Defense of an Expanded Historical Range for the Mexican Wolf: A Comment on Heffelfinger et al.

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In a recent review, Heffelfinger *et al.* (2017) argue that historical and recent genetic data on the Mexican wolf (*Canis lupus baileyi*) are not sufficient justification for a proposed historical range expansion. According to Heffelfinger *et al.*, the observations of “experts” who saw wolves in the wild prior to extirpation and morphologic analysis of historical specimens should carry more weight in designation of a historical range. We strongly disagree with this assertion and below argue for the primacy of genetic data. We assert that reintroductions and wildlife management plans should develop definitive expectations based on evolutionary hypotheses, and use genetic data to test them. The field of evolutionary genetics has experienced a revolution given genome wide typing and sequencing approaches, and we hope that Heffelfinger *et al.* might value this dramatic change when considering conservation recommendations and future research possibilities.

1. Morphology and evolutionary inference. Size, which is the principle phenotypic character used to deduce the original historical distribution of Mexican wolves (Bogan & Melhop 1983; Nowak 1995), is not a reliable indicator of evolutionary distinction at the subspecies level as it can be plastically altered by habitat and prey size/abundance. Taxonomy is best served by a focus on characters which have near perfect heritability, such as DNA sequence changes, and which define evolutionary groups in a web-of-life framework (Arnold 2015; vonHoldt *et al.* 2017). The use of size as diagnostic indicator of ancestry for Mexican wolves presumes that it maps to phylogeny. However, this is often not the case in wolves (e.g. Fan *et al.* (2016)). In fact, none of the five currently supposed North American gray wolf subspecies based on morphologic characters are well matched with partitions based on nuclear genetic markers (vonHoldt *et al.* 2011; Schweizer *et al.* 2016). A single genetic unit may contain wolves of varying size, hence slightly larger wolves outside the original Mexican wolf range may share a common ancestry with them, which is consistent with the genetic findings of Leonard *et al.* (2005) and Hendricks *et al.* (2016).

2. The opinion of experts and typological thinking. Heffelfinger *et al.* suggest that field observations made before extirpation should dominate definitions of geographic range. However, early historical observations are weak data for range inference and opinions of “experts” (as defined by Heffelfinger *et al.*) were developed under a typological framework in large part prior to acceptance of the modern evolutionary synthesis and did not incorporate evolutionary thinking. Even minor variations, often observed in just a few specimens, were used to define subspecies and “races”, and this Victorian legacy has carried over into modern times. For example, in the Southern US, historically black wolves were defined as a distinct species and then subspecies, *Canis rufus niger*. However, genetic analysis of gray wolves and coyotes now suggest that the black coat coloration came from hybridization with dogs (Leonard *et al.* 2002; Anderson *et al.* 2009). The modern systematic framework for taxonomy uses shared-derived traits to define clades, such as those based on mtDNA or nuclear sequence data. These clades are

then the basis for evolutionary taxonomic units (e.g. Moritz (1994)). As such, size is a dubious character for evolutionary inference at best and average size may differ between populations depending on how they are defined and sample size. Some populations, such as the Mexican wolf, may be so narrowly defined that size does not overlap with other populations despite sharing a close evolutionary history. Under a modern view of process and admixture in current wolves, larger wolves observed by past naturalists may have been admixed or, despite size differences, are genetically and evolutionarily Mexican wolves. Large intergradation zones likely existed between Mexican wolves and other adjoining populations as suggested by the historical genetic data (Leonard *et al.* 2005). Admixture zones should be part of reintroduction plans and admixed individuals can receive protection (Arnold 2015; vonHoldt *et al.* 2017). Hence, a simple typological model as advocated by Heffelfinger *et al.* is not appropriate for conservation or reintroduction.

3. Limitations of genetic data. Heffelfinger *et al.* find that the sample sizes included in Leonard *et al.* (2005) and Hendricks *et al.* (2016) are inadequate for genetic data to delineate historical range. Specifically, the authors suggest that the process of drift and incomplete lineage sorting explain the distinct mtDNA clade for Mexican wolves. This kind of argument ignores the general pattern so elegantly reviewed by John Avise in his 1996 and 2002 books summarizing hundreds of studies that show clades based on mtDNA data often correspond with geography and define the science of phylogeography (the correspondence between genes and geography). To dismiss the finding of a distinct mtDNA clade, observed in modern and historical specimens, as a random event in lineage sorting is without foundation. The clade has a geographic coherence not expected for lineage sorting and recent analyses place the mtDNA clade in a worldwide context showing that it is highly distinct from other modern NA wolves (Koblmüller *et al.* 2016). In fact, the limited geographic sampling of the genetic studies is in part compensated by the large number of polymorphisms in complete genome sequence data used to reconstruct evolutionary history (vonHoldt *et al.* 2011; 2016). We maintain the Mexican wolf is one of the best defined groupings below the species level of any large North American vertebrate have been based on mtDNA sequence, microsatellite loci, genome wide SNPs and complete genome sequence data (vonHoldt *et al.* 2011; 2016).

4. Historical range definition. In the absence of more extensive genetic data and given the questionable inferences from body size and historical observations, niche projections in Hendricks *et al.* (2016) provide an alternative hypothesis for geographic range. Heffelfinger *et al.* argues against our ecological modeling because we predict suitable habitat exists as far north as southern Oregon. That areas far from the historical geographic range have suitable habitat, does not contradict its use for a guide to historical range, rather, criteria such as continuity or possible dispersal must be used in addition to defend an expanded historical geographic range. Much of the additional range we find in the Grand Canyon ecoregion and Southern Rockies, is confirmed by other landscape scale analysis (Sneed 2001) and niche based studies (Carroll *et al.* 2014) and with observations of long range dispersal and admixture zones in modern wolves. Further, a web-of-life framework explains the evidence for a historical hybridization of *C.l. baileyi* and *C. l. mogollonensis*, which extends the historical range northwards, and allows for future admixture in this region (vonHoldt *et al.* 2017).

Given the difficulty of establishing Mexican wolves in the US and Mexico, which contrasts with the considerable success of Yellowstone-Idaho reintroduction (Wayne & Hedrick 2011), expanded historical range is desperately needed, and as discussed above, is supported by ecological and genetic evidence. Further, climate change is likely to increase the proportion of historical range northwards, and a modern consideration of climate points to the need for a dynamic view of historical geographic range.

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