

Of bears, conservation genetics, and the value of time travel

Svante Pääbo*

Max Planck Institute for Evolutionary Anthropology, Inselstrasse 22, D-04103 Leipzig, Germany

Population genetics is a historical discipline in the sense that it analyzes the distribution of genetic variants in populations to make inferences about evolutionary processes and events in the past. But it is time trapped, because population geneticists, unlike for example paleontologists or archaeologists, are limited to the analysis of contemporary materials and cannot go back in time to study directly the genetics of previous populations. The enthusiasm for the study of DNA in ancient remains stems partly from the hope that one would be able to overcome this time trap and add a temporal aspect to the study of population genetics (1). Although progress in this direction has been made over the past 10 years, it has often been frustratingly slow. The reason is that very few remains contain retrievable old DNA, and that contamination by modern DNA poses a great problem. As a result, molecular time travel has been achieved only in cases where a single or few representatives of extinct animal species can give insights about their relations with extant species, such as the relationship of the marsupial wolf with extant marsupials (2), moas with extant flightless birds (3), or ground sloths with present-day sloths (4). In contrast, diachronical population studies have been limited to the last 100 years from which voucher specimens exist in zoological museums (e.g., ref. 5). Now, Leonard *et al.* (6) present a study where population genetics is taken further back in time—to brown bears preserved since the last glaciation in the permafrost of Alaska and Northern Canada. Their results provide insights about the history of bears and are provocative in their implications for conservation genetics.

Frozen Bears. Although not much is understood about factors that influence the degradation of DNA in the fossil record, it is abundantly clear that low temperature makes for good preservation. Thus, studying permafrost remains is clearly a wise decision if one wants to retrieve ancient DNA. For example, whereas only a few Egyptian mummy samples of hundreds studied yield believable DNA sequences, permafrost remains have much higher

success rates in spite of being up to 10 times older. In Leonard *et al.*'s study, seven of the nine bones tested yielded DNA sequences.

Bears represent another good choice for study because, excepting humans, the mitochondrial DNA sequences of few other mammalian species have been as extensively studied as those of bears (7–9). The maternally inherited mitochondrial DNA is the logical focus of this study not only because of the available sequence information, but also because its high copy number per cell makes it less difficult to retrieve from ancient remains. Furthermore, mitochondrial DNA studies have largely been responsible for the advent of a field called phylogeography (10), the study of how DNA sequences are related to each other and to geography. The phylogeography of brown bears is particularly interesting.

In phylogenetic trees, bear mitochondrial DNA types fall largely into four clades of related sequences, designated I through IV. Although clade I exists only in western Europe, clades II and IV exist in Europe, Asia, and North America. Within the Americas, where brown bears are believed to have existed only since some 50,000 years ago, clades II through IV are present but in a phylogeographic pattern such that clade II is present only on islands off the coast of Northwestern Canada, clade IV occurs in Southern Canada and the contiguous United States, and the subclade IIIb exists in Northern Canada and Eastern Alaska, whereas subclade IIIa is found in Eurasia and Western Alaska (Fig. 2A in ref. 6). One interpretation of several possible (9) for this pattern is that the distribution of these mitochondrial clades represents different “waves of immigration” by brown bears to North America. Leonard *et al.*'s rendering of the data is that clade II would represent a first wave and clades IV and clade III, a second and a third wave, respectively. Furthermore, these clades have been suggested to be “evolutionary significant units” for conservation purposes (9), on the argument that the mitochondrial divergences between the clades represent a substantial time of separation of popula-

tions, qualifying them for treatment as entities worthy of separate management and conservation.

Leonard *et al.* (6) succeeded in retrieving DNA from four bones from the Fairbanks area that date to the end of the last glaciation (about 15,000 years ago). All of these samples carry mitochondrial clade III, the same variant found in contemporary bears of the area. However, among another three bones that are 34,000 to 43,000 years old, one from Fairbanks belongs to clade III, whereas the two others that come from the Yukon Territory belong to clades II and IV, although only clade III exists in the bears in the Fairbanks and Yukon areas today. Thus, before the last glacial maximum around 18,000 years ago, what was presumably a single population (Fairbanks and the Yukon Territory) contained three mitochondrial DNA clades that are now restricted to separate geographic areas. Although the number of samples analyzed is limited, this finding illustrates the value of going back in time to examine the basis of current phylogeographic patterns and can serve to illustrate some problems with drawing conclusions for conservation from genetic studies.

Diachronical Population Genetics. In an area such as the Americas, where many species have arrived from Eurasia, it is tempting to associate mitochondrial clades with colonization events. However, what is often overlooked is that although Beringia, the Ice Age land mass connecting North America and Siberia, is generally envisaged as a “landbridge,” it existed for many thousands of years and was in no respect a “one-way bridge.” Thus, there is no reason to assume that colonization took place in a few defined “waves.” Rather, animals as well as humans lived in Beringia and migrated both back and forth continuously between what is today Asia and North America (11). In light of this, it is not very surprising that some 40,000

See companion article on page 1651.

*To whom reprint requests should be addressed. E-mail: paabo@eva.mpg.de.

years ago, all the bear mitochondrial clades that today exist in different parts of North America coexisted in Beringia. However, it means that later events must be responsible for the phylogeographic patterns seen today. As the authors indicate (6), one explanation is genetic drift resulting in lineage sorting, i.e., the chance survival of only single mitochondrial types in small bear populations during the last glacial maximum when many species were restricted to small ice-free refugia. This explanation has been invoked previously not only for the phylogeographic patterns seen for clades I and III in European bears (12), but also for a whole host of other species in North America (10). The beauty of the bear situation is that ancient bear remains have been found in some of the likely refugia, so that in the future this explanation can be tested.

Conservation Genetics. Leonard *et al.* further say that the coexistence of clades II, III, and IV about 36,000 years ago raises doubts about the claim that these clades represent “evolutionary significant units” that should be managed separately (9). This may indeed be the case, but to my mind this finding can also be taken to question the value of genetic studies for management questions in general.

It seems that there exist two general lines of argument in conservation genetics that are largely incompatible. First, it is often claimed that genetic variation in a population is a good thing in itself and that one should therefore attempt to conserve it whenever possible. Second, it is argued that “evolutionary significant units” and “management units” defined by monophyly of mitochondrial sequences and differences in allele frequencies between populations, respectively (13), should not be allowed to interbreed either in captivity or as a result of wildlife management measures (e.g., ref. 9). Obviously, the latter idea of regarding “genetic purity” of

“subspecies” or “stocks” as a value in itself is contrary to the first idea that genetic variation should in itself be a good thing for the survival of a population. A case in point is that of the three supposed “subspecies” of chimpanzees that have been promoted as separate entities on the basis of geographic location and mitochondrial sequences, although they cannot be distinguished morphologically and behaviorally, and their nuclear sequences fail to fall into monophyletic groups (14). Another case in point are Sumatran and Bornean orang-utans that, after their mitochondrial sequences and minisatellite allele frequencies were found to be substantially different, were proposed to be two species (15, 16), although they produce fertile offspring. As a result, “hybrids” are now not allowed to reproduce in captivity and long-time relationships between captive animals have been broken up. The wisdom of this policy is called into question not only by the fact that Sumatra and Borneo were connected by land until 10,000–20,000 years ago but also by the recent finding that nuclear sequences from the two groups of orang-utans do not form monophyletic clades (Kaessmann and Wiebe, personal communication). However, Leonard *et al.*'s claim that the finding of cooccurrence of mitochondrial types now separated geographically in North America some 36,000 years ago would be an argument for not managing contemporary bears carrying these mitochondrial types as separate entities strikes me as equally arbitrary as the contrary claim. Who is to say if 36,000 years of separation is enough to qualify as a management unit? This question cannot be answered by any genetic arguments. In fact, from a genetic point of view, I see no reason to keep populations that can have fertile offspring separate because interbreeding will, in most cases, only increase the chances that alleles survive in the population. Indeed, a thorough reappraisal of

the role of genetic studies for conservation is needed to clarify when they can contribute to management decisions. Initial efforts in that direction are under way (e.g., ref. 17).

Prospects. Although the study of phylogeographic patterns in both extant and extinct populations often has little to say about management decisions, it is of great value to understand the history of populations, for example how climatic and other environmental changes during the last glaciation have affected them. Such knowledge may be relevant in view of the great environmental changes that our planet has experienced and is likely to experience in the near future. For this pursuit, the permafrost represents a great source. First, not only bears but also a very large number of other vertebrate species have been preserved there, often in very large numbers, and much of this material is already stored in museums. Second, preservation conditions are so good that not only mitochondrial DNA but also single-copy nuclear genes can be retrieved at least in some cases (18). In other places where large numbers of individuals can be studied, such as coprolite deposits or packrat middens (19), preservation conditions are less excellent, such that technical advances, for example the repair of damage in the DNA (20), may be needed before these deposits become amenable for molecular analyses on a large scale. It should be stressed, however, that even in the case of permafrost remains, the technical difficulties involved in the retrieval and verification of DNA sequences are substantial and require a large amount of dedication in terms of resources and skills. Leonard *et al.* have demonstrated that these difficulties can be overcome on a scale that makes studies of populations feasible.

I am grateful to P. Morin, L. Vigilant, and R. Ward for constructive discussions.

- Pääbo, S., Higuchi, R. G. & Wilson, A. C. (1989) *J. Biol. Chem.* **264**, 9709–9712.
- Thomas, R. H., Schaffner, W., Wilson, A. C. & Pääbo, S. (1989) *Nature (London)* **340**, 465–467.
- Cooper, A., Mourer-Chauviré, C., Chambers, G. K., von Haeseler, A., Wilson, A. C. & Pääbo, S. (1992) *Proc. Natl. Acad. Sci. USA* **89**, 8741–8744.
- Höss, M., Dilling, A., Currant, A. & Pääbo, S. (1996) *Proc. Natl. Acad. Sci. USA* **93**, 181–185.
- Thomas, W. K., Pääbo, S., Villablanca, F. X. & Wilson, A. C. (1990) *J. Mol. Evol.* **31**, 101–112.
- Leonard, J. A., Wayne, R. K. & Cooper, A. (2000) *Proc. Natl. Acad. Sci. USA* **97**, 1651–1654.
- Taberlet, P. & Bouvet, J. (1994) *Proc. R. Soc. London Ser. B* **255**, 195–200.
- Talbot, S. L. & Shields, G. F. (1996) *Mol. Phylogenet. Evol.* **5**, 477–494.
- Waits, L. P., Talbot, S. L., Ward, R. H. & Shields, G. F. (1998) *Cons. Biol.* **12**, 408–417.
- Awise, J. C. (2000) *Phylogeography* (Harvard Univ. Press, Cambridge, MA).
- Guthrie, R. D. (1990) *Frozen Fauna of the Mammoth Steppe* (Chicago Univ. Press, Chicago, IL).
- Taberlet, P., Fumagalli, L., Wust-Saucy, A.-G. & Cosson, J.-F. (1998) *Mol. Ecol.* **7**, 453–464.
- Moritz, C. (1994) *Trends Ecol. Evol.* **9**, 373–375.
- Kaessmann, H., Wiebe, V. & Pääbo, S. (1999) *Science* **286**, 1159–1162.
- Xu, X. & Arnason, U. (1996) *J. Mol. Evol.* **43**, 431–437.
- Zhi, L., Karesh, W. B., Janczewski, D. N., Frazier-Taylor, H., Sajuthi, D., Gombek, F., Andau, M., Martenson, J. S. & O'Brien, S. J. (1996) *Curr. Biol.* **6**, 1326–1336.
- Paetkau, D. (1999) *Cons. Biol.* **13**, 1507–1509.
- Greenwood, A. D., Capelli, C., Possnert, G. & Pääbo, S. (1999) *Mol. Biol. Evol.* **16**, 1466–1473.
- Hadly, E. A., Kohn, M. H., Leonard, J. A. & Wayne, R. K. (1998) *Proc. Natl. Acad. Sci. USA* **95**, 6893–6896.
- Poinar, H. N., Hofreiter, M., Spaulding, W. G., Martin, P. S., Stankiewicz, A., Bland, H., Evershed, R. P., Possnert, G. & Pääbo, S. (1998) *Science* **281**, 402–406.