancient samples of extinct cave hyenas (*Crocuta crocuta spelaea*), dating from 37 to >50 kbp, and the four different haplotypes found divided evenly into two clades. One clade was found in the center of the range while the other was distributed throughout the total range. The authors also examined four published samples of Neanderthals dating from 29 to 42 kbp. In addition to the small sample size, there was little genetic variation among the samples, no clades could be identified, and inference about phylogeography was not possible.

An obvious lesson from both the North American brown bear data and the samples of the four European species is that extrapolating past population structure from contemporary data will be difficult in many circumstances. More recent events, such as glaciation and formation of refuges might result in lineage sorting and generate genetic differences. Such patterns are more likely to arise for mtDNA than for nDNA variation because of lower female than male rates of gene flow in many species. For example, nDNA microsatellite analyses have demonstrated male-mediated gene flow in brown bears across the mtDNA clade boundaries in North America (Paetkau *et al.*, 1998) and Europe (Waits *et al.*, 2000). Population genetic theory indicates that many different scenarios for past population structures can explain patterns of contemporary genetic varia-

tion. For example, bottlenecks might quickly generate genetic distance between groups (Hedrick, 1999), a factor of substantial significance in endangered species. Again, bottlenecks are expected to have a much greater effect on mtDNA than autosomal genes, primarily because of the general four-fold difference in effective population size between them.

Inferences of population structure drawn from mtDNA or nDNA, regardless of when it was formed, do at least give an indication of the potential for adaptive differences between groups. However, population structure for neutral molecular markers and adaptive variation might not be consistent under a number of different situations. For example, studies of the response to human-mediated environmental factors indicate that adaptive change can occur very quickly, particularly when populations are isolated from each other. On the other hand, even when molecular markers indicate there is extensive gene flow, adaptive differences can still show geographic patterns associated with environmental variation (Karju *et al.*, 1996).

Finally, these recent studies of ancient DNA have led to some controversial statements being made about their implications for conservation genetics. For example, Pääbo (2000) stated that a 'thorough reappraisal of the role of genetic studies for conservation is needed to clarify when they can contribute to management decisions', and Hofreiter *et al.* (2004) commented that 'conservation geneticists are often torn between the wish to prevent inbreeding depression and the desire to preserve

populations that have been historically separated as distinct gene pools (often referred to as 'evolutionary significant units')'.

Conservation genetics is a young and evolving field that draws from basic theory in population genetics, phylogenetics, and evolution to make applied recommendations for conservation and management of endangered populations and species. It is continuing to incorporate current information and approaches from basic science as it develops (Hedrick, 2001). Inbreeding depression is an important immediate concern for many endangered species, either with a history of small population size or few founders (Hedrick and Kalinowski, 2000). In the longer term, consideration of the amount of potentially adaptive genetic variation within and among taxa is significant. Identifying groups potentially containing important adaptive variants or independent evolutionary history was the basis of developing the concept of ESUs (Moritz, 2002). Recently, genetic rescue of species that have lost genetic variation over time or accumulated detrimental variants has become of greater concern in isolated, small populations. However, as with many topics in evolutionary genetics, the success of genetic rescue depends on many factors and should be undertaken with caution and be methodically evaluated (Talmon *et al.*, 2004). There is not necessarily a conflict between these different goals despite there often being multiple, not fully complementary, objectives in conservation genetics. Informed genetic and evolutionary perspectives are potentially important contributors to both the understanding of the past evolutionary history of endangered species and their future conservation.

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