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Featured Article

Clarifying Historical Range to Aid Recovery of the Mexican Wolf

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ABSTRACT We assessed historical, morphological, and genetic information on the range of the Mexican wolf (*Canis lupus baileyi*) to plan the recovery of this endangered subspecies. Early accounts of its range included the Sierra Madre Occidental, Mexico, and southeastern Arizona, southwestern New Mexico, and sometimes western Texas, USA. Such accounts are supported by ecological, physiographic, and morphological data. Recent suggestions to depict a more extensive northern periphery have been based primarily on a fragmented geographic sampling of genetic markers assumed to be diagnostic at subspecies level. Some of these genetic markers, found in extant Mexican wolves, reportedly also occur in a few individuals far to the north of the range defined in early accounts. Extending the historical range northward would necessitate drawing that line far north of transitions in wolf phenotype, breaks in vegetation associations, barriers to gene flow, and differences in prey base. We review morphologic, genetic, and ecological information to illustrate why such historical range extensions are not supported. The historical distribution of the Mexican wolf likely does not correspond to the detected distribution of certain molecular markers. The historical range of the Mexican wolf should not be altered through the identification of similar habitat in other locations, the distribution of inadequately sampled molecular markers, or by theoretical arguments about movement capacity. Rather, it should respect the original descriptions that were made when the animal was still present on the landscape, and which are concordant with ecological relationships, physiography, morphology, and the principles of population genetics. Clarifying the historical range of the Mexican wolf accurately will be foundational to developing a scientifically defensible recovery plan. © 2017 The Wildlife Society.

KEY WORDS *Canis lupus baileyi*, historical range, Mexican wolf, morphometrics, phylogeography, recovery.

The Mexican wolf (*Canis lupus baileyi*) is an endangered subspecies indigenous to southwestern North America (Nelson and Goldman 1929). There are at least 143 individuals currently living in the wild in Arizona, New Mexico, and Mexico, and about 240 in 48 captive-breeding facilities in the United States and Mexico. Efforts to recover the Mexican wolf have been underway for >30 years (U.S. Fish and Wildlife Service [USFWS] 1982) and disagreement regarding an accurate depiction of its historical range has figured prominently in recovery planning.

When the Mexican wolf was more common on the landscape and originally described in the literature, its range was defined as southern Arizona, southwestern New Mexico, and the Sierra Madre of Mexico south at least to southern Durango (Nelson and Goldman 1929). In the following decades, observers working in this region reaffirmed this geographic range based on body size and skull morphology through first-hand observation and examination of Mexican wolves and specimens (Bailey 1931; Young and Goldman 1944; Hoffmeister 1986; Nowak 1995, 2003). In recent years, the analysis of molecular markers has led some to suggest the historical range of the Mexican wolf may have extended as far north as Nebraska and northern Utah (Leonard et al. 2005), and as far west as southern California (Hendricks et al. 2015, 2016). Distribution of those molecular markers has led those researchers and others to suggest a larger geographic area could be used for recovery of the 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 Endangered Species Act (ESA). The ESA instructs to conserve listed taxa and the ecosystems upon which they depend. Further, USFWS regulations do not allow release of an endangered taxon outside its "... probable historic range, absent a finding by the Director in the extreme case that the primary habitat of the species has been unsuitably and irreversibly altered or destroyed..." (50 CFR 17.81[a]). It logically follows that recovery of the Mexican wolf must start with a scientifically and legally defensible understanding of the geographic area it originally and regularly inhabited.

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To assess the original distribution of the Mexican wolf, we reviewed the literature for collection records of wolves from throughout the southwestern United States and Mexico, deliberately expanding our search beyond the traditionally defined northern boundary of its range to ensure coverage of the transition zone between subspecies. These records included measurements, comparisons, and direct observations of wolf phenotype throughout the Southwest. We also reviewed studies of wolf skull morphometrics to assess and clarify the original physical differentiation among wolves throughout the Southwest. Analyses and comparisons spanned the areas of intergrade between putative subspecies and ecological zones. Finally, we evaluated more recent genetic work on historical wolf specimens from throughout North America.

THE PREHISTORY OF THE MEXICAN WOLF

Relevant paleontological evidence is fragmentary and indefinite. Some fossils indicate that wolves or immediate precursors crossed into ice-free parts of Alaska and northwestern Canada in the middle Pleistocene. However, the species in its present form probably did not penetrate south of the Beringian region until the late Rancholabrean (Kurten 1968; Nowak 2002, 2003; Tedford et al. 2009). A few mid-Pleistocene specimens from Arkansas and Nebraska, once referred to the gray wolf (Nowak 1979, Kurten and Anderson 1980), more likely represent Armbruster's wolf (*C. armbrusteri*), part of a separate New World lineage (Nowak 2002, 2003; Tedford et al. 2009). The gray wolf may have entered North America in several waves, perhaps corresponding to interglacial phases (Nowak 1995, 2003; Chambers et al. 2012). The smallest North American skull of an adult gray wolf examined by Nowak (1979) was from San Josecito Cave in the state of Nuevo Leon, Mexico. It is part of a fauna dated at 27,000–11,000 years before present (YBP; Arroyo-Cabrales et al. 1995) and suggests Mexican wolves may have been established in Mexico by the late Pleistocene.

A subsequent gray wolf wave from Eurasia apparently spread southward from Beringia in the late Pleistocene and occupied much of western North America, where it now is known as the Great Plains wolf (*C. lupus nubilus*; Nowak 1995); it intermixed with and exchanged mitochondrial DNA (mtDNA) haplotypes and nuclear DNA (nDNA) alleles with descendants of the earlier invasion (Currat et al. 2008, Chambers et al. 2012). This Pleistocene blending created a wide zone of mtDNA intergradation between the 2 genetic clades described by Leonard et al. (2005). The time of secondary contact between the earliest wolf immigrants and subsequent immigration events is not precisely known, but at the close of the Pleistocene (11,000 YBP), glacial withdrawal may have allowed entrance to the last wave of immigrants, now recognized as the Northwestern or Alaskan wolf (*C. l. occidentalis*), which currently occupies northern Alaska, western Canada, and (partly through human agency) the northern Rocky Mountains of the conterminous United States (Weckworth et al. 2010, 2011).

Mexican wolves are the primary extant carriers of an mtDNA lineage that has been hypothesized to reflect an early wave of wolves that entered North America from Eurasia during the Pleistocene (Vila et al. 1999, Weckworth et al. 2005, vonHoldt et al. 2011, Chambers et al. 2012). This lineage is not unique to Mexican wolves, and it is not known how prevalent it was in intermediate regions, such as the Southern Rockies, from which wolves have been extirpated.

At the close of the Pleistocene, most of the American Southwest was cloaked in woodland plant communities to elevations as low as 259 m (Van Devender 1977). This continuous block of woodland connected the southern Rocky Mountains, high-elevation forests in central Arizona and New Mexico, and the forested mountains throughout northern Mexico. Wolves at that time would have existed as a semi-continuous population across this woodland area. By 8,000 YBP, however, post-glacial climates caused rapid, widespread, and synchronous retreat of the southwestern woodlands northward and upslope, leaving behind a matrix of desert scrub and grassland in which isolated blocks of woodland persisted in the mountains of northern Mexico, central and southern Arizona, and New Mexico (Van Devender 1977, Van Devender and Spaulding 1979). After these relatively swift and dramatic changes, vegetation associations remained mostly unchanged for 8,000 years to the present (Van Devender and Spaulding 1979).

The primary prey of the Mexican wolf was Coues' white-tailed deer (*Odocoileus virginianus couesi*; Parsons 1996, Brown 2002), a diminutive subspecies (Heffelfinger 2006). Coues' white-tailed deer occur throughout the American Southwest, primarily in partially isolated mountains above 1,200 m (Heffelfinger 2006). Although it ranges up to 3,600 m (Bailey 1931), the highest densities of Coues' white-tailed deer are found between 1,200 m and 2,100 m (Knipe 1977, Heffelfinger 2006). This affinity to the higher-elevation Madrean pine (*Pinus* spp.)-oak (*Quercus* spp.) woodland areas results in a discontinuous distribution of ungulate biomass throughout the Southwest, separated by expanses of desert scrub and grasslands. Likewise, the distribution of the Mexican wolf corresponded closely to these elevations, habitat types, and prey distribution. According to Brown (2002:19), nearly all Mexican wolf specimens were collected in "pine-clad mountains, oak woodlands, pinyon-juniper forests, and intervening and adjacent grasslands above 4,500 feet" (1,372 m).

The fragmentation of habitat and prey distribution between the Sierra Madre and the southern Rocky Mountains could have reduced wolf movement across this region over the past 8,000 years, facilitating the accumulation of genetic traits adaptive to local ecological conditions. Mexican wolves have been recognized as genetically, morphologically, and ecologically differentiated

from other wolf subspecies (Bogan and Mehlhop 1983, Vila et al. 1999, vonHoldt et al. 2011).

HISTORICAL DESCRIPTION AND DISTRIBUTION OF THE MEXICAN WOLF

In considering the historical range of the Mexican wolf, topological taxonomic designations may not be as useful as the actual descriptions of phenotype made by the experts of the day (based on first-hand experience). These observers were familiar with the Mexican wolf at a time when it was common, and had experience across the region, including zones of intergradation between Mexican wolves and more northerly forms.

When Nelson and Goldman (1929:165) first described the Mexican wolf, they reported that it occurred in "Southern and western Arizona, southern New Mexico, and the Sierra Madre and adjoining tableland of Mexico as far south, at least, as southern Durango." They noted that north of this distribution "Specimens from the Escudilla Mountains in extreme east-central Arizona, and from the Mogollon Mountains region of New Mexico are generally larger and grayer and evidently grading toward the more northern *nubilus* type of animal" (Fig. 1).

In their seminal work, Young and Goldman (1944:469) described the historical range of the Mexican wolf as the "Sierra Madre and adjoining tableland region of western Mexico, formerly extending north to southeastern Arizona (Fort Bowie), southwestern New Mexico (Hatch), and western Texas (Fort Davis), south to the valley of Mexico; still living in the northern part of Sierra Madre, the exact southern and eastern limits undetermined. . . ." The southern-most record, from the state of Oaxaca, is of "an old male wolf, *C. lupus baileyi* . . . killed in March, 1945, in the vicinity of Tequisistlan . . ." (Goodwin 1969:224). Goldman (1944:465) described the wolves of the Mogollon Rim as "somewhat intermediate in characters, as well as geographic position, between *youngi* and the smaller race *baileyi*, which ranged north from the Sierra Madre and the high plateau region of Mexico into southeastern Arizona and southwestern New Mexico."

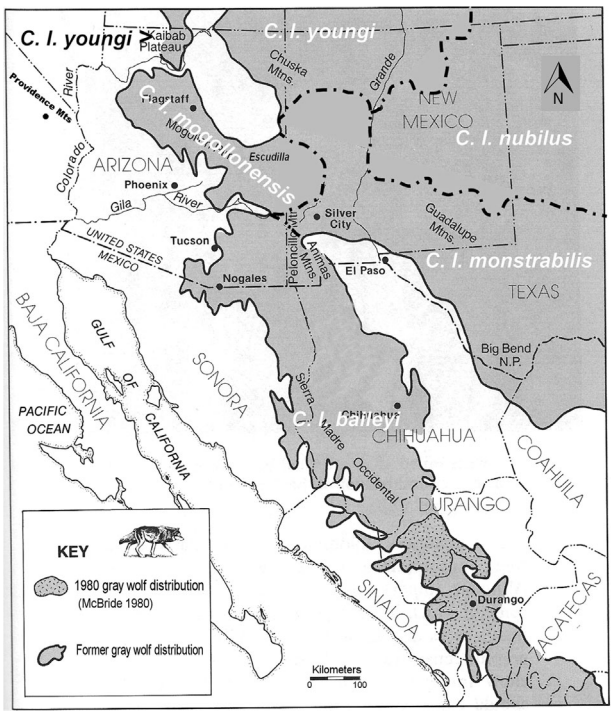

Figure 1. Historical range of southwestern wolves with subspecies designations noted (adapted from Brown 2002).

Young and Goldman (1944) and others described differences in distribution, overall size, and skull size and shape between Mexican wolves and other southwestern wolves. The Southern Rocky Mountain wolf (*C. l. youngi*) reportedly ranged from Utah and Wyoming down to northern Arizona and New Mexico. Nowak (1995, 2003) subsequently suggested the southern Rocky Mountain wolf is a synonym of the Great Plains wolf, which was the designation for the wolf throughout the Great Plains and south into northeastern New Mexico. Historical accounts clearly describe the wolves that formerly occupied the Great Plains, northern Arizona, and northern New Mexico as being larger and differentiated from the Mexican wolf (Nelson and Goldman 1929, Bailey 1931, Young and Goldman 1944; Fig. 1).

Just a few years after it was first described, Bailey (1931) delineated the northern limits of his eponym, indicating that specimens from the United States-Mexico border region were smaller than the Great Plains wolf (including the Southern Rocky Mountain wolf in northern New Mexico), but that a large series of skulls from the Mogollon Mountain region contained specimens more referable to the Great Plains wolf (Bailey 1931:303; Nowak 1995, 2003). The Mogollon Mountain wolf (*C. l. mogollonensis*) was "decidedly larger" than the Mexican wolf and said to occupy central Arizona across the Mogollon Rim and into New Mexico (Young and Goldman 1944). That wolf also was reportedly smaller than the Great Plains wolf to the north, and "On the south it passed rather abruptly into *C. l. baileyi*" (Young and Goldman 1944:464).

The Texas gray wolf (*C. l. monstrabilis*) was similar in size to the Great Plains wolf to the north and larger than the Mexican wolf (Young and Goldman 1944:467, Nowak 1995). The range of the Texas gray wolf was said to be "Formerly southern and most of western Texas (apparently replaced by *baileyi* in extreme western part), southeastern New Mexico, and south into northern Mexico. . ." (Young and Goldman 1944:466). The Mexican wolf was unknown in Texas until wolf populations native to the state were extirpated and an individual was killed near Fort Davis in western Texas in 1941 (Scudday 1977). This wolf "may have been a wanderer from northern Chihuahua" (Young and Goldman 1944:471).

The status of the Texas gray wolf in Mexico is uncertain. Young and Goldman (1944:414, 466, 468) indicated that its range extended across northeastern Mexico, including Coahuila, Nuevo Leon, and Tamaulipas, but the only specimen they listed, which was also the only record of the Texas gray wolf in Mexico noted by Hall (1981), was a skull

(United States National Museum [USNM] 1380) of disputed provenance (Bogan and Mehlhop 1983) from a small, young individual of unknown sex that does not closely resemble either the Texas gray wolf or the Mexican wolf. There thus is no material on which to reliably determine the kind of wolf that historically occurred east of Chihuahua. Leopold (1959) mentioned various records of wolves from the Sierra del Carmen in northwestern Coahuila, and Young and Goldman (1944:53) stated that wolves were continually entering the United States from Coahuila and from Chihuahua and Sonora. Baker (1956) wrote that the wolf formerly occurred throughout Coahuila but had become restricted to a few places in the West. He suggested that the Texas gray wolf may once have occurred in eastern Coahuila, and that the Mexican wolf was expanding eastward from Chihuahua into western Coahuila. McBride (1980) noted that wolves were apparently absent from northern and eastern Coahuila. They were only known to him southwest of Muzquiz, Coahuila (27°52′17.54″N, 101°31′7.05″W) on the eastern boundary of Chihuahua.

MORPHOMETRIC RELATIONSHIPS

There have been several efforts to evaluate large collections of wolf specimens. Bogan and Mehlhop (1983) analyzed measurements from 253 adult wolf skulls from throughout the Southwest and reported that wolves from northern New Mexico and southern Colorado were distinct from Mexican wolves in southeastern Arizona, southern New Mexico, and Mexico. Specimens from the Mogollon Rim in central Arizona were intermediate between those 2 forms, with females showing affinity to the larger northern group and males being more similar to Mexican wolves in the south. They recognized the Mogollon Rim as a wide zone of intergradation but suggested including wolves from this area (Mogollon Mountain wolves) with Mexican wolves. Such inclusion, which would effectively extend the range of Mexican wolves far north of southern Arizona and New Mexico, was considered forced by Brown (2002) and was contradicted by the morphometric analyses of Hoffmeister (1986) and Nowak (1995).

Hoffmeister (1986:466) noted a marked size difference between the measurements of 28 Mexican wolf skulls from southeastern Arizona and southwestern New Mexico when compared with 5 skulls from the Mogollon Rim. This led him to place Mogollon Mountain wolf in the synonymy of Southern Rocky Mountain wolf to the north, and retain Mexican wolf as a distinct subspecies. Nowak (1995) suggested a reduction in the number of recognized subspecies in the Southwest, and indeed throughout the Holarctic, but retained Mexican wolf and recommended against synonymizing the Mogollon Mountain wolf of the Mogollon Rim of Arizona and New Mexico with the Mexican wolf. His analysis showed the Mogollon Mountain wolf to have closer affinity to the larger wolves to the north, which he included with the Great Plains wolf. Whether one assigns the wolves of the Mogollon Rim to their northern or southern neighbor, what emerges from these morphometric studies is a consistent picture of a sharp difference in body size between the southern and northern portions of New Mexico and Arizona.

More recently, Hendricks et al. (2016) suggested the original range of the Mexican wolf extended as far west as southern California. This claim was based on the skull (Museum of Vertebrate Zoology [MVZ]:Mammals [MAMM]:33389) of a male wolf, collected in the Providence Mountains in the Mojave Desert in 1922 (Fig. 1), which had been assigned by Young and Goldman (1944) to Southern Rocky Mountain wolf. Hendricks et al. (2016) compared 15 measurements of that skull to those of the approximately 160 other complete North American male wolf skulls listed as gray wolves by Young and Goldman (1944) and O'Keefe et al. (2013:S1). Of those, Young and Goldman (1944) had identified 8 as Cascade Mountains wolf (*C. l. fuscus*), 17 as Great Plains wolf, 19 as Northern Rocky Mountain wolf (*C. l. irremotus*), 12 as Southern Rocky Mountain wolf, 7 as Texas gray wolf, and 11 as Mogollon Mountain wolf. Nowak (1995), however, had placed those 6 subspecies, which occupied the western half of the conterminous United States, in the synonymy of the Great Plains wolf, and both O'Keefe et al. (2013) and Hendricks et al. (2016) followed that procedure. Nowak (1995) also showed that one of the specimens, identified as Northern Rocky Mountain wolf by Young and Goldman (1944), most likely represented an invading individual of Northwestern or Alaskan wolf; that specimen is not considered in the following evaluation.

Hendricks et al. (2016: Appendix B) implied that the California specimen is morphometrically more similar to the Mexican wolf than to the Great Plains wolf (including Southern Rocky Mountain wolf). Nonetheless, a principal component analysis performed by Hendricks et al. (2016: Appendix C) indicated that morphometrically the California skull is not representative of Mexican wolf.

Individual specimens are sometimes difficult to assign to subspecies, and over the years, there has been some moderation in the reported overall characterization of the Mexican wolf. Nelson and Goldman (1929) presented a rather extensive suite of cranial and pelage features said to distinguish the subspecies. However, after a comprehensive review of all North American wolves, Young and Goldman (1944) could not refer to a single non-measurable character of the skull that clearly separated Mexican wolf from neighboring subspecies. It generally was described as a small, dark wolf, with a skull having a slender rostrum and widely spreading zygomata. In his comparison of Mexican wolf and Southern Rocky Mountain wolf (in which he included Mogollon Mountain wolf), Hoffmeister (1986) mentioned only the smaller size of the former, though he indicated that such distinction was pronounced and warranted subspecific designation. Hoffmeister's (1986) graphical analyses, mainly expressing size, show no overlap of Mexican wolf and southern Rocky Mountain wolf, though sample size of the latter was small. Nowak's (1995) multivariate analysis, using a much larger sample of Southern Rocky Mountain wolf and other subspecies that he placed in the synonymy of the Great Plains wolf, shows very little overlap between those others and Mexican wolf. The measurements that Nowak (1995) reported to contribute most to the separation of

Mexican wolf were reflective of some of the distinguishing characters originally pointed out by Nelson and Goldman (1929) and Young and Goldman (1944); small size, high skull, relatively widely spreading zygomata, and narrow rostrum.

In any case, there is agreement that small size, relative to other North American gray wolves, characterizes the Mexican wolf. Hoffmeister (1986) reported the Mexican wolf to even be smaller than some red wolves (*C. rufus*), though Nowak (1995) found Mexican wolves to be generally larger and that the skulls of the 2 taxa were completely separable by multivariate analysis. The skull of the male gray wolf collected in southern California in 1922, as discussed by Hendricks et al. (2016), is not small for the species. For the 6 nominal subspecies listed by Young and Goldman (1944) to occupy the western half of the conterminous United States (excluding Mexican wolf), the California skull exceeds the means of the combined sample of males in 11 of the 15 measurements (Table 1). The California skull exceeds the means of each of those 6 subspecies in $\geq$8 of the 15 measurements. The skull of this California wolf also exceeds the mean of each measurement of the 11 male Mexican wolves listed by Young and Goldman (1944) and exceeds all specimens of Mexican wolf in 12 of the 15 measurements. In his analyses, Nowak (1995) used 10 cranial measurements, mostly different from those of Young and Goldman (1944) but demonstrated the same pattern as above. Nowak (1995) placed the same 6 western subspecies, aside from Mexican wolf, in the synonymy of the Great Plains wolf. His sample of that group was 91 males. The California skull exceeds the mean of that combined sample in 7 of the 10 measurements, exceeds the means of every one of Young and Goldman's (1944) original subspecies in 6 of the 10 measurements, and exceeds the mean of 21 Mexican wolves in all 10 measurements (Table 2).

The southwestern wolf skulls available for study reveal a pattern of larger wolves in northern Arizona and New Mexico and smaller individuals in the southern parts of those states and in Mexico. These differences in skull morphometrics are valuable indices to the geographic barriers to gene flow contributing to the differentiation of infraspecific variation in phenotype. Because the Mexican wolf subspecies is listed under the ESA, understanding these differences is imperative to satisfy the legal mandate to recover the listed entity.

GENETIC RELATIONSHIPS

Leonard et al. (2005) analyzed mtDNA variation in 34 museum specimens of wolves from the west-central conterminous United States, a broad region some 2,000 km^2 from which there are no living descendants. They identified 2 haplotypes among 6 Mexican wolves (excluding their samples JAL 474, which was a coyote [*Canis latrans*], and JAL 477, which was a misidentified Great Plains wolf from Colorado). One of these haplotypes had a continental distribution, spanning from Alaska to Labrador to Mexico. The second haplotype was only observed in Mexican wolves, although it was similar to 3 other haplotypes detected immediately to the north, in a region spanning from Nebraska to Utah to northern New Mexico in their small sample set.

Leonard et al. (2005) hypothesized that the 4 related haplotypes with comparatively southerly observations, which they termed the southern clade, were a vestige of an early wave of immigration into the continent. However, that is not the only possibility. When random genetic drift is visualized as a coalescent process, in which a group of related haplotypes trace their ancestry to a single ancestral female, and when that process is layered over a real landscape under the constraint of finite female dispersal, it is inevitable that some clades will adopt geographic patterns. Even in a population system that is comparatively free of internal discontinuity, the descendants of a given female will be geographically associated. The data of Leonard et al. (2005) lack the power to test between the hypothesis that the southern clade reflects evolutionary history, and the hypothesis that the coalescence of this clade was in the south unrelated to population history, with the geographic pattern of its subsequent distribution reflecting only a spatially explicit coalescent process (i.e., random drift in the real world).

Notably, the observation of a continent-spanning mtDNA haplotype in the Mexican wolf is owed to 2 museum specimens, which could easily have escaped collection or analysis. Without these specimens, the temptation would have been to view the second, southern Mexican wolf haplotype as diagnostic of subspecies, and to interpret the lack of variation in this subspecies as evidence of isolation. This example illustrates the danger of assigning too much meaning to observations that are based on sample sizes that would be considered inadequate in a contemporary analysis of population genetics (or morphology), and emphasizes the extent to which our capacity to understand the historical population genetics of wolves was eroded when the species was extirpated from such a vast geographic region.

Hendricks et al. (2016) analyzed 6 historical specimens (including MVZ:MAMM:33389 from CA) and reported that the California specimen shared alleles at 4 single nucleotide polymorphisms (vonHoldt et al. 2011) and a mitochondrial haplotype, with Mexican wolves. Notwithstanding the small sample size and enormous sampling gap for intervening and surrounding regions, Hendricks et al. (2015, 2016) interpreted these genetic variants as diagnostic of Mexican wolf ancestry. We believe this interpretation oversteps the power of the data. Basing taxonomy below the species level on a few molecular markers, or indeed a single genetic marker (i.e., mtDNA), is problematic (Cronin 1993, Paetkau 1999). This problem is compounded by small sample size and discontinuous sampling.

The importance of continuous sampling is illustrated by work on the pronghorn (*Antilocapra americana*), where an initial genetic analysis detected northern and southern mtDNA clades (Lou 1998). Lee et al. (1994) sampled 330 pronghorn from 29 populations and reported that mtDNA haplotype A occurred at high frequencies in populations within the historical range of the Mexican pronghorn (*A. a. mexicana*). Subsequently, Reat et al. (1999) analyzed another

Table 1. Means of 15 cranial measurements of male wolves listed by Young and Goldman (1944) for the 6 nominal subspecies they reported to occupy the western half of the conterminous United States, Mexican wolves, and comparative measurements of the skull (MVZ:MAMM:33389) of a male wolf collected in the Providence Mountains in the Mojave Desert, California, USA, 1922.

Group, identified by Young and Goldman's (1944) original name	*N*	Greatest length	Condylobasal length	Zygomatic breadth	Squamosal constriction	Width of rostrum	Interorbital breadth	Postorbital constriction	Length of mandible	Height of coronoid process	Maxillary tooth row, crown length	Upper carnassial, crown length (outer side)	Upper carnassial crown width	First upper molar, antero-posterior diameter	First upper molar, transverse diameter	Lower carnassial, crown length
Cascade Mountains wolf (*C. lupus fuscus*)	8	256.6	237.4	137.7	78.63	44.91	49.33	42.68	185.45	81.49	106.54	25.45	13.90	16.70	22.79	29.14
Northern Rocky Mountain wolf (*C. l. irremotus*)	19	258.9	239.7	140.5	79.77	46.17	45.82	37.99	184.48	76.19	107.88	25.91	14.18	17.03	23.24	29.47
Mogollon Mountain wolf (*C. l. mogollonensis*)	11	255.8	233.7	140.6	81.26	45.19	46.43	40.34	182.36	78.42	105.03	25.52	14.42	16.55	22.78	29.16
Texas gray wolf (*C. l. monstrabilis*)	7	255.8	234.8	136.9	78.30	45.50	45.61	39.61	178.99	77.80	105.86	25.83	14.49	16.56	23.03	29.46
Great Plains wolf (*C. l. nubilus*)	17	253.9	233.5	136.8	77.52	44.94	47.06	39.10	180.90	76.86	106.42	25.45	13.87	16.70	22.92	29.29
Southern Rocky Mountain wolf (*C. l. youngi*)	11	258.6	242.3	141.9	80.95	47.26	47.53	40.94	187.94	78.23	109.16	25.70	13.98	16.89	22.92	29.46
Above combined	75	256.6	236.9	139.2	79.36	45.67	46.84	39.75	183.35	77.95	106.91	25.65	14.11	16.77	22.97	29.34
California 1922 (MVZ:33389)	1	252.1	232.3	150.0	80.0	44.9	49.0	44.9	186.2	82.6	107.4	25.9	15.1	17.1	22.7	30.1
Mexican wolf (*C. l. baileyi*)	11	241.0	222.3	134.5	76.80	41.10	43.06	38.26	171.28	74.57	99.93	24.85	13.21	15.81	20.92	27.04

Table 2. Means of 10 cranial measurements of male wolves listed by Nowak (1995) for the 6 nominal subspecies reported by Young and Goldman (1944) to occupy the western half of the conterminous United States and Mexican wolves, and comparative measurements of the skull (MVZ:MAMM:33389) of a male wolf collected in the Providence Mountains in the Mojave Desert, California, USA, 1922.

Group, identified by Young and Goldman's (1944) original name	*N*	Greatest length	Zygomatic breadth	Alveolar length of maxillary tooth row	Maximum width across upper cheek teeth	Palatal width at first premolars	Width of frontal shield	Height from tooth row to orbit	Depth of jugal	Crown length of upper carnassial	Crown width of second upper molar
Cascade Mountains wolf (*C. lupus fuscus)*	10	257.4	138.7	85.82	81.71	31.33	69.29	40.67	20.72	25.52	13.47
Northern Rocky Mountain wolf (*C. l. irremotus*)	14	253.9	139.7	86.41	83.14	31.13	62.74	38.98	18.99	25.52	13.47
Mogollon Mountain wolf (*C. l. mogollonensis*)	17	253.5	140.4	84.34	81.11	31.06	66.65	39.81	19.26	25.37	13.65
Texas gray wolf (*C. l. monstrabilis*)	7	257.4	138.3	84.40	79.51	31.63	65.06	40.27	18.84	25.56	13.16
Great Plains wolf (*C. l. nubilus*)	15	256.7	137.5	84.93	80.55	31.95	65.57	39.87	19.77	25.39	13.19
Southern Rocky Mountain wolf (*C. l. youngi*)	28	257.5	140.0	86.25	83.18	32.79	66.55	39.45	19.89	25.65	13.81
Above combined	91	256.0	139.3	85.51	81.91	31.82	66.01	39.71	19.62	25.51	13.54
California 1922 (MVZ:33389)		252.1	150.0	86.8	80.9	32.2	70.2	41.5	19.0	25.9	14.5
Mexican wolf (*C. l. baileyi*)	21	243.9	136.3	81.78	77.40	29.98	60.62	38.95	18.79	24.49	12.59

389 samples from Arizona and documented that haplotype A was the most common and widely distributed haplotype throughout the range of the northern subspecies (*A. a. americana*) in that state, rendering it of no use in describing the historical range of Mexican pronghorn.

Even if mtDNA patterns have their origins in population history, they may not reflect current population relationships. For example, a relictual polar bear (*Ursus maritimus*) population that is thought to have become isolated at the end of the Pleistocene in the Alexander Archipelago of southeast Alaska retains the mitochondrial signal of its polar bear matriline, but 92–94% of its genome has been converted to brown bear (*U. arctos*) ancestry through male-mediate gene flow into the islands (Cahill et al. 2015). The contemporary population relationships in these islands are with geographically neighboring brown bear populations (Paetkau et al. 1998), notwithstanding the pure polar bear mitochondrial ancestry. This includes genetic exchange between semi-isolated pockets of large coastal brown bears, which are not a cohesive genetic group, and neighboring interior populations of the dramatically smaller-bodied ecotype (grizzly bears). There are several other mtDNA discontinuities in the North American range of brown bears (Waits et al. 1998), the historical meaning of which is less clear, and none of these mtDNA boundaries are associated with meaningful discontinuities in contemporary genetic structure (Paetkau et al. 1998). By contrast, the bears of the Kodiak Archipelago are thought to have been demographically isolated since the end of the Pleistocene but show no meaningful mtDNA differentiation (Talbot and Shields 1996).

In contemporary population genetics, we understand that the power and accuracy of an analysis of individual origins hinges on having a sample size from each potential source population on the order of 30–50 individuals, with each individual genotyped at a number of markers sufficient to reasonably sample the independently assorting regions of the genome, thus averaging out the random effects of drift on any one part of the genome (Paetkau et al. 2004). Furthermore, we apply statistical testing to assess whether a given individual's ancestry can be assigned to a particular population by ruling out all the others (Piry et al. 2004). If we observe a particular genetic variant in a few individuals from location A, and in one individual from location Z, we cannot automatically assume populations at locations A and Z are the same, especially with a large sampling gap around, and between, those 2 locations. This is effectively what has been done by recommending the expansion of the known range of Mexican wolves based on one morphologically large (Great Plains wolf) specimen from California that carries some genetic variants that are also common in a small sample of Mexican wolves, and that may or may not have been common elsewhere throughout their range. This single individual's genotype does not provide a rigorous basis for assuming a special historical relationship between geographically separated regions in a poorly sampled landscape.

The recommendation that southern California and parts of Baja California be added to the recognized range of the Mexican wolf creates interesting tension around the definition of the subspecies. It is an expectation of taxonomic thinking that subspecies be rooted in geography and that the members of a subspecies be more closely related to one another than to members of other subspecies (Brewster and Fritts 1995). As illustrated by the case of coastal Alaskan brown bears, ecological factors (the availability of a rich food resource in the form of salmon) can bring about similar and dramatic changes in body size, appearance, and reproductive parameters in populations that are not directly connected by gene flow. This superficial convergence caused coastal brown bear populations that are isolated from one another, but connected through interior grizzly bear populations, to be erroneously grouped as a subspecies (Paetkau et al. 1998).

Returning to the case of the Mexican wolf, if the California specimen were grouped with Mexican wolves by morphology, which it turns out not to be (above), it would be unclear whether this reflected parallel changes driven by common ecological forces, or historical association between regions. Furthermore, we are only beginning to understand the extent to which heritable changes in gene expression in response to environmental conditions (epigenetics) can facilitate phenotypic adaptation (Bossdorf et al. 2008).

Similarly, the observation that models can identify suitable habitat for Mexican wolves east and west of the Nevada and western Arizona deserts does not argue that wolves on either side of that void share common history, any more than the identification of a patch of similar habitat on a different continent would. Given that the populations connecting these regions did not share a long and open genetic boundary, it is not plausible that wolves east and west of these desert areas would be members of a single cohesive group, namely Mexican wolf, notwithstanding the ecological commonalities that might exist between these regions.

An artificially inflated historical range based on fragmented sampling of molecular markers could lead to recovery planning and actions that are not only a breach of legal responsibilities but ecologically problematic. Implementation of recovery plans based on erroneous information may have irreversible consequences if the listed entity is exposed to hybridization with nonlisted conspecifics or ill-adapted to extralimital ecological conditions.

MOVEMENT AND EXTRALIMITAL REPORTS OF MEXICAN WOLVES

Wolves sometimes make long-distance movements (Fritts 1983, Linnell et al. 2005, Wabakken et al. 2006), although dispersal may occur more often to areas within familiar habitats (Gese and Mech 1991, Geffen et al. 2004, Muñoz-Fuentes et al. 2009). Although they undoubtedly made such movements in historical times, we have no evidence to demonstrate how far north Mexican wolves may have routinely traveled. Differentiation along ecological breaks in vegetation associations or prey type has been documented in wolves in Europe and North America, even well within their dispersal distance (Geffen et al. 2004; Carmichael et al. 2007; Musiani et al. 2007; Muñoz-Fuentes et al. 2009; Weckworth et al. 2011). The phenotypic differentiation of the Mexican

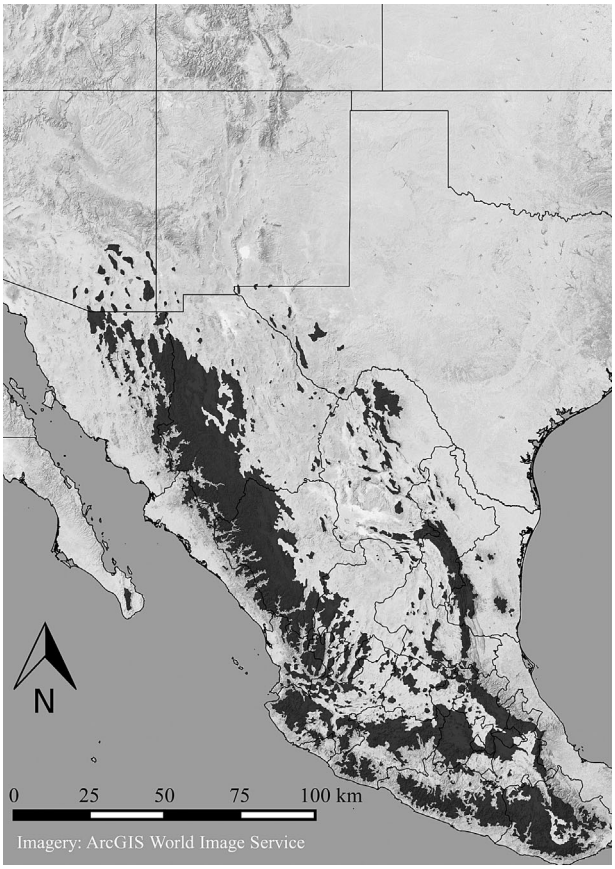

Figure 2. Genetic and phenotypic differences in animals have been documented to align with ecological boundaries and the distribution of the Madrean pine-oak woodlands (dark gray) is concordant with the historical distribution of the Mexican wolf and many other iconic southwestern subspecies.

wolf is concordant with the geographic range of the Madrean pine-oak woodlands (Fig. 2) and other endemic subspecies of this vegetation association (e.g., Montezuma quail [*Cyrtonyx montezumae mearnsi*], Coues' white-tailed deer, Gould's turkey [*Meleagris gallopavo mexicana*]). Differences in prey and vegetation associations are consistent with the original description of Mexican wolf range (Brown 1982, Heffelfinger 2006).

There have not been any wolves described phenotypically as Mexican wolves documented north of Arizona or New Mexico. The historical accounts contain a few instances of possible Mexican wolves outside the traditionally recognized historical range. It is important to address the circumstances of each report to assess its relevancy toward recovery planning.

1. Young and Goldman (1944) present a picture that appears to be a wolf killed in 1921 near Truxton, in northwestern Arizona, but do not list it anywhere as a specimen examined (Fig. 3). Because this specimen was not preserved and has not been available to be examined in subsequent analyses (Bogan and Mehlhop 1983, Hoffmeister 1986, Gipson and Ballard 1998, Boitani 2003:321, Nowak 2003), its origin, taxonomic status, and validity as a wolf are unknown.
2. Nowak (1995:385) described a male Mexican wolf that was killed in 1957 near Concho, Arizona (Fig. 3). This wolf aligns morphometrically with Mexican wolf, but was collected within the range of Mogollon Mountain wolf, as designated at the time. Hoffmeister (1986) also discussed a specimen taken in 1935 about 150 km farther south, near Clifton, and assigned it to Southern Rocky Mountain wolf on a geographical basis but expressed doubt as to whether it actually belonged to that subspecies. Nowak (1995), who suggested that Southern Rocky Mountain wolf is part of the Great Plains wolf, did not subject that specimen (USNM 251527) to multivariate analysis because it lacked several necessary components (in particular, the bones of the zygomatic arch were missing, which precluded measurements of zygomatic width, height to orbit, and depth of jugal).
3. The somewhat famous wolf (or wolves) known as the Aguila Wolf was killed by Charlie Gillham in 1924 after being credited with an 8-year spree of livestock depredation. This wolf reportedly ranged in low-elevation Sonoran Desert and semi-desert grasslands north and west of Wickenburg, Arizona (Brown 2002; Fig. 3), but it is morphometrically referable to the Great Plains wolf (Hoffmeister 1986:469).
4. Two male wolves were killed in 1970 in Brewster County about 27 km south of the town of Alpine, Texas (Scudday 1972; Fig. 3). Skull measurements of these 2 wolves (Sul Ross State University [SRSU]1258, SRSU1261) were consistent with those of Mexican wolves. Because both animals were the same age and the first wolves known in the area in decades, they were assumed to be littermates that had traveled up from Mexico. Brown (2002:99–100) indicated that several other Mexican wolves had crossed from Mexico and been killed in Brewster County in the late 1920s, but there is only 1 additional extant specimen of Mexican wolf from Texas, a female killed 26 km northwest of Fort Davis (Fig. 3). That specimen is the basis of Young and Goldman's (1944) and Hall's (1981) inclusion of west Texas in the historical range of the subspecies. Although Scudday (1972) indicated the animal had been taken in 1944, the tag on the skull (USNM 266568) shows the actual date as 1941. Young and Goldman (1944:53, 471) wrote that wolves had been believed extirpated in that area, and they did not include any part of Texas in their description of the then current range of gray wolf, further suggesting the Fort Davis animal was a wanderer from northern Chihuahua. In 1942, a male gray wolf was killed nearby, in the vicinity of Presidio on the Rio Grande; the skull is in the United States National Museum (272332) and identified as a Texas gray wolf. It was not available to Young and Goldman (1944:466), who thought Texas gray wolf was probably extinct. In greatest length (257.0 mm), the skull exceeds all available specimens of Mexican wolves, though in other dimensions it is equaled or slightly exceeded by a few skulls of Mexican wolves.
5. Leonard et al. (2005) erroneously reported as Mexican wolves 2 specimens (USNM 3188 and USNM 3191)

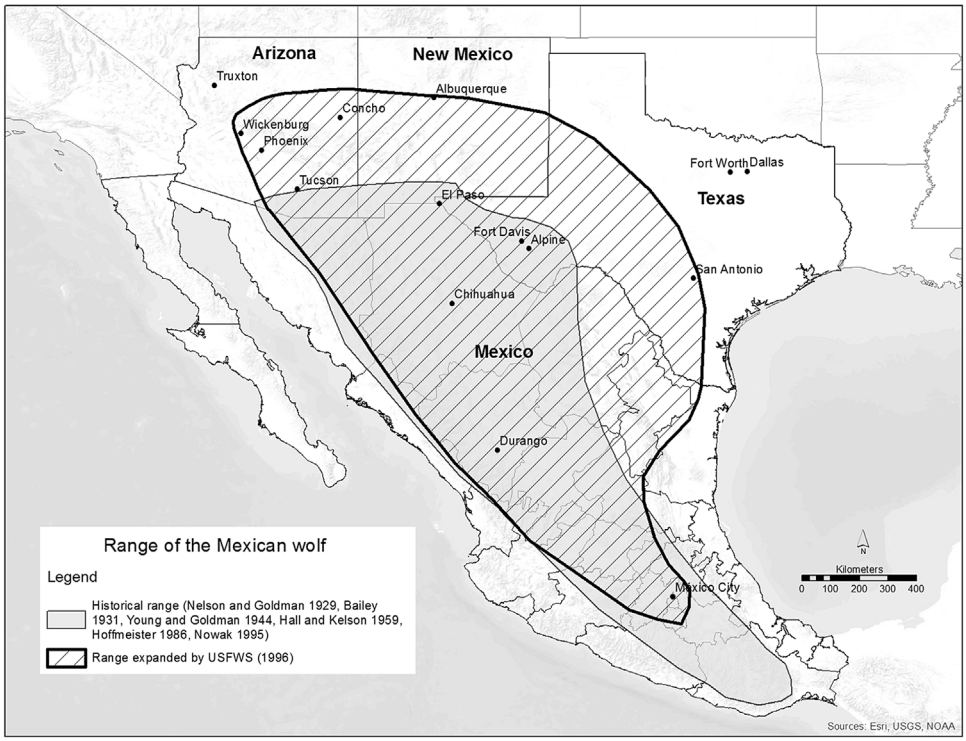

Figure 3. Generalized historical range of the Mexican wolf defined by most authorities compared with the range expanded by Parsons (1996) and adopted by the United States Fish and Wildlife Service (USFWS 1996:1–4) as "probable historic range."

collected in 1856 near Fort Massachusetts in the San Luis Valley of extreme southern Colorado. These were reported to have been collected in New Mexico because of confusion resulting from Fort Massachusetts having been in New Mexico Territory at the time but later being included in the boundaries of the state of Colorado. These 2 specimens were labeled Great Plains wolf when collected in 1856 and Hailer and Leonard (2008) clarified them to be Great Plains wolf.

RECENT RECOMMENDATIONS TO EXPAND HISTORICAL RANGE

Notwithstanding some disagreement on the status of wolves from the Mogollon Rim (above), most sources prior to the mid-1990s were in agreement and defined the historical range of the Mexican wolf as southeastern Arizona, southwestern New Mexico, and portions of Mexico (Nelson and Goldman 1929, Bailey 1931, Young and Goldman 1944, Hall and Kelson 1959, Hall 1981). Of this historical range (Fig. 3), 10% occurs in the United States (99,852 km^2) and the remainder in Mexico (885,064 km^2). More recently, Hoffmeister (1986) and Nowak (1995, 2003) agreed with those previous sources.

Based on a review of ecological, morphological, and genetic data, Parsons (1996:106) published a map that "defines the 'probable historic range' of *C. l. baileyi* for the purposes of reintroducing Mexican wolves in the wild in accordance with provisions of the ESA and its regulations." This new range map (Fig. 3), which was accepted by the Mexican Wolf Recovery Team (USFWS 1996), added a 322-km (i.e., 200-mile) buffer to the existing range, citing the dispersal capacity of wolves, and thus aligned with Bogan and Mehlhop (1983) and against Hoffmeister (1986) and Nowak (1995, 2003) in regards to the status of the intermediate form, Mogollon Mountain wolf. This range map was adopted and included in the 1996 Federal Environmental Impact Statement (USFWS 1996) as the probable historical range of the Mexican wolf. The current wild population of Mexican wolves in the United States resides within the expanded 322-km buffer, north of the historically described range.

In 2003, the USFWS established 3 Distinct Population Segments (DPS) for wolves nationwide, including a Southwestern DPS covering Arizona, New Mexico, southern Utah, southern Colorado, western Texas, and western Oklahoma (USFWS 2003). This was a significant expansion far outside any earlier depiction of Mexican wolf historical range. Soon after the establishment of the Southwestern DPS, a recovery team was assembled and began working on a revision to the 1982 Recovery Plan (USFWS 2010). Court rulings in 2005, however, voided the 3 DPSs and all recovery planning ceased, including the recovery of Mexican wolves in Utah and Colorado.

In December 2010, a new Mexican Wolf Recovery Team (MWRT) was assembled to revise the 1982 plan (USFWS 1982). After working for 1 year, a draft Recovery Plan was presented by the Science and Planning Subgroup (SPS) to the full MWRT (USFWS, unpublished report). This draft included recovery criteria that established 2 of 3 recovery areas outside of "probable historic range" as defined in the 1996 Final Environmental Impact Statement (USFWS

1996:1–3, Parsons 1996). Much of the justification for this additional range expansion relied on the presence of southern clade (Leonard et al. 2005) haplotypes in Nebraska and northern Utah, which we reject as an inadequate method for assessing population relationships (above). This second major expansion of the historical range of the Mexican wolf northward was also rationalized by the SPS based on the ability of wolves to disperse long distances from the already-expanded range, opening the door to an endless logical loop of additional buffers justified by dispersal capacity. Indeed, the longest straight-line movement documented by a wolf is >1,000 km (Wabakken et al. 2006), which, under this logical framework, would expand Mexican wolf historical range to the Arctic Circle in just a few iterations.

Hendricks et al. (2016) argued that the historical range of the Mexican wolf has been underestimated because it was based on a small number of specimens, genetic markers common in current Mexican wolves were found in wolves collected outside historical range, and ecologically suitable habitat exists outside the historical range of the Mexican wolf. However, the substantial records of southwestern wolf phenotype and skull morphometrics provide a unified depiction of historical range for the Mexican wolf, the genetic analysis is weakened to the point of inutility by inadequate sampling prior to extirpation, and the existence of suitable habitat in geographically disjunct locations is not evidence of a taxon's existence in those locations, wherever they may be.

Despite reporting and depicting suitable habitat, the Hendricks et al. (2016) distributional model actually reflects probability of occurrence based on collection locations of historical Mexican wolf specimens. After including all northern (Great Plains wolf) samples possessing a southern clade haplotype, the model results show southern Oregon has the same probability of occurrence of Mexican wolves as the southwestern areas purported to be newly discovered historical range, including the collection location of the California specimen (MVZ:MAMM:33389; Hendricks et al. 2015:figure 2). Even with the inclusion of northern wolves to train the model for Mexican wolf habitat, 4 of 7 wolves with a southern clade mitochondrial haplotype are still in areas mapped as unsuitable (Hendricks et al. 2016: figure 2). Regardless, the relative suitability of habitat to an animal that thrives from deserts to the arctic is not relevant to the accurate description of its historical range. Further, the designation of habitat by Hendricks et al. (2016: figure 2) as "Not suitable due to human activity and land cover" is largely truncated at the United States-Mexico border, indicating this factor is depicted as either overly pessimistic in Mexico or overly optimistic in the United States, thereby casting doubt on its accuracy and usefulness as a model parameter in this case.

MANAGEMENT IMPLICATIONS

Defining the historical distribution of Mexican wolves is important because of its direct bearing on how parts of the ESA are implemented. Recovery efforts attempted outside the subspecies' historical range when suitable habitat exists within would make the program vulnerable to legal challenge, thereby delaying recovery of this endangered subspecies (Parsons 1996).

The Mexican wolf was defined by expert observers who had the opportunity to view the animal in numbers in the wild, and who identified an unequivocal reduction in body size that they viewed as worthy of taxonomic distinction. The range of this subspecies was bounded by plausible geographic discontinuities in the form of scrub and grassland north and south of the Mogollon Rim. Although contemporary workers continue to accept the conclusion of those early experts, that the Mexican wolf is an identifiable and distinct entity, some have recommended repeated range expansions. Extending the historical range north and west of central Arizona and New Mexico would not only dismiss the scientific evidence upon which the Mexican wolf was originally based, it would locate a subspecies boundary well into the vast contiguous range to the north, where there is no plausible basis for a genetic discontinuity of the sort needed to permit the development and retention of the unique qualities that define a subspecies.

Recent recommendations to extend the historical range far to the north and west have placed heavy weight on the detection of genetic variants that are also observed in the Mexican wolf. However, because of low sample sizes and discontinuous sampling, the genetic data lack the power to explicitly test competing hypotheses, one of which is that the distribution of genetic variants by the forces of random genetic drift created geographic associations that are not diagnostic of population history. Unfortunately, the loss of surrounding populations without adequate sampling probably means that genetic tools will never have the power to prove or disprove hypotheses regarding the locations of historical genetic discontinuities in the southern range of North American wolves.

The original and subsequent descriptions of Mexican wolf historical range (Fig. 3; Nelson and Goldman 1929; Young and Goldman 1944; Nowak 1979, 1995, 2003), remain the most defensible. Given this historical range and the recent success shown by rapid growth of the wild population of Mexican wolves, the most scientifically sound approach is to base recovery efforts within the range accepted by USFWS in 1996 (Fig. 3).

The historical range of the Mexican wolf should not be altered through the identification of similar habitat in other locations, the distribution of inadequately sampled molecular markers, or by theoretical arguments about movement capacity. Rather, it should respect the original expert descriptions that were made when the animal was still present on the landscape, and which are concordant with ecological relationships, physiography, morphology, and the principles of population genetics.

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