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December 10, 2012

Benjamin N. Tuggle
Director, Southwest Region
U.S. Fish and Wildlife Service
Post Office Box 1306
Albuquerque, NM 87103

Dear Dr. Tuggle:

Wolf recovery planning is among the most daunting of conservation challenges. I appreciate the enormous responsibility you bear in leading and directing the Mexican wolf recovery planning effort. Reverence for the sanctity of the scientific process and science inputs to recovery planning has been perhaps your most dominant theme in all recovery planning discussions, and the Department shares and admires your commitment in this regard.

For three decades, the Arizona Game and Fish Department (Department) has invested significant time and resources to restore Mexican wolves in Arizona. Our shared goal has been to achieve a self-sustaining population of wolves that would no longer be in danger of extinction.

The Department actively sought and welcomed the opportunity to be a member of the Mexican wolf Science and Planning Subgroup (SPS) and to contribute scientific expertise to the recovery planning process. Over the course of that effort, it became obvious that there are significantly divergent perspectives within the SPS on how best to recover the subspecies and the scientific underpinnings used to develop recovery criteria.

As you are aware, Jim Heffelfinger routinely raised and documented these concerns over the course of his work with the SPS (Dissenting Opinion 8/12/11; review comments on Draft Recovery Plan versions dated 9/13/2011, 12/2011, 4/14/2012, and 5/1/2012; and, e-mails to the SPS dated 1/16/12 and 7/13/12). While Jim was informed that he could provide a dissenting opinion and it would be incorporated into the administrative record, there is no guarantee that these dissenting opinions will be seen in the SPS recommendations.

Jim requested that he be allowed to resign from the SPS after the group failed to meaningfully address perceived flaws in the recovery planning process. Not wanting to take such action without vetting these concerns, I assembled an internal scientific review team. They likewise found serious flaws in the proposed draft recovery criteria and the process by which they were developed. After a thorough review of the expert panel's findings (see attached), the Department considers the concerns to be valid and strongly believes the SPS is focused on recovery criteria that are not biologically sound.

I have elected to honor Jim's request to no longer serve as a member of the SPS. Because of the Service's recent action to identify the gray wolf as the listed species rather than the Mexican wolf, the future of the planning effort remains unclear to me. Nonetheless, the Department will continue to participate and serve on the larger Mexican Wolf Recovery Team, should it continue to serve you.

The Department has been and remains committed to establishing a viable population of Mexican wolves in the subspecies' historic range. To be successful, the recovery planning process must be objective, transparent, and yield recovery criteria that are biologically appropriate, emphasize core historical range with a bi-national approach, and are achievable on the complex biological and socioeconomic landscape of the Southwestern United States.

Sincerely,

Larry D. Voyles
Director

Attachments

cc: Sherry Barrett, Mexican Wolf Recovery Coordinator, USFWS
Steve Spangle, Field Supervisor, Arizona Ecological Services, USFWS
Tracy Melbihess, Mexican Wolf Recovery Plan Manager, USFWS

Mexican Wolf Recovery Criteria: AZGFD Technical Review
December 4, 2012

Background and Context

In 2010, the U.S. Fish and Wildlife Service (Service) chartered its 4th iteration of a Recovery Team for the endangered Mexican wolf. The Recovery Team includes a Science and Planning Subgroup (SPS), tasked with developing specific recovery criteria for delisting the subspecies. Over the course of these efforts, the Department employee serving on the SPS identified a number of scientific concerns with the draft recovery criteria and the process by which they were developed.

In November 2012, an internal review team was convened to provide an objective, technical review of these concerns. The review team examined each concern, considering the available scientific information, underlying logic, and weight of evidence. The team then prepared a revised and augmented narrative summary of Department concerns, which is presented here. Detailed supporting information and citations from the scientific literature are provided in appended endnotes.

Overall Evaluation

The review team's assessment is that the following concerns have merit and are supported by the scientific literature. Major deficiencies in draft recovery criteria are:

- Recovery is focused on areas in the U.S. well outside historical range of the Mexican wolf, with inadequate attention to areas located within core historical range in Mexico.
- The recovery criteria do not reflect an integrated, bi-national approach, and do not fully incorporate recovery efforts underway in Mexico.
- Numerical recovery criteria are arbitrary and may not be consistent with historical wolf abundance in Arizona.
- The number of wolves proposed likely exceeds that required for wolves to no longer be in danger of extinction and may not be achievable in areas where prey and winter conditions are considerably different than where the Mexican wolf evolved.
- The population viability analysis (PVA) used to support numerical recovery criteria has deficiencies that limit its usefulness.
- The specified level of natural wolf dispersal among subpopulations may be challenging to attain and will be very difficult, time-consuming and expensive to monitor.

Some of the recovery criteria may be impossible to achieve (or document attainment), even after self-sustaining wolf populations have been established in one or more recovery areas. This appears to reflect a more theoretical approach taken by the SPS, which does not adequately consider the realities of a high-profile reintroduction effort on a multi-dimensional political and biological landscape.

Department Concerns

Selection and Prioritization of Recovery Areas. The draft plan and recovery criteria emphasize 3 areas within the U.S.: 1) Mogollon Rim in central Arizona, 2) Grand Canyon area and southern Utah, and 3) Vermejo Ranch in Northern New Mexico northward to Denver, Colorado.

- These areas are well outside historical range of the Mexican wolf as described in the scientific literature[1].
- Existing genetic data suggest that Mexican wolves have distinctive characteristics, however; the genetic data are incomplete and insufficient to justify northward expansion of the recovery area[2].
- Available historical, morphological, and biogeographic information argue strongly for focusing recovery efforts within core historical range. Several large tracts of suitable habitat have been identified within historical range of the wolf in Mexico[3], but are not being considered as primary recovery areas to count towards recovery.
- Selection of at least one recovery area appears to reflect personal interests of SPS members[4].
- Reintroductions north of historical range present a potential and undesirable risk of genetic swamping of this apparently unique taxon[5].

Integration of Conservation Efforts in the U.S. and Mexico. The draft recovery criteria focus on recovery efforts in the U.S., with minimal emphasis on those in Mexico.

- There are many examples of integrated, bi-national recovery efforts for species whose historical ranges occur in the U.S. and Mexico (e.g., jaguar, ocelot, California condor, Kemps-Ridley sea turtle, and black-footed ferret). Such an approach is appropriate for the Mexican wolf, but inadequately reflected in recovery criteria developed by the SPS.
- Mexican government agencies, academic institutions, and conservation organizations are actively engaged in wolf recovery, and have begun releasing animals into the wild. These efforts have likewise not been given appropriate consideration in development of the recovery criteria.
- Recovery criteria for other endangered species (e.g., masked bobwhite) include populations in both countries[6]. In contrast, draft recovery criteria developed by the SPS consider wolves in Mexico as supplemental and not contributing to meeting numerical recovery objectives.
- The potential value of adding areas in Mexico to the recovery criteria was not adequately examined in the current PVA[7].

Numerical Population Objectives for Recovery. Several alternatives are under consideration, each representing a metapopulation of 750-850 individuals, containing 3 primary core populations of 200-300 wolves, maintained for a period of 8 years.

- These numbers are arbitrary and should have been more fully evaluated with respect to potentially suitable habitat within historical range in the United States and Mexico, historical data on wolf densities within those areas[8], and current densities of wolves in Arizona and New Mexico.
- The proposed number likely exceeds that needed for wolves to no longer be in danger of extinction[9]. Considerably smaller populations of wolves (of multiple subspecies) have successfully

persisted across their range[10]. Numbers proposed by the SPS are more appropriate to a restoration than a recovery effort.

- The PVA analysis used to support numerical recovery criteria failed to evaluate the relative outcomes of meaningful alternative recovery scenarios. Although it compared various sizes and numbers of populations, results only confirm a basic tenet of conservation biology – that larger populations have lower extinction risk, and seem to reflect pre-determined, desired outcomes[11].
- There are many apparent shortcomings in the PVA, including arbitrary manipulation of key parameters in the model[12], insufficient documentation[13], and limited sensitivity analysis[14].
- The PVA is heavily influenced by inputs and assumptions about the relationship between genetics and demographic parameters and may, as a result, overestimate risk of extinction[15].

Calculations based on wolf pack territory spacing and prey biomass were used to assess the potential to support specific numbers of wolves in selected recovery areas.

- These calculations are fraught with uncertainty due to multiple, confounded variables and complex relationships among these variables[16].
- Ungulate biomass - wolf density relationships were derived from more productive northern ecosystems where wolves, other predators, and their prey base coexisted for long periods[17]. These calculations are retrospective and may not yield reliable predictions of the number of wolves that might be supported in recovery areas for the Mexican wolf[18].

Dispersal Among Recovery Areas. The draft criteria specify a minimum of 0.5 effective migrants per generation (4 years). This means one wolf must naturally disperse into each of the 3 populations every 8 years and successfully reproduce.

- This level of natural immigration may be difficult to achieve, given the spatial arrangement of proposed recovery areas and lack of connectivity among them.
- It will be extremely difficult and expensive to document attainment[19].
- Relying on natural dispersal alone deprives managers of an effective and comparatively inexpensive tool (translocation) that could be used to increase genetic variability among and within recovery areas. The Service has long-recognized the role of human-assisted migration in wolf recovery[20].

Additional Concerns

The review team also considered 2 additional concerns, reflecting factors not currently incorporated in the draft recovery criteria, but which have figured prominently in discussions by the SPS.

Climate Change. It has been suggested that predicted climate changes across the Southwest necessitate recovery outside historical range.

- This assertion is contrary to the generalist and adaptable nature of wolves and their prey, and is inconsistent with their evolutionary history[21].

Human-caused Losses. It has been suggested that recovery criteria should include a threshold for maximum allowable human-caused loss of wolves in the recovery areas.

- Reducing human-caused loss is an important recovery action, but as a formal criterion will do little to functionally reduce wolf mortality[22].
- The number of human-caused losses is irrelevant if the wolf population is stable or increasing. The overall mortality rate is of greater concern[23].
- Suggested thresholds could limit managers' willingness to deal with wolves causing damage or other conflicts[24].
- There is considerable disagreement in the scientific literature over how to measure this factor, which may be difficult to define and would be time-consuming and expensive to measure[25].

Notes

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[1] The gray wolf, *Canis lupus*, is a widely distributed animal whose geographic range in North America was not fragmented historically by natural barriers to dispersal, and for which historical gene flow appears to have been significant and widespread. The Mexican wolf, *C. l. baileyi*, is an entity occupying the extreme southwestern edge of that much larger distribution. Its historical range included primarily the Sierra Madre Occidental in Mexico and did not extend farther north than extreme southeastern Arizona and southwestern New Mexico. The majority of that distribution was isolated from other wolves (only the extreme northern end in Arizona and New Mexico came in contact with other wolves, historically), and Mexican wolves occupied habitats unlike those found elsewhere in the range of gray wolves, thus setting the stage for localized differentiation (Bailey 1931, Brown 1983, Hoffmeister 1986, Chambers et al. 2012).

While the Mexican portion of the distribution of *C. l. baileyi* is clearly circumscribed, the northern distributional limit of *C. l. baileyi* is not well defined, and therefore by extension, neither is the zone of intergradation into *C. l. nubilus* (or *mogollonensis*). Ecological limitations of arid communities east of the Sierra Madre Occidental (Brown 1983) may have prevented long distance wolf dispersal and kept those southernmost populations isolated. Animals in Arizona and New Mexico had no such limits, and wolf habitat (albeit vegetatively different) graded into the southern Rockies and Great Plains. While there is ample evidence that *C. l. baileyi* is morphologically distinct (Bogan and Mehlhop 1983, Hoffmeister 1986, Nowak 1995, Chambers et al. 2012), Bogan and Mehlhop (1983) proposed that morphology of wolves living along the Mogollon Rim in Arizona suggested a zone of intergradation between *C. l. baileyi* and northern gray wolves. Although most of the variation seemed to be explained by skull size, *C. l. baileyi* was consistently identifiable. Importantly, they included large numbers of Mexican museum specimens in their studies.

[2] There are clear problems with interpretation of the available genetic data. Vilà et al. (1999) and Leonard et al. (2005) have been used as "strong" evidence for a genetically unique *C. l. baileyi.* Each conducted a genetic analysis of 425 base pairs of mitochondrial DNA control region, which is only a small fraction (< 3%) of the mitochondrial genome. This resulted in the identification of 60 or so haplotypes (mitochondrial genotypes), and only 16 phylogenetically informative sites (Vilà et al. 1999), i.e., there were many genetic types, but only a few characters that could be used to infer genetic relationships. Vilà et al. (1999) acknowledged that their analysis resulted in "an absence of large-scale geographical structure," such that it would be difficult to definitively identify subspecies or other entities across the range of wolves in North America.

Both Vilà et al. (1999) and Leonard et al. (2005) identified haplotype *lu33*, which was found only in members of the captive Mexican wolf population and in 4 historical samples taken from within the historical distribution (1 southwestern NM, 1 southeastern AZ, 2 Chihuahua). That particular haplotype suggests a unique history that might have been shared only by members of the *C. l. baileyi* subspecies. Also, an analysis of microsatellites indicated the three captive Mexican wolf lineages were more closely related to one another than to any other North American gray wolf populations (García-Moreno et al. 1996).

However, the mtDNA analyses suggested different histories for haplotype *lu33*. Vilà et al. (1999) suggested that the Mexican wolf haplotype was ancestral to all other North American *and* Eurasian wolves. Leonard et al. (2005) came to very different conclusions, suggesting that *lu33* and a few other haplotypes comprised a "southern clade" that included animals from Mexico, extreme southwestern New Mexico, and southeastern Arizona, but also included a few individuals from Oklahoma, Nebraska, northern New Mexico, Colorado and northern Utah. Statistical support for the "southern clade" was sorely lacking, i.e., the chance that the "southern clade" was, in fact, a distinct entity was less than 50%, essentially no different than random; the remaining "branches" within that tree were also poorly supported. The differences in the results presented in the two studies, and the extraordinarily poor support for the "southern clade" in Leonard et al. (2005) suggests that more caution is warranted than was exercised in the interpretation of those data.

Chambers et al. (2012:2) reviewed "the scientific support in the currently available scientific literature for 1) recognizing...subspecies, of North American wolves...[and]...recommending at least general geographic boundaries for...[those] subspecies." They noted that (p. 2) "... there are large gaps in geographic coverage, particularly for genetic data. Recent studies... of DNA markers from museum specimens have attempted to address these gaps, but as yet they represent relatively few individuals." Nonetheless, later in their review, Chambers et al. (2012:35) emphasized grouping of the "southern clade" as proof the Mexican wolf is a genetically unique animal, "divergent from other North American wolves."

Genetic data suggest a unique history to wolves from Mexico and extreme southern Arizona and New Mexico (a *baileyi* haplotype, *lu33*; microsatellites); however, a more thorough analysis of museum specimens, including larger portions of mitochondrial or nuclear genes, is necessary to understand that history more fully.

Haplotypes apparently linked to *lu33* (i.e., the other samples in the "southern clade") were found in animals from as far away as northern Utah, Colorado, Nebraska and Oklahoma, suggesting a couple of possibilities: 1) a common genetic source (i.e., "incomplete sorting" of highly variable ancestral haplotypes, leaving similar remnants of that ancestral genetic pattern); this would be consistent with the the Vilà et al. (1999: fig. 1) analysis, or 2) occasional gene flow from southern Arizona and New Mexico through somewhat fragmented habitat northward to the southern Rockies and Great Plains (see Bailey 1931 and Brown 1983). Leonard et al. (2005:15) felt that evidence for geographical (= subspecies) structure was insufficient and recommended that "ecological rather than genetic heritage should guide reintroduction." Nonetheless, they went on (p. 16) to contradict that conclusion, stating that their "genetic results provide a wider geographical mandate for reintroduction [of *C. l. baileyi*] and suggest admixture was a characteristic of past populations that might enhance the adaptive potential of reintroduced stocks" indicating, "[t]he wide distribution of the southern clade suggests that gene flow *was extensive across the recognized limit of the subspecies* (p. 15, emphasis added). Recent attempts by USFWS and the SPS to extend historical range of Mexican wolves northward rely heavily on this assertion. However, it is not clear what subspecies limits they recognized.

The Department has consistently urged the USFWS to be clear and consistent regarding issues of subspecies recognition and geographic distribution, with respect to subsequent listing or recovery strategies. We have argued the need to clearly define a subspecies' distribution prior to listing and setting of recovery objectives. Unfortunately, and because the characteristics used to define subspecies are often arbitrary, subspecies distributions depend on who is drawing the maps and how much information is available (see Young and Goldman 1944, Hoffmeister 1986, Nowak 1995, García-Moreno et al. 1996,).

For example, the Tucson shovel-nosed snake became a candidate for listing in 2010. This subspecies was described in 1941, on the basis of "unique" color pattern, from creosote flats habitats at the eastern edge of the Sonoran Desert between Phoenix and Tucson. Its distribution was inconsistently defined and comprised a narrow strip at the eastern periphery of a species widely distributed throughout the Sonoran and Mohave deserts. The Department pointed out inconsistencies regarding where the subspecies distribution ended and the zone of intergradation began, and the extent of that zone. The Service had indicated that "[c]urrent practice...is to objectively describe the ranges of different subspecies...with narrative descriptions, maps, or both...", and that "including all shovel-nosed snakes in the intergrade zone...would not be consistent with current scientific practice... therefore, *we do not consider shovel-nosed snakes within the intergrade zone to be members of the Tucson shovel-nosed snake subspecies*" (USFWS 2010, emphasis added). While a consistent approach is prudent, in most cases of subspecies, it is nearly impossible to apply those rules effectively. Moreover, "current scientific practice," as represented by phylogenetic approaches to systematics, has moved away from the subspecies concept and zones of intergradation are seldom recognized; this has been the case for more than a decade.

Wood et al. (2007) provided an extensive analysis of shovel-nosed snake mtDNA sequence variation that included 1068 base pairs from the 16S rRNA and ND1 genes, and resulted in 157 phylogenetically informative sites (compare with wolf genetic analyses, above). The result of that analysis demonstrated that Tucson shovel-nosed snakes comprised the extreme end of an east-west cline of genetic variation, suggesting that subspecific recognition was not warranted. A follow-up study using nuclear DNA is underway to test that hypothesis further.

If the SPS is going to apply a taxonomic standard to define Mexican wolf distribution, the objective basis must be made clear. The putative zone of intergradation has been interpreted narrowly using morphometrics and historical accounts, e.g., extending north through the White Mountains, Mogollons, Datils, etc., and more broadly by Leonard et al. (2005), e.g., extending well into Colorado, southern Utah or even Oklahoma or Nebraska. Unfortunately, the current genetic data are insufficient to make such delineations. Further, the presence of "southern clade" haplotypes outside of the presumed historical range should not be construed as evidence of an extended historical distribution of Mexican wolves. This is especially important if the Service continues to not recognize animals within the zone of intergradation as "members" of that subspecies, whether currently or historically.

[3] Araiza et al. (2012) prioritized six previously identified areas within historical range of the Mexican wolf in northern Mexico as potential sites for reintroduction. Using a GIS framework, areas were ranked based on habitat quality and probability of human-caused mortality. Enrique Martinez-Meyer (Universidad Nacional Autónoma de Mexico) revisited this analysis, without constraint to the six pre-identified polygons. Preliminary results were presented to the SPS in October 2012, who used them to delineate two large areas of suitable Mexican wolf habitat that could serve as recovery areas in historical range.

[4] Prior to appointment to the SPS, one member was hired by Ted Turner for the expressed purpose of establishing Mexican wolves on Mr. Turner's Vermejo Park Ranch (http://www.livestockweekly.com/papers/97/04/03/3wolfbio.html), one of the currently proposed recovery areas outside historical range. The landscape modeling effort that identified this recovery area was conducted by that individual and 2 other SPS members using funds provided by the Turner Endangered Species Fund. That analysis scored this private ranch the same as a U.S. National Park and also as roadless, despite having 600 coal bed methane wells and 200 miles of new roads.

[5] Wolves from the successfully-recovered Northern Rocky Mountain metapopulation have already dispersed southward into Utah and Colorado. One wolf from Yellowstone National Park reached Highway 70 in Colorado (Colorado Wolf Management Working Group 2004), the northern boundary of the Mexican wolf recovery area currently proposed by the SPS. While arguing for a wider geographical mandate for reintroduction, Leonard et al. (2005) failed to consider potential consequences of such events, i.e., the potential for genetic swamping by northern gray wolves coming into contact with Mexican wolves while recovering populations are still low.

[6] The Recovery Plan for the masked bobwhite (U.S. Fish and Wildlife Service 1995:37) specifies the following recovery criteria:

> "The masked bobwhite will be considered for reclassification from endangered to threatened when four separate, viable populations are established (consisting of two populations in the United States and two or more in Mexico) and have been maintained for 10 consecutive years. The criteria for full delisting the species are not known at this time. The earliest estimated date for downlisting is 2007."

[7] Populations in Mexico were modeled as small and isolated (based on initial delineations of potential reintroduction areas) and did not reflect the full extent of potential habitat and populations that might be supported south of the border.

[8] The proposed number of wolves likely exceeds that historically present in one recovery area (Grand Canyon Ecosystem). Numbers of wolves removed during intensive predator control efforts provide a useful index of historical abundance. Mann and Locke (1931) summarized predator removal on the Kaibab Plateau between 1907-1930, which included 4,849 coyotes, 781 mountain lions, 554 bobcats, and 30 wolves.

[9] The final Environmental Impact Statement (FEIS) for the recovery of wolves in the Northern Rocky Mountains revisited the number and configuration needed for a viable wolf metapopulation. Twenty of 25 leading wolf experts agreed that a metapopulation of 10 breeding pairs of wolves in each of 3 areas for 3 successive years with some level of movement between areas would achieve recovery objectives (U.S. Fish and Wildlife Service 1994:Appendix 9).

[10] Fuller et al. (2003:Table 6.9) list 7 small wolf populations (<200 animals) that have persisted in North America and Europe. Perhaps the most extreme example is Isle Royale National Park, where a small (12-50 animals), isolated and highly-inbred wolf population (derived from 1 female and 1-2 males) has persisted in for >60 years without negative demographic consequences (Mech and Cronin 2010).

[11] Population viability analyses (PVAs) are computer simulation-based theoretical models used to examine population viability under specified management and/or environmental conditions. Viability is assessed as the risk of extinction or quasi-extinction (falling below some predefined size). A great deal of emphasis was originally placed on using PVAs to identify minimum viable population or to assess the urgency of recovery efforts (Shaffer 1981, Gilpin and Soulé 1986). However, subsequent assessments identified limitations of PVAs and provided recommendations for their appropriate use (Beissinger and Westphal 1998, Ellner et al. 2002, Reed et al. 2002). Specific recommendations that have relevance to our review of the SPS's PVA are 1) model validity is contingent on appropriateness of the model's structure and data quality, 2) results should include appropriate assessment of confidence, 3) model construction and results should be subject to external review, 4) more research is needed on determining the influence of density dependence, and 5) PVA should not be used to determine minimum population size or the specific probability of reaching extinction.

The PVA analysis done by the SPS largely serves to illustrate the obvious -- that larger populations have reduced risk of extinction, a basic tenet of conservation biology. Reed et al. (2002) cautioned that PVAs are most appropriate for evaluating potential scenarios, but should not be used to determine minimum population sizes. The analysis appears to be used as justification for pre-determined numbers of wolves deemed desirable by some members of the SPS. The SPS acknowledges that PVAs should be used to evaluate relative versus absolute risks of extinction, and the analysis does compare the risk of extinction associated with several recovery scenarios. However, these comparisons focused on combinations of different sizes and numbers of populations. If additional scenarios included populations > 250 animals, we anticipate that they would have resulted in even lower extinction risk.

An approach that would have been more informative, but was not pursued, is to evaluate habitat within historical range, including Mexico, to estimate the minimum number of wolves likely be supported within each area based on observed densities in currently occupied areas, and to assess permeability of the landscape between blocks of suitable habitat. This information could have formed the basis of an evaluation of relative risks associated with alternative scenarios (in this case representing various recovery areas and connectivity levels), as recommended by PVA modelers (e.g., Beissinger and Westphal 1998, Reed et al. 2002).

[12] Key parameters in the PVA have been arbitrarily set or manipulated and in some cases, appear to have been derived by working backwards from a desired outcome (population size or number of effective migrant wolves per generation). Specific examples include:

- When used in the PVA model, the observed mortality rate of Mexican wolves in the Blue Range Wolf Recovery Area was too high for modeled populations to persist, so mortality rates were arbitrarily reduced for simulation purposes. Consequently, model outputs reflect a baseline of unknown relevance to recovering wolf populations in the Southwest.

- "Percent of females breeding" is the most influential parameter affecting probability of extinction. The literature contains estimates ranging from 33-77%. The SPS arbitrarily selected a value of 50%. Using higher or lower values results in very different model outcomes.

- A separate model based on data from initial lineages of Mexican wolves showed a relationship between inbreeding coefficient of the dam and litter size. This was extrapolated to overall population persistence for all recovering Mexican wolf populations. This parameter significantly affects probability of extinction, removing it brings the probability of extinction to near zero.

- Catastrophic events in Mexican wolf populations were modeled using the frequency and severity of canine distemper outbreaks in wolf pups in the Northern Range of Yellowstone National Park. The effect of an 80% reduction in percent of females breeding and 5% reduction in survival rates (of all classes) is an arbitrary and uncertain surrogate for episodic catastrophes that might affect recovering Mexican wolf populations. This parameter also has a significant influence on the results; removing it from the model also brings the probability of extinction to near zero.

- The model simulated harvest of wolves out of subpopulations after they reached subpopulation goals (but not necessarily satisfy recovery criteria). It is inappropriate to include post-delisting management (harvest) in a PVA for recovery.

[13] The SPS has not provided a systematic narrative of the PVA modeling approach nor obtained external review of the methodology, as recommended by Reed et al. (2002).

[14] Sensitivity analysis is an important element of PVA analysis -- systematically exploring the influence of demographic parameters which typically carry considerable uncertainty (Ellner et al. 2002) and identifying the range of uncertainty around estimated extinction risk (Reed et al. 2002). In this modeling effort, the SPS seems to have taken an ad-hoc approach, focused more on desired outcomes (e.g., population size) than parameters driving population persistence -- which have been incorporated into recovery criteria for other species (e.g., Channel Island fox; U.S. Fish and Wildlife Service 2012a).

[15] The relationship between inbreeding and demographic parameters and their influence on long-term population viability is poorly understood. Fredrickson et al. (2007) and Asa et al. (2007) present evidence that inbreeding depression influences reproduction in Mexican wolves. However, the long-term implications on recovery are not clear. Fredrickson (2011) noted that inbreeding depression may be reduced with improvements to captive breeding and release decisions. While genetic purging was considered a mechanism to offset the negative impacts of inbreeding depression (e.g., Ralls and Ballou 1986), more recent studies have not consistently supported this relationship (Kalinowski et al. 2000, Boakes et al. 2007). This uncertainty should be more fully considered in development and interpretation of a PVA.

[16] Estimates of the number of territories that could exist on the landscape and calculations of pounds of edible biomass available to wolves were done as simple mathematical exercises, not with the expectation of obtaining estimates of carrying capacity for wolves. Predictions based on available biomass are confounded by spatial and temporal variations and interactions among numerous factors. These include: prey species availability, vulnerability, and selection by wolves; interactions with other large predators; effects of scavengers; prey cached, then lost to spoilage or not retrieved; and uncertain dietary preferences in new ecosystems (Fuller et al. 2003; L.D. Mech and T. Fuller, personal communications to J. Heffelfinger).

[17] Fuller et al. (2003:Figure 6.2) present significant, positive linear relationship between ungulate biomass and wolf density during winter. These data reflect long-established wolf populations in the U.S. (Alaska, Michigan, Minnesota) and Canada (Alberta, Quebec, Yukon Territory). Because the Mexican wolf evolved with smaller prey (e.g., Coues' white-tailed deer and javelina) in a milder climate, it's unclear if these relationships would apply in proposed recovery areas where larger ungulates (e.g., elk) represent the bulk of prey biomass and occur in habitats that can have deep, persistent snow during winter.

[18] These regression analyses were not intended to predict wolf carrying capacity, but rather to illustrate a general relationship between ungulate biomass and wolf density at a continental scale in instances where predators and prey had coexisted, not at a time prior to the release or reestablishment of wolves (T. Fuller, personal communication to J. Heffelfinger).

[19] Small, re-introduced populations of Mexican wolves (*C. l. baileyi*), present an extra challenge to documenting gene flow among subpopulations. Because reintroduction programs often begin with small numbers of individuals that share a common gene pool, "the ability to detect genetically effective migration between [populations] is confounded by shared close relatives among founding populations." (vonHoldt et al. 2010: 4413).

Documenting natural immigration of wolf individuals who then become alpha breeders in new areas will thus be rather difficult and extremely expensive. Among reintroduced wolf populations in the Northern Rocky Mountains, documenting "genetically effective dispersal" among three recovery areas required extensive and laborious measures (vonHoldt et al. 2010). Earlier attempts to examine genetic exchange among 200 individuals found no evidence for natural gene flow (vonHoldt et al. 2008).

Later, vonHoldt et al. (2010) sampled 656 individual wolves across the Northern Rocky Mountains. Their efforts required blood/tissue collection via helicopter darting and post-mortality sampling, and each individual was assessed for 26 microsatellite loci (more than twice the usual number of loci used in a majority of published microsatellite studies). They also used date of birth/death, sampled from juveniles in a known subpopulation, radio-telemetry, and known dispersal data, as well as field-based behavioral observations, to further verify the genetic assignments and determine the minimum number of migrants and genetically effective dispersal events that had occurred over the first decade of recovery.

No less effort would be required to demonstrate genetically effective dispersal among Mexican wolf populations, given that their founders came from 7 captive animals (Hedrick et al. 1997). The level of genetic diversity is much lower in Mexican wolves than in recovered northern grey wolf populations, i.e., low overall genetic heterozygosity (García-Moreno et al. 1996), and one mtDNA haplotype found in wolves from the historical range of Mexican wolves versus multiple haplotypes found in northern grey wolves (Vilà et al. 1999, Leonard et al. 2005).

[20] The final rule for delisting the gray wolf in Wyoming (U.S. Fish and Wildlife Service 2012b) noted that:

> "For more than 15 years, we have concluded that movement of individuals between the metapopulation segments could occur either naturally or by human-assisted migration management... Intensive migration management might become necessary if 1 of the 3 subpopulations should develop genetic or demographic problems... human-assisted migration should not be viewed negatively and would be necessary in other wolf recovery programs."

Assisted migration has been part of recovery criteria for other species (e.g., the Concho water snake; U.S. Fish and Wildlife Service 1993:33):

> "Movement of an adequate number of Concho water snakes is assured to counteract the adverse impacts of population fragmentation. These movements should occur... until such time that the Service determines that Concho water snake populations in the three reaches are viable and 'artificial movement' among them is not needed."

The post-delisting monitoring plan for the Concho water snake (U.S. Fish and Wildlife Service 2011) indicated use of additional translocations if needed.

[21] Wolves inhabited northern latitudes in Eurasia prior to migrating into North America in at least three distinct migratory events, the first some 500,000 years B.P. (Weckworth et al. 2010, Chambers et al. 2012). They were subject to fluctuating climates and temperatures of the Pleistocene Epoch (~2.5 million years ago to ~11,000 years before present), a dynamic period characterized by cold, glacial periods and warm interglacial periods that cycled roughly every 100,000 years. In modern history, wolves have inhabited regions where temperatures range from -40 to +40°C, in areas as varied as Israel and Greenland (Mech 1995).

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. Wolves successfully occupy a variety of ecosystems in North America and Eurasia and take a wide variety of prey (e.g., all species of North American ungulates and smaller mammals such as beaver and hares; Mech 1995). Their natural history and adaptability suggest they can persist within historical range in the face of shifts in vegetative communities and associated vertebrate prey.

[22] A small minority of the public is responsible for illegal killing of Mexican wolves; regardless how written, recovery criteria will not alter behavior of those individuals. To date, 23% (14/61) of human-caused losses in Arizona and New Mexico have been the result of vehicle collisions

(http://www.fws.gov/southwest/es/mexicanwolf/pdf/MW_causes.pdf),which are likewise unaffected by recovery criteria.

[23] This issue has arisen for other listed species such as grizzly bears. The 1993 Grizzly Bear Recovery Plan (U.S. Fish and Wildlife Service 1993) initially developed a recovery criterion with a threshold for percent of human-caused mortality allowed. This criterion was later amended (U.S. Fish and Wildlife Service 2007) for all bears (except those still dependant on sows) to apply only to total mortality since the source of mortality is not relevant as long as total losses do not inhibit recovery.

[24] In grizzly bear recovery areas, roadkills and other human-caused losses result in a reluctance to remove problem animals (Montana Fish Wildlife and Parks 2002:54). Not honoring previous agreements for management removal of Mexican wolves (U.S. Fish and Wildlife Service 1998) will further erode support for wolf recovery.

[25] Creel and Rotella (2010) predicted substantial harvest-related declines in Montana wolf populations, asserting that human-caused losses could be sustained only if <22.4%, a number lower than assumed in wolf management plans and previous studies (Fuller et al. 2003, Adams et al. 2008, Murray et al. 2010). Gude et al. (2011) replicated the analyses of Creel and Rotella (2010), including annual variation in wolf recruitment and excluding suspect field data, yielding a predicted sustainable level of human-caused mortality of 48.4% , regardless of recruitment. Population simulations by Gude et al. (2012) were consistent with field observations and previous population estimates by Montana Fish Wildlife and Parks, whereas declines predicted by Creel and Rotella (2010) were not. A subsequent reanalysis of data used by Creel and Rotella (2010) and Gude et al. (2011) by SPS yielded yet another estimate of sustainable human-caused mortality (17%; manuscript in prep). These estimates are currently a source of debate in the scientific community and have extended to the review of Wyoming's wolf management plan (Atkins 2011).

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