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Perspective

Perils of recovering the Mexican wolf outside of its historical range

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ABSTRACT

The Mexican wolf (*Canis lupus baileyi*) was included in the 1973 Endangered Species Act listing of the gray wolf (*C. lupus*), but then listed separately as a subspecies in 2015. Early accounts of its range included the Sierra Madre Occidental of Mexico, southeastern Arizona, southwestern New Mexico, and sometimes western Texas, supported by ecological, biogeographic, and morphological data. There have been multiple unsuccessful attempts to revise the original 1982 recovery plan and identify areas suitable for Mexican wolf reintroduction. Despite the fact that 90% of its historical range is in Mexico and widespread suitable habitat exists there, previous draft recovery plans recommended recovery mostly outside of Mexico and well north of the subspecies' historical range. Planning recovery outside historical range of this subspecies is fraught with problems that may compromise, thwart, or impede successful recovery. Dispersal of Mexican wolves northward and continued movements southward by Northwestern wolves (*C. l. occidentalis*), along with allowing establishment of Mexican wolves north of their historical range before they are recovered, may lead to premature and detrimental intraspecific hybridization. Interbreeding of Northwestern wolves from Canadian sources and Mexican wolves does not represent the historical cline of body size and genetic diversity in the Southwest. If Northwestern wolves come to occupy Mexican wolf recovery areas, these physically larger wolves are likely to dominate smaller Mexican wolves and quickly occupy breeding positions, as will their hybrid offspring. Hybrid population(s) thus derived will not contribute towards recovery because they will significantly threaten integrity of the listed entity. Directing Mexican wolf recovery northward outside historical range threatens the genetic integrity and recovery of the subspecies, is inconsistent with the current 10(j) regulations under the ESA, is unnecessary because large tracts of suitable habitat exist within historical range, is inconsistent with the concepts of restoration ecology, and disregards unique characteristics for which the Mexican wolf remains listed.

1. Mexican wolf recovery efforts

Federal efforts to prevent the extinction of the Mexican wolf (*Canis lupus baileyi*) began with the passage of the Endangered Species Act (ESA) in 1973 when this subspecies was included in the listing of *Canis lupus* at the species level. Wolf taxonomy has undergone review through time, including a substantial revision through which the number of recognized subspecies of the gray wolf in North America was reduced from 24 to 5 (Nowak, 1995). Throughout these revisions, however, the Mexican wolf subspecies has always been recognized as the most morphologically and genetically unique of all North American *C. lupus* subspecies (Vilá et al., 1999; Nowak, 1995, 2003; vonHoldt et al., 2011, 2016).

In 2015, the United States Fish and Wildlife Service (USFWS) amended the status of the subspecies *C. l. baileyi* by individually listing it as an endangered subspecies, and importantly, as a separate entity from all other *C. lupus* (U. S. Fish and Wildlife Service, 2015a). By listing the Mexican wolf subspecies separately, the USFWS clearly intended to protect, conserve, and recover the unique characteristics of this subspecies and the habitats upon which it relies.

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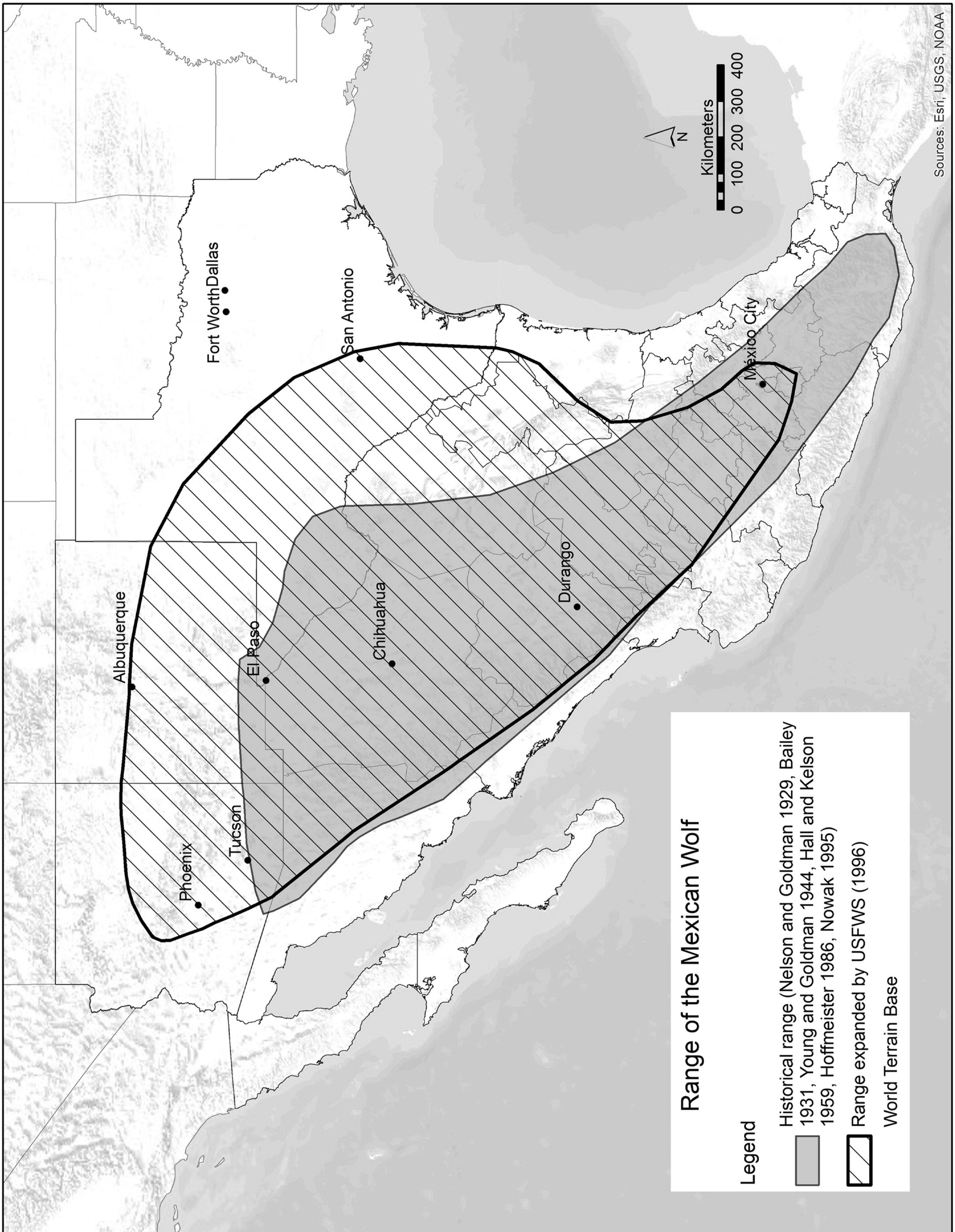

Fig. 1. Range of the Mexican wolf (*Canis lupus baileyi*). Depicted are both the historical range defined by most authorities compared with the range expanded by Parsons (1996) and adopted by USFWS (1996) as "probable historic range."

The original recovery plan for the Mexican wolf, finalized in 1982, includes a prime objective: "To conserve and ensure the survival of *Canis lupus baileyi* by maintaining a captive breeding program and re-establishing a viable, self-sustaining population of at least 100 Mexican wolves in the middle to high elevations of a 5000-square-mile area within the Mexican wolf's historic range." (USFWS, 1982).

When the 1982 recovery plan was drafted there were no known wild Mexican wolves in the United States or Mexico. Therefore, recovery would require establishment of a reintroduced population within the subspecies' historical range. In the 1996 final Environmental Impact Statement "Reintroduction of the Mexican Wolf Within Historic Range in the Southwestern United States" the USFWS recognized that the proposed 1998 reintroduction site in central Arizona was already at the northern extent of an expanded definition of probable historical range that "included the core geographic range of *C. l. baileyi*, plus an approximately 200-mile extension to the north and northwest of that area" (USFWS, 1996:1–3, Fig. 1–1). Mexican wolves have been released in east-central Arizona and west-central New Mexico, where the population is currently managed by an interagency field team consisting of state, federal, and tribal agencies. The USFWS has initiated 3 separate attempts (1995, 2003, 2010) to revise the 1982 Recovery Plan, but none have been successful. Two contentious issues central to past attempts to revise the recovery plan were identifying specific areas where future recovery will occur and developing criteria for determining recovery and delisting.

2. Geography of recovery considerations

2.1. Historical range

The historical range of the Mexican wolf has been an important topic of discussion by past Mexican wolf recovery teams because it is central to achieving an effective and scientifically defensible recovery plan. 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." Subsequent authors concurred with this original range description (Heffelfinger et al., 2017a and citations therein). Further, Heffelfinger et al. (2017a) assessed the historical, morphological and genetic information and clarified the historical range of the Mexican wolf, aligning it with the original descriptions made when the animal was still on the landscape.

Citing Bogan and Mehlhop (1983) and the dispersal capacity of wolves in general, Parsons (1996:104) 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 was accepted by the Mexican Wolf Recovery Team (USFWS, 1996), which effectively added a 322-km dispersal buffer to the recognized historical range (Fig. 1).

Recent suggestions (Leonard et al., 2005; Hendricks et al., 2016; Hendricks et al., 2017) to depict a more extensive northern periphery have been based primarily on a fragmented geographic sampling of genetic markers assumed to be diagnostic at the subspecies level (Heffelfinger et al., 2017a,b). Some such markers, found in extant Mexican wolves, also occur in a few phenotypically large individuals as far north as Nebraska and northern Utah and as far west as California. Extending the historical range of the Mexican wolf northward to that degree is in conflict with well-documented transitions in wolf phenotype (Bogan and Mehlhop, 1983; Hoffmeister, 1986; Nowak, 1995, 2003), differences in vegetation associations (Geffen et al., 2004), restrictions to gene flow (Van Devender and Spaulding, 1979), and dramatic differences in prey base (Carmichael et al., 2001). The detection of these genetic markers in a few museum specimens does not help inform the historical distribution of gray wolf subspecies. Not enough is known about the historical distribution of these scattered and sporadically sampled genetic markers to warrant dramatic changes to the well-established historical distribution of the Mexican wolf (Heffelfinger et al., 2017a,b).

All sources prior to the mid-1990s were in agreement that core historical range of the Mexican wolf included southeastern Arizona, southwestern New Mexico, and portions of Mexico with some intergrade in central Arizona and New Mexico (Bogan and Mehlhop, 1983). Of this historical range, about 90% occurs in Mexico (885,064 km^2) with the remainder in the United States (99,852 km^2, Fig. 1).

The importance of recovery within historical range has been well articulated in the literature (Robinson, 2005; Vucetich et al., 2006; Carroll et al., 2010). The historical distribution, ecological adaptations, and evolutionary history of the Mexican wolf dictate that historical range in Mexico serve as the focal area for recovery. Mexico's version of a recovery plan, the Programa de Acción (PACE), was finalized in 2009 with the participation of a wolf technical advisory subcommittee. This action plan established the necessary steps to reintroduce Mexican wolves in Mexico (CONANP, 2009).

2.2. Habitat suitability in Mexico

Several studies have assessed habitat-quality and suitability for the Mexican wolf in the U.S. and Mexico (Araiza, 2001; Carroll et al., 2005, 2006; Martínez-Gutiérrez, 2007; Araiza et al., 2012; Hendricks et al. 2016; USFWS 2017: Appendix B). Despite different methodologies, these studies have identified remaining habitat patches in both countries. In a model very similar to Carroll et al. (2006), considered the best available science in the 2010–2012 recovery planning effort, Carroll et al. (2005) estimated that suitable habitat in Mexico could support up to 2600 wolves.

To address ESA regulations requiring reestablishment of populations within historical range of the subspecies, an updated habitat suitability analysis was developed in conjunction with the current recovery plan (USFWS, 2017: Appendix B). This analysis used global datasets and geospatial data blended for both countries to allow for a consistent bi-national evaluation of habitat suitability and was considered the best available information of environmental, vegetative, topographic, and human presence (population density and road density) across the historical range of *C. l. baileyi*. This detailed habitat suitability analysis indicates that the current wild population of Mexican wolves in the United States is near the northern periphery of the climatic and vegetative niche defined by historical specimen locations (USFWS, 2017: Appendix B). Results indicate that the Sierra Madre Occidental forms a continuum of suitable habitat that includes at least 64,000 km^2 of high-quality habitat surrounded by a connected matrix of lower quality habitat centered in the mountains of Sonora, Chihuahua, Durango, Zacatecas, and Jalisco. In addition, suitable habitat also exists in the Sierra Madre Oriental, in the states of Coahuila, Nuevo León, Tamaulipas, and San Luis Potosí in smaller, more scattered patches that include around 9259 km^2 of high-quality habitat (USFWS, 2017: Appendix B). In the United States, blocks of high-quality habitat were found in the current Mexican Wolf Experimental Population Area (MWEPA) in Arizona-New Mexico, which has been the focus of most recovery efforts to date. These spatially-explicit analyses are a valuable first step in identifying potential recovery areas to direct and focus subsequent efforts. Further work to quantify prey availability and evaluate human attitudes towards wolves in suitable habitat is an important element for successful wolf recovery. (USFWS, 2017: Appendix B).

2.3. Significant portion of range

The ESA provides for the conservation of threatened and endangered species defined as one "which is in danger of extinction throughout all or a significant portion of its range…" or likely to become so in the foreseeable future (16 U.S.C. § 1532). Some have suggested the significant portion of range language should require restoration of the species to the majority of its historical range before delisting (Vucetich et al., 2006; Carroll et al., 2010). If this interpretation were ever accepted, the Mexican wolf could not be recovered without a significant portion of recovery occurring in Mexico.

Recovery frameworks are often based on the ecological principles of Representation, Resiliency, and Redundancy (Shaffer and Stein, 2000; Wolf et al., 2015). These emphasize establishment and protection of populations across the range of ecological communities in historical range (Representation), recovery of ecologically effective populations (Resiliency), and more than one population recovered (Redundancy) (Shaffer and Stein, 2000; Wolf et al., 2015). These principles can only be satisfied if Mexico plays a major role in recovering the Mexican wolf; population viability analyses show that recovery depends upon this (USFWS, 2017: Appendix A). The Sierra Madre Occidental region in Mexico was identified in the most recent spatially explicit analyses as highly suitable for successful wolf recovery based on climate, vegetation association and 2 measures of human threat (road density and human habitation). Excluding, or marginalizing, this vast area from Mexican wolf recovery in favor of ecological environments in the U.S. unrelated to those in which the subspecies evolved is clearly inconsistent with the principles of representation and resiliency.

2.4. Legal framework

Although the ESA does not explicitly mandate recovery within historical range, the geographic context is implicit in the criterion for listing an entity as endangered, i.e., "in danger of extinction throughout all or a significant portion of its range" (the range occupied by the species at the time of listing)." Following passage of the ESA, the vast majority of candidate and ultimately listed species (or subspecies) had experienced significant declines or extirpations within areas that were occupied historically and recovery efforts have been focused within the historical range of those species. Introductions of listed species outside historical range are uncommon and restricted to situations where habitat loss or introduced predators rendered historical range unsuitable (e.g., for the Micronesian kingfisher [*Todiramphus cannamominus*] and Guam rail [*Gallirallus owstoni*]) (Jachowski et al., 2014).

The legal framework for recovery outside currently occupied range largely rests with the experimental population provision contained in Section 10(j) of the ESA. The legislative history of Section 10(j) and its amendments indicate Congress intended that reintroductions under Section 10(j) occur within the species' historical range. Thus, Section 10(j) does not explicitly authorize releases outside historical range (16 U.S.C. §1539(j)). The USFWS explicitly included a geographic restriction that prohibits introductions of experimental populations outside historical range unless "…the primary habitat of the species has been unsuitably and irreversibly altered or destroyed" (50C.F.R. §17.81(a)). In 1984, the USFWS acknowledged this geographic restriction was necessary to comply with the purposes and policies of the ESA and to remain consistent with a long-standing policy opposing introduction of listed species outside historical range (Endangered and Threatened Wildlife and Plants; Experimental Populations, 49 FR 33885–01, at 33890). Under this regulatory framework, establishing Mexican wolf populations outside the subspecies' historical range is strictly prohibited unless that range "has been unsuitably and irreversibly altered or destroyed." (50C.F.R. §17.81(a)). This has neither been demonstrated nor is evident with regard to the Mexican wolf, for which large tracts of suitable habitat exist within historical range in the United States and Mexico (USFWS, 2017: Appendix B).

2.5. Climate change

Climate change has increasingly been an important consideration in recovery planning. Wolves currently inhabit regions where temperature extremes range from −40 to +40 °C, and use habitats as varied from the Arabian Peninsula to the Arctic Circle (Mech, 1995). Wolves successfully occupy a variety of diverse ecosystems in North America and Eurasia and kill a wide variety of prey (e.g., from small mammals to all species of North American ungulates) (Mech, 1995).

The Mexican wolf evolved fulfilling an ecological role in the Sierra Madre Occidental of Mexico that is unique among other wolf ecotypes. Implicit in its listing as a separate entity under the ESA is the need for recovery planning that includes its primary ecological setting.

Martinez-Meyer et al. (2006) modeled suitability of potential reintroduction areas in Mexico, with respect to potential climate changes. Their analysis identified a number of areas expected to remain suitable for Mexican wolves under an altered climate. The likelihood that climate change will irreversibly alter or destroy Mexican wolf historical habitat in the foreseeable future is contrary to the generalist and adaptable nature of wolves and their prey, and improbable.

3. Perils of extra-limital recovery

3.1. Extra-limital habitat evaluation

Carroll et al. (2005) evaluated habitat suitability for Mexican wolves in the southwestern U.S. and Mexico. This analysis was the result of work done by members of the 2004–05 Mexican wolf recovery team charged with developing a recovery plan for the Southwestern Gray Wolf Distinct Population Segment (DPS) that included all of Arizona and New Mexico, southern Colorado, southern Utah, western Oklahoma, western Texas, and Mexico. Carroll et al.'s (2005) habitat suitability analysis was heavily influenced by the application of a spatially explicit adjustment to base mortality risk. The adjustment was chosen to reflect assumed differential risk to wolves due to land ownership, wherein all lands throughout Mexico represented a high risk (+175% of base rate) and specific areas in the United States (National Parks, Department of Defense lands, and the privately-owned Vermejo Park Ranch) represented a decreased risk (50% of base rate). The habitat analysis did not reduce wolf mortality risk for Mexico's protected natural areas managed by the Comisión Nacional de Áreas Naturales Protegidas (CONANP) or remote privately owned ranches as was done for areas in the United States. The overall effect of this mathematical adjustment was that the model universally decreased the suitability of Mexico for wolf recovery and selectively boosted suitability of the Vermejo Park Ranch and Grand Canyon National Park.

Based on this spatial analysis, Carroll et al. (2005) recommended 3 introduction sites: 1) the current recovery area in Arizona and New Mexico, 2) northern Arizona and southern Utah (Grand Canyon), and 3) northern New Mexico and southern Colorado (variously referred to as Vermejo, Carson NF and Southern Rockies). However, this effort to evaluate habitat north of Mexican wolf historical range was rendered irrelevant when the Southwestern Wolf DPS was vacated by court ruling in 2005 and the recovery team was dissolved.

Based largely on their artificial adjustment of mortality risk by country and land ownership, Carroll et al. (2006) accepted the 3 core areas identified by Carroll et al. (2005) which subsequently formed the basis for the 3 populations proposed by the Science and Planning Subgroup of the Mexican wolf recovery team in 2012. Carroll et al. (2014:77) then continued to reference these 3 recovery areas without further discussion of how they were identified. Despite critical shortfalls inherent in their identification, these 3 areas, exclusive of Mexico, continue to be inappropriately referenced by some as the best available science upon which to base the geography of recovery.

3.2. Habitat connectivity

Carroll et al. (2014) modeled connectivity among the 3 previously proposed recovery areas of Mexican wolves relative to existing populations of Northwestern wolves in the Rocky Mountains. This analysis artificially prevented these 3 Mexican wolf populations from growing or expanding northward through areas of highly connected habitat, but allowed periodic dispersal movements to the south, west, and east where habitat connectivity is much lower. By placing an artificial restriction on the northern spatial extent of both the proposed Southern Rockies and Grand Canyon Mexican wolf populations, Carroll et al. (2014) viewed the habitat to the north of these 2 areas only in terms of connectivity linkages rather than core habitat, which is not biologically reasonable. This restrictive population definition influences all subsequent habitat connectivity and linkage analyses. In the proposed Southern Rockies population, based on the Carroll et al. (2003) habitat analysis, there is a high level of habitat connectivity throughout western and central Colorado. In fact, their proposed Southern Rockies Mexican wolf population has substantially higher connectivity to all habitat in western and central Colorado than with the proposed Grand Canyon recovery area or existing Mexican wolves in central Arizona and New Mexico. Thus, if Mexican wolves were released or allowed to successfully establish in southern Colorado, they would doubtless expand their distribution northward throughout western Colorado given high habitat connectivity and prey availability to the north. The largest and most productive deer and elk herds are in northwest Colorado (Edward, 2000; Colorado Parks and Wildlife, unpublished data). Therefore, it is unlikely that a Southern Rockies Mexican wolf population would remain confined to southern Colorado and northern New Mexico and freely interchange only with other Mexican wolf populations to the south.

Likewise, potential habitat in northern Arizona and occupied habitat in Idaho and Wyoming is highly connected through Utah. There is a continuous string of elk habitat and populations connecting Utah's northern and southern borders from the Bear River Range in the north to the Paunsaugunt Plateau in the south (Utah Division of Wildlife Resources, unpublished data), a corridor that was likely used by the Wyoming wolf arriving in the Grand Canyon in 2014.

Because of this habitat continuity, one would expect populations of *C. l. baileyi* occupying southern Colorado and Utah or northern Arizona and New Mexico to have relatively frequent exchange with Northwestern wolves from Wyoming, Idaho, and Montana. Mexican wolves would also be expected to disperse and establish throughout the entirety of western Colorado and much of Utah, which could lead to detrimentally premature genetic interchange between Northwestern gray wolves and Mexican wolves before the latter is recovered.

3.3. Wolf movements

Wolves are noted for long range movements and genetic interchange among distant populations (Brewster and Fritts, 1995). Although no wolf packs are currently known from Utah or Colorado, dispersing Northwestern wolves from the Northern Rockies population have already been documented in both states and are expected to establish eventually (Colorado Wolf Management Working Group, 2004; Utah Division of Wildlife Resources, 2005).

Northern wolves have even dispersed farther south into areas previously proposed for Mexican wolf recovery (Fig. 2, Table 1). In October 2014, a 2-year old female Northwestern wolf collared near Cody, Wyoming was documented on the Kaibab Plateau near Grand Canyon National Park in northern Arizona. The wolf was repeatedly sighted in that area for more than 2 months. In July 2008, a wolf with black pelage was documented near the Vermejo Park Ranch in northern New Mexico. No Mexican wolves have ever been documented with black pelage so this animal was assumed to be a wolf from the Northern Rocky Mountains (J. P. Greer, Arizona Game and Fish Department, personal communication). Neither of these two areas are part of Mexican wolf historical range, but both have been proposed as recovery areas (Carroll et al., 2006, 2014).

3.4. Genetic swamping

Genetic swamping has been a critical challenge for other endangered canids, notably the Eastern red wolf (*C. rufus*, Kelly et al., 1999). Genetic swamping of Mexican wolves by northern wolves is more than a theoretical possibility – it presents an existential threat to recovery of the Mexican wolf as a distinct entity. All available information suggests releasing, or allowing colonization of, Mexican wolves into extra-limital areas north of central Arizona and New Mexico will result in intraspecific hybridization with expanding populations of the Northwestern gray wolf. The risk of intraspecific genetic swamping is particularly high during early phases of Mexican wolf recovery, when the number of wolves on the ground in recovery areas is relatively small. This risk is further compounded by the potential for Mexican wolves to move from extra-limital recovery areas northward through well connected habitat into areas occupied by Northwestern gray wolves. Mexican wolves from the current Arizona-New Mexico population have dispersed distances in excess of 250 km (J. P. Greer, Arizona Game and Fish Department, personal communication).

The Mexican wolf as a subspecies developed in near-allopatry, centered in the high-elevation mountains of Mexico, and mostly separated by fragmented habitat and discontinuous prey distribution from the other wolf subspecies to the north (Heffelfinger et al., 2017a,b). The unique phenotypic differentiation of Mexican wolves could not have developed, or maintained itself, if they had shared an extensive zone of intergradation with adjacent ecotypes. Contemporary hybridization through secondary contact between Mexican and larger Northwestern wolves from Canada does not represent the restoration of a natural cline in southwestern ecotypes (Heffelfinger et al., 2017a,b).

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 a dominant 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) used a 14-year dataset from wolves in Yellowstone National Park, USA, to demonstrate that body mass of breeders was the main determinant of litter size and survival of the litter. Their analysis estimated that for every 10 kg increase in breeding female body weight, litter survival increased 39%. 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 obtaining and defending breeding positions and maximizing genetic contribution to the population.

In addition to a body size differential, several characteristics of the current wild Mexican wolf populations make them vulnerable to detrimental genetic swamping by Northwestern wolves: 1) high levels of disruptive human-caused mortality, 2) small pack size, and 3) elevated levels of inbreeding. A vast majority of all Mexican wolf mortalities are caused by humans (USFWS, 2017). When wolf populations are exploited and have high rates of human-caused mortality the 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 Northwestern wolves were accepted into other packs. Immigrating wolves are also more readily adopted by smaller packs where additional individuals, especially males, have a greater chance of increasing the fitness of existing pack members (Fritts and Mech, 1981; Ballard et al., 1987; Cassidy et al., 2015). The wild 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 immigrant Northwestern wolves. Inbreeding avoidance in wolves has been well-documented (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),

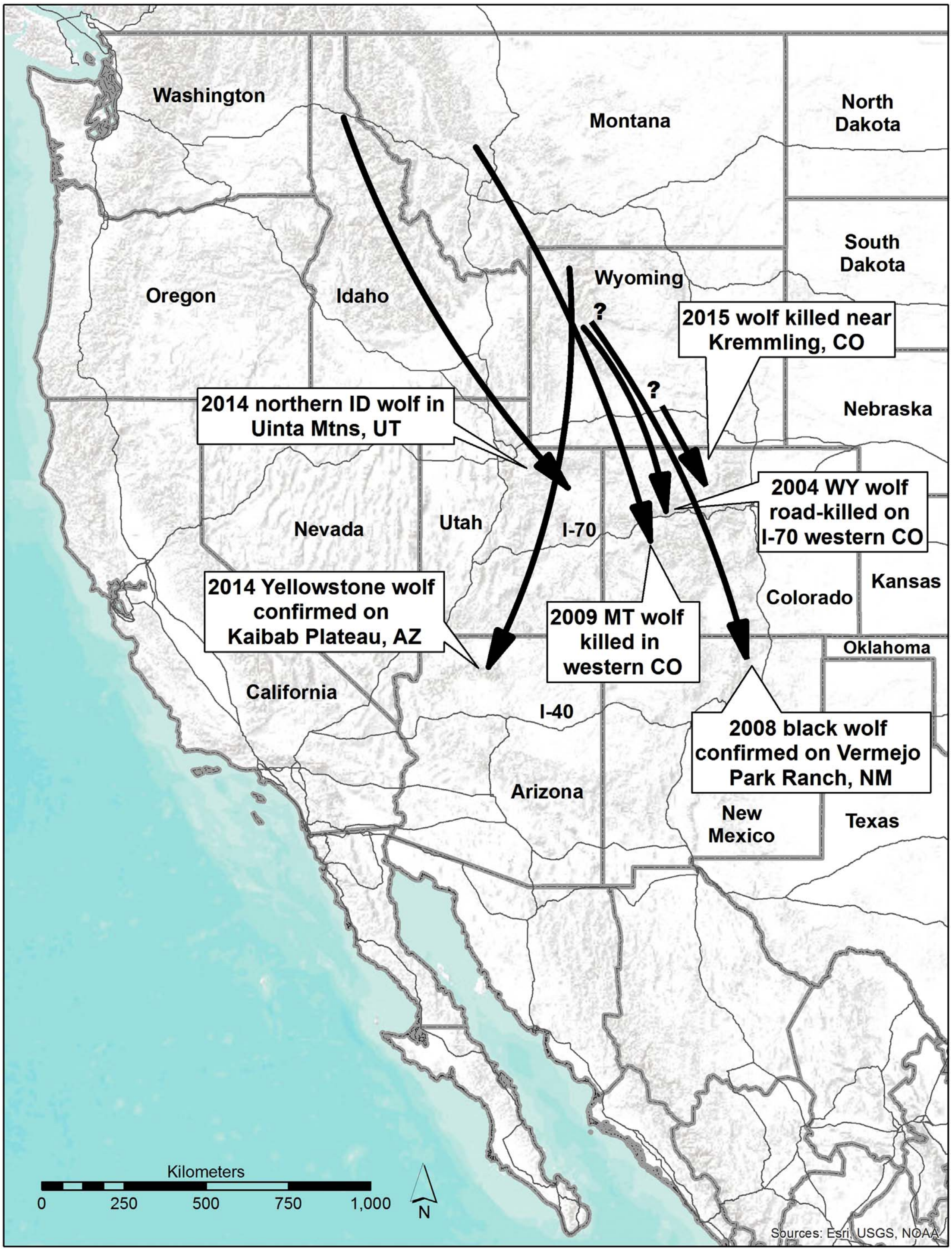

Fig. 2. Documented southward movements of gray wolves (*Canis lupus*) from established populations in the northern Rocky Mountains, 2004–2016.

which means a new wolf immigrant, unrelated to all Mexican wolves, would have a disproportionately high probability of being adopted and attain a breeding position (vonHoldt et al., 2008; Geffen et al., 2011; Åkesson et al., 2016).

Although not seen in the Northern Rockies, the success of 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 precipitated the expansion of hybridized coyotes into the northeast (Monzón et al., 2013). These larger hybridized coyotes are no longer the typical canonical coyote and now assume a different ecological niche as predators of adult white-tailed deer. A similar situation of wolves with Northwestern ancestry hybridizing with smaller Mexican wolves would likely result in a similar failure to retain the very characteristics that make this separately listed entity unique.

Wayne and Shaffer (2016) have suggested Mexican wolves be purposefully hybridized with the larger gray wolf on the grounds that the Southern Rockies once held such an intermediate form of wolf. However, extensive skull measurements and documentation of phenotypic differences by those having experience with historical populations of wild southwestern wolves clearly place the zone of intergradation between the Mexican wolf and a larger Plains wolf (*Canis lupus nubilus*) in

Table 1
Examples of long-distance dispersal of Northwestern wolves (*Canis lupus occidentalis*) into or near areas once considered for Mexican wolf (*C. l. baileyi*) recovery.

Date	Details
June, 2004	A wolf was found dead on the side of I-70 in western Colorado, after moving southward from Wyoming. This interstate freeway was the northern boundary of the Mexican wolf recovery area proposed by the 2010–2012 Science and Planning Subgroup of the Mexican Wolf Recovery Team.
July, 2008	A wolf with black pelage was observed near the Vermejo Park Ranch in northern New Mexico and also recorded on trail cameras in the area. No Mexican wolves have ever been documented with black pelage so this animal was assumed to be a gray wolf from the Northern Rocky Mountains population (J. P. Greer, Arizona Game and Fish Department, personal communication). The Vermejo Park Ranch and surrounding public land has been repeatedly proposed as a Mexican wolf recovery area (Carroll et al., 2006, 2014).
April, 2009	A female wolf from southwestern Montana was traveling southward when she was killed in western Colorado, north of I-70. The GPS collar she wore revealed that her circuitous route took her 4,800 km through western Wyoming, northern Utah, and Colorado in a southerly direction
April, 2015	Other wolves have traveled southward into Colorado, including another uncollared male that was killed near Kremmling, Colorado.
Between 2002 and 2015	Wolves have been confirmed in Utah on at least 12 occasions and many other unconfirmed sightings have been reported (K. Hersey, Utah Division of Wildlife Resources, personal communication). Although most of the activity has been observed in the northern portions of the states, Leonard et al. (2005) suggested northern Utah be considered for Mexican wolf recovery and several confirmed wolves have demonstrated remarkable dispersal abilities. For example, an adult male first collared in the northern Idaho panhandle was documented moving east through the Uinta Mountains of northeastern Utah during late summer 2014. No location data were collected during the dispersal, but minimum straight-line distance was greater than 1,000 km.
October, 2014	A northern gray wolf that was later identified as a 2-year old female collared near Cody, Wyoming was documented on the Kaibab Plateau near Grand Canyon National Park of northern Arizona. The wolf was repeatedly sighted in that area for more than 2 months. The Kaibab Plateau is not part of Mexican wolf historical range, but it has been proposed as a recovery area (Carroll et al., 2006, 2014). The wolf was then recorded moving back north through Utah before being inadvertently killed approximately 290 km north of the Grand Canyon and 210 km north of the Utah/Arizona border on the foothills of the Tushar Mountains.

central Arizona and New Mexico, not further north in the Southern Rockies (as summarized by Heffelfinger et al., 2017a,b).

How the ESA should treat hybrids has been a topic of discussion since its passage in 1973 (Rhymer and Simberloff, 1996; Haig and Allendorf, 2006). While drafts have been proposed, a policy on hybridization was never finalized. The USFWS is currently left without clear direction on how to consider either the role of the ESA in protecting hybrids, or importantly in this case, the implications of hybrids contributing to the recovery and delisting of protected species.

The USFWS purposely created hybrids between the endangered Florida panther (*Puma concolor coryi*) and Texas pumas (*Puma concolor stanleyana*) after some were convinced the listed taxa would cease to exist without genetic and demographic intervention (Pimm et al., 2006). Indeed, the Florida panther was suffering from several serious physical abnormalities because of high levels of inbreeding. This effort was a last resort to save the subspecies from extinction and done in a controlled manner with all remaining pure Texas individuals removed after 8 years. The Mexican wolf population has grown an average of 16% annually since 2009 (USFWS Files), making their trajectory quite different from the dire situation of the Florida panther. The exception made for the Florida panther in no way sets a precedent to allow listed entities to hybridize freely with similar species and subspecies and still contribute to recovery. Uncontrolled and unneeded hybridization early in the recovery of the Mexican wolf would compromise the recovery and delisting of the Mexican wolf because the product of this hybridization between the Mexican wolf and Northwestern gray wolf will not be representative of the listed entity (*C. l. baileyi*).

Preservation of the unique Mexican wolf subspecies is the obvious objective of its discrete subspecies listing status and must be the goal of recovery planning. Recovery of that subspecies will not be achieved without including those in Mexico already working towards that goal and focusing Mexican wolf recovery in historical range where its unique characteristics will continue to be geographically buffered, as they were historically, from freely mixing with northern gray wolf subspecies. Mexican wolves can be successfully returned to the southwestern landscape including habitat within historical range in both the United States and Mexico, but focusing efforts outside of their historical range will likely jeopardize the recovery effort.

4. Conclusions

The recent decision by the U.S. Fish and Wildlife Service to list the Mexican wolf as a distinct taxonomic entity separate from all other gray wolf subspecies (USFWS, 2015b) provides clear and unambiguous direction to recover the unique genetic and physical attributes of the subspecies. Directing recovery efforts in extra-limital habitats presents significant risks to recovery efforts for the Mexican wolf through genetic swamping by Northwestern gray wolves. Offspring of a Northwestern gray wolf and Mexican wolf would have a disproportionate probability of becoming a breeder due to the larger size of its parent and the additional effects of heterosis (Shull, 1948; Monzón et al., 2013). Some extra-limital recovery areas proposed (Carroll et al., 2003, 2006, 2014) could prove disastrous if hybridized wolves spread back into core populations in historical range.

A comprehensive habitat suitability analysis of the Mexican wolf's historical range (USFWS, 2017: Appendix B), as well as ongoing collaboration between US and Mexican officials and top Mexican scientists and managers (J. Bernal, CONANP, personal communication) demonstrate capacity, interest, and motivation for recovering Mexican wolves within historical range. The Mexican wolf remains one of the top three priority species for recovery by the Mexican government (F. Abarca, personal communication). Further, CONANP has launched a program to evaluate human dimension aspects related to wolf recovery in Mexico. Staff have been hired to administer many programs in areas where Mexican wolves have been released in Mexico. These opportunities need to be fully explored and exhausted prior to further consideration of extralimital recovery areas. Mexican wolves must be recovered within their historical range.

Recovery outside historical range is inconsistent with the purposes and objectives of the ESA, prohibited by current 10(j) regulations, unnecessary due to abundant and widespread high quality habitat in Mexico, inconsistent with the concepts of restoration ecology, and represents a disregard for the unique characteristics for which the Mexican wolf was listed. Besides being ecologically insufficient and inappropriate, abandoning or marginalizing the subspecies' core historical range in Mexico in favor of areas well north of historical range will likely lead to litigation (Phillips, 2000) and only delay critical progress in expanding Mexican wolf populations to achieve successful recovery.

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References

Åkesson, M., Liberg, O., Sand, H., Wabakken, P., Bensch, S., Flagstad, Ø., 2016. Genetic rescue in a severely inbred wolf population. Mol. Ecol. 25, 4745–4756.

Araiza, M., 2001. Determinación de sitios potenciales para la reintroducción del lobo gris mexicano. In: Universidad Nacional de Costa Rica. Dissertation. Programa Regional de Manejo de Vida Silvestre para Mesoamérica y el Caribe. Universidad Nacional de Costa Rica, Heredia, Costa Rica.

Araiza, M., Carrillo, L., List, R., Lopez Gonzalez, C.A., Martinez Meyer, E., Martinez Gutierrez, P.G., Moctezuma Orozco, O., Sanchez Morales, N.E., Servin, J., 2012. Consensus on criteria for potential areas for wolf reintroduction in Mexico. Conserv. Biol. 26, 630–637.

Baker, J., Meade, A., Pagel, M., Venditti, C., 2015. Adaptive evolution toward larger size in mammals. Proc. Natl. Acad. Sci. 112, 5093–5098.

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

Bogan, M.A., Mehlhop, P., 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., Paquet, P.C., Donelon, S., Ream, R.R., Pletscher, D.H., White, C.C., 1995. Transboundary movements of a recolonizing wolf population in the Rocky Mountains. In: Carbyn, L.N., Fritts, S.H., Seip, D.R. (Eds.), Ecology and Conservation of Wolves in a Changing World. Canadian Circumpolar Institute, Occasional Publication Number 35, pp. 135–140.

Brewster, W.G., Fritts, S.H., 1995. Taxonomy and genetics of the gray wolf in western North America: a review. In: Carbyn, L.N., Fritts, S.H., Seip, D.R. (Eds.), Ecology and Conservation of Wolves in a Changing World. Occasional Publication No. 35, Canadian Circumpolar Institute, pp. 353–374.

Carmichael, L.E., Nagy, J.A., Larter, N.C., Strobeck, C., 2001. Prey specialization may influence patterns of gene flow in wolves of the Canadian northwest. Mol. Ecol. 10, 2787–2798.

Carroll, C., Phillips, M.K., Schumaker, N.H., Smith, D.W., 2003. Impacts of landscape change on wolf restoration success: planning a reintroduction program based on static and dynamic models. Conserv. Biol. 17, 536–548.

Carroll, C., Phillips, M.K., Lopez-Gonzalez, C.A., 2005. Spatial Analysis of Restoration Potential and Population Viability of the Wolf (*Canis lupus*) in the Southwestern United States and Northern Mexico. Klamath Center for Conservation Research, Orleans, CA. http://www.klamathconservation.org/docs/carrolletal2005_text.pdf, Accessed date: 26 May 2017.

Carroll, C., Phillips, M.K., Lopez-Gonzalez, C.A., Schumaker, N.H., 2006. Defining recovery goals and strategies for endangered species: the wolf as a case study. Bioscience 56, 25–37.

Carroll, C., Vucetich, J.A., Nelson, M.P., Rohlf, D.J., Phillips, M.K., 2010. Geography and recovery under the U.S. endangered species act. Conserv. Biol. 24, 395–403.

Carroll, C., Fredrickson, R.J., Lacy, R.C., 2014. Developing metapopulation connectivity criteria from genetic and habitat data to recover the endangered Mexican wolf. Conserv. Biol. 28, 76–86.

Cassidy, K.A., MacNulty, D.R., Stahler, D.R., Smith, D.W., Mech, L.D., 2015. Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. Behav. Ecol. 26, 1352–1360.

Colorado Wolf Management Working Group. 2004. Findings and Recommendations for Managing Wolves that Migrate into Colorado. https://cpw.state.co.us/Documents/WildlifeSpecies/SpeciesOfConcern/Wolf/recomendations.pdf (Accessed 30 June 2017).

Comisión Nacional de Áreas Naturales Protegidas (CONANP), 2009. Programa de Acción para la Conservación de la Especie. Lobo Gris Mexicano, Mexico, D.F., Mexico (52 pp).

Edward, R., 2000. A brief history of wolf extirpation & restoration in the southern Rockies. In: Phillips, M., Fascione, N., Miller, P., Byers, O. (Eds.), Wolves in the Southern Rockies. A Population and Habitat Viability Assessment: Final Report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota, USA, pp. 86–94.

Fritts, S.H., Mech, L.D., 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildl. Monogr. 80, 3–79.

Geffen, E., Anderson, M.J., Wayne, R.K., 2004. Climate and habitat barriers to dispersal in the highly mobile grey wolf. Mol. Ecol. 13, 2481–2490.

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

Haig, S.M., Allendorf, F.W., 2006. Hybrids and policy. In: Scott, J.M., Goble, D.D., Davis, F.W. (Eds.), The Endangered Species Act at Thirty, Volume 2: Conserving Biodiversity in Human-Dominated Landscapes. Island Press, Washington, DC, USA, pp. 150–163.

Heffelfinger, J.R., Nowak, R.M., Paetkau, D., 2017a. Clarifying historical range to aid recovery of the Mexican wolf. J. Wildl. Manag. 81 (5), 766–777. http://dx.doi.org/10.1002/jwmg.21252.

Heffelfinger, J.R., Nowak, R.M., Paetkau, D., 2017b. Revisiting revising Mexican wolf historical range: a reply to Hendricks et al. J. Wildl. Manag. 81, 1334–1337.

Hendricks, S.A., Sesink Clee, P.R., Harrigan, R.J., Pollinger, J.P., Freedman, A.H., Callas, R., Figura, P.J., Wayne, R.K., 2016. Re-defining historical geographic range in species with sparse records: implications for the Mexican wolf reintroduction program. Biol. Conserv. 194, 48–57.

Hendricks, S.A., Koblmuller, S., Harrigan, R.J., Leonard, J.A., Schweizer, R.M., vonHoldt, B.M., Kays, R., Wayne, R.K., 2017. Defense of an expanded historical range for the Mexican wolf: a comment on Heffelfinger, et al. J. Wildl. Manag. 81, 1331–1333.

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

Jachowski, D.S., Kester, D.C., Steen, D.A., Walters, J.R., 2014. Redefining baselines in endangered species recovery. J. Wildl. Manag. 79, 3–9.

Kelly, B.T., Miller, P.S., Seal, U.S., 1999. Population and Habitat Viability Assessment Workshop for the Red Wolf *(Canis rufus)*. Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, Minnesota, USA.

Leonard, J.A., Vilà, C., Wayne, R.K., 2005. Legacy lost: genetic variability and population size of extirpated U.S. grey wolves (*Canis lupus*). Mol. Ecol. 14, 9–17.

MacNulty, D.R., Smith, D.W., Mech, L.D., Eberly, L.E., 2009. Body size and predatory performance in wolves: is bigger better? J. Anim. Ecol. 78, 532–539.

Martínez-Gutiérrez, P.G., 2007. Detección de áreas de actividad potenciales para la reintroducción del lobo mexicano (Canis lupus baileyi) en México. In: Thesis. A.C. México, Instituto de Ecología.

Martinez-Meyer, E., Peterson, T., Servin, J.L., Kiff, L.F., 2006. Ecological niche modeling and prioritizing areas for species reintroductions. Oryx 40, 411–418.

Mech, L.D., 1995. The challenge and opportunity of recovering wolf populations. Conserv. Biol. 9, 270–278.

Mech, L.D., Boitani, L., 2003. Wolf social ecology. In: Mech, L.D., Boitani, L. (Eds.), Wolves, Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois, USA, pp. 1–34.

Messier, 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Can. J. Zool. 63, 239–245.

Monzón, J., Kays, R., Dykhuizen, D.E., 2013. Assessment of coyote-wolf-dog admixture using ancestry-informative diagnostic SNPs. Mol. Ecol. 23, 182–197.

Nelson, E.W., Goldman, E.A., 1929. A new wolf from Mexico. J. Mammal. 10, 165–166.

Nowak, R.M., 1995. Another look at wolf taxonomy. In: Carbyn, L.N., Fritts, S.H., Seip, D.R. (Eds.), Ecology and Conservation of Wolves in a Changing World. Canadian Circumpolar Institute, University of Alberta, Canada, pp. 375–397.

Nowak, R.M., 2003. Wolf evolution and taxonomy. In: Mech, L.D., Boitani, L. (Eds.), Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois, USA, pp. 239–258.

Parsons, D., 1996. Case study: the Mexican wolf. New Mexico Journal of Science 36, 101–123.

Phillips, M., 2000. Restoring Mexican wolves to the Southern Rockies: why not? In: Phillips, M., Fascione, N., Miller, P., Byers, O. (Eds.), Wolves in the Southern Rockies. A Population and Habitat Viability Assessment: Final Report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota, USA, pp. 96–103.

Pimm, S.L., Dollar, L., Bass Jr., O.L., 2006. The genetic rescue of the Florida panther. Anim. Conserv. 9, 115–122.

Rhymer, J.M., Simberloff, D., 1996. Extinction by hybridization and introgression. Annu. Rev. Ecol. Syst. 27, 83–109. http://dx.doi.org/10.1146/annurev.ecolsys.27.1.83.

Robinson, M.J., 2005. Prospects for Mexican gray wolf recovery on the Sky Islands. In: Gottfried, G.J., Gebow, B.S., Eskew, L.G., Edminster, C.B. (Eds.), Connecting mountain islands and desert seas: biodiversity and management of the Madrean Archipelago II. USDA Forest Service Proceedings RMRS-P-36, Fort Collins, Colorado, USA, pp. 341–344.

Shaffer, M.L., Stein, B.A., 2000. Safeguarding our precious heritage. In: Stein, B.A., Kutner, L.S., Adams, J.S. (Eds.), Precious Heritage: The Status of Biodiversity in the United States. Oxford University Press, New York, New York, USA, pp. 301–321.

Shull, G.H., 1948. What is "Heterosis"? Genetics 33, 439–446.

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

Stahler, D.R., Smith, D.W., Landis, R., 2002. The acceptance of a new breeding male in to a wild wolf pack. Can. J. Zool. 80, 360–365.

Stahler, D.R., MacNulty, D.R., Wayne, R.K., VonHoldt, B., Smith, D.W., 2013. The adaptive value of morphological, behavioral and life-history traits in reproductive female wolves. J. Anim. Ecol. 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. U. S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.

U. S. Fish and Wildlife Service, 2015a. Endangered and threatened wildlife and plants; endangered status for the Mexican wolf. Final rule. Fed. Regist. 80, 2488–2512.

U. S. Fish and Wildlife Service, 2015b. Endangered and threatened wildlife and plants; revision to the regulations for the nonessential experimental population of the Mexican wolf. Fed. Regist. 80, 2512–2567.

U.S. Fish and Wildlife Service, 1982. Mexican Wolf Recovery Plan. Region 2, Albuquerque, New Mexico, USA.

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, Accessed date: 30 June 2017.

Utah Division of Wildlife Resources, 2005. Utah Wolf Management Plan. (Publication #05–17. 81 pages).

Van Devender, T.R., Spaulding, W.G., 1979. The development of vegetation and climate in the southwestern United States. Science 204, 701–710.

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

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

vonHoldt, B.M., Pollinger, J.P., Earl, D.A., Knowles, J.C., Boyko, A.R., Parker, H., Geffen, E., Pilot, M., Jedrzejewski, W., Jedrzejewska, B., Sidorovich, V., Greco, C., Randi, E., Musiani, M., Kays, R., Bustamante, C.D., Ostrander, E.A., Novembre, J., Wayne, R.K.,

2011. A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. Genome Res. 21, 1–33.
vonHoldt, B.M., Cahill, J.A., Fan, Z., Gronau, I., Robinson, J., Pollinger, J.P., Shapiro, B., Wall, J., Wayne, R.K., 2016. Whole genome sequence analysis shows that two endemic species of North American wolf are admixtures of the coyote and gray wolf. Sci. Adv. 2 (7) (13pp).
Vucetich, J.A., Nelson, M.P., Phillips, M.K., 2006. The normative dimension and legal meaning of endangered and recovery in the U.S. endangered species act. Conserv. Biol. 20, 1383–1390.
Wayne, R.K., Shaffer, H.B., 2016. Hybridization and endangered species protection in the molecular era. Mol. Ecol. 25, 2680–2689.
Wolf, S., Hartl, B., Carroll, C., Neel, M.C., Greenwald, D.N., 2015. Beyond PVA: why recovery under the endangered species act is more than population viability. Bioscience 65, 200–207.