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Letter to the Editor

Revisiting Revising Mexican Wolf Historical Range: A Reply to Hendricks et al.

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Hendricks et al. (2017) questioned 4 elements of our clarification of Mexican wolf (*Canis lupus baileyi*) historical range and our criticism of their expansion proposals far to the north and west. With current recovery planning focused on ample habitat in Mexico, Arizona, and New Mexico (Martínez-Meyer et al. 2017), calls to expand historical range descriptions based on poorly understood distribution of molecular markers (Leonard et al. 2005, Hendricks et al. 2016) serve only to impede progress. The subspecies is on its way to recovery; in the United States, wild population growth has averaged 16% annually since 2009. Mexico has a comparably expanding population of 32 wild wolves with documented reproduction in each of the last 4 years (U.S. Fish and Wildlife Service [USFWS] 2017). Success can continue, if not derailed by misinformation on Mexico's ability to contribute to recovery of its eponymous wolf. We appreciate the opportunity to discuss using the best available science to define historical range of endangered species. Such dialogue is crucial to developing recovery strategies with a solid scientific foundation to maximize success and reduce litigation.

MORPHOLOGY AND EVOLUTIONARY INFERENCE

Nearly all taxa listed under the Endangered Species Act (ESA) are based on classical phenotypic assessment. It is not our position that skull morphology and historical records should outweigh sufficient genetic data. We agree with Hendricks et al. (2017) on the importance of using all available genetic, morphometric, and ecological information for taxonomic decisions. Although Heffelfinger et al. (2017) was not about taxonomic validity of the Mexican wolf, we devoted much space to those same 3 areas of study to fully discuss usefulness of all available data to clarify historical range. Genetic support for expanding that range as far north as Nebraska and west to California is insufficient to outweigh the coalescence of morphometric, historical records, phylogeographic concordance with other taxa, vegetation, and suitable habitat patterns.

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Some cranial differences may be taxonomically uninformative, but this taxon has been well-delineated in every morphometric analysis, and that delineation was consistently associated with historical range as clarified by Heffelfinger et al. (2017). Hendricks et al. (2017) asserted, "...none of the 5 currently supposed North American gray wolf subspecies based on morphometric characters are well matched with partitions based on genome-wide nuclear genetic markers (vonHoldt et al. 2011, Schweizer et al. 2016)." However, Schweizer et al. (2016) did not assess Mexican wolf specimens and vonHoldt et al. (2011:7) found "... in the New World, Mexican wolves appear as the most genetically distinct group, ..." The later finding is supported by other genome-wide analyses (Fan et al. 2016).

Skulls are subject to environmental plasticity, but that does not discredit their use in taxonomy (Bogan and Mehlhop 1983, Nowak 1995). Likewise, the variation of skull size through evolutionary time does not invalidate their use for evaluating distribution. Contrary to the citation by Hendricks et al. (2017), Fan et al. (2016) did not address size as a diagnostic phylogenetic indicator. Skull size and proportion may be environmentally affected, with eventual adaptation resulting from directional selective pressures. The Mexican wolf phenotype evidently results from long-term genetically based adaptive changes, representing a subspecies that was listed separately under ESA, and thus must be the focus of recovery.

THE OPINION OF EXPERTS AND TYPOLOGICAL THINKING

The appropriate framework for studying Mexican wolf historical range involves population and ecological relationships, not divergence of subspecific taxonomic units. The ESA seeks to represent complex distributional arrangement of natural populations. Current recovery guidance directs that recovery plans include 3 R's: representation, redundancy, and resiliency. Representation cannot occur north of historical range in areas unrepresentative of the evolutionary processes that shaped the Mexican wolf, while ignoring the 90% of such range in Mexico.

The Mexican wolf is not a casualty of outdated Victorian thinking (vonHoldt et al. 2016, Hendricks et al. 2017). It is

more distinct, physically and genetically, than any other North American subspecies (vonHoldt et al. 2016). Hendricks et al. (2017) asserted that larger northern wolves in Nebraska and northern Utah were "genetically and evolutionarily Mexican wolves." That view only considers genetics to the exclusion of all other information. The goal is to recover the Mexican wolf, not an assembly of phenotypically and geographically diverse wolves with certain molecular markers of unknown historical distribution.

Reviewing pre-extirpation geographic distribution illustrates how partial isolation from larger wolves to the north allowed for the universally recognized multi-factor differentiation of the Mexican wolf (Heffelfinger et al. 2017: figure 1). This well-documented distribution pattern, centered in Mexico, is inconsistent with a wide mid-continent zone of intraspecific intergradation (Leonard et al. 2005, Hendricks et al. 2016, 2017). Considering wolves from Nebraska to Mexico City as one genetic unit based on fragmentary sampling of genetic markers (Leonard et al. 2005) disregards abrupt shifts in morphology, habitat, prey, and multi-species ecological concordance.

LIMITATIONS OF GENETIC DATA FOR THE DEFINITION OF HISTORICAL RANGE

The discussion of historical relationships among wolf populations in Hendricks et al. (2017) is anchored in the hierarchical, bifurcating framework of evolutionary genetics, even as they discuss the likely presence of intergradation. Both single-locus (i.e., mitochondrial) analysis and single-individual, multi-thousand-locus analysis (i.e., genomics) can be informative when studying phylogeny but not for understanding relationships across space. For example, in brown bears (*Ursus arctos*) of southeast Alaska the distribution of mitochondrial haplotypes is dramatically discordant with current population relationships, grouping together island populations not recently exchanging individuals, and missing contemporary connections between certain islands and the mainland (Paetkau et al. 1998).

The southern clade purported to represent diagnostic markers for Mexican wolf heritage comprises 4 mtDNA haplotypes. Only 1 was found in known Mexican wolves, the rest in wolves phenotypically described as northern subspecies. It is problematic that the genetic argument for expanding historical range is based on the detection of these 4 haplotypes in 12 wolf specimens across 2,000 km^2 of west-central North America (Leonard et al. 2005) and 1 sample from California (Hendricks et al. 2016). The subjective manner in which single-locus data are interpreted is questionable, as illustrated by the meaning assigned to a single California specimen with a mitochondrial haplotype seen in Mexican wolves, while ignoring a Mexican wolf with the lu32 haplotype that was common in a similarly small sample of Labrador wolves (*C. l. labradorius* [=*nubilus*]). No one would argue that this Arizona wolf had Labrador heritage. Nuclear DNA evidence of Mexican wolf ancestry in the California specimen suffers from the same lack of geographic sampling and thus it cannot be determined if those alleles are diagnostic of Mexican wolves, especially considering those alleles were also found in other subspecies in northern California, Oregon, and Nevada (Hendricks et al. 2016: table 1).

For illustration, 2 studies of polar bears (*Ursus maritimus*), each based on hundreds of individuals, provided broadly consistent quantitative descriptions of population relationships, despite 1 study using 17 markers and the other 5,441 markers (Malenfant et al. 2015). These studies could not have identified locations and severities of the many genetic discontinuities in this species' range by sampling a handful of individuals, no matter how well characterized those individuals' genomes were. This example illustrates that adequate samples of both genetic loci and geographically distributed individuals are required to understand connections across a landscape, and that a shortfall in 1 sample size (of the genome or of individuals) cannot be overcome by simply increasing the other. Indeed, the suggestion that intensive genetic study of 1 or a few individuals can adequately describe population relationships is the genetic analogue of Victorian typological thinking. The unfortunate reality is that wolves across the southern United States and Mexico were not well sampled prior to extirpation, so we are unable to quantify the extent to which particular haplotypes or autosomal alleles are diagnostic of Mexican wolves. Because of this limitation, genetic methods cannot illuminate historical population relationships with the detail provided by other sources of information (Heffelfinger et al. 2017).

HISTORICAL RANGE DEFINITION

Our paper focused on defining historical range, not advocating recovery zones. In fact, preferences for such zones are not germane to objective evaluation of data supporting delineation of historical range. The range defined by Parsons (1996:104) included historical range "plus a 322-km extension to the north and northwest" including the area of historical admixture as clarified by Heffelfinger et al. (2017). This range has been officially adopted (USFWS 1996, 2017) "for purposes of reintroducing Mexican wolves" (Parsons 1996:104). Listed separately as a subspecies in 2015, the Mexican wolf must be recovered for its genetic, ecological, and physical differences.

Admixture zones are important in Mexican wolf recovery as evidenced by the introductions in the United States in an area of intergradation with more northerly wolves (*C. l. nubilus*; Heffelfinger et al. 2017). In the current absence of the latter, eventual gene flow with Northwestern wolves (*C. l. occidentalis*) could be desirable. However, forcing recovery in areas periodically occupied by Northwestern wolves would result in premature admixture, contrary to recovery goals (USFWS 2017).

We did not misrepresent habitat suitability models with historical demography inferences. We agree with Hendricks et al. (2017), and pointed out, that one cannot infer continuous historical range simply because a model identifies suitable habitat there. The strongest argument against use of the habitat suitability model of Hendricks et al. (2016) for

recovery is not inclusion of Oregon, but exclusion of Mexico from serious consideration (Hendricks et al. 2016, 2017). Martínez-Meyer et al. (2017) used advanced analytical tools to identify extensive high quality habitat in historical range including Mexico and that habitat is sufficient to successfully recover the Mexican wolf (Miller 2017, USFWS 2017). Past recovery planning failed to adequately evaluate all historical range for suitable habitat, resulting in plans to recover beyond historical range. This shortcoming has been rectified, making the current Mexican wolf Recovery Plan draft a truly binational effort to return the subspecies to its historical range. Ignoring Mexico in recovery planning is indefensible when best available science shows abundant suitable habitat in Mexico.

Carroll et al. (2014) did not evaluate potential areas for suitable Mexican wolf habitat. They simply referenced earlier work originating from a report (Carroll et al. 2004) that was never peer reviewed but is the original source indicating the Grand Canyon and Southern Rockies are the best places for recovery. This flawed report exaggerates suitability of northern areas while dismissing habitat in Mexico. Additionally, Carroll et al. (2004) classified a large private ranch in northern New Mexico as roadless and the same as a national park, despite it containing 600 active coalbed methane wells and the associated road network. This outdated assessment has been eclipsed by Martínez-Meyer et al. (2017), which represents the best available science on Mexican wolf habitat suitability.

Sneed's (2001:153) Grand Canyon habitat analysis was by his own admission "preliminary results from research done on a limited number of factors in the northern Arizona section of the ecoregion." In fact, only 6 of 26 planned factors were covered, work was never completed, and release of Great Lakes wolves in the Grand Canyon was recommended. Hence, that source is not a useful analysis of the area to inform recovery.

Hendricks et al. (2017) and others suggested climate change as a reason for northward recovery, yet no one has adequately explained why Mexican wolves cannot be recovered within historical range despite that factor. Climate change has accelerated fire frequency and intensity and increased beetle infestations and tree mortality, which have positively affected habitat for ungulate prey in the Southwest. The recovery plan draft concluded climate change does not threaten recovery in historical range (USFWS 2017). Wolves currently inhabit regions with temperatures from -40°C to 40°C and use varied habitats from Arabia to the Arctic. Climate change is unlikely to unsuitably and irreversibly alter or destroy habitat in Mexican wolf historical range within a relevant timeframe.

Recovery should incorporate selective forces that produced and maintained this southwestern subspecies. The northern areas identified by Hendricks et al. (2016:50) "represent more fringe habitats in terms of suitability for the Mexican wolf." It is important to protect evolutionary and ecological processes and the role of an endangered taxon (vonHoldt et al. 2016). If that role can be restored by recovery in historical range, there is no justification for expansion.

RECOVERY WITHOUT REVISING RANGE

The current recovery plan is based on a newly updated population viability model (Miller 2017) that is far more complex and realistic than all previous versions. It shows recovery is not only possible within historical range but highly (>90%) probable (USFWS 2017). Efforts are now appropriately focused on returning a small wolf subspecies to its ecological role in the American Southwest and Mexico. Challenges lie ahead, but efforts to force recovery into environments lacking evolutionary forces that shaped the Mexican wolf threaten our best chance for recovery in nearly 4 decades.

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