Journal of Heredity Advance Access published May 11, 2015

American Genetic Association

Journal of Heredity, 2015, 1–2
doi:10.1093/jhered/esv028
Letter to the Editor

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Mexican Wolves Are a Valid Subspecies and an Appropriate Conservation Target

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Cronin et al. (2015) used nearly 124 000 single nucleotide polymorphisms (SNP) to estimate genetic differentiation among wolves within southeastern Alaska and between wolves, coyotes, and dogs in other areas of North America. In their major emphasis, they found that wolves within the 6 game management units (GMU) of southeastern Alaska had "considerable" genetic differentiation (means of pairwise $F_{ST} = 0.11–0.15$ depending on how the GMU were grouped for contrasts). They concluded wolves occupying the 6 GMU were not a homogenous group, and that the differentiation within southeastern Alaska was similar to that among some pairwise comparisons of wolf populations in other areas of North America. Based on these findings and the lack of reciprocal monophyly of mtDNA haplotypes of these wolves, found in other studies, they concluded that the wolves of southeastern Alaska should not be considered a separate wolf subspecies.

Cronin et al. (2015) also found that SNP differentiation was high between 8 Mexican wolves (*Canis lupus baileyi*) and other wolf populations in North America. Pairwise F_{ST} values between Mexican wolves and wolves from Minnesota, the Northern Rocky Mountains of the United States, British Columbia, and central Alaska ranged from 0.22 to 0.25. Differentiation was even greater between Mexican and southeastern Alaska wolves (pairwise $F_{ST} = 0.34$) and similar to F_{ST} values found by Cronin et al. (2015) for interspecific comparisons between wolves, coyotes, and dogs (pairwise $F_{ST} = 0.28–0.34$). The high differentiation of Mexican wolves relative to other North American wolves found by Cronin et al. (2015) is consistent with results from previous studies that have found Mexican wolves to be genetically the most distinct subspecies of wolf in North America (Garcia-Moreno et al. 1996; Hedrick et al. 1997; vonHoldt et al. 2011).

This substantial genetic differentiation suggests there may be important differences between Mexican wolves and other grey wolves, including observed morphological differences. Mexican wolves differ from other North American wolves in their skull morphology (Bogan and Mehlhop 1983; Nowak 1995), small body size (Nowak 1995), and distinctive pelage. Historically, they occupied habitats in the southernmost portion of the geographic range of grey wolves in North America, and were found as far south as Puebla, Mexico (Leopold 1959).

Cronin et al. also stated "extant and historic samples show that Mexican wolves lack mtDNA monophyly, share haplotypes with wolves in other areas and with coyotes (Leonard et al. 2005; Hailer and Leonard 2008), and extant Mexican wolves came from only 7 founders that may have included dog ancestry (although data indicate this is improbable and/or of small genetic importance, Garcia-Moreno et al. 1996; Hedrick et al. 1997). These factors indicate that designation of a Mexican wolf subspecies is of questionable validity."

First, the fact that extant Mexican wolves descended from only 7 founders is not relevant to whether Mexican wolves are a subspecies. A number of other endangered species and subspecies are known to have descended from similarly small numbers of founders. Second, there is no indication of dog ancestry in extant Mexican wolves from the studies cited by Cronin et al. (2015) and a recent comprehensive search for dog ancestry in Mexican wolves using 172 000 SNPs (Fitak 2014).

Finally, phylogenetic analysis of mtDNA haplotypes suggests that the 3 most widely recognized grey wolf subspecies in North America, Mexican wolves, *C. l. nubilus*, and *C. l. occidentalis*, each originated from successive waves of wolf colonization from Eurasia during the Pleistocene with Mexican wolves descending from the earliest of these waves (Vilà et al. 1999). Vilà et al. (1999) attributed the observed phylogenetic patterns of haplotypes as resulting from "past episodes of isolation followed by admixture" as successive waves of wolves colonized southward.

Subsequently, Leonard et al. (2005, see also Hailer and Leonard 2008) examined mtDNA haplotypes from recent and historic wolves collected from Mexico, the American southwest, the southern Rocky Mountains, and the Great Plains. They found that all Mexican wolves from the captive breeding program and 4 of 6 historic Mexican wolves had haplotypes that formed a "unique southern clade." Of the 2 other historic Mexican wolves, one had a haplotype common among more northern wolves, and the other had a coyote-like haplotype, suggesting a past hybridization event. In addition, 6 of 18 historic wolves identified as *C. l. nubilus* and 2 of 6 *C. l. youngi* (a subspecies no longer recognized) also had southern clade haplotypes. Southern clade haplotypes were found as far north as Nebraska and northern Utah among sampled historic wolves. Leonard et al. (2005) concluded that the southern Rocky Mountains region supported a "large zone of intergradation" between Mexican and *nubilus* wolves. These results suggest that lack of mtDNA monophyly among historic Mexican wolves may be a result of "past episodes of isolation followed by admixture" as suggested by Vilà et al. (1999). As a perspective, many species (or subspecies) of plants and animals naturally form hybrid zones where the hybridization does not compromise the distinctiveness of the parental species, based on morphology and genomes, for example, Mexican wolves. In fact, hybridization of grey wolves with coyotes and eastern wolves in the Great Lakes area has not compromised the genetic integrity of grey wolves to the west of the hybrid zone (Koblmuller et al., 2009). In some cases, such hybridization may even have positive effects by providing new adaptive genetic variation to one or both parental species (Hedrick 2013).

Speciation is a complex and highly variable process. This is reflected in the many different definitions of species that have been proposed, each based on different and sometimes conflicting properties, for example, monophyly, intrinsic reproductive isolation, common niche (de Quieroz 2007). But because the various properties proposed in the many species definitions may be attained at different times and in different orders among lineages undergoing speciation, requiring any individual property to define speciation could be considered arbitrary and potentially misleading. Instead, de Quieroz (2007) proposed that the presence of one or more of the various properties used in species concepts may each serve as lines of evidence for speciation, but that no individual property would be required.

Cronin et al. (2015), however, in examining the work of others on mtDNA variation in Mexican wolves would apparently require reciprocal monophyly of mtDNA haplotypes as a condition for recognizing subspecies. Applying the approach of de Quieroz (2007) to identifying subspecies, the absence of reciprocal monophyly would not be a reason to deny designation of a subspecies, if other ecological or genetic differences were present. Although Moritz (1994) proposed that populations should show reciprocal monophyly of mtDNA haplotypes as a required property on which to identify evolutionarily significant units (ESU), he recognized that smaller segments of a species or ESU may warrant conservation attention. For this purpose, Moritz (1994) proposed recognition of management units defined as "…populations with significant divergence of allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of the alleles."

Crandall et al. (2000), however, subsequently argued that ecological and genetic evidence suggesting adaptive variation are more relevant to identifying conservation units. The strong genetic differentiation of Mexican wolves from other grey wolves as found by Cronin et al. (2015) and others, as well as their morphological differences and historical range, support the conservation validity of Mexican wolves. Even the near-monophyly of Mexican wolf mtDNA found by studies of others and discussed by Cronin et al. (2015), provides more than enough evidence to justify the continuing status of Mexican wolves as a valid subspecies (*C. l. baileyi*) and an appropriate target for conservation.

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