Historical range of the Mexican wolf and current recovery location in the United States

The Mexican wolf (*Canis lupus baileyi*) as a subspecies evolved its uniqueness in the high-elevation mountains of Mexico and small island mountain habitats of the desert southwest; mostly separated from the other wolf subspecies to the north by fragmented habitat and discontinuous prey distribution (Heffelfinger et al. 2017a,b). The unique physical and genetic differences of Mexican wolves could not have developed and maintained themselves, if they shared an extensive zone of genetic exchange with larger northern wolves. Mexican wolf historical range (Nelson and Goldman 1929; Young and Goldman 1944; Nowak 1979, 1995, 2003), is supported by best available science on ecological relationships, physiography, wolf morphology, and the principles of population genetics (Heffelfinger et al. 2017a, Martinez-Meyer et al. 2021).

The Service acknowledges that intergradation zones between Mexican wolves and other gray wolf populations likely occurred in central Arizona and New Mexico (Bogan and Mehlhop 1983, Heffelfinger et al. 2017) as incorporated into the historical range expanded by Parsons (1996). The Service continues to recognize the concordance in the scientific literature depicting the Sierra Madre of Mexico and southern Arizona and New Mexico as Mexican wolf core historical range and will continue to recognize the expanded range as per Parsons (1996) that extends into central New Mexico and Arizona (USFWS 1996).

Historically, Mexican wolves were associated with montane woodlands characterized by sparsely to densely forested mountainous terrain and adjacent grasslands in habitats found at elevations of 1,219-1,524 m (4,500-5,000 ft) (Brown 1988). Wolves were known to occupy habitats ranging from foothills characterized by evergreen oaks (*Quercus* spp.) or pinyon (*Pinus edulis*) and juniper (*Juniperus* spp.) to higher elevation pine (*Pinus* spp.) and mixed conifer forests. Factors making these habitats attractive to Mexican wolves likely included prey and availability of water. White-tailed deer (*Odocoileus virginianus couesi*) and mule deer (*O. hemionus*) were believed to be the primary sources of prey (Brown 1988, Bednarz 1988, Bailey 1931, Leopold 1959), and Mexican wolves may have consumed more vegetative material and smaller animals than gray wolves in other areas (Brown 1988) as do coyotes in southern latitudes (Hidalgo-Mihart et al. 2001). The difference between historical versus current prey preference in the United States is likely due to the lack of elk in large portions of historical Mexican wolf range.

Recovery of Mexican wolves in the United States is currently occurring in areas approximately 200 miles north of the Mexican wolf core historical range (USFWS 1996). Based on a review of ecological, morphological and genetic data, Parsons (1996) published a map that delineates "the 'probable historic range' of *C. l. baileyi* for the purposes of reintroducing Mexican wolves in the wild in accordance with provisions of the Endangered Species Act (ESA) and its regulations." The expanded range map developed by (Parsons 1996: fig. 2) added a 322-km (200-mile) northward extension of the core historical range and was adopted and included in the 1996 Final Environmental Impact Statement (USFWS 1996) prior to the release of the first Mexican wolves in the U.S. In 2015, the Service revised the Mexican wolf 10(j) area and expanded the area of

Mexican wolf recovery to include all of Arizona and New Mexico south of Interstate 40 to the Mexican border (USFWS 2015).

Establishing an experimental population of northern gray wolves in Colorado will increase the connectivity of northern gray wolves to Mexican wolves. Although wolves are noted for long-range movements and genetic interchange among distant populations, even as far as 678 miles (Wabakken et al. 2007) few wolves originating from the north have been documented in Northern Arizona and New Mexico. In October 2014, a 2-year old female wolf collared near Cody, Wyoming was documented on the Kaibab Plateau in northern Arizona. In July 2008, a wolf with black pelage was documented near the Vermejo Park Ranch in northern New Mexico that was most likely a wolf from the Northern Rocky Mountains since no black phase Mexican wolf has ever been documented (Odell et al. 2018). The wild Mexican wolf population in the U.S. is approximately 350 miles from the proposed population release sites in Colorado, a distance that is within the known travel distance for wolves and hence, reasonable management options are essential to maintaining the integrity of the Mexican wolf genome.

Maintaining genetic integrity has been a critical challenge for other endangered canids, notably the Eastern red wolf (*C. rufus*, Kelly et al. 1999). The loss of genetic integrity of Mexican wolves by hybridization with northern wolves would impede recovery efforts of the separately listed Mexican wolf. In 2015, the USFWS changed the status of the Mexican wolf from being listed together with all other subspecies of gray wolf (*C. lupus*) to being listed as Endangered as a separate entity (*C. l. baileyi*) under the ESA. The separate listing of the Mexican wolf is supported by all genetic (Vila et al. 1999, vonHoldt et al. 2011) and physical morphometric analyses conducted (Bogan and Mehlhop 1983, Hoffmeister 1986, Nowak 1995). The ESA requires all federal and cooperating state agencies to conserve listed taxa and releasing northern wolves closer to the existing nonessential experimental population of Mexican wolves could risk the recovery of the latter without mechanisms in place to keep the populations separate.

Best available information suggests the risk of loss of genetic integrity is particularly high during early phases of Mexican wolf recovery, when the number of wolves on the ground in recovery areas is relatively small. Generally, dispersing wolves are adopted into packs (Boyd et al. 1995) and can assume vacant breeding positions (Fritts and Mech 1981, Stahler et al. 2002, vonHoldt et al. 2008, Sparkman et al. 2012), usurp an existing breeder (Messier 1985, vonHoldt et al. 2008), or bide their time to ascend to breeding positions (vonHoldt et al. 2008). Body size is an important determinant of individual fitness and a driving evolutionary force (Baker et al. 2015). Stahler et al. (2013) demonstrated that body mass of breeders was the main determinant of litter size and survival of the litter. Hunting success is also tied directly to larger body size, which has obvious fitness advantages (MacNulty et al. 2009). This physical superiority offers a decisive advantage for northern wolves obtaining and defending breeding positions in the small Mexican wolf population.

In addition to a body size differential, several demographic characteristics of the current wild Mexican wolf populations make them vulnerable to loss of genetic integrity by admixture of northern wolves. When wolf populations have high rates of mortality, the social turmoil results in a higher rate of acceptance of wolves dispersing from other packs (Ballard et al. 1987, Mech and Boitani 2003:16). Ballard et al. (1987) noted that 21% of dispersing wolves were accepted into other packs. Immigrating wolves are also more readily adopted by smaller packs where additional individuals, especially males, increase hunting efficiency and survival of existing pack members (Fritts and Mech 1981, Ballard et al. 1987, Cassidy et al. 2015). The wild U.S. population of Mexican wolves has consistently maintained a relatively small pack size (mean = 4.1, 1998-2016, USFWS 2017), which means they would more readily accept immigrating wolves from the north. Inbreeding avoidance in wolves has been well-documented, where wolves more readily mate with unrelated wolves (vonHoldt et al. 2008, Geffen et al. 2011, Sparkman et al. 2012). The current wild populations of Mexican wolves have inbreeding levels higher than most wolf populations (USFWS 2017), which means a new wolf immigrant, unrelated to all Mexican wolves, would have a disproportionately high probability of attaining a breeding position (vonHoldt et al. 2008, Geffen et al. 2011, Åkesson et al. 2016).

Wolf introgression into coyotes in the northeastern U.S. has been attributed to the advantage of larger body size (Monzón et al. 2013). This dominance of breeding positions by larger wolves has allowed the expansion of hybridized coyotes into the northeast. Likewise, a situation of wolves with Canadian genomes hybridizing with smaller Mexican wolves could result in a similar failure to retain the genetic, physical, and ecological characteristics that resulted in Mexican wolves being listed separately.

Allowing wolves that evolved on the northern end of the North American genetic and body size cline to breed with the separately listed Mexican wolf on the southern end of the continental cline could impact the genetic integrity of the Mexican wolf and risk ongoing recovery efforts. To maintain this separation and protect Mexican wolf genetic integrity, we will simultaneously issue a 10(a)(1)(A) permit to be held by the Service authorizing our state and federal partners to assist in the capture and return of wolves originating from the Colorado experimental population.

Relevant Literature

Adams, J.R., L. M. Vucetich, P. W. Hedrick, R. O. Peterson, and J. A. Vucetich. 2011. Genomic sweep and potential genetic rescue during limiting environmental conditions in an isolated wolf population. Proceedings Biological Science. Nov 22;278(1723):3336-44. doi: 10.1098/rspb.2011.0261. Epub 2011 Mar 30.

Åkesson, M., O. Liberg, H. Sand, P. Wabakken, S. Bensch and Ø. Flagstad. 2016. Genetic rescue in a severely inbred wolf population. Molecular Ecology 25:4745-4756.

Baker, J., A. Meade, M. Pagel, and C. Venditti. 2015. Adaptive evolution toward larger size in mammals. Proceedings of the National Academy of Sciences 112:5093-5098.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs 98.

Bogan, M. A., and P. Mehlhop. 1983. Systematic relationships of gray wolves (*Canis lupus*) in southwestern North America. Occasional Papers of the Museum of Southwestern Biology 1:1–20.

Boyd, D. K., P. C. Paquet, S. Donelon, R. R. Ream, D. H. Pletscher, and C. C. White. 1995. Transboundary movements of a recolonizing wolf population in the Rocky Mountains. Pages 135-140 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors, Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Occasional Publication Number 35.

Cassidy, K. A., D. R. MacNulty, D. R. Stahler, D. W. Smith, and L. D. Mech. 2015. Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. Behavioral Ecology 26:1352-1360.

Fritts, S. H., and L. D. Mech. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildlife Monographs 80:3-79.

Geffen, E., M. Kam, R. Hefner, P. Hersteinsson, A. Angerbjorn, L. Dalen, E. Fuglei, K. Noren, J. Adams, J. Vucetich, T. Meier, L. D. Mech, B. VonHoldt, D. Stahler, and R. K. Wayne. 2011. Kin encounter rate and inbreeding avoidance in canids. Molecular Ecology 20:5348–5358.

Heffelfinger, J. R., R.M. Nowak, and D. Paetkau. 2017a. Clarifying historical range to aid recovery of the Mexican wolf. Journal of Wildlife Management 81:766-777. DOI: 10.1002/jwmg.21252

Heffelfinger, J. R., R.M. Nowak, and D. Paetkau. 2017b. Revisiting revising Mexican wolf historical range: A reply to Hendricks et al. Journal of Wildlife Management 81:1334-1337.

Hoffmeister, D. F. 1986. Mammals of Arizona. University of Arizona Press and Arizona Game and Fish Department, Tucson, USA.

Kelly, B. T., P. S. Miller, and U. S. Seal, editors. 1999. Population and habitat viability assessment workshop for the red wolf (Canis rufus). Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, Minnesota, USA.

MacNulty, D. R., D. W. Smith, L. D. Mech, and L. E. Eberly. 2009. Body size and predatory performance in wolves: is bigger better? Journal of Animal Ecology 78:532-539.

Martínez-Meyer, E., A. González-Bernal, J. A. Velasco, T. L. Swetnam, Z. Y. González-Saucedo, J. Servín, C. A. López González, J. K. Oakleaf, S. Liley, and J. R. Heffelfinger. 2021. Rangewide habitat suitability analysis for the Mexican wolf (*Canis lupus baileyi*) to identify recovery areas in its historical range. Diversity and Distributions 27:642–654.

Mech, L. D. and L. Boitani. 2003. Wolf Social Ecology. Pages 1-34 in L. D. Mech and L. Boitani, editors, Wolves, Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois, USA.

Messier, 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Canadian Journal of Zoology 63:239-245.

Monzón, J., R. Kays, and D. E. Dykhuizen. 2013. Assessment of coyote-wolf-dog admixture using ancestry-informative diagnostic SNPs. Molecular Ecology 23:182-197.

Nelson, E. W., and E. A. Goldman. 1929. A new wolf from Mexico. Journal of Mammalogy 10:165–166.

Nowak, R. M. 1979. North American Quaternary *Canis*. Monograph of the Museum of Natural History (University of Kansas) 6:1–154.

Nowak, R. M. 1995. Another look at wolf taxonomy. Pages 375–397 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Occasional Publication No 35. Canadian Circumpolar Institute, Edmonton, Alberta, Canada.

Nowak, R. M. 2003. Wolf evolution and taxonomy. Pages 239–258 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Odell, E. A., J. R. Heffelfinger, S. S. Rosenstock, C. J. Bishop, S. Liley, A. González-Bernal, J. A. Velasco, and E. Martínez-Meyer. 2018. Perils of recovering the Mexican wolf outside of its historical range. Biological Conservation 220:290-298. https://doi.org/10.1016/j.biocon.2018.01.020

Sparkman, A. M., J. M. Adams, T. D. Steury, L. P. Waits, and D. L. Murray. 2012. Pack social dynamics and inbreeding avoidance in the cooperatively breeding red wolf. Behavioral Ecology 23:1186–1194.

Stahler, D. R., D. W. Smith, and R. Landis. 2002. The acceptance of a new breeding male in to a wild wolf pack. Canadian Journal of Zoology 80:360-365.

Stahler, D. R., D. R. MacNulty, R. K. Wayne, B. VonHoldt, and D. W. Smith. 2013. The adaptive value of morphological, behavioral and life-history traits in reproductive female wolves. Journal of Animal Ecology 82:222-234.

U.S. Fish and Wildlife Service. 1996. Reintroduction of the Mexican wolf within its historic range in the southwestern United States: final environmental impact statement. USFWS, Region 2, Albuquerque, New Mexico, USA.

U.S. Fish and Wildlife Service. 2015. Revision to the Regulations for the Nonessential Experimental Population of the Mexican Wolf (80 FR 2512, January 16, 2015), Albuquerque, New Mexico.

U.S. Fish and Wildlife Service. 2017. Mexican Wolf Biological Report: Version 2. Region 2, Albuquerque, New Mexico, USA. https://www.fws.gov/southwest/es/mexicanwolf/pdf/2017MexicanWolfBiologicalReportFinal.pdf.

Vila, C., I. R. Amorim, J. A. Leonard, D. Posada, J. Castroviejo, F. Petrucci-Fonesca, K. A. Crandall, H. Ellegren, and R. K. Wayne. 1999. Mitochondrial DNA phylogeography and population history of the gray wolf *Canis lupus*. Molecular Ecology 8:2089–2103.

vonHoldt, B. M., D. R. Stahler, D. W. Smith, D. A. Earl, J. P. Pollinger, and R. K. Wayne. 2008. The genealogy and genetic viability of reintroduced Yellowstone grey wolves. Molecular Ecology 17:252–274.

vonHoldt, B. M., J. P. Pollinger, D. A. Earl, J. C. Knowles, A. R. Boyko, H. Parker, E. Geffen, M. Pilot, W. Jedrzejewski, B. Jedrzejewska, V. Sidorovich, C. Greco, E. Randi, M. Musiani, R. Kays, C. D. Bustamante, E. A. Ostrander, J. Novembre, and R. K. Wayne. 2011. A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. Genome Research 21:1–33.

Wabakken, P., H. Sand, I. Kojola, B. Zimmermann, J. Arnemo, H. C. Pedersen, and O. Liberg. 2007. Multi-stage, long-range dispersal by a GPS-collared Scandinavian wolf. Journal of Wildlife Management 71: 1631-1634.

Young, S. P., and E. A. Goldman. 1944. The wolves of North America. American Wildlife Institute, Washington, D.C., and Dover Publishers, New York, New York, USA.