

Wishful thinking: imagining that the current Great Lakes wolf is the same entity that existed historically

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Invited reply

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Mech (2009) asserts that our results (Leonard & Wayne 2008) are not representative of the Great Lakes wolf that was restored. His conclusion is based on the assertions that: (i) wolves 'segregate' genetically, (ii) current and historic samples were not from the same localities, and, finally, (iii) the numerical delisting conditions were met and hence followed all the legal criteria. We address each of these issues below.

- (i) *Wolves 'segregate' genetically.* Wolves only show weak patterns of differentiation over small geographical distances (Lehman *et al.* 1991; Roy *et al.* 1994, 1996). Specifically, Geffen *et al.* (2004) find a strong association between genetic divergence and ecological differences between habitats on a continental scale. The close ties between the Minnesota, Wisconsin and Michigan populations are explicitly acknowledged under the delisting plan, which allowed for a lower numerical limit because these populations were closely connected (Fish & Wildlife Service 2003). Without evidence for isolation or distinct habitat differences, asserting that these populations are genetically distinct on this limited geographical scale calls into question the numerical limits of delisting and its legal basis and is not supported by the evidence in Geffen *et al.* (2004).
- (ii) *Representativeness of our historic sample.* Regrettably, we could not find historical wolves from Minnesota to include in our study. However, with regard to our samples from Wisconsin and Michigan, we feel they are representative of northeastern Minnesota and the Great Lakes recovery area. It is thought that the founders of the Wisconsin and Michigan populations derive from northeastern Minnesota, and this was the basis for defining the recovery area to include all three states (Fish & Wildlife Service 2003). It is likely that these areas were similarly connected in the historic population. Finally, the focus on Minnesota in Mech's (2009) letter seems somewhat misplaced; the delisting concerns all three states, hence the analysis of specimens in the entire Great Lakes region is relevant to delisting.

Two unfortunate oversights by Mech (2009) are pertinent to the representativeness of our historic sample. The first concerns the distribution of the modern haplotypes in our sample. As we state in the first line of the Methods section, we choose 68 recent wolves to *represent the diversity* of coyote-like and wolf-like mtDNA haplotypes from Lehman *et al.* (1991). This previous study sampled 160 wolves from the Great Lakes area, including 88 from north and northeastern Minnesota and 51 from southern Ontario. Both areas are likely sources for the founders of the Wisconsin and Michigan populations (Lehman *et al.* 1991; Fish & Wildlife Service 2003). The population sampled in northeastern Minnesota by Lehman *et al.* clearly represents a substantial portion of the recovery area in that state. As discussed in Lehman *et al.* (1991), all haplotypes found in recent Minnesota wolves were also found to the east in Ontario. In other words, haplotypes unique to northeastern Minnesota were not found, which does not support Mech's (2009) assertion that the population is genetically distinct. Unfortunately, the mtDNA haplotypes in Lehman *et al.* (1991) were based on restriction fragment polymorphisms that are not directly comparable with the sequences generated from the historic samples. For this reason, we sequenced a representative subset of the haplotypes found throughout Minnesota and Ontario for comparison.

Secondly, Mech's (2009) critique ignores a central finding of our paper. Mech states correctly that 31 per cent of the recent population has historic haplotypes. However, all haplotypes are not equal and the dominant haplotypes missing in the recent sample belong to a divergent group of sequences (GL1, GL3, GL5, GL6 and GL8) that probably derive from a wolf unique to the Great Lakes area. These divergent haplotypes are lost at the expense of coyote-like and grey wolf sequences, which become more frequent in the recent sample (although some are shared with the historic sample). Without considering the phylogenetic distribution of haplotypes, the comparison is misleading. Furthermore, it is unlikely that the recent wolves sampled by Lehman *et al.* (1991) included this divergent group of sequences since we sequenced representatives from all restriction fragment haplotypes and none were genetically close to the historic sequences. In fact, we find these divergent sequences in 9 out of 17 historic samples, and the possibility of missing this divergent group of sequences in our sequenced sample of 68 wolves or the 88 wolves restriction fragment length polymorphism typed from northeastern Minnesota is slim (e.g. the binomial probability of observing one or more divergent haplotypes in the recent sample of 68 wolves is $p > 0.999$ if the collective frequency of these haplotypes is 10%).

- (iii) *The delisting is legal.* We never question the legality of the delisting, but rather its rationale. The delisting document has extensive discussion of hybridization and the taxonomic problems of

The accompanying comment can be viewed on page 65 or at <http://dx.doi.org/doi:10.1098/rsbl.2008.0440>

Great Lakes wolves (Fish & Wildlife Service 2003), but this issue is ignored in the delisting requirements. The cause of the hybridization is not well understood, and it may stem from human activities that could be mitigated, and thus deserves some consideration.

In summary, we stand firmly by our conclusion that both coyote and grey wolf mitochondrial haplotypes have introgressed into the population of wolves around the Great Lakes. Nearly all genetic studies of wild vertebrates can be questioned to some extent on sampling grounds, but in this case, our conclusion that the historic population contained a greater proportion of unique sequences is robust given our sampling regime and the known history of wolves in the recovery area.

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