

NEWS AND VIEWS

PERSPECTIVE

Molecules and beyond: assessing the distinctness of the Great Lakes wolf

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The dog family, Canidae, is a widely distributed group of species that have evolved and radiated relatively recently into 16 genera and 36 recognized species (Nowak 1999). Specific taxonomic designations for some canid taxa can be unclear due to frequent interspecific hybridization among species in both historical and contemporary times, and our imperfect molecular genetic approaches for determining among a series of hypotheses regarding hybridization and evolution. In this issue of *Molecular Ecology*, Koblmüller *et al.* tackle the difficult topic of Great Lakes wolf taxonomy and present data that suggest this taxon is currently genetically distinct despite a long history of human persecution and hybridization with related taxa.

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There are multiple hypotheses regarding the evolutionary history and contemporary composition of the canid complex found around the Great Lakes region of North America. Solutions to these issues are paramount in assessing the legal status and thus protection of these canids. The first unresolved question is whether grey wolves and coyotes are the only canid species in the region, with the eastern/Great Lakes wolf a subspecies of the grey wolf (Nowak 2002), or whether the eastern wolf is its own species. For those who agree the eastern wolf exists as a distinct species, the debate once focused on whether this species arose as a hybrid between coyotes and grey wolves (Lehman *et al.* 1991) or whether the coyote and eastern wolf recently diverged to form sister taxa (Wilson *et al.* 2000). The next element

of this debate presumes the eastern wolf was indeed a distinct entity historically, regardless of its evolutionary origin, and focuses instead on whether the composition of wolves that recolonized the Great Lakes area after heavy human persecution has the same genetic composition as that of a prerecovery populations.

Historical understandings are complicated by the fact that species distributions ebb and flow over time due to natural and anthropogenic causes, leading to changes in distributions of pure species, historical hybrids, and contemporary hybrids. Furthermore, our contemporary genetic snapshot requires us to analytically delineate whether haplotypes found in multiple taxa are products of incomplete lineage sorting, historical or contemporary hybridization. Sorting the evolutionary history of these canids that existed pre-European arrival and comparing it to the existing canids around the Great Lakes is no simple task.

Taxonomic status

In this study, Koblmüller *et al.* examine maternally, paternally and bi-parentally inherited molecular markers to test whether the Great Lakes wolves are either a unique population or an ecotype of the grey wolf. The authors examine 18 historical Great Lakes wolves from Ontario, Quebec, Minnesota, Wisconsin, Michigan and New York and show that the mitochondrial haplotypes of these historical samples all group with a coyote-clade. However, the contemporary Great Lakes wolves group with both a coyote-clade and a grey wolf-clade (although more Great Lakes wolves share haplotypes with grey wolves than with coyotes). Y-chromosome data show historical samples all grouping with a wolf-clade, and like the mitochondrial DNA (mtDNA), the contemporary samples group with both the coyote and grey wolf-clade. In addition to the mtDNA and Y-chromosome data, the authors analysed microsatellite data which show support for two groups, a grey wolf-Great Lakes wolf group, and a coyote group. If the authors use the next supported clustering result, three groups are supported; these separate the Great Lakes wolf from the grey wolf and the coyote. These results are similar to a factorial correspondence analysis where the first axis separates wolves from coyotes, and the second separates Great Lakes wolves from grey wolves, and eastern coyotes from western coyotes. Most importantly, the microsatellite data show that despite the overall separation between western grey wolves, Great Lakes wolves and coyotes, there are some Great Lakes wolf individuals with apparent mixed ancestry. Some Great Lakes wolf individuals with high proportions of eastern coyote autosomal DNA had wolf-like mtDNA and Y-chromosomal haplotypes; while other Great Lakes wolf individuals with grey wolf autosomal DNA had

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Fig. 1 A photograph of Great Lakes wolves. (Photo by John A. Vucetich)

coyote-clade mtDNA and Y-chromosomal haplotypes. This suggests relatively recent incidents of hybridization drive these results, as opposed to incomplete lineage sorting or only historical hybridization.

Unfortunately, this paper will not be the end to the eastern canid controversy. One problem that these authors and others have noted is the fact that insufficient sampling may be a problem (Mech 2008; Schwartz & McKelvey 2009; Wheeldon & White 2008; Koblmüller *et al.* 2009). Until a study has the following elements in its design, we will likely continue to see a stream of papers open to challenges:

- 1 Contemporary geographical sampling that matches the distribution of all wild species of concern (in this case: coyotes, eastern wolves/Great Lakes, and grey wolves). The gap in grey wolf samples may have accentuated the separation on the grouping analyses between the Great Lakes wolves and the grey wolf.
- 2 Historical (predisturbance) samples from as wide a distribution as possible (in this case, pre-European, or pre-coyote arrival).
- 3 An adequate variety of molecular markers with different inheritance patterns. Ideally, but not necessarily, some of these markers would be of known function and thus potentially under selection.
- 4 Good reference samples from the edges of the distribution of each species.
- 5 Samples from wolf breeders or pet registries to assess human-induced movement: between 1989 and 1998, the Wisconsin Department of Natural Resources documented 21 cases of free-roaming wolf/dog hybrids (WDNR 1999). These animals may represent an introgression source to the wild populations.

This study meets many of the criteria suggested above, although perhaps lacks the well-distributed contemporary samples of coyotes, grey wolves, and Great Lakes wolves which could influence results — as they admit. Resolving this sampling issue will require large-scale collaborations among previously competing teams of researchers.

Setting aside sampling issues, Koblmüller *et al.*'s results indicate that 'the Great Lakes wolves are genetically distinct despite the recent demographic bottleneck caused by persecution and habitat depletion in the early 1900s, and high degrees of ancient and recent introgression of coyote mtDNA and Y-chromosome haplotypes'. Thus, Koblmüller *et al.* believe that the Great Lakes wolves have maintained their genetic integrity and they therefore represent a 'discrete wolf taxon'. Combining these results with a recent paper by two of the paper's co-authors (Leonard & Wayne 2008) produces the understanding that the Great Lakes wolf has remained discrete, but because of the recent admixture, it has not been restored.

Broader implications

By all accounts, the return of wolves to the Great Lakes region has been successful (Fig 1). In less than 35 years, their abundance has increased fivefold and their geographic range has more than doubled. Although controversies persist about whether they exist in enough places to be considered recovered, no one disputes that where wolves exist in the Great Lakes, they are doing superbly — both in terms of population viability and ecological function. Even when it comes to how genetics might affect population demography, no one takes issue with Great Lakes wolves. However, Koblmüller *et al.* conclude that hybridization between the Great Lakes wolves and coyotes appears to be ongoing, and still has the ability to challenge the integrity of the Great Lakes wolves.

Therefore, should we celebrate the wolf population's viability and their contributions to ecosystem health or be alarmed about their genetic integrity? It is not clear that the integrity Koblmüller *et al.* discuss is at all a threat to viability or ecosystem health. Then, why be concerned about 'genetic integrity' or other aspects of population genetics that do not affect population viability (in a conventional demographic sense) or ecosystem health?

More specifically, should we conserve evolutionary processes which include, on occasion, fuzzy taxon boundaries? Or, should we seek to preserve evolutionary states (e.g. the wolf that used to be here 250 years ago)? Even this alternative raises profoundly difficult questions like, 'what if such preservation is impossible?' and 'how different would two populations have to be before we would agree that the first (historical) population is *too* different from the second (contemporary) population?'. Ultimately, at what point is integrity lost or genetic restoration complete?

These critical questions remain unanswered as they are not questions that science can fundamentally address. Their answers require an understanding not only on matters of science, but also how to evaluate normative (value) judgements. While scientific propositions are assessed by scientific methods, normative propositions of this kind are assessed by principles of ethics (Vucetich *et al.* 2006). Ultimately, Koblmüller *et al.* and Leonard and Wayne (2008) are valuable for highlighting the importance of properly identifying and handling the normative aspects of conservation genetics.

The broader community of conservation scholars is beginning to have a deepening appreciation for the profound importance and difficulty of handling the normative aspects of conservation. Rigorous arguments have been developed about what ecosystem health and population viability are, and why we ought to

conserve them. We have been told we should conserve biodiversity at all levels. And environmental ethicists have developed rigorous arguments for why we should respect, for their own sake, individuals, populations, and ecosystems. But, what justification is needed for being concerned over genetic integrity, except when it serves population or ecosystem health? Should concern for genetic integrity arise because it is valuable in its own right?

The integrity of conservation genetics depends on rigorous treatment of questions like these. Doing so will be difficult and will require collaboration between science and environmental philosophy; the first step of this process is the collection of valuable scientific data such as those collected by Koblmüller *et al.*

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