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Draft Mexican Wolf Revised Recovery Plan

5_07_2012
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DRAFT

U.S. Fish and Wildlife Service
Southwest Region (Region 2)
Albuquerque, New Mexico
20xx

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PREFACE

(Note to Reviewer: The below paragraph is mandatory language that must be included somewhere in the introductory sections of a recovery plan; anything else in this section is optional. Let’s wait until we’ve got more of the plan put together to determine whether we need anything else.)

The purpose of a recovery plan is to provide a scientifically based, logical, and effective roadmap for the recovery of a species. It explains what is needed for species recovery and how to get there. Recovery plans are advisory documents, not regulatory documents. A recovery plan does not commit any entity to implement the recommended strategies or actions contained within it for a particular species, but rather provides guidance for ameliorating threats and implementing proactive conservation measures, as well as providing context for implementation of other sections of the ESA, such as section 7(a)(2) consultations on Federal agency activities, development of Habitat Conservation Plans, or the creation of experimental populations under section 10(j).

DRAFT

54 **DISCLAIMER**

55 (Note to Reviewer: The text in this section is standard, required “legalese” language in all
56 recovery plans so please do not provide edits.)

57

58 Recovery plans delineate reasonable actions believed to be required to recover and/or protect
59 listed species. Plans published by the U.S. Fish and Wildlife Service (FWS), are sometimes
60 prepared with the assistance of recovery teams, contractors, state agencies, and other affected
61 and interested parties. Recovery teams serve as independent advisors to FWS. Plans are reviewed
62 by the public and submitted to additional peer review before they are adopted by FWS.

63 Objectives of the plan will be attained and any necessary funds made available subject to
64 budgetary and other constraints affecting the parties involved, as well as the need to address
65 other priorities. Recovery plans do not obligate other parties to undertake specific tasks and may
66 not represent the views nor the official positions or approval of any individuals or agencies
67 involved in the plan formulation, other than FWS. They represent the official position of FWS
68 only after they have been signed by the Regional Director as approved. Approved recovery plans
69 are subject to modification as dictated by new findings, changes in species status, and the
70 completion of recovery tasks.

71

72 By approving this document, the Regional Director will certify that the data used in its
73 development represent the best scientific and commercial data available at the time it was
74 written. Copies of all documents reviewed in development of the plan are available in the
75 administrative record located at New Mexico Ecological Services Field Office, U.S. Fish and
76 Wildlife Service, 2105 Osuna Dr., NE, Albuquerque, NM, 87113, #505-346-2525 or 1-800-299-
77 0196.

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85

86 **ACKNOWLEDGEMENTS**

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88 which convened from 2011 to 20xx to develop this recovery plan. The team was comprised of four
89 subgroups:

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141 Melbihess, Mexican Wolf Recovery Team Manager, Southwest Region.

142
143 (continue list as needed, Colby Gardner/Kevin Winters/GIS, etc?)

144
145
146 The writing of the plan took place in several stages. Much of the background material was modified extensively by
147 members of the Science and Planning Subgroup from the 2010 Mexican Wolf Conservation Assessment through
148 team review and updated field data and information. The Recovery Strategy and Recovery Criteria subsections were
149 written by members of the Science and Planning Subgroup. The Tribal Perspectives chapter was written by
150 members of the Tribal Subgroup and the Agency Subgroup. The.... (i.e., explain how the plan was written, that
151 there was not necessarily “consensus” throughout, name individual contributors if desired, etc).

152 **LITERATURE CITATION AND AVAILABILITY**

153

154 Literature citation should read as follows:

155 U.S. Fish and Wildlife Service. 20xx. Draft Mexican Wolf Revised Recovery Plan. Region 2,
156 Albuquerque, New Mexico, USA.

157

158 Copies of the document can be requested from:

159

160 U.S. Fish and Wildlife Service

161 New Mexico Ecological Services Field Office

162 2105 Osuna Drive NE

163 Albuquerque, New Mexico 87113

164 Telephone #: 505-346-2525 or 1-800-299-0196

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174 Copies are also available on-line at:

175 <http://www.fws.gov/southwest/es/mexicanwolf>

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259 **EXECUTIVE SUMMARY**
260 (Note to Reviewer: We will write this section last.)

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261 **I. BACKGROUND**

262

263 A. Brief Overview

264 (Note to Reviewer: This section should orient the reader to the situation.)

265

266 *Recovery Planning*

267

268 The Mexican Wolf Revised Recovery Plan (Plan) is the first recovery plan developed for the
269 Mexican wolf that contains the required recovery plan elements specified by the Endangered
270 Species Act (ESA, or Act) (section 4(f)(1)):

271 i) a description of such site-specific management actions as may be necessary to achieve
272 the plan's goal for the conservation and survival of the species;

273 ii) objective, measurable criteria which, when met, would result in a determination, in
274 accordance with the provisions of this section, that the species be removed from the
275 list; and

276 iii) estimates of the time required and the cost to carry out those measures needed to achieve
277 the plan's goal and to achieve intermediate steps toward that goal.

278

279 Two other recovery plans have been written for the Mexican wolf: the 1982 Mexican Wolf
280 Recovery Plan, which was written by a recovery team established by the Service and signed by
281 the Service and the Dirección General de la Fauna Silvestre in Mexico; and the Programa de
282 Recuperación del Lobo Mexicano (Programa de Recuperacion), written by a team of scientists in
283 Mexico, in 1999 (SEMARNAT 2000). Both of these plans acknowledge the binational historical
284 range of the Mexican wolf within the United States and Mexico, but each plan was written
285 within the context of the federal laws governing its content: the 1982 Mexican Wolf Recovery
286 Plan was written pursuant to the Service's obligation to develop recovery plans for species
287 protected by the Act, whereas Mexico's plan was written pursuant to the Mexican federal law
288 protecting wildlife, Norma Oficial Mexicana NOM-059-ECOL-1994.

289

290 The 1982 Mexican Wolf Recovery Plan did not contain all three of the recovery plan elements
291 specified in section 4(f)(1) of the Act. The recovery team could not foresee full recovery and

292 eventual delisting of the Mexican wolf due to its dire status in the wild and the lack of suitable
293 habitat within the historical range due to anthropogenic activities. Therefore, they stopped short
294 of providing the objective and measurable recovery criteria required by the Act. Instead, the
295 recovery team laid out a “prime objective”:

296 “To conserve and ensure the survival of *Canis lupus baileyi* by maintaining a captive
297 breeding program and re-establishing a viable, self-sustaining population of at least 100
298 Mexican wolves in the middle to high elevations of a 5,000-square-mile area within the
299 Mexican wolf’s historic range (USFWS 1982:23).”

300 The recovery actions and attending time and cost estimates in the 1982 Recovery Plan focused
301 on information gathering and management recommendations in support of this prime objective.
302 The Service initiated revision to the 1982 Mexican Wolf Recovery Plan in the mid-1990s and
303 early 2000’s. These revisions were not finalized due to logistical issues, including litigation
304 related to gray wolf reclassifications (see National Gray Wolf Recovery, below).

305
306 Mexico’s 1999 Programa Recuperacion was not required by law to set a numeric goal for
307 recovery. It did, however, establish an objective to reach population levels that would ensure
308 long-term viability by reintroducing Mexican wolves into several areas in Mexico (V:
309 Objectives, VI: Strategies, Projects, and Actions) (SEMARNAT 2000). The document explained
310 that Mexico supported reintroduction on both sides of the Mexico-United States border, and
311 stated that it would be difficult to find appropriate habitat for reintroduction in Mexico. The plan
312 suggested that the best habitat may exist within the Sierra Madre Occidental and the Sierra
313 Madre Oriental mountain ranges (SEMARNAT 2000).

314
315 The 201x Mexican Wolf Revised Recovery Plan replaces and supersedes the Service’s 1982
316 Mexican Wolf Recovery Plan, but it does not replace, supersede, or otherwise affect Mexico’s
317 Programa de Recuperacion. [More here as necessary to broadly describe national/bi-national
318 aspects of this plan.]

319
320 *Recovery Implementation in the United States and Mexico*

321 Recovery efforts for the Mexican wolf have been underway in the United States and Mexico for
322 several decades. Both countries have adopted a two-pronged approach to recovery: maintaining

323 a captive population of Mexican wolves, and re-establishing wild populations by releasing
324 captive wolves into designated reintroduction areas to establish viable populations that count
325 toward recovery..

326
327 The Mexican wolf captive breeding program established in the late 1970's saved the Mexican
328 wolf from extinction. The breeding program was founded by three of the last six Mexican
329 wolves removed from the wild in Mexico. The first Mexican wolf pups were conceived and born
330 in captivity in the United States in 1981 (Parsons 1996, Hedrick et al. 1997, Lindsey and
331 Siminski 2007). Mexico formally joined the captive breeding effort in 1987 (SEMARNAT
332 2000), and by 1994, the binational breeding program had produced a captive population of 92
333 wolves. These founding wolves and their offspring were initially referred to as the Certified
334 lineage, later renamed the McBride lineage. In 1995, two additional lineages of pure Mexican
335 wolves, the Ghost Ranch lineage, founded by two wolves, and the Aragon lineage, founded by
336 two wolves, were integrated into the captive breeding program to increase the genetic diversity
337 of the founder population and reduce the potential for inbreeding depression to hinder recovery
338 (Parsons 1996, Hedrick et al. 1997). Ultimately then the founding base of the captive population
339 included only seven pure Mexican wolves (Hedrick et al. 1997).

340
341 Today, the binational captive breeding program continues to conserve the subspecies' genome
342 and provide healthy offspring for release to the wild (Parsons 1996, Lindsey and Siminski 2007).
343 The program has been managed pursuant to breeding protocols and genetic and demographic
344 goals established by the Association of Zoos and Aquariums' Species Survival Plan (AZA
345 Mexican Wolf SSP) since 1994 (Siminski and Spevak 2011). The captive breeding program
346 currently houses 283 wolves in 52 facilities, 34 of which are in the United States and 18 of which
347 are in Mexico (Siminski and Spevak 2011). In an analysis of the captive population in 2011, the
348 calculated retention of the original gene diversity of the founding seven wolves was 83.3 percent
349 (Siminski and Spevak 2011). However, even with optimal management the genetic diversity in
350 the captive population will continue to decline and could eventually compromise the Mexicana
351 wolf's ability to survive in the wild (cite).

352

353 The United States and Mexico have both initiated re-establishment of the Mexican wolf in the
354 wild by releasing captive-bred wolves into areas of suitable habitat in each country. In the
355 United States, Mexican wolves were reintroduced to the wild in 1998 (cite annual report); as of
356 December 31, 2011, a population of approximately 58 wild Mexican wolves inhabits the
357 southwestern United States (update, cite). Mexico reintroduced Mexican wolves to the wild in
358 2011; as of MONTH, 2012 x wild Mexican wolves inhabit Mexico (update, cite). These
359 reintroduction efforts are independent of the captive breeding program, although closely
360 coordinated. The United States and Mexico also communicate their reintroduction plans with
361 one another, share equipment, and transfer information and technology through staff visits to
362 each country. Implementation of reintroductions occurs according to the legal frameworks and
363 management provisions relevant to each country.

364
365 In the United States, plans for the reintroduction of the Mexican wolf to the wild began to
366 develop in the early-1990s, stimulated in part by a suit filed against the Service by seven
367 environmental organizations for failure to implement provisions of the ESA (Wolf Action
368 Group, et al. vs. United States, Civil Action CIV-90-0390-HB, U.S. District Court, New
369 Mexico). During this time, the Service formed a new recovery team to revise the 1982 Mexican
370 Wolf Recovery Plan with updated scientific information and recovery criteria. The draft
371 recovery plan developed by the new recovery team was not finalized. The prime objective of the
372 1982 recovery plan to establish a population of at least 100 wolves in the wild was maintained as
373 a guiding recommendation for the reintroduction. Several analyses were conducted to assess
374 locations for the reintroduction (Johnson et al. 1992, USFWS 1993), culminating with the Final
375 Environmental Impact Statement, “Reintroduction of the Mexican Wolf within its Historic
376 Range in the Southwestern United States,” (FEIS) (USFWS 1996).

377
378 By 1998, the plans for the reintroduction were solidified in the final rule, “Establishment of a
379 Nonessential Experimental Population of the Mexican Gray Wolf in Arizona and New Mexico”
380 (Final Rule) (63 FR 1752-1772, January 12, 1998), and in March of that year, 11 Mexican
381 wolves from the captive breeding program were released to the wild. The Final Rule established
382 the Mexican Wolf Experimental Population Area (MWEPA) in central Arizona and New
383 Mexico, and designated the reintroduced population as a non-essential experimental population

384 under section 10(j) of the ESA (Figure x). This designation was justified because wolves
385 released to the wild would be genetically redundant to the captive breeding program and because
386 it allowed for regulatory flexibility in managing released wolves and their progeny, an important
387 consideration at the time for gaining public support (63 FR 1752-1772, January 12, 1998; Brown
388 and Parsons 2001). The rule stipulated that the reintroduction of wolves would take place within
389 the Blue Range Wolf Recovery Area, a 17,775 km² (6,845 mi²) area within the MWEPA that
390 included the Apache National Forest in east-central Arizona and the Gila National Forest in
391 west-central New Mexico. The remainder of the MWEPA outside of the BRWRA was
392 considered recovery habitat for the Mexican wolf and provided a transition zone between the
393 non-essential experimental designation of the BRWRA to the endangered designation that
394 applied to Mexican wolves elsewhere (i.e., wolves outside of the MWEPA have full endangered
395 status under the classification provided by the 1978 gray wolf listing) (63 FR 1752-1772,
396 January 12, 1998).

397
398 The strategy for the reintroduction was to release 14 family groups of wolves into the Blue
399 Range Wolf Recovery Area over a period of five years in order to establish the population (63 FR
400 1752-1772, January 12, 1998). The FEIS projected that the population target of at least 100 wild
401 wolves and 18 breeding pairs would be reached in 2006 (USFWS 1996). Because a source
402 population of Mexican wolves did not exist in the wild, the reintroduction would be initially
403 dependent on captive-bred wolves. As of December 31, 2011, the minimum estimate for the
404 BRWRA population is 58 wolves, about half of the minimum population objective (USFWS
405 2011).

406
407 In 2000, the White Mountain Apache Tribe (WMAT) agreed to allow wolves to inhabit Fort
408 Apache Indian Reservation (FAIR), and in 2002 signed an agreement allowing direct release of
409 wolves onto the reservation providing an additional 500 mi² (6,475 km²) of wolf habitat.

410
411 In October 2011, Mexico released five captive wolves to the wild in Sonora (Araiza et al. in
412 press). Four of these wolves were illegally killed by poison within several months of release.
413 Mexico plans on releasing additional wolves in this area, and in other areas targeted for
414 reintroduction, in the near future. Since Mexico developed its Programa de Recuperacion,

415 researchers in Mexico have conducted several habitat analyses to identify areas of suitable
416 habitat for the establishment of wild wolf populations (see Section I.H. and Modeling Appendix
417 Section 5.B.).

418
419 With the recent release of wolves in Mexico close to the United States-Mexico border, there is
420 potential for wolves from Mexico to disperse into the United States. Based on the current Code
421 of Federal Regulations (cite), such wolves would be considered “endangered” anywhere in the
422 Southwest other than within the boundaries of the Mexican wolf non-essential experimental
423 population (see Figure x). Wolves entering into this zone from Mexico will be managed
424 pursuant to a management plan developed by the Service, in coordination with the states of
425 Arizona, New Mexico, and Texas, and Mexico (cite).

426

427 *National Gray Wolf Recovery*

428 Since the Service’s listing of the gray wolf in the coterminous United States in 1978 (43 FR
429 9607-9615, March 9, 1978), the Service has implemented three gray wolf recovery programs in
430 different regions of the country: the Western Great Lakes (Minnesota, Michigan, and Wisconsin,
431 administered by the Service’s Great Lakes, Big Rivers Region), the Northern Rocky Mountains
432 (Idaho, Montana, and Wyoming, administered by the Service’s Mountain-Prairie Region and
433 Pacific Region), and the Southwest (Arizona, New Mexico, Texas, Oklahoma, Mexico,
434 administered by the Service’s Southwest Region). Recovery plans were developed in each of
435 these areas to organize and prioritize recovery criteria and actions appropriate to the unique local
436 circumstances of the gray wolf. As such, the three gray wolf recovery programs have functioned
437 independently from one another since their inceptions. The Service also initiated a red wolf
438 (*Canis rufus*) recovery program in 1982 in the eastern United States that it continues to
439 implement today.

440

441 Progress toward recovery of gray wolves in the Western Great Lakes, Northern Rocky
442 Mountains, and Southwest has differed substantially between the regions over the last four
443 decades.

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B. Status of the Species

(Note to Reviewer: This section should provide the species’ federal and state status, and FWS recovery priority status; the rest of the section should note things of importance related to species status.)

The gray wolf, *Canis lupus*, is currently listed as endangered with a recovery priority number of (X) (cite 1978 FR or update with reclassification if applicable). The Service originally listed the Mexican wolf subspecies in 1976 (41 FR 17736-17740, April 28, 1976). In 1978, this and several other gray wolf subspecies-level listings were subsumed into a species-level listing to protect the gray wolf species throughout its range in the coterminous United States and Mexico (43 FR 9607-9615, March 9, 1978). This reclassification provided a commitment that the Service would maintain a conservation focus on recognized gray wolf subspecies. The Service’s Mexican wolf program is conducted as a component of the agency’s gray wolf recovery obligations under the ESA.

In addition to its listed status under the ESA, the gray wolf is also protected under State wildlife statutes in the Southwest. The gray wolf is managed as a species of Special Concern and is identified as a Species of Greatest Conservation Need (endangered) in Arizona (Wildlife of Special Concern in Arizona 1996), and listed as state endangered in New Mexico (Wildlife Conservation Act, 17-2-37 through 17-2-46 NMSA 1978) and Texas (Texas Statute 31 T.A.P). Wolves are considered “protected wildlife” in Utah; they cannot be harvested unless the Wildlife Board establishes an open season for harvest (Utah Code Annotated, Title 23). The gray wolf is not included on Utah’s Sensitive Species List, as the species is not considered a resident in Utah at this time and because the ESA provides protection. Wolves are listed as endangered by Colorado (Colorado Revised Statutes 33-2-105, “Nongame, Endangered, or Threatened Species Conservation Act”, Title 33). The gray wolf is not listed or protected by State law in Oklahoma.

Mexico formally recognized the Mexican wolf as an endangered subspecies under the Norma Oficial Mexicana NOM-059-ECOL-1994, a Mexican Federal law protecting wildlife. The Mexican wolf subspecies continues to be protected under the Ley de Vida Silvestre (2000), Norma Oficial Mexicana NOM-059-ECOL-2001 (2002).

480 C. Description

481 (Note to Reviewer:)

482

483 The gray wolf, *Canis lupus*, is a member of the dog family (*Canidae: Order Carnivora*). The
484 genus *Canis* also includes the red wolf (*C. rufus*), Eastern wolf (*Canis lycaon*), dog (*C.*
485 *familiaris*), coyote (*C. latrans*), several species of jackal (*C. aureus*, *C. mesomelas*, *C. adustus*)
486 and the dingo (*C. dingo*) (Mech 1970, Chambers et al. 20xx). The Mexican wolf, *C. l. baileyi*, is
487 a subspecies of gray wolf (Nelson and Goldman 1929). Type localities of previously recognized
488 subspecies are documented in Young and Goldman (1944). The type locality of *Canis lupus*
489 *baileyi* is Colonia Garcia, Chihuahua, Mexico based on a gray wolf killed during a biological
490 investigation in the mountains of Chihuahua, Mexico in 1899. Thirty years later this animal was
491 combined with additional specimens to define the Mexican wolf (*Canis lupus baileyi*) (Nelson
492 and Goldman 1929).

493

494 Gray wolves often vary considerably in size, although males typically weigh between 36-55 kg
495 (80-120 lbs), are 1.5 to 2 m (5-6.5 ft) long from tip of nose to tip of tail, and 66 to 81 cm (26-32
496 in) high at the shoulder. Females are typically 15-20 percent smaller than males in weight and
497 length (Mech 1970). The Mexican wolf is the smallest extant gray wolf in North America;
498 adults weigh 23-41 kg (50-90 lbs) with a length of 1.5-1.8 m (5-6 ft) and height at shoulder of
499 63-81 cm (25-32 in) (Young and Goldman 1944, Brown 1983). Gray wolves exhibit significant
500 variety in pelt color; the most commonly observed pelt is a mottled charcoal gray, but pelt color
501 can range from white, cream, brown and red, to dark gray and black (Mech 1970). Individual
502 wolves may exhibit any or all of these colors (Fuller 2004). Mexican wolves are typically a
503 patchy black, brown to cinnamon, and cream color, with primarily light underparts (Brown
504 1983); solid black or white Mexican wolves do not exist as seen in other North American gray
505 wolves (USFWS 2008).

506

507

508

509 D. Taxonomy and Distribution

510

511 *Taxonomy*

512

513 It is likely that all gray wolves evolved from the small, early canids that were widespread in
514 North America and the Old World during the Pliocene, some 2 to 4.5 million years ago (Nowak
515 2003). The modern gray wolf, with the possible exception of the wolves of southeastern Canada
516 and northeastern United States (Wilson et al. 2003), likely evolved in Eurasia from wolves that
517 crossed into Eurasia from North America. A branch of these wolves (i.e., *Canis lupus*) then
518 reinvaded North America during the middle Pleistocene (around 300,000 years ago) via the
519 Bering Strait land bridge (Wayne et al. 1992, Brewster and Fritts 1995, Nowak 1995, Parsons
520 1996, Nowak 2003: Table 9.2). It is hypothesized that there were at least three waves of
521 colonization from Eurasia each from different wolf lineages in response to changing glacial ice
522 patterns and openings in the Bering Sea (Nowak 1995, Nowak 2003, Wayne and Vilá 2003). The
523 Mexican wolf may represent the last surviving remnant of the initial wave of gray wolf migration
524 (vonHoldt et al. 2011). Once in North America, wolves dispersed southward and eastward,
525 gradually spreading across most of North America and Mexico (Nowak 2003).

526

527 *C. l. baileyi* has been recognized as a subspecies of gray wolf since its description by Nelson and
528 Goldman (1929; Goldman 1937). Goldman (1944, pp. 389-636), provided the first
529 comprehensive treatment of North American wolves; this gray wolf classification scheme was
530 subsequently followed by Hall and Kelson (1959, Hall 1981). Since that time, gray wolf
531 taxonomy has undergone substantial revision, including a major taxonomic revision in which the
532 number of recognized gray wolf subspecies was reduced from 24 to 5 (Nowak 1995). However,
533 the distinctiveness of *C. l. baileyi* and its recognition as a subspecies continues to be supported
534 by both morphometric and genetic evidence. The Mexican wolf's uniqueness is due at least in
535 some part to its long term isolation in Mexico. What is not known is if the uniqueness was
536 brought about by selective pressures related to ecological conditions or arose as a result of
537 random genetic drift or both.

538

539 Three published studies of morphometric variation conclude that *C. l. baileyi* is a
540 morphologically distinct and valid subspecies. Bogan and Mehlhop (1983) analyzed 253 gray
541 wolf skulls from southwestern North America using principal components analysis and
542 discriminant function analysis. They found that *C. l. baileyi* was one of the most distinct of the
543 five subspecies of gray wolves in the Southwest recognized at that time. Hoffmeister (1986)
544 conducted principal component analysis of 28 skulls, also recognizing *C. l. baileyi* as a distinct
545 southwestern subspecies. Nowak (1995) analyzed 580 skulls from across North America using
546 discriminant function analysis. He concluded that *C. l. baileyi* was one of only five distinct North
547 American gray wolf subspecies that should continue to be recognized.

548

549 Genetic research provides additional validation of the recognition of *C. l. baileyi* as a subspecies.

550 Three studies demonstrate that Mexican wolves have unique genetic markers that distinguish
551 them from other North American gray wolves. Hedrick et al. (1997; see also Garcia-Moreno et
552 al. 1996; Wayne 19995) examined data for 20 microsatellite loci, from samples of Mexican
553 wolves (N=38), northern gray wolves (N=55), coyotes (N=39), and dogs (N=27). They
554 concluded that Mexican wolves were divergent and distinct from other sampled northern gray
555 wolves, coyotes and dogs. They also determined that data from two captive groups of putative
556 Mexican wolves were consistent with the conclusion that these animals were in fact Mexican
557 wolves, and that these groups should be interbred with the captive certified lineage of Mexican
558 wolves (now known as the McBride lineage) that had founded the captive breeding program.

559 Leonard et al. (2005) examined mitochondrial DNA sequence data from 34 pre-extermination
560 wolves collected from 1856 to 1916 from the historic ranges of *C. l. baileyi* and *C.l. nubilus*.

561 They compared these data with sequence data collected from 96 wolves in North America and
562 303 wolves from Eurasia. They found that the historic wolves had the twice the diversity of
563 modern wolves, and that two-thirds of the haplotypes were unique. They also found that
564 haplotypes associated with Mexican wolves formed a unique southern clade distinct from that of
565 other North American wolves. A clade is a taxonomic group that includes all individuals (in this
566 case DNA haplotypes) that have descended from a common ancestor. VonHoldt et al. 2011
567 investigated the taxonomy of wolves and coyotes world-wide using 48,000 single nucleotide
568 polymorphisms (SNPs) and found Mexican wolves to be the most genetically distinct group of
569 New World gray wolves, again supporting the validity of the subspecies.

570

571 Most recently, Chambers et al. (2012, in review) reviewed the scientific literature related to *C. l.*
572 *baileyi*'s classification as a subspecies and concluded that this subspecies' recognition remains
573 well-supported.

574

575 *Distribution*

576 Gray wolves were once abundant and widespread in North America. Before European settlement, the gray wolf
577 ranged from the Canadian high arctic through the United States to central Mexico (Mech 1970, Wayne and Vilá
578 2003), with the exception of the southeastern United States which was occupied by the red wolf (U.S. Fish and
579 Wildlife Service 1989). The scientific literature contains several descriptions of Mexican wolf historical range in
580 Mexico and the United States that generally concur with one another but vary in their interpretation of the northern
581 boundary of historical range.

582

583 Based on morphology (mostly skull and pelage characteristics) 24 subspecies of gray wolf have
584 been described in North America (Hall and Kelson 1959). Five of these subspecies occurred in
585 the southwestern United States and Mexico: *C. l. baileyi*, *C. l. mogollonensis*, *C. l. monstrabilis*,
586 *C. l. nubilus*, and *C. l. youngi*. Original descriptions of Mexican wolf range by Young and
587 Goldman (1944) and Hall and Kelson (1959) delineated range for each of *C. l. baileyi*, *C.l.*
588 *monstrabilis*, and *C.l. mogollonensis* (Figure). Hall (1981) described the range of *C. l. baileyi*
589 as including only a small portion of extreme southwestern New Mexico and southeastern
590 Arizona. Bogan and Mehlhop (1980, 1983) generally combined *C. l. mogollonensis* and *C. l.*
591 *monstrabilis* with *C. l. baileyi*, thereby extending *C. l. baileyi*'s range north to central Arizona
592 and central New Mexico (Figure) through the area that Goldman had identified as an intergrade
593 zone with an abrupt transition from *baileyi* to *mogollensis*. Bogan and Mehlhop's analysis did not
594 indicate a sharp transition zone between *baileyi* and *mogollonensis*, rather the wide overlap
595 between the two subspecies led them to synonymize *baileyi* and *mogollonensis*. The Service
596 adopted the findings of Bogan and Mehlhop in the 1982 Mexican Wolf Recovery Plan, thus
597 supporting reintroduction of *C. l. baileyi* north of *C. l. baileyi*'s range as originally conceived by
598 Young and Goldman (1944) and Hall and Kelson (1959). Subsequently, Hoffmeister (1986) added
599 to the taxonomic confusion by regarding *C. l. mogollonensis* as a synonym of *C. l. youngi* rather than as
600 a synonym of *C. l. baileyi*.

601

602 Brown (1983) stated that in southern Arizona, Mexican wolves inhabited the Santa Rita,
603 Tumacacori, Atascosa-Pajarito, Patagonia, Chiricahua, Huachuca, Pinaleno, and Catalina
604 mountains, west to the Baboquivaris and east into New Mexico in the late 19th and early 20th
605 centuries. In central Arizona, he described a mixing ground where Mexican wolves and several
606 formerly recognized subspecies of gray wolf were interspersed (Brown 1983). He also stated
607 that Mexican wolves and up to four formerly recognized subspecies were present throughout
608 New Mexico, with the exception of low desert areas, and were documented as numerous or
609 persisting in areas including the Mogollon, Elk, Tularosa, Diablo and Pinos Altos mountains, the
610 Black Range, Datil, Gallinas, San Mateo, Mount Taylor, Animas, and Sacramento mountains
611 (Brown 1983). Brown (1983) described Mexican wolves frequenting the borderlands between
612 Mexico and the US, and claimed that they were abundant in the Sierra Madre and the altiplano
613 (high plains) of Mexico.

614

615 In 1995, Nowak proposed a major shift from the identification of 24 subspecies of North
616 American gray wolves to only 5 subspecies (1995), recognizing *C. l. baileyi* as a subspecies, but
617 grouping *C. l. mogollonensis* and *C. l. monstrabilis* with *C. l. nubilus*, providing a more
618 restrictive range for *C. l. baileyi* than Bogan and Mehlhop (Figure). It is important to note that
619 Nowak (1995) agreed with Bogan and Mehlhop (1983) that the range of *C. l. mogollonensis* in
620 Arizona was a transition zone where *C. l. baileyi* intergraded with more northern *C. lupus*.
621 Parsons (1996) added knowledge of dispersal patterns to the historic range of *C. l. baileyi*
622 proposed by Nowak (1995) and concluded that historically Mexican wolves ranged as far north
623 as central New Mexico and east-central Arizona (Figure). In 1996, the Service adopted the
624 historical range proposed by Parsons (1996) and included it in the final EIS for the reintroduction
625 of Mexican wolves into the BRWRA (SUFWS 1996). This version of historical range was more
626 restrictive than that defined by Bogan and Mehlhop (1908, 1983) but more expansive than that
627 defined by Nowak (1995) due to the inclusion of a 200-mile northward extension of Nowak's
628 (1995) range to account for contemporary knowledge of wolf movements (USFWS 1996). After
629 conducting an exhaustive review of molecular genetics and morphological data, Chambers et al.
630 (200xx) supported the Service's decision to adopt the findings of Bogsan and Mehlhop (1980,
631 1983) in the 1982 Mexican wolf recovery plan.

632

633 Evidence of historical gene flow across the various surmised boundaries of *C. l. baileyi* suggests
634 that Mexican wolves likely intergraded with other gray wolves in a wide zone at the northern
635 extent of their range. Wolves' dispersal behavior as revealed by numerous telemetric studies
636 (Mech and Biotani 2003) has long led to the contemporary conclusion that there were large
637 zones of intergradation across the North American landscape (Young and Goldman 1944, Mech
638 1970, Brewster and Fritts 1995) and indicates that the periphery of Mexican wolf historical range
639 occurred somewhere within such a zone in the southwestern U.S. These zones of intergradation
640 allowed for considerable genetic exchange between wolf subspecies (Leonard et al. 2005,
641 Chambers et al. 20xx). On this matter Mech (1970) wrote: "Wherever subspecies meet, their
642 characters tend to blend as a result of interbreeding, or intergradation ...". Analyses of historic
643 specimens (Leonard et al. 2004) demonstrate that the gray wolves that inhabited northern
644 Arizona, Utah, northern New Mexico, and southern and central Colorado had genetic markers
645 associated with the Mexican wolf. This research shows that within the time period that the
646 historic specimens were collected (1856-1916) a mitochondrial DNA haplotype characteristic of
647 northern wolves was found as far south as Arizona, and individuals with southern clade
648 haplotypes (associated with the Mexican wolf) occurred as far north as northern Utah and
649 Nebraska (Leonard et al. 2005).

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651 A few historical reports of Mexican wolf locations indicate that wolves from one area began to
652 occupy habitat recently vacated due to predator eradication efforts. Scudday (1977) reported on
653 two male Mexican wolves collected in 1970 in Brewster County, Texas and concluded that *C. l.*
654 *baileyi* "was a late comer to Texas, probably moving in as *C. l. monstrabilis* was eliminated in
655 the Trans-Pecos region." Gish (1977) thought that *C. l. baileyi* increasingly moved into Arizona
656 from Mexico and southwestern New Mexico as other subspecies were eliminated in Arizona.
657 Nowak (1995) noted that a male Mexican wolf taken in 1957 near Concho, Arizona, was well
658 within the original range of *C. l. mogollonensis* (subsequently synonymized by Nowak with
659 *nubilis*). By 2002, Nowak (personal communication with Mike Phillips) had concluded that the
660 two animals collected from Brewster County, Texas and the one animal collected near Concho,
661 Arizona represented a 160 km northward extension of the historical range that he had
662 recommended for the subspecies in 1995.

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668 E. Historical Population Trends

669 Population estimates of gray wolves, and specifically Mexican wolves, prior to the advent of
670 extermination efforts in the late 1800s and early to mid-1900s are not available for the Southwest
671 or Mexico. This is due primarily to a lack of available data on wolf abundance, but also in some
672 part to difficulty in interpreting anecdotal accounts of wolf abundance. Brown (1983)
673 summarized historical distribution records for the wolf from McBride (1980) and other sources
674 that repeatedly indicated, at least for the southwestern United States, that wolves were common.
675 His map (Brown 1983: 10) shows most records in the southwestern United States as being from
676 the Blue Range and the Animas region of New Mexico. The high number of wolf bounties
677 collected in southern Colorado and northern New Mexico suggest that wolves were abundant in
678 that area as well (Robinson 2005). Wolves appear to have been less numerous in northern
679 Arizona during this time period, with only 30 wolves reported killed on or near the North Kaibab
680 between 1907 and 1926 (Russo 1964). Young and Goldman (1944) stated that in 1916-1918 the
681 wolf was fairly numerous in Sonora, Chihuahua, and Coahuila. Brown (1983) described the
682 Sierra Madre Occidental in the Mexican states of Sonora, Chihuahua, and Durango as a
683 stronghold for the Mexican wolf. Leonard et al. (2005) analyzed mitochondrial DNA sequences
684 of 34 pre-extermination wolves and found that they had more than twice the diversity of their
685 modern conspecifics, implying a historic population of several hundred thousand wolves in the
686 western U.S. and Mexico.

687

688 The status of the Mexican wolf declined rapidly to near extinction during the 1900's. The
689 intensification of human settlement, agriculture, and livestock operations in the Southwest in the
690 1800's led to human persecution of wolves due to wolf depredation of livestock (Brown 1983,
691 Robinson 2005). Federal control programs and extermination campaigns, coupled with habitat
692 alteration resulting from settlement patterns, led to the near extinction of the gray wolf in the
693 Southwest by the early 1900s (Brown 1983). By 1925, poisoning, hunting, and trapping efforts
694 had drastically reduced wolf populations in all but a few remote areas of the southwestern United
695 States, and control efforts shifted to wolves in the borderlands between the United States and
696 Mexico (Brown 1983). Bednarz (1988) estimated that breeding populations of Mexican wolves
697 were extirpated from the United States by 1942. The use of increasingly effective poisons and

698 trapping techniques during the 1950s and 1960s eliminated remaining wolves north of the
699 border, although occasional reports of wolves crossing into the United States from Mexico
700 persisted in to the 1960s. By the time of Leopold (1959), the formerly continuous wolf
701 distribution in northern Mexico had contracted to encompass the Sierra Madre Occidental in
702 Chihuahua, Sonora, and Durango, as well as a disjunct population in western Coahuila (from the
703 Sierra del Carmen westward). Leopold (1959) found conflicting reports on the status of the
704 Coahuila population and stated that wolves were likely less abundant there than in the Sierra
705 Madre Occidental. McBride (1980) surveyed the distribution of the last wild populations of
706 Mexican wolves. He mapped three general areas where wolves were recorded as still present in
707 the Sierra Madre Occidental: 1) northern Chihuahua/Sonora border (at least eight wolves); 2)
708 western Durango (at least 20 wolves in two areas); and 3) a small area in southern Zacatecas.
709 McBride (1980) believed that wolves did not occur in northern and eastern Coahuila despite the
710 existence of what he judged to be excellent wolf habitat there. Although occasional anecdotal
711 reports have been made during the last three decades that a few wild wolves still inhabit forested
712 areas in Mexico, no publically available documented verification exists.

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721 F. Current Population Trends and Distribution

722 (Note to Reviewer: The text below has been adapted from the CA. Entire section needs to be
723 updated through 2012 annual reports as available. Needs graphs/visuals.)

724

725

726 *United States*

727 The population trends and distribution of the current wild nonessential experimental Mexican
728 wolf population in the BRWRA are well documented, as monitoring of the population has been
729 ongoing since its inception in 1998. Between one and 21 wolves have been released into the the
730 BRWRA every year since 1998, with the exception of 2005, 2007, 2009, 2010 (update with 2011-
731 2012) in which no wolves were released (cite online stats or 2011 annual report). As of December
732 31, 2012, the Blue Range population consisted of a minimum of xx wolves and xx breeding pairs
733 (cite end of year count/annual report). The growth of the population from its initial end-of-year
734 count of four wolves in 1998 to a minimum of xx wolves today is attributed to continued releases
735 and to natural reproduction (AMOC and IFT: TC-11).

736

737 The growth of the Blue Range population has been more modest than expected based on the agency's
738 initial predictions (cite FEIS). Between 1998 and 2003, the Blue Range population tracked fairly
739 closely to FEIS projections for population count, reaching (a minimum of) 55 wolves in 2003,
740 but was consistently below the FEIS's estimated number of breeding pairs. The population
741 decreased significantly in 2004-2005 and then rebounded to a high of 59 wolves in 2006, the
742 year in which the FEIS projected the population target of 100 would be met. Between 2007-2011,
743 the population has fluctuated between a minimum count of 42-xx wolves and two (2011?) to four
744 breeding pairs. Thus, the population has remained around the halfway point of the population target
745 since 2003, with fewer breeding pairs than estimated (cite USFWS: Mexican Wolf Blue Range
746 Reintroduction Project Statistics or 2011 annual report) (Figure/s).

747

748 *BRWRA Project Evaluation*

749 Evaluation of the BRWRA reintroduction project has been on-going since its inception to identify
750 biological and regulatory issues affecting its progress. Initial observation of the population from
751 1998-2000 documented that most of the captive-bred wolves that were released into the BRWRA
752 were successfully establishing home ranges, breeding, and killing native prey, alleviating some
753 apprehension over the use of captive born wolves (Brown and Parsons 2001). Challenges for the
754 reintroduction, as seen after its first few years, included the intense management response
755 necessary to address wolves dispersing outside of the BRWRA (which necessitated their removal due to
756 the regulations established in the 1998 Final Rule), wolf-livestock interactions, the possible
757 consequences of limited genetic diversity, and sociopolitical acceptance of the reintroduction
758 (Brown and Parsons 2001), as evidenced by a very high level of illegal killing.

759
760 Two formal agency reviews of the reintroduction project were conducted at three and five years
761 after its inception to determine whether the reintroduction should continue, or be modified or
762 terminated, as stipulated in the Final Rule (63 FR 1752-1772, January 12, 1998). The technical
763 component of the 3-Year Review, commonly referred to as the Paquet Report, assessed the progress
764 of the reintroduction from its inception to 2001. The review was conducted by four independent
765 researchers under contract to the Service: Paul Paquet, John Vucetich, Leah Vucetich, and Michael
766 Phillips. Paquet et al. (2001) found that continuation of the population's documented
767 reproduction and survival rates would result in slower progress achieving the population target of
768 at least 100 wolves than estimated during the planning of the reintroduction. They concluded
769 that several factors were ultimately hindering the biological success of the project: 1) the small
770 size of the Primary Recovery Zone of the BRWRA, which limited the establishment phase of the
771 project by constraining the number and location of wolves that could be released; 2) the
772 requirement that wolves stay within the BRWRA, which did not allow for natural dispersal
773 movements; and, 3) the Service's objective to establish a population of at least 100 wolves,
774 which was not deemed an adequate size for long-term viability (Paquet et al. 2001:60-61). To
775 address these issues, Paquet et al. (2001) recommended the Service initiate a recovery team to
776 revise the 1982 Mexican Wolf Recovery Plan, modify the Final Rule to allow initial releases into
777 the Gila National Forest, allow wolves to establish territories outside of the BRWRA, and require
778 livestock operators on public lands to take some responsibility for managing/removing carcasses
779 to reduce the likelihood of wolves becoming habituated to feeding on livestock.

780

781 The 5-Year Review evaluated the reintroduction from 1998 to 2003, but also included analysis of
782 some aspects of the project through 2005. This review was conducted by the Mexican Wolf Adaptive
783 Management Oversight Committee (AMOC) and the Interagency Field Team, the multi-agency group
784 leading the project and the multi-agency staff in charge of day to day operations, respectively. In the
785 Technical Component of the Review, which addressed the biological progress of the project,
786 AMOC concluded that at least until 2003, progress toward establishment of a population of at
787 least 100 wolves had generally proceeded in line with projections from the FEIS. However, they
788 also recognized that guidelines in the Final Rule requiring removal of wolves that establish home
789 ranges outside of the BRWRA, or at landowner's request, are contrary to normal wolf
790 movements, resulting in higher levels of wolf releases and removals than projected in the FEIS.
791 Further, they found that wolves spending a greater proportion of their lives in the wild are more
792 likely to be successful, and therefore wolves ought to be translocated, rather than permanently
793 removed, after their first removal event except in extreme situations (AMOC and IFT: TC-24).
794 The review recommended further analysis of potential modification of the Final Rule, including
795 expansion of external boundaries, expansion of a recovery zone designated for release of wolves,
796 additional provisions for harassment and take of wolves, creation of an incentives program to
797 mitigate wolf nuisance and livestock issues, analysis of social and economic impacts associated
798 with any MWEPA modifications under consideration, and provisions for another review of the
799 reintroduction project in 2009-2010 (AMOC and IFT: ARC). Following the completion of the 5-
800 Year Review in 2005, the Service determined that the reintroduction should continue, and
801 acknowledged that modifications to the Final Rule were necessary (USFWS 2006b).

802

803 The status of the reintroduction project is also documented and evaluated in annual Interagency Field
804 team reports. Since the 5-Year Review, FWS and partner agencies have acknowledged in these
805 reports that the population is lagging behind the projections of the FEIS, citing the high mortality
806 and removal rates of the population as responsible for this trend (USFWS 2005:27) and
807 concluding that changes in management are needed to support population growth (AGFD et al.
808 2007:13, AGFD et al. 2008).

809

810 In 2010, the Service contracted with a former employee, Tracy Melbhiess, to develop an assessment of
811 the reintroduction project within the context of gray wolf recovery. The Mexican Wolf Conservation
812 Assessment found that (...wild population faces a number of challenges; risk of extinction averted due to
813 captive breeding program but wild population is susceptible to failure due to small size, lack of
814 redundancy, cumulative effect of stressors/threats, etc.).

815

816 *Mexico*

817 In October 2011, Mexico initiated the establishment of a wild Mexican wolf population in the Sierra San
818 Luis Complex of northern Sonora and Chihuahua, Mexico. Officials released five captive-bred Mexican
819 wolves into the San Luis Mountains in Sonora just south of the US-Mexico border (SEMARNAT e-press
820 release, 2011). As of February 2012, four of the five released animals were confirmed dead due to
821 ingestion of illegal poison (USFWS, our files). One wolf remains near the area in which it was released
822 (USFWS, our files). Additional releases are tentatively planned for 2012-2013 to continue efforts to
823 establish a wild population.

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826 G. Life History

827 (Note to Reviewer: This section is copied directly from CA. Needs updating with 2009/2010/2011
828 annual reports.)

829

830 Basic descriptive life history information is well documented for gray wolves, although less so
831 for the Mexican wolf since the subspecies had been extirpated before useful studies could be
832 conducted. What we have learned in the recent past from captive breeding programs and the
833 BRWRA project is that the Mexican wolf does not manifest any particularly unique life history
834 strategies compared to other gray wolf subspecies.

835

836 In the wild, gray wolves typically live 4 to 5 years, although they can reach 13 years (Mech
837 1988). They reach sexual maturity at two years of age (Mech 1970). Wolves have one
838 reproductive cycle per year, and females are capable of producing a litter of pups, usually four to
839 six, each year (Mech 1970). Litters are born in spring in a den or burrow that the pack digs
840 (Mech 1970, Packard 2003). Pups weigh about one pound (0.5 kg) at birth (Mech 1991), and
841 remain inside the den for at least four weeks, during which time their eyes open and the animals
842 learn to walk (Packard 2003). Pup mortality during the denning period is difficult to document
843 due to lack of access to den sites (Fuller et al. 2003).

844

845 Documentation in the BRWRA of wild-born wolves breeding and raising pups has been made
846 for 11 years in a row (2001-2012), and in 2012 approximately x percent of wolves in the Blue
847 Range population were wild-born (cite). In the wild, Mexican wolf pups are generally born
848 between early April and early May (AMOC and IFT 2005: TC-6). Pup counts are conducted
849 opportunistically after the denning period, but prior to October, at which point Mexican wolf
850 pups are difficult to distinguish from adults (AMOC and IFT 2005: TC-6). Average litter size
851 has been estimated at 3.26 (n = 95) pups in the reintroduced population (USFWS files), which is
852 noticeably smaller than Mexican wolf litters in captivity (4.6 pups/litter) (AMOC and IFT: TC-
853 17-18), gray wolf litters elsewhere (AMOC and IFT: TC-12, see Fuller et al. 2003), or the
854 historical litter sizes of wild Mexican wolves reported by McBride (4.5 pups) (1980). Pup
855 counts, however, are documented at some substantial time from whelping (post den emergence), thus
856 some mortality would be expected prior to initial wild counts, and may explain the difference between the

857 number of pups counted in the wild and captivity. Note that red wolf litter sizes (2.8 pups/litter)
858 during their initial restoration were similar (Phillips et al. 2003).

859
860 Recent analyses of the captive and reintroduced populations suggest the low litter sizes observed
861 in the reintroduced population may be influenced by the level of inbreeding (Fredrickson et al.
862 2007). In the Blue Range population, the number of pups observed in packs producing cross-
863 lineage pups (those descended from outbred F1 wolves created by the merging of the founding
864 lineages) was 52 percent greater than packs producing pure McBride wolves, indicating that
865 inbreeding may be negatively affecting litter sizes because fitness was greatest in the less-inbred
866 cross-lineage wolves (Fredrickson et al. 2007). Several other factors may also explain small
867 litter sizes in the reintroduced population due to early pup mortality: 1) wolves may be limited
868 seasonally by the amount of vulnerable prey; 2) litter sizes may be an historical adaptation to the
869 environment; or, 3) wolves released from captivity may be less capable of exploiting vulnerable
870 prey, potentially further affected by frequent management that decreases their ability to fully
871 exploit their home ranges (AMOC and IFT: TC-18). Additionally, cryptic poaching of pups may
872 be occurring before litters are censused (Liberg et al. 2012). Mexican wolf females from the wild
873 population brought into captivity before or shortly after whelping pups had an average litter size
874 matching that of the captive population (4.6 pups/litter, n = 6), suggesting that more Mexican
875 wolf pups are born than are observed in the wild. Since litter size at birth and early pup mortality
876 are unknown (AMOC and IFT 2005: TC-18), either could explain the small number of pups
877 observed during pup counts.

878
879 During the first few months of life, gray wolf pups are gradually weaned from their parents,
880 transitioning from nursing to feeding on semi-liquid regurgitated food provided by adult wolves
881 at the den site, to consuming solid food. During this period, pups grow rapidly, likely due to
882 high prey availability during summer months and pup survival is typically highest in those areas
883 of high prey availability (Fuller et al. 2003). Wolves are referred to as pups up to one year of age
884 and yearlings when between one and two years of age (Packard 2003).

885
886 Pups begin hunting with adults when 4 to 10 months old (Packard 2003), remaining with their
887 family until they disperse to establish a new territory. Wolves exploit their prey by hunting in

888 packs. Adult wolves typically experience a feast or famine existence, gorging on freshly killed
889 prey after successful hunts and subsequently able to survive for days with low food intake
890 (Peterson and Ciucci 2003). Wolves buffer these extremes of food availability by burying food
891 for later consumption, scavenging carcasses, and have the ability to use a variety of prey and
892 habitat types (Peterson and Ciucci 2003, Mech 1991, Weaver et al. 1996).

893
894 Wolf survival rates vary seasonally, as shifts in prey availability occur (Fuller et al. 2003).
895 Annual survival rate of yearling and adult gray wolves is estimated at 0.55 to 0.86 (Fuller et al.
896 2003: table 6.6). Documented causes of death include starvation, disease, human-caused
897 mortality, and interactions with other wolves or predators (Ballard et al. 2003, Fuller et al. 2003).
898 In the Blue Range population, causes of mortality have been largely human-related, including
899 vehicle collision, illegal gunshot, lethal control, and capture complications, although
900 dehydration, brain tumor, infection, snakebite, disease, mountain lion attack, and unknown
901 causes have also been documented (AMOC and IFT 2005: TC-12). Between 1998 and
902 December 31, 2011, illegal gunshot (43 of 88 deaths) and vehicle collision (14 of 68 deaths)
903 were the two most prevalent causes of death (USFWS 2012: Population Statistics). Wolf
904 population can compensate to a degree for relatively high mortality rates by means of increased
905 reproduction, but current mortality rates in the Blue Range may exceed this level (Weaver et al.
906 1996, Oakleaf in prep., Vucetich et al. in review) The average annual survival rate of the Blue
907 Range population between YEAR-YEAR is xx (or a corresponding failure rate of xx, which
908 includes both mortality and management removal of wolves), a rate considered too low for
909 natural population growth (cite).

910
911 Wolves are social animals that live in hierarchical families, referred to as packs. Wolf packs
912 consist of a breeding pair (formerly “alpha” (Packard 2003)) and their subordinate pup and
913 yearling offspring (Mech 1970) although many variations of this typical pack structure have been
914 observed (Mech and Boitani 2003). The minimum number of breeding pairs observed in the
915 Blue Range population is documented by the IFT in the annual end-of-year population count.
916 “Breeding pair” as defined in the Final Rule as, “...an adult male and an adult female wolf that
917 have produced at least two pups during the previous breeding season that survived until
918 December 31 of the year of their birth” (50 CFR 17.84(k)(15)). Over the span of the

919 reintroduction, the number of breeding pairs meeting the Final Rule definition has ranged from
920 zero to seven pairs (USFWS 2012: Population Statistics). During two years, the Service
921 interpreted the Final Rule to include any adult male and adult female associated with any two
922 surviving pups at the end of the year, even if the adult pair did not breed (e.g., one member of a
923 breeding pair is replaced by a new wolf that raises pups born to the former pair). This
924 interpretation resulted in the number of breeding pairs counted being higher than if only the pairs
925 that produced pups that survived until the end of the year were counted (AGFD et al. 2006,
926 AGFD et al. 2007). Additional breeding events occur within the population, but do not meet the
927 Final Rule definition for a breeding pair, making the original definition of “breeding pair”
928 conservative. For example, in 2008, wild-born, wild-conceived pups were produced by seven
929 packs (AGFD et al. 2008), but only XX of these packs had at least two surviving pups, and their
930 biological parents, at the end of the year. Pack size in the Blue Range population between 1998
931 and 2012 ranged from 2 to x (mean = x) wolves (). Bednarz (1988) estimated historic Mexican
932 wolf pack size as two to eight animals. Brown (1983) reported that Mexican wolf packs
933 typically included fewer than 6 wolves. A wolf pack is typically some variation on a mated pair
934 and offspring, sometimes of varying ages (Mech and Boitani 2003).

935
936 To secure food, water, and shelter, a pack establishes an area, or territory, that is maintained
937 through scent-marking (Peters and Mech 1975), howling (Harrington and Mech 1983), and direct
938 defense (Mech and Boitani 2003). Wolf packs move within their respective territories as they
939 forage and defend their territories (Mech and Boitani 2003). Wolves’ daily movements vary in
940 response to the distribution, abundance, and availability of prey. Seasonal movements vary as
941 well: while rearing pups, adult wolves leave the den, returning throughout the day to care for
942 their young. When pups are old enough to travel with adults, packs become nomadic, traveling
943 throughout the territory, sometimes returning to rendezvous sites (Mech and Boitani 2003).
944 Daily pack movements of less than 10 miles per day to over 40 miles in a 24-hour period have
945 been documented in different wolf populations in different seasons (see Mech and Boitani 2003).

946
947 In addition to movements within territories, wolf travels typically include dispersal movements
948 (Mech and Boitani 2003). An individual wolf, or rarely a group, will disperse from its natal pack
949 in search of vacant habitat or a mate; dispersers are typically younger wolves of 9 to 36 months

950 of age (Packard 2003). A yearling might make several dispersal forays before completely
951 disassociating from the family (Messier 1985). These dispersals may be short trips to a
952 neighboring territory, or may be a long journey to find a mate and establish a territory. Dispersal
953 of more than 655 mi (1092 km) has been documented in northern populations (Wabakken et al.
954 2007). Between 1998 and 2012, xx wolf dispersals (natural dispersals and post-release
955 movements) were documented in the Blue Range population, with an average distance of xx mi
956 +/- x mi (x km +/- x km). This is likely an under-representation of true movement distances, due
957 to management response required by the nonessential experimental-population designation when
958 wolves disperse outside of the BRWRA. Wolves in the BRWRA primarily dispersed
959 northwestward or southeastward, in the direction that mountain ranges lie within the area
960 (AMOC and IFT 2005: TC-13).

961
962 Dispersing gray wolves usually travel alone and tend to have a high risk of mortality (Fuller et al.
963 2003). In the Blue Range population, x known mortalities were documented in association with
964 dispersal between 1998-2012 (including natural dispersal and movements directly after release to
965 the wild) (USFWS our files). Wolves that disperse and locate a mate and an unoccupied patch of
966 suitable habitat usually establish a territory (Rothman and Mech 1979, Fritts and Mech 1981).

968 H. Ecology and Habitat Characteristics/Ecosystem

969 (Note to Reviewer: This section copied directly from CA. Needs to be updated with
970 2009/2010/2011 annual reports.)

971
972 Wolves, historically the most widely distributed large terrestrial mammal, can be found
973 throughout much of the Northern Hemisphere where sufficient ungulate prey exists and the risk
974 of being killed by humans is not excessive (Fuller et al. 2003). These two factors, prey biomass
975 and human-associated mortality risk (and the resultant variation in wolf fecundity rate and
976 survival rate, respectively) define the extent of suitable habitat for the Mexican wolf and other
977 wolf subspecies (Fuller et al. 2003, Carroll et al. 2006, Mladenoff et al. 2009).

978
979 The gray wolf hunts in packs, primarily pursuing medium to large hoofed mammals, potentially
980 supplementing its diet with small mammals (Mech 1970). Wolf density is positively correlated
981 to the amount of ungulate biomass available and the vulnerability of ungulates to predation
982 (Fuller et al. 2003).

983
984 Although vegetation and climate vary greatly across the range of the Mexican wolf, the region as
985 a whole is generally more arid than regions of North America such as the Northern Rocky
986 Mountains (NRM) and the western Great Lakes states to which wolves have previously been
987 recovered (Brown 1983). Because of the semi-arid climate, primary productivity in the southwest
988 is generally lower than in these areas (Carroll et al. 2006). In consequence, prey species available
989 to Mexican wolves may be smaller in size, have lower population growth rates, exist at lower
990 densities, and exhibit patchy distributions.

991
992 Historically, Mexican wolves were associated with montane woodlands characterized by
993 sparsely- to densely-forested mountainous terrain and adjacent grasslands in habitats found at
994 elevations of 1219-1524m (4,500-5,000 ft) (Brown 1983). Wolves were known to occupy
995 habitats ranging from foothills characterized by evergreen oaks (*Quercus* spp.) or pinyon (*Pinus*
996 *edulus*) and juniper (*Juniperus* spp.) to higher elevation pine (*Pinus* spp.) and mixed conifer
997 forests. Factors making these habitats attractive to Mexican wolves likely included an
998 abundance of prey, availability of water, and the presence of hiding cover and suitable den sites.

999 Early investigators reported that Mexican wolves probably avoided desert scrub and semidesert
1000 grasslands that provided little cover, food, or water (Brown 1983). Wolves traveled between
1001 suitable habitats using riparian corridors, and later, roads or trails (Brown 1983). Elevation in
1002 the BRWRA ranges from 1219-3353 m (4,000-11,000 ft), ranging from semi-desert grasslands to
1003 conifer forests, with ponderosa forests dominating the area in between (USFWS 1996).

1004

1005 Wolf pack territories vary in size depending on prey density or biomass and pack size; minimum
1006 territory size is the area in which sufficient prey exist to support the pack (Fuller et al. 2003).

1007 Bednarz (1988) predicted that reintroduced Mexican wolves would likely occupy territories
1008 ranging from approximately 78 to 158 square miles (mi^2) (200-400 square kilometers (km^2), and
1009 hypothesized that Mexican wolf territories were historically comparable in size to those of small
1010 packs of northern gray wolves, but possibly larger, due to habitat patchiness (that is,

1011 mountainous terrain that included areas of unsuitable lowland habitat) and lower prey densities
1012 associated with the arid environment. Between 1998 and 2010, home range size of 80 denning
1013 packs in the Blue Range population averaged $182 \text{ mi}^2 \pm 24 \text{ mi}^2$ ($464 \text{ km}^2 \pm 298 \text{ km}^2$ (179 mi^2
1014 $\pm 115 \text{ mi}^2$) (John Oakleaf, pers. comm., 2012). The average home range size for 22 non-
1015 denning packs during the same time period was $330 \text{ mi}^2 \pm 272 \text{ mi}^2$ ($855 \text{ km}^2 \pm 704 \text{ km}^2$).
1016 Pack home range size for denning packs has remained remarkably consistent since the beginning
1017 of this wolf recovery effort.

1018

1019 *Wolves and Prey*

1020 Wolves play a variable and complex role in ungulate population dynamics depending on predator
1021 and prey densities, prey productivity, vulnerability factors, weather, alternative prey availability,
1022 and habitat quality (Boutin 1992, Gasaway et al. 1993, Messier 1994, Ballard et al. 2001).

1023 Ungulates employ a variety of defenses against predation (e.g., aggression, altered habitat use,
1024 gregariousness, migration) (MacNulty et al. 2007), and wolves are frequently unsuccessful in
1025 their attempts to capture prey (Mech and Peterson 2003, Smith et al. 2004). Generally, wolves
1026 tend to kill less-fit prey (e.g., young, old, injured) that are predisposed to predation (Mech and
1027 Peterson 2003, Smith and Bangs 2009). Wolves may reduce prey density, especially during
1028 periods of adverse weather or habitat conditions, but only in extreme circumstances have they

1029 been documented exterminating a prey population, and then only in a relatively small area (Mech
1030 and Peterson 2003).

1031
1032 Historically, Mexican wolves were believed to have preyed upon white-tailed deer (*Odocoileus*
1033 *virginianus*), mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), collared peccaries
1034 (javelina) (*Pecari tajacu*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*),
1035 jackrabbits (*Lepus spp.*), cottontails (*Sylvilagus spp.*), and small rodents (Parsons and
1036 Nicholoupolos 1995). White-tailed deer and mule deer were believed to be the primary sources
1037 of prey (Brown 1983, Bednarz 1988, Bailey 1931, Leopold 1959), but Mexican wolves may have
1038 consumed more vegetative material (Brown 1983:134) and smaller animals as do coyotes in southern
1039 latitudes (Hidalgo-Mihart et al. 2001).

1040
1041 Wolves are highly-adaptable prey generalists and available evidence suggests that Mexican
1042 wolves can efficiently capture a range of ungulate prey species of widely varying size. Elk have
1043 comprised the bulk of the biomass in the diet of wolves reintroduced to the Blue Range area of
1044 Arizona (Paquet et al. 2001, Reed et al. 2006, Carrera et al. 2008, Merkle et al. 2009a), and elk
1045 kill rates by Mexican wolves are similar to those for northern wolf subspecies (Oakleaf et al. in
1046 prep.). Data from the Blue Range indicate that elk are the preferred prey (Brown and Parsons
1047 2001, Reed et al. 2006, Merkle et al. 2009a), with wolves showing a preference for calf elk over
1048 adult elk (AMOC and IFT 2005: TC-14). AMOC and IFT (2005) reported that wolf activity in
1049 the BRWRA appears to be located in areas of high elk density. Mexican wolves are also feeding
1050 on adult and fawn deer, cattle, small mammals, and occasionally birds (Reed et al. 2006). The
1051 difference between historical versus current prey preference is probably due to the lack of elk in
1052 historical Mexican wolf range except for very low densities at the northern periphery in central
1053 Arizona and New Mexico and yet elk are very common in the current Mexican wolf range in the
1054 BRWRA (AMOC and IFT: TC-1). Although white-tailed and mule deer are present, the Mexican
1055 wolves' preference for elk may be related to the gregariousness, relative abundance, naïveté, and
1056 consistent habitat use by elk. There is also a possibility some of the dominance of elk in their diet
1057 was skewed by data collection methods of analyzing only large scats in order to minimize the
1058 probability of including coyote scat (Reed et al. 2006, Carrera et al. 2008).

1059

1060 Mexican wolf predation rates are well within the range of other wolf populations (Mech and
1061 Peterson 2003) suggesting no unusual difficulty killing elk. Given that wolves often hunt in
1062 groups, multiple wolves can be involved in attacks on elk (MacNulty et al. 2012) which
1063 ameliorates the effect of the elk's large size. Further, the size ratio of wolf to elk in the Blue
1064 Range (1:11) is no greater than wolves preying on bull bison in Yellowstone National Park
1065 (1:20) and wolves preying on bull moose (1:10) on Isle Royale suggesting that size of prey is not
1066 a good predictor of hunting success. Considering all the prey of Mexican wolves, they are less
1067 variable in size compared to other multi-prey wolf systems in North America (Mech and
1068 Peterson 2003). Studies of wolf hunting behavior in Yellowstone National Park also indicate
1069 that wolf hunting strategy is plastic and capable of adjusting for variously sized prey (MacNulty
1070 2007). In fact, virtually all wolves in a particular location (e.g. population) prey on more than
1071 one species of prey and wolf hunting strategies reflect this variability. For example, in
1072 Yellowstone one pack successfully preys on a range of species from deer to bison (Smith et al.
1073 2004). Wolves have adapted their hunting strategy by varying age, size (males vs. females),
1074 behavior, and hunting group size all within one pack depending on the situation (Kaffmann et al.
1075 2007) and species of prey indicating a wide adaptability to successfully capture a range of prey
1076 types (MacNulty et al. 2009a, MacNulty et al. 2009b, MacNulty et al. 2012. Deer and elk
1077 typically flee in the presence of a large predator, whereas bison typically stand their ground
1078 causing wolves to respond differently. For Mexican wolves, their primary prey, deer and elk,
1079 behave similarly making adjustment to each easier compared to other wolf populations with
1080 diverse prey. In short, while the historical literature indicates that Mexican wolves preyed
1081 primarily on deer (USFWS 1982, Brown 1983, USFWS 1996), current research shows
1082 successful adaptation to elk with normal to high consumption rates and even a preference for elk
1083 when they are sympatric with deer.

1084
1085 Kill rates of individual wolves vary significantly, from 0.5 to 24.8 kg/wolf/day (1 to 50
1086 lbs/wolf/day), based on a variety of factors such as prey selection, availability and vulnerability
1087 of prey, and the effects of season or weather on hunting success (Mech and Peterson 2003, see
1088 Table 5.5). Minimum daily food requirements of a wild, adult gray wolf have been estimated at
1089 1.4 kg/wolf (3 lbs/wolf) to 3.25 kg/wolf (7 lbs/wolf), or about 13 to 30 adult-sized deer per wolf
1090 per year, with the highest kill rate of deer reported as 6.8 kg/wolf/day (15 lbs/wolf/day) (Mech

1091 and Peterson 2003, Peterson and Ciucci 2003). . Prior to the Blue Range reintroduction, it was
1092 estimated that Mexican wolves would need to kill 1 mule deer every 12-13 days (29/year) or 1
1093 white-tailed deer every 8-9 days (43/year, Johnson et al. 1992). Stark et al. (in prep) used
1094 clusters of wolf GPS locations to estimate kill rates of Mexican wolves in the BRWRA and
1095 estimated a kill rate of 6.53 kg/wolf/day in early winter (assuming 68% of an elk is edible
1096 biomass), and a 9.42 kg/wolf/day consumption rate in late winter (March), for an overall winter
1097 estimate of 8.59 kg/wolf/day. Most studies in other wolf/ungulate systems show a lower kill rate
1098 in the summer (perhaps only 70% of winter kill rates) due to a higher diversity of food items
1099 available at that time (Messier 1994, Metz et al. 2012). Using kill rates from Stark et al. (in
1100 prep.), an independent analysis by the SPS estimated each Mexican wolf would kill 19.9 elk per
1101 year if feeding on only elk. Assuming elk comprise 80% of the biomass consumed and deer
1102 comprise 8%, each wolf would annually kill approximately 16 and 6.5-11 elk and deer (both
1103 species), respectively.

1104
1105 Ungulate population dynamics in the Southwest differ from that of the same species in other
1106 ecoregions due to the lower overall primary productivity of the habitat (Short 1979). Vegetative
1107 communities in the arid southwestern forests are not as lush and productive as similar-looking
1108 communities in the Rocky Mountains. The lower productivity of the vegetative community
1109 influences productivity upwards through several trophic levels resulting in lower inherent
1110 herbivore reproductive rates in the Southwest than in their northern counterparts (Heffelfinger
1111 2006:156). In addition, recruitment differs between southwestern and northern ungulate
1112 populations because winter precipitation comes as rain rather than snow. Lack of widespread
1113 winterkill of ungulates means that lower recruitment is needed to sustain a stable population
1114 compared to northern ungulate populations. Southwestern deer herds require 35-50 fawns per
1115 100 does to remain stable (Heffelfinger 2006:158), while those in the northern Rocky Mountains
1116 require 66: fawns 100 does for population maintenance (Unsworth et al. 1999). As in deer,
1117 southwestern elk seem to have adopted a life history strategy of lower overall recruitment and higher
1118 survival.

1119
1120 Similarly, predator-prey dynamics may differ in the Southwest compared to other systems...
1121 Predator populations are sustained more by the productivity of prey populations than by the

1122 standing biomass at one point in time (Seip 1995, National Research Council 1997, Carbone and
1123 Gittleman 2002). In southwestern deer populations, a compensatory response in deer survival or
1124 recruitment would not be expected because deer density is kept mostly below a fluctuating carrying
1125 capacity via chronically low recruitment. Computer population simulations of Arizona and New Mexico
1126 deer herds showed that an increase in adult doe mortality by only 5-10% was enough to cause population
1127 declines because of low and erratic recruitment and no compensatory response (Short 1979). However,
1128 Heffelfinger (1999) pointed out that "... time and time again, deer research in Arizona has found that
1129 habitat conditions are what primarily drive deer populations up and down, with other factors like
1130 overgrazing, habitat change, predation, poaching, and human encroachment playing secondary roles." As
1131 in deer, southwestern elk have a similar life history strategy of lower overall recruitment and higher
1132 survival. With a high adult cow elk survival (90-97%, Ballard et al. 2000), there is little room for
1133 existing sources of mortality to compensate for additional sources of mortality, except for those herd units
1134 and time periods that female elk are being harvested to manage the population.

1135
1136 Wolves may also impact ecosystem diversity beyond that of their immediate prey source in areas where
1137 their abundance affects the distribution and abundance of other species (sometimes referred to as
1138 "ecologically effective densities" (Soule et al. 2003, 2005). For example, in a major review of large
1139 carnivore impacts on ecosystems, Estes et al. 2011 concluded that structure and function as well as
1140 biodiversity is dissimilar between systems with and without carnivores. In the Southwest, one should
1141 expect that increasing numbers of wolves as a result of recovery, along with other carnivores, could have
1142 impacts on biodiversity and ecosystem processes. This may occur through two mechanisms: a behavioral
1143 mediated or numeric response on prey – or both (Terbough et al. 1999). Such effects have been attributed
1144 to gray wolf reintroduction in Yellowstone National Park and elsewhere (e.g., Ripple and Beschta 2003,
1145 Wilmers et al. 2003, Ripple and Beschta 2004, Hebblewhite et al. 2005, Ripple and Beschta 2011). Such
1146 a trophic cascade was caused by wolf effects on elk (numeric/behavioral or both is yet to be determined)
1147 which caused a response in willow which in turn created habitat and forage for songbirds and beavers
1148 (Hebblewhite and Smith 2010, Baril et al. 2011). Impacts like this may be an outcome of wolf recovery in
1149 the Southwest. However, wolves have yet to have a demonstrable trophic cascade effect in the BRWRA
1150 likely due to the low densities of Mexican wolves in the area (Beschta and Ripple 2010).

1151
1152 Livestock are another widely available potential source of prey for Mexican wolves in the
1153 BRWRA. Historically, records of Mexican wolf exploitation of livestock were prominent
1154 (Young and Goldman 1944, McBride 1980, Brown 1983, Bednarz 1988); this is not surprising

1155 given that such reports were made by government and private wolf control agents whose jobs
1156 focused on depredate animals (and see Gipson and Ballard 1998, Gipson et al. 1998). When
1157 the reintroduction began, sheep and cattle grazing were permitted on approximately 69 percent of
1158 the BRWRA, with about half of the allotments being grazed year-round (USFWS 1996).
1159 Program projections predicted that at the population objective of at least 100 Mexican wolves,
1160 depredation levels of 1-34 cattle per year would occur (USFWS 1996). Between 1998 and 2012,
1161 x confirmed cattle depredations were documented, or an average depredation rate of x cattle per
1162 100 wolves per year. This depredation rate may represent an underestimate due to incomplete
1163 detection of wolf-killed cattle, which has been demonstrated in XXXX(Oakleaf et al. 2003,
1164 Breck et al. 2011). Between 1998 and 2012, xx wolves were removed as a result of xxx
1165 confirmed depredations (xxx cattle, xx sheep, and x horses) (USFWS our files), or one wolf
1166 removal per xx confirmed depredations.

1167

1168 *Wolves and Non-prey*

1169 Wolves also interact with non-prey species. Although these interactions are generally not well
1170 documented, competition and coexistence may occur between wolves and other large, medium,
1171 or small carnivores (Ballard et al. 2003). In the Southwest, wolves may interact with other
1172 wolves, coyotes, mountain lions (*Puma concolor*), and black bears (*Ursus americanus*) (AMOC
1173 and IFT 2005: TC-3). Aggression among wolves is typically associated with food shortages as
1174 wolves venture into neighboring territories to locate prey (Mech and Boitani 2003).
1175 Observations of wolf and coyote interactions in other regions have documented decreased coyote
1176 density in areas of high wolf density and that wolves occasionally kill or eliminate coyotes
1177 (Ballard et al. 2003, Merke et al. 2009). A current study of Mexican wolf and coyote diets in the
1178 BRWRA shows that wolves and coyotes have similar diets consisting mainly of elk (Carrera et
1179 al. 2008). It is not known whether coyotes are scavenging elk carcasses from wolf kills (cite?) or
1180 preying on elk directly (Gese et al. 1994), although both behaviors have been documented in
1181 other areas. It is hypothesized that this shared source of prey may cause competition between
1182 wolves and coyotes that will result in wolves killing coyotes when coyotes visit wolf kills to
1183 scavenge (Carrera et al. 2008), as has been documented in Yellowstone National Park (Merkle et
1184 al. 2009b).

1185

1186 Bednarz (1988) hypothesized that wolves and mountain lions interacted historically, given their
1187 overlapping habitats and shared prey source of deer, but suggested that wolves may have
1188 exploited gentler sloping terrain, with mountain lions hunting in steeper craggy mountainous
1189 terrain. The potential for competition between wolves and lions certainly exists in areas where
1190 spatial overlap is extensive and prey selection patterns are similar (see Kunkel et al. 1999),
1191 although differences in hunting behavior and prey vulnerability to wolves and mountain lions
1192 have been observed (see Husseman et al. 2003). One Mexican wolf death from a mountain lion
1193 attack has been recorded in the BRWRA (AMOC and IFT 2005: TC-12). Gray wolves have been
1194 known to kill black bears near their dens and to take over kill sites occupied by black bears
1195 (Ballard and Gipson 2000, Ballard et al. 2003), but interactions between Mexican wolves and
1196 black bears have not been documented. Two other Mexican wolf deaths have been attributed to
1197 predators, but identification of specific predators was not provided (USFWS 2004, USFWS
1198 2006a, USFWS 2009: Population Statistics).

1199 *Wolf–Human Interactions*

1200 Wolves’ reactions to humans include a range of non-aggressive to aggressive behaviors, and may
1201 depend on their prior experience with people. For example, wolves that have been fed by
1202 humans, reared in captivity with frequent human contact or otherwise habituated to humans may
1203 be more apt to show fearless behavior towards humans than wild wolves; diseased wolves may
1204 also demonstrate fearless behavior (McNay 2002, Fritts et al. 2003). In North America, wolf-
1205 human interactions have increased in the last three decades, likely due to increasing wolf
1206 populations and increasing visitor use of parks and other remote areas (Fritts et al. 2003).
1207 Generally, wild wolves are not considered a threat to human safety (McNay 2002) and are less so
1208 (as measured by the number of attacks/carnivore species) than other carnivores that are currently
1209 common in the western U.S. and Mexico (citation). An inquest jury has attributed one recent
1210 human death in Canada to wolves, although a number of wildlife experts disagree whether
1211 wolves or a black bear were responsible for the death (Paquet and Walker 2006). During March
1212 2010, a woman jogging alone in rural Alaska was killed by wolves (Butler et al. 2011).

1214

1215 In the BRWRA, wolf-human interactions have been documented. For example, between 1998
1216 and 2012, xx cases of wolf-human interactions were documented in the BRWRA. The majority

1217 of these incidents (xx percent) were considered investigative searches in which wolves ignored
1218 human presence. In several cases (xx percent), wolves approached humans in a non-threatening
1219 manner, and in x reports wolves displayed aggressive behavior (charging) toward humans
1220 (USFWS our files). A majority of the interactions involved wolves recently released from
1221 captivity, suggesting that wolves released from captivity may be prone to initial tolerance of
1222 humans, despite appropriate captive management techniques and selection criteria for release
1223 candidates that promote and select for intolerance (shyness), respectively (AMOC and IFT 2005:
1224 TC-22).

1225

1226 Wolves are known to kill dogs virtually everywhere the two coexist (Fritts et al. 2003), thus the
1227 presence of dogs may provoke investigative or aggressive behavior. Dogs were present in many
1228 of the cases above (including xx charges) in which the aggression appeared to focus on the dogs
1229 rather than the humans (USFWS our files). Aversive conditioning (rubber bullets, cracker
1230 shells) or translocation or removal of the wolf was applied in response.

1231

1232 Humans also can be a significant source of mortality for wolves. Human-caused mortality is a
1233 function of human densities in and near occupied wolf habitat and human attitudes toward
1234 wolves (Kellert 1985, Fritts and Carbyn 1995, Mladenoff et al. 1995). Sources of mortality may
1235 include accidental incidents such as vehicle collision, or intentional incidents such as illegal
1236 shooting or poisoning. In areas where humans are tolerant to the presence of wolves, wolves
1237 demonstrate an ability to persist in the presence of a wide range of human activities (e.g., near
1238 cities and congested areas) (Fritts et al. 2003). Past recommendations estimated suitable
1239 Mexican wolf habitat to occur where human density is less than 12 people per square mile (2.56
1240 km²), with an optimum density of less than 6 people per square mile (Johnson et al. 1992). In
1241 keeping with these guidelines, the BRWRA was selected in part due to its low human population
1242 density (estimated at 0.31/km² or 0.8/mi² prior to the reintroduction) (USFWS 1996: Table 3-3).
1243 In the BRWRA, illegal shooting is the biggest mortality source for Mexican wolves (USFWS
1244 2009: Population Statistics) (and see “Physical Description and Life History”, and factor (E) in
1245 “5-factor analysis”).

1246

1247

1248 I. The Geography of Recovery

1249 (IMPORTANT Note to Reviewer: This subsection is not standard in a recovery plan. I have
1250 swapped out the “Critical Habitat” section that typically occurs here in the recovery plan with
1251 this one, based on the FWS recovery planning guidance, “If important habitat has been identified
1252 as needed for recovery but has not been designated as critical habitat, be sure to note this in this
1253 section and include the necessary management of the habitat in the recovery actions section.” We
1254 can/will make clear that the areas discussed here are NOT being recommended for critical habitat
1255 / that critical habitat cannot be designated for 10j species. Rather, this subsection provides an
1256 opportunity to broadly explain what the Southwestern landscape looks like from the perspective
1257 of the wolf recovery effort. Thus at minimum it should contain a description of ecologically
1258 suitable habitat; *it could* also include an overview of non-ecological factors that the team wants
1259 acknowledged, such as land ownership (including tribal lands), land use, binational aspects, etc.
1260 We need additional team discussion about what might be useful and appropriate in this section,
1261 but this may be the place to address some of the non-biological concerns raised at our August
1262 and November 2011 meetings. As I think about this section more, it may be better placed
1263 AFTER the recovery criteria...we need to flesh it out and see where it fits the best.)

1264
1265 Because Mexican wolf recovery will require reintroduction projects to restore populations it is
1266 essential to define the region where such efforts would be scientifically sound and ecologically
1267 feasible. It is also important to carefully assess the major social, cultural, political, and economic
1268 characteristics of the region that may influence implementation of Mexican wolf recovery
1269 activities. Defining the ecological basis for Mexican wolf recovery includes consideration of
1270 historical range and current range, and current and future habitat conditions, including, most
1271 importantly, prey availability and conflicts with humans. This information is given context by
1272 the policy framework created by applicable federal, state, and international laws and regulations,
1273 as well as by social aspects of this region pertinent to Mexican wolf recovery such as land
1274 ownership, tribal boundaries, international relations with Mexico, and ranching and other
1275 economically and culturally significant land uses that have potential to conflict with wolf
1276 recovery. This subsection of the plan provides a holistic description of the landscape within
1277 which Mexican wolf recovery is ecologically appropriate and biologically feasible.

1278

1279 We first describe initial analyses of potential Mexican wolf habitat that occurred prior to the
1280 widespread availability of digital data on habitat attributes. We then discuss how the two factors
1281 limiting wolf distribution (prey abundance and human-caused mortality) have been evaluated in
1282 more recent studies using geographic information systems (GIS) (below and Appendix X).
1283 Because of the contrasts in available digital data between the US and Mexico, we review habitat
1284 distribution in each nation separately. The available digital data in the two nations allows us to
1285 make quantitative comparisons between sites within each nation, but only qualitative
1286 comparisons of sites between nations.

1287
1288 *Initial Analyses of Habitat Suitability in the United States*

1289 In the course of planning for Mexican wolf recovery in the 1990s, the FWS evaluated the habitat
1290 suitability of five potential core areas in Arizona and New Mexico (with those within each of the two
1291 states being evaluated separately). Bednarz (1989) evaluated the suitability of the White Sands Missile
1292 Range (WSMR, see Figure 1 for this and other locations) in central New Mexico, finding it suitable in
1293 terms of habitat security but marginal in habitat productivity (prey abundance). A later assessment
1294 concluded that the area could only support 20 to 30 wolves (Green-Hammond 1994). Johnson et al.
1295 (1992) evaluated four areas in Arizona: the Blue, Galiuro-Pinaleno, Chiracahua, and Atascosa-Patagonia
1296 ranges (Figure 1). The New Mexico portion of the current Blue Range Wolf Recovery Area (BRWRA) was
1297 not considered in either Johnson et al. (1992) or Bednarz (1989). The Arizona portion of the BRWRA was
1298 scored by Johnson et al. (1992, see also Groebner et al. 1995) as highest in 7 of 13 habitat factors. The
1299 Atascosa/Patagonia ranges were the only one of the remaining three areas to approach the BRWRA in
1300 quality (highest in 5 of 13 habitat factors). Parsons (1995) produced a comprehensive reassessment of
1301 all 5 of the proposed sites in Arizona and New Mexico. He found that, based on the sum of scores for
1302 seven factors affecting wolf habitat suitability (habitat area, ungulate density, water availability,
1303 livestock density, human density, road density, and effects on threatened species), WSMR scored
1304 highest, followed by the Blue Range, and more distantly, the Atascosa/Patagonia Mountains. The
1305 contrast between these results and those of others who discount the potential of the WSMR (e.g.,
1306 Paquet et al. 2001, Carroll et al. 2005), is due to the fact that habitat area, for which WSMR scores very
1307 low, is only one of seven factors given equal weight in Parsons (1995). USFWS (1996) evaluated four
1308 alternatives for Mexican wolf restoration and chose a preferred alternative involving
1309 reintroduction to the BRWRA, with potential use of WSMR as a second core area if necessary.

1310 The preferred alternative notwithstanding, given the lack of robust prey populations the WSMR
1311 offers little actual support for Mexican wolf recovery..

1312

1313 Sneed (2001) evaluated suitability of wolf habitat in the Grand Canyon and Mogollon Rim
1314 region in northern and central Arizona. While this area includes some habitat with relatively low
1315 ungulate density due to the arid climate, other portions of the area such as the Kaibab Plateau
1316 support ungulate densities comparable to mesic forest ecosystems of the NRM (> 8 deer/km²).

1317 Sneed (2001) concluded that the North Kaibab and South Colorado Plateau could support
1318 between 115 and 187 wolves.

1319

1320 *GIS Assessment of Habitat Suitability in the US: Factors Associated with Wolf Fecundity*

1321 A large body of literature links wolf redundancy (productivity) with ungulate biomass available per
1322 wolf (Fuller et al. 2003). Consequently, estimates of potential wolf fecundity can be based on
1323 surveys of abundance of prey species. However, these data are challenging to assemble across a
1324 multi-state region because methods for estimating ungulate abundance vary between
1325 jurisdictions. A comprehensive survey of available data on prey abundance in the US was
1326 developed as part of this recovery plan, and is discussed below.

1327

1328 Because best available data on prey abundance is inconsistent between areas due to differences
1329 in collect methods and resolution, it is also useful to evaluate potential wolf fecundity based on
1330 surrogate variables for prey productivity that are consistently measured for the areas in question.
1331 Past studies have found good concurrence between such surrogate variables and actual prey
1332 abundance in Colorado and Utah (Carroll et al. 2003a, Carroll 2003). The drawbacks of using
1333 surrogate variables (e.g., vegetation patterns) for estimating prey abundance are countered by the
1334 benefits of obtaining consistent and comparable data across a wide region. This, of course,
1335 facilitates comparison of areas within the wide region. Facilitated comparisons notwithstanding it
1336 is true that ungulate abundance may differ between two areas with similar vegetation due to
1337 contrasting levels of hunting pressure by humans. Although prey species in the US are often
1338 managed near carrying capacity, in some areas of Mexico prey abundance may be locally
1339 depleted by heavy hunting pressure, lowering the match between vegetation productivity and
1340 prey abundance (i.e., wolf habitat)(Lara-Diaz et al. 2011).

1341
1342 Carroll et al. (2005, 2006) developed a binational evaluation of habitat for the Mexican wolf
1343 using predicted prey abundance based on vegetation data, with a focus on 13 evaluation areas
1344 (Figure 1). The National Land Cover Dataset (NLCD) was used for the United States. NLCD
1345 data were derived from Landsat TM imagery at a resolution of 30 m, and contains 21 landcover
1346 classes. Landcover types from both the US and Mexican data sets were ranked as to their value
1347 as wolf habitat (see Tables 4 and 5 in Carroll et al. 2005) based on expert opinion and historical
1348 records (Brown 1983, C. Lopez-Gonzalez pers. comm.).

1349
1350 Because ungulate prey density may vary greatly within a particular vegetation type due to
1351 variation in primary productivity and other factors, Carroll et al. (2005, 2006) augmented the
1352 vegetation data with a satellite imagery-derived metric, tasseled-cap greenness (Crist and Cicone
1353 1984). Variables such as greenness that are derived directly from unclassified satellite imagery
1354 are correlated to varying degrees with ecological factors such as net primary productivity and
1355 green phytomass that influence the abundance of ungulates (Cihlar et al. 1991, Merrill et al. 1993,
1356 White et al. 1997). Summer greenness values were found to be strongly correlated with ungulate
1357 density in the northern Rocky Mountains and Pacific Northwest (Carroll et al. 2001b, 2003a).
1358 Carroll et al. (2005, 2006) combined greenness levels with ranking of vegetation types to
1359 produce a composite ranking (Figure 2). This prey productivity or potential fecundity layer also
1360 incorporated the negative effect of terrain (slope) on prey availability to wolves (Paquet et al.
1361 1996). Because the season of maximum productivity varies across the region, Carroll et al.
1362 (2005, 2006) used the maximum greenness level found in either March or July (2001) MODIS
1363 imagery.

1364
1365 *GIS Assessment of Habitat Suitability in the US: Factors Associated with Wolf Survival*

1366 As with fecundity estimates, wolf survival estimates in different habitat types would ideally be based on
1367 models of the relationship of habitat variables to wolf survival from other recovery areas such as the
1368 NRM. However, although analysis of NRM survival data has occurred (e.g., Murray et al. 2010), these
1369 studies have not yet produced models of the relationship between survival and habitat variables as has
1370 been done for other carnivore species (e.g., grizzly bears; Schwartz et al. 2010). However, a large body

1371 of literature links wolf survival with surrogates for human caused mortality such as roads and population
1372 (reviewed in Fuller et al. 2003).

1373 Previous studies have incorporated “habitat effectiveness” as a composite metric for relative mortality
1374 risk to large carnivores based on roads and human population (Figure 3). This has proven to be a useful
1375 surrogate for wolf mortality risk in the northern Rocky Mountains (Merrill et al. 1999, Carroll et al.
1376 2003a, 2003b). In the analysis of Carroll et al. (2005, 2006), roads data for the US were derived from
1377 USGS Digital Line Graphs (DLG) coverage at 1:100,000 scale (USGS, unpublished data) (Figure 3).

1378 Population data for the US was derived from 1990 and 2000 censuses (US Census Bureau 2001)
1379 at the census block scale. Human population growth from 2000 to 2025 was predicted based on
1380 growth rates from 1990 to 2000. Road density was predicted to increase at 1% per year
1381 (Theobald et al. 1996).

1382

1383 Because much of the data relating human population and roads to wolf mortality come from
1384 areas without the public lands grazing patterns found in the western US, less is known about the
1385 quantitative effects of livestock density, and resulting depredation-related removals, on wolf
1386 survival (but see Treves et al. 2011 for an example from the Great Lakes states). For this
1387 document data on livestock abundance for the US was derived from the 1997 US Census of
1388 Agriculture at the county level (Figure 4). Livestock data are therefore at a substantially coarser
1389 scale than available human population data.

1390

1391 *Identification of Potential Core Areas of Suitable Habitat within the US*

1392 Once data on both potential wolf fecundity and survival is collected, one is faced with the
1393 challenge of estimating the relative influence of habitat factors related to fecundity and survival
1394 in determining persistence of wolf populations. For example, habitat suitability for southwestern
1395 Colorado which has very high prey abundance and likely moderate human impacts to any wolf
1396 population) (i.e., those anthropogenic activities that might affect wolf fecundity and survival by
1397 altering habitats needed by prey and providing increased access that might lead to elevated levels
1398 of human-caused mortality) may be contrasted with habitat suitability for the Grand Canyon
1399 region and western Texas both of which have lower prey abundance and but likely lower human
1400 impacts as well. Similarly, arid ecosystems in many areas of the southwestern US likely have
1401 relatively low human impacts but also support prey abundance near the lower threshold for wolf

1402 persistence. Because previous reintroductions in the western US were to sites in the Greater
1403 Yellowstone Ecosystem and central Idaho which have both high prey abundance and low human
1404 impacts, they do not provide detailed guidance as to the relative strength of these two factors.
1405

1406 An effective strategy for wolf recovery involves establishing well-distributed source populations
1407 in core areas of highly suitable habitat and then allowing natural dispersal to re-establish a
1408 regional metapopulation. For a core area of suitable habitat to include potential reintroduction
1409 sites it would need to contain areas of highly secure habitat that are well situated to facilitate
1410 growth of the regional wolf metapopulation. The several habitat suitability assessments that have
1411 been conducted over the last 20 years indicate that only three major core areas of suitable habitat
1412 exist in the area encompassing the Mexican wolf's historical range and adjacent areas in
1413 Arizona, New Mexico, southern Colorado and southern Utah that are capable of supporting
1414 Mexican wolf populations of sufficient size to contribute to recovery. The three core areas of
1415 suitable habitat are 1) the Blue Range Wolf Recovery Area and adjacent public lands, 2) the
1416 Grand Canyon and adjacent public lands in northern Arizona and southern Utah (as
1417 circumscribed by interstate highways 15 and 70), and 3) Carson National Forest/San Juan
1418 National Forest and other connected areas of public lands and private lands with conservation
1419 management in northern New Mexico and southern Colorado (as circumscribed by interstate
1420 highways 70 and 25) (Table 1). We describe these areas using regional-scale habitat data, but a
1421 more detailed evaluation of local land ownership, land use, and prey abundance patterns would
1422 be necessary in subsequent stages of recovery (e.g., development of an Environmental Impact
1423 Statement before conducting reintroductions to restore populations that count toward recovery).
1424 An additional area in western Texas which has some attributes of suitable habitat is also
1425 described here.
1426

1427 Although some areas which are not currently suitable habitat might become so in future decades
1428 due to recovery actions, this plan's recovery strategy focuses primarily on the three areas
1429 identified above because they are currently capable of expeditiously advancing wolf recovery.
1430 Expeditious recovery (i.e., consistent with the timeline set forth in this plan) is necessary to
1431 fulfill recovery objectives because any additional time that captive and wild Mexican wolf
1432 populations remain at their current low levels accentuates genetic threats and reduces recovery

1433 potential. The accumulating genetic effects of the current population bottleneck lend urgency to
1434 recovery and require a focus on areas that currently could support relatively rapid growth of
1435 Mexican wolf populations due to high survival rates and abundant prey.

1436
1437 The three major core areas of suitable habitat are each projected to become more distinct and
1438 separated as landscape change factors such as exurbanization continue (Carroll et al. 2006). All
1439 areas except western Texas include large tracts of public lands subject to conservation mandates
1440 (National Park, wilderness) where wolves are predicted to experience the lowest human-induced
1441 mortality. While the Grand Canyon and northern Arizona and southern Utah core area and
1442 northern New Mexico/southern Colorado core area are both located north of the Mexican wolf's
1443 historical range, in the recent past they each supported a closely related subspecies (*C. l. nubilus*)
1444 that has for over half a century been restricted to the western Great Lakes states and Canada
1445 (Nowak 1995) due to 20th century extermination campaigns (Robinson 2005). The two areas are
1446 proximate to (Brown 1983, Bogan and Mehlhop 1983, Hoffmeister 1986, Nowak 1995) or well
1447 within (Leonard et al. 2005) the zone of gray wolf subspecies intergradation that characterized
1448 the southwest historically. For these reasons and others to be discussed, northern
1449 Arizona/southern Utah and northern New Mexico/southern Colorado are appropriate for
1450 inclusion in the Mexican wolf recovery program.

1451

DRAFT

1453 Table 1. Ecological attributes of core areas of suitable Mexican wolf habitat. All metrics are expressed as per km² unless noted. Isolation is center-to-center
 1454 distance from nearest neighboring potential core area. Wolves per 1000 km² is based on the model of Fuller et al. (2003). 'Total wolves' indicates estimates of
 1455 potential population size based on previously-published studies and the analysis in this document.

1456	Area name		Total Size	Size	Isolation (km)	Cattle	Deer biomass	Deer Biomass
1457	Prey biomass	Wolves (per 1000 km ²)	Total wolves					
1458				Good habitat			(DEPU)	Best habitat
1459	Best habitat							
1460								
1461	Overall							
1462	<u>US</u>							
1463	1. Blue Range		>25,000		400	1-5	5.6	
1464	22	>250						
1465	2. Grand Canyon		>25,000		400	<1	4.1	
1466	17	>250						
1467	3. Carson/San Juan		>25,000		450	1-7	7.6	
1468	28	>250						
1469	4. Western Texas		24,000		250	1-3	2-4?	
1470	10-17?	200?						
1471								
1472	<u>Mexico</u>							
1473								
1474	Best habitat							
1475	1. Sierra San Luis/Ajos-Bavispe		25,900	15,700	300	5	1-2	2.41
1476	2.89	13	80					
1477	2. Tutuaca/Sierra Tarahumara		21,200		300	4	1-2	2
1478	2.4	11.4	80					
1479	3. Chihuahua/Durango		29,975	8,300	350	7	1-2	3.6
1480	4.32	17.8	60					
1481	4. Sierra de Valparaiso/Sierra de Urica/Mezquital		12,667		350	6	1-2	0.68
1482	0.82	6.2	24					
1483	5. Maderas del Carmen/Serranias de Burro		19,564		250	6	1-2	0.6
1484	0.72	5.9	85-100					
1485	6. Sierra Plegada		17,968		450	7	1-2	0.23
1486	0.28	4.4	60-140					

1487 *Description of Core Areas of Suitable Habitat in the US*

1488 1. Blue Range: The Blue Range Wolf Recovery Area (BRWRA) covers 17,545 km² and is
1489 located on the Apache-Sitgreaves and Gila National Forests (NFs) along the Arizona/New
1490 Mexico border. Since 1998 the FWS has released Mexican wolves into this area. The Mogollon
1491 Rim area lies along a block of forested public lands (e.g. Tonto NF) stretching between the Blue
1492 Range and Grand Canyon sites. The two areas (Blue Range and the Mogollon Rim) would likely
1493 function as a semi-continuous block of suitable wolf habitat in the absence of management
1494 actions to limit wolf populations or movement. However, Carroll et al. (2006) concluded that the
1495 wolf survival would be lower in the Mogollon Rim area than in the Blue Range due to greater
1496 levels of threat factors (primarily roads) in the former area. We do not identify the Mogollon
1497 Rim as a separate core area of suitable habitat both because of its greater threat levels and
1498 because it does not represent a geographically disjunct block of potential wolf habitat that would
1499 support a spatially and demographically distinct population.

1500
1501 2. Grand Canyon (Northern Arizona/Southern Utah as circumscribed by interstate highways 15
1502 and 70): This core area encompasses the Grand Canyon and adjacent public lands in northern
1503 Arizona and southern Utah. The area is centered on the Grand Canyon National Park (4900 km²)
1504 and adjacent of Kaibab and Coconino NF lands (13,300 km²). The Grand Canyon National Park
1505 is not predominantly highly productive wolf habitat, although wolves within its boundaries
1506 would likely benefit from low rates of human-caused mortality. Adjacent public lands on the
1507 Kaibab Plateau, other portions of the Kaibab National Forest, and areas in southern Utah such as
1508 the Paunsaugunt Plateau are more mesic with greater prey densities as described below.

1509
1510 With the exception of the Blue Range, the Northern Arizona/Southern Utah core area may have
1511 the highest probability of enhancing regional wolf populations through dispersal (Carroll et al.
1512 2005, 2006). This is due to both a large area of public lands with low mortality risk for wolves,
1513 and substantial connectivity from that habitat southward through the Mogollon Rim towards the
1514 Blue Range and northward to the public lands of the mountains of southern and central Utah and
1515 north to Wyoming and Idaho.

1516

1517 3. Carson National Forest/San Juan National Forest (Northern New Mexico/Southern Colorado
1518 as circumscribed by interstate highways 70 and 25): This core area of suitable habitat
1519 encompasses connected areas of extensive public lands and private lands with conservation
1520 management in northern New Mexico and southern Colorado. The New Mexico portion of this
1521 area includes sections of the Carson National Forest (6,000 km²), Santa Fe National Forest
1522 (6,400 km²), Vermejo Park Ranch (2,300 km²), 268 km² of additional private lands protected
1523 under conservation easements, and the Taos Pueblo (391 km²) of which 230 km² are managed as
1524 wilderness by the tribe. The Valle Vidal Unit of the Carson National Forest (407 km²) is
1525 managed with special emphasis on wildlife and fisheries resources. For example, 88% of the
1526 roads present in 1982 have since been closed or removed to enhance wildlife and fisheries
1527 habitat. Given tightly restricted access to Vermejo Park Ranch and careful monitoring of traffic
1528 and road use that is allowed, when considering human-caused mortality of wolves the ranch is
1529 functionally roadless.

1530
1531 The Colorado portion of this area extends across portions of the San Juan National Forest (8,345
1532 km²), Rio Grande National Forests (7,440 km²), and Grand Mesa, Uncompahgre, and Gunnison
1533 National Forests (12,600 km²). The San Juan Mountains contain 4,000 km² of Wilderness Areas
1534 and 4,000 km² roadless areas including significant lower-elevation ecosystems. Relatively low
1535 levels of livestock grazing occur public land and private conservation land throughout the area
1536 (Bennett 1994).

1537
1538 Similarly to the Grand Canyon, the northern New Mexico/southern Colorado core area would aid
1539 the reestablishment of well-distributed wolf populations northward to the public lands in western
1540 Colorado. However, these sites appear to have somewhat higher vulnerability to habitat
1541 reduction or isolation by landscape change than does the Grand Canyon region (Carroll et al.
1542 2005). This is due to a higher proportion of private lands in lower elevation valleys, as well as
1543 the generally higher predicted rate of landscape change in Colorado and New Mexico (Carroll et
1544 al. 2005).

1545
1546 4. Western Texas: Approximately 24,000 km² of potentially suitable habitat occurs in western
1547 Texas (Carroll et al. 2006). This area is assessed as suitable in the model of Carroll et al. (2005)

1548 due primarily to low numbers of roads and human settlements. Potential prey productivity is low
1549 but likely sufficient to support low densities of wolves (Table 1). This area lies between the
1550 Davis Mountains and the Pecos River watershed in Jeff Davis, Brewster, Pecos, Terrell and Val
1551 Verde Counties, from approximately State Route 385 on the west to State Route 163 on the east.
1552 The few public landholdings (Davis Mountains State Park, Seminole Canyon State Park) in this
1553 area are relatively small in size. Private lands under conservation easements total approximately
1554 270 km². Big Bend National Park, while large in size, lies to the south of this area and does not
1555 offer extensive suitable habitat due to its aridity. The area of suitable habitat in western Texas is
1556 distant (700 km) from the nearest core area of suitable habitat in New Mexico, but relatively near
1557 (250 km) the potential reintroduction area in the northern Coahuila identified by Araiza et al.
1558 (2006).

1559

1560 *Other Areas of Arizona and New Mexico*

1561 The US/Mexico border region is likely to serve as sink habitat for wolves under current
1562 conditions (Carroll et al. 2006) despite the presence of some potentially suitable habitat such as
1563 the 305 km² Galiuro Wilderness. Sites in this area that have previously been proposed as
1564 reintroduction locations (e.g., Galiuro/Pinaleno, Chiricahua Mountains, and Atascosa/Patagonia
1565 Mountains [Johnson et al. 1992]) appear, based on the model of Carroll et al. (2005), to be poor
1566 choices for such efforts. However, the area's key role in facilitating dispersal between US and
1567 Mexican wolf populations suggests that it be given significant attention in recovery planning,
1568 through recovery actions which increase the likelihood of these sites being naturally recolonized
1569 by dispersers from the Blue Range or Mexican populations. The importance of binational
1570 population connectivity is further highlighted by the recent release of Mexican wolves in
1571 northern Sonora ~100 km south of the Arizona/New Mexico border.

1572

1573 *Data on Prey Distribution and Abundance in the US*

1574 Carroll et al. (2003a, 2005, 2006) used spatially explicit population models (SEPM) to assess the
1575 potential of prey populations to support wolf populations in the southwestern US with
1576 differential emphasis on the three core areas of suitable habitat. Abundance estimates of
1577 ungulate prey are not collected in some areas of the western US and where they do exist they
1578 show strong inconsistencies across state boundaries. Therefore, as a surrogate for ungulate

1579 abundance they used tasseled-cap greenness (Crist and Cicone 1984), a metric derived from
1580 MODIS (Moderate Resolution Imaging Spectroradiometer) satellite imagery from mid-July 2003
1581 and 2004 (Wharton and Myers 1997). “Pseudo-habitat” variables such as greenness are
1582 correlated to ecological factors like net primary productivity and green phytomass (Cihlar et al.
1583 1991, Merrill et al. 1993, White et al. 1997) and thus with ungulate abundance (Carroll et al.,
1584 2001b, 2003a). Furthermore, the large body of published research on relationships between wolf
1585 demographics and habitat (as reviewed by Fuller et al. 203) strengthens the power of conceptual
1586 models such SEPM. SEPM for the Blue Range, Grand Canyon, and northern New
1587 Mexico/southern Colorado core areas indicated that prey populations in each were sufficient to
1588 support > 250 wolves (Table 1) (Carroll et al. 2005, 2006).

1589
1590 As a validation of the GIS modeling that used a surrogate variables to estimate prey populations
1591 (as described above), J. Heffelfinger (while a member of the Science and Planning Subgroup)
1592 assembled ungulate abundance estimates from game surveys for selected areas in the US portion
1593 of the region. These data were provided primarily by the state game departments of Arizona,
1594 New Mexico, Utah, and Colorado. Survey and population estimation methodology varied
1595 between jurisdictions but data were reduced to animal density as a common denominator. Survey
1596 data were summarized at the spatial resolution of game management units (GMU), with the
1597 exception that New Mexico summarized data over general regions. Members of the SPS
1598 calculated a standard Ungulate Biomass Index (UBI) for several areas of interest (Fuller et al.
1599 2003). Using estimated densities of elk, white-tailed deer, and mule deer from several areas
1600 considered in this document as potential recovery areas, the resultant UBI was calculated and
1601 compared to a regression equation showing the relationship between UBI and wolf density in 31
1602 studies throughout North America (Fuller et al. 2003, fig. 6.2). Based on this regression
1603 equation, wolf density would be estimated at 21 wolves/1000 km² for the Blue Range/Mogollon
1604 Rim, 17 wolves/1000 km² for the Grand Canyon area, and 28 wolves/1000 km² for Carson/San
1605 Juan (J. Heffelfinger, unpublished data assembled while a member of the Science and Planning
1606 Subgroup). Since elk make up a majority of the Mexican wolf diet, the same exercise was
1607 conducted for elk alone yielding wolf density estimates of 18, 12, and 25 wolves/1000 km² for
1608 the Blue Range/Mogollon Rim, Grand Canyon area, and Northern New Mexico/Southern
1609 Colorado areas, respectively.

1610
1611 These predicted wolf densities were extrapolated to previously identified core areas using
1612 hexagons of >60% predicted wolf occupancy from spatially explicit models (Carroll et al. 2006).
1613 Respective wolf densities for the core areas were applied to the number of 500 km² hexagons
1614 with at least 60% probability of occupancy to estimate the total number of wolves that could be
1615 supported in these areas. These calculations indicate each of the three core areas identified are of
1616 sufficient size and currently support ungulate biomass sufficient to support > 250 wolves (Table
1617 2).

1618
1619 Before wolves were reintroduced to the BRWRA, in the FEIS it was estimated that the area
1620 contained adequate prey to support a population of at least 100 wolves (USFWS 1996). Prior to
1621 the outset of reintroductions a population of 15,800 elk (average density 3.7 elk/km²) and 57,170
1622 deer (average density 13.4deer/km²) were estimated to inhabit the BRWRA. The 3-year review
1623 of the reintroduction project indicated that elk in the area could support about 213 wolves and
1624 when combined with deer could support about 255 wolves, based on calculations of standing
1625 biomass and estimated consumption rates (Paquet et al. 2001:47). This estimate was solely for
1626 the BRWRA and did not include the capacity of the FAIR and other areas of Mogollon Rim to
1627 support wolves. Data collected since the BRWRA project began indicate that the wolf
1628 population there is not limited by food (see *BRWRA Project Evaluation*).

1629
1630 All estimates of wolf densities and corresponding estimates of population size that can be
1631 expected to persist in the US core areas should be viewed cautiously. Game management units
1632 and occupancy polygon boundaries did not correspond exactly to the potential core areas of
1633 suitable habitat, so predicted densities and numerical values are approximations. Additionally, it
1634 is uncertain to what extent the regression equation of Fuller et al. (2003) applies to less
1635 productive arid southwestern environments where ungulate population dynamics may differ to a
1636 degree from those in mesic ecosystems. Seasonality of prey availability and vulnerability may
1637 also affect wolf carrying capacity differently in areas where altitudinal migration of ungulates
1638 occurs, versus areas that receive little or no snow. These shortcomings notwithstanding,
1639 extrapolating each density estimate across the respective core areas affirmed that the US portion

1640 of the Mexican wolf recovery region that extended into Utah and Colorado could potentially
 1641 support > 900 wolves (Table 2).

1642

1643

1644 Table 2. Based on ungulate biomass and their areal extent each of the three core areas identified
 1645 are expected to support > 250 wolves.

1646

Core Area	Area (km ²) with 60%+ Predicted Wolf Occupancy	UBI based on all Deer & Elk	Predicted wolf density (/1000km ² based on Deer & Elk)	Predicted No. of Wolves (based on Deer & Elk)	UBI based on Elk only	Predicted wolf density (/1000km ² based on Elk only)	Predicted No. of Wolves (based on Elk only)
Carson/San Juan (northern New Mexico/southern Colorado)	11,500	7.6	28	322	6.5	25	288
Grand Canyon (northern Arizona/southern Utah)	23,000	4.1	17	391	2.6	12	276
BRWRA/Mogollon Rim	20,500	5.6	22	442	4.5	18	369

1647

1648

1649

1650

1651

1652 Effects of Future Landscape Change on Habitat in the US

1653 Potential effects of landscape change on wolf habitat are summarized based on the results of
 1654 Carroll et al. (2006). That study estimated potential change in human-associated impact factors
 1655 (i.e., roads and human population) by proportionately increasing road density and by increasing
 1656 human population on the basis of current trends derived from a time series of human census data.
 1657 The study predicted human population growth from 2000 to 2025 based on growth rates from
 1658 1990 to 2000, but adjusted the predicted 2025 population to match state-level predictions based
 1659 on more complex socioeconomic models. Road density projections incorporated an increase of
 1660 1% per year (proportional to the current road density at the 1-km² scale), a rate half of that seen

1661 in the most rapidly growing portions of our study region (e.g., western Colorado; Theobald et al.
1662 1996).

1663
1664 Wolf habitat in New Mexico and Colorado are most vulnerable to landscape change because
1665 habitat in those states is relatively more fragmented than in Arizona and is experiencing more
1666 rapid development. Outside of those two states, the US southwest shows vulnerability levels
1667 similar to those in the US Northern Rockies - about a 25% decline in wolf carrying capacity over
1668 25 years (Carroll et al. 2003, 2006). Carroll et al. (2005, 2006) predicted that, absent
1669 management actions to mitigate threat factors, future wolf populations in the southwestern US
1670 may be primarily confined to the highest quality habitat in the core areas previously discussed.
1671 Future landscape change would also compromise the already modest connectivity between the
1672 Blue Range and the Sierra Madre Occidental (Sonora/Chihuahua) via occupied habitat along the
1673 Arizona/New Mexico border.

1674
1675 *Connectivity between US core areas*

1676 Earlier studies concluded that potential wolf population connectivity between the Blue Range and Grand
1677 Canyon core areas is greater than between the Blue Range and the Carson/San Juan core area (Carroll et
1678 al. 2005, 2006). We analyzed potential connectivity in more detail using the Connectivity Analysis Toolkit
1679 software (Carroll et al. 2011). We used a habitat model based on data used in previous studies (Carroll et
1680 al. 2006) as input to an analysis of shortest-path betweenness centrality (BC) and current-flow BC
1681 (Carroll et al. 2011). Shortest-path BC identifies the single best linkage between each pair of core areas,
1682 whereas areas of high current flow BC reveal connectivity 'pinchpoints' where much potential dispersal
1683 flow is being routed through relatively limited habitat. Results indicate that the best linkage in the
1684 southwestern US corresponds to a rate intermediate between the well-connected populations in the
1685 northern Rocky Mountains (i.e., Greater Yellowstone to central Idaho and central Idaho to northwestern
1686 Montana) and the poorly connected populations (i.e., Greater Yellowstone to northwestern Montana).
1687 Recovery actions designed to facilitate dispersal between populations in the southwestern US
1688 (especially those that reduce or eliminate human-caused mortality) will be critically important to
1689 recovery and may focus on the most important shortest-path linkages while giving additional
1690 attention to areas with high current flow as well. Such recovery actions may be essential in
1691 ensuring that connectivity-related recovery criteria are achieved.

1692

1693 *Results of Previous GIS Analyses of Habitat Suitability in Mexico*

1694 In Mexico, several previous analyses have evaluated the extent of potential habitat. Araiza et al.
1695 (2002) evaluated GIS data from Sonora, Chihuahua, and Coahuila and identified an area in the
1696 northern Sierra Madre Occidental with relatively high levels of habitat security (low road density
1697 and human settlement). However, field measurements of prey abundance indicated deer densities
1698 in this area were near the lower limit for wolf population persistence. This suggested that
1699 augmentation of deer herds through revised grazing techniques and reduced hunting might be
1700 necessary before the area could support wolves (Araiza 2002).

1701

1702 Sanchez and Guevera (2006) examined habitat potential in Coahuila and Nuevo Leon and
1703 identified areas of as potential habitat in northern Coahuila (Sierra del Carmen) and central
1704 Nuevo Leon (Sierra Plegada). Servín et al. (2007) analyzed historic wolf distribution records
1705 using the Genetic Algorithm for Rule-Set Prediction (GARP) method and regional-scale GIS
1706 data on vegetation type, elevation, temperature, and precipitation to define the probable historic
1707 distribution and ecological niche of the Mexican wolf. Areas with land use unsuitable for current
1708 occupation by wolves (human-altered habitats) were then excluded from the historic distribution
1709 to produce an estimate of the area of remaining suitable habitat. A large portion of the Sierra
1710 Madre Occidental (90,000 km²) was predicted to be suitable for wolves under these assumptions,
1711 whereas little habitat remained in other areas such as Nuevo Leon and Tamaulipas (Servín et al.
1712 2007).

1713

1714 Carroll et al. (2005) identified and compared four potential core areas of suitable habitat in
1715 Mexico: the Sierra San Luis (northern Chihuahua/Sonora), Maderas del Carmen (northern
1716 Coahuila), an area in northwestern Durango near the Chihuahua border, and the Tutuaca reserve
1717 area (west-central Chihuahua near the Sonora border). Of the four, the Durango site contained
1718 the most productive habitat for wolves, but the Tutuaca and Maderas del Carmen sites appeared
1719 to have lower risk of conflict with livestock production.

1720

1721 Martinez Meyer et al. (2006) developed a habitat model based on climate, vegetation, and human
1722 impacts (Figure 5). The study predicted that only 2% of the area with suitable climate and

1723 vegetation also showed low human impacts (i.e., those anthropogenic activities that might affect
1724 wolf fecundity and survival by altering habitats needed by prey and providing increased access
1725 that might lead to elevated levels of human-caused mortality). These core areas of potential
1726 habitat were found widely distributed across northern Mexico in small patches (<100km² in
1727 size). Of the 7,265 km² of currently suitable habitat with low human impacts, 2,284 km² was
1728 predicted to retain suitability under future climate.

1729
1730 Martinez-Gutierrez (2007) identified two areas of >600 km² in size in the northern Sierra Madre
1731 Occidental (western Chihuahua near the border with Sonora) with habitat suitability and low
1732 human-associated mortality risk (Figure 6). The more southerly of these areas falls within the
1733 Tutuaca core area (see below). Additionally, several additional areas of between 200 and 500
1734 km² in size were identified in the same region of northern Sierra Madre Occidental as well as in
1735 western Durango.

1736
1737 *Habitat Factors Associated with Wolf Fecundity: Vegetation Data for Mexico*
1738 Several studies, including Carroll et al. (2005, 2006), have used vegetation data from the 2000
1739 National Forest Inventory (Palacio-Prieto et al. 2000). This inventory mapped land cover across
1740 Mexico at a scale of 1:250,000 based on Landsat TM imagery. Land cover was assigned to one
1741 of 75 classes, with a minimum mapping unit (MMU) of approximately 1 km². The vegetation
1742 data (Palacio-Prieto et al. 2000) for Mexico is the first detailed national vegetation data set for
1743 the area and provides a more accurate record of human-altered land cover types than did the
1744 Mexican roads data described below.

1745
1746 *Habitat Factors Associated with Wolf Fecundity: Climate Data for Mexico*
1747 Species distribution models based on climate data are termed “climatic niche” models. These
1748 models are most commonly applied to allow first approximations of potential effects of global
1749 climate change on large suites of taxa (Thomas et al. 2004). Because many of these species are
1750 poorly-known, and relevant non-climatic environmental variables may be unavailable over the
1751 global or continental extent of analysis, more detailed and biologically-informed models may not
1752 be feasible. Servín et al. (2007) and Martinez Meyer et al. (2006) used the Genetic Algorithm for
1753 Rule-set Prediction (GARP) to predict the potential distribution of the Mexican wolf. Stockwell

1754 and Peters (1999) proposed that the GARP method they developed identifies the ecological niche
1755 of a species, defined as the multi-dimensional environmental space which contains those
1756 ecological conditions under which the species can maintain populations without immigration
1757 (Grinnell 1917, MacArthur, 1972). As climatic niche models are increasingly applied to inform
1758 single-species conservation strategies, the assumption that such models adequately describe a
1759 species “fundamental niche” have been questioned, particularly when the mechanisms by which
1760 climate influences physiology and demography of the species of interest are unknown (Elith and
1761 Leathwick 2009). Although climatic niche models might be expected to suggest overarching
1762 limiting factors within which finer-scale habitat relationships operate, results may be misleading
1763 in the absence of relevant finer-scale habitat variables (Pearson and Dawson 2003, Carroll 2010).

1764
1765 To develop input data for GARP, available occurrence points are divided evenly into training
1766 and extrinsic test data sets; the former set is again divided evenly into true training data (for
1767 model rule development) and intrinsic test data sets (for model rule evaluation and refinement).
1768 Although input data was derived from historical records, GARP projects results onto current
1769 landscapes to estimate the current geographical distributions of suitable areas. GARP is designed
1770 to work based on presence-only data; absence information is included via sampling of pseudo-
1771 absence points from those pixels where the species has not been detected. GARP works in an
1772 iterative process of rule selection, evaluation, testing, and incorporation or rejection: firstly, a
1773 method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules), and is
1774 then applied to the training data and a rule developed; rules may evolve by several means
1775 (truncation, point changes, crossing-over among rules) to maximize predictivity. Predictive
1776 accuracy (for intrinsic use in model refinement) is then evaluated based on 1,250 points re-
1777 sampled from the intrinsic test data and 1,250 pseudo-absence points. Change in predictive
1778 accuracy between iterations is used to evaluate whether particular rules should be incorporated
1779 into the model, and the algorithm runs either 1,000 iterations or until convergence.

1780
1781 Martínez Meyer et al. (2006) predicted Mexican wolf distribution based on a niche model
1782 developed with data on topography (elevation, slope, aspect, topographic index) and annual
1783 means of climate variables (diurnal temperature range, precipitation, maximum, minimum, and
1784 mean temperatures, solar radiation, wet days, and vapor pressure) (Figure 5). Martínez-Gutiérrez

1785 (2007) used 14 climatic variables (average annual temperature, mean diurnal range, seasonal
1786 temperature, annual temperature range, average temperature of wettest quarter, mean
1787 temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest
1788 quarter, annual precipitation, seasonal rainfall (coefficient of variation), precipitation of wettest
1789 quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of
1790 coldest quarter) and three topographic variables (elevation, slope and topographic index) (Figure
1791 6). Both studies subsequently filtered suitable areas based on data on human-associated threats
1792 (e.g., roads) and other factors.

1793

1794 *Habitat Factors Associated with Wolf Fecundity: Prey Data for Mexico*

1795 Estimates of prey abundance in Mexico are limited in spatial extent in comparison to those
1796 collected by state game agencies within the US. For this reason, the most comprehensive
1797 evaluation of potential wolf reintroduction areas in Mexico (Araiza et al. 2006) relied on expert-
1798 based estimates of prey abundance within core areas of suitable habitat. Estimates for all of the
1799 six areas were between 2 and 4 deer per km², which would correspond to densities of 10-17
1800 wolves/1000 km² based on the model of Fuller et al. (2003). Subsequent studies (Arellano et al.
1801 2009, Lara-Diaz 2011) using standardized survey methods have found similarly low prey
1802 densities within potential wolf habitat in northern Mexico. Another potential source of prey
1803 abundance data derives from information collected by Game Management Areas (UMA). UMA
1804 are required to base the number of hunting permits sold on estimates of prey abundance.
1805 Although these estimates are often greater than 2-4 deer per km², the lack of standardized
1806 methodology, limited area sampled, and financial motivation to inflate estimates cause these data
1807 to be of limited relevance to recovery planning.

1808

1809 The diversity of prey available to Mexican wolves in ecosystems of the Sierra Madre Occidental
1810 in Mexico may be higher than in the United States, which might partially compensate for the low
1811 abundance of wild ungulates. In a prey survey in Sierra Madre Occidental, Servín et al. (2007)
1812 found that ungulates (deer) constituted 84% of total wild prey biomass (1.92 of 2.28 kg/ha),
1813 whereas medium-sized and small prey (i.e., rabbits, hares, and rodents) constituted
1814 approximately 16%.

1815

1816 *Habitat Factors Associated with Wolf Survival: Available Data for Mexico*

1817 The relative proportion of private to public lands is higher in northern Mexico than in the
1818 southwestern US. Privately owned land makes up a majority of the states of Northern Mexico:
1819 Chihuahua 84.9%, Sonora 76.8%, Coahuila 73.9%, Nuevo Leon 69.4%, Zacatecas 59.3%, and
1820 Durango 54.7%. Remaining lands are typically held in communal (ejidal) rather than public
1821 ownership. Public lands cover less than 10% of northern Mexico. State and federal nature
1822 reserves cover approximately 4.4% of Nuevo Leon and 2.8% of Tamaulipas (Cantu et al. 2001).
1823 Consequently, most wolves would have to inhabit private lands in Mexico, although some of
1824 these large landholdings are well protected against trespass and deer populations are well-
1825 managed for commercial hunting operations. As a consequence, some large ranches might play
1826 a role in lowering the extinction risk of reintroduced wolves.

1827

1828 Transportation infrastructure (e.g. roads) data for Mexico, as used in several studies including
1829 Carroll et al. (2005, 2006), are derived from the Inventario Nacional de Infraestructura para el
1830 Transporte (INIT), a national database created from state and local level roads data sources at
1831 1:50,000 or coarser scales (Backhoff Pohls et al. 2000). Due to its coarse-scale source, the INIT
1832 data potentially excludes a large proportion of the unpaved roads within northern Mexico (Figure
1833 3). To compensate for this omission in areas of Mexico that showed human-altered land cover
1834 types but no roads (at a resolution of 1 ha), Carroll et al. (2005, 2006) set minimum road
1835 densities of 1.24 km/km² for pasture and 2.0 km/km² for other human-altered lands, based on an
1836 evaluation of road densities in similar land cover types in the US.

1837

1838 Population data for Mexico is typically derived from census databases at the locality scale
1839 (INEGI 2000). The locality is the finest scale of census data collected in Mexico, and thus
1840 approximately corresponds to the census block in the United States. However, locality data is
1841 available as point locations rather than the polygons used to delineate US census blocks.

1842 Livestock data for Mexico may be derived from the Census of Agriculture at the municipality
1843 level (Census of Agriculture 1991). Because available data on human settlement patterns and
1844 roads is relatively sparse in Mexico, data on livestock density may allow more realistic
1845 evaluation of potential wolf survival in remote areas.

1846

1847 *Potential Core Areas of Suitable Habitat in Mexico*

1848 Potential core areas of suitable habitat in Mexico are found along the mid to higher elevations

1849 (2400 – 3200 m) of the Sierra Madre Occidental, as well as in two smaller mountain ranges

1850 located in Coahuila (Maderas del Carmen) and Nuevo Leon (Sierra Plegada) (Figures 7 and 8).

1851 Due to the continuous band of forest habitat at higher elevations of the Sierra Madre Occidental,

1852 wolves historically may have been widely distributed through this region. In contrast, the

1853 Maderas del Carmen and Sierra Plegada are relatively isolated from other areas of temperate

1854 forest habitat (Araiza et al. 2006, in press) (Figures 7 and 8).

1855

1856 In 2006, a workshop convened researchers involved with several of the studies described above,

1857 in order to derive a consensus opinion of which areas held potential for wolf reintroduction in

1858 Mexico (Araiza et al. 2006, in press). Because these six areas have subsequently formed the

1859 focus of recovery planning in Mexico, we describe them in detail here. Araiza et al. (in press)

1860 subsequently analyzed habitat suitability and human-associated mortality risk within each of the

1861 six larger areas to identify optimal sites in which to focus recovery efforts. Using historical

1862 occurrence records, Araiza et al. (in press) ranked vegetation types as to suitability. The study

1863 then developed three alternate scenarios for human-associated risk (low, intermediate, and high

1864 risk) that made alternate assumptions as to the extent of the zone around roads and human

1865 settlements in which wolves would experience increased mortality. Although the expert's

1866 workshop (Araiza et al. 2006) had concluded that patches of suitable habitat larger than 10,000

1867 km² were most suitable for reintroductions, no single patch in any of the six areas met that

1868 criterion (Araiza et al. in press). However, the largest clusters of suitable patches were found in

1869 Sonora-Chihuahua (area 1) and Chihuahua-Durango (area 3) (15,705 and 8,344 km² in area,

1870 respectively - Figure 7; under the intermediate risk assumptions - Figure 8).

1871

1872 The six potential core areas of suitable habitat identified by Araiza et al. (2006, in press) (Table

1873 1, Figure 7) generally correspond with core areas identified in the various habitat models cited

1874 above. Many of these areas are not under legal protection, because past conservation efforts in

1875 Mexico have primarily focused on Desert and Tropical Forest biomes. The Mexican wolf

1876 conservation program thus has stimulated broader awareness by the Mexican federal government
1877 of the need to protect areas of temperate forests in northern Mexico.

1878

1879 *Description of six candidate core areas of suitable habitat in Mexico (numbering as shown in*
1880 *Table 1 and Figure 7)*

1881 1. Sierra San Luis/ Ajos-Bavispe (Sonora/Chihuahua): This area, of 10-15,000 km² in extent,
1882 lies in the northern portion of the states of Chihuahua and Sonora, abutting the US border and the
1883 northern end of the Sierra Madre Occidental. Vegetation ranges from lower elevation desert
1884 grassland to montane forest. The area is estimated to support 2-4 deer/ km². Livestock density is
1885 approximately 5 cattle/ km². In October 2011, five wolves were released in this area. Araiza et al.
1886 (2006) estimated that the area could support 80 wolves.

1887

1888 2. Tutuaca/Sierra Tarahumara (Chihuahua): This area, of 10,000 km² in extent, lies in the Sierra
1889 Madre Occidental in the central and southern portions of the state of Chihuahua. Vegetation is
1890 primarily montane pine and pine-oak forest and grassland. A protected area of the same name
1891 (Refugio de la Fauna Silvestre Tutuaca) lies within this area. The area is estimated to support 2-4
1892 deer/ km² (Araiza et al. 2006) and may range up to 6 deer/ km² in some areas (J. Servín, unpubl.
1893 data). Livestock density is about 4 cattle/ km². It is estimated the area could support 80 wolves
1894 (Araiza et al. 2006).

1895

1896 3. Chihuahua/Durango: This area, of 15,000 km² in extent, lies in the central Sierra Madre
1897 Occidental on the border of the states of Chihuahua and Durango. Vegetation is montane pine,
1898 pine-oak, and oak forest and grassland. The area is estimated to support 2-4 deer/ km² (Araiza et
1899 al. 2006) and may range up to 7 deer/ km² in some areas (J. Servín, unpubl. data). Livestock
1900 density is about 7 cattle/ km². Road density is less than 0.23 km/km². It is estimated the area
1901 could support 60 wolves (Araiza et al. 2006).

1902

1903 4. Sierra de Valparaiso/Sierra de Urica/Mezquital (Zacatecas/Durango): This area, of 6,000 km²
1904 in extent, lies in the southern Sierra Madre Occidental on the border of the states of Durango,
1905 San Luis Potosi and Zacatecas. Vegetation is montane pine, pine-oak, and oak forest, grasslands,
1906 and mesquite shrublands. The area is estimated to support 2-4 deer/ km² (Araiza et al. 2006) and

1907 may range up to 6 deer/ km² in some areas (J. Servín, unpubl. data). Livestock density is about 6
1908 cattle/ km². Road density is low at approximately 0.08 km/km². It is estimated the area could
1909 support 24 wolves (Araiza et al. 2006).

1910

1911 5. Maderas del Carmen/Serranias de Burro (Northern Coahuila): The area of the Sierra del
1912 Carmen in northern Coahuila, of 13,000 km² in extent, is characterized by pine-oak and oak
1913 forest, grassland and mesquite shrubland vegetation. The area is estimated to support 2-4 deer/
1914 km². Livestock density is about 6 cattle/km². Road density is less than 0.23 km/km². It is
1915 estimated the area could support 85-100 wolves (Araiza et al. 2006).

1916

1917 6. Sierra Plegada (Nuevo Leon/Tamaulipas): This mountain range, of 17,000 km² in extent, lies
1918 primarily in the state of Nuevo Leon. Vegetation is primarily montane pine-oak and oak forest,
1919 grassland, and mesquite shrubland, with a sub-tropical forest influence in the eastern portion of
1920 the area. The area is estimated to support 2-4 deer/km². Livestock density is about 7 cattle/km².
1921 Road density, although averaging less than 0.23 km/km², is somewhat higher than in the Sierra
1922 Madre Occidental. It is estimated the area could support 60-140 wolves (Araiza et al. 2006).

1923

1924 *Connectivity Between Potential Core Areas of Suitable Habitat in Mexico*

1925 Araiza et al. (2006) considered all of the six areas described above as adequately connected with
1926 at least one other potential core area of suitable habitat. However, the authors noted that areas in
1927 the southern Sierra Madre Occidental (i.e., areas 1 through 4, Figure 7) were likely to be better
1928 connected to the wolf metapopulation than were areas to the east in Coahuila and Nuevo Leon
1929 (areas 5 and 6, Figure 7). It is difficult to quantitatively assess potential connectivity between the
1930 six areas, beyond conclusions based on the general distribution of suitable montane habitat,
1931 because of the coarse resolution of available data on mortality risk factors (e.g., roads).

1932 However, Martinez Gutierrez (2007) reported that habitat between core areas 1 through 4 of
1933 suitable habitat was of marginal quality because of a high level of human impacts (Figure 9).

1934 For example, the habitat between the Tutuaca/Sierra Tarahumara (area 2, Figure 7) and
1935 Chihuahua/Durango (area 3, Figure 7) (and the southern portion of the Tutuaca area itself) is
1936 within a “zone of concentrated [mortality] risk” due to high human presence (Martinez Gutierrez
1937 2007). In other cases, both the regional-scale GIS analysis and expert knowledge were used to

1938 reveal important patterns to the suitability of habitat between the six potential reintroduction
1939 areas in Mexico. For example, the southern boundary of the Sierra San Luis/Ajos-Bavispe
1940 reintroduction area (area 1, Figure 7) was defined by the presence of the logging town of
1941 Madera, which itself is surrounded by a heavily roaded and logged landscape.

1942
1943 To ensure detection of such patterns within the potential reintroduction areas Araiza et al (in
1944 press) performed a detailed modeling of risk under alternate assumptions of risk levels (i.e., high,
1945 intermediate, and low) associated with human population centers and road. Their analysis
1946 revealed that within the core areas of suitable habitat (i.e., areas 1 through 6, Figure 7) the most
1947 suitable areas for reintroductions are somewhat fragmented (Figure 10). It follows logically
1948 from their work that areas of low risk and preferred habitat are even more uncommon and
1949 fragmented between the six core areas of suitable habitat. The Mexican wolf recovery plan for
1950 Mexico that was written by a team of scientists in Mexico also concluded that it would be
1951 difficult to find appropriate habitat for wolves (SEMARNAT 2000).

1952
1953 Servín et al. (2007) proposed that the six Mexican core areas of suitable habitat in Mexico might
1954 form two disjunct metapopulations. The larger metapopulation would include the four areas in
1955 the Sierra Madre Occidental (i.e., areas 1 through 4, Figure 7), with interchange of dispersers
1956 along the Sierra Madre Occidental from Sonora to Zacatecas, with potentially connections with
1957 the Blue Range Wolf Reintroduction Area in Arizona and New Mexico. The two areas in eastern
1958 Mexico (Coahuila and Nuevo Leon, areas 5 and 6, Figure 7) could potentially exchange
1959 dispersers with Mexican wolf populations in Texas and New Mexico.

1960
1961 We considered the relative distance between the various Mexican core areas and with the US
1962 core areas to qualitatively evaluate the connectivity between sites (Table 1). Areas in eastern
1963 Mexico (Sierra Plegada and Maderas del Carmen) are qualitatively better connected to each
1964 other than to the other 4 potential core areas in western Mexico. This is due to barriers created
1965 by large areas of unsuitable low-elevation habitat and the human population between these areas.
1966 However, higher-elevation areas may offer some potential for connectivity between the Sierra
1967 Plegada core area (6 in Figure 7) and areas 3 and 4 in the states of Durango and Zacatecas (J.
1968 Servin, pers. comm.). The four areas in the Sierra Madre Occidental are largely connected with

1969 each other and to a lesser degree, through the Sierra San Luis Complex, to the Blue Range core
1970 area in the US.

1971

1972 *Comparing potential core areas of suitable habitat in Mexico*

1973 Araiza et al. (2006) estimated potential size of wolf populations in the six core areas of suitable
1974 habitat in Mexico (Table 1). These estimates indicate that the areas have varying potential to
1975 contribute to recovery. Areas in the Sierra Madre Occidental are more likely to form part of a
1976 connected metapopulation than are the two eastern areas. Additionally, the two areas in the
1977 northern Sierra Madre Occidental are predicted to support larger wolf populations (80 wolves
1978 each) than are the two areas in the southern Sierra Madre Occidental (60 and 24 wolves).
1979 However, the relative potential for successful reintroductions within each of these areas may also
1980 depend on public attitudes and details of land use that are not quantifiable using available data
1981 (Servín et al. 2007).

1982

1983 *Comparing potential core areas of suitable habitat between the US and Mexico*

1984 Although we sought to use the best available data in both the US and Mexico, we encountered
1985 inconsistencies in the resolution and completeness of data between the two nations. This
1986 inconsistency was greatest for the roads data, as the mapped roads network in Mexico was quite
1987 sparse when compared to the relatively complete mapping of four-wheel drive routes in the US
1988 (INIT, USGS)(Figure 4). In contrast, human population data was relatively consistent in scale
1989 between the two nations. Carroll et al. (2005, 2006) concluded that the sparseness of the
1990 available data on mapped human impacts (roads and altered habitat types) in remote areas of the
1991 Sierra Madre Occidental strongly affected estimates of potential wolf habitat. The authors
1992 therefore concluded that their model results for the Sierra Madre Occidental (cores areas 1
1993 through 4, Figure 7) should be used only as an initial comparison of habitat suitability among
1994 sites within Mexico to be followed by local surveys of land use and prey abundance.

1995

1996 Available vegetation data also differed between the two nations. Such data was available at a
1997 finer spatial scale in the US than Mexico. Conversely, thematic detail (floristic types) was greater
1998 for the Mexican data. However, due to the generalized nature of the rankings of vegetation by
1999 wolf habitat value (both due to generalist nature of wolf habitat associations and lack of detailed

2000 data on Mexican wolf natural history) and the large extent of wolf territories, both the thematic
2001 and spatial detail of the vegetation data is sufficient for the recovery planning.

2002

2003 These bi-national contrasts in the data used in the studies reviewed above limit quantitative
2004 comparison of habitat suitability between US and Mexican potential core areas of suitable
2005 habitat. For example, Carroll et al. (2005) concluded that “the resolution of the habitat data was
2006 still inconsistent between US and Mexico to an extent that significantly limits comparability
2007 between Mexican and US reintroduction sites.”

2008

2009 *Implications of comparison of core areas of suitable habitat*

2010 Despite the challenges arising from bi-national contrasts in available data, we conclude based on
2011 qualitative comparisons that potential core areas in the US are likely to support larger wolf
2012 populations than potential core areas in Mexico (Table 1). The Mexican wolf recovery plan
2013 developed by a team of scientists in Mexico similarly concluded that it would be difficult to find
2014 appropriate habitat for reintroduction to Mexico (SEMARNAT 2000). The core areas identified
2015 in the US are 24,000-25,000 km² in extent. Core areas identified by Araiza et al. (2006) in
2016 Mexico were 6,000-17,000 km² in extent. Although the subsequent analysis by Araiza et al. (in
2017 review) expanded the potential recovery areas to encompass areas of 12,000 to 30,000 km² in
2018 extent, they noted that areas of low or moderate mortality risk formed no more than half of these
2019 expanded areas (e.g., 10,500 of the total 30,000 km² comprising the Chihuahua/Durango
2020 potential recovery area). Notably, the core areas in the US are defined by large tracts of federal
2021 land managed per longstanding, legally mandated conservation prescriptions that ensure that the
2022 risk to wolves from human-caused mortality is relatively low. Such public land is absent in the
2023 core areas in Mexico.

2024

2025 In addition to the contrast in patterns of land ownership between the US and Mexico that would
2026 affect wolf survival, contrast in prey density between the US and Mexico core areas results in a
2027 sharply different estimates of the number of wolves that could be potentially supported in each of
2028 the core areas. Ungulate biomass in US core areas (with the exception of western Texas, where
2029 prey density is likely low) was 4.1-7.6 deer equivalents (UBI)/km² vs. 2-4 deer/km² in Mexico.
2030 Although habitat exists in the in the U.S./Mexico border area, the area would likely serve as a

2031 mortality sink for wolves (Carroll et al. 2005). The Service concluded that other than the
2032 BRWRA, since other reintroduction sites in the border country were isolated and could each
2033 support only 5 to 30 wolves that they offered little support to Mexican wolf recovery (U.S. Fish
2034 and Wildlife Service 1996). This is consistent with Service findings that the small isolated gray
2035 wolf population that inhabits Isle Royale National Park (Peterson et al. 1998) does not contribute
2036 to gray wolf recovery in the Western Great Lakes states (U.S. Fish and Wildlife Service 1992,
2037 U.S. Fish and Wildlife Service 2011).

2038
2039
2040

2041 *Recommended Recovery Region for the Mexican Wolf*

2042 Studies of Mexican wolf habitat suitability in the US and Mexico as summarized above and
2043 Appendix 1 indicate that the most feasible and expeditious recovery strategy will require a
2044 recovery region that includes Mexico, extreme western Texas, Arizona, New Mexico, southern
2045 Utah (as circumscribed by interstate highways 15 and 70), and southern Colorado (as
2046 circumscribed by interstate highways 70 and 25) (Figure 11). Three core areas of suitable habitat
2047 exist within this recovery region and include: 1) the BRWRA and adjacent public lands, 2) the
2048 Grand Canyon and adjacent public lands in northern Arizona and southern Utah (circumscribed
2049 by interstate highways 15 and 70), and 3) Carson and San Juan National Forests and other
2050 connected areas of public lands and private lands with conservation management in northern
2051 New Mexico and southern Colorado (circumscribed by interstate highways 70 and 25). Primary
2052 reintroduction sites could be found within each of these core areas since they all include large
2053 patches of high quality habitat on public or private lands subject to conservation mandates
2054 (National Park, wilderness, conservation easements) where wolves would experience relatively
2055 low human-caused mortality. The uncertainty introduced by climate change notwithstanding,
2056 these core areas of suitable habitat are projected to persist under potential future landscape
2057 changes (Carroll et al. 2006). Based on GIS modeling of current habitat conditions it is
2058 estimated that these three core areas in the US could support > 250 wolves (Table 1) and the
2059 entire US portion of the recovery region could support > 1,000 wolves (Carroll et al., 2003,
2060 2006). In an independent assessment of standing ungulate biomass Heffelfinger (unpublished
2061 data assembled while serving on the Science and Planning Subgroup) used ungulate density

2062 estimates and concluded that current abundance levels in the entire US portion of the recovery
2063 region could support > 900 wolves.

2064
2065 Although some areas which are not currently suitable habitat might become suitable in future
2066 decades due to recovery actions, this plan's recovery strategy focuses primarily on areas that are
2067 currently among the most highly secure and productive areas for wolf recovery. Expedient
2068 recovery (that is, consistent with the timeline set forth in this plan) is necessary to fulfill recovery
2069 objectives because any additional time that captive and wild Mexican wolf populations remain at
2070 their current low population size accentuates genetic threats and reduces future recovery
2071 potential. In other words, the accumulating genetic effects of the current population bottleneck
2072 lend urgency to recovery, and require a focus on areas where growth of Mexican wolf
2073 populations will be relatively rapid due to high survival rates and adequate prey abundance.

2074
2075 *Relevance to Historical Range*
2076 Two of the core areas of suitable habitat, the Grand Canyon and adjacent public lands in northern
2077 Arizona and southern Utah (as circumscribed by interstate highways 15 and 70), and the Carson
2078 and San Juan National Forests and other connected areas of public lands and private lands with
2079 conservation management in northern New Mexico and southern Colorado (as circumscribed by
2080 interstate highways 70 and 25) are located north of the Mexican wolf's historical range. For the
2081 following reasons it is appropriate to include both areas in the Mexican wolf recovery region.

- 2082
- 2083 • The Mexican wolf is a close living relative to the gray wolf subspecies that occupied the
2084 areas historically.
 - 2085 • The Mexican wolf is the closest geographic source of wolves to the areas.
 - 2086 • The Mexican wolf is capable of surviving and thriving in the areas.
 - 2087 • Of all gray wolf subspecies, the Mexican wolf is in greatest need of conservation
2088 assistance.
 - 2089 • Including areas in Mexican wolf recovery region that are located outside the subspecies'
2090 historical range is consistent with the best available science.
 - 2091 • The Mexican wolf is not recoverable unless the areas are included in the recovery region.

2092

2093 Each of these reasons is discussed below.

2094

2095 The Mexican Wolf is a Close Living Relative to the Gray Wolf Subspecies That Occupied the
2096 Areas Historically.

2097 The Mexican wolf is a close living relative to the gray wolf subspecies that occupied the areas
2098 historically. These two core areas are proximate to (Brown 1983, Bogan and Mehlhop 1983,
2099 Hoffmeister 1986, Nowak 1995) or well within (Leonard et al. 2005) the large zone of gray wolf
2100 genetic intergradation that characterized the southwest historically (see Taxonomy). Leonard et
2101 al. (2005) interpret the geographic distribution of genetic markers as evidence that historical gene
2102 flow among the Mexican wolf and other wolf “subspecies” was extensive in time and space and
2103 supports an area for recovery of the Mexican wolf that extends well beyond the subspecies
2104 historical range.

2105

2106 The Mexican Wolf is the Closest Geographic Source of Wolves to the Areas.

2107 The Minnesota wolf (*C. l. nubilus*), a close relative of the Mexican wolf, was probably
2108 widespread throughout the southwestern US historically (Nowak 1995) until it was extirpated
2109 from the region over 50 years ago (Brown 1983, Robinson 2005). In response, at least a few
2110 Mexican wolves moved north to occupy the vacated habitat in New Mexico and Arizona (Gish
2111 1977, Scudday 1977, Nowak 1995). Nowak (1986:1-2) considered the relevance of the shifting
2112 range when he endorsed the reintroduction of the Mexican wolf “beyond its designated range on
2113 the grounds that it could have occupied such sites naturally, if other wolves had not already been
2114 there, and indeed, may have been attempting to do so after the other wolves had been extirpated
2115 ... Suppose, however, that there had been no gray wolves to the immediate north of the range of
2116 bailey. In that case, there is no reason to think that baileyi would not have kept right on going to
2117 eventually occupy a large part of the western United States ... The genus Canis is remarkably
2118 adaptable to a variety of conditions. The main factor limiting the distribution of a particular
2119 species or subspecies seems not to be different habitat conditions, but rather the presence of
2120 another kind of Canis. It has not been unusual for one subspecies of gray wolf to invade and
2121 establish itself in the range of another subspecies that had disappeared.”

2122 After conducting an exhaustive review of molecular genetics and morphological data (Chambers
2123 et al. 20xx) the senior author concluded: "I think drawing a line to represent the geographical
2124 limits of the taxon *C. l. baileyi* (its boundary if you will) will always be problematical (I dislike
2125 that term, but it actually fits this situation)... I am fearful that in defining a subspecies range, that
2126 some may try to manage to maintain that boundary. A lesson from our range-wide review of
2127 North American wolves is that there are genetic lineages of wolves that correspond to some
2128 subspecies groupings, but the geographical relationships of these lineages has been dynamic over
2129 time. Even if one maps a range for a subspecies for any given time, it would be a mistake both
2130 biologically and in terms of management to treat a boundary as a static line. They never have
2131 been static."

2132 Wide-ranging wolves from the BRWRA affirm Nowak's expectation about range expansion and
2133 indicate that the subspecies' current range extends north of the historical range proposed by
2134 Parsons (1996). Two wolves from the BRWR traveled to the edge of the historical range and
2135 two beyond that range (see Life History). The wolf's ability to colonize distant, unoccupied
2136 habitat is well known (Mech and Boitani 2003) and is one reason why the USFWS recognizes
2137 the importance of long distance movements by gray wolves for defining the boundaries of
2138 recovery areas (U.S. Fish and Wildlife Service 2009:15126 – 15127). It is quite possible that the
2139 four wolves that traveled considerable distances from the BRWRA could have survived and
2140 reproduced (assuming the presence of other Mexican wolves) in areas well outside the historical
2141 range if they had not been captured and returned to the BRWRA. The proximity of the BRWRA
2142 population and the wide-ranging capabilities of wolves combine to indicate that northern
2143 Arizona/southern Utah and northern New Mexico/southern Colorado will be part of the
2144 subspecies' future range due to similar forays by other young dispersing wolves.

2145

2146 The Mexican Wolf is Capable of Surviving and Thriving in the Areas.

2147 Data collected from the BRWRA, especially those concerning food habitats (see Wolves and
2148 Prey), indicate that Mexican wolves are capable of living as far north as southern Utah and
2149 southern Colorado. This is not surprising given the broad ecological abilities of gray wolves.

2150

2151 Of All Gray Wolf Subspecies, the Mexican Wolf is in Greatest Need of Conservation Assistance.

2152 As noted previously (see Taxonomy and Distribution) early taxonomists identified five gray wolf
2153 subspecies that inhabited the southwestern US including three (*C. l. mogollonensis*, *C. l.*
2154 *monstrabilis*, *C. l. youngi*) that have been have been extinct for decades and a fourth (*C. l.*
2155 *nubilus*) that is represented in the wild by a robust population in the western Great Lakes states
2156 and eastern Canada. This subspecies was extirpated from the southwestern US over 50 years ago
2157 (Brown 1983, Robinson 2005). The fifth southwestern subspecies, *C. l. baileyi*, is represented in
2158 the wild by only one small population in the BRWRA (see Current Population and Trends).
2159 Given its precarious status in the wild, the Mexican wolf is the most endangered gray wolf
2160 subspecies (Phillips et al. 2000) and has been targeted as a conservation priority by the Wolf
2161 Specialist Group for the International Union for the Conservation of Nature (IUCN) (L.D.
2162 Mech, pers. comm.). Including northern Arizona/southern Utah and northern New
2163 Mexico/southern Colorado in the Mexican wolf recovery region is strongly indicated from a
2164 conservation perspective.

2165
2166 Including Areas in the Mexican Wolf Recovery Region That Are Located Outside the
2167 Subspecies' Historical Range is Consistent With the Best Available Science.

2168 Defining a Mexican wolf recovery region that extends outside the historical range for the
2169 subspecies is consistent with the conclusion reached by the IUCN Conservation Breeding
2170 Specialist Group and other experts involved in a comprehensive wolf population and habitat
2171 viability analysis (Phillips et al. 2000). Additionally, it is consistent with the findings of the
2172 science and planning subgroup of the recovery team that was assembled to develop a recovery
2173 plan for the gray wolf southwestern distinct population segment (DPS) that was adopted by the
2174 USFWS in 2003 and included the southern half of Utah and Colorado (Federal Register
2175 68:15804 – 15875). Members of that subgroup concluded that *C. l. baileyi* was the most
2176 appropriate source stock for recovering the DPS (U.S. Fish and Wildlife Service 2003).

2177
2178 More broadly, defining a recovery region that extends outside a species or subspecies historical
2179 range following a comprehensive assessment of historical, contemporary, and future conditions
2180 is supported by leading ecological research (Lomolino 2006, Caro 2007, McLachlan et al. 2007,
2181 Davis et al. 2011). In an increasingly dynamic and uncertain world (Dimento and Doughman
2182 2007, Brown 2011, Orr 2010), recovering taxa outside purported historical ranges (assisted

2183 migration) based on diligently assembled scholarship from the best available science may
2184 become increasingly common (Lomolino 2006, Caro 2007, Hunter 2007, McLachlan et al. 2007,
2185 Hayward 2008, Davis et al. 2011, Marris 2011). While this approach is not without risk
2186 (Rubenstein et al. 2006, Ricciardi and Simberloff 2009, Marris 2011:111-132), it seems
2187 environmentally benign when it involves species that are defined by ecologically similar
2188 subspecies with historical distributions that included extensive zones of intergradation. Such an
2189 approach to recovery will allow such species (or subspecies) to experience greater security than a
2190 more conservative approach based on an exclusive focus on subspecies' historical ranges. The
2191 Mexican wolf is one such subspecies: it arises from a species that is defined by many subspecies
2192 all of which were ecological generalists with historical ranges that included wide zones of
2193 ecologic and genetic intergradation (Brewster and Fritts 1995, Mech and Boitani 2003:11 17, Von
2194 Holdt et al. 2011, Chambers et al. submitted).

2195

2196 The Mexican Wolf is Not Recoverable Unless the Areas are Included in the Recovery Region.
2197 Due to alteration of the historic habitat inhabited by Mexican wolves from human development
2198 and resource use, defining a recovery region for the Mexican wolf that focused solely on
2199 historical range would preclude recovery (see Geography of Recovery). The authors of the 1982
2200 Mexican Wolf Recovery Plan concluded the same and commented: "In formulating a recovery
2201 plan objective for any subspecies of *C. lupus*, one must realistically view, not only the causes of
2202 the wolf's past endangerment, but also present trends toward ever-increasing human needs –
2203 whether real or perceived – for space and for the renewable and nonrenewable resources present
2204 or producible in wolf habitat" (USFWS 1982:23). The tension between recovery and habitat
2205 availability within historical range led them to conclude that recovery of the Mexican wolf was
2206 not possible. That conclusion remains valid. This problem is remedied by including areas
2207 outside the Mexican wolf's historical range in the recommended recovery region.

2208

2209 *Land Ownership Status and Use in the US and Mexico*

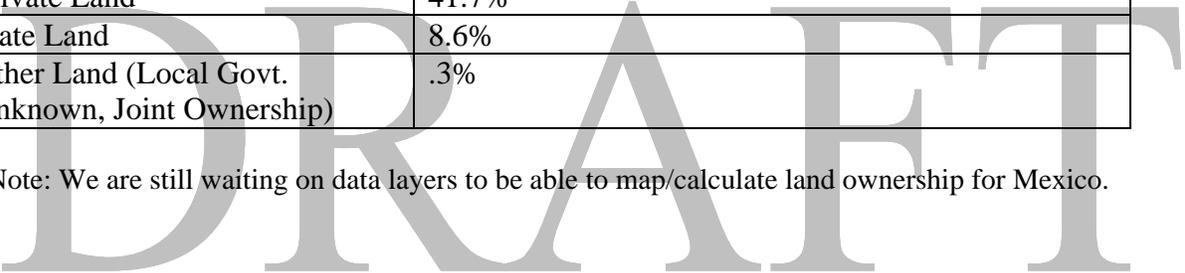
2210 Recovery plans in the United States for wide-ranging species such as the wolf typically assume
2211 that the primary responsibility for species conservation will fall on federal lands, with additional
2212 activities potentially occurring on private and other non-federal lands when these actions are also
2213 necessary for recovery. A mixed pattern of land ownership characterizes that portion of the

2214 Mexican wolf recovery region in Utah, New Mexico, and Arizona (Figure 9, Table 3). In
 2215 contrast western Texas is nearly all privately owned which seriously compromising the
 2216 usefulness of otherwise suitable wolf habitat there to serve as a primary reintroduction area.
 2217 Regulations limiting wolf mortality in western Texas (e.g., limitations on hunting of wolves)
 2218 could, however, allow a population of wolves to become established there due to natural
 2219 dispersal from either the Blue Range or any wolf populations resulting from future
 2220 reintroductions in the northern portion of Coahuila state (Mexico).

2221
 2222 Table 3*. Land ownership in the Mexican wolf recovery area.
 2223

Category of Land Type (Landownership)	Amount of land type found within the Recommended Mexican Wolf Recovery Region in the U.S. (percentage)
Federal Land	36.6%
Native American Land	12.8%
Private Land	41.7%
State Land	8.6%
Other Land (Local Govt. Unknown, Joint Ownership)	.3%

2224
 2225 *Note: We are still waiting on data layers to be able to map/calculate land ownership for Mexico.
 2226
 2227



2228
 2229
 2230
 2231
 2232 Mexico

2233 Ejidos and communities

2234
 2235

2236 *Policy-Related Considerations*

2237 ESA

2238 An exclusive focus on historical range is not mandated in the ESA or related USFWS policies.
 2239 There is no direct reference to historical range in the ESA, and only one ESA related policy
 2240 makes reference to it [50 CFR 17.81(a)]: “The Secretary may designate as an experimental
 2241 population a population of endangered or threatened species that has been or will be released into
 2242 suitable natural habitat outside the species current range (but within its probable historic range)

2243 ...”. But even here the USFWS Director has discretion based on current conditions [50 CFR
2244 17.81(a)]: “... an experimental population can be established outside a species historic range if
2245 the Director finds that the primary habitat of the species has been unsuitably or irreversibly
2246 altered or destroyed.” The best available science (see Geography of Recovery) indicates that 1) a
2247 lack of suitable habitat in the Mexican wolf’s historical range precludes recovery, and 2)
2248 recommending a recovery region that includes sufficient suitable habitat from areas outside the
2249 subspecies historical range is appropriate.

2250
2251 USFWS has supported endangered species reintroductions in areas that were not necessarily
2252 considered historical habitat for other listed species including the black-footed ferret (*Mustela*
2253 *nigripes*) near Janos, Mexico (Anderson et al. 1986,
2254 <http://www.fws.gov/mountainprairie/species/mammals/blackfootedferret/archives.htm>);
2255 California condor (*Gymnogyps californianus*) in northern Arizona (Mesta 1996, USFWS 1996,
2256 Snyder and Snyder 2000, USFWS 2012); westslope cutthroat trout (*Oncorhynchus clarki lewisi*)
2257 in southwestern Montana (USFWS 2007); and the gray wolf in the northern Rocky Mountains
2258 (Fritts et al. 1997). Since the plains gray wolf (*Canis lupus nubilus*) seemingly occupied that
2259 area historically rather than the northwestern gray wolf (*Canis lupus occidentalis*) from Alberta
2260 and British Columbia, Canada (Nowak 2003), the former, which is common in the Great Lakes
2261 states, could have been used for reintroductions rather than the latter which was used because the
2262 animals were familiar with the habitats and prey of the northern Rocky Mountains (Fritts et al.
2263 1997).

2264
2265 The Mexican wolf recovery region recommend in this plan is similar to the area delineated for
2266 southwestern gray wolf (*Canis lupus*) distinct population segment (DPS) that was adopted by the USFWS
2267 in 2003 (Federal Register 68:15804 – 15875). While the language authorizing the DPS was silent on the
2268 topic of gray wolf subspecies, the science and planning subgroup of the team that was assembled to
2269 develop a recovery plan for the DPS concluded that *C. l. baileyi* was the most appropriate source stock
2270 for recovering the DPS (USFWS 2003).

2271

2272

2273 State Policies

2274 Describe state game commissions, state laws/regulations/commission policies/rules, management
2275 plans, etc. related to wolves.

2276

2277 Binational US-Mexico Policy Coordination

2278 As previously described (see Background), Mexico and the United States have worked
2279 independently yet collaboratively on Mexican wolf recovery for over three decades. Today, both
2280 countries are actively engaged in the binational captive breeding program and in efforts to re-
2281 establish the Mexican wolf in the wild. Recognition of the historical cross-border distribution of
2282 the Mexican wolf paired with recognition that the two countries' legal frameworks for species
2283 protection differ, leads both countries to desire the establishment of a bi-national collaborative
2284 framework that is mutually supportive yet respectful of each country's autonomy.

2285

2286 Smaller populations in Mexico as well as in the US (e.g., Texas) could be critically important for
2287 ensuring connectivity between larger core areas in each country, as well as meeting
2288 representation goals (Shaffer and Stein 2000). The modest potential for connectivity between US
2289 and Mexican wolf populations suggests that recovery planning would benefit from a binational
2290 coordination. However, determining the appropriate degree of coordination, and the respective
2291 roles of actions in US and Mexico, is difficult given contrasting policy contexts and biological
2292 realities in the two nations.

2293

2294 There are many similarities between Mexico and the United States in the regulatory context of
2295 Mexican wolf conservation. Both have federal legal frameworks for recovery: Mexico's Ley
2296 General de Vida Silvestre (2000), NOM 059 ECOL 2001 (2002), and the United States' ESA
2297 of Both nations have developed recovery plans for the Mexican wolf. Mexico's Programa de
2298 Recuperacion del Lobo Mexicano was published in 1999; the United States' Mexican Wolf
2299 Recovery Plan was published in 1982, and was co-signed by Mexico's Direccion General de la
2300 Fauna Silvestre. In both nations, Federal agencies lead the recovery efforts: Mexico's Direccion
2301 General de Vida Silvestre (DGVS) and the US Fish and Wildlife Service (FWS). Both nations
2302 have comparable advisory committees for recovery: Mexico's Subcomite Technico Consultivo
2303 Nacional para la Recuperacion del Lobo Mexicano (STCN RLM); the United States' Mexican
2304 Wolf Recovery Team. In both nations, the parties interested in and affected by wolf recovery

2305 actions include state and local governments, as well as non-governmental organizations and
2306 private property owners.

2307

2308 There are, however, also significant differences in the regulatory context between Mexico and
2309 the United States. Whereas the US ESA mandates development of species-specific recovery
2310 criteria, Mexico's red list of endangered species (NOM 059 ECOL 200 1) has downlisting
2311 criteria that apply to broad categories of species, one of which includes the Mexican wolf.

2312

2313 Local and Regional Culture

2314

2315

2316 *Etc...*

2317

2318 *Summary Description of Recovery Area*

2319

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2320 J. Reasons for Listing/Threats Assessment

2321 (Note to Reviewer: I have provided an explanation of what this subsection of the plan should provide
2322 directly from the Service’s recovery planning guidance: “This subsection should include an
2323 overview of the species’ decline, and its causes of decline (to the extent they can be
2324 determined). The causes of decline, or threats, may be past, continuing from the past into the
2325 future, newly identified, and reasonably anticipated in the future (including, but not limited
2326 to, those that have been temporarily curtailed but are likely to recur). Where possible, this
2327 subsection should also identify the source of threats, e.g., if the threat is siltation in a stream,
2328 the source could be urban runoff, watering cattle, removal of riparian vegetation, recreational
2329 uses, etc. Noting the source helps tailor the recovery action(s) needed. When discussing each
2330 threat and its source(s), the geographic scope, severity, and frequency of the various threats
2331 should be indicated, noting those that present greater or lesser threats to the species.
2332 Uncertainties with respect to threats to the species should be identified as well...To provide
2333 continuity among the listing package, this section and the recovery criteria, threats that were
2334 listed in the final rule should be addressed in this section and discussed in terms of the five
2335 listing factors. If the species was recently listed, much of this information can be taken from
2336 the “Factors Affecting the Species” section of the listing rule. Plans should assess any new
2337 threats, changes in severity of threats, and threats that have been reduced or removed since
2338 publication of the final listing rule.)”

2339
2340 The ESA defines an “endangered species” as “any species which is in danger of extinction
2341 throughout all or a significant portion of its range” 16 U.S.C 1532(6). Similarly, a
2342 “threatened species” is “any species which is likely to become an endangered species within
2343 the foreseeable future throughout all or a significant portion of its range” 16 U.S.C 1532(20).
2344 A species is listed as threatened or endangered if one or more of the following five factors in
2345 section 4(a)(1) of the ESA are determined to be responsible for its condition (a process
2346 referred to as a 5-factor analysis):

- 2347 (A) the present or threatened destruction, modification, or curtailment of its habitat or
2348 range;
- 2349 (B) overutilization for commercial, recreational, scientific, or educational purposes;
- 2350 (C) disease or predation;

2351 (D) the inadequacy of existing regulatory mechanisms; or,
2352 (E) other natural or manmade factors affecting its continued existence.

2353

2354 Subsequent 5-factor analyses are conducted while a species is listed to periodically assess its
2355 status and ensure that conservation actions are addressing current threats. Finally, a 5-factor
2356 analysis is conducted when a species is proposed for delisting due to recovery to ensure that
2357 none of the factors continue to threaten or endanger the species.

2358

2359 Several 5-factor analyses have been conducted for the Mexican wolf. In the initial proposal
2360 to list the Mexican wolf as endangered in 1975, the Service found that threats from habitat
2361 loss (factor (A)), sport hunting (factor (B)), and inadequate regulatory protection from human
2362 persecution (factor (D)) were responsible for the subspecies' decline and near extinction (40
2363 FR 17590-17591, April 21, 1975). In the 1978 listing of the entire gray wolf species as
2364 endangered throughout the coterminous United States and Mexico (except for Minnesota,
2365 where it was classified as threatened), the Service identified the same threats (43 FR 9607-
2366 9615, March 9, 1978).

2367

2368 In 2003, when the Service reclassified the gray wolf into three distinct population segments,
2369 the agency conducted a 5-factor analysis of the Mexican wolf as a part of the SWDPS (68 FR
2370 15804-15875, April 1, 2003). The reclassification rule stated that habitat destruction or
2371 modification (factor (A)) was not currently considered a threat or deterrent for restoration of
2372 southwestern (Mexican) gray wolves based on the 1982 Mexican Wolf Recovery Plan which
2373 stated that sufficient habitat existed at that time to support current reintroduction objectives.
2374 "Take" for commercial or recreational purposes (factor (B)) was not considered a threat. 16
2375 U.S.C 1532(19). Diseases and parasites (factor (C)), which are known to be an important
2376 consideration in wolf conservation, were not known to be significant factors in the decline of
2377 the Mexican wolf, and there was no reason to believe they would hinder recovery. Illegal
2378 killing ("human predation", considered factor (C) in the rule) was recognized as a factor that
2379 may slow, but not likely preclude, recovery in the Southwest. Regulatory protection of
2380 reintroduced Mexican wolves was deemed adequate (factor (D)). Finally, public attitudes
2381 toward gray wolves were cited as a primary determinant in the long-term recovery status of

2382 wolves (factor (E)), and the rule anticipated that the potential for human-wolf interactions
2383 would increase as the number of wolves increased.

2384

2385 The Mexican Wolf Conservation Assessment (USFWS 2010 add cite) contained an updated 5-
2386 factor analysis specific to the Blue Range population (...summarize findings...). The draft
2387 reclassification....

2388

2389 The following 5-factor analysis identifies current and anticipated threats throughout the entire area
2390 considered potentially suitable recovery habitat for the Mexican wolf (see Geography of Recovery),
2391 thus the geographic scope of this assessment is larger than that in the Conservation Assessment or the
2392 draft rule to reclassify.... When available, information on the source, geographic scope, severity,
2393 frequency, and overall known or perceived magnitude of each threat is provided.

2394

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(This table is a result of team brainstorm at February 2012 meeting; we will continue to revise it...)

Factor A: Habitat Attribute	Stressor	Geographic Scope	Severity / Intensity	Occurrence (Past/present/future; single episode vs. continuous; regular vs. sporadic; likelihood)	Overall Magnitude	Response
Prey Availability / Biomass						
	Forage production					
	Competition between livestock and other prey for forage					
	Spread of non-native vegetation (inedible? lower nutrition?)					
	Change in vegetation due to livestock grazing (inedible? lower nutrition?)					
	Wolf predation					Ungulate mortality
	Ungulate Disease (See Factor C.)					Ungulate mortality; ___ in wolves
Habitat Quantity to Support Core Populations						

	Increasing urbanization					Decreased ability for natural wolf range expansion; decreasing habitat availability over time in areas of low human inhabitation; increased likelihood of wolf-human interactions
	Increasing road density / traffic					Mortality from vehicular collision; behavior modification? (denning, dispersal)
	Quantity of public land					Private lands have a greater potential for human-wolf interactions
	Wildfire					Mortality; prey availability?

	Climate Change					
	Regional Drought Cycles					Mortality? Prey availability?
Habitat Connectivity to Support Migration Between Subpopulations						
	Increasing urbanization in US and Mexico					
	Increasing road density / traffic in US and Mexico					Mortality from vehicular collision during dispersal events; no genetic exchange between subpopulations
	Borderlands activities and infrastructure					
Habitat Quality						
	Increasing urbanization in US and Mexico					Behavior disturbance (
	Regional Drought					

	Cycles					
	Climate Change					
	Wildfire					
Factor B. Overutilization						
Incidental take by FWS and partner agencies	Vaccinations and medical treatment; capture and control actions					Mortality
Factor C. Disease						
Rabies						
	Transmission by domestic canids					Mortality
	Transmission by wild canids or other animals					Mortality
	Lack of labeled vaccines for wolves					
Parvovirus						
	Transmission by domestic canids					Mortality
	Transmission by wild canids or other animals					
Distemper						
	Transmission by domestic canids					
	Transmission by wild canids					

Corona virus						
Chronic wasting disease						Mortality to ungulates;
Predation (on wolf by other predators)	Competition between predators					Mortality
Factor D. Regulatory Mechanisms						
Legislative efforts to delist wolves in UT, AZ, NM	Public opinion					
Illegal / accidental take of Mexican wolves						
	McKittrick policy / difficulty successfully prosecuting offenders					
	Nighttime spotlight hunting					
	Misidentification					
	Lack of law enforcement capacity					
Progress / status of BRWA						

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reintroduction						
	BRWRA Regulations BRWRA boundary, SRZ/PRZ. Removals due to depredations, boundary removals, etc.					
Funding mechanisms to support reintroduction and recovery						
Mechanisms to regulate hybrids						
Mechanisms that reduce forage (repetitive with factor A?)	Competing management regimes stemming from single species management focus (e.g., MSO vs MW?)					
Insufficient 7(a)(1)(A)	Budgetary and staffing constraints of federal agencies					
Management by litigation	Public opinion; lack of policy direction from USFWS (SPR, use of DPS policy, etc).					
Lack of a (binational)	FWS priorities, US-Mexico coordination					

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recovery plan						
Factor E. Other						
Tribal participation in recovery						
	Lack of funding, economic impacts					
	Competing land uses					
	Cultural values					
Stakeholder participation in recovery						
	Inadequate public education					
	Social and economic impacts					
	USFWS intolerance of local communities, culture					
Lack of funding to support recovery implementation						
	Political support					
Interagency coordination to support recovery						

Foothold traps						
Human tolerance						
	Release sites too close to human inhabitation					
	Fear of wolves, negative perceptions of wolves					
	Dislike of federal government					
	Economic impacts of reintroduction					
	Wolf habituation to humans					
Progress of BRWRA						
	Lack of response to 3 year and 5 reviews					
	Depredation and boundary related removals					
	Human-caused mortality (all sources; poisoning, road kill, other)					
	Lack of incentives, funding, resources to support implementation, esp. in local communities to reduce interactions,					

	especially depredation;					
	management of human habituated wolves, aversive conditioning					
	communication with affected parties					
	monitoring of uncollared wolves					
	Lack of trust (of USFWS) due to failure to live up to commitments					
Genetic health						
	Lack of gene flow					
	Hybridization with dogs and coyotes					
	Genetic swamping by northern wolves					
	Low levels of genetic variation, lack of robustness					
	Limited capacity of captive breeding program					
Use of livestock protection collars						

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K. Conservation Efforts

(Note to Reviewer: This section is not intended to be a laundry list of all conservation efforts, rather it is a concise list of those efforts that most contribute to recovery. Due to the specific situation with the Mexican wolf, i.e., that it is contained within the BRWRA, I'm not sure this section is terribly relevant. We may just want to reiterate the reintroduction projects and captive breeding program with some mention of important partners, etc. Perhaps also the Interdiction Council?)

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2416 L. Biological Constraints and Needs

2417 (Note to Reviewer: Recovery planning guidance says, “Based on all of the above, identify
2418 any biological constraints or needs of the species that need to be considered in planning and
2419 management. The purpose of this section is to state up front any known limiting factors that
2420 are biologically inherent in the species and non-modifiable, and which *must be honored* when
2421 designing any management/recovery program for that species. Examples might include
2422 extremely delayed maturity which requires unusually high annual survival in juvenile stages;
2423 needs for a particular and rare habitat for one or another life history stage; or a need for a
2424 minimum population size for successful breeding behavior.”

2425

2426 Perhaps we focus here on the “basic three”, prey, large area, and security from humans?

2427 Whatever constraints we list, this section will not provide new information; rather it will
2428 refer back to where the constraints are initially discussed (probably in the Background or
2429 Threats Assessment) and reemphasize them as critical considerations for the recovery effort.
2430 This section should be just a few pages or less in length.)

2431

2432

2433 *Large Area with Security from Human Exploitation*

2434

2435

2436

2437

2438 *Prey*

2439 Historical data indicate that Mexican wolves preyed extensively on the diminutive Coues
2440 white tailed deer (*Odocoileu virginianuscouesi*) prompting some to suggest that the
2441 subspecies was an ecological or habitat specialist (Brown 1983:6 12). An early assessment of
2442 Mexican wolf ecology was completed by McBride (1980). On the notion that the Mexican
2443 wolf was a habitat specialist fine tuned to the Madrean montane forests, evergreen
2444 woodlands, and adjacent grasslands in Mexico, extreme southeast Arizona, and southwest
2445 New Mexico (Brown 1983:7), McBride (1980:13) wrote: "*While it might appear that wolves*

2446 *are attracted to certain vegetative associations, they are actually responding to the*
2447 *availability of prey."*

2448

2449 Historically Mexican wolves in Mexico probably preyed differentially on Coues white tailed
2450 deer simply because of its relative abundance. Supporting this notion are studies that indicate
2451 that elk (*Cervus elaphus*), the most abundant wild ungulate in the BRWRA, is the primary
2452 prey of Mexican wolves there despite an abundance of mule deer (*Odocoileus hemionus*) and
2453 white-tailed deer (*Odocoileus virginianus*) (Reed et al. 2006, Carrera et al. 2008, Merkle et
2454 al. 2009a). Consequently, this recovery plan is based on the expectation that the Mexican
2455 wolf is an ecological generalist, like all other gray wolf subspecies, and can successfully
2456 subsist on both small and large ungulates. This expectation does not detract from the
2457 Mexican wolf's genetic uniqueness. It is, however, impossible to know if this uniqueness
2458 resulted from selective pressures brought about by the specific ecological conditions of the
2459 southwestern US and Mexico or a result of random genetic drift that attends any sexually
2460 reproducing organism.

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M. Tribal Perspectives on Mexican Wolf Recovery

2464 (Note to Reviewer: This subsection under development by Tribal Subgroup, 6-2012.)

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N. Binational Coordination for Mexican Wolf Recovery

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2470 (Note to Reviewer: The 3 paragraphs below were developed by the 2002 DPS team; perhaps
2471 they can serve as a model for us? Also, Carlos has drafted some text that for now I placed in
2472 Section III Recovery Actions as a placeholder to develop a US-Mexico MOU.)

2473

2474 “Despite their independent authorities, the two countries are similar in many ways regarding
2475 gray wolf conservation. Both have legal frameworks for recovery: Mexico’s Ley General de
2476 Vida Silvestre (2000), NOM-059-ECOL-2001 (2002) and the Endangered Species Act of
2477 1983. Both countries have developed recovery plans for the Mexican wolf – Mexico’s
2478 Programa de Recuperacion del Lobo Mexicano was published in 1999; the United States’
2479 Mexican Wolf Recovery Plan was published in 1982, and was co-signed by Mexico’s
2480 Direccion General de Vida de la Fauna Silvestre. In both countries, Federal agencies lead the
2481 recovery efforts: Mexico’s Direccion General de Vida Silvestre (DGVS) and the U.S. Fish
2482 and Wildlife Service. Both countries have comparable advisory committees for recovery:
2483 Mexico’s Subcomite Technico Consultivo Nacional para la Recuperacion del Lobo
2484 Mexicano (STCN-RLM); the Service’s Mexican wolf recovery team. In both countries, the
2485 parties interested in and affected by wolf recovery actions include State and local
2486 governments, as well as nongovernmental organizations and private property owners.

2487

2488 There are, however, significant differences between Mexico and the United States in
2489 approaches and limitations to Mexican wolf recovery. The listed entity in Mexico is the
2490 subspecies, *Canis lupus baileyi*; it is listed as extinct in the wild. In the United States, the
2491 gray wolf species, *Canis lupus*, is listed [UPDATE as necessary], with a suggested focus on
2492 the subspecies. Mexico’s red list of endangered species (NOM-059-ECOL-2001) has down-
2493 listing criteria that apply to broad categories of species, one of which includes the Mexican
2494 wolf. The United States’ recovery plan does not include downlisting or delisting criteria
2495 [UPDATE!]. Once a Federal recovery plan has been approved, Mexico has fewer legal
2496 mechanisms by which non-federal entities can constrain or advocate implementation of
2497 recovery actions than does the United States.

2498

2499 Clearly, the SWDPS Recovery Plan, when approved, will have legal standing in guiding
2500 recovery actions in the United States. It may also provide recommendations useful to
2501 recovery efforts in Mexico. Thus, the recovery plan can be an invaluable resource for
2502 complementary efforts in Mexico. However, Mexico is singularly responsible for enacting
2503 and implementing recovery regulations, plans, and approaches in Mexico. Its authorities and
2504 decisions are not subject to U.S. approval. Conversely, the recovery program in Mexico in
2505 terms of law, policy, and activity may provide insights for and be useful to complementary
2506 efforts in the United States, but decision made by Mexico for Mexico are not binding on the
2507 United States. Also, by necessity and force of law, each country must respect the other's
2508 independent authority for law enforcement, i.e., Mexico cannot address law enforcement
2509 within the MOU proposed below" (excerpted from a white paper drafted by members of the
2510 2003 SWDPS recovery team)

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2514 **II. RECOVERY STRATEGY, GOALS, OBJECTIVES, AND CRITERIA**

2515 (Note to Reviewer:)

2516

2517 **A. Recovery Strategy**

2518 The ultimate goal of this Recovery Plan is to recover the Mexican wolf so that
2519 protections afforded by the ESA are no longer necessary, thus allowing for delisting. The
2520 objectives of the Recovery Plan describe a scenario in which the Mexican wolf's
2521 population is stable or increasing, well distributed, and affected only by manageable
2522 threats. This Recovery Plan was developed using the best scientific information available
2523 and a "step-down" approach of objectives, criteria, and actions. As part of this approach,
2524 we have developed a state-of-the-science modeling framework that can provide
2525 information for numerous Mexican wolf recovery actions and management decisions.
2526 This modeling effort is described in detail in Appendix [].

2527

2528 Recovery criteria are specific statements that describe the conditions under which the
2529 Service would consider the Mexican wolf to be recovered. Recovery criteria aim to
2530 establish wild, self-sustaining populations of Mexican wolves which show attributes that
2531 demonstrate that threats have been ameliorated and, consequently, serve as objective,
2532 measurable guidelines to assist in determining when an endangered species has
2533 recovered to the point that it may be downlisted to threatened, or that the protections
2534 afforded by the ESA are no longer necessary and the species may be delisted. Recovery
2535 actions are those activities that are needed to accomplish the recovery criteria by
2536 addressing the specific threats that threaten or endanger the Mexican wolf.
2537 Implementation of the full suite of recovery actions to achieve this will involve
2538 participation from the States, Federal agencies, non-federal landowners, and the public.

2539

2540 Currently the most important biological threats to the Mexican wolf are 1) excessive
2541 mortality due to human-associated factors, 2) overall small population size due to the
2542 existence of only one wild population, that is itself small and exhibits a low rate of
2543 growth, and 3) continuing loss of genetic diversity in both the captive and wild
2544 populations. To address these threats, a successful recovery strategy must:

- 2545 1. Manage the captive population to produce reintroduction stock with an optimal
2546 genetic composition and prospects for survival in the wild;
2547 2. Reduce mortality of wild wolves so that multiple populations restored via
2548 reintroductions can quickly grow to a sufficient size and persist with minimal
2549 management to minimize further loss of genetic diversity;
2550 3. Maintain habitat connectivity to ensure that these restored populations are effectively
2551 connected by dispersing wolves.

2552

2553 **B. Recovery Goals, Objectives and Criteria**

2554

2555 **Recovery Goals**

2556 The goal of the Mexican wolf recovery plan is to improve the status of the species so it
2557 can be removed from protection under the ESA (i.e., delist the species). The interim goal
2558 is to downlist the Mexican wolf to threatened status under the ESA. This recovery plan
2559 was developed using the best scientific information available and a “step-down”
2560 approach of objectives, criteria, and actions. As part of this approach we developed a
2561 state-of-the-art modeling framework that provided insight into numerous recovery
2562 actions and related management options.

2563

2564 **Recovery Objectives**

2565 The objectives of this recovery plan are:

- 2566 1. To establish a sufficient number of Mexican wolf populations that each are
2567 sufficiently large and distributed such that the subspecies no longer requires listing under
2568 the ESA; and
2569
2570 2. To ensure that threats have been reduced or eliminated such that the requisite
2571 Mexican wolf populations are stable or increasing.

2572

2573 **Recovery Criteria**

2574 There are five recovery criteria in this recovery plan that are discussed below. Recovery
2575 criteria are achievable targets that we believe can result from implementation of the

2576 recovery actions in this recovery plan. Recovery criteria serve as objective, measurable
2577 guidelines to assist in determining when an endangered species has recovered to the point
2578 that it may be downlisted to threatened, or that the protections afforded by the ESA are no
2579 longer necessary and the species may be delisted. Achievement of these criteria will take
2580 time and is intended to be measured over the life of the plan, not on a short-term basis.
2581 Consequently, recovery criteria should not simply be considered near-term
2582 recommendations. The recovery criteria in this recovery plan represent the best
2583 assessment of the conditions that should result in a determination that delisting the
2584 Mexican wolf is warranted. Once the criteria are achieved the Service should complete a
2585 formal regulatory rule-making process to delist the species.

2586

2587 **Recovery Actions**

2588 Recovery actions are activities (both field-based and administrative) that need to be
2589 implemented to achieve Mexican wolf recovery. Based on the statutory criteria for
2590 determining whether a species should be listed [16 U.S.C. § 1533(a)(1)], not all recovery
2591 actions need to be implemented for the Service to consider initiating the delisting
2592 process. A change in status (downlisting or delisting) requires a separate rule-making
2593 process based on an analysis of the same five factors (referred to as the listing factors)
2594 considered in the listing of a species, as described in section 4(a)(1) of the ESA. These
2595 include:

2596

- 2597 A. The present or threatened destruction, modification, or curtailment of its habitat or range;
- 2598 B. Overutilization for commercial, recreational, scientific, or educational purposes;
- 2599 C. Disease or predation;
- 2600 D. The inadequacy of existing regulatory mechanisms; and
- 2601 E. Other natural or manmade factors affecting its continued existence.

2602

2603 **3.1 Reclassification to Threatened Under the ESA (downlisted)**

2604 The Mexican wolf can be reclassified to threatened when the following two criteria are met:

2605 **Criterion 1 – Adequate population size for a sufficient period of time:** Three populations,
2606 with a census population of ≥ 100 wolves each, have simultaneously been maintained in the
2607 wild for 8 successive years (2 successive generations).

2608

2609 **Criterion 2 – Stable or increasing population trend:** The trend for each of the three
2610 populations has been stable or increasing over 8 years (2 generations), as measured by a
2611 statistically reliable monitoring effort.

2612

2613

2614 **3.2 Reclassification to Unprotected Under the ESA (delisted)**

2615 The Mexican wolf can be delisted when the following five criteria are met:

2616

2617 **Criterion 1 – Adequate Population Size for a Sufficient Period of Time:**

2618 Option 1: A metapopulation of ≥ 850 wolves distributed among 4 populations in the wild that
2619 have simultaneously persisted for 8 successive years (2 successive generations) at or above the
2620 following sizes: three primary core populations with a census population of ≥ 200 wolves each
2621 and a total population size of at least 750 wolves, and a secondary core population with a census
2622 population of ≥ 100 wolves.

2623

2624 Option 2: A metapopulation of ≥ 750 wolves distributed among 3 populations in the wild that
2625 have simultaneously persisted for 8 successive years (2 successive generations) with a census
2626 population of ≥ 200 wolves each. Wolves in excess of the minimum number required for the 3
2627 populations must occur as part of one or more of the 3 populations.

2628

2629 Option 3: A metapopulation of ≥ 750 wolves distributed among 3 populations in the wild that
2630 have simultaneously persisted for 8 successive years (2 successive generations) with a census
2631 population of ≥ 250 wolves each.

2632

2633 **Criterion 2 – Adequate Population Connectivity:** Immigration into each of the 3 populations
2634 via natural dispersal at a rate not less than 0.5 genetically effective migrants per generation (4
2635 years), averaged over a period of 2 successive generations (8 successive years), as measured by

2636 a statistically reliable monitoring effort. If the metapopulation includes ≥ 850 wolves then
2637 immigration into one of the 3 populations may be less than 0.5 genetically effective migrants
2638 per generation.

2639

2640 **Criterion 3 – Stable Population Trend:** The overall population trend of Mexican wolves
2641 throughout the range is stable or increasing over 8 years, as measured by a statistically reliable
2642 monitoring effort.

2643

2644 **Criterion 4 – Post-delisting Monitoring:** To monitor the continued stability of the recovered
2645 Mexican wolf, a post-delisting monitoring plan has been developed and is ready for
2646 implementation within the States of Arizona, Colorado, New Mexico, and Utah, as required in
2647 section 4(g)(1) of the ESA.

2648

2649 **Criterion 5 - Regulatory Mechanisms:** State management plans and adequate post-
2650 delisting regulatory protection are available.

2651

2652 * A "wolf population" is defined as a group of wolf packs that are relatively spatially
2653 contiguous and demographically connected by typical dispersal events, and are relatively
2654 spatially and demographically disjunct from other wolf populations, except for long distance
2655 dispersal events as specified above.

2656

2657 **3.3 Justification for Recovery Criteria**

2658 This section explains the rationale for the recovery criteria.

2659

2660 **Guiding Principles for Mexican Wolf Recovery**

2661 To identify appropriate criteria for recovery of the Mexican wolf, the Service used four
2662 Biological Indicators (abundance, redundancy, connectivity, and trend) and six “Guiding
2663 Principles” to help ensure recovery of Mexican wolf.

2664

2665 ***Four Biological Indicators***

2666

- 2667 1. Abundance
2668
2669 2. Redundancy
2670
2671 3. Connectivity
2672
2673 4. Trend
2674

2675 ***Six Guiding Principles:***

- 2676
2677 1. Ensure sufficient abundance and trend indices to support population viability;
2678
2679 2. Ensure sufficient redundancy in populations;
2680
2681 3. Ensure sufficient connectivity among populations;
2682
2683 4. Ensure distribution of populations across representative habitats;
2684
2685 5. Ensure future adaptive potential by reducing the loss of genetic diversity.
2686
2687 6. Consider and accommodate uncertainty arising from climate change, disease,
2688 environmental stochasticity, and other factors;

2689
2690

2691 **Rationale for Delisting Criteria**

2692 Four categories of threats compromise the future of the Mexican wolf: reduced
2693 genetic diversity (due to inbreeding and genetic drift), demographic viability,
2694 environmental stochasticity, and catastrophes (disease outbreaks, etc.). Loss of genetic
2695 diversity is an inevitable consequence of small finite population size for any sexually
2696 reproducing organism like the Mexican wolf. However, if small, relatively genetically
2697 compromised populations are connected by immigration, the genetic diversity

2698 maintained by the meta-population approaches that of one population as large as the sum
2699 of the connected populations. Thus, sufficient connectivity among Mexican wolf
2700 populations can help maintain genetic diversity, the viability of each of the small
2701 populations, and the long-term adaptive potential of the subspecies. Genetic threats are
2702 greater for the Mexican wolf than for other wolf subspecies because only 7 wolves were
2703 available as founders for the captive population which is the source of all Mexican
2704 wolves alive today. Effects of demographic viability and environmental stochasticity
2705 on population persistence also generally diminish as the size and connectivity of
2706 populations within a metapopulation increases.

2707 Loss of genetic diversity, due to the pronounced population bottleneck that the
2708 Mexican wolf experienced, is a function of both small population size and the length of
2709 time that the population remains at a small size. Thus recovery criteria and associated
2710 recovery actions that are projected to result in rapid population growth and expeditious
2711 recovery are strongly preferred over those that would require more time. For example,
2712 an area that could support a core population under current habitat conditions should be
2713 strongly favored over an area that would require time consuming habitat restoration.
2714 Reintroductions projects should be designed to effect rapid population growth. A tepid
2715 or modest approach to population restoration will not serve Mexican wolf recovery well.

2716 Environmental stochasticity generated by variation in environmental conditions
2717 (e.g., drought, fire, prey fluctuations) and catastrophes (episodic threats like disease
2718 outbreaks) challenge wild populations of most species, including wolves. In the case of
2719 the Mexican wolf, these “background” threats are especially problematic because of the
2720 subspecies’ eroded genetic diversity which has and will continue to compromise its
2721 adaptive potential. If a wolf population experienced no unfavorable variation in
2722 environmental conditions or disease occurrence, a small, genetically compromised
2723 population would probably be able to persist with greater certainty. Conversely, if the
2724 wolf population was genetically robust then it would have sufficient resilience (greater
2725 adaptive potential) to withstand the impact of these background threats. To achieve the
2726 same level of resiliency, a population derived from inbred and interrelated founders must
2727 be larger than a population derived from outbred and unrelated individuals, in order to

2728 avoid the genetic damage that occurs in a small inbred population during demographic
2729 downturns associated with background threats.

2730 We used the 3-stage modeling framework to evaluate what level of population
2731 size, abundance, persistence, and connectivity are necessary for the Mexican wolf to be
2732 likely able to withstand the threats described above in the presence of minimal
2733 management. The criteria detailed below are appropriate because they serve as effective
2734 redress of the general threats that compromise the Mexican wolf's future in a manner
2735 that ensures that the subspecies no longer fits the ESA's definition of threatened or
2736 endangered. Restoration of smaller populations than those recommended below would
2737 be too small to withstand threats unique to each with a sufficient degree of certainty, and
2738 would also result in a metapopulation with an insufficient level of connectivity to
2739 withstand threats common to all. The several components of the recovery criteria are
2740 thus interrelated and mutually supporting in ensuring recovery of the Mexican wolf in a
2741 manner that comports with the spirit and intent of the ESA.

2742
2743 **Criterion 1 – Adequate Population Size for a Sufficient Period of Time.** A
2744 metapopulation size of 750 wolves distributed among three populations \geq of 200 wolves
2745 each that have simultaneously persisted for 8 successive years (2 generations), is
2746 considered highly robust to threats from environmental stochasticity as well as
2747 inbreeding and demographic stochasticity (see Modeling Appendix). Populations of this
2748 size and base persistence (i.e. 8 successive years), when connected within a
2749 metapopulation, are resistant to threats to viability arising from loss of genetic variation.
2750 Three populations are designated because 1) this number allows a metapopulation of
2751 sufficient size and maximizes redundancy given the configuration of suitable habitat; and
2752 2) arrangement of the three populations facilitates natural dispersal among populations
2753 and thus retention of genetic variability. Any secondary core population(s) would help to
2754 ensure distribution of populations across representative habitats. Two generations (8
2755 successive years) was designated because it is a meaningful biological period of time
2756 that is of sufficient duration to allow reliability in trend data that would indicate that
2757 threats to population persistence have been reduced. Underlying these conclusions are

2758 several themes emerging from the results of the 3-stage modeling framework (see
2759 Modeling Appendix):
2760 1) Multiple large populations are necessary for Mexican wolf recovery.
2761 2) Smaller secondary core populations, with the possible exception of the Sonora-Sky
2762 Island population, will likely contribute minimally to sustaining a viable regional wolf
2763 metapopulation.
2764 3) Due to its poor genetic composition, the Blue Range population (BRP) in isolation
2765 underperforms the other two requisite populations. However, when three populations are
2766 present, the BRP's central location allows it to receive dispersal from the two other
2767 populations, making its performance comparable to theirs.

2768
2769 The criterion for metapopulation size (750) is larger than the numeric recovery criterion
2770 for the Northern Rocky Mountains (450 wolves) and smaller than that for wolves in the
2771 Great Lakes states (1,350 to 1,450 wolves). The extent of genetic threats to Mexican
2772 wolves make recovery for this subspecies qualitatively different than for recovery of the
2773 metapopulation in the Northern Rocky Mountains that was established from outbred,
2774 unrelated individuals translocated from two disparate and naturally populations in
2775 Canada. Concerning the Great Lakes states, wolves there also were genetically diverse
2776 having arose from a large historic population that extended into Canada. Additionally,
2777 the extant population in the region included about 1,000 wolves at the time it was listed
2778 under the ESA. Recovery criteria were, therefore, developed that called for at least a
2779 modest increase in population size (35% to 45%).

2780
2781 **Criterion 2 – Adequate Population Connectivity.** A rate of natural dispersal, between
2782 three populations of the size specified above, of 0.5 genetically effective migrants per
2783 generation, is sufficient to alleviate threats to viability arising from loss of genetic
2784 variation. This rate of natural dispersal was also feasible given rates observed in other
2785 regions, and taking into account the lower levels of habitat connectivity evident between
2786 the three core areas of suitable habitat in the US portion of the recommended Mexican
2787 wolf recovery region.

2788

2789 **Recovery Criterion 3 – Stable Population Trend.** A stable or increasing population trend
2790 over 8 successive years (2 generations) supports the conclusion that threats have been
2791 adequately alleviated.

2792

2793 **Recovery Criterion 4 – Post-delisting Monitoring.** Continued population monitoring is
2794 necessary to ensure that the subspecies does not again fall to threatened or endangered
2795 status.

2796

2797 **Recovery Criterion 5 - Regulatory Mechanisms:** Adequate state management plans
2798 and other regulatory protection indicate that threats arising from inadequacy of regulatory
2799 mechanisms have been remedied.

2800

2801 **Rationale for Downlisting Criteria**

2802

2803 **Recovery Criterion 1 – Adequate Population Size.** The establishment of three primary
2804 core populations of 100 individuals each indicate reduction in threats to viability arising
2805 from loss of genetic variation and other factors.

2806

2807 **Recovery Criterion 2 – Stable Population Trend.** A stable or increasing population trend
2808 over 8 successive years (2 successive generations) supports the conclusion that threats to
2809 population persistence have been reduced.

2810

2811 **Modeling Approach**

2812

2813 Several modeling tools are available to inform development of recovery criteria based on
2814 best available science. It is important to acknowledge the strengths and weaknesses of
2815 each type of model and to consider information from multiple models in an appropriate
2816 decision-support context. We employed state-of-the-art modeling tools in a multi-step
2817 analysis for evaluating alternative recovery criteria. Collectively, these modeling tools
2818 allow comparison of estimated population viability (probability of population recovery)

2819 and distribution among alternative recovery scenarios under a variety of potential
2820 conditions. The modeling approach consisted of three main steps:

2821

2822 **Step 1 Population Simulation Model** - Because of the magnitude of genetic threats to
2823 the Mexican wolf, we selected a population simulation model (Vortex; Lacy et al. 2010)
2824 with the capability to explore how genetic threat factors vary with population size,
2825 population growth rate, and metapopulation structure. This informs development of
2826 criteria for the size, number, and connectivity of subpopulations required to reduce the
2827 loss of genetic diversity to ensure the Mexican wolf's long-term adaptive potential.

2828

2829 **Step 2 Habitat-based Model** – The Vortex model lacks sophisticated treatment of
2830 spatial dynamics or habitat. Once Step 1 of criteria development was is completed, a
2831 second stage of the process was used to determined where on the landscape the requisite
2832 populations could be restored given the distribution of suitable habitat. Information
2833 sources for this step in modeling included results from a spatially-explicit population
2834 model (PATCH; Carroll et al. 2006).

2835

2836 **Step 3 Connectivity Model** - The Vortex analysis suggested that population
2837 connectivity was especially beneficial for persistence in Mexican wolves due the
2838 subspecies being derived from inbred and interrelated founders. We therefore examined
2839 what rate of natural dispersal between primary core populations was sufficient for
2840 population persistence and could be achieved give the distribution of suitable habitat. We
2841 did this by relating observed connectivity rates in other regions to relative habitat
2842 connectivity between primary core populations in those regions, and extrapolating to
2843 evaluate rates expected given habitat connectivity between potential primary core
2844 populations of Mexican wolves.

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III. RECOVERY PROGRAM

(Note to Reviewer:)

A. Recovery Action Outline

Recovery actions are near-term recommendations to guide the activities needed to accomplish the recovery objectives and achieve the recovery criteria. This Recovery Plan presents [] actions that address overall recovery. These actions are organized following the five listing factors described earlier.

A. The present or threatened destruction, modification, or curtailment of its habitat or range;

B. Overutilization for commercial, recreational, scientific, or educational purposes;

C. Disease or predation;

D. The inadequacy of existing regulatory mechanisms; and

E. Other natural or manmade factors affecting its continued existence

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B. Recovery Narrative

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C. Threats Tracking Table

This table demonstrates how the recovery criteria and/or recovery actions ameliorate threats to the Mexican wolf.

Factor	Threat	Criteria	Recovery Action	

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2898 IV. IMPLEMENTATION SCHEDULE
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V. LITERATURE CITED

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4497 **APPENDIX A. GLOSSARY AND LIST OF ABBREVIATIONS**

4498	3-Year Review	Mexican Wolf Recovery: Three Year Program Review and Assessment
4499		
4500	5-Year Review	Mexican Wolf Blue Range Reintroduction Project 5-Year Review
4501		
4502	AGFD	Arizona Game and Fish Department
4503	AMOC	Adaptive Management Oversight Committee
4504	AMOC and IFT	Adaptive Management Oversight Committee and
4505		Interagency Field Team, commonly used as a literature citation
4506		referencing these committees as authors of sections of the 5-
4507		Year Review, including the Technical Component (TC),
4508		Administrative Component (AC), or AMOC Recommendations
4509		Component (ARC)
4510	AMWG	Adaptive Management Working Group
4511	APA	Administrative Procedures Act of 1946
4512	AZA	Association of Zoos and Aquariums
4513	Blue Range population	Wolves in the BRWRA, FAIR, and surrounding areas
4514	BRWRA	Blue Range Wolf Recovery Area, as designated by the Final
4515		Rule (50 CFR 17.84(k))
4516	DPS	Distinct Population Segment
4517	EIS	Environmental Impact Statement
4518	ESA	Endangered Species Act of 1973, as amended
4519	FAIR	Fort Apache Indian Reservation of the White Mountain Apache
4520		Tribe
4521	FEIS	Final Environmental Impact Statement of 1996 (for proposed
4522		reintroduction of Mexican wolves)
4523	Final Rule	Final “nonessential experimental population” or “10(j)” rule of
4524		1998 for Mexican wolf reintroduction in Arizona and New
4525		Mexico, 50 CFR 17.84(k)
4526	Great Lakes	USFWS gray wolf recovery program administered out of the
4527		Great Lakes, Big Rivers Region (Region 3)
4528	IFT	Interagency Field Team (for the Reintroduction Project, see
4529		below)
4530	MVP	Minimum Viable Population
4531	MWEPA	Mexican Wolf Experimental Population Area
4532	NEPA	National Environmental Policy Act of 1969
4533	NMDGF	New Mexico Department of Game and Fish
4534	Northern Rockies	USFWS gray wolf recovery program administered out of the
4535		Mountain-Prairie Region (Region 6) and Pacific Region
4536		(Region 1)
4537	PVA	Population Viability Analysis
4538	SOP	Standard Operating Procedure for the Reintroduction Project
4539	SSP	Species Survival Program
4540	SWDPS	Southwestern Gray Wolf Distinct Population Segment

4541	SWDPS Recovery Team	Southwestern Gray Wolf Distinct Population Segment (with
4542		emphasis on the Mexican gray wolf, <i>Canis lupus baileyi</i>)
4543		Recovery Team
4544	USDA-WS	US Department of Agriculture-Animal Plant Health Inspection
4545		Service, Wildlife Services
4546	USFWS or Service	US Fish and Wildlife Service
4547	USFS	USDA Forest Service
4548	WMAT	White Mountain Apache Tribe
4549		

DRAFT

Appendix 1. Modeling and analysis procedures used to evaluate recovery criteria for the Mexican wolf

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I. INTRODUCTION

This document provides a description of the modeling process used by the U.S. Fish and Wildlife Service (Service) to identify and evaluate appropriate recovery criteria for the Mexican wolf (*Canis lupus baileyi*). We consistently based our evaluations on the best scientific information available, while acknowledging that this information is incomplete. We do our best to recognize and articulate uncertainties, and the relative strength of evidence for information versus our use of professional judgment or other sources of information for making recommendations. The approach we have adopted makes use of the best available quantitative modeling tools, and is designed to be thorough, transparent, and repeatable.

Our criteria development process began with the statutory definition of recovery, which is aimed at ameliorating threats to an extent that the species no longer requires listing under the ESA. This would occur at the point at which Mexican wolf populations are stable or increasing and distributed such that the Mexican wolf is unlikely to become threatened again in the foreseeable future. Based on this definition, as well as precedent set by other recovery plans and principles from the field of conservation biology, we developed a set of Guiding Principles that generally identified what is essential for recovering the Mexican wolf.

Recovery criteria should be objective and measurable, and comprehensively address all aspects of the definitions of endangered and threatened species contained in the Endangered Species Act (ESA). To identify appropriate criteria for recovery of the Mexican wolf, the Service used four Biological Indicators (abundance, redundancy, connectivity, and trend) and six Guiding Principles:

1. Ensure sufficient abundance and trend indices to support population viability;
2. Ensure sufficient redundancy in populations;
3. Ensure sufficient connectivity among populations;
4. Ensure distribution of populations across representative habitats;
5. Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, demographic stochasticity, and other factors;
6. Conserve genetic diversity and adaptive potential.

II. JUSTIFICATION FOR GUIDING PRINCIPLES

A. THE THREE RS: RESILIENCY, REDUNDANCY AND REPRESENTATION

Guiding Principles:

Ensure sufficient redundancy in populations;

Ensure distribution of populations across representative habitats;

Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, and other factors.

The conservation principles of resiliency, redundancy and representation (the ‘3R’ criteria) developed by Shaffer and Stein (2000) are widely applied in recovery planning (USFWS 2009, 2011). In essence, the 3R framework states that, to be considered recovered, a species should be present in many large populations arrayed across a range of ecological settings. The 3R framework parallels the intent of the ESA in that it links the concepts of geography and viability by combining protection of representative examples of ecosystem types or species’ populations with two additional factors typically associated with population viability. First, resiliency may be associated with factors such as population size that describe a single subpopulation and its ability to persist (Shaffer & Stein 2000). Second, redundancy of such subpopulations in a metapopulation enhances the viability of each and provides a margin of safety for the species (DenBoer 1968).

The concept of redundancy acknowledges that demographic persistence is enhanced by creation of a metapopulation, in which multiple subpopulations are linked by dispersal. This is in part due to “spreading of risk”, since episodic threats such as disease outbreaks may not affect all subpopulations simultaneously (DenBoer 1968). A comprehensive set of demographic recovery criteria should include criteria on the size of individual subpopulations, the number of subpopulations, and the degree of metapopulation connectivity. The status of two populations of the same size would differ if one was stable while the other was declining. Demographic recovery criteria should thus specify both the required state or status and trend over time in population size and demographic rates.

Recovery criteria that explicitly address the geographic distribution of recovered populations should also typically be present in recovery plans. For example, the recently revised Recovery Plan for the Northern Spotted Owl (*Strix occidentalis caurina*) requires demographically stable populations in each of eleven recovery units (USFWS 2011). Such criteria help fulfill the ESA’s mandate (contained in the preamble of the Act) to conserve the ecosystems on which species depend. Fulfillment of geographic criteria promotes recovery of ecological-effective populations (Soule et al. 2005), and help increase resilience of populations to climate change (Carroll et al. 2010).

Geographic criteria are complementary to genetic and demographic criteria in that a species that meets geographic criteria is also more likely to be considered recovered in terms of the other types of criteria (Carroll et al. 2010). Conservation planners have frequently proposed representation as an important complement to viability-related goals because it allows consideration of biological diversity at multiple scales (e.g., populations, ecotypes, and species)(Shaffer & Stein 2000).

B. POPULATION VIABILITY ANALYSIS (PVA) AS A TOOL FOR ADDRESSING RESILIENCY AND REDUNDANCY IN RECOVERY PLANNING

Guiding principles:

Ensure sufficient abundance and trend indices to support population viability;

Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, demographic stochasticity, and other factors.

Recovery criteria appropriately focus on addressing factors that affect the demographic status and trends of the population (Caughley 1994) and its geographic distribution. In terms of population status, recovery criteria are typically expressed as the population size necessary to increase probability of persistence (reduces probability of extinction) to acceptable levels (expressed as <x% probability of extinction over x years). A population viability analysis (PVA) model may be used to evaluate alternative criteria in terms of their implications for population persistence. Even if expressed in terms of results from PVA models, such criteria can be seen as implicitly threat-based. The Service has concluded that “PVA should not be viewed as a replacement for criteria based on threats, but as a supplement to them. The criteria describe the conditions under which it is anticipated the PVA would indicate long-term viability” (Interim Recovery Guidance 5.1:18).

Scientific peer reviewers of previous wolf conservation plans (e.g., Washington state; WDFW 2010) have characterized the role of PVA as “an analytical tool that can be used proactively to evaluate how various management options affect the likely persistence of a species and understand what aspects of a population are critical to its growth...PVA cannot be used to make precise estimates of wolf sustainability...but PVA definitely can and should be used to evaluate the relative likelihood that recovery targets will produce self-sustaining wolf populations” (Fuller et al. 2010). Based on these and other published recommendations, we concluded that a rigorous PVA was essential for developing recovery criteria for the Mexican wolf.

Lambda, a measure of population growth rate, is the amount that the population must be multiplied by to give the population size in the next year. A population with lambda of 1 is stable. Long-term studies of the wolf metapopulation in the Northern Rocky Mountains suggest that both central Idaho and Yellowstone populations have shown lambdas significantly

exceeding 1 (Smith et al. 2010). In contrast, at least until 2009, demographic rates from the Blue Range population suggest a lambda below 1, characteristic of a population that would decline in the absence of supplementation (Oakleaf et al. in prep.).

Deterministic lambda can be estimated using simple models. If deterministic factors are favorable (lambda exceeds 1), a population has the potential for a stable or increasing trend, and more complex PVA models become useful in evaluating additional stochastic threats that may further limit growth of small populations. If deterministic lambda exceeds 1, a population may show high probability of persistence if a) lambda sufficiently exceeds 1 in normal years that it can recover from stochastic factors such as disease outbreaks; and b) population size and metapopulation connectivity are sufficient to mitigate threats related to low levels of genetic diversity.

To illustrate the context of the PVA, we present a conceptual diagram of the influence of demographic and genetic factors on viability (Figure 1). For a population to fall within the ‘zone of viability’ both demographic and genetic threats must be mitigated. Currently, Northern Rocky Mountains (NRM) wolf populations fall largely within that zone. The small and semi-isolated Swedish wolf population is an example of a population with favorable levels of deterministic demographic threats (low mortality and abundant prey), but which is threatened by genetic factors. The Blue Range Mexican wolf population has historically fallen outside the zone of viability due to both low genetic diversity and deterministic threats to demographic viability. Recovery actions must be designed to move the population towards viability on both threat axes. Progress on a single axis (e.g., reducing mortality rates) is not in itself sufficient to achieve long-term viability.

C. DEVELOPING CRITERIA FOR METAPOPOPULATION CONNECTIVITY

Guiding Principle: Ensure sufficient connectivity among populations.

The ESA requires that recovery plans define objective and measurable recovery criteria that comprehensively address the threats that led to listing of the taxa as threatened or endangered. The three fundamental processes of a population are reproduction, mortality, and dispersal. To be considered self-sustaining, a recovered population should be able to perform these fundamental processes without the direct assistance of humans. For example, one could not consider a population to be recovered if it required the regular addition of individuals from a captive population to offset either low recruitment or survival in the wild. For the same reason, a population would not be considered recovered if it did not exhibit critical levels of natural dispersal.

Wolves are able to travel and disperse more widely than most terrestrial mammals. Natal dispersal averages 100 km (Boyd and Pletscher 1999). Numerous long-distance dispersal events (greater than 800 km) have been recorded (Boyd and Pletscher 1999). Two recent long-distance dispersal events from the NRM metapopulation demonstrate the potential for restoring natural population connectivity in the western U.S. In 2010, a female wolf from Yellowstone (341F) dispersed over 1,000 km to Colorado. In 2011, a male wolf from eastern Oregon (OR7) dispersed over 900 km to California.

Unexploited wolf populations typically show a considerable degree of genetic and demographic connectivity (Wayne and Hedrick 2011). Wolves were historically present throughout their range in the contiguous 48 states as a largely continuous population with some degree of genetic isolation-by-distance (i.e. increasing genetic difference with increasing geographical distance) and additional heterogeneity reflecting specific ecological factors (Carmichael et al. 2007, Musiani et al. 2007, Muñoz-Fuentes et al. 2009). However, due to loss of suitable habitat, human intolerance, and other factors, wolf distribution in most areas of the contiguous 48 states (i.e. outside of Alaska), even after delisting, is likely to consist of subpopulations which are relatively small when compared to historic population sizes (which have been estimated at 380,000; Leonard et al. 2005). As has been discussed in relevant wolf recovery plans and conservation documents for the NRM region (e.g., FWS 1994), connectivity among these subpopulations is necessary to alleviate genetic and demographic threats posed by small population size. Considering the natural genetic population structure of gray wolves and their distributional range in the recent past, it follows that recovery must be secured by ensuring connectivity at the metapopulation level. Population connectivity is thus a necessary component of criteria for recovery and delisting of the Mexican wolf.

For subpopulations to benefit from the genetic diversity of the larger metapopulation, they must be linked via 'genetically-effective' dispersal, which can be specified as the number of effective migrants (those migrants that survive to produce offspring in the recipient population) per generation. The ratio between genetically effective migrants and the total (census) number of migrants may be similar to the N_e/N ratio, but it is also possible that the two ratios differ. Therefore direct assessment of genetically effective migrants (vonHoldt et al. 2010) is preferable to indirect methods based on total number of migrants. To facilitate development of objective and measurable connectivity criteria, we developed methods for using the Vortex model to evaluate alternate recovery criteria expressed in terms of the number of genetically effective migrants.

Because of the wolf's dispersal ability, achieving adequate connectivity via natural dispersal (rather than artificial translocation) is relatively feasible in wolf metapopulations. VonHoldt et al. (2010) documented a minimum estimate of 5.4 effective migrants per generation (over the metapopulation as a whole) in the NRM, and concluded that sufficient gene flow from natural dispersal was occurring to counteract the loss of future genetic variation within populations

because of drift. The vonHoldt et al. (2010) study covered approximately 2.4 wolf generations from 1995 through 2004 when the NRM region contained between 101 and 846 wolves. The study documented 1 genetically effective natural dispersal from Central Idaho into the Greater Yellowstone population for an average effective migration rate of 0.42 migrants per generation, lower than that into either of the two other NRM wolf populations (0.83 migrants each per generation for Central Idaho and Northwest Montana). However, the migration rates documented in vonHoldt et al. (2010) represent minimum estimates recorded over a period in which the metapopulation size grew by 800%.

Achieving natural population connectivity for Mexican wolves does not require expensive habitat restoration measures, but rather management to sustain survival of dispersers. Mitigation of threat factors (e.g., overexploitation) to a level sufficient to allow natural dispersal between populations will also help achieve additional recovery goals. Recovery of metapopulations that are large enough to ensure long-term genetic potential may also help achieve goals for recovery of ecologically effective populations, consistent with the Endangered Species Act's mandate to restore self-sustaining wild populations of species and the ecosystems on which such species depend (ESA, Section 2(b) Purposes).

Connectivity may be important both within and beyond the Mexican wolf metapopulation. For example, genetic data indicate that historically, the southern Rocky Mountains were part of a zone of intergradation between Mexican wolves and more northern wolf subspecies (Leonard et al. 2005). If wolves from the NRM, disperse southward (as occurred with wolf 341F in 2010, see below) and breed with free-ranging Mexican wolves, resultant gene flow has the potential to restore genetic variation that has been lost from Mexican wolves (genetic restoration, Hedrick 2005), and increase the fitness of Mexican wolves (genetic rescue, Tallmon et al. 2004). However, it is important to evaluate the potential effects of such gene flow from northern populations (e.g., genetic swamping) on the unique characteristics of the Mexican wolf genome (see Section III.B.9 below).

Recovery criteria focused on natural connectivity rather than artificial translocation are consistent with the intent of the ESA, which requires recovery of self-sustaining wild populations where feasible. The Services' (FWS and National Marine Fisheries Service (NMFS)) joint Section 7 Handbook (p. 4-36) defines the term "recovery" as "the process by which species' ecosystems are restored and/or threats to the species are removed so self-sustaining and self-regulating populations of listed species can be supported as persistent members of native biotic communities." The Services have an extensive history of emphasizing recovery of self-sustaining wild populations (i.e., those that do not require measures such as controlled propagation or artificial translocation for their persistence) in recovery plans. For example, the Florida panther (*Puma concolor coryi*) recovery plan states "Restoring endangered or threatened animals or plants to the point where they are again secure, self-sustaining members of their ecosystems is a primary goal of the Service's endangered species program" (60 FR 478). Similarly, the Peregrine

Falcon (*Falco peregrinus*) recovery plan states “Recovery is the process by which the decline of an endangered or threatened species is arrested or reversed and threats to its survival are neutralized so that long-term survival in nature can be ensured. The goal of this process is the maintenance of secure, self-sustaining wild populations of species with the minimum investment of resources” (63 FR 45446). In delineating critical habitat for Canada lynx (*Lynx canadensis*), the Service emphasized that “retaining connectivity with larger lynx populations in Canada is important to ensuring long-term persistence of lynx populations in the United States” (74 FR 8641).

III. STAGES IN MODELING APPROACH

A. OVERVIEW

Several modeling tools are available to inform development of recovery criteria based on best available science. It is important to acknowledge the strengths and weaknesses of each type of model and to consider information from multiple models in an appropriate decision-support context. We employed state-of-the-art modeling tools in a multi-stage analysis for evaluating alternative recovery criteria. Collectively, these modeling tools allow comparison of estimated population viability (probability of population recovery) and distribution among alternative recovery scenarios under a variety of potential conditions. The evaluation approach the modeling team developed consists of three main stages:

Stage 1 - Population Simulation Model

This stage is relevant to the following Guiding Principles:

1. Ensure sufficient abundance and trend indices to support population viability;
2. Ensure sufficient redundancy in populations;
5. Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, demographic stochasticity, and other factors; and
6. Conserve genetic diversity and adaptive potential.

Because of the magnitude of genetic threats to the Mexican wolf, we selected a population simulation model (Vortex; Lacy et al. 2010) with the capability to explore how genetic threat factors vary with population size and metapopulation structure. This informs development of criteria for the size, number and connectivity of subpopulations. Details of Stage 1 analysis are described in Appendix 2.

Stage 2 - Habitat-based Model

This stage is relevant to the following Guiding Principles:

1. Ensure sufficient abundance and trend indices to support population viability;
4. Ensure distribution of populations across representative habitats; and
5. Consider and accommodate uncertainty arising from climate change, disease, environmental stochasticity, and other factors.

The Vortex model lacks sophisticated treatment of spatial dynamics or habitat. Once Stage 1 of criteria development is completed, a second stage of the process determined where on the landscape such criteria could be achieved given distribution of suitable habitat. Information sources for this second stage included results from a spatially-explicit population model (PATCH; Carroll et al. 2006). The PATCH model lacks consideration of genetic issues, so if used in isolation would underestimate extinction risk for taxa with genetic threats such as the Mexican wolf.

Stage 3 - Connectivity Model

This stage is relevant to Guiding Principle 3. Ensure sufficient connectivity among populations.

The Vortex analysis suggested that population connectivity was especially important for persistence in Mexican wolves due the current population being derived from only seven founders. We therefore examined what rate of natural dispersal between primary core populations was sufficient for population persistence and could be achieved given the distribution of suitable habitat. We did this by relating observed connectivity rates in other regions to relative habitat connectivity between primary core populations in those regions, and extrapolating to evaluate rates expected given habitat connectivity between potential primary core populations of Mexican wolves.

B. DETAILS OF HABITAT-BASED MODEL

1. OVERVIEW

We developed information on habitat suitability as the second stage of a two stage modeling process. The first stage was development of criteria for subpopulation and metapopulation size and connectivity as described above. This analysis was informed by a simulation model, Vortex, which does not require information on spatial distribution of habitat (see Appendix 2 for more information). The second stage was to determine where a metapopulation of the size and connectivity suggested as necessary for viability by the Vortex analysis could be recovered given the distribution of suitable habitat. This stage of analysis is designed to address the question: what potential recovery areas are large and secure enough that they might be expected to achieve numeric recovery criteria sufficient to alleviate genetic and other threats? We have prepared a comprehensive summary of best available information concerning the distribution and suitability

of habitat for Mexican wolves in the United States and Mexico (Section I.H.). We reference Section I.H. where appropriate in this appendix rather than repeat this material. It is appropriate to provide a general assessment of habitat suitability in the recovery plan, in order to provide general guidance on geographic locations that would be best suited for achieving recovery criteria. However, a detailed assessment of habitat data for individual areas would be more appropriately presented as part of an Environmental Impact Statement associated with future actions to implement recovery in those areas.

Conservation planners assess the distribution of wildlife habitat (including potentially suitable but currently unoccupied areas) with the aid of computer models of varying complexity. Broadly speaking, large carnivores such as the wolf can persist in areas where there is sufficient food and where persecution by humans is low (Fuller et al. 2003, see also Section I.H.). A simple model of recovery potential could therefore highlight large roadless areas with sufficient productivity or extensive forest habitat. More complex spatially explicit population models (SEPMs) might also begin with data on road density and productivity, but would then integrate additional information on species characteristics such as demographic rates and dispersal behavior. For example, social carnivores, such as the wolf, often require larger territories than solitary species of similar size, and may thus be more vulnerable to landscape fragmentation (Carroll et al. 2003a). Unlike the simpler model, an SEPM can provide insights on the effects of population size and connectivity on viability and can help identify the locations of population sources and the degree of threat to those areas from landscape change (Carroll et al. 2003b). An effective recovery strategy requires establishing well-distributed source populations in core areas of highly suitable habitat and then allowing natural dispersal to re-establish a regional metapopulation. To merit attention as a potential reintroduction site, a 'core area of suitable habitat' would need to be both be relatively secure habitat and be well situated to facilitate growth of the regional wolf metapopulation.

Spatially explicit population models (SEPM) are a class of simulation models that are both individual-based and retain spatially-explicit information on habitat distribution (DeAngelis and Gross 1992). These models track the fates of many individuals through time as they move across a grid of cells, age, reproduce and die. The behavior of large numbers of individuals collectively determine the aggregate characteristics that form the model output. SEPM span a range of complexity, depending on the degree of biological realism and number of demographic parameters they incorporate. Model output may include the mean population size, mean time to extinction, or the percentage of suitable habitat occupied. Because these models can incorporate habitat-specific demographic parameters, the development of SEPM has allowed data gathered from intensive demographic studies to be combined with GIS maps of landscape composition and pattern in dynamic models (Murphy and Noon 1992). If SEPM results are considered in the proper context, they have the potential to offer insights on both spatial and non-spatial factors that might influence the success of recovery efforts.

2. THE PATCH MODEL AND ANALYSES OF HABITAT IN THE UNITED STATES

PATCH, the SEPM used in the previously-published study described below (Carroll et al. 2006), links the survival and fecundity of individuals or groups of animals to GIS data on mortality risk and habitat productivity at the scale of an individual or pack territory (Schumaker et al. 2004). Territories are allocated by intersecting the GIS data with an array of hexagonal cells. The different habitat types in the GIS maps are assigned weights based on the relative levels of fecundity and survival expected in those habitat types. Base survival and reproductive rates, derived from published field studies, are then supplied to the model as a population projection matrix. The model scales these base matrix values using the habitat weights within each hexagon, with lower means translating into lower survival rates or reproductive output. Each individual in the population is tracked through a yearly cycle of survival, fecundity, and dispersal events. Environmental stochasticity is incorporated by drawing each year's base population matrix from a randomized set of matrices whose elements were drawn from a beta (survival) or normal (fecundity) distribution. Adult organisms are classified as either territorial or floaters. The movement of territorial individuals is governed by a parameter for site fidelity, but floaters must always search for available breeding sites. Movement decisions use a directed random walk that combines varying proportions of randomness, correlation, and attraction to higher-quality habitat (Schumaker et al. 2004). The PATCH model lacks consideration of genetic issues, so if used in isolation would underestimate extinction risk for taxa with genetic threats such as the Mexican wolf. Hexsim, the successor to PATCH, was recently used in recovery planning for the Northern Spotted Owl (Dunk et al. 2012).

We summarize below the results from a previously-published study (Carroll et al. 2006) that were used as one source of information for evaluating areas in the United States in this second stage of the modeling process. More recent studies (Araiza et al. 2012) were used to evaluate potential recovery areas in Mexico. Carroll et al. (2006) identified four potential reintroduction sites in the United States, based on the results of initial SEPM simulations. These sites were labeled Carson (northern New Mexico), Grand Canyon (northern Arizona), Mogollon Rim (central Arizona), and San Juan Mountains (southwestern Colorado). A fifth site in the Blue Range Wolf Recovery Area (BRWRA; Arizona and New Mexico) was also included to provide comparability with current recovery program results. Each of these sites was evaluated in detail by simulating the effects of releasing wolves at that site alone. Each reintroduction site comprised five adjacent potential wolf territories, totaling 2500 km². The model approximated the standard reintroduction protocol (Bangs and Fritts 1996) by introducing five breeding-age females in the first year and setting survival for the first 5 years at close to 100% under the assumption that new animals would be released to replace mortality among the initial releases.

In addition to the current reintroduced population in the Blue Range, the Grand Canyon reintroduction site showed a high probability of success (low extinction rates) and rapid geographic expansion. Several other reintroduction sites showed higher, but still relatively low,

extinction rates. The probability that a reintroduction at a single site will fail (extinction probability) under scenario A ranges from near zero (0 of 1000 simulations) for the Blue Range and Grand Canyon sites to near 10% for the Mogollon Rim and San Juan Mountains sites. Under scenario C (which projected future landscape change trends), the extinction probability for the Mogollon and San Juan Mountains sites increases to 16–20%. The probability of extinction for the Blue Range, Grand Canyon, and Carson sites also increased slightly but remained low (< 3%). Occupancy of the larger (10,000-km²) restoration zone surrounding each 2500-km² reintroduction site gives a sense of the extent of suitable habitat that might be important in the early stages of population establishment. The Blue Range restoration zone has the highest occupancy, at 72.5%, followed closely by the Carson and Grand Canyon zones. The Grand Canyon zone is more resilient to landscape change than the Blue Range or Carson; thus, it shows the highest wolf population density among US restoration zones under scenario C. A scenario that incorporated cattle density as an additional mortality risk factor resulted in a similar ranking of restoration zones, except that the San Juan Mountains zone appeared less vulnerable, and thus only the Mogollon zone showed high relative extinction risk.

The regional population size achieved at the end of the SEPM reintroduction simulations (year 200) gives an indication of the ability of a particular reintroduction site to enhance the broader regional population, an ability that is due to factors such as ease of dispersal to other suitable habitat. The Grand Canyon site achieves the highest regional population within the US SWDPS. As a result of sink habitat and other barriers to population spread, the largest regional US population achieved from a single reintroduction is only 59.9% of the maximum population size achieved in the equilibrium scenario (scenario A) that began with all habitat occupied. However, a regional population of 89.3% of the maximum population size is eventually achieved by using three reintroduction sites (Blue Range, Grand Canyon, and Carson). At the end of the 200-year simulations, this reintroduced population occupied 54.3% to 57.5% (depending on assumptions about dispersal distance) of the suitable habitat under scenario A, 26.3% to 26.6% under scenario C, and 100% of the region's ecoregions under both scenarios. Population predictions in peripheral areas with fragmented habitat were most sensitive to alternate assumptions about maximum dispersal distance (e.g., New Mexico, with 13% relative change), with most other areas showing less than 5% relative change. Extinction probability at individual reintroduction sites was not sensitive to dispersal parameterization, with a doubling of maximum dispersal distance generally producing changes in extinction risk of less than 0.5% (absolute percentage), with a maximum of 1.6% change.

3. ANALYSES OF HABITAT IN MEXICO

We primarily used results from more recent studies (Araiza et al. 2006, Araiza et al. 2012) to evaluate potential recovery areas in Mexico, consistent with our goal to use the best currently available data. However, it is relevant to briefly review here Carroll et al. (2005)'s comparison

of four potential recovery areas in Mexico. The areas analyzed correspond to four areas described in Araiza et al. (2006, 2012; see Table 1): Sierra San Luis/Ajos-Bavispe (Chihuahua/Sonora near U.S. border), Tutuaca/Sierra Tarahumara (westcentral Chihuahua), Chihuahua/Durango, and Maderas del Carmen/Serranias de Burro (northern Coahuila). Carroll et al. (2005) concluded from the SEPM analysis that the Durango site contained the most productive wolf habitat, but the Tutuaca and Carmen sites appeared to have lower risk from conflict with livestock production. Under current landscape conditions, the PATCH model projected that northern Mexico as a whole might support 82% as many wolves as could be supported in the southwestern US (2600 versus 3166).

Although the analysis of Carroll et al. (2005) served as a useful initial comparison between potential recovery areas in Mexico, the authors cautioned against using results to compare habitat between the US and Mexico or to make absolute estimates of wolf carrying capacity in Mexico. Because of these concerns, results from analysis of the Mexican sites were not included in the subsequent peer-reviewed paper (Carroll et al. 2006). Accuracy of Carroll et al. (2005)'s analysis of sites in Mexico was reduced by two factors. Firstly, Carroll et al. (2005) concluded that the sparseness of the available digital data on human impacts (roads and altered habitat types) in Mexico affected their estimates of potential wolf habitat in Mexico "to an extent that significantly limits comparability between Mexican and US reintroduction sites." Secondly, Carroll et al. (2005)'s analysis of prey productivity was based on surrogate data (vegetation types, greenness). These surrogate data are likely to show lower correlation with actual prey density in Mexico than in the United States because 1) estimates of prey abundance in Mexico with which to test surrogate data are more limited in Mexico, and 2) what prey data are available indicate that prey populations are further below ecological carrying capacity than in the southwestern US (Araiza et al. 2006, Arellano et al. 2009, Lara-Diaz 2011). For the above reasons, the results of Carroll et al. (2005) for wolf recovery areas in Mexico have largely been superseded by more recent studies.

In 2006, a workshop convened researchers involved with several of the studies described above, in order to derive a consensus opinion of which areas held potential for wolf reintroduction in Mexico (Araiza et al. 2006). Six areas were identified as having the greatest potential to support populations of Mexican wolves. This conclusion was based on several sources of expert judgement and qualitative analysis. For example, Martínez Gutiérrez (2007) first identified patches with suitable vegetation, and then identified areas with low levels of roads and settlements within those patches. The area between the Tutuaca/Sierra Tarahumara and Chihuahua/Durango area could be identified as unsuitable in this analysis based on high levels of roads and settlements. In other cases, both the regional-scale GIS analysis and expert knowledge were used by Araiza et al. (2006). Subsequently, Araiza et al (2012) performed more detailed modeling of risk as described below which confirmed that areas of lowest risk are somewhat fragmented even within the 6 recovery areas.

In a subsequent analysis, Araiza et al. (2012) performed a quantitative analysis of habitat suitability and human-associated mortality risk to validate and extend the expert-based conclusions. Historical locations of wolves were compared with historical vegetation types using a utilization-availability analysis. Contemporary vegetation types were ranked in six quality classes based on a combination of the results obtained in the selection analysis and the current status of transformation. Point data on the locations of population centers was buffered to a zone of influence based on their population size. Roads were also buffered based on reported zones of avoidance (Kaartinen et al. 2005). Three alternate scenarios were developed for human-associated risk (low, intermediate, and high risk) that made alternate assumptions as to the extent of the zone around roads and human settlements in which wolves would experience increased mortality. Information on vegetation suitability and distance to settlements and roads maps were combined to identify large patches of the high quality habitat in which further fieldwork to evaluate prey availability was conducted. The largest clusters of suitable patches were found in Sonora-Chihuahua (area 1) and Chihuahua-Durango (area 3)(15,705 and 8,344 km² in area, respectively, under the intermediate risk assumptions)(see Section I.H.).

Araiza et al. (2006) estimated potential size of wolf populations in the six core areas of suitable habitat in Mexico. Subsequent fieldwork to evaluate prey availability (Lara-Diaz 2011, J. Servín unpublished data) further refined these estimates (see Table 1). Based on these sources, the two areas in the northern Sierra Madre Occidental are predicted to support larger wolf populations (80 wolves each) than are the two areas in the southern Sierra Madre Occidental (60 and 24 wolves). However, the relative potential for successful reintroductions within each of these areas may also depend on public attitudes and details of land use that are not quantifiable using available data (Servín et al. 2007).

4. CONCLUSIONS FROM HABITAT ANALYSES

Several conclusions emerged from our review of the results of Carroll et al. (2006) , Araiza et al. (2012) and other relevant data on e.g., prey abundance (section I.H.):

1) Under current habitat conditions, three major core areas of suitable habitat exist in the area encompassing Arizona, New Mexico, southern Colorado and southern Utah. The three core areas of suitable habitat are a) the Blue Range Wolf Recovery Area and adjacent public lands, b) the Grand Canyon and adjacent public lands, and c) two linked areas of public lands and private lands with conservation management in northern New Mexico and southern Colorado (labeled Carson and San Juans in Carroll et al. (2006))(see section I.H.). These areas are projected to become more distinct and separated as landscape change factors such as exurbanization continue (Carroll et al. 2006). Each of the three areas (but not western Texas) holds a secure core area of

public lands subject to conservation mandates (National Park, wilderness) where wolves are predicted to experience the lowest human-induced mortality.

2) The US/Mexico border area is likely to serve as sink habitat for wolves under current conditions (Carroll et al. 2006). However, the area's key role in facilitating dispersal between US and Mexican wolf populations suggests that it be given significant attention in recovery planning, through recovery actions which increase the likelihood of these sites being naturally recolonized by dispersers from the Blue Range or Mexican populations.

3) Potential recovery areas in Mexico contain areas of suitable habitat that are smaller and have lower prey abundance than those in the U.S. In particular, the contrast in prey density between the US and Mexico core areas results in a contrast in estimates of the number of wolves that could be potentially supported in each of the core areas. They are thus unlikely to support the primary core populations necessarily for metapopulation persistence but may play a role in increasing connectivity and distribution of populations across representative habitats. Secure habitat (areas with low human-associated mortality risk) are appears smaller and more fragmented within potential recovery areas in Mexico. Smaller secondary core populations (e.g., in Mexico or Texas) may be important for enhancing connectivity, as well as meeting representation goals.

5. POTENTIAL SHIFTS IN SUITABLE HABITAT UNDER CLIMATE CHANGE

Previous studies (Carroll et al. 2006) have projected effects of development trends on suitable habitat but have not evaluated potential effects of climate change. To evaluate this potential threat, we used data on projected shifts in biome boundaries in the southwestern US in the period 2000-2062 (50 years from date of recovery plan). The MC1 model (Daly et al. 2000, Bachelet et al. 2001) is a DGVM (dynamic global vegetation model). Such models add complexity in terms of the interaction of vegetation components (competition, etc.) but have low thematic resolution (biomes are broad categories)(Figure 6). Spatial resolution is also limited by the resolution of the climate model inputs. The figures contrast projections from three GCMs (general circulation models) developed by three different research groups (CSIRO, Hadley, and MIROC). Results from two contrasting IPCC emissions 'storylines' are also contrasted (Figure 5). The A1 storyline and scenario family describes a future world of very rapid economic growth, global population that peaks in mid-century and declines thereafter, and the rapid introduction of new and more efficient technologies. The A1 scenario family develops into three groups that describe alternative directions of technological change in the energy system. The three A1 groups are distinguished by their technological emphasis: fossil intensive (A1FI), non-fossil energy sources (A1T), or a balance across all sources (A1B). The A2 storyline and scenario family describes a very heterogeneous world. Emissions under the two storylines are similar at first, but eventually the A2 scenario projects higher emissions.

The MC1 biome projections suggest that there is substantial variation between the projections of the different models. There are greater contrasts between GCMs than between the A2 (Figure 7) and A1B (Figure 8) storylines. However, there is agreement between model projections in many areas. The greatest change in vegetation and above-ground carbon may occur to the south of the Blue Range and along the southern edge of the Mogollon Rim. A northward expansion of both temperate and subtropical grassland is shown. The steep elevational gradient of the Mogollon Rim prevents a large northward shift in biome boundaries in that area. Southern Arizona remains primarily desert with some expansion of subtropical grassland, especially to the south of the Blue Range. The Blue Range and potential recovery areas in northern Arizona and New Mexico are currently primarily temperate grassland or conifer forest, with some subalpine areas in the San Juan Range. These areas remain primarily temperate grassland or conifer, with the exception that in the more extreme projections of the MIROC GCM, the subalpine areas in the San Juans are replaced by temperate conifer habitat. Given the limitations of the biome classification, it appears from these projections that potential wolf habitat in central and northern Arizona and New Mexico will remain relatively stable under climate change for the next 50 years. This suggests that core habitat areas identified based on current habitat condition (e.g., in Carroll et al. 2006) will remain suitable under future projected climates. We have described here the mapped information on climate change impacts we considered in stage 2 of the modeling process. We considered additional non-mapped information on potential climate change impacts as part of the threats assessment (Section I).

C. DETAILS OF CONNECTIVITY MODEL

1. OVERVIEW

The most commonly proposed rule of thumb for connectivity is the “one genetically effective migrant per generation” rule (Frankel & Soule 1981; Allendorf 1983). This rule states that one migrant per generation into a subpopulation is sufficient to minimize the loss of polymorphism (the occurrence of multiple alleles at one locus) and genetic heterozygosity within subpopulations. Because this generalized rule depends on simplifying assumptions (e.g. ideal populations whose effective population size equals census size), other researchers have suggested a more ambitious rule of up to 10 effective migrants per generation (Mills & Allendorf 1996; Vucetich & Waite 2000).

One (or 10) migrants per generation is applicable across a range of population sizes because genetic effects of population size and connectivity are interrelated. Because genetic drift is stronger in a small population, a greater proportion of heterozygosity is lost per generation and divergence of allele frequencies is faster. However, when a small population receives a single migrant, that migrant comprises a larger proportion of the population and has a larger impact in

restoring genetic variation. This was illustrated in the wild with the recent genomic sweep of the Isle Royale wolf population by a single immigrant from the mainland (Adams et al. 2011).

A connectivity criterion of one effective migrant per generation (“migrant”) was supported by evidence from the Vortex analysis that a higher connectivity rate was especially beneficial for population persistence in Mexican wolves due the subspecies derived from inbred and interrelated founders. Additionally, data from the Northern Rocky Mountains (NRM) suggested that such a rate had been achieved there between 2 of 3 primary core populations (vonHoldt et al. 2010). The 1 migrant rate was also endorsed as a recovery criterion in the NRM wolf delisting documents (FWS 2011).

2. METHODS

We projected connectivity rates between primary core populations in the Mexican wolf metapopulation by relating observed connectivity rates in an extant wolf metapopulation (the NRM) to relative habitat connectivity (in both the NRM and the southwestern US). Habitat data inputs were derived from the habitat model used in Carroll et al. (2006). Observed connectivity rates in NRM were derived from vonHoldt et al. (2010) with the adjustment suggested by Hebblewhite et al. (2010) to account for the fact that vonHoldt et al. (2010) analyzed data from a subsample of the NRM wolf population.

Connectivity between wolf populations was based on two metrics: least-cost distance and resistance distance. Least-cost distance is the basis of the corridor delineation methods available in most GIS software. These methods analyze raster data representing cost of movement as distance, and use computationally efficient algorithms to identify the route between two predetermined endpoints that has the shortest total distance (least total cost). Least-cost distance was calculated using the Linkage Mapper software (McRae 2011).

In contrast to least-cost distance, which focuses on a single optimal path, resistance distance considers movement across multiple paths. Resistance is calculated using algorithms from electrical circuit theory. These methods treat landscapes as conductive surfaces, i.e. networks of nodes connected by resistors. Current flow models integrate the contributions of all possible pathways across a landscape or network. As in electrical circuits, the addition of new pathways increases connectivity by distributing flows across more routes (McRae et al. 2008). Resistance distance was calculated using the Circuitscape software (McRae et al. 2008).

3. RESULTS

Linkages between primary core populations were ranked similarly under both metrics (least-cost distance and resistance distance). The “shortest” (best) linkages were between central Idaho and

both northwestern Montana and Yellowstone (figure 9 and 10). Effective migration rates of 1.67 and 0.83 EMPG, respectively have been estimated for these linkages (accounting the adjustment suggested by Hebblewhite et al. (2010) of doubling rates documented in vonHoldt et al. (2010)). Projected connectivity between the Blue Range and Grand Canyon primary core populations was somewhat less than that of the two “best” linkages described above. Projected connectivity between the Blue Range and southern Colorado/northern New Mexico primary core populations was somewhat less than that of between the Blue Range and Grand Canyon. The Grand Canyon and southern Colorado/northern New Mexico primary core populations were projected to be poorly connected, with distances similar to that between Yellowstone and northwestern Montana, a linkage where no effective migrants have been documented (vonHoldt et al. 2010).

Based on these results, rates equivalent to or somewhat below 0.83 EMPG might be expected between 2 of three primary core populations in the southwestern U.S., but few direct migrants would be expected between the Grand Canyon and southern Colorado/northern New Mexico. Given these projections, a connectivity criterion of 0.5 EMPG for the Mexican wolf in the southwestern US (specifically between the Blue Range and both Grand Canyon and Carson) would be analogous to a 1 EMPG criterion for the NRM (specifically between central Idaho and both NW Montana and Yellowstone). Limited dispersal expected between Grand Canyon and Carson would be analogous to the low or no dispersal between Yellowstone and northwestern Montana. Thus the three largest populations would be connected as an archipelago rather than a network. Although not ideal, this arrangement has the benefit of providing increased demographic and genetic support to the centrally located Blue Range population.

Araiza et al. (2006) considered all of the six potential recovery areas in Mexico described above as adequately connected with at least one other potential core area of suitable habitat. However, the authors noted that areas in the southern Sierra Madre Occidental (e.g., Chihuahua/Durango and Valparaiso/Mezquital) were likely to be better connected to the wolf metapopulation than were areas to the east in Coahuila and Nuevo Leon. Servín et al. (2007) proposed that the six Mexican core areas of suitable habitat in Mexico might form two disjunct metapopulations. The larger metapopulation would include the four areas in the Sierra Madre Occidental, with interchange of dispersers along the Sierra Madre Occidental from Sonora to Zacatecas. The two areas in eastern Mexico (Coahuila and Nuevo Leon) could potentially exchange dispersers with any Mexican wolf populations in Texas. The four areas in the Sierra Madre Occidental might be largely connected with each other and to a lesser degree, through the Sierra San Luis Complex, to the Blue Range primary core population. However, realized dispersal rates (expressed as EMPG) are influenced by both habitat connectivity and the size of the source population. The projected smaller size of secondary core populations would lower realized connectivity rates between those populations. This would not affect dispersal rates from primary core populations (e.g., Blue Range) to adjacent secondary core populations (e.g., Sky Islands-Sonora).

IV. CONCLUSION

A. NORMATIVE ELEMENTS OF RECOVERY CRITERIA DEVELOPMENT

Because a population's extinction risk is never zero, establishing risk thresholds in listing and recovery actions involves a normative dimension (i.e., specifying what level of endangerment is acceptable) and a scientific dimension (i.e., determining whether a species meets that level of endangerment) (Vucetich et al. 2006). Although the U.S. Congress mandated that agencies consider "solely" the best science in making listing decisions (16 U.S.C. §1533 (3b)(1A)(a1)), lawmakers addressed the normative nature of such decisions only qualitatively when they emphasized in the ESA the high degree of protection they intended to afford to biodiversity.

While the ESA's legislative history indicates that Congress intended the Act to afford a high level of security to listed species, the statute established no numeric risk thresholds which would provide an explicit judgment as to the minimal likelihood of persistence and minimal geographic distribution that would separate species considered secure or recovered from those considered threatened or endangered. While the ESA does not explicitly define quantitative thresholds for acceptable risk, this does not mean that administrative agencies may apply such risk thresholds inconsistently. To be effective, conservation strategies must be based on the rates of species' population dynamics, that is, the time from endangerment to recovery. Clear and consistent implementation of statutes helps to maintain the continuity in conservation policy necessary to realize the essentially ethical goals of the ESA.

Although threat assessment criteria prioritize which species are most at risk of extinction, they typically do not offer justification for why one level of risk is acceptable and another is not (IUCN 2001). Wilhere (2012) noted that recovery plans seldom contain explicit statements of acceptable extinction risk, but among those that did the recovery criteria span two orders of magnitude of risk. Gilpin (1987), one of the few authors to consider the normative aspects of this issue, argued for considering risks of extinction for 200-year time frames simply because he believes humanity's immediate challenge is to eke through the next two centuries while losing as few species as possible. Shaffer (1981) adopted a 99% persistence probability for 1000 years as a viability criterion for grizzly bears. Soule (1987) and Shaffer (1992) expressed concern that targeting a minimum population level is inadequate for sound conservation (because by design they provide minimal capacity for populations to withstand unforeseen circumstances) and larger populations are necessary to ensure long-term persistence.

The statutory language is consistent with this concern to the extent that it does not require the agencies to define recovery for a given species as the absolute minimum population size and geographic distribution that equates to a specified persistence level. For species that are experiencing severe declines, the recovery goal is often to reverse the decline and restore the population to a previous status rather than some minimum size. Recovery goals may also address

the minimum population size necessary for a species to be ecologically functional. For example, recovery plans may set a lower acceptable level of risk for species that play disproportionately large roles in their ecosystems (Estes et al. 2011), in order to increase the probability of conserving “ecosystems on which species depend,” one of the ESA’s express purposes (16 U.S.C. §1531 (a)(5)(b)).

While data for many species are too limited for quantitative PVA-based risk estimates, such estimates are possible for relatively well-studied taxa such as the gray wolf. However, scientists have generally rejected use of a single point estimate of minimum viable population size in recovery planning. They argue that PVA results should be used instead to provide information on the general relation between risk and factors such as abundance, genetic diversity, and distribution (Shaffer et al. 2002). Most estimates of minimum viable population size are probably too low because they underestimate long-term uncertainty in stochastic events. Recovery goals may appropriately include a margin of safety to ensure that unanticipated future events do not cause species to fall below the threshold that would again make listing warranted.

One benefit of considering geographic distribution or population redundancy as a recovery criterion (see section II above) is that situations in which a species is well distributed geographically in multiple populations will generally correspond with the conditions necessary for genetic viability. However, evaluating the appropriate levels of geographic distribution for listing and recovery similarly involves normative and biological determinations.

Consistent with best practice in recovery planning, we used point estimates of population viability (from the Vortex model) as one source of information in a decision-support context. We considered 100 years as an appropriate timeframe for evaluating effects of population size on genetic health, but deemphasized the significance of arbitrary thresholds (95%, 99%). We use such thresholds as only one of several factors for evaluating alternate recovery options, and focus primarily on patterns of how persistence changes with population size across a range of thresholds and alternative parameter sets. For example, in the Vortex simulations, populations of ≥ 250 individuals had low extinction rates ($< 1\%$ over 100 years) and maintained substantial numbers of wolves, especially when multiple connected populations were connected via dispersal. In contrast, smaller populations of 150 individuals had relatively high extinction risk (4-17% over 100 years). However, several aspects of model parameters and structure were potentially overly optimistic, and these multiple factors could act synergistically to reduce population viability. Consistent with Congress’ intent to institutionalize caution in order to avoid uncertainty about a species’ future status, we identified criteria that provide a margin of safety because they resulted in conditions under which the species is unlikely to become threatened or endangered again in the foreseeable future: 1) a low predicted potential for extinction ($< 1\%$ over 100 years), and 2) a greater than 50% probability that populations would meet specified size criteria (200, 250, or 350) over the long term. Due to the role wolves play in their ecosystems

(Estes et al. 2011), such precautionary criteria also increase the probability of conserving ecosystems and ecosystem function (16 U.S.C. §1531 (a)(5)(b)).

B. ADDRESSING UNCERTAINTY

The appropriate role of PVA models in recovery planning is not to predict outcomes, but rather to provide one of several sources of information that support decisions on appropriate recovery criteria. Therefore sensitivity analyses using a range of parameters are often more informative than would be a single estimate based on the best estimate of parameter values. Results from PVA models are subject to two general sources of uncertainty. Model parameters such as mortality and fecundity rates are based on best available field data but are uncertain both in their accuracy for the studied population and their generality to the range of populations which the PVA is attempting to evaluate (i.e., subpopulations in several different potential recovery areas). More importantly, model structure introduces uncertainty into the results. For example, density dependent variation in reproductive rates affects the level of threat from ‘catastrophes’ (e.g., diseases). If reproductive rate increases at low population sizes, populations recover more quickly from population decline associated with episodic threats. Thus alternate assumptions concerning density dependence can significantly alter PVA estimates of metrics such as extinction risk.

Despite these sources of uncertainty, PVA models can provide qualitative insights on the relative level of threat to different populations, and relative strength of the different threat factors (demographic, disease, genetic) at different population sizes. To derive guidance from the PVA despite model uncertainty, we used an ‘ensemble modeling’ approach. We developed multiple alternate plausible model structures and evaluated these across a range of plausible parameters. We evaluated the sensitivity of results to a range of demographic and genetic parameters and based decisions where possible on metrics that were relatively robust to variation in input parameters. Decisions concerning recovery criteria were informed based on the ‘strength of evidence’ across multiple models, combined with an approach based on the precautionary principle that sought to minimize both Type I and Type II error. “By identifying the sources and magnitude of our uncertainties, we can build better criteria and more accurately target those aspects of our criteria that may bear refining in the future” (Interim Recovery Guidance 5.1:18).

Although more demographic data exists for the wolf than for most species, the plausible range of demographic parameters nonetheless causes simulations to span a range of outcomes from deterministic decline ($\lambda < 1$) to deterministic increase ($\lambda \gg 1$) for all alternative recovery criteria. Increasing the magnitude of catastrophes and genetic effects accentuated contrasts between alternate recovery criteria, whereas increasing or decreasing demographic rates (deterministic λ) reduced the contrasts between alternate recovery criteria. The stochastic and genetic factors that cause contrasts in persistence between populations of different

sizes are significant for demographic parameter sets in the middle of the range of plausible values, but generally not for demographic parameter sets at the extremes of this range.

Although it is often recommended that PVAs focus on ranking scenarios rather seeking a ‘magic’ MVP number, this is of limited utility given the idealized nature of the scenarios we evaluated. It is intuitive that 3 subpopulations of 250 will persist longer than 2 subpopulations of 250. It is more informative to focus on the question: over the range of demographic rates at which stochastic and genetic factors are important, what thresholds caused by population size and connectivity are evident? This allows the PVA to complement analyses of other recovery criteria such as representation goals.

Additional uncertainty is inherent in the analysis due to several factors. Firstly, the reproductive system as modeled does not represent the complexities of breeding in social animals such as wolves. Incorporating realistic wolf social dynamics would reduce the N_e/N ratio of the population because reproductive contribution would be more unequal between individuals. Secondly, potential effects of inbreeding on survival were not modeled. Although this effect was not evident in past studies of Mexican wolves (Fredrickson et al. 2007), findings from other species suggest that this may be due to lack of sufficient data. Thirdly, survival rates were based on optimistic assumptions concerning the ability to mitigate current threat factors. Fourthly, we considered disease and other catastrophes at acting at a relatively low magnitude and predominantly affecting fecundity rather than survival. Finally, we did not quantitatively evaluate metapopulation size necessary for maintaining long-term adaptive potential (mutation-drift balance). Conversely, other assumptions such as concerning density dependence would increase the pessimism of the Vortex results. We addressed this issue through sensitivity analysis where feasible (e.g., impact of increased inbreeding effects). In some cases, the best available models were inadequate to assess these factors (e.g., mutation-drift balance, wolf social structure). As stated above, given uncertainty, and to be consistent with Congress’ intent to institutionalize caution in order to avoid uncertainty about a species’ future status, we identified criteria that provide a margin of safety because they predicted a low potential for extinction (<1% over 100 years).

C. SUMMARY

The Service employed a 3 stage process to evaluate potential recovery criteria for the Mexican wolf. Stage 1 consisted of comparison of population performance across a range of scenarios with alternative metapopulation size and structure. Based on the results of these comparisons, we evaluated in Stage 2 which areas within the recovery region held suitable habitat sufficient to recover populations of the necessary size. In Stage 3, we evaluated what rates of dispersal could be expected between the areas identified in Stage 2. The process was then iterated to evaluate persistence of a metapopulation with the projected dispersal rates. The composite set of recovery

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criteria represents an effort to maximize efficiency and realism by focusing on well-connected high quality habitat while maintaining the best possible population performance. The composite set of recovery criteria represents an assessment, based on best available scientific data, of what conditions are necessary to recover Mexican wolf populations to the point at which they are unlikely to become threatened or endangered again in the foreseeable future.

Figure 1. Conceptual diagram of analysis context of Mexican wolf PVA.

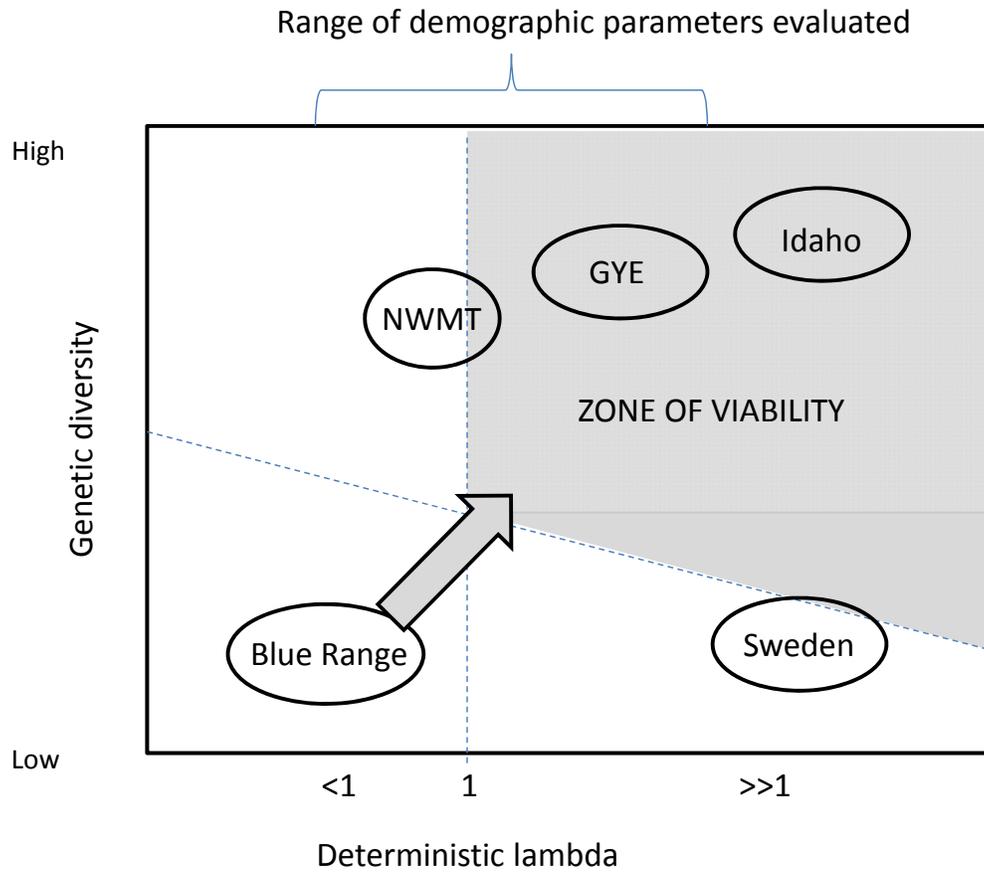


Figure 5. Contrasts in projected emissions between IPCC storylines.

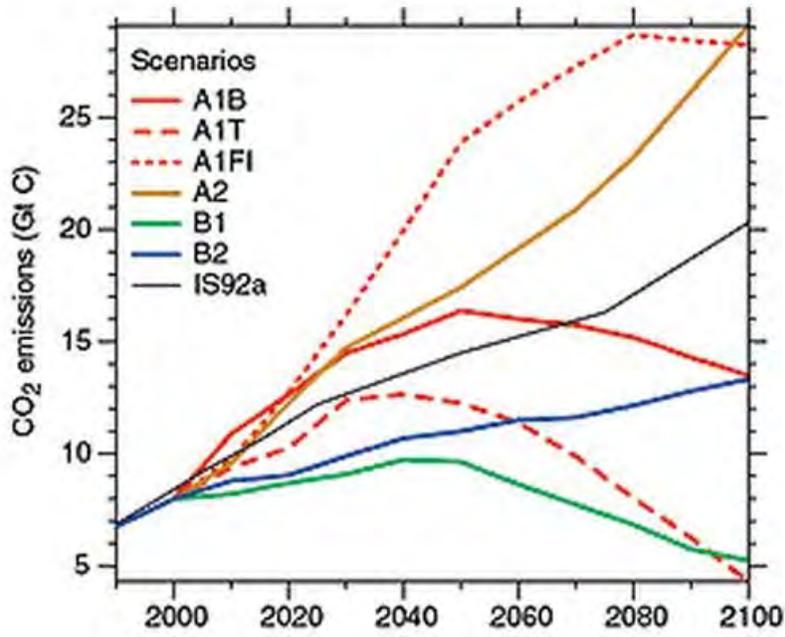


Figure 6. Current (2000) biomes as predicted by the MC1 model. Potential wolf recovery areas as derived from Carroll et al. (2006) are outlined.

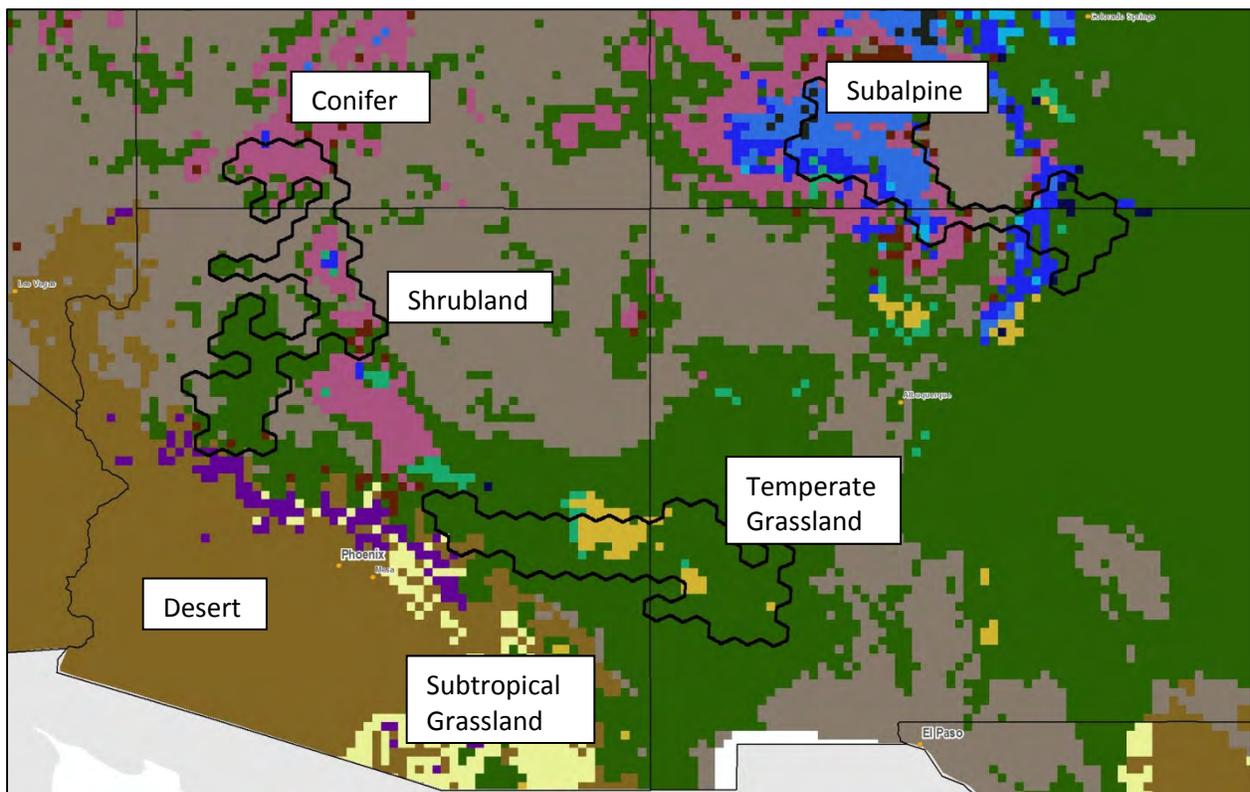


Figure 7. Projected biomes for 2062 under A2 scenario: a) CSIRO, b) Hadley, and c) MIROC GCM

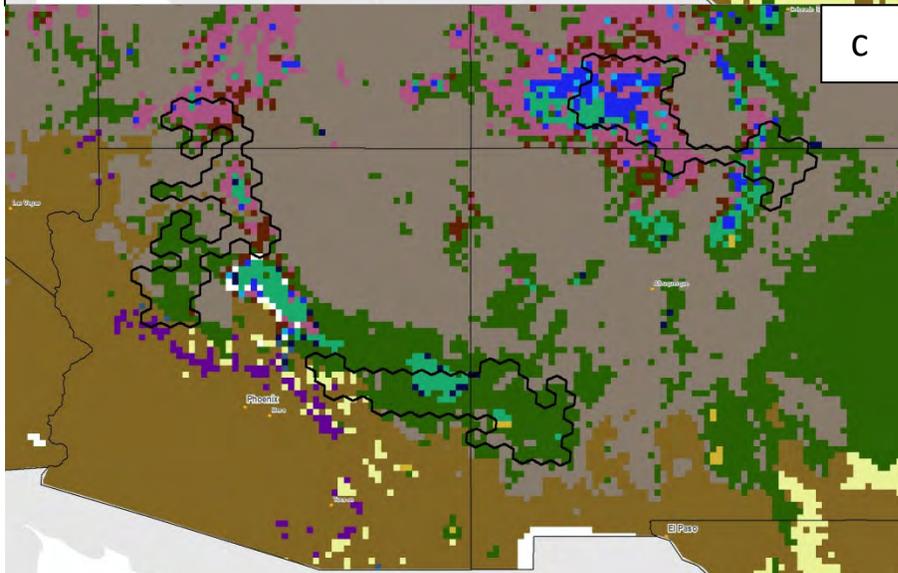
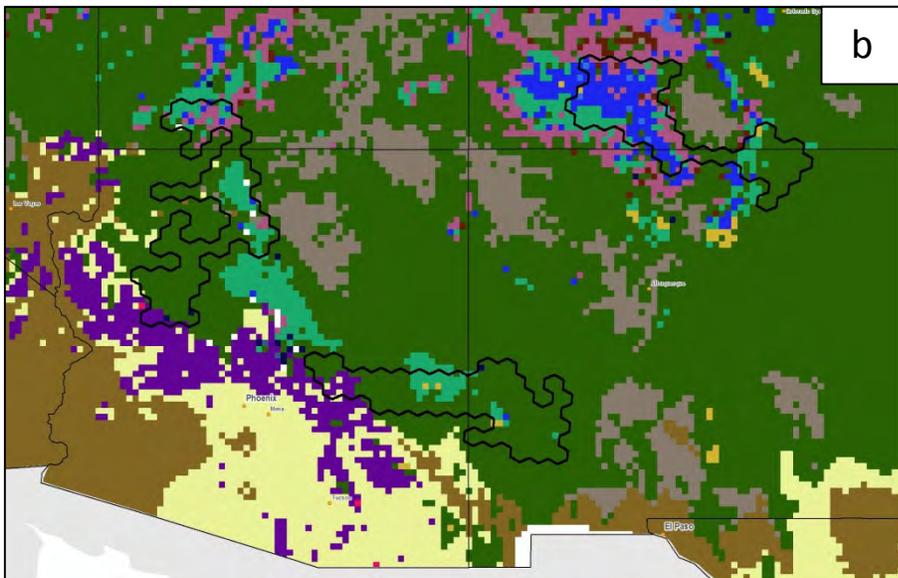
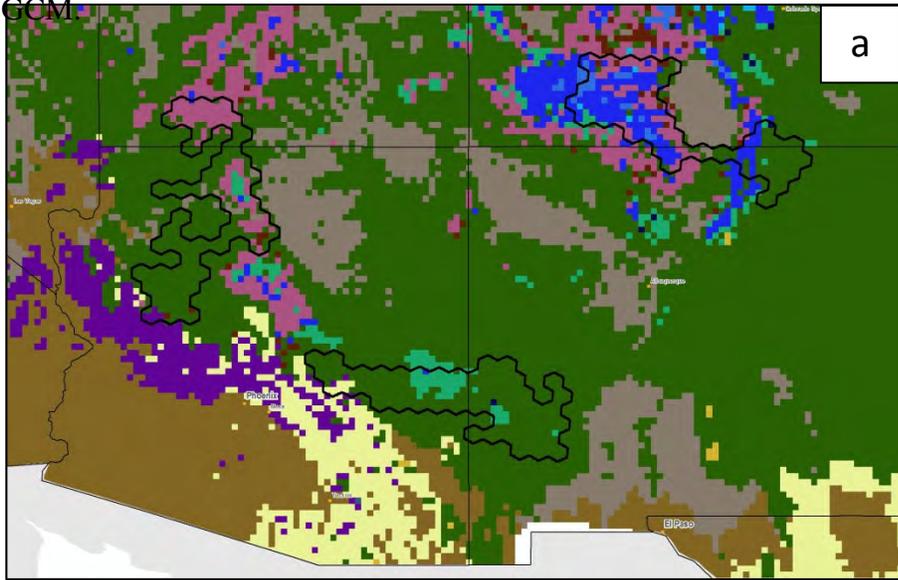


Figure 8. Projected biomes for 2062 under A1B scenario: a) CSIRO, b) Hadley, and c) MIROC GCM.

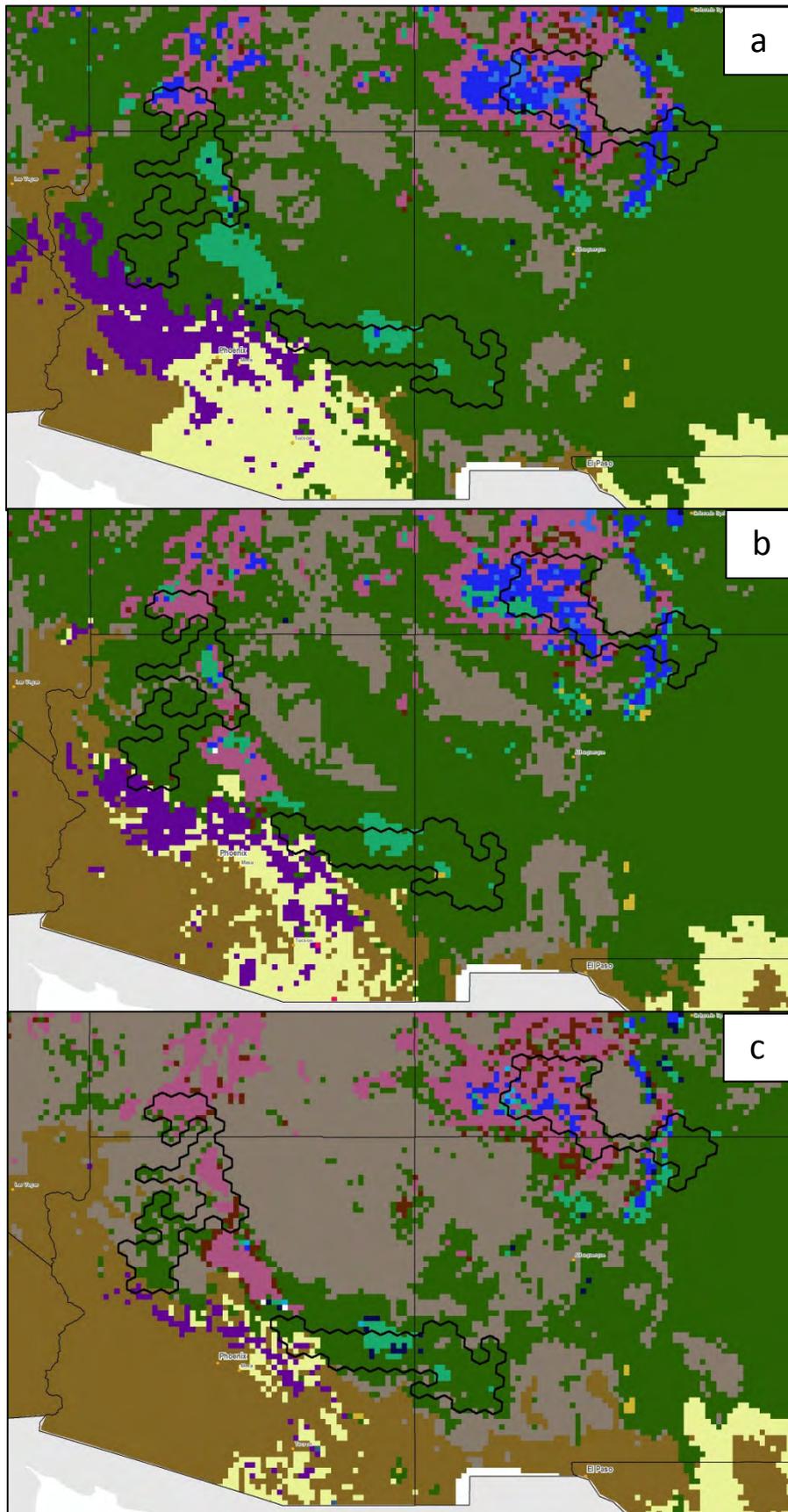


Figure 9. Map of potential linkages and relative connectivity rate (as inverse of least cost distance), between existing or potential wolf population core areas in the western US. Link colors range from green (better connected, or lower least cost distance) to red (worse connected).

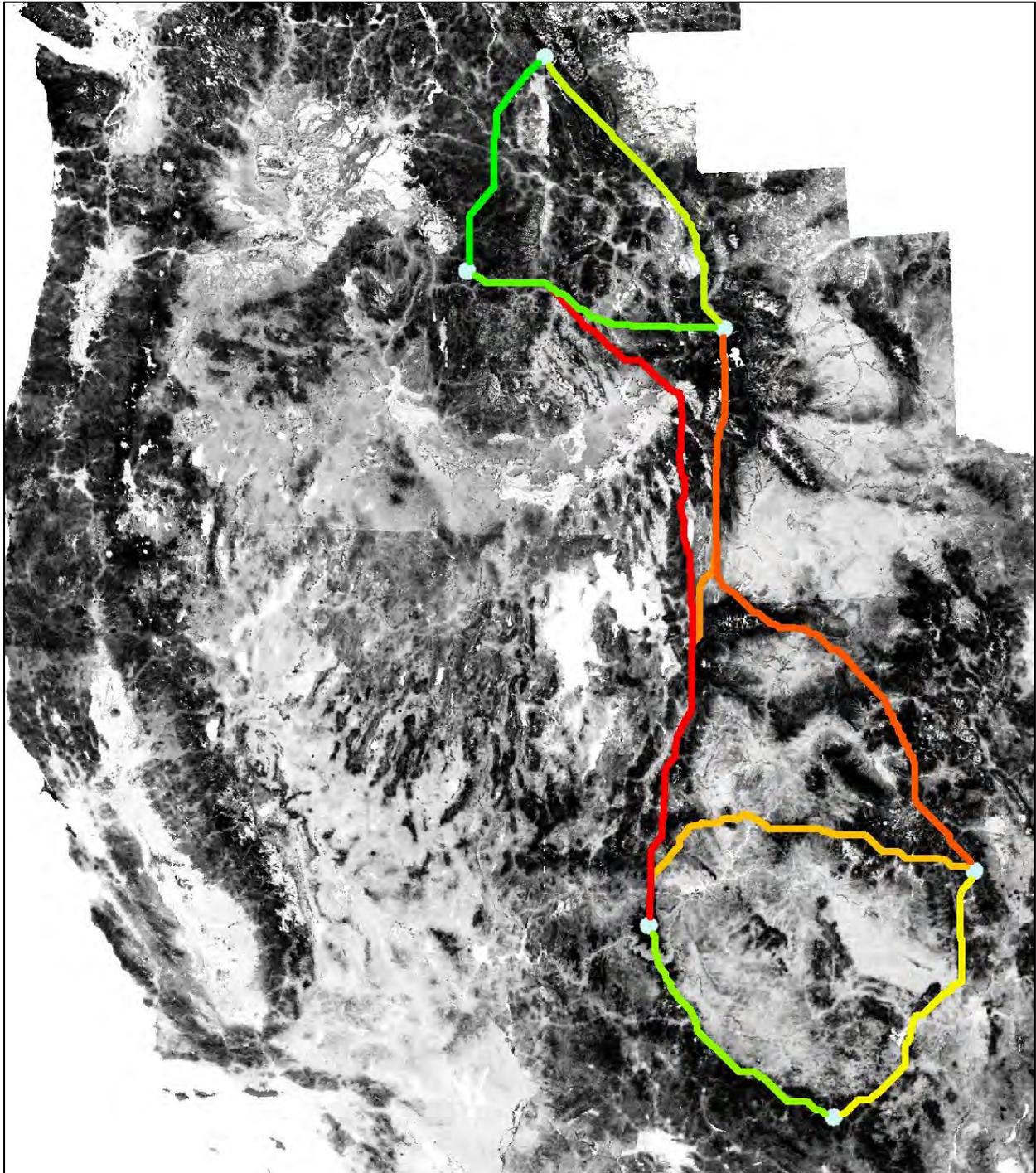
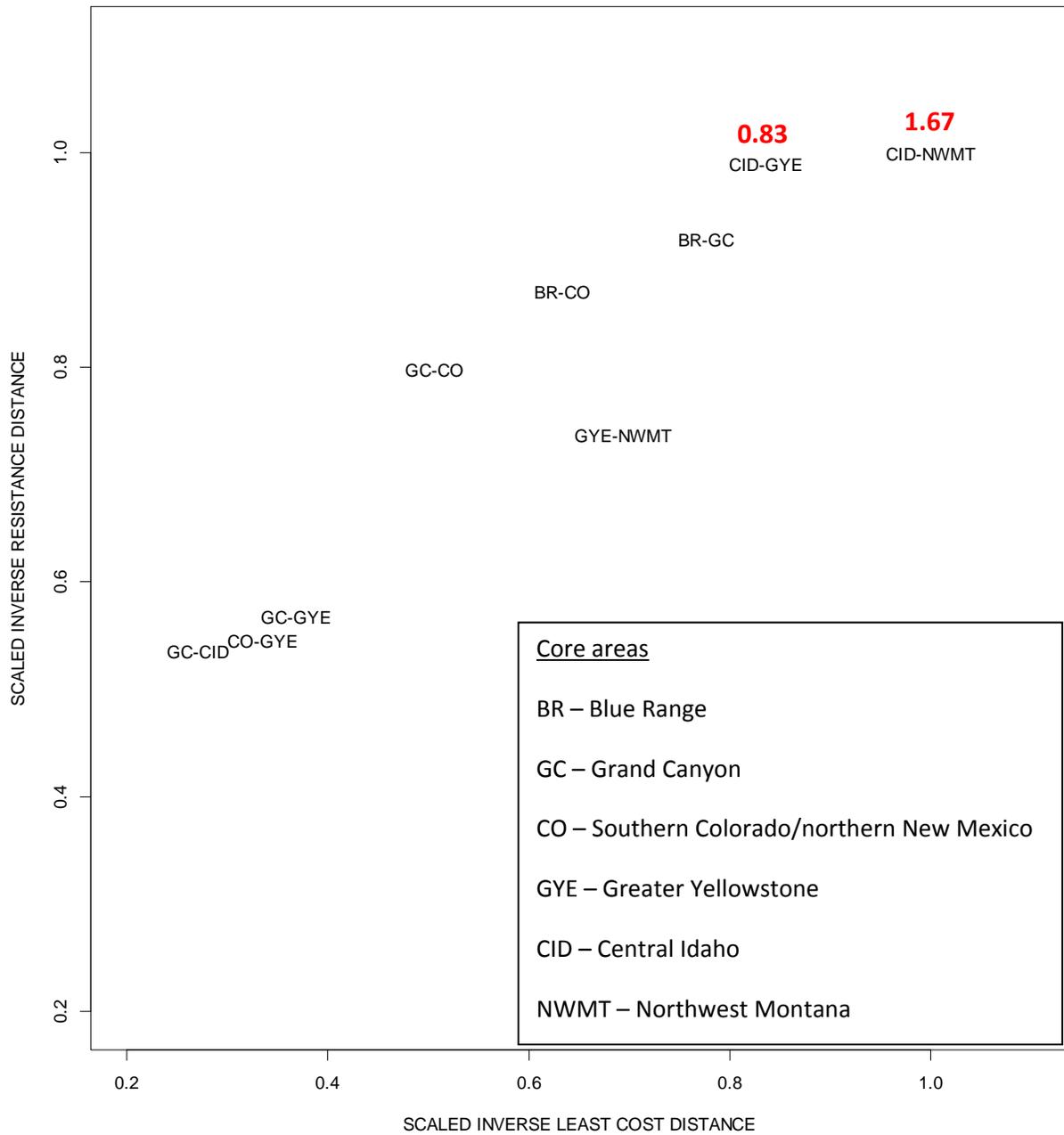


Figure 10. Potential connectivity (inverse of distance), expressed as inverse least cost and resistance distance, between existing or potential wolf population core areas in the western US. Values in red are estimates of effective migration rates per generation in the NRM based on Vonholdt et al. 2010 (multiplied by 2 to account for incomplete sampling).



ASSESSING POTENTIAL RECOVERY SCENARIOS AND IDENTIFYING FACTORS AFFECTING SUCCESS

Richard Fredrickson

December 3, 2013

A. CONSERVATION OF GENETIC DIVERSITY AND ADAPTIVE POTENTIAL AND ASSESSING POTENTIAL RECOVERY SCENARIOS

1. OVERVIEW: USING GENETICS TO INFORM VIABILITY CRITERIA

The increase in knowledge of conservation genetics over the last decade has made development of genetic criteria an increasingly important component of recovery planning (Allendorf and Luikart 2006, Frankham et al. 2010). Genetic criteria are especially relevant for taxa such as the Mexican wolf that are currently genetically depauperate (Hedrick et al. 2007). Genetic criteria are important because the genetic composition of a population affects both short-term demographic trends and viability (via inbreeding depression or accumulation of genetic load; Hedrick and Fredrickson 2010) and the long-term potential of the population to adapt to changing conditions. Genetic robustness may be defined as the genetic capacity to survive and respond to environmental changes within populations, among populations, and across the range (Redford et al. 2011).

The ESA's primary goal is recovery of wild populations that are self-sustaining over the long term. This requires that recovered populations experience minimal loss of genetic health. Because much of our knowledge of the importance of genetics in recovery stems from relatively recent research, some have argued that genetic criteria are 'theoretical' and thus of limited relevance to real-world wolf conservation (Fritts et al. 1995). On the contrary, evidence for the relevance of genetics to wolf population persistence arises from multiple lines of evidence including theory, captive wolf populations, and wild wolf populations. For example, the Isle Royale wolf population was long used as an example of a small and isolated population without apparent genetic issues. New research demonstrates that this population shows effects of inbreeding and also documents a recent example of genetic rescue via dispersal from the larger mainland population (Raikonen et al 2009, Adams et al 2011).

Due to recent advances in genetic research, genetic recovery criteria are increasingly ‘objective and measurable’ in wild populations as required under the ESA. Genetic health can be measured via population-level metrics such as heterozygosity and allelic diversity (Frankham et al. 2010). Additionally, new methods allow assessment of individual-level metrics such as the number of genetically-effective migrants between subpopulations. For example, vonHoldt et al. (2010) assessed the level of genetically-effective dispersal in the Northern Rocky Mountains (NRM) wolf metapopulation and concluded that the metapopulation currently met connectivity criteria that would be sufficient to limit loss of heterozygosity to <1% per generation.

The relatively recent nature of much conservation genetics research in wild populations has resulted in a scarcity of in-depth analyses of the effects of genetics on persistence. This has led to two divergent viewpoints. On the one hand, some authors have concluded that, because detailed genetic data are often unavailable, general ‘rules of thumb’ may be used to determine recovery criteria (e.g., MVP (minimum viable population) numbers) across a range of taxa (Traill et al. 2010). Other authors have contested these generalizations. For example, Flather et al. (2011) reanalyzed the data used by Traill et al. (2007, 2010) and concluded that there is little evidence for a pattern across taxa supporting generalized MVP thresholds. The broader and more defensible conclusion from Traill et al. (2007, 2010)’s meta-analyses is that a comprehensive consideration of genetic threat factors can greatly increase estimates of the MVP required for long-term viability. Although genetic rules of thumb may be insufficient in isolation for devising recovery criteria, they are helpful in contextualizing results from more detailed species-specific PVAs such as we conducted.

2. USING EFFECTIVE POPULATION SIZE (N_e) TO INFORM CRITERIA

Effective population size, or N_e , is a useful and appropriate metric to inform recovery and recovery criteria for a variety of reasons, including: 1) it integrates ecological as well as purely “genetic” considerations, and 2) it gives insight to the current and future genetic functioning of populations. Typically, the metrics produced by PVAs that seem most directly relevant to recovery criteria, such as probability of extinction, are highly sensitive to uncertainty in model parameters and structure. Effective population size (N_e) provides a metric that is relevant to recovery and potentially more robust to model uncertainty. The effective population size of a set of individuals denotes the number of individuals in an “ideal” population that would give rise to the same rates of inbreeding accumulation or random genetic drift that is observed in the set of individuals in question. An ‘ideal’ population is defined as a random mating population in which all parents have an equal probability of being the parents of any individual progeny (Hedrick 2005).

Effective population size is an appropriate metric to inform recovery criteria because it can be directly linked to genetic effects on viability. For example, heterozygosity is expected to be lost

from a population at a rate of $1/2 N_e$ per generation. Therefore a population with an N_e of 50 is expected to lose 1% of existing heterozygosity per generation.

Effective population size is a more robust metric than alternate genetic metrics such as inbreeding coefficient (F). Whereas effective population size provides information on the current functioning of the population (e.g. the relative strengths of genetic drift and natural selection, the rate at which heterozygosity is expected to be lost), mean inbreeding coefficient simply provides a snapshot in time of the estimated levels of identity by descent (homozygosity resulting from inbreeding accumulation). Subpopulations with rapid inbreeding accumulation will also tend to be those that go extinct earlier, leaving the remaining populations with relatively low inbreeding. Effective population size integrates considerations of subpopulation census size and connectivity in a non-arbitrary manner. A small subpopulation will require greater connectivity to achieve the same N_e as a larger subpopulation with low connectivity.

Molecular markers may be used to estimate the effective population size through a variety of statistical methods (Aspi et al. 2006). A review of genetically effective population sizes among wildlife populations (Frankham 1995) found that comprehensive estimates of effective population size were on average 10% of census population sizes, whereas a more recent review found an average ratio of 14% (Palstra & Ruzzante 2008). The estimated N_e / N ratios in gray wolves range from ca. 0.2 – 0.42 (Aspi et al. 2006; Peterson et al. 1998; vonHoldt et al. 2008). Two recent studies on wolves found that effective sizes were 28% and 42% of census population sizes (Aspi et al. 2006; vonHoldt et al. 2008), but the ratio for the Mexican wolf population is expected to be lower than that of the wolf populations in these studies because of its high mean kinship suggesting that on average wolves in the Blue Range population are about as related to one another as full siblings born to unrelated parents (Siminski and Spevak 2013). The high relatedness results in part from the high number of wolf removals from 2005 through 2007 combined with few releases of minimally related wolves over the last nine years. In addition, These removals resulted in unequal contributions from wolves in breeding positions that are still evident in the population. Finally the the long history of small litter sizes and low recruitment of wolves to alpha status in the Blue Range would also be expected to reduce the ratio of effective to census population sizes. In contrast, the Greater Yellowstone area population studied by Von Holdt et al. (2008) was founded by 31 presumably outbred and unrelated wolves drawn from two large wolf populations in Canada. This population quickly grew to much larger size minimizing the loss of genetic variation and accumulation of inbreeding. And the Finnish wolf population (Aspi et al. 2006) had relatively high gene flow, around 3 migrants per generation, from the larger and genetically differentiated Karelian wolf population to the east in Russia for at least part of the sampling period (Aspi et al. 2009).

3. ESTIMATING AN EFFECTIVE POPULATION SIZE THAT MINIMIZES SHORT-TERM GENETIC EFFECTS AND MAINTAINS LONG-TERM ADAPTIVE POTENTIAL

The 50/500 rule is perhaps the mostly widely-accepted ‘rule of thumb’ for consideration of effective population size in conservation planning (Frankham 1980). The ‘50’ component specifies that populations important for conservation should have a minimum effective population size of at least 50 to minimize inbreeding accumulation in the short-term until populations can be grown to much larger size. This would correspond to a maximum rate of inbreeding accumulation of 1% per generation, which is approximately half the maximum rate tolerated by domestic animal breeders (Franklin 1980). Allendorf & Ryman (2002) proposed a stricter criteria in which the recommended effective population size should allow retention of 95% of heterozygosity over a 100 year period, which in wolves would be equivalent to loss of <0.2% of heterozygosity per generation, or an N_e of ~250. While the 1% per generation rule underlying the $N_e = 50$ rule was approximate, it was based on a literature review over a wide variety of taxa of the inbreeding coefficient (and associated effective population size) that led to substantial inbreeding depression over the short term. This criterion is a well-established generalization that can be tested against species-specific modeling as we do here.

In their review of MVP rules of thumb, Flather et al. (2011) critique use of the 50/500 rule, stating that "the 50/500 values of N_e] are simply viability goals for maintaining genetically diverse populations; they provide little direct connection with extinction risk." However, although we agree with Flather et al. (2011) that the specific threshold embodied in the 50 rule may be somewhat arbitrary, the genetic processes they represent are directly connected with extinction risk and should be assessed in any comprehensive PVA.

In order to maintain its ability to adapt to new environments (such as caused by climate change or novel diseases), a population should be of sufficient size to maintain a balance between loss of alleles via genetic drift and new alleles produced by mutation. The ‘500’ portion of the 50 / 500 rule specifies that retention of allelic diversity through a long-term balance between mutation and genetic drift requires that a population or metapopulation maintain an $N_e \geq 500$, which in wolves might require a census population of >2500. More recent studies suggest that an N_e of 500 may be inadequate. Estimates of “evolutionary” MVP, the minimum population size required for species to adapt to changing environments through evolution, have ranged from effective population sizes of 500-1000 (Franklin et al. 1980; Franklin & Frankham 1998) to 5,000 (Lynch & Lande 1998).

Population sizes of these magnitudes would secure long-term sustainability of the population, addressing both genetic and demographic requirements (Frankham et al. 2002). Recovery of wolf populations of thousands of individuals, that obtain effective population sizes that secure a potential for future evolution, is challenging to achieve at the scale of any one region but may be feasible at broader scales (Carroll et al. 2006). Recovery goals should consider 1) securing sufficiently high population sizes within the present fragments (subpopulations) within the

historical range and adjacent areas and 2) securing sufficient connectivity among the subpopulations through natural migration.

4. GENETIC THREATS AND STRATEGIES FOR THEIR AMELIORATION IN THE MEXICAN WOLF

Addressing genetic threats are especially relevant to ensuring recovery of the Mexican wolf due to their few founders, strong inbreeding and inbreeding depression, and continuing history of small population sizes (Hedrick and Fredrickson 2010). Mexican wolves were rescued from extinction by the establishment of three captive lineages founded by a total of seven wolves (Hedrick et al. 1997). These lineages were managed separately until the mid-1990's by which time all three lineages had become strongly inbred. Inbreeding coefficients (f) for McBride, Aragon, and Ghost Ranch lineage pups born in the mid-1990's averaged about 0.23, 0.33, and 0.64, respectively. Heterozygosity was also low. Observed heterozygosity at 20 microsatellite loci averaged 0.457, 0.128, and 0.255 for McBride, Aragon, and Ghost Ranch lineage wolves, respectively. Although the McBride lineage was fixed for a single allele at two loci, the Aragon and Ghost Ranch lineages were fixed at 11 loci (Hedrick et al. 1997). Overall, heterozygosity was about half of that observed for other subspecies of northern gray wolves. At that time the "captive population" consisted of three tiny, separate, and highly inbred populations that were each experiencing severe genetic bottlenecks.

Out of concern for the low number of founders and rapid inbreeding accumulation the decision was made to merge the three lineages. Pairings between McBride lineage wolves and Aragon lineage wolves and between McBride and Ghost Ranch lineage wolves began in 1995 with the first F1 pups born in 1997. Although both parents of each F1 wolf were strongly inbred, the F1 wolves themselves were expected to be free of inbreeding and free of any deleterious effects on fitness due to inbreeding, called inbreeding depression. Ultimately 47 F1 wolves were produced from 1997 to 2002. Upon reaching maturity, the F1 wolves were paired among themselves, backcrossed with pure McBride wolves, and paired with the descendants of F1 wolves called "cross-lineage" wolves.

Although the F1 wolves had high reproductive fitness relative to wolves from the three founding lineages, there was evidence of strong inbreeding depression among cross-lineage wolves in captivity affecting dams, sires, and pups (Asa et al. 2007; Fredrickson et al. 2007). There was also evidence of strong inbreeding depression in the reintroduced Blue Range population.

Despite the merging of the three founding lineages, and a rapid increase in size, the captive population of Mexican wolves is still small with limited potential to support recovery. As of September 2013, it consisted of 248 wolves, of which 36 were reproductively compromised, leaving 212 wolves as the managed population (Siminski & Spevak 2013). The age structure of the population, however, is heavily skewed with wolves eight years old and above comprising

about 51% of the population. This senescent age structure has resulted from the high reproductive output of the F1 wolves and their descendants in captivity along with the combination of few releases of captive-born wolves to the reintroduced Blue Range population (BRP), and removals of wolves from the Blue Range population to captivity. It is estimated that more than half of the alleles from the seven founders have been lost from the population. The genetically effective population size (N_e) is estimated to be 21 and the ratio of effective to census size (N_e / N) is estimated to be 0.098 (Siminski & Spevak 2013). Thus the captive population is expected to lose about 2.4% of its heterozygosity each generation.

Data from about 6,000 SNPs suggest that while heterozygosity was restored in the F1 wolves, heterozygosity among cross-lineage wolves has declined to levels similar to that of mid-1990's McBride lineage wolves (R. Fitak, unpublished data).

Unfortunately the reintroduced Blue Range population is currently a poor representation of the genetic variation remaining in the captive population. Founder representation is more strongly skewed than in the captive population. Mean inbreeding levels are 61% greater in the BRP (0.1924 versus 0.1197), and only about two thirds of the alleles present in the captive population are estimated to be in the Blue Range population (Siminski & Spevak 2013). In addition, the estimated mean relatedness (mean kinship) of wolves in the Blue Range is about 50% greater than that in the captive population, with wolves on average about as related to one another as full siblings born to unrelated parents (Siminski & Spevak 2013). Without substantial management action to improve the genetic composition of the BRP, inbreeding will accumulate and heterozygosity and alleles will be lost much faster than in the captive population. A program of selective removals and initial releases over several years could greatly improve the genetic composition of the Blue Range as well as increase its demographic vigor.

Recovering Mexican wolves will entail reintroducing genetically diverse wild populations and growing them quickly to large sizes. Rapid growth of reintroduced populations is needed to minimize heterozygosity loss and inbreeding accumulation while the populations are small. This has not been done, however, in the Blue Range. Given the sizes of habitat patches potentially available for reintroductions, these restored populations would still lose heterozygosity at a rapid rate if they were isolated. Ensuring substantial levels of connectivity between the reestablished populations, however, could greatly slow heterozygosity loss and inbreeding accumulation within each population. In the long-term, failure to establish genetically diverse and connected wild populations would compromise the Mexican wolf's demographic vigor as well as its ability to adapt to future environmental challenges.

B. DETAILS OF VORTEX POPULATION SIMULATION MODEL

1. OVERVIEW OF VORTEX MODEL

Vortex is a simulation model of the effects of deterministic forces as well as stochastic demographic, environmental and genetic events on wildlife populations. It is an attempt to model the many factors composing the “extinction vortex” (Soule & Mills 1998) that can threaten the persistence of small populations (hence, its name). VORTEX models population dynamics as discrete, sequential events that occur according to probabilities that are random variables following user-specified distributions. VORTEX simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, dispersal between populations, harvest, supplementation, and then truncation of populations (if necessary) to the carrying capacity, and finally incrementing age by one year. The simulation of the population is iterated many times to generate the distribution of fates that the population might experience. VORTEX is an individual-based model. That is, it creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. VORTEX keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of the events occur.

We parameterized Vortex based on best available information from the Mexican wolf population (Fredrickson et al. 2007) and, where appropriate, other wolf populations. Vortex output allows tracking of both demographic criteria (population size, time to extinction) and genetic criteria (heterozygosity, allelic diversity, inbreeding coefficient). We evaluated both of these classes of output metrics under a range of scenarios with varying a) subpopulation size [$N=100-350$]; b) number of subpopulations [3-4], and c) dispersal rate between subpopulations [0-2 “effective” migrants per generation]. We compared results from populations founded by outbred and unrelated individuals with results based on populations founded by individuals with pedigree data based on the current captive and wild Mexican wolf populations.

In order to assess the effects of stochastic and genetic factors within a PVA, it is common to analyze parameter sets that contain ‘boosted’ demographic rates when data from existing populations suggest current demographic rates are inadequate for population persistence, under the assumption that deterministic factors that affect these rates will need to be addressed as a first priority, in order for criteria mitigating stochastic and genetic factors to be relevant (Caughley 1994). We first evaluated deterministic population growth rates (λ) across a range of sets of demographic rates derived from field data (Oakleaf unpublished data). Because mortality rates based on these data resulted in population growth rates < 1 , we then selected a baseline set of mortality rates based on data from the Greater Yellowstone Area that allowed population persistence ($\lambda > 1$). This allowed us to evaluate additional threats from stochastic and genetic factors. We then added parameterization of catastrophes (disease). We evaluated

population persistence and genetic metrics for the ensemble of scenarios across a range of population size and connectivity.

2. MORTALITY RATES

We first evaluated deterministic lambda (intrinsic population growth rate) for the Blue Range population of Mexican wolves based on mortality rates from Oakleaf (unpublished data) and found that lambda was substantially below 1. Consequently we used mortality rates based on those observed in the Greater Yellowstone area (GYA) which were intermediate to those estimated for the northwestern Montana and central Idaho wolf populations (Smith et al. 2010). For pups, we used an annual mortality rate of 24.4% with a standard deviation of 5.072. For yearlings and adults Smith et al. (2010) estimated an annual mortality rate of 22.9% in the GYA. To explore how different levels of yearling / adult mortality may affect Mexican wolf populations we used three mortality values in our simulations, 22, 23.5, and 25%. We estimated process variance for adult / yearling mortality from the GYA data used in Smith et al. (2010) by subtracting the variance due to annual demographic stochasticity from the total variation associated with annual adult / yearling mortality. From this we calculated a coefficient of variation of 0.2127 for adult / yearling mortality. We then used this value to set standard deviations for the three yearling / adult mortality rates used in our simulations.

3. DOWNLISTING CRITERION RELATED TO MORTALITY RATES

Wolf populations are generally limited in distribution to areas where the risk of being killed by humans is not excessive (Fuller et al. 2003). High rates of human-caused mortality are documented as a specific threat factor for Mexican wolves (see Section I.i.). We developed a downlisting criterion that addresses this threat factor. The criterion is expressed as in terms of the estimated rate of human-caused losses during an 8 year period. This criterion is relevant to downlisting (and not delisting) because wolf populations of a size that merit downlisting (150 individuals per population) will exist far enough below carrying capacity that the primary limiting factor on population growth will be human-associated mortality. At the time of delisting, populations will be closer to carrying capacity and may also be limited by other environmental factors. We derived an appropriate downlisting criterion from a separate analysis as described below (Vucetich et al. in review). However, a population that meets this criterion will also show total mortality rates similar to those assumed in the Vortex baseline scenarios. Thus our conclusions as to appropriate criteria for population size and connectivity will be more relevant for a metapopulation that meets the downlisting criterion for human-associated mortality.

Annual survival rate (S) is the proportion of animals in a population that survive from one year to the next. Evidence clearly indicates that S has an important influence on the population

dynamics of wolves (e.g., Fuller et al. 2003; Peterson et al. 1998). That is, as S decreases there is a strong tendency for λ , the population growth rate, to decrease. Population growth rate is the fundamental determinant of a population's numerical dynamics. Because recruitment rate (the process that balances mortality rate) in the Mexican wolf population is affected by inbreeding depression, the population may be more sensitive to fluctuations in S than most other wolf populations. Significant human-caused mortality (m_{hc}) (poaching, vehicle collisions, lethal management removal actions, etc.) occurs in most wolf populations. Four recently published papers present analyses that quantify the relationship between m_{hc} and S for wolf populations (Adams et al. 2008; Creel and Rotella 2010; Murray et al. 2010, Sparkman et al. 2011). Collectively these papers indicate that S and r tend to decrease as m_{hc} increases.

Previous analyses of m_{hc} and r were based on data that would also allow one to calculate the probability that r would fall below any specified level, given m_{hc} . For this reason, we developed this downlisting criterion by first reasoning that the rate of human-caused losses should be low enough to correspond with a reasonably high chance that the population's growth rate would be sufficiently positive to allow reasonably fast growth as the population begins to recover from its status of endangered to threatened. The need for a reasonably fast growth rate is further justified by the irreparable damage that inbreeding may cause if the population grows too slowly during these early stages of recovery. Based on this reasoning, we calculated the value of m_{hc} that corresponds to a relatively low risk (25%) of r falling below 2.5%/yr. We refer to this threshold value as X .

The downlisting criteria are expressed as: the estimate for the expected value for the average rate of human-caused losses during an 8-year period should be less than X . Mexican wolves have also been experiencing high rates of management removals from the wild. These removals are functionally equivalent to a mortality event from the perspective of the free-ranging population. For this reason, the downlisting criterion that we develop will pertain to the rate of human-caused losses, where losses include human-caused mortalities (poaching, vehicle collisions, etc.) and management removals.

We calculated X by analyzing data collected from wolf populations across North America where m_{hc} and r had been monitored. One set of such data was compiled by Creel and Rotella (2010). Those data included: 1) 18 populations from across North America (originally compiled by Fuller et al. (2003), where each population had been observed for one or several years; and 2) 29 estimates from wolf populations living in the Northern Rocky Mountains. We used this data set along with others to make our calculations. Based on the analysis of Vucetich et al. (in review), we propose that to be considered for downlisting, the best estimate for the expected value for the average rate of human-caused losses during an 8-year period should be less than 17%.

4. REPRODUCTIVE PARAMETERS

The following parameters related to reproduction were set to values that are standard for previous Vortex analyses of wolf populations:

- 1) Mating system: Long Term Monogamous
- 2) Age of first reproduction for females/males = 2 years
- 3) Maximum age of reproduction = this was set to 11 years, but functionally wolves older than 9 years old could not reproduce (see Density Dependence below)
- 4) Maximum number litters per year = 1
- 5) Maximum number progeny per litter = 11
- 6) Probability of female in breeding pool having no litter: 0
- 7) Sex Ratio = 50/50
- 8) % Males in Breeding Pool = 100

Fecundity for wolf populations in the Vortex simulations is a function of litter size and the proportion of adult females breeding. The function for litter size was based on Fredrickson et al. (2007) as described below. Previous Mexican wolf PVAs have set the proportion of adult females breeding at 50% (Seal 1990) to 60% (IUCN 1996). vonHoldt et al. (2010) used an estimate of 35% for the Yellowstone population, while a PVA for the Algonquin (Ontario) wolf population used a value of 57% derived from the mean from estimates ranging from 50-64% (Ewins et al. 2000). We set the proportion of adult females breeding at 50%, with an SD of 12.5% for our simulations but the sensitivity analysis of Carroll et al. 2013 also conducted simulations incorporating a density dependent function for this parameter (see below).

5. DENSITY DEPENDENCE, CARRYING CAPACITY, AND HARVEST

Two forms of density dependence were incorporated into the simulations. The first was density dependence on survival of adults greater than 6 years old. In well-studied populations of northern gray wolves, relatively few adults live past eight years old (e.g. Smith et al. 2010). And very few females produce pups after eight years. But in the BRP, a relatively large proportion of wolves have been documented to survive to up to 11 years while retaining alpha status, even though only one female wolf is known to have produced pups after nine years old. It is thought that the longevity of wolves in the BRP is a function of the small population size and low density of the population, and that as the population gets larger the proportion of very old wolves will drop.

Consequently we have incorporated a function into the simulations that causes mortality to increase with age past six years, and the rate of mortality increases is greater at high wolf densities (Figure 1). At very low wolf densities, wolves may live up to 11 years, but at high wolf densities no wolves live past nine years old. For example, mortality rates for nine year old

wolves increased from 31.5% to 93.5% as wolf numbers increased from 10% of K to 75% of K , when the baseline mortality rate was 22%.

In the simulations below we set the % of adult females breeding at a constant value of 50 with a standard deviation of 12.5. In the sensitivity analysis of Carroll et al. 2013, however, we investigated the effects density dependence on the % of adult females breeding. We developed a density dependent function (Figure 2) based on data from Yellowstone National Park (Smith and Stahler unpublished) from years in which both the numbers of females breeding was known and total wolf numbers could be estimated. With this function, about 59% of adult females were expected to breed each year when populations were at very low densities. At maximal densities ($N = K$), however, only 30% of adult females were expected to breed in a given year. The standard deviation of the % adult females breeding with density dependence was set to 25% of the mean value for each year.

Targeted sizes for individual populations in simulations ranged from 100 to 300 individuals. We assumed that “recovered” wolf populations would likely exist at numbers below ecological carrying capacity due to human caused mortality. Consequently, in the simulations we set carrying capacities of individual populations to 133% of the targeted size. Vortex uses carrying capacity (K) to impose a ceiling model of density-dependence on wolf numbers, i.e. if wolf numbers are above K at the end of a timestep, Vortex randomly kills additional wolves until the population size is equal to K . To maintain wolf numbers below K , we used the “Harvest” function in Vortex. We parameterized the function to “harvest” wolves each year that the population size exceeded the target population size, beginning in year 25. By this time, population size had reached or exceeded K in most iterations. When harvest occurred, 12.5% of the wolves above the target population size were taken, from each of four sex / age classes: male pups, female pups, male yearling and adult, and female yearlings and adults. We set the standard deviation in carrying capacity due to environmental variation (drought, etc.) to 10%.

Previous Mexican wolf PVAs (Seal 1990, IUCN 1996) did not incorporate density dependence in reproduction. We propose that limiting density dependence to survival is the most parsimonious strategy because 1) data is scarce on the response of reproductive parameters to density, and 2) once Mexican wolf subpopulations reached moderate densities, dispersal to adjacent areas with lower survival rates would be expected, and thus ‘saturated’ conditions would rarely occur given the fragmented distribution of wolf habitat in the southwestern U.S.

6. DISEASE AND OTHER “CATASTROPHIC” EVENTS

We parameterized episodic threats based on data from the Yellowstone wolf population which showed distemper outbreaks occurring on average of every 5 years, and affecting primarily fecundity rather than survival (Fecundity: 20% of baseline, Survival (all age classes): 95% of

baseline). Because we did not model additional episodic threats such as other diseases or drought, this can be seen as an optimistic parameterization of catastrophes. All catastrophes were 'local' rather than 'global', i.e., were not simultaneous across populations. Carroll et al. (2013), however, considered frequencies of catastrophes from four to six years as part of their sensitivity analysis.

7. GENETIC EFFECTS

Previous Vortex wolf PVAs have either ignored genetic effects (Ewins et al. 2000), or used a fraction of the default number of lethal equivalents in Vortex (3.14), which is a median value obtained in a study of captive populations of 40 mammalian species (Ralls et al. 1988). This likely represents an underestimate of inbreeding effects in wild populations (e.g. Keller and Waller 2002). The Mexican wolf PVAs of Seal (1990) and IUCN (1996) set this value at 1.7 and 3.14 LE, respectively.

Fredrickson et al. (2007), however, found evidence of strong negative effects of inbreeding on reproduction in both the captive and wild populations of Mexican wolves. Among captive wolves with ancestry from at least two of the founding lineages, they found that inbreeding accumulation in the both sires and dams rapidly reduced the probability of a pair producing at least one live pup. Of those pairings that produced at least one live pup, inbreeding in the dam and in the pups were found to have strong negative effects on litter size. In the BRP they also found that inbreeding accumulation in the pups reduced observed litter sizes, but a lack of data prevented them from meaningfully examining the effects of parental inbreeding on litter sizes. These results are consistent with those of Asa et al. (2007) who found that inbreeding reduced semen quality in Mexican wolves.

Strong inbreeding effects have also been observed in other wolf populations. In the Scandinavian wolf population, inbreeding accumulation has been found to reduce both litter sizes and the probability of a wolf attaining a breeding position (Liberg et al. 2005; Bensch et al. 2007). Inbreeding has also been tied to high incidences of severe skeletal defects among Scandinavian and Isle Royal wolves (Raikonen et al. 2006; 2009). And the recent genomic sweep of the Isle Royale wolf population by a single immigrant from the mainland illustrates the low relative fitness of the highly inbred Isle Royale wolves (Adams et al. 2011). More generally, inbreeding depression has been shown to be common in wild populations where inbreeding is occurring, resulting in reduced individual fitness and producing population level effects among a wide range of plants, invertebrates and vertebrates (e.g. Keller & Waller 2002).

In the simulations we incorporated inbreeding effects on litter size using the best model from the Blue Range data in Fredrickson et al. (2007). Although this is a significant advance in realism

relative to previous Mexican wolf PVAs, our treatment of inbreeding likely underestimates of the overall effects of inbreeding depression among wild Mexican wolves.

8. FOUNDING POPULATIONS

For the simulations we assumed that releases to found new populations of Mexican wolves would begin in 2018 and be completed by spring of 2022. Thus the simulations are assumed to begin in the spring of 2022.

To “update” the Blue Range population to 2022, we first constructed a Blue Range pedigree based on the results of the January 2013 wolf count. During this count 75 wolves and 14 packs were detected, but one wolf was permanently removed leaving 74 wolves. Based on the results of the count we assumed there would be one unknown pair among the uncollared wolves detected, and that one radio collared yearling female disperser that was traveling with another wolf would form a new pair. We also assumed that the Hawks Nest alpha male (whose collar does not work) would pair with an undetected wolf. In the spring of 2013 the USFWS had two pairs together in captivity with intentions of releasing both in 2013. We assumed that both would be released before pups were produced. In total, we assumed there would 79 wolves and 17 pairs in the BRP at the start of 2013. Two of the pairs, however, had alphas that are post-reproductive (10+ years old) and would not produce pups in the simulations, leaving 15 reproductive pairs in the BRP in spring 2013.

To “update” the BRP from spring 2013 to spring 2022 we ran a simulation with only the BRP for nine years, with an adult mortality rate of 22.75%. The median population size for the BRP at year 9 was 121 wolves, based on 1000 iterations. We next ran single iteration simulations until we got an ending population size close to 121. From this simulation we used simulation output from Vortex to extract the pedigree over the previous nine years. The simulation we chose had N=122 wolves at year 9. The information extracted from the simulation included not just the pedigree, but the sexes and ages of the wolves alive at the end of the simulation (2022). So in the simulations presented below the BRP was started with 122 wolves and 21 pairs.

We next created new wolves and wolf pairs to found new wild populations during the period 2018 – 2022. Because few of the existing captive wolves will be suitable for release during this period, we first created a new generation of captive wolves which could be used in releases. In total, a pool of about 800 wolves was generated from which founding wolves could be selected. We used the program PMx (Ballou et al. 2011) to select wolves from the pool to create two populations of ten pairs and two populations of nine pairs. Individuals chosen for each population were to be minimally related and collectively provide a good representation of the existing genetic variation in the existing captive and wild populations. We then used PMx to pair the wolves in each population. The result was four new populations of 20, 20, 18, and 18 wolves that each had better representation for the existing genetic variation than the current captive population.

The wolves selected by this process, however, would result in some individual wolves producing offspring for the released populations with up to five different mates. This is unrealistic for the captive population. So we then revised the parental pairings so that the individual wolves producing the release wolves would have no more than two mates over time.

Once the 38 founding pairs were determined, a timetable was developed for when each pair would be released. For the Grand Canyon and Southern Rockies populations, we assumed that two new pairs would be released each year from 2018 to 2022 for a total of 10 pairs released into each population. These alphas potentially produced offspring each year after release. They also experienced mortality so that by 2022 only about half of the founding pair members were still alive. We then paired single alphas and 2 – 4 year old offspring among themselves such that at the start of 2022 each population had a total of 50 wolves and 10 pairs. Sex was randomly assigned for descendants of the founding pairs. We used the same process for the Mexican populations, but used only 7 of the 9 pairs noted above, resulting in starting populations of 35 wolves with seven pairs in 2022. Throughout the process of developing the new populations, no artificial insemination was used. All wolves were produced by natural pairings. Table 1 presents the numbers of wolves and packs used to found simulated wolf populations. Departures from these numbers are noted in the results below.

9. CONNECTIVITY BETWEEN POPULATIONS

Carroll et al. (2006) identified three major core areas of suitable habitat in the area encompassing Arizona, New Mexico, southern Colorado and southern Utah which may be most suitable for restoring large populations ($N \geq 250$) of Mexican wolves. The three core areas of suitable habitat are a) the Blue Range Wolf Recovery Area and adjacent public lands, b) the Grand Canyon and adjacent public lands, and c) two linked areas of public lands and private lands with conservation management in northern New Mexico and southern Colorado (labeled Carson and San Juans in Carroll et al. (2006))(see section I.H.).

In addition two areas in the western Sierra Madre of Mexico have been identified that may each be able to support around 100 wolves (Araiza et al. 2007; C. Lopez personal communication). The northern area (Sonora) spans the Sonora / Chihuahua border from New Mexico south about 240 km. The southern area (Durango) is primarily in southwestern Durango extending south into Zacatecas.

Based on habitat modeling for the southwestern USA, we assumed that the Grand Canyon and southern Rockies populations would both be linked by dispersal to the Blue Range, but there would be no natural dispersal between the Grand Canyon and southern Rockies. Similarly, we also assumed that the Sonora population would be linked by dispersal to both the Blue Range and Durango populations, but that there would be no natural dispersal between Durango and the

Blue Range. For these networks of populations we simulated three levels of connectivity between populations in our simulations: no dispersal between populations, dispersal sufficient to provide an average of 1 genetically effective mpg (1 mpg) to each population, and dispersal sufficient to provide 2 genetically effective mpg to the centrally located Blue Range and 1 genetically effective mpg to each of the other populations (2/1/1 mpg). Simulations were parameterized such that the burden of providing immigrants into the Blue Range was equitably split among neighboring populations based on population size. Dispersal between populations was modeled as a constant proportion of young wolves (1 – 4 years old) moving to a neighboring population each timestep.

We defined an effective migrant as a wolf that immigrated into a non-natal population, paired and produced at least one pup in its new population. We quantified the number of effective migrants into each population by tallying the numbers of effective migrants reported by Vortex in each iteration from years 31 -100 and dividing the total by the number of wolf generations. We used a generation time of 4.2 years. Numbers of effective migrants reported are averages over all iterations for each population. Iterations of a given population were omitted from the calculation of effective migrants if a donor population became extinct during the iteration. In the simulations, we attempted to ensure that populations received at least the minimum number of effective migrants. We also attempted to limit the numbers of effective migrants into each population to no more than 10% above the desired average. We chose the years 31 – 100 for quantifying effective migrants, because migration rates were typically highest early in the simulations e.g. years 20-35, and declined over time. By omitting a portion of the highest migration years we ensured that our parameterization of dispersal rates provided for migration even when populations were below targeted sizes.

10. CONTEXT: COMPARISON WITH PREVIOUS VORTEX-BASED MEXICAN WOLF PVAS

The Vortex software used in the PVA simulates the life cycle of individuals in a population and the interacting effects of the population's demographic and genetic composition. Although Vortex does not evaluate habitat distribution and other spatial issues, its detailed evaluation of genetic issues complements results from habitat models. Although Vortex has been used in previous Mexican wolf recovery planning efforts (Seal 1990, IUCN 1996), we now have better genetic and demographic data and a more developed software (Vortex version 10) that allow more complex analyses than were previously possible. Neither of the previous Mexican wolf PVAs rigorously addressed genetic issues. The 1990 PVA simulations suggested that a population of 100 or more animals would have less than 5% probability of extinction over the 100 year time period (Seal 1990). However, because larger populations were required in order to retain a large proportion of the starting heterozygosity, the authors speculated that “in order to biologically recover the Mexican wolf, a meta-population of at least 1000 wolves will need to be free-ranging in the wild.”

The 1996 PVA (IUCN 1996) predicted that the risk of extinction over a 100-year time frame for a population reintroduced into the White Sands Recovery Area was considerable. In contrast, the authors concluded that a population inhabiting the Blue Range Recovery Area would have a reduced risk of extinction due to its larger size. The authors found considerable sensitivity of the Blue Range population to catastrophic events (drought, disease). They also cautioned that “the genetic picture Vortex paints is an optimistic one, since the program assumes that each new individual supplemented to the existing population is completely unrelated to all individuals in that population. Because of the very-restricted number of founders making up the captive Mexican wolf population, captive individuals will have some degree of relatedness to each other as well as to those individuals recently reintroduced into the wild.” The current PVA is the first to quantitatively assess the speculations concerning genetic MVPs in the 1990 and 1996 PVAs. Our analysis using pedigree data confirmed earlier concerns regarding increased extinction risk to populations derived from inbred founders.

In addition to the enhanced genetic capabilities of the current version of Vortex, we have substantially increased the amount and types of information that can be output from each simulation. For example, for each population it is now possible to quantify the numbers of census and effective migrants received, the rate of inbreeding accumulation, and changes in heterozygosity, and census population sizes in each timestep of each iteration in a simulation.

Finally, we have extensively tailored the simulation to incorporate several important aspects of wolf natural history including: 1) allowing wolves to survive past their reproductive years, when the population is at low density, 2) incorporating density dependent survival senescence for older wolves, 3) incorporating realistic dispersal between populations by limiting the pool of potential dispersers to young, non-breeding wolves and assigning increased mortality to those that move between populations, 4) preventing full sibling and parent-offspring pairings, 5) inclusion of a density dependent function for the % adult females breeding based on empirical data (used in sensitivity analysis of Carroll et al. 2013), and 6) incorporating a mechanism to allow wolf populations to be maintained at densities substantially below carrying capacity.

Finally, we have also incorporated perhaps the most defining feature of the wolf social system – the monopolization of breeding opportunities by a subset of adult wolves. In natural wolf populations, breeding is typically limited to a single adult male and female in each pack, and these individuals restrict breeding by others for the duration of their tenure as breeders. From a population genetic perspective this has the effect of excluding some wolves from contributing their genes to future generations and reducing the contribution by other wolves. This aspect of the wolf social system reduces the genetically effective population size (N_e) of natural wolf populations. All of these enhancements make the demographic and population genetic functioning of the simulated populations more realistic.

C. RESULTS OF VORTEX SIMULATIONS

We used Vortex in a two-step process to identify scenarios that may provide a suitable basis for recovery criteria. We first considered seven scenarios that varied widely in the numbers and sizes of populations included. Based on the results from the first step, we identified three scenarios to examine in greater detail.

1. FOUR SCENARIOS

Because previous Vortex modeling indicated that multiple large populations of Mexican wolves will be needed for recovery and habitat availability indicated these large populations will need to be in the USA, we further investigated three potential recovery scenarios. Scenario 1 required three populations each with at least 250 wolves for a total of at least 750 wolves (3x250). The second recovery scenario was an adaptation of scenario 1 that would allow greater management flexibility. It required three populations of at least 200 wolves for a minimum of 750 total wolves; the “extra” 150 wolves could be distributed among any of the three populations. The most extreme outcome of this scenario would be two populations of 200 and one population of 350. This would also potentially be the most detrimental configuration. To better understand the potential viability costs and benefits of this proposed management flexibility we simulated two different metapopulations with two populations of 200 wolves along with a single population of 350 wolves. The first assumed at least 350 wolves would be maintained in the Grand Canyon population and at least 200 wolves would be maintained in each of the other two populations (Grand Canyon 350). The second assumed that at least 350 wolves would be maintained in the Blue Range and that the Grand Canyon and Southern Rockies populations would each support at least 200 wolves (Blue Range 350). In the simulations below, the Grand Canyon and Blue Range populations were the strongest and weakest populations, respectively. It should be noted that because Vortex is not truly a spatially explicit simulation model the locations of the “Grand Canyon” and “Southern Rockies” populations are interchangeable, i.e. the population called Grand Canyon below could have instead been called the Southern Rockies. The third recovery scenario required three populations of at least 250 wolves as well as a fourth population of at least 100 wolves in Mexico (3x250 + Sonora). Requiring at least one population be established and maintained in Mexico would expand the geographic range of the recovered Mexican wolf population and address significant portion of range concerns. Finally we simulated a fourth scenario which was not considered a recovery scenario. This scenario would require at least 250 wolves in the Blue Range and two populations in Mexico each supporting at least 100 wolves (Blue Range+2MX100).

2. SCENARIO 1: 3X250

At the start of the simulations the three populations differed in their mean kinship levels. The Blue Range had a mean kinship of 0.2446, whereas the Grand Canyon and southern Rockies had lower mean kinships of 0.194, and 0.1954, respectively (Table 2). Mean kinship is a measure of the average relatedness of each individual to all individuals in the population including itself. A mean kinship of 0.25 would mean that on average individuals in the population were as related to each other as are full siblings from unrelated parents. In the absence of immigration from other populations, the initial mean kinship of a population will affect how quickly heterozygosity is lost and inbreeding accumulates. The simulated BRP started with a mean kinship slightly less than the actual Blue Range (0.2472) despite being “advanced” by nine years. The low mean kinship of the simulated Blue Range relative to the actual Blue Range is in large part a result of the inclusion of two new pairs that were planned for release in 2013. One of these pairs was released but one member died and the other was brought back into captivity. The other pair was not released. Mean kinships for the Grand Canyon and southern Rockies at the start of the simulations were 26 and 25% lower, respectively, than that for the Blue Range, but substantially higher than that for the captive population (0.1665; Table 3).

When there was no dispersal between populations, the Blue Range initially increased rapidly in size from 122 wolves at the start of the simulations. By year 24 the mean size of extant iterations had peaked at 244 wolves when there was 22% adult mortality (Figure 3A). Wolf numbers declined steeply starting at year 25 due to the initiation of harvests, and continued to decline to the end of the simulation. By year 100 the mean size of extant iterations had declined to 134 wolves – only eight more than the Blue Range started with at year zero. In contrast, the Grand Canyon began the simulation with 50 wolves and increased rapidly to a mean of 241 wolves at year 24 (Figure 3B). Initiation of harvest at year 25 resulted in a small decline in mean population size, followed by a slow decline in numbers to a mean of 193 wolves among extant populations. The southern Rockies population performed similarly to the Grand Canyon ending the simulation with a mean size of 189 wolves. Despite starting the simulation with nearly 2.5 times as many wolves as the Grand Canyon (and southern Rockies) the Blue Range ended the simulation with 44% fewer wolves. The differences in mean sizes of the three populations was a result of the differences in initial mean kinships of the populations and provided an illustration of the effects that the composition of the starting populations may have on their viability.

With 1 mpg and 22% adult mortality the Blue Range peaked at 213 wolves before declining to a mean of 156 wolves at year 100 (Figure 3A). But for the first 68 years of the simulation the mean population size of the Blue Range with 1 mpg was smaller than that with no dispersal between populations. This illustrated the demographic cost of the 1 mpg dispersal regime to the centrally located Blue Range. Whereas the Blue Range sent out about 2 migrants per generation (1 mpg each to the Grand Canyon and southern Rockies), the other populations each sent about 0.5 migrants per generation to the Blue Range. The demographic cost of this dispersal regime was in large part a result of the high mortality rate (62.5%) assumed for wolves dispersing between populations. In addition some wolves which successfully moved to non-natal populations died

before producing a pup and were not considered as genetically effective migrants. With 25% adult mortality, the demographic cost of the 1 mpg dispersal regime to the Blue Range became extreme (Figure 3C). Mean wolf numbers peaked at 129 wolves in year 6 before declining to a mean of 49 wolves at year 100. For the entire 100 year period the Blue Range had fewer wolves than with no dispersal between populations. It should be noted that the Blue Range received a mean of 1.28 mpg (Table 3), notably above the 1 - 1.1 mpg range targeted. Without these “extra” migrants the Blue Range would have supported even fewer wolves over time. The mean number of migrants received by the Blue Range was increased to ensure that the Grand Canyon and southern Rockies each received at least 1 mpg. Based on many trial simulations it appeared that the parameter space in which the Blue Range could send at least 1 mpg to each of the two peripheral populations while receiving 1 – 1.1 mpg may have been very limited.

With 2/1/1 mpg, there was still a demographic cost to the Blue Range in the early years of the simulations. When there was 22% adult mortality, mean population size for the Blue Range with 2/1/1 mpg lagged that with no dispersal for the first 27 years of the simulation (Figure 3A). But for the remaining 73 years, the Blue Range was larger than that with no dispersal between populations. At year 100, the Blue Range averaged 216 wolves with 2/1/1 mpg, and exceeded that with no dispersal between populations by 82 wolves on average. With 25% adult mortality, the demographic cost of 2/1/1 mpg extended through the first 48 years (Figure 3C). But by year 100, the Blue Range averaged 117 wolves, exceeding that with no dispersal between populations by an average of 58 wolves.

In contrast to the Blue Range, the Grand Canyon had the highest mean population sizes with 1 mpg (Figure 3B and D). But with 2/1/1 mpg, the peripheral Grand Canyon population bore a small demographic cost relative to 1 mpg as a result of having to send twice as many migrants to the Blue Range. The southern Rockies population performed similarly to the Grand Canyon. Although mean wolf numbers were relatively steady after harvests began for the Blue Range with 2/1/1 mpg and for the Grand Canyon with 1 mpg when there was 22% adult mortality (Figure 3A and B), the modest harvest “buffer” incorporated into the simulations was inadequate to allow wolves to be maintained above the numerical criteria for delisting. Incorporation of a numerical buffer above the 250 wolf goal would have allowed populations to remain “recovered” even while being harvested.

The adult / yearling mortality rates used in these simulations had a large effect on the numbers of wolves present and whether wolves were able to maintain their numbers over time. Mean peak wolf numbers and mean numbers of wolves at year 100 were highest with 22% adult mortality (Figure 3). With 23.5% and 25% adult mortality, mean peak wolf numbers for the Blue Range were 15% and 35% lower, respectively, than with 22% adult mortality and 2/1/1 mpg. For the Grand Canyon mean peak wolf numbers with 23.5% and 25% adult mortality were 11% and 27% lower, respectively, with 2/1/1 mpg.

Mean number of wolves at year 100 among extant iterations in the Blue Range were 17% and 46% lower when there was 23.5% and 25% adult mortality, respectively, than with 22% adult mortality and 2/1/1 mpg. For the Grand Canyon, mean wolf numbers at year 100 with 23.5% and 25% adult mortality were 16% and 38% lower, respectively, with 2/1/1 mpg. By year 30, the mean numbers of wolves among extant iterations had stabilized following the initiation of harvests when there was 22% adult mortality and 2/1/1 mpg (Figure 3A and B). From year 30 to the end of the simulations, the mean numbers of wolves present in the Blue Range and Grand Canyon populations declined by 2% and 5% respectively. But with higher adult mortality the mean trend in wolf numbers from year 30 to year 100 became increasingly negative. With 23.5% adult mortality, the Blue Range and Grand Canyon populations declined by 5% and 12%, respectively. And with 25% adult mortality, both populations declined by 22% by year 100 (Figure 3C and D).

Whereas the mean size of the Blue Range initially increased and then sharply declined over the last 76 years of simulations when there was no dispersal between populations (Figure 3A and C), mean expected heterozygosity declined in a roughly linear fashion throughout the 100 year period of the simulations (Figure 4A and C). With 1 mpg, heterozygosity losses at year 100 were reduced by 60, 49, and 41% with 22, 23.5 and 25% mortality, respectively, relative to when there was no dispersal between populations, despite the substantial demographic costs of this dispersal regime to the Blue Range. When there was 2/1/1 mpg heterozygosity losses were reduced by 89, 85, and 68% with 22, 23.5, and 25% mortality, respectively, relative to when there was no dispersal between populations (Figure 4A and C).

The Grand Canyon population also grew rapidly in size up to year 24, but the subsequent declines in population size in the absence of dispersal between populations were not as extreme as that for the Blue Range (Figure 3). When there was no dispersal between populations mean expected heterozygosity declined rapidly for approximately the first 20 years but then slowed (Figure 4B and D). This suggested that the genetically effective size of the population increased as the population grew from 50 wolves at the start of the simulations to much larger sizes. But the proportion of initial mean expected heterozygosity lost by year 100 was similar to that of the Blue Range. With 2/1/1 mpg, heterozygosity losses at year 100 were reduced by 35, 35 and 27% with 22, 23.5, and 25% adult mortality, respectively, relative to when there was no dispersal between populations. Heterozygosity loss was similar for the 1 mpg and 2/1/1 mpg dispersal regimes even though census population sizes were somewhat larger with 1 mpg (Figure 3B and D). By year 100, mean expected heterozygosity among extant populations was 1-2% higher in the Blue Range than in the Grand Canyon for all three mortality rates considered. With 1 mpg, however, mean expected heterozygosity at year 100 was 2-4% lower for the Blue Range.

Each of the simulated populations had a significant heterozygosity excess at the start of the simulations, a characteristic of populations that have suffered a genetic bottleneck. A heterozygosity excess occurs when the observed heterozygosity for a population is greater than the heterozygosity expected based on Hardy-Weinberg genotypic proportions (expected

heterozygosity). A heterozygosity excess arises as rare or uncommon alleles are lost quickly from the population due to the strong genetic drift associated with small effective population sizes during a genetic bottleneck. In this case the loss of alleles is immediately reflected in the calculated expected heterozygosity even though actual genotypic frequencies within the population have not yet reverted to Hardy-Weinberg proportions.

Although all simulated populations had heterozygosity excesses at the start of the simulations, the Blue Range was unique in starting with a relatively low heterozygosity excess and having its excess increase over the 100 period of the simulation, in some cases. In contrast, the Grand Canyon and southern Rockies started the simulations with high heterozygosity excesses, but ended with reduced excesses in all cases. An increasing heterozygosity excess indicates the population is still losing alleles at a rapid rate as the bottleneck continues. A declining heterozygosity excess indicates that the population is moving towards a new genotypic equilibrium following a bottleneck.

When there was no dispersal between populations, the Blue Range heterozygosity excess increased over time for all adult mortality levels, but the heterozygosity excess for the Grand Canyon declined over time (Figure 5). Results for the southern Rockies were similar to that of the Grand Canyon (not shown). Increases in adult mortality rate resulted in increased heterozygosity excesses at year 100 for all populations. When there was 1 mpg and 22% adult mortality the Blue Range heterozygosity excess at years zero and 100 were identical. But with 23.5 or 25% mortality the Blue Range heterozygosity excess increased over time. For the Grand Canyon, the heterozygosity excesses remaining at year 100 with 1 mpg were reduced relative to that with no dispersal. When there was 2/1/1 mpg the Blue Range heterozygosity excess declined over the 100 years of the simulation with 22 and 23.5% adult mortality. But with 25% adult mortality the Blue Range heterozygosity excess increased over time. The excess, however, was < half that observed with 1 mpg. For the Grand Canyon, the heterozygosity excess at year 100 was nearly identical to that observed with 1 mpg, for all three mortality rates.

In addition to having lower census population sizes, greater heterozygosity losses, and more prolonged genetic bottlenecks, the Blue Range also had higher extinction rates than the Grand Canyon and southern Rockies populations. We defined the extinction rate as the percentage of iterations that became extinct at any time during the simulation, even if they were later recolonized by dispersers. When adult mortality was 22% and there was no dispersal between populations the Blue Range became extinct in 18% of iterations, but the Grand Canyon and southern Rockies became extinct in only 10 and 12% of iterations, respectively (Figure 6A). Although the Blue Range started the simulation with nearly 2.5 times as many wolves as the other populations (122 versus 50), it had an extinction rate 73 and 46% higher than the other two populations. When there was 1 mpg, extinction rates for all three populations were greatly reduced but the Blue Range still had the greatest rate. But with 2/1/1 mpg the Blue Range had the lowest extinction rate.

When adult mortality rates were increased to 23.5%, extinction rates roughly doubled for all populations with 1 mpg, except for the Blue Range which increased five-fold (Figure 6B). The Blue Range extinction rate with 1 mpg was about triple that of the Grand Canyon and southern Rockies. But with 2/1/1 mpg the Blue Range again had the lowest extinction rate. With 25% adult mortality extinction rates were high for all three populations, but they were highest for the Blue Range, except when there was 2/1/1 mpg (Figure 6C). With no dispersal between populations extinction rates were 63, 38, and 49% for the Blue Range, Grand Canyon and southern Rockies populations, respectively. With 1 mpg, extinction rates were 51, 21, and 24% for the Blue Range, Grand Canyon and southern Rockies populations, respectively. With 2/1/1 mpg, extinction rates were 20, 22, and 24%, respectively. Extinction rates for the Grand Canyon and southern Rockies were similar with either 1 mpg or 2/1/1 mpg. The extinction cost to these populations from the 2/1/1 mpg dispersal regime was very minimal, but the benefits to the Blue Range in the form of dramatically lower extinction rates were large.

Among the nine simulations described above, there was a strong, negative relationship between mean population size at year 100 for extant iterations and variability in population size, as quantified by the coefficient of variation (standard deviation / mean; Figure 7). This suggested that factors that act to decrease population size also increase the relative amount of variation around the mean. Conversely, factors (or management actions) that increase population size also act to reduce variability in population size. Increased variability in population size is known to increase extinction risk, decrease stochastic population growth rates, and is a component of the “extinction vortex” experienced by small populations. It is interesting to note that at least three disparate factors acted to affect mean population sizes in these nine simulations: degree of connectivity, adult / yearling survival rate, and the degree of relatedness within populations. But the tandem effects on the coefficient of variation were linear, for mean population sizes at least as low as 59 wolves. Similar negative, linear relationships were observed for other simulation sets described below, although the slopes varied (results not shown). The four smallest populations in Figure 7 are representations of the Blue Range with either zero or 1 mpg and either 23.5 or 25% adult mortality.

Finally, the 2/1/1 mpg dispersal regime also increased the percentage of iterations in which all three populations met the numerical delisting criterion. With 2/1/1 mpg, all three populations met the delisting criterion in 90, 69, and 32% of iterations with 22, 23.5, and 25% adult mortality, respectively (Table 4). This represented 11, 47, and 78% increases relative to 1 mpg. The percentage of iterations in which all three populations exceeded the numerical criterion for being endangered at some point during years 81-100 was also increased with 2/1/1 mpg, relative to 1 mpg (Table 5). But few iterations exceeded the criterion with either 2/1/1 or 1 mpg.

3. SCENARIO 2: GRAND CANYON 350 AND BLUE RANGE 350

In Scenario 1, 3x250, simulations without dispersal between populations indicated that the Grand Canyon was demographically the strongest population. Consequently in scenario 2 we first examined the effects on population viability if the numerical recovery goal for this population was set at 350 wolves and the Blue Range and southern Rockies had recovery goals of at least 200 wolves each. But because the Blue Range was the central population and demographically weaker than the other two populations, we also examined metapopulation viability when the numerical goal for the Blue Range was set at 350 wolves with the Grand Canyon and Southern Rockies required to support at least 200 wolves each. In simulations that included populations with numerical recovery goals that were $< >$ 250 wolves, we assumed for the purposes of this analysis that the population would be considered “endangered” if its eight year running mean dropped below 60% of its numerical goal. Consequently populations with numerical goals of 350 and 200 were considered endangered when their eight year mean dropped below 210 and 120 wolves, respectively.

For this scenario, and for scenarios 3 and 4, we ran simulations with 22 and 23.5% adult / yearling mortality, but we did not run simulations with 25% adult / yearling mortality. As the adult mortality rate increased it became increasingly difficult to parameterize dispersal rates for each population that would achieve the desired connectivity rates. This difficulty arose because the parameter space for achieving the desired numbers of migrants per generation decreased as adult mortality increased, particularly with the 1 mpg dispersal regime. In some cases, it appeared that the parameter space did not exist in which the desired connectivity could be achieved. These cases are noted in the text.

a. Grand Canyon 350

The main themes apparent from the 3x250 scenario were present in the Grand Canyon 350 simulations. When there was 22% adult mortality and 2/1/1 mpg, the mean size of the Blue Range peaked at 192 wolves at year 23 (Figure 8A). Following the initiation of harvests at year 25 the mean size declined, but the Blue Range was able to maintain itself at or above 174 wolves from years 30 through 71. But ultimately the Blue Range declined by 5% to a mean of 166 wolves at year 100. With 1 mpg, the demographic costs of this dispersal regime relative to 2/1/1 mpg were apparent. The Blue Range reached a maximum mean population size of 173. Following the start of harvests mean population size declined linearly to a mean of 111 wolves at year 100. This was 33% lower than the size of the Blue Range at year 100 with 2/1/1 mpg.

As before, wolf numbers were slightly higher in the Grand Canyon and southern Rockies with 1 mpg than with 2/1/1 mpg (Figure 8C and E). With 22% adult mortality and 1 mpg, the mean size of extant populations in Grand Canyon reached 335 before harvest began. Following a dip due to the start of harvests, mean wolf numbers increased to 341 before declining to 317 wolves at year 100 (Figure 8C). In the southern Rockies mean wolf numbers reached 210 wolves before harvesting began when there was 22% adult mortality and 1 mpg (Figure 8E). But in contrast to the Grand Canyon, the southern Rockies population did not continue to increase in later years.

Instead mean population size declined to 164 wolves at year 100. This constituted a 14% drop in wolf numbers from year 30 (Figure 8E).

With 23.5% adult mortality, the Blue Range reached a mean population size of 162 wolves at year 20 when there was 2/1/1 mpg (Figure 8B). Mean wolf numbers declined slightly shortly before the start of harvests at year 25, suggesting that without harvests mean wolf numbers among extant populations in the Blue Range may not have reached 200. By year 100, the mean number of wolves among extant iterations in the Blue Range had dropped to 129 – 32% lower than that with 22% adult mortality. With 1 mpg and 23.5% adult mortality, the mean number of wolves in the Blue Range peaked in year 8 at 136. By year 100 the mean number of wolves had dropped to 47. This was 64% fewer wolves than with the 2/1/1 mpg dispersal regime.

In the Grand Canyon, mean wolf numbers among extant iterations dipped at the start of harvests, but then continued to increase when there was 23.5% adult mortality (Figure 8D). Mean wolf numbers peaked in year 50 at 309 with 1 mpg. By year 100 mean wolf numbers were slightly higher with the 2/1/1 mpg dispersal regime than with 1 mpg (268 vs. 266 wolves). Mean wolf numbers at year 100 with 23.5% adult mortality and 1 mpg were 17% lower than with 22% adult mortality.

In the southern Rockies, mean wolf numbers among extant populations peaked at 192 wolves in year 24 when there was 23.5% adult mortality and 1 mpg. By year 100, mean wolf numbers were greater with 2/1/1 mpg than with 1 mpg (128 vs. 124). With 23.5% adult mortality and 1 mpg wolf numbers were 24% lower than with 22% adult mortality at year 100.

All three populations had patterns of mean expected heterozygosity over time that were qualitatively similar to those with the 3x250 scenario, despite the differences in census population sizes (Figure 9). Mean expected heterozygosity at year 100 for the Grand Canyon was about 0.01 greater than in the 3x250 scenario for each of the four simulations. Heterozygosity at year 100 for the Blue Range and southern Rockies was lower than in the 3x250 scenario for all simulations. Across the four simulations, mean heterozygosity in the Blue Range averaged 0.008 less than in the 3x250 simulations; the greatest difference, 0.012, occurred when there was 1 mpg and 23.5% adult mortality. The southern Rockies averaged 0.012 less than in the 3x250 scenario, with the greatest difference, 0.015, again occurring when there was 1 mpg and 23.5% mortality.

Heterozygosity excesses increased over time for the Blue Range when there was 1 mpg, but excesses decreased or were about the same at years zero and 100 when there was 2/1/1 mpg (Figure 10A). Heterozygosity excesses for the Grand Canyon and southern Rockies populations dropped substantially by year 100 in all four simulations (Figure 10C). The excess was eliminated in the Grand Canyon when there was 1 mpg and 22% adult mortality. Relative to the 3x250 scenario, heterozygosity excesses were increased for the Blue Range and decreased for the Grand Canyon (Figures 5 and 10).

The Grand Canyon also had lower extinction rates than in similar simulations under the 3x250 scenario. Simulations with 22% adult mortality had approximately half the extinctions as in the 3x250 scenario, but extinction rates were already low in the 3x250 simulations (Figures 6A and 12A). With 23.5% mortality, the Grand Canyon had about 20% fewer extinctions than in the 3x250 scenario. Extinction rates for the Blue Range and southern Rockies were somewhat higher than in similar simulations of the 3x250 scenario, particularly for the Blue Range with 1 mpg and 23.5% mortality (34.3 vs. 20.2%).

Mean metapopulation sizes at year 100 were slightly larger than those under the 3x250 scenario when there was 1 mpg (Figure 12), but the sums of population extinctions were higher (Figure 13). This metric simply sums the number of iterations in which each population became extinct. The maximum number of extinctions possible was 3,000 for these simulations. With 2/1/1 mpg, however, mean metapopulation sizes were slightly smaller than in the 3x250 scenario, and the numbers of population extinctions were lower than with 3x250 (22% adult mortality) or slightly higher (23.5% adult mortality). The percentages of iterations in which all three populations met their numerical delisting goals (350, 200, 200 for the Grand Canyon, Blue Range, and southern Rockies, respectively) were slightly lower than under the 3x250 scenario when there was 1 mpg (Table 4). With 2/1/1 mpg, however, the percentages of iterations in which all three populations met numerical goals were nearly identical between this scenario and the 3x250 scenario. Finally, the percentages of iterations in which all three populations exceeded their numerical thresholds for being endangered during years 81 -100 (>210, 120 and 120 for the Grand Canyon, Blue Range, and southern Rockies, respectively) were somewhat lower than under the 3x250 scenario (Table 5).

b. Blue Range 350

When there was 22% adult mortality and 2/1/1 mpg, mean population size among extant iterations for the Blue Range peaked at 325 wolves in year 24 (Figure 14A). After a dip following the start of harvesting, mean wolf numbers slowly increased through the remainder of the simulation ending with a mean of 319 wolves among extant iterations. With 1 mpg, mean wolf numbers decreased following the start of harvests and continued to slowly decrease through year 100. By year 100 mean population size among extant iterations for the Blue Range with 1 mpg was 262 wolves, 22% lower than that with 2/1/1 mpg (Figure 14A). The Grand Canyon and southern Rockies populations performed similarly to each other. Both had higher mean wolf numbers with 1 mpg (Figure 14C and E). With 1 mpg and 22% adult mortality, mean population sizes among extant iterations peaked at 204 and 197 wolves in year 24, for the Grand Canyon and southern Rockies, respectively. Both populations then declined in mean size through year 100. With 2/1/1 mpg, the mean sizes of extant iterations were 7 and 5% lower by year 100 for the Grand Canyon and southern Rockies, respectively.

Increasing the adult mortality rate to 23.5% had the greatest effect on the Blue Range. With 2/1/1 mpg, mean size of extant iterations peaked at 272 wolves at year 24, but then increased further to 276 before decreasing to a mean of 250 wolves by year 100. By year 100 the mean sizes of extant populations were 22 and 32% lower with 2/1/1 mpg and 1 mpg, respectively, than that with 22% adult mortality. For the Grand Canyon and southern Rockies, the increase in adult mortality exacerbated the demographic costs of the 2/1/1 mpg dispersal regime relative to the 1 mpg, as determined by the increased differences between mean wolf numbers for the two dispersal regimes (Figure 14D and F). This was not seen with the 3x250 scenario nor in the Grand Canyon 350 simulations (Figure 8E and F). By year 100 the mean sizes of extant populations for the Grand Canyon were 29 and 15% lower with 2/1/1 mpg and 1 mpg, respectively, than that with 22% adult mortality. For the Southern Rockies, the mean sizes of extant populations at year 100 were 30 and 17% lower with 2/1/1 mpg and 1 mpg, respectively, than that with 22% adult mortality.

Mean expected heterozygosity at year 100 for the Blue Range was greater than that in the 3x250 scenario for all four simulations (Figures 4 and 15). When there was 2/1/1 mpg, mean expected heterozygosity at year 100 for the Blue Range was also greater than that for the Grand Canyon and southern Rockies populations. But when there was 1 mpg, the Blue Range had the lowest expected heterozygosity at year 100. This pattern was also present among simulations in the 3x250 scenario. When there was 22% adult mortality and 2/1/1 mpg, the mean expected heterozygosity of the Blue Range initially declined at the start of the simulation, but then increased as a result of gene flow to a level before slowly declining to year 100.

For the Grand Canyon and southern Rockies populations mean expected heterozygosity at year 100 was lower than that in similar simulations for the 3x250 scenario as a result of their smaller census population sizes. Mean expected heterozygosity was greatest when there was 1 mpg (Figure 15C – F), as in the 3x250 scenario. For the southern Rockies, mean expected heterozygosity at year 100 was greater than that in similar simulations for the Grand Canyon 350 scenario in three of four cases. But the differences were not large.

Mean heterozygosity excesses at year 100 for the Blue Range were greatly reduced relative to that with the Grand Canyon 350 simulations (Figure 10A and B) and the 3x250 scenario (Figure 5). For the Grand Canyon, excesses were greater than in the Grand Canyon 350 simulations (Figure 10C and D) and the 3x250 scenarios (Figure 5). For the southern Rockies, mean excesses were lower than those with the Grand Canyon 350 simulations when there was 1 mpg, but slightly higher when there was 2/1/1 mpg (Figure 10E and F) even though the population size targets were the same in the two scenarios. Interestingly, at year 100 the excesses were smallest with 1 mpg for both the Grand Canyon and southern Rockies in the Blue Range 350 simulations, suggesting that the reduced population size and greater emigration demands required in the 2/1/1/ mpg simulations slowed the elimination of the initial heterozygosity excess.

With the Blue Range 350 simulations, extinction rates for the Blue Range were reduced relative to the Grand Canyon 350 simulations particularly when there was 1 mpg (Figure 11A and B). With 22% adult mortality, Blue Range extinction rates were reduced from 7% to 2%, and with 23.5% adult mortality extinction rates were reduced from 34% to 9%. Blue Range Extinction rates were also lower than with the 3x250 scenario when there was 1 mpg (Figures 6 and 11). With 2/1/1 mpg, Blue Range extinction rates were similarly low for both scenarios. For the Grand Canyon, extinction rates were similar to those with the Grand Canyon 350 simulations and 3x250 scenarios when there was 1 mpg, but higher when there was 2/1/1 mpg (Figures 8 and 11). For the southern Rockies, extinction rates were similar to those under the 3x250 scenario when there was 1 mpg and when there was 2/1/1 mpg and 22% adult mortality. But when there was 2/1/1 mpg and 23.5% mortality, extinction rates were 55 and 71% higher, respectively, than those under the 3x250 scenario.

Mean metapopulation sizes were slightly greater than either the Grand Canyon 350 simulations or the 3x250 scenarios and the summed population extinctions substantially lower when there was 1 mpg (Figures 12 and 13). When there was 2/1/1 mpg and 22% adult mortality, metapopulation sizes and summed extinctions were similar for the Blue Range350 and Grand Canyon 350 simulations, and 3x250 scenarios (Figures 12 and 13). With 2/1/1 mpg and 23.5% adult mortality, however, the Blue Range 350 scenario resulted in a slightly smaller mean metapopulation size and higher summed extinctions than the either Grand Canyon 350 simulation and the 3x250 scenario (Figures 12 and 13). But overall, mean metapopulation sizes were larger and summed extinctions fewer with 2/1/1 mpg than with 1 mpg.

The percentages of iterations in which all three populations met their numerical delisting goals (350, 200, and 200 for the Blue Range, Grand Canyon, and southern Rockies, respectively) were greater than either the 3x250 or Grand Canyon 350 scenarios when there was 1 mpg (Table 4). With 2/1/1 mpg, however, the percentages of iterations in which all three populations met numerical goals were slightly lower than the 3x250 scenario and the Grand Canyon 350 simulations. But like mean metapopulation size, delisting rates were higher with 2/1/1 mpg than with 1 mpg.

The percentages of iterations in which all three populations exceeded their numerical criteria for being endangered during years 81 -100 (>210, 120 and 120 for the Grand Canyon, Blue Range, and southern Rockies, respectively) were also somewhat higher than the 3x250 scenario and the Grand Canyon 350 simulations when there was 1 mpg (Table 5). But when there was 2/1/1 mpg, percentages were somewhat lower.

c. Costs and Benefits

Of these two extreme scenarios, the Blue Range 350 scenario appeared to provide greater overall benefits with fewer costs than the GC350 scenario, particularly when there was 1 mpg. The Blue Range 350 scenario had highest mean metapopulation sizes at year 100 and the fewest numbers

of population extinctions when there was 1 mpg. When there was 2/1/1 mpg and 22% adult mortality the three scenarios had nearly the same mean metapopulation sizes and summed extinctions (Figures 12 and 13). When there was 2/1/1 mpg and 23.5% adult mortality, the 3x250 scenario had the largest mean metapopulation size, but the other two scenarios were only slightly lower. The 3x250 scenario also had the lowest summed extinctions, but the GC350 simulation had nearly as few extinctions. The Blue Range350 simulation had the highest summed extinction rate with about 33% more extinctions. But the overall population extinction rate was still only 7.5%.

The Blue Range350 scenario had the highest % of iterations in which all three populations met the delisting criteria when there was 1 mpg (Table 4). When there was 2/1/1 mpg, the 3x250 scenario had the highest % and the Blue Range350 scenario had the lowest, but the differences were small. The same pattern was evident for the % of iterations in which all three populations exceeded the numerical criteria for being endangered (Table 5).

The Blue Range350 scenario had the lowest heterozygosity excesses and the highest expected heterozygosity at year 100 for the Blue Range. Similarly, the GC350 scenario had the lowest heterozygosity excesses and the highest expected heterozygosity at year 100 for the Grand Canyon. Heterozygosity was highest at year 100 for the southern Rockies under the 3x250 scenario. The 3x250 scenario had intermediate levels of heterozygosity at year 100 for the Blue Range and Grand Canyon.

Collectively, these results suggested that the level of management flexibility allowed under this scenario is unlikely to impede recovery or substantially reduce the viability of the recovered metapopulation.

4. SCENARIO 3: 3X250 + SONORA

This scenario was the same as Scenario 1 except that it added a fourth population which had a numerical goal of at least 100 wolves. In the simulations we assumed that the fourth population, “Sonora”, would be located in northern Mexico along the border of Sonora and Chihuahua. Therefore the only population with which it was likely to be connected by natural dispersal was the Blue Range. Because the Sonora population was much smaller than the other populations, we assumed it would likely not be able to provide 1 mpg to the Blue Range, but it likely would provide some migrants. For the 2/1/1 dispersal regime in this scenario, dispersal was parameterized such that the Blue Range would receive a total of about 2 mpg from the three peripheral populations. But the Blue Range would attempt to provide 1 mpg to each of the three peripheral populations. Thus the 2/1/1 dispersal regime in this scenario had the potential to be more stressful on the Blue Range than the previous scenarios. We founded the Sonora population with seven pairs, and the simulations started with a total of 35 wolves. Overall, the inclusion of

Sonora reduced the demographic performance of the Blue Range but slightly enriched it genetically. Sonora had little effect, however, on the Grand Canyon and southern Rockies populations, relative to the 3x250 scenario.

When there was 22% adult mortality and 2/1/1 mpg, the Blue Range reached a maximum mean population size among extant iterations of 224 wolves in year 24 (Figure 16A). Following the dip in wolf numbers caused by the initiation of harvests, the mean population size slowly increased before declining during the last few years of the simulation. At year 100 the Blue Range averaged 203 wolves among extant populations. When there was 1 mpg the Blue Range peaked in year 20 with a mean population size of 178. The early peak in mean wolf numbers suggested that the Blue Range had already started to decline before the start of harvests. By year 100 the Blue Range declined to a mean of 111 wolves which was 45% fewer wolves than that with the 2/1/1 mpg dispersal regime and less than the 122 wolves in the Blue Range at the start of the simulation (Figure 16A). Relative to similar simulations in the 3x250 scenario, the mean Blue Range size at year 100 when there was 2/1/1 mpg was only 6% lower than in the 3x250 scenario, but when there was 1 mpg mean population size was 29% lower than with the 3x250 scenario. With 23.5% adult mortality, mean population sizes for the Blue Range at year 100 were 145 and 56 wolves with 2/1/1 mpg and 1 mpg, respectively (Figure 16B). Relative to the 3x250 simulations, the Blue Range ended the simulations with 19 and 40% fewer wolves.

In contrast, mean population sizes among extant iterations over time for the Grand Canyon and southern Rockies were similar to that under the 3x250 scenario for 22 and 23.5% adult mortality and both dispersal regimes (Figure 16C and D). Mean population sizes among iterations extant at year 100 for the Grand Canyon and southern Rockies were 227 and 221, respectively, when there was 22% adult mortality and 1 mpg. When there was 23.5% adult mortality and 1 mpg, mean population sizes at year 100 were 185 and 181 for the Grand Canyon and southern Rockies, respectively.

Sonora grew rapidly at the start of the simulations to a mean population size among extant populations of 109 wolves at year 23 when there was 22% adult mortality and 1 mpg (Figure 16E). As with the other peripheral populations (Grand Canyon and southern Rockies), Sonora peaked at a smaller mean size of 105 wolves at year 23 when there was 2/1/1 mpg (Figure 16E). The flattening of the curves prior to the start of harvesting appeared to be caused by the truncation of an increasing number of iterations at the carrying capacity of 133 wolves. Following the start of harvesting, mean population sizes declined steadily to 71 and 75 at year 100 for simulations with 1 mpg and 2/1/1 mpg, respectively. When there was 23.5% adult mortality, Sonora peaked in year 23 with mean population sizes of 101 and 97 wolves when there was 1 mpg and 2/1/1 mpg, respectively (Figure 16F). By year 100, mean population sizes among extant iterations had declined to 51 and 58 wolves when there was 1 mpg and 2/1/1 mpg, respectively. Mean population sizes over time were little affected by the choice of dispersal regime with either 22 or 23.5% adult mortality. It is interesting to note, however, that for the first portion of the simulations, those with 1 mpg supported greater mean numbers of wolves,

consistent with the demographic cost to peripheral populations of the 2/1/1 mpg dispersal regime. But by the end of the simulations, the 2/1/1 mpg dispersal regime supported higher mean wolf numbers and reduced the extinction rate for the Sonora population (see below). As the Blue Range declined in size with 1 mpg, its ability to send migrants to the peripheral populations also declined, and fewer migrants were received by each of the peripheral populations. With 2/1/1 mpg, the Blue Range supported substantially higher wolf numbers in the latter half of the simulations. For the small Sonora population, the additional migrants it received from the Blue Range with 2/1/1 mpg outweighed the added costs of this dispersal regime. But for the relatively large and stable Grand Canyon and southern Rockies populations the demographic costs of the 2/1/1 mpg dispersal regime were not outweighed by the benefits of receiving more migrants in the later years of the simulations.

Despite smaller census population sizes than that under the 3x250 scenario, mean expected heterozygosity for the Blue Range at years 24 and 100 exceeded that with the 3x250 scenario when there was 2/1/1 mpg for both 22 and 23.5% adult mortality rates. In addition, the maximum mean heterozygosity for the Blue Range (0.7579 at years 48 and 49) exceeded that at simulation start (0.7555) when there was 2/1/1 mpg and 22% adult mortality (Figure 17). Although the difference was slight, this did not occur under the 3x250 scenario. These differences between the two scenarios appeared to be a result of the inclusion of immigrants from a third donor population, Sonora. Although the mean number of migrants per generation received by the Blue Range was only slightly greater than that under the 3x250 scenario (2.21 vs. 2.02; Table 3), the inclusion of migrants from a third differentiated population (Sonora) appeared to genetically enrich the Blue Range.

With 1 mpg, however, mean expected heterozygosity for the Blue Range was lower than that under the 3x250 scenario. By year 100, heterozygosity was 1.2 and 1.6% lower than similar simulations under the 3x250 scenario when adult mortality was 22 and 23.5%, respectively. This outcome, reduced heterozygosity, was not surprising given that the Blue Range received an average of 1.12 and 1.13 mpg with 22 and 23.5% adult mortality, respectively, but exported totals of 2.96 and 2.53 mpg on average to the three peripheral populations (Table 3). In contrast, under the 3x250 scenario the Blue Range received an average of 1.03 and 1.12 mpg, and exported a mean of 2.15 and 2.02 mpg with 22 and 23.5% adult mortality, respectively to the two peripheral populations (Table 3). Even though mean wolf numbers among extant populations were substantially lower than under the 3x250 scenario, mean expected heterozygosity was only slightly lower.

Although the three peripheral populations in the simulation with 1 mpg and 23.5% adult mortality were intended to each receive an average of 1 – 1.10 mpg, they received an average of about 0.84 (Table 3). This shortfall was a result of the combination of increased emigration demands on the Blue Range to meet connectivity goals and the demographic decline of the Blue Range. The increased demographic demands on the Blue Range for emigration, relative to that under the 3x250 scenario, appeared to accelerate the decline of the Blue Range. In the

simulations, it may not have been possible for the Blue Range to provide 1 mpg to each of three populations while receiving a total of 1 mpg, when adult mortality was < 23.5%. This dynamic was also seen in 3x250 scenario with 25% adult mortality and 1 mpg. In this case the Blue Range received an average of 1.28 mpg even though the target was 1-1.10 mpg. Several simulations with < 1.10 mpg into the Blue Range suggested that the Blue Range would only be able to provide 1 mpg to the two peripheral populations if it received substantially more than 1.10 mpg. This dynamic was also apparent for the BR + 2MX100 simulations with 1 mpg (see below). In these cases, the centrally located Sonora population was unable to provide 1 mpg to the two peripheral populations under the 1 mpg dispersal regime (Table 3).

For the Grand Canyon (Figure 17 C and D) and southern Rockies, the choice of dispersal regime had only a small effect on mean expected heterozygosity (Figure 17C and D). At year 100 mean expected heterozygosity for the Grand Canyon was about 0.735 with 22% adult mortality and 0.719 with 23.5% mortality for both dispersal regimes. For the southern Rockies mean expected heterozygosity at year 100 was about 0.730 and 0.715 with 22 and 23.5% adult mortality, respectively. Expected heterozygosities, however, were less than that with the 3x250 scenario, but the differences were slight. When there was 2/1/1 mpg and 23.5% adult mortality the mean expected heterozygosity for the Grand Canyon and southern Rockies were 1.8 and 1.6% lower, respectively, at year 100 than that under the 3x250 scenario. But in all other cases the differences were <1%.

For Sonora, the pattern of mean expected heterozygosity over time (Figure 17E and F) was similar to that observed for mean population size among extant iterations (Figures 16E and F). Heterozygosity was initially highest with 1 mpg, but by the end of the simulations heterozygosity was greatest with the 2/1/1 mpg dispersal regime for both 22 and 23.5% adult mortality. With 2/1/1 mpg, mean expected heterozygosity at year 100 was 3.1 and 4.7% greater than that with 1 mpg with 22 and 23.5% adult mortality, respectively. Mean expected heterozygosity dropped as low as 0.648 with 23.5% adult mortality and 1 mpg (Figure 17F).

Heterozygosity excess for the Blue Range increased over time when there was 1 mpg, but with 2/1/1 mpg it declined or was similar to that at the start of simulations (Figure 18A). The excesses at year 100, however, were greater than those for the Blue Range under the 3x250 scenario (Figure 5). Excesses for the Grand Canyon and southern Rockies declined over time in all cases and the excesses at year 100 were similar to those in the 3x250 scenario. For Sonora, the heterozygosity excess at year 0 was higher than the other three populations. Although the excesses declined over time with both dispersal regimes, the decline was greater with 2/1/1 mpg (Figure 18B).

Extinction rates were greatly reduced for the Blue Range and Sonora when there was 2/1/1 mpg versus 1 mpg (Figure 19). When there was 22% adult mortality the extinction rate for the Blue Range was reduced from 10% with 1 mpg to <1% with 2/1/1 mpg, and the extinction rate for Sonora was reduced from 9 to 4%. For simulations with 23.5% adult mortality, the extinction

rate for the Blue Range was reduced from 33% with 1 mpg to 5% with 2/1/1 mpg, and the extinction rate for Sonora was reduced from 32 to 18% with 2/1/1 mpg. For the Grand Canyon and southern Rockies, there was little difference in extinction rates due to dispersal regime. But extinction rates were 4-6 times greater with 23.5% adult mortality than with 22% mortality.

For the Grand Canyon and southern Rockies populations there was little difference in extinction rates between this and the 3x250 scenario. But for the Blue Range extinction rates were 150 and 60% higher than those under the 3x250 scenario when there was 1 mpg (Figures 6 and 19). When there was 2/1/1 mpg extinction rates were roughly similar between the two scenarios.

Mean metapopulation sizes at year 100 exceeded that for the 3x250 scenario in three of four simulations by 2 – 9% (Figure 20). The exception was when there was 1 mpg and 23.5% adult mortality. In this case mean metapopulation size under 3x250 was 3% larger. For the current simulations, mean metapopulation size was 19 and 22% smaller with 1 mpg than 2/1/1 mpg, with 22 and 23.5% adult mortality, respectively. But the summed population extinctions for the three large populations were higher somewhat higher than with 3x250, in three of four cases (Figure 21). The exception this time was Summed extinctions were lower than the 3x250 simulation when there was 2/1/1 mpg and 22% adult mortality, but the difference was small. Summed extinctions for the current simulations were 4.8 and 2.5 times higher with 1 mpg than 2/1/1 mpg, with 22 and 23.5% adult mortality, respectively.

Although the Sonora population met numerical delisting criteria in 88-97% of iterations, the proportion of iterations in which all three of the other populations met numerical criteria for delisting ranged from 33 to 90% (Table 6). This was 28 and 31% lower than in the 3x250 scenario when there was 1 mpg (Table 4). The similarity in delisting rates for the Blue Range and the three large populations suggested that the Blue Range was the primary determinant of when all three large populations simultaneously met delisting criteria (Tables 4 and 6). When there was 2/1/1 mpg, delisting rates for the three large populations were 90% for both this and the 3x250 scenarios when there was 22% adult mortality. But with 23.5% adult mortality the 3x250 scenario had a higher delisting rate (69 vs. 59%; Tables 4 and 6). Interestingly, Sonora had higher rates of delisting than the Blue Range except when there was 2/1/1 mpg and 22% mortality (Table 6).

Similarly, inclusion of the Sonora population reduced the percentage of iterations in which the three large populations exceeded the numerical criteria for being endangered in the years 81-100 relative to the 3x250 scenario (Tables 5 and 7). And Sonora exceeded numerical criteria for being endangered far more often than the Blue Range when there was 1 mpg, but not when there was 2/1/1 mpg (Table 7).

5. SCENARIO 4: BLUE RANGE + 2MX100

This scenario assumed three populations would be restored: the Blue Range in the US supporting at least 250 wolves and two small populations in Mexico each supporting at least 100 wolves. The two populations in Mexico were assumed to be located along the border of Sonora and Chihuahua states (Sonora) and in the southern portion of the western Sierra Madre (Durango). We assumed that these populations would be connected in a linear fashion by natural dispersal, with Sonora as the central population. This differed from the previous scenarios in that for this scenario the Blue Range was a peripheral rather than the central population, and it was the only large population. We based the Sonora and Durango starting populations on the pedigrees of the Grand Canyon and southern Rockies populations, respectively. But instead of founding each population with 10 pairs and starting the simulations with 50 wolves in each population, we chose seven pairs to found each population and started the simulations with 35 wolves in each of the two Mexican populations. Thus the Sonora population in this scenario was different from the Sonora population in Scenario 3. Overall, this scenario was characterized by low census population sizes, rapid heterozygosity loss, and high extinction and endangerment rates, particularly for the centrally located Sonora population.

Mean population size among extant iterations over time for the Blue Range was similar to that under the 3x250 scenario when there was no dispersal between populations (Figures 3 and 22). But unlike that under the 3x250 scenario, mean population size after the start of harvesting was greatest with 1 mpg. In addition, the mean number of wolves did not plateau after the start of harvesting, but instead declined from year 25 to 100. By year 100 wolf numbers averaged 171 and 118 for simulations with 22 and 23.5% adult mortality, respectively. It should be noted, however, that that under 1 mpg, the Blue Range received only about 0.77 mpg (Table 3). With 2/1/1 mpg, mean wolf numbers at year 100 were 7 and 9% lower than that with 1 mpg, when there was 22 and 23.5% adult mortality, respectively. This difference represented the demographic cost of the 2/1/1 mpg dispersal regime to the peripherally located Blue Range, relative to 1 mpg. Mean population sizes at year 100 with 1 mpg were 21 and 34% smaller than that under the 3x250 scenario with 2/1/1 mpg and 22 and 23.5% adult mortality, respectively. Relative to the peripheral populations under the 3x250 scenario (Grand Canyon and southern Rockies), the Blue Range averaged about 22 and 36% fewer wolves at year 100 when there was 1 mpg and adult mortality was 22 and 23.5%, respectively.

The centrally located Sonora population grew the fastest at the start of the simulations when there was no dispersal between populations and peaked at substantially higher mean population sizes than simulations with dispersal between populations (Figure 22C and D). But by year 100, simulations without dispersal between populations averaged only 26 and 17 wolves among extant iterations when there was 22 and 23.5% adult mortality, respectively. This was less than the 35 wolves at the start of simulations. Simulations with 2/1/1 mpg supported the greatest mean numbers of wolves at year 100. With 22% adult mortality the Sonora population averaged 49 wolves at year 100; with 23.5% adult mortality Sonora averaged 34 wolves at year 100.

Mean population sizes among extant iterations for Durango were similar with either 2/1/1 mpg or 1 mpg dispersal regimes (Figure 22E and F). But by year 100, simulations with 2/1/1 mpg supported means of 60 and 40 wolves, with 22 and 23.5% adult mortality, respectively, which was slightly higher than mean population sizes with 1 mpg. It should be noted, however, that Durango received only about 0.77 mpg under 1 mpg (Table 3). If Durango had received the full 1 mpg, its mean population sizes would have been larger than that with 2/1/1 mpg. The dispersal shortfall into Durango and the Blue Range resulted from the small and declining population size of Sonora. By year 100 Durango supported 22 and 18% more wolves than Sonora when there was 2/1/1 mpg with 22 and 23.5% adult mortality, respectively.

The Blue Range retained greater expected heterozygosity over time than either of the other two populations, even though it started with the lowest mean expected heterozygosity (0.755 versus 0.795 for Sonora and Durango). Mean expected heterozygosity in the Blue Range declined in a nearly linear fashion with or without dispersal between populations (Figure 23A and B). When there was no dispersal between populations, mean heterozygosity for the Blue Range dropped to 0.65 and 0.62 at year 100, with 22 and 23.5% adult mortality, respectively. When there was dispersal between populations, mean expected heterozygosity was similar for the two dispersal regimes even though mean census population sizes were larger with 1 mpg (Figure 22A and B). At year 100, expected heterozygosity averaged about 0.69 and 0.66 with 22 and 23.5% adult survival, respectively. Relative to that under the 3x250 scenario, the Blue Range averaged 3-10% lower heterozygosity at year 100 than that under the 3x250 scenario.

Mean expected heterozygosity for Sonora dropped to 0.545 and 0.524 at year 100 in the absence of dispersal between populations, with 22 and 23.5% adult mortality, respectively (Figure 23C and D). But with 2/1/1 mpg, mean heterozygosity at year 100 dropped to only 0.681 and 0.65 for 22 and 23.5% adult mortality, respectively. With 1 mpg, mean expected heterozygosity at year 100 was 5% lower than that with 2/1/1 mpg. Relative to the central population under the 3x250 scenario (Blue Range) with 2/1/1 mpg, mean heterozygosity at year 100 for Sonora was 8 and 11% lower with 22 and 23.5% adult mortality, respectively.

For Durango, mean expected heterozygosity was highest when there was 2/1/1 mpg (Figure 23E and F). At year 100, expected heterozygosity averaged 0.665 and 0.633 with 22 and 23.5% adult survival, respectively. With 1 mpg, mean heterozygosity at year 100 was 2.8% lower. As noted above, the Blue Range and Durango each received about 0.77 mpg under the 1 mpg dispersal regime (Table 3). This suggested that the demographic costs to Durango of the 2/1/1 mpg dispersal regime were more than offset by providing additional support to the struggling Sonora population. This additional support allowed Sonora to provide one mpg to each of the peripheral populations. Relative to the peripheral populations from the 3x250 scenario, mean heterozygosity at year 100 for Durango was about 9 and 13% lower for 22 and 23.5% adult mortality, respectively.

Mean heterozygosity excesses at year 100 for the Blue Range were somewhat different than with 3x250. With 1 mpg heterozygosity excesses were 11 and 24% lower than that in the 3x250 scenario, for 22 and 23.5% adult mortality, respectively (Figures 5 and 24A). With 22% adult mortality the excesses at year zero and 100 were equal under the 3x250 scenario, but in the current scenario the excess had declined by year 100. With 23.5% adult mortality, the excess in the current scenario increased over time, but to a lesser amount than that in the 3x250 scenario.

With 2/1/1 mpg, mean heterozygosity excesses for the Blue Range at year 100 were 97 and 132% larger than that in the 3x250 scenario when adult mortality was 22 and 23.5%, respectively. Although the excesses decreased in both scenarios relative to that at year zero, when there was 22% adult mortality, with 23.5% adult mortality the excess increased substantially from year zero to 100. Under the 3x250 scenario, the excess decreased over time under these circumstances. The change in the pattern of heterozygosity excesses in the Blue Range appeared to result from the different position of the Blue Range in the metapopulation. In the current scenario, the Blue Range was not the central population, but a peripheral population. Throughout the simulations considered here, the 2/1/1 mpg dispersal regime provided demographic and genetic benefits to the central population, but presented costs to peripheral populations, in most cases. The primary exception to this pattern was Durango in the current scenario. Durango benefited demographically and genetically from the 2/1/1 mpg dispersal regime because it and the central Sonora populations were so small, particularly late in the simulations.

Sonora (in this scenario) and Durango had the highest initial heterozygosity excesses (0.054 and 0.055 respectively) of all the populations considered among the four scenarios. When there was no dispersal between populations, heterozygosity excesses increased over time in all cases (Figure 24 B and C) suggesting a deepening genetic bottleneck. In all previous cases, heterozygosity excesses decreased over time among populations that had initial excesses > 0.04 (i.e. Grand Canyon, southern Rockies, and Sonora in scenario 3) when there was no dispersal between populations. With 1 mpg, excesses at year 100 were smaller than those when there was no dispersal between populations, but the excesses at year 100 were still $>$ that at year zero in three out of four cases (Figure 24B and C). For Sonora the excess at year 100 with 1 mpg and 23.5% adult mortality was only marginally lower than that with no dispersal. With 2/1/1 mpg mean heterozygosity excesses were lower in Sonora and Durango than that at year zero when there was 22% adult mortality. But when there was 23.5% adult mortality, excesses still exceeded that at year zero. Consistent with previous scenarios, however, the centrally located Sonora population derived substantially greater benefit from the 2/1/1 mpg dispersal regime than the peripheral Durango population.

Extinction rates for the Blue Range were similar to that under the 3x250 scenario, when there was no dispersal between populations (Figures 6 and 25). But with either 1 mpg or 2/1/1 mpg, extinction rates were greater than with 3x250. With 1 mpg, extinction rates for the Blue Range were 95 and 26% higher than that under the 3x250 scenario with 22 and 23.5% adult mortality.

With 2/1/1 mpg, extinction rates were 14 times and 11 times higher than that under the 3x250 scenario with 22 and 23.5% adult mortality. Although Blue Range extinction rates were high relative to those under the 3x250 scenario, they were low relative to that for Sonora and Durango.

With no dispersal between populations, Sonora and Durango had similar extinction rates. With 22% adult mortality, extinction rates were 69 and 71% for Sonora and Durango, respectively. With 23.5% adult mortality, extinction rates were 87 and 86% for Sonora and Durango, respectively. With 1 mpg extinction rates were substantially lower, but still very high. For Sonora, 38 and 70% of iterations became extinct when there was 22 and 23.5% adult mortality, respectively. For Durango, 26 and 56% of iterations became extinct. With 2/1/1 mpg, Extinction rates for Sonora dropped to 14 and 48% for 22 and 23.5% adult mortality. Durango had 17 and 47% extinction rates.

Mean metapopulation sizes at year 100 were far lower than that for any of the other three scenarios. And the summed extinctions were far higher than with the other scenarios. When there was 1 mpg, mean metapopulation sizes at year 100 for extant iterations averaged 139 and 85 wolves with 22 and 23.5% adult mortality, respectively. The summed extinctions were 1,559 and 2,110 with 22 and 23.5% adult mortality, respectively. In other words, with 22% adult mortality there was a mean population extinction rate of 52%, and with 23.5% adult mortality the mean population extinction rate was 70%. When there was 2/1/1 mpg, mean metapopulation sizes at year 100 averaged 237 and 142 wolves for extant iterations, with 22 and 23.5% adult mortality, respectively, still substantially lower than the 450 wolf numerical goal. And the summed extinctions were 720 and 1,493, with 22 and 23.5% adult mortality, respectively. This translated into mean population extinction rates of 24 and 50% with 22 and 23.5% adult mortality, respectively.

The % of iterations in which all three populations reached numerical criteria for delisting was highest when there was 2/1/1 mpg (Table 8). But the Blue Range was most likely to meet delisting criteria with 1 mpg. In the simulations with 1 mpg the % of iterations meeting delisting criteria for the Blue Range was > that under the 3x250 scenario. With 2/1/1 mpg, however the Blue Range met delisting criteria less often than under the 3x250 scenario. These results were consistent with the Blue Range having the highest mean population sizes with 1 mpg (Figure 22) in the current scenario. In contrast, Sonora was most likely to meet delisting criteria with 2/1/1 mpg, consistent with this population having the greatest mean population sizes and lowest extinction rates with 2/1/1 mpg (Figures 22 and 24). The percentages of iterations in which Durango met delisting criteria were similar with either dispersal regimen and similar to the Blue Range. Overall, all three populations met delisting criteria in 58 and 30% of iterations when there was 1 mpg and 22 and 23.5% adult mortality, respectively. With 2/1/1 mpg, all three populations met delisting criteria in 72 and 39% of iterations when there was 22 and 23.5% adult mortality, respectively.

Numerical criteria for being endangered in the last 20 years of the simulations were exceeded by all three populations in < 8% iterations (Table 9). Of the three populations, Sonora was most likely to become endangered. Overall, patterns were similar to that with delisting except that Durango was slightly more likely to exceed endangered criteria with 2/1/1 mpg than with 1 mpg (Table 9).

D. DISCUSSION

1. FACTORS AFFECTING POPULATION VIABILITY AND RECOVERY

In the simulations, we highlighted the effects of adult / yearling mortality rates, connectivity between populations, and the composition of the founding populations based on mean kinship. We did this because each of these may have substantial effects on population viability and the prospect for recovery under the Endangered Species Act. But we also highlighted these because they can be affected by management.

The Blue Range had the highest initial mean kinship of all the populations considered in the simulations (0.2446 versus 0.1940 – 0.2064 for other simulated populations; Table 2). The effects of the Blue Range population's high mean kinship were illustrated in simulations with no dispersal between populations. With the 3x250 scenario the Blue Range and the Grand Canyon both peaked at similar mean population sizes around year 24, but the Blue Range ended the simulations with 31-50% fewer wolves than the Grand Canyon and about 70% higher extinction rates, despite starting with nearly 2.5 times as many wolves. In addition, the Blue Range lost heterozygosity faster than the Grand Canyon and southern Rockies populations. And its heterozygosity excess increased over time suggesting ongoing genetic bottlenecks, whereas the excesses in the other two populations decreased over time. Similar simulations with each population founded by 20 outbred and unrelated wolves (mean kinship = 0.025) and no dispersal between populations averaged 52% larger populations and 60% larger metapopulation sizes at year 100 with 40% fewer extinctions, when there was 22% adult / yearling mortality. With 25% adult / yearling mortality, populations and metapopulations averaged 144 and 236% more wolves at year 100, with 66% fewer population extinctions (results not shown). These results suggested that recovery prospects for Mexican wolves would be enhanced by establishing genetically diverse populations that have low relatedness within each population. These results further suggested that growing the Blue Range larger without substantially improving its poor genetic composition will impede recovery of Mexican wolves and reduce the overall viability of the "recovered" metapopulation.

The adult mortality rate also had large effects on simulation outcomes. When there was no dispersal between populations in the 3x250 scenario, increasing the adult mortality rate from 22

to 23.5% reduced the mean number of wolves among extant iterations by 32% in the Blue Range at year 100. Further increasing the adult mortality rate to 25% reduced mean wolf numbers in the Blue Range at year 100 by 56% relative to 22% adult mortality. For the Grand Canyon, increasing the adult mortality rate from 22% to 23.5 and 25% reduced the mean numbers of wolves at year 100 by 19 and 40%, respectively. Similarly, in the southern Rockies, increasing the adult mortality rate from 22% to 23.5 and 25% reduced the mean numbers of wolves at year 100 by 22 and 42%, respectively. In addition, increasing the adult mortality rate from 22 to 23.5% doubled the extinction rate for all three populations. Increasing the adult mortality rate to 25% raised the extinction rate about 3.5 – 4 fold for the three populations relative to that with 22% adult mortality. The adult mortality rate also affected heterozygosity. Increasing the adult mortality rate from 22% to 23.5 and 25% increased the loss of mean expected heterozygosity by 19 and 39%, respectively in the Blue Range, and by 13 and 30%, respectively, in the Grand Canyon. Increasing the adult mortality rate from 22 to 25% also doubled the mean heterozygosity excesses at year 100 for the Blue Range and Grand Canyon (Figure 5). It should be noted that the range of mortality rates used in the simulations have been associated with vigorous wolf populations, e.g. Smith et al (2010), estimated a mean adult / yearling mortality rate of 22.9% for wolves in the Greater Yellowstone Area. It should also be noted that the consistent performance differences between the three populations were driven by differences in starting mean kinships.

The two dispersal regimes interacted with adult / yearling mortality rates in the Blue Range to affect the mean numbers of wolves among extant iterations and heterozygosity excesses. In the 3x250 scenario, when there was 1 mpg the mean numbers of wolves at year 100 increased 16 and 2% with 22 and 23.5% adult mortality, respectively, relative to that with no dispersal between populations. But with 25% adult mortality, the mean number of wolves present at year 100 was 17% less than that with no dispersal. This represented a linear decrease in wolf numbers as the adult mortality rate increased. The 2/1/1 mpg dispersal regime, however, greatly increased the mean numbers of wolves present at year 100, but in a non-linear manner. With 22, 23.5, and 25% adult mortality, mean wolf numbers were increased by 61, 98, and 100%, respectively, relative to that with no dispersal between populations.

The two dispersal regimes also had different effects on Blue Range heterozygosity excesses at year 100. With 1 mpg heterozygosity excesses were lower than that with no dispersal between populations when there was 22% adult mortality. But with 23.5 and 25% adult mortality heterozygosity excesses with 1 mpg were greater than that with no dispersal between populations. With 2/1/1 mpg, however, heterozygosity excesses were much lower than with either 1 mpg or no dispersal between populations for all three adult survival rates. But with 2/1/1 mpg heterozygosity excesses increased in a non-linear manner with adult mortality increased with the greatest increase occurring when adult mortality increased from 23.5 to 25% (Figure 5).

Overall, the 2/1/1 mpg dispersal regime outperformed 1 mpg in every viability and recovery metric considered in all four scenarios. The reasons were that 2/1/1 mpg better supported the

central population in each scenario. And the costs of this dispersal regime to the peripheral populations were small while the benefits to the central populations were large. And in a few cases even the peripheral populations benefitted over the long-term with 2/1/1 mpg. In contrast, with 1 mpg the central population bore a large demographic cost relative to 2/1/1 mpg, while the peripheral populations somewhat benefitted.

Under the 1 mpg dispersal regime, the central populations were required to export enough wolves to provide a total of about 2 mpg to the two peripheral populations, in scenarios 1, 2, and 4. But each of the peripheral populations provided only about 0.5 mpg to the central population. This suggests the central population bore four times the demographic cost of the peripheral populations. But because the Blue Range was on average smaller than the Grand Canyon and southern Rockies (except in the Blue Range350 simulations), a greater percentage of its young wolves were required to disperse than that from the other populations to achieve a given effective number of migrants. And the relative burden on the central population increased as adult mortality rates increased. It should be noted that most dispersers did not become effective migrants. Most (62.5%) died before reaching their destinations, which also disproportionately increased the number of wolves leaving the central populations. Of the dispersing wolves that survived, only a fraction paired in the new population and produced at least one pup.

In scenario 3 (3x250 + Sonora), the central population was required to provide a total of about three mpg, while receiving a total of 1 mpg. In this case mean wolf numbers were substantially lower and extinction rates substantially higher for the central Blue Range than in similar simulations under 3x250. This was not a problem specific to the Blue Range. In scenario 4 the Blue Range was a peripheral population and Sonora was the central population. Sonora performed similarly to Durango when there was no dispersal between populations. But with 1 mpg, Durango had substantially larger mean population sizes and lower extinction rates. With 2/1/1 mpg the demographic differences between Sonora and Durango narrowed greatly.

Carroll et al. (2013) conducted a relative sensitivity analysis (Table 10; Cross & Beissinger 2001) focused on the 3x250 scenario to examine the relative effects of nine parameters and two categorical variables (density dependent reproduction and initial composition of populations) on extinction risk and two levels of quasi-extinction corresponding to the proposed threatened and endangered statuses for scenario 1 (<250 wolves and <150 wolves, respectively). For this analysis, mean parameter values for eight of the continuous parameters were randomly drawn from a range within +20% of the mean values used in the simulations above. In addition, the target population sizes of the three populations were varied from 50 – 350 wolves, with each of the three populations having the same target sizes. One thousand parameter sets were generated and 100 iterations were run for each parameter set. They then used logistic regression to provide a quantitative ranking of the relative importance of the 11 covariates considered for each of the three outcomes considered (extinction and dropping below the two quasi-extinction thresholds).

They found that the mean adult mortality rate and the % of adult females in the breeding pool were the two covariates that had the greatest effects on all three population outcomes (Table 10). For the probability of extinction the “population size threshold” (target population size) and the strength of inbreeding depression were close runners-up. For the two levels of quasi-extinction, the strength of inbreeding depression was the third most important variable.

The number of effective migrants per generation was of secondary importance in determining extinction and quasi-extinction rates, based on the standardized regression coefficients. The analysis varied the numbers of mpg from zero to 2.4. But the dispersal regime, which provided at least two times as many migrants to the Blue Range as to each of the other populations, was not varied. This was similar to the 2/1/1 mpg dispersal regime considered here, but given that all three populations used the same dispersal rates the Blue Range probably received slightly more effective migrants than the two peripheral populations combined. Simulations with the 2/1/1 mpg dispersal regime had low extinction rates when adult mortality was moderate, e.g. 22% (Figure 6A), suggesting that sensitivity analysis iterations with connectivity rates > 1 mpg would have very low extinction rates except when adult mortality rates were high. But simulations with zero mpg had high extinction rates (Figure 6). Thus it appeared that most of the potential benefits of increasing connectivity to avoid extinction occurred in the lower portion of the connectivity range used in the sensitivity analysis. The relative insensitivity of simulation outcomes to the higher dispersal rates (>1 mpg) used in the sensitivity analysis would have reduced the relative importance ranking of connectivity.

“Variation between existing and new populations” (initial mean kinship of populations) was among the covariates with the least effects on extinction and quasi-extinction rates in the analysis (Table 9). The dispersal regime used in the sensitivity analysis, however, may have somewhat masked the effects of initial mean kinship on population outcomes. In the simulations described above, the performance of the centrally located Blue Range, which had the highest initial mean kinship, was enhanced with the 2/1/1 mpg dispersal regime. For example, the Blue Range had the lowest extinction rates (Figure 6) and highest mean expected heterozygosity at year 100 (Figure 4) of the three populations with 2/1/1 mpg, even though it started with the lowest heterozygosity and had the highest extinction rates when there was no dispersal between populations. In contrast, when the Blue Range was simulated as a peripheral population and the Grand Canyon was the central population the Blue Range had the highest extinction rates, lowest mean expected heterozygosity at year 100, and smaller mean population sizes at year 100 than when it was simulated as the central population (results not shown). As noted above, the dispersal regime used in the sensitivity analysis was similar to 2/1/1 mpg in that the central population received at least twice as many mpg as the peripheral populations. And thus it would be expected to have had similar positive effects on the Blue Range. If a dispersal regime similar to 1 mpg were included in the sensitivity analysis. Or if initial mean kinships of the peripheral populations were varied while the mean kinship of the central population remained constant, a truer picture of the relative importance of population mean kinships would be apparent. A

common management goal for small pedigreed populations managed for conservation is to minimize mean kinship. This is done to minimize the rate of inbreeding accumulation in populations. In populations with inbreeding depression, populations with low mean kinship will be less impacted by inbreeding depression and demographically more vigorous. If mean kinship of the Blue Range were to be reduced by genetic management, it would facilitate Mexican wolf recovery and support a stronger metapopulation. Conversely, if the Grand Canyon and southern Rockies populations were established with higher mean kinships than that assumed in the simulations, this would be expected to reduce their short and long-term performance and make recovery more difficult to attain and more tenuous to maintain. It should be noted that that it may be possible to establish new populations with lower mean kinships than those used in the simulations for peripheral populations, if new populations are reintroduced soon. If the Mexican wolf gamete bank is used in the creation of new populations it may be possible to reestablish populations with lower mean kinship than what currently exists in the captive population. It is encouraging, however, that the simulations suggested that relatively low rates of dispersal between populations has the potential to somewhat ameliorate the poor genetic composition of the Blue Range.

The population size threshold was the third or fourth most important covariate in determining whether a population became extinct or quasi-extinct (Table 10). That most populations in the simulations described above became extinct or quasi-extinct in a majority of iterations suggested that the minimal harvest buffer we incorporated would likely be inadequate to prevent populations from falling below the targeted population sizes once delisting targets are met. But the strong performance of the population size threshold suggested that adding numerical management buffers above the targeted population sizes would substantially reduce the probability of needing to relist Mexican wolves once they are delisted. In contrast, the sensitivity analysis suggested that reducing the efficiency by which wolves in excess of the target numbers are hunted would likely be ineffective in preventing the need for relisting.

Density dependent reproduction had the fifth largest effect on extinction rates in the sensitivity analysis (Table 10). Data from Yellowstone National Park suggested that the % of adult females that breed each year may be density dependent (Smith and Stahler unpublished data). The function used ranged from 30% of adult females breeding when the census population size (N) was equal to the carrying capacity (K) to a maximum of 60% when N / K approached zero (Figure 1). When the population size was 57% of K, the % adult females breeding dropped to 50%. Including density dependent reproduction decreased the probability of extinction. But it had relatively lesser effects on the probabilities of a population dropping below 150 and 250 wolves, ranking 8th and 12th, respectively (Table 10). This suggested that including density dependent reproduction in simulations reduced the probability of extinction but had relatively little effect on whether the population would drop below the quasi-extinction thresholds.

It should be noted that the sensitivity analysis by Carroll et al. (2013) may have under represented the effects of parameters that have wide variation (>20%) in mean rates or high

variability and in parameters with a high degree of uncertainty. Mortality rates for young of the year mammals are often high and highly variable. If the long-term Mexican wolf pup mortality rate turns out to be higher and / or more variable than considered in Carroll et al. (2013) its relative importance in determining extinction and quasi-extinction may also increase. In addition there is high uncertainty in the frequency and nature of catastrophes that may occur among reintroduced Mexican wolf populations. The catastrophe parameterization used by Carroll et al. (2013) and in the simulations described above was based on the observed occurrence of distemper in Yellowstone National Park. Available data suggested parvovirus outbreaks have occurred on a five-year periodicity within the Park. But it remains uncertain how often comparable catastrophes may occur among reintroduced Mexican wolf populations. If a wider range of parvovirus periodicity had been considered this parameter would likely have had a higher relative importance.

The results of the simulations presented here and in the sensitivity analysis by Carroll et al. (2013) suggest that our recovery criteria appropriately focus on major threats to Mexican wolf viability and recovery under the Endangered Species Act. Focusing management efforts on these metrics should facilitate recovery. And once Mexican wolves are delisted, continued monitoring of these metrics should inform management to prevent the need to relist Mexican wolves in the future.

2. REALISM

Although we incorporated a high degree of realism into the simulation model, there were two aspects of the simulations that were not realistic: the modeling of heterozygosity and some aspects of inbreeding depression.

In the founding pedigrees we assumed that each of the original seven Mexican wolf founders carried two unique alleles at each locus. This led to mean observed heterozygosities for neutral genetic variation ranging from 0.774 to 0.848 for the various populations at the start of the simulations. Empirical estimates of observed heterozygosity among Mexican wolves, however, have been much lower. Hedrick et al. (1996) used 20 microsatellite loci to estimate mean observed heterozygosity among McBride, Ghost Ranch, and Aragon lineage wolves. Based on these data, they estimated McBride lineage wolves had the highest observed heterozygosity at 0.457, while Ghost Ranch and Aragon wolves had mean heterozygosities of 0.128 and 0.255, respectively. They also found that the Ghost Ranch and Aragon wolves were fixed for single alleles at 11 of the 20 loci. Fitak (unpublished data) found similar results based on about 6,000 unlinked single nucleotide polymorphisms (SNPs) with genotypic frequencies consistent with Hardy Weinberg proportions. Recent McBride lineage wolves had a mean observed heterozygosity of 0.310, while Ghost Ranch and Aragon lineage wolves averaged 0.194 and

0.273, respectively. In addition F1 wolves created from pairings between McBride and Ghost Ranch wolves averaged 0.409, while wolves created by pairings between McBride and Aragon wolves averaged 0.460. As expected, heterozygosity for the F1 wolves was substantially higher than those of the founding lineages. Observed heterozygosity for a sample of 21 cross-lineage wolves born 2006 – 2008, were lower than that for the F1 wolves, averaging 0.360. Most of these cross-lineage wolves were born in the Blue Range. Thus, the heterozygosity values from the simulations were not approximations of what might be achieved in actual reintroduced populations of Mexican wolves. But they are still useful for illustrating relative differences between populations, scenarios, and simulation conditions, as well as exploring the interplay of demography, genetics and management options.

Our parameterization of inbreeding depression on litter sizes was based on the findings of Fredrickson et al. (2007). Although this constitutes the best available information, we did not include the potential for a portion of the genetic load to be purged over time. Inbreeding depression is thought to be primarily a result of the full expression of deleterious alleles that have become homozygous as a result of inbreeding (Charlesworth and Willis 2009). But theory suggests that purging in small populations is likely to be limited to lethal alleles (those that result in the death of individuals with two copies; Hedrick 1994, Wang et al. 2000, Whitlock et al. 2000). And while lethal alleles may be eliminated or reduced in frequency in small populations, many other mildly and moderately deleterious alleles may simultaneously become fixed (homozygous in all individuals) with little or no net reduction in the overall genetic load (Hedrick 1994; Wang et al. 2000; Whitlock et al. 2000). This mixed result may occur because natural selection is weak and genetic drift is strong in small populations (Hedrick 2005). As a consequence, natural selection may only operate effectively on alleles with large effects (positive or deleterious) in small populations. But given the Mexican wolf's history of long-term small population size and close inbreeding, it is possible that lethal alleles carried by the seven Mexican wolf founders may have already been purged or reduced in frequency. If further purging were to occur among reintroduced Mexican wolf populations the strength of inbreeding depression may be reduced if the fitness increases resulting from the elimination of lethal alleles was not offset by the increased frequency of moderately and mildly deleterious alleles. It is possible, however, that the strength of inbreeding depression estimated by Fredrickson et al. (2007) for wolves in the Blue Range may have been underestimated. In the captive population of Mexican wolves, they found that inbreeding levels in dams, sires, and pups affected the numbers of pups produced. But it was not possible to investigate potential inbreeding effects associated with dams and sires in the Blue Range due to the nature of the available data.

3. LIMITATIONS

Although our simulations explored a wide range of conditions, there were some we did not consider. These included the possibilities that dispersal between populations may be density dependent, and that populations may have different mean adult mortality rates or that mortality rates vary over time within populations. We also did not consider the effects of potential directional changes in carrying capacity over time. Finally we did not consider possible management options related to implementation of the recovery plan.

a. Dispersal

In our simulations, dispersal between populations was modeled by moving a mean percentage of young, unpaired wolves between populations each timestep from the start of the simulations. Thus even when populations were small, some dispersal between populations was occurring. If, however, dispersal among Mexican wolves may be driven by positive density dependence, i.e. the percentage of young wolves that emigrate from a population each year increases and decreases as the population increases and decreases in size, this could affect the simulation outcomes in a variety of ways. First, when all populations are small, e.g. at the start of simulations, there could be fewer effective migrants per generation than in the simulations described above (depending on parameterization). This may reduce the demographic costs of dispersal between populations, thereby reducing the rate of extinctions among small populations. If so, this could be particularly important for the centrally located Blue Range population with the 1 mpg dispersal regime. When all populations are large, the increased rate of effective migration may reduce the probability of decreasing to small size. If one population was small, while its neighbor(s) was large, the small population may be more likely to be demographically and / or genetically rescued by adjacent populations. But at the same time the large neighboring populations may be at increased risk of declining in size as a result of receiving few migrants.

Wolves, however, may be compelled to move between populations by considerations other than a crowded landscape. At least four Mexican wolves have made long-distance movements out of the Blue Range Wolf Recovery Area travelling straight line distances of 158 – 291 km before being recaptured, despite the small size of the Blue Range population (<59 wolves). When populations are small and wolf densities are low, finding a minimally related mate may be difficult, particularly in a population such as the Blue Range which has such high mean kinship. Consistent with this, Von Holdt et al. (2008) found that wolves in the recovering Yellowstone population used a variety of behavioral mechanisms to avoid inbreeding, and concluded that the population had levels of genetic variation similar to a population managed to retain variation and minimize inbreeding accumulation. This suggests that our assumption that some wolves will disperse (or at least attempt to) between populations even when source populations are small may be valid.

b. Adult mortality, carrying capacity, and recovery implementation

If mean adult mortality rates vary between populations, those with higher mortality may be slower to reach the delisting criteria and may be less able to maintain a given population size. Thus it may cause differences between populations in their long-term census sizes. Populations with higher mortality may also be more likely to become extinct. If mean adult mortality rates vary over time within a population, this could cause variation in population size between different periods. It would also be expected to reduce the retention of heterozygosity relative to a population with equivalent constant mean mortality rate.

Carrying capacity could change as a result of changes to prey populations. This could potentially be driven by management of prey populations and / or by changes in habitat. Climate change may have the potential to drive changes in both prey and habitat. Climate in the southwestern United States is projected to become warmer and drier with longer droughts. This is expected to result in increased disturbance by forest fires and forest insects. Over time this is expected to change the areal extent of forests and their nature in the Southwest (Adams et al. 2009; Cayan et al. 2010; Raffa et al. 2008; Seager & Vecchi 2010; Williams et al. 2010).

Finally, our simulations did not explore scenarios related to implementation of the recovery plan. For example we did not explore the potential consequences of substantially improving the genetic composition of the Blue Range, nor did we consider the use of artificial insemination or in vitro fertilization techniques in the founding of new Mexican wolf populations. Similarly, we did not explore the potential benefits of artificial migration, e.g. between the Grand Canyon and southern Rockies populations. We also did not attempt to determine the size of numerical management buffers that may be needed to avoid relisting of Mexican wolves once they have been delisted. Although it would be possible to investigate these topics and others via simulations, this was beyond the scope of our task.

4. SCENARIO REVIEWS

Scenario 1: 3x250

Under scenario 1, the Blue Range was able to support a roughly stable mean population size only when there was 22% adult mortality and 2/1/1 mpg (Figure 3). Under these circumstances, the Blue Range was also able to maintain stable levels of heterozygosity (Figure 4), low extinction rates (Figure 6), contain its heterozygosity excess (Figure 5) and meet the numerical delisting criterion in 90% of iterations (Table 3). Increasing the adult mortality or using the 1 mpg dispersal regime caused deterioration in all viability and recovery metrics considered.

In contrast, the choice of dispersal regime had relatively small effects on the Grand Canyon and southern Rockies populations. But both populations were strongly affected by increases in adult mortality rates. The greatest mean metapopulation sizes were, however, supported by the

2/1/1 mpg (Figure 12). These simulations, as well as those from the other three scenarios strongly support the adoption of the 2/1/1 dispersal regime as part of the recovery criteria, rather than the 1 mpg dispersal regime.

None of the three populations in these simulations were able to maintain mean population sizes over time greater than 250 wolves. The GC350 and Blue Range 350 simulations under scenario 2, however, suggest that all three populations could be maintained above 250 wolves if the numerical threshold for harvests was set higher than 250 wolves.

Scenario 2: 3x200=750

This scenario was intended to allow some management flexibility in achieving and maintaining a recovered Mexican wolf metapopulation. Under this recovery scenario unequal minimum census population sizes for the three populations would be allowed, which could lead to unequal genetically effective population sizes for the three populations. If taken to an extreme a metapopulation composed of populations with highly unequal effective population sizes could have reduced viability relative to one in which component populations were of more equal sizes. We simulated two extreme variations of this scenario. The first assumed that the peripheral Grand Canyon population would be managed to maintain at least 350 wolves, while the Blue Range and southern Rockies would each be managed to maintain at least 200 wolves. The Grand Canyon population had the lowest mean kinship and was demographically the strongest of the three populations. The second variation assumed that the central Blue Range population would be managed to support at least 350 wolves, while the other two populations would be managed to each support at least 200 wolves.

When there was 1 mpg, the Blue Range 350 variation performed better than the GC 350 variation and the 3x250 scenario. The Blue Range350 variation had the highest mean metapopulation sizes at year 100 (Figure 12) and the lowest number of population extinctions (Figure 13). It also had the highest % of iterations meeting delisting criteria and exceeding the endangerment criteria in the last 20 years of the simulations. Overall the GC350 variation performed the worst. Although it supported slightly higher mean metapopulation sizes at year 100 than the 3x250 scenario, it also had the most population extinctions, the lowest delisting rate, and the lowest % of iterations that exceeded endangerment criteria at the end of the simulations.

When there was 2/1/1 mpg, the 3x250 scenario and the Blue Range 350 and GC 350 variations performed similarly. The Blue Range 350 variation, however, had slightly lower mean metapopulation sizes at year 100, higher numbers of population extinctions, and slightly lower delisting and higher rates endangerment than the other two options.

These simulations suggested that this scenario allows a level of management flexibility that will likely not have a large negative effect on viability. In addition, other considerations suggested that allowing this level of management flexibility will likely not be detrimental to recovered Mexican wolf populations. First Mexican wolves will likely not be maintained at these extreme

numerical disparities and relative census sizes of recovered populations will likely change over time. Secondly, the recovered Mexican wolf population may be maintained at numbers substantially greater than 750 wolves, to minimize the probability of needing to relist Mexican wolves in the future. Maintaining a numerical buffer on each recovered population would reduce the functional differences between the scenarios. Finally the viability of the Blue Range may be increased by genetic management prior to delisting and / or the reintroduced Grand Canyon and southern Rockies populations may be founded by wolves with greater relatedness, reducing their long-term viability.

Long-term adult mortality rates and the choice of dispersal regime will likely have much larger effects on management outcomes than the management flexibility allowed under this scenario. These simulations, however, did not explore the potential effects of management flexibility when populations have substantially different adult mortality rates. The simulations also did not explore the effects of directional changes in relative wolf abundance over time among the three populations. If the smallest population increased in size to become the largest population, while the largest population became the smallest, this could cause an overall reduction in heterozygosity over time as individuals and genes from the formerly small population proliferate in the other two populations. This dynamic may, however, be minimized by land ownership patterns and prey abundances that suggest the southern Rockies may be most capable and the Grand Canyon region may be least capable of supporting large populations of Mexican wolves.

Collectively, these results suggested that Scenario 2 which allows management flexibility in the numerical targets for delisting is unlikely to be severely detrimental to the recovered Mexican wolf population relative to the 3x250 scenario.

Scenario 3: 3x250 + Sonora

This scenario would extend the geographic scope of the recovered Mexican wolf metapopulation into Mexico. It would also broaden the array of ecological communities inhabited by Mexican wolves. The inclusion of Sonora in the simulations, however, had mostly negative effects on the Blue Range and on overall metapopulation viability relative to the 3x250 scenario. The Grand Canyon and southern Rockies populations, however, largely performed similarly with or without Sonora.

The positive effects of including Sonora were limited. With Sonora, mean metapopulation sizes at year 100 were greater in three of four of the simulations (Figure 20). The sum of extinctions among the three large populations was lower (Figure 21) and mean expected heterozygosity for the Blue Range was higher when there was 2/1/1 mpg and 22% adult mortality. However, extinctions among the three large populations were higher and mean expected heterozygosity lower when there was 2/1/1 mpg and 23.5% adult mortality as well as when there was 1 mpg.

Additional negative effects on the Blue Range included 29 and 40% smaller mean population sizes at year 100 than that with the 3x250 scenario when there was 1 mpg, and 6 and 19%

smaller population sizes when there was 2/1/1 mpg, with 22 and 23.5% adult mortality, respectively. When there was 1 mpg, extinction rates for the Blue Range were 156 and 63% higher with Sonora than without, with 22 and 23.5% adult mortality, respectively. But with 2/1/1 mpg Blue Range extinction rates were only slightly higher with Sonora.

In addition, the % of iterations in which all three large populations exceeded numerical criteria for being endangered was lower with Sonora (Tables 5 and 7). And delisting rates for the three large populations were lower in three of four cases (the fourth simulation was tied; Tables 4 and 6).

The Sonora population outperformed the Blue Range when there was 1 mpg, driven by the demographic costs of this dispersal regime to the centrally located Blue Range. At year 100 the mean population size for the Blue Range was 34 and 22% of the target population size of 250 wolves, but Sonora was 71 and 51% of its target population size of 100 wolves, with 22 and 23.5% adult mortality, respectively. In addition, extinction rates for Sonora were somewhat lower than those for the Blue Range.

But with 2/1/1 mpg the Blue Range outperformed Sonora. Mean population sizes at year 100 for the Blue Range were 81 and 58% of the target population size of 250 wolves, while population sizes for Sonora were 75 and 58% of targeted numbers, with 22 and 23.5% adult mortality, respectively. Extinction rates for the Blue Range were also much lower than that for Sonora (Figure 19).

Although, the addition of Sonora increased mean metapopulation sizes relative to the 3x250 scenario, it appeared to reduce the viability of the metapopulation. Overall, Sonora and the Blue Range had smaller relative population sizes and were substantially more extinction prone than the Blue Range in the 3x250 scenario. In addition, there is substantial uncertainty whether the Sonora / Chihuahua area identified for potential reintroduction of Mexican wolves would be able to support 133 wolves in the foreseeable future, as assumed in the simulations.

Based on expert opinion, it was thought the Sonora and Durango reintroduction areas may each be able to support about 100 wolves (Araiza et al. 2007; C. Lopez Gonzalez personal communication). There is, however, little data available to inform estimates of ecological carrying capacity in these areas. Further, even if there is the biological potential to support at least 100 wolves in these areas, land ownership and land use patterns, and road densities may make the goal of 100 wolves difficult to achieve, as suggested by the recent unsuccessful reintroduction attempts into the Sonora area. Thus it is unclear whether either Sonora or Durango will be able to support 100 wolves in the foreseeable future. Consequently, the sum of available information suggests that recovery under scenario 3 may be more difficult to achieve and presents a higher risk of failure than scenarios 1 and 2.

Scenario 4: Blue Range +2MX100

This scenario was characterized by populations that declined steadily from the start of harvests to very low sizes by year 100 and by higher extinction rates and lower heterozygosity retention than the other three scenarios. As a result, this scenario had the lowest % of iterations exceeding the numerical delisting criteria and only 8% or fewer iterations exceeding the numerical criteria for being endangered in the last 20 years of the simulation.

With 1 mpg, mean sizes of extant metapopulations at year 100 were only 53 and 32% of the targeted 450 wolves, with 22 and 23.5% adult mortality, respectively. Mean metapopulation sizes at year 100 for the 3x250 scenario were 78 and 58% of the targeted population size of 750 wolves (Figure 20). Summed extinctions across the three populations were 720 and 1,493, with 22 and 23.5%, respectively (Figure 21). This was 10.3 and 4.5 times greater than the summed extinctions for the 3x250 scenario. Averaged over the three populations, the mean population extinction rate for this scenario was 49.8% with 23.5% adult mortality.

Although none of the three populations performed well, Sonora, the central population, performed the worst. The mean sizes of extant populations at year 100 were only 37 and 20 wolves, and extinction rates for Sonora were 38 and 70% with 22 and 23.5% adult mortality, respectively. Durango fared somewhat better. But mean sizes of extant populations at year 100 were only 56 and 38 wolves, and extinction rates for Durango were 26 and 56% with 22 and 23.5% adult mortality, respectively. The Blue Range performed the best. Mean sizes of extant populations at year 100 were 171 and 118 wolves with 22 and 23.5% adult mortality, respectively, slightly higher than that with the 3x250 scenario. But with extinction rates of 8 and 24% with 22 and 23.5% adult mortality, respectively, more iterations became extinct than with the 3x250 scenario.

With 2/1/1 mpg, mean metapopulation sizes at year 100 were 56 and 34% of the targeted size of 450 wolves. This was substantially lower than that under the 3x250 scenario which supported 86 and 71% of the targeted 750 wolves at year 100. The summed population extinctions, 385 and 1,238 with 22 and 23.5% adult mortality, respectively, were 9 and 8.4 times greater than that with the 3x250 scenario. The centrally located Sonora population supported averages of 49 and 34 wolves at year 100 among extant iterations and had extinction rates of 15 and 48% with 22 and 23.5% adult mortality, respectively. Durango supported mean population sizes among extant populations of 60 and 40 wolves at year 100, and had 17 and 47% extinction rates, with 22 and 23.5% adult mortality, respectively. The Blue Range supported 159 and 108 wolves on average at year 100, along with extinction rates of 7 and 29%, with 22 and 23.5% adult mortality, respectively.

These results suggested that this alternative would be the least likely to result in delisting of Mexican wolves and the most likely to result in the need to relist Mexican wolves under the Endangered Species Act - if they were ever delisted. Coupled with the high uncertainty, noted above, of whether the Sonora and Durango regions will each be capable of supporting 100

wolves in the foreseeable future, makes this alternative unacceptable as recovery criteria for Mexican wolves.

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Table 1. Numbers of wolves, packs and pairs used to found populations and the range of target population sizes.

Population	Target population sizes	Number of wolves at founding	Pairs at founding
Blue Range	200 – 350	122	21
Grand Canyon	200 - 350	50	10
Southern Rockies	200 - 350	50	10
Sonora	100	35	7
Durango	100	35	7

Table 2. Mean kinship for founding populations, the reintroduced Blue Range population, and the captive population as of fall 2013.

Population	Mean kinship
Blue Range (simulated)	0.2446
Blue Range (actual) ^a	0.2472
Grand Canyon	0.194
Southern Rockies	0.1954
Sonora (Scenario 3)	0.2064
Sonora (Scenario 4)	0.2053
Durango	0.2049
SSP population ^a	0.1665

^aSiminski and Spevak (2013).

Table 3. Mean numbers of effective migrants per generation into each population from years 30 to 100.

Simulation	Dispersal regime	Mortality rate (%)	Blue Range	Grand Canyon	S. Rockies	Sonora	Durango	
3x250	1 mpg	22	1.03	1.06	1.09	na	na	
		23.5	1.12	1.00	1.02	na	na	
		25	1.28	1.01	1.03	na	na	
	2/1/1 mpg	22	2.02	1.04	1.04	na	na	
		23.5	2.21	1.07	1.07	na	na	
		25	2.06	1.06	1.07	na	na	
	GC350 BR&SR200	1 mpg	22	1.10	1.01	1.00	na	na
			23.5	1.10	0.99	0.99	na	na
		2/1/1 mpg	22	2.03	1.01	1.02	na	na
23.5			2.07	1.02	1.01	na	na	
BR350 GC&SR200		1 mpg	22	1.05	1.05	1.06	na	na
			23.5	1.07	1.02	1.03	na	na
	2/1/1 mpg	22	2.04	1.02	1.02	na	na	
		23.5	2.04	1.04	1.04	na	na	
3x250 + Sonora 5 pairs	1 mpg	22	1.11	1.00	1.00	0.99	na	
		23.5	1.11	0.84	0.85	0.86	na	
	2/1/1 mpg	22	2.20	1.00	1.01	1.06	na	
		23.5	2.24	1.02	1.03	1.04	na	
3x250 + Sonora 7 pairs	1 mpg	22	1.12	1.00	0.99	0.97	na	
		23.5	1.13	0.84	0.85	0.84	na	
	2/1/1 mpg	22	2.21	0.99	1.00	1.03	na	
		23.5	2.24	1.01	1.01	1.01	na	
BR + 2MX100	1 mpg	22	0.77	na	na	1.13	0.77	
		23.5	0.76	na	na	1.17	0.78	
	2/1/1 mpg	22	0.99	na	na	2.39	1.01	
		23.5	1.03	na	na	2.26	0.98	

Table 4. Percentage of iterations in which all three populations met numerical delisting criteria (the mean size of each population averaged over eight years was ≥ 250 wolves for 3x250 simulations; >350 and ≥ 200 wolves for the Grand Canyon 350 and Blue range 350 simulations).

Adult / yearling mortality rate (%)	3 x 250	Grand Canyon 350	Blue Range 350
1 mpg			
22	81	79	86
23.5	47	42	58
25	18	na	na
2/1/1 mpg			
22	90	90	89
23.5	69	68	62
25	32	na	na

Table 5. Percentage of iterations in which all three populations exceeded the numerical criteria for being endangered during the last 20 years of the simulations (the mean size of each population averaged over eight years was ≥ 150 wolves for 3x250 simulations; ≥ 210 and ≥ 120 wolves for the Grand Canyon 350 and Blue range 350 simulations).

Adult / yearling mortality rate (%)	3 x 250	Grand Canyon 350	Blue Range 350
1 mpg			
22	27	24	37
23.5	8	3	15
25	1	na	na
2/1/1 mpg			
22	44	38	37
23.5	20	19	15
25	4	na	na

Table 6. Percentage of iterations in which all four populations, just the three large populations, the BR and Sonora met numerical delisting criteria for the 3x250+Sonora scenario (the mean population size averaged over eight years was ≥ 250 wolves for the BR, GC, and SR populations, and ≥ 100 for Sonora).

Adult / yearling mortality rate (%)	All 4 populations	BR+GC+SR	BR	Sonora
1 mpg				
22	64	65	66	97
23.5	31	33	37	88
2/1/1 mpg				
22	86	90	96	95
23.5	54	59	72	89

Table 7. Percentage of 3x250+Sonora iterations in which all four populations, the three large populations, the BR, and Sonora exceeded numerical criteria for being endangered during the last 20 years of the simulations for the option (the mean size of each population averaged over eight years was ≥ 150 wolves for the BR, GC, and SR populations, and > 60 for Sonora).

Adult / yearling mortality rate (%)	All 4 populations	BR+GC+SR	BRP	Sonora
1 mpg				
22	12	17	21	52
23.5	1	3	6	24
2/1/1 mpg				
22	26	41	68	57
23.5	7	14	32	35

Table 8. Percentage of iterations in which all three populations, the BR, Sonora, and Durango populations met numerical delisting criteria for the BRP+2MX100 scenario (the mean population size averaged over eight years was ≥ 250 wolves for the BR and ≥ 100 for Sonora and Durango).

Adult / yearling mortality rate (%)	All 3 populations	BR	Sonora	Durango
1 mpg				
22	58	92	64	90
23.5	30	79	40	77
2/1/1 mpg				
22	72	90	80	91
23.5	39	71	54	73

Table 9. Percentage of iterations in which all three populations, the BR, Sonora, and Durango populations exceeded numerical criteria for being endangered during the years 81-100 under the BRP+2MX100 scenario (the mean population size averaged over eight years was ≥ 150 wolves for the BR and ≥ 60 wolves for Sonora and Durango).

Adult / yearling mortality rate (%)	All 3 populations	BR	Sonora	Durango
1 mpg				
22	5	49	12	32
23.5	<1	25	2	10
2/1/1 mpg				
22	8	44	24	38
23.5	1	19	8	13

Table 10. Results of sensitivity analysis of Vortex population model assessed using standardized coefficients from logistic regression of parameter sets against probability of extinction and quasi extinction (reproduced from Carroll et al. 2013).

Parameter	Minimum	Maximum	z value for probability of		
			extinction	Quasi-ex-150	Quasi-ex-250 ^a
Adult mortality ^b	18.32	27.48	167.46	162.48	111.15
Percentage of females in breeding pool	40	60	-160.67	-156.80	-104.49
Population size threshold	50	350	-158.63	-136.53	-72.03
Strength of inbreeding depression ^c	6.586	9.789	152.81	141.54	92.90
Density dependent reproduction	categorical		-92.42	-54.95	-8.35
Effective migrants per generation	0.0	2.4	-88.13	-56.17	-35.49
Average number of years between disease events	4	6	76.54	81.23	41.31
Pup mortality ^b	19.52	29.28	75.37	60.22	43.56
Variation between existing and new populations ^d	categorical		-34.12	-32.62	-24.79
Carrying capacity buffer ^e	1.07	1.60	-5.44	-51.50	-52.47
Harvest efficiency ^f	6.4	9.6	-3.86	-2.44	-12.65

Footnotes

a Quasi-extinction occurs when the 8-year running mean population size falls below 150 or 250. All regressions are based on 1000 scenarios derived from randomized parameter sets, with 100 replicate runs per scenario. Standardized regression coefficients (z-values), created by dividing a regression coefficient by its standard error, are unitless values whose magnitude indicates the relative importance of a parameter in the model.

b From Smith et al. (2010) for Greater Yellowstone Area wolf population.

c Slope parameter in equation of Fredrickson et al. (2007) relating litter size to inbreeding coefficient.

d Variation in population performance arising from contrasts between populations in initial pedigree.

e Ratio of ecological carrying capacity to the population size threshold parameter.

f Reciprocal of proportion of the population above the population-size threshold that is removed annually.

Figure 1. Mean mortality rates with density dependent senescence when the baseline mortality rate was 22% for a range of census population sizes relative to the carrying capacity (N/K).

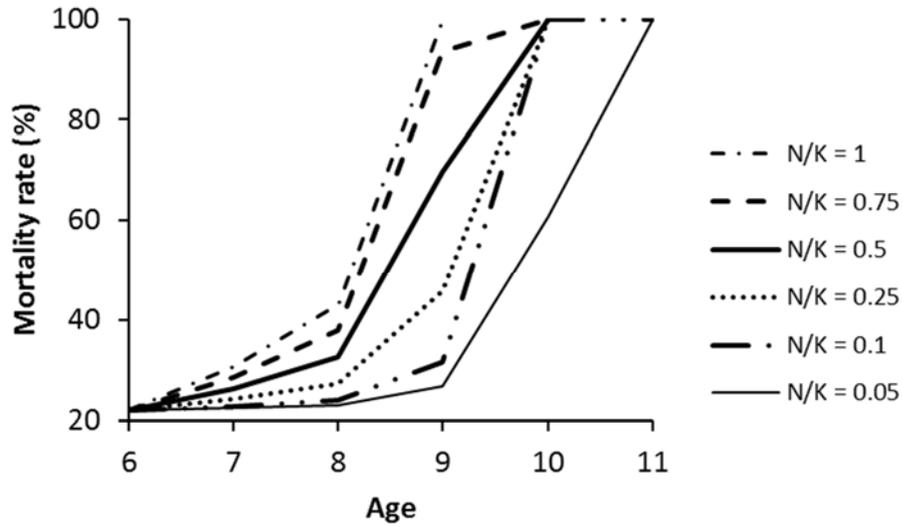


Figure 2. Mean % of adult females breeding when there was density dependent reproduction for census population sizes relative to carrying capacity (N/K) ranging from 0 to 1.

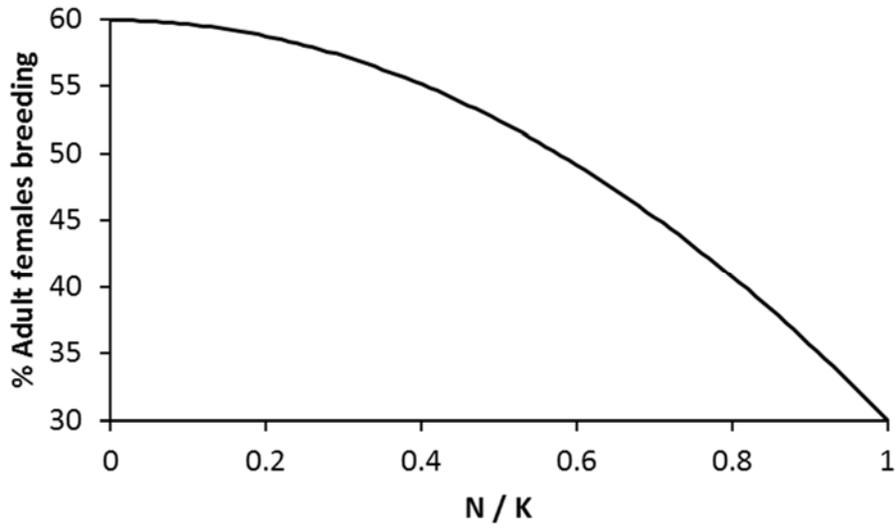
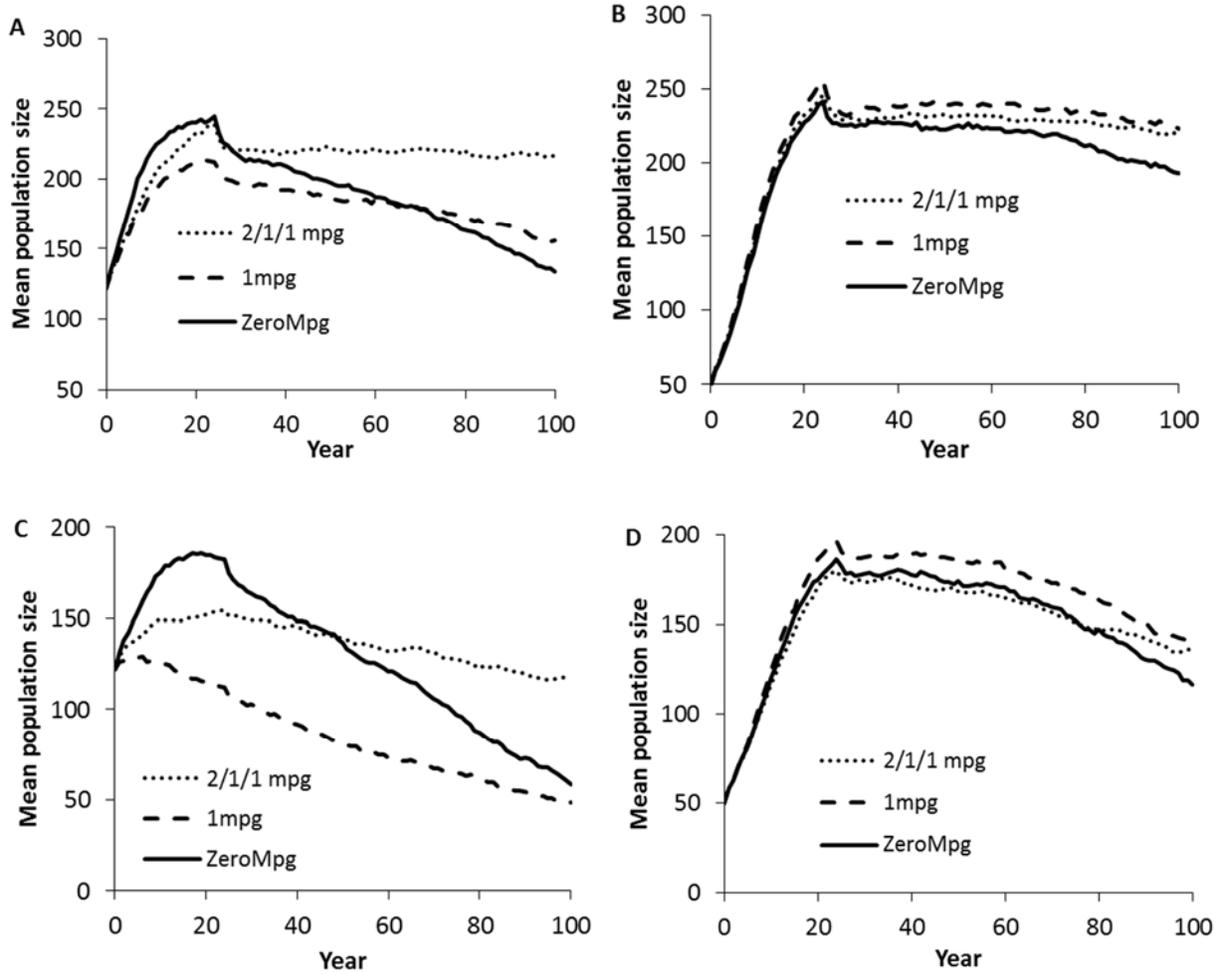


Figure 3. Mean census population size among extant iterations over time under the 3x250 scenario for the BR and Grand Canyon populations: A) BR with 22% mortality; B) Grand Canyon with 22% mortality; C) BR with 25% mortality; and D) Grand Canyon with 25% mortality.



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Figure 4. Mean expected heterozygosity over time for the 3x250 scenario of the Blue Range and Grand Canyon populations with 22% yearling / adult mortality (A, B) and 25% mortality (C, D).

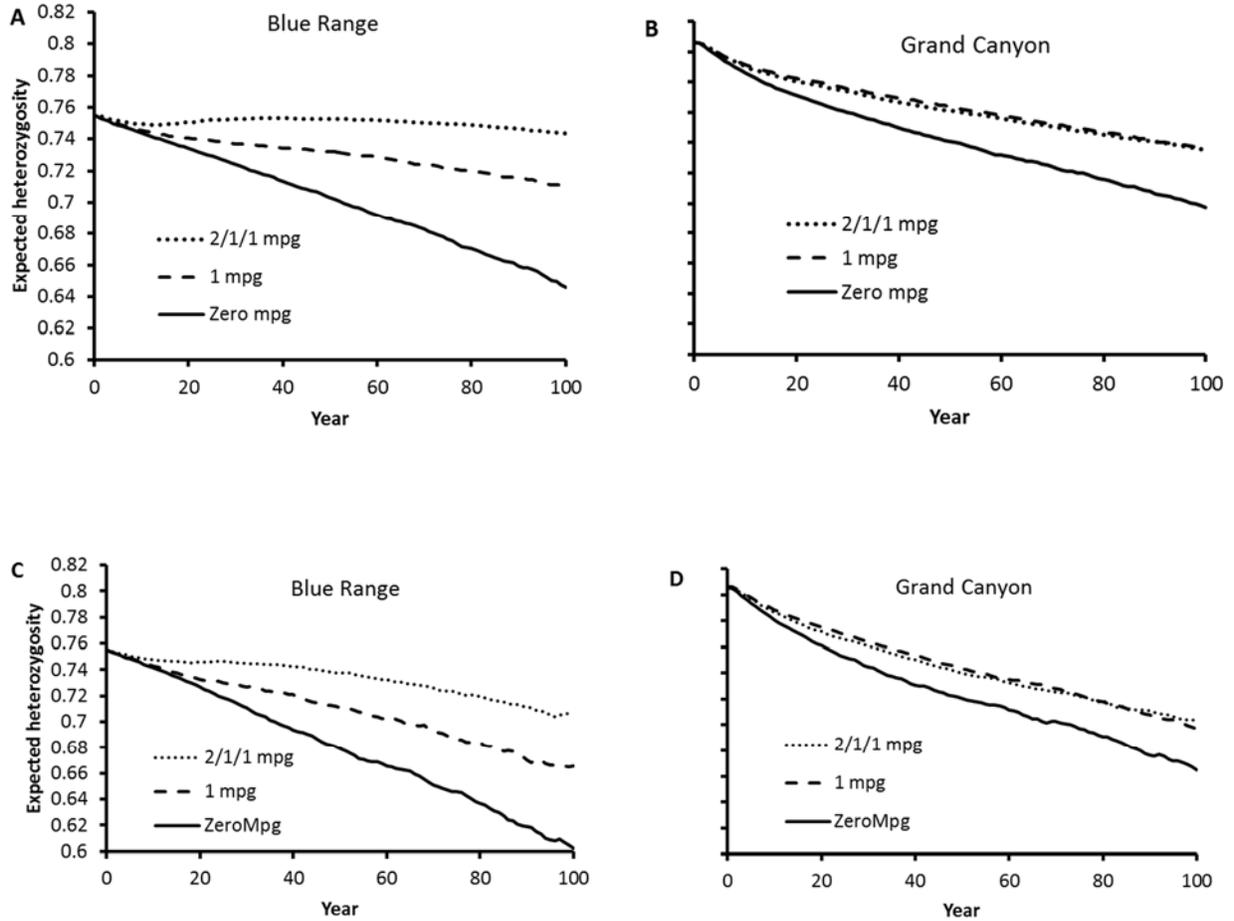
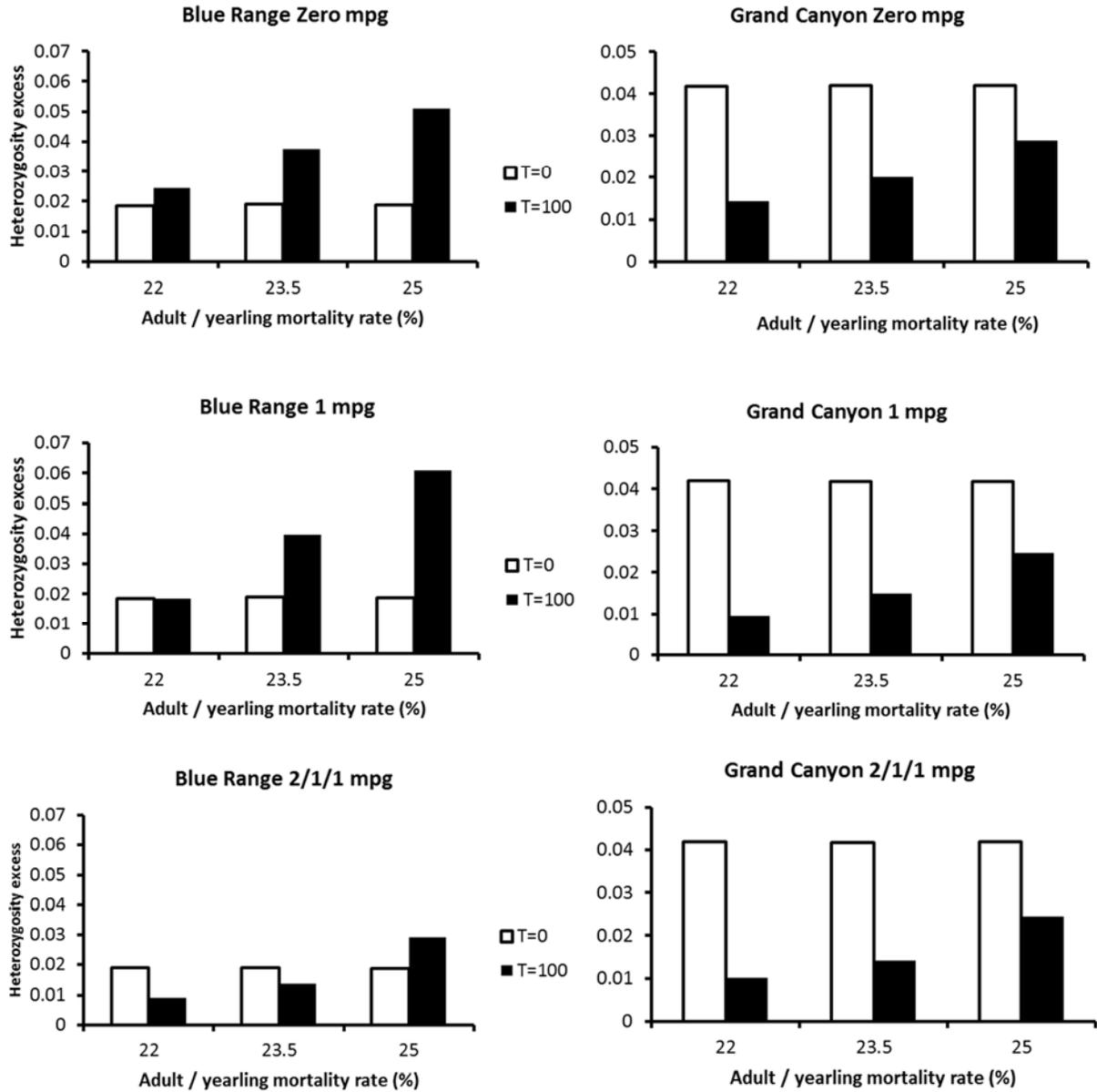


Figure 5. Heterozygosity excesses at years zero and 100 for the Blue Range and Grand Canyon populations under the 3x250 scenario.



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Figure 6. Population extinction rates for the 3x250 scenario with three different adult / yearling mortality rates and three dispersal regimes: A) 22% annual mortality; B) 23.5% annual mortality; and C) 25% annual mortality.

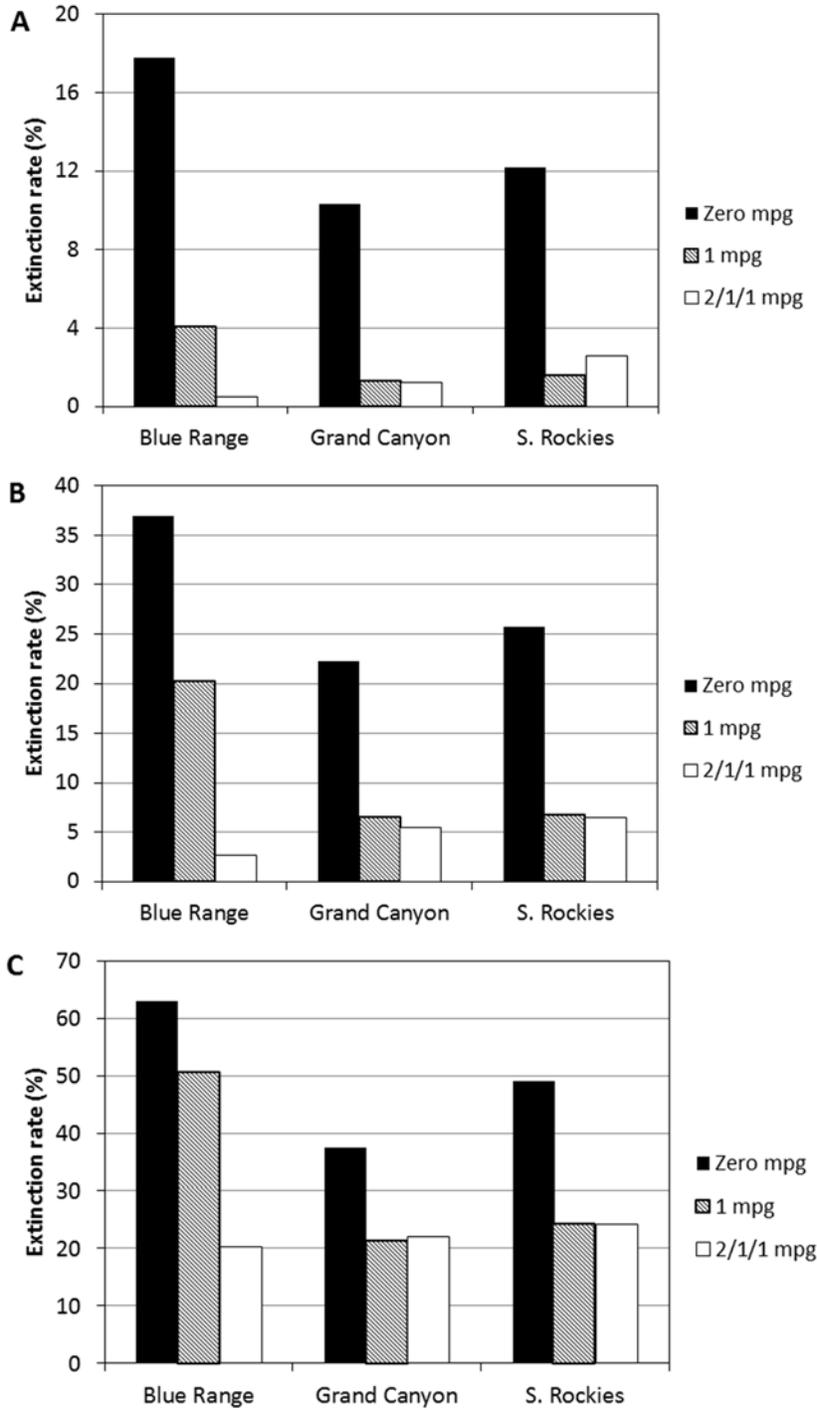


Figure 7. Relationship of mean size of extant populations at year 100 and its coefficient of variation from the 3x250 scenario with three levels of adult / yearling mortality (22, 23.5, and 25%) and three levels of population connectivity. Each symbol represents a single population from a simulation.

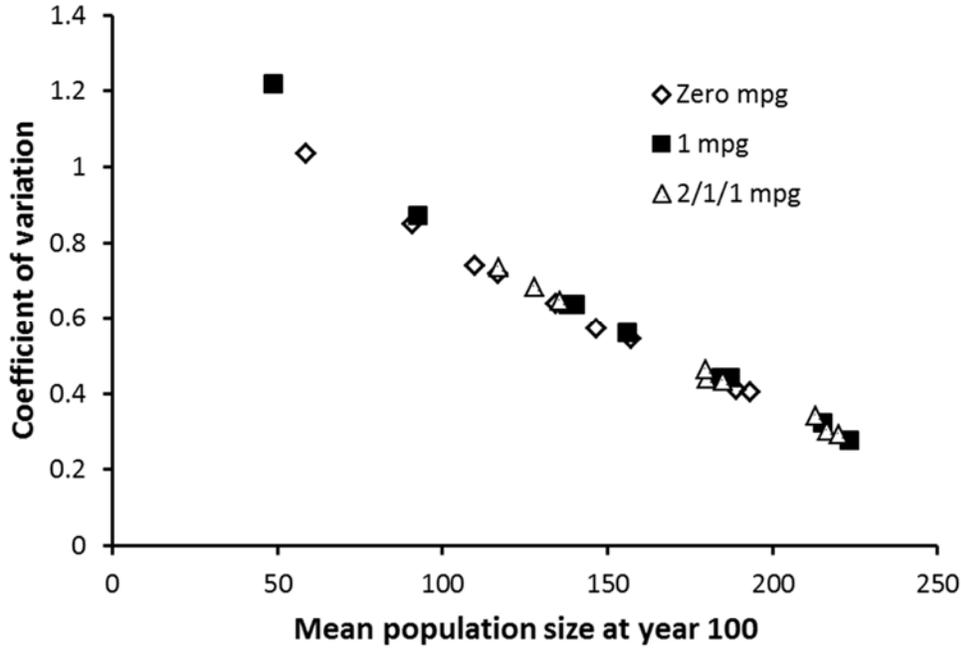
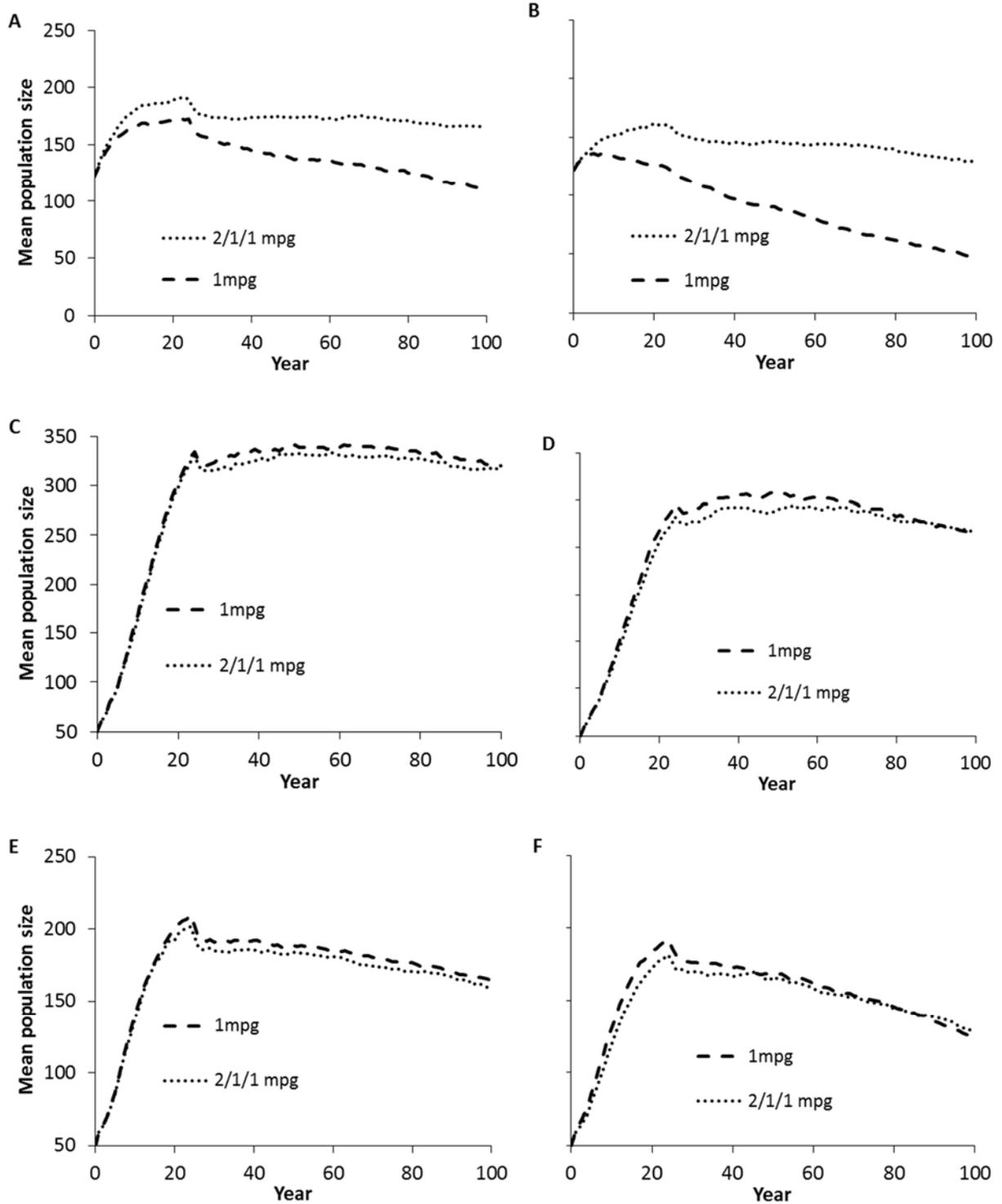


Figure 8. Mean census population sizes among extant iterations over time for the Grand Canyon 350 simulations: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) southern Rockies with 22% adult mortality; and F) southern Rockies with 23.5% adult mortality.



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Figure 9. Mean expected heterozygosity over time for the Grand Canyon 350 simulations: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) southern Rockies with 22% adult mortality; and F) southern Rockies with 23.5% adult mortality.

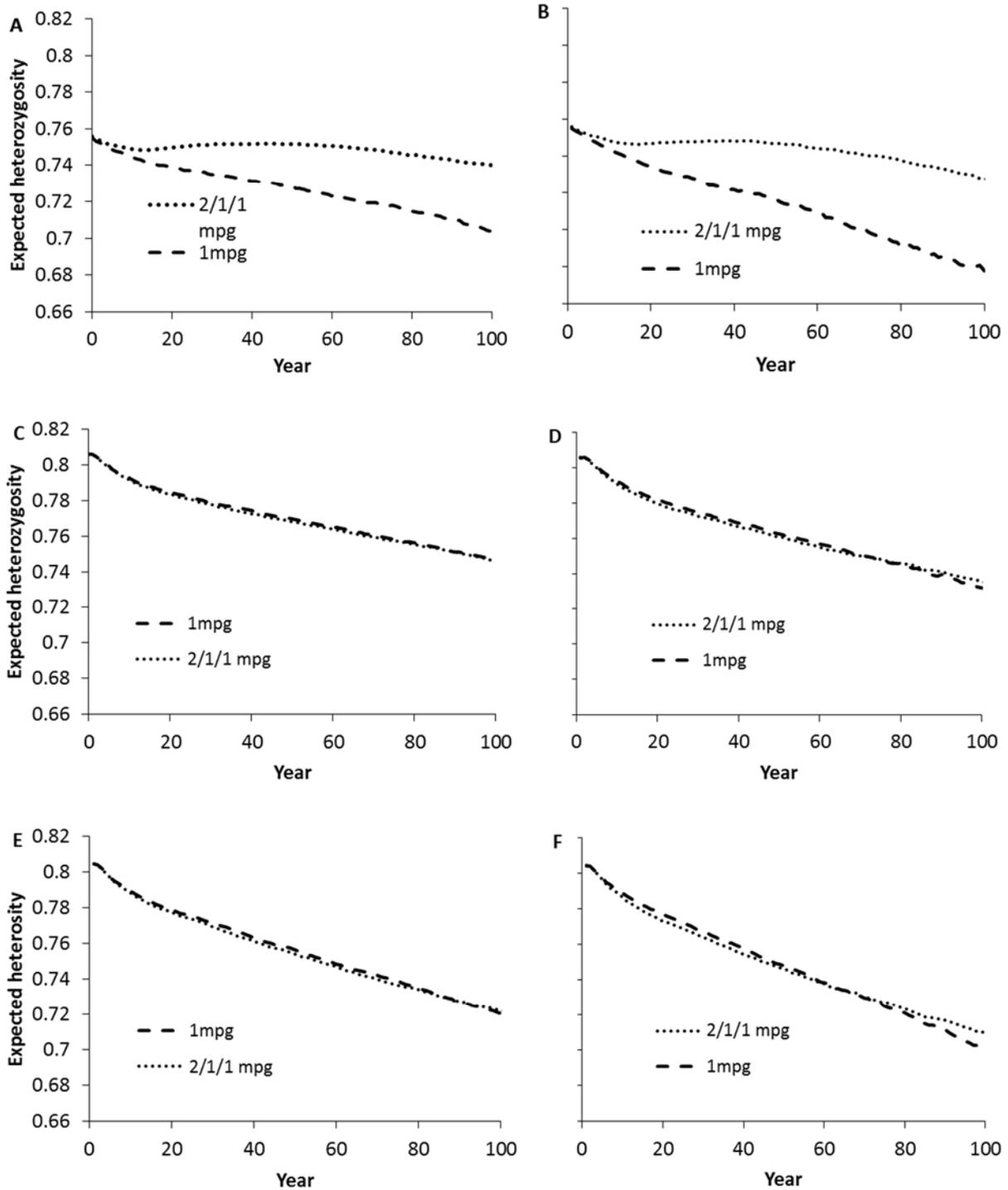


Figure 10. Mean heterozygosity excesses for the Grand Canyon 350 simulations (A, C and E) and BRP 350 simulations (B, D, and F) simulations: A, B) Blue Range; C, D) Grand Canyon; E, F) southern Rockies.

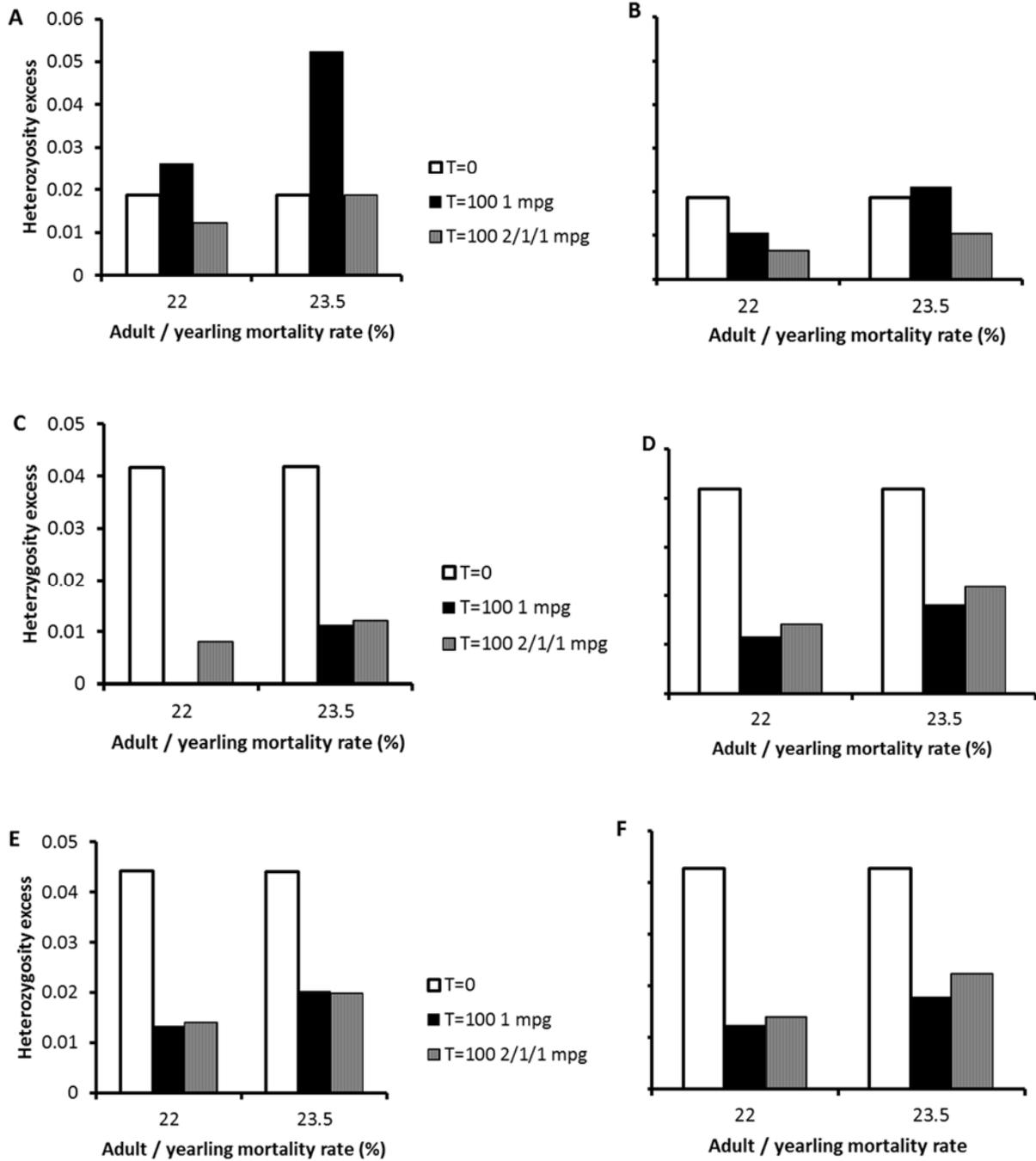


Figure 11. Subpopulation extinction rates for Grand Canyon 350 simulations (A,C) and BRP 350 simulations (B,D) with two adult / yearling mortality rates and two dispersal regimes: A) 22% adult mortality Grand Canyon 350; B) 22% adult mortality BRP 350; C) 23.5% adult mortality Grand Canyon 350; and D) 23.5% mortality BRP350.

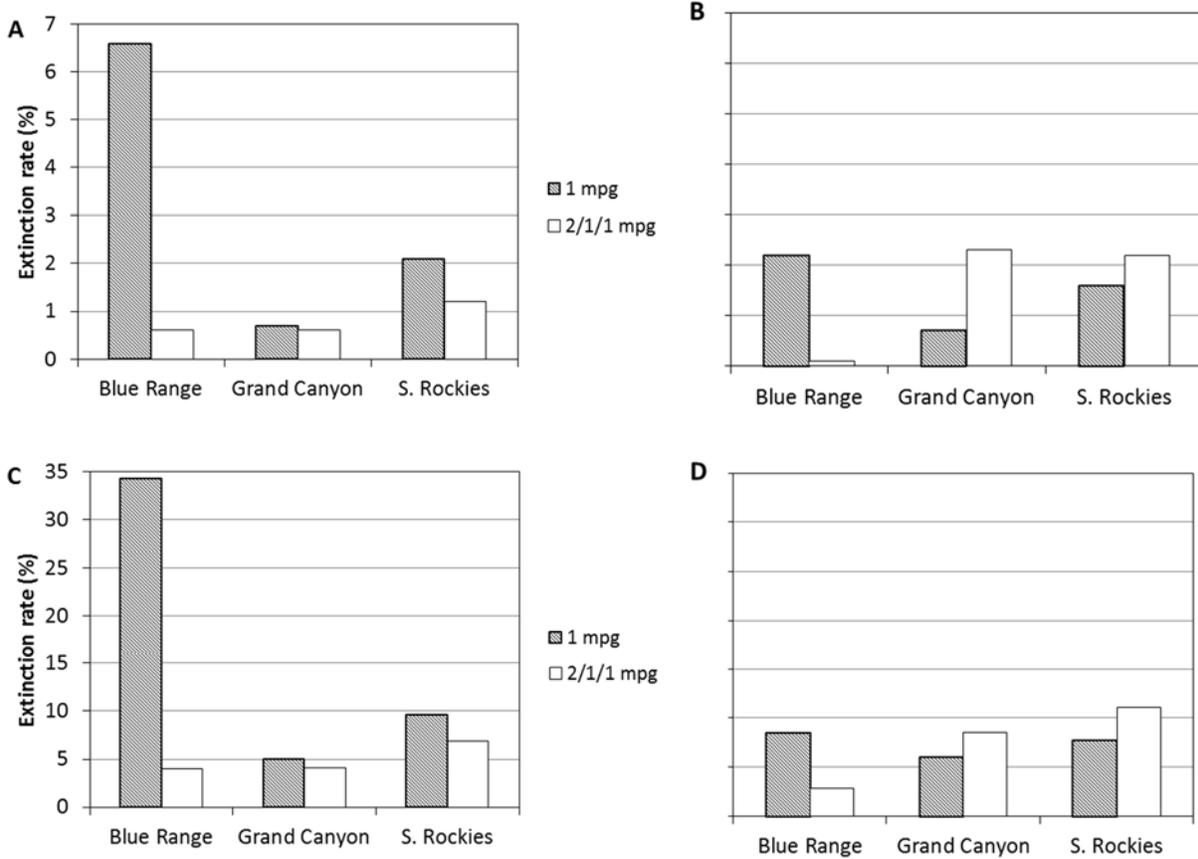


Figure 12. Mean metapopulation size at year 100 for the 3x250, the Grand Canyon 350, and BRP 350 simulations.

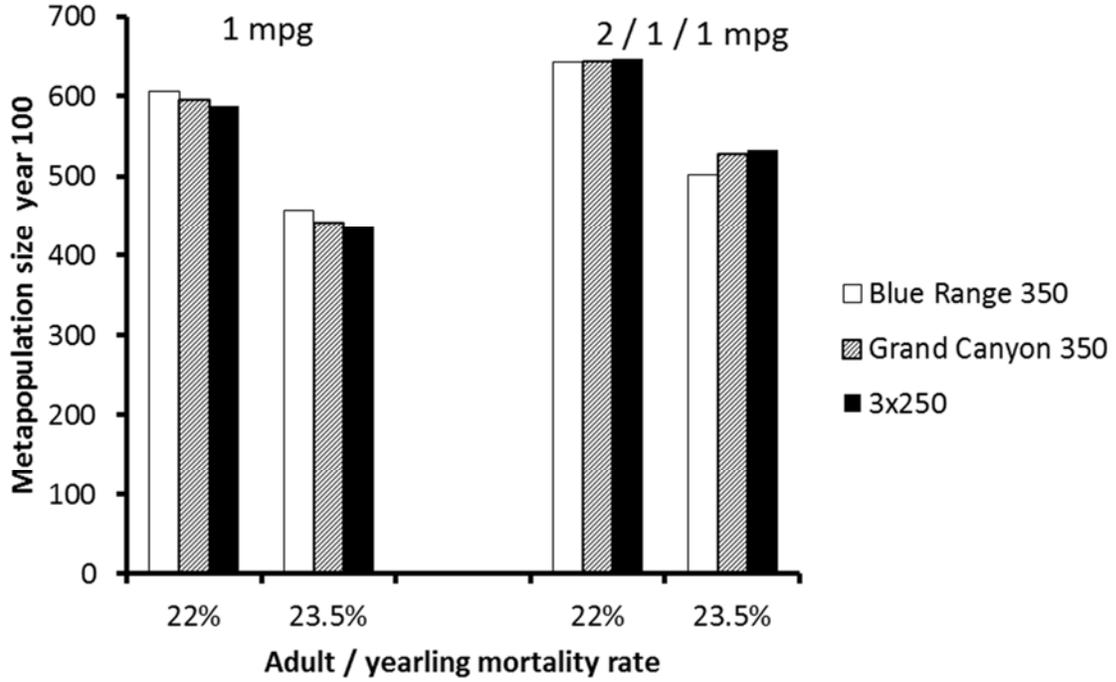


Figure 13. Total number of population extinctions for the 3x250, the Grand Canyon 350, and BRP 350 simulations.

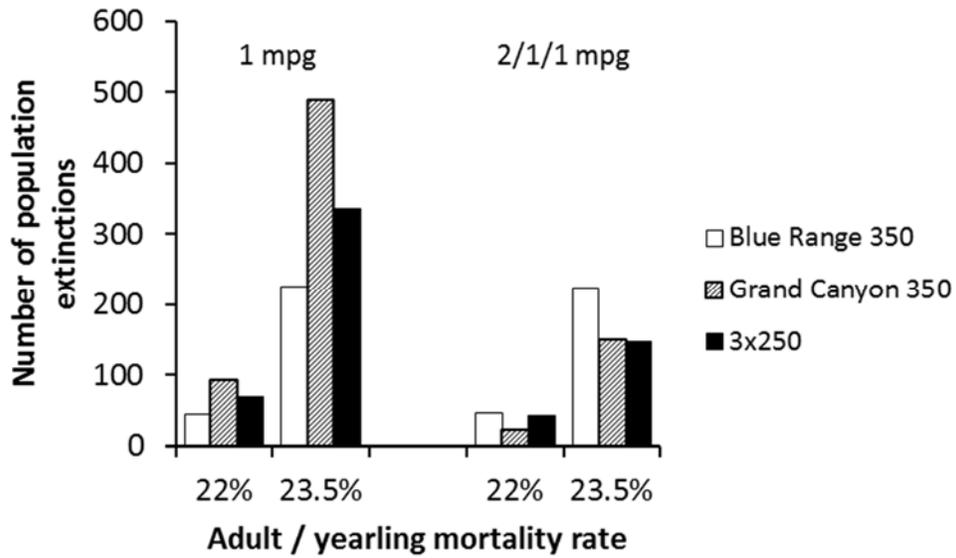
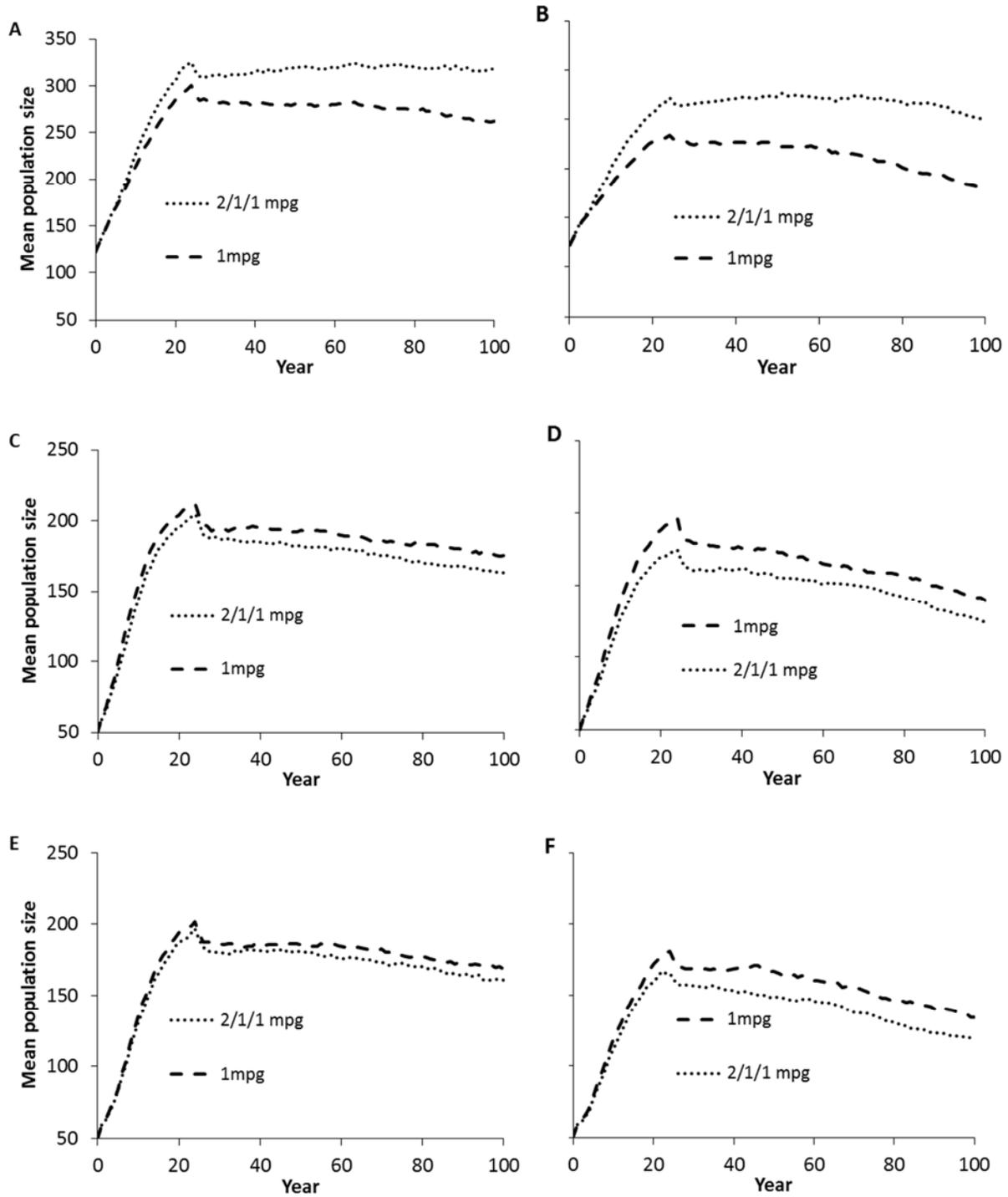


Figure 14. Mean census population sizes among extant iterations over time for BRP 350 simulations: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) southern Rockies with 22% adult mortality; and F) southern Rockies with 23.5% adult mortality.



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Figure 15. Mean expected heterozygosity over time for BRP 350 simulations: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) southern Rockies with 22% adult mortality; and F) southern Rockies with 23.5% adult mortality.

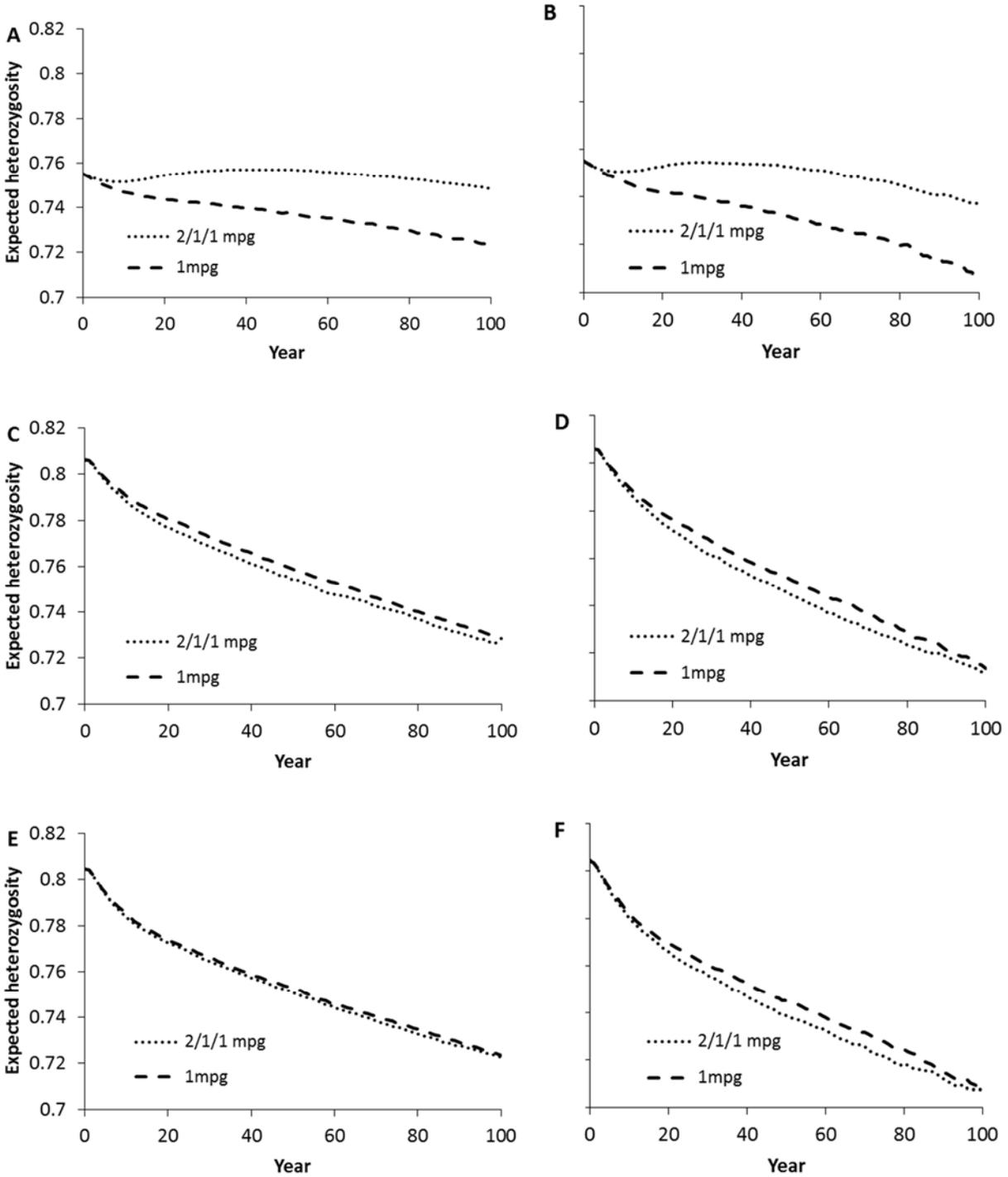
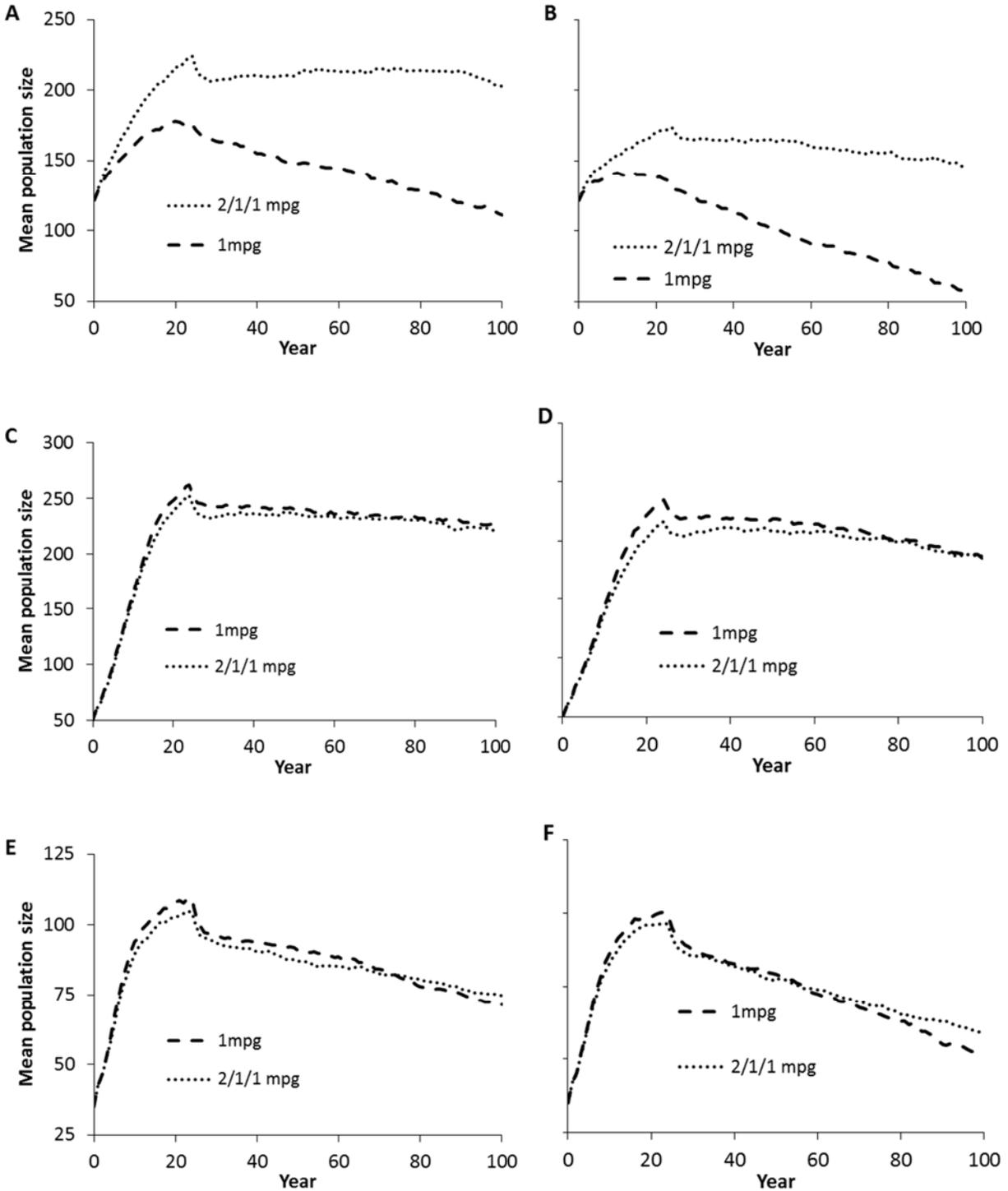


Figure 16. Mean census population sizes among extant iterations over time for the 3x250 + Sonora scenario: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) Sonora with 22% adult mortality; and F) Sonora with 23.5% adult mortality.



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Figure 17. Mean expected heterozygosity over time for the 3x250 + Sonora scenario: A) BR with 22% adult mortality; B) BR with 23.5% adult mortality; C) Grand Canyon with 22% adult mortality; D) Grand Canyon with 23.5% adult mortality; E) Sonora with 22% adult mortality; and F) Sonora with 23.5% adult mortality.

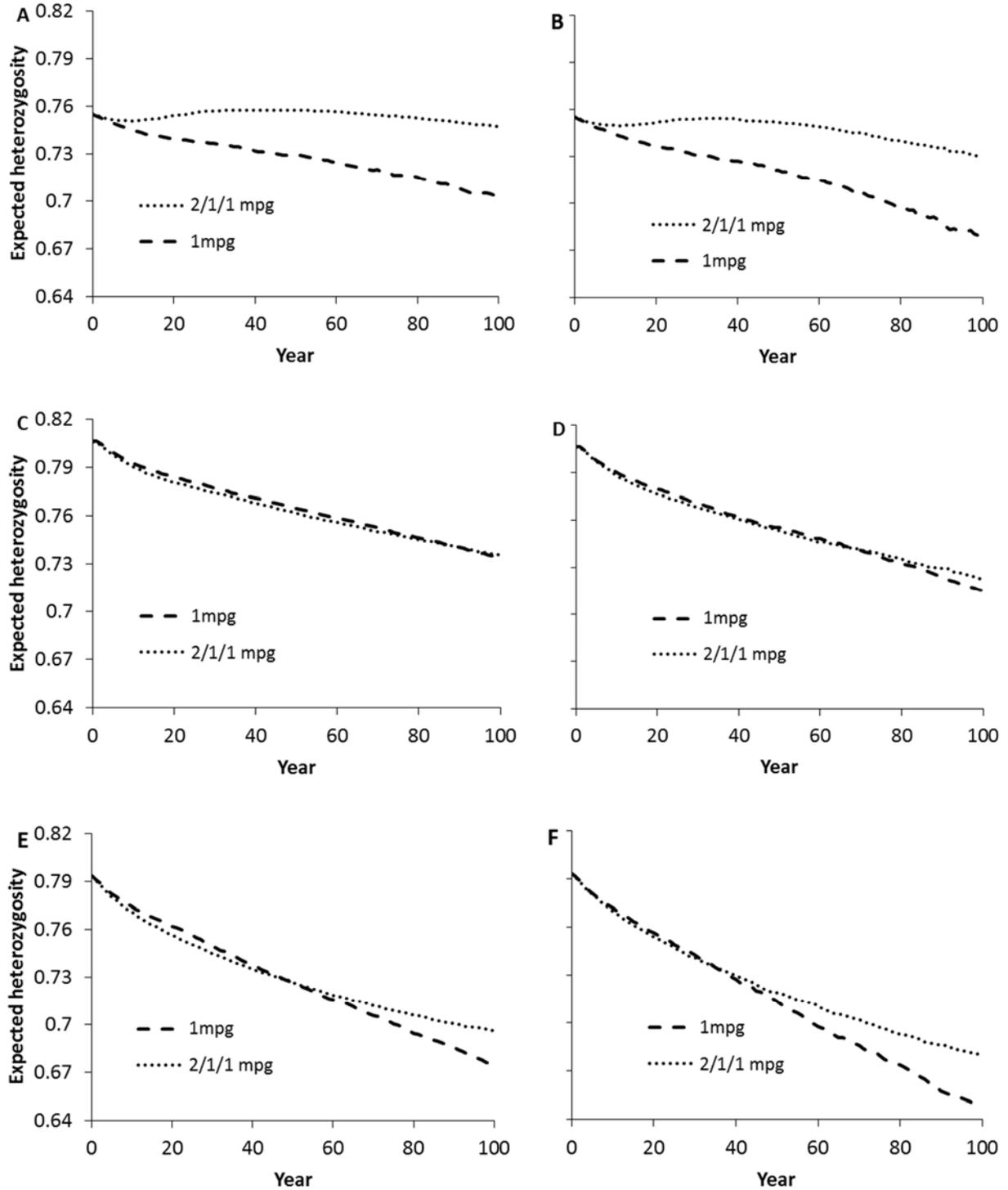
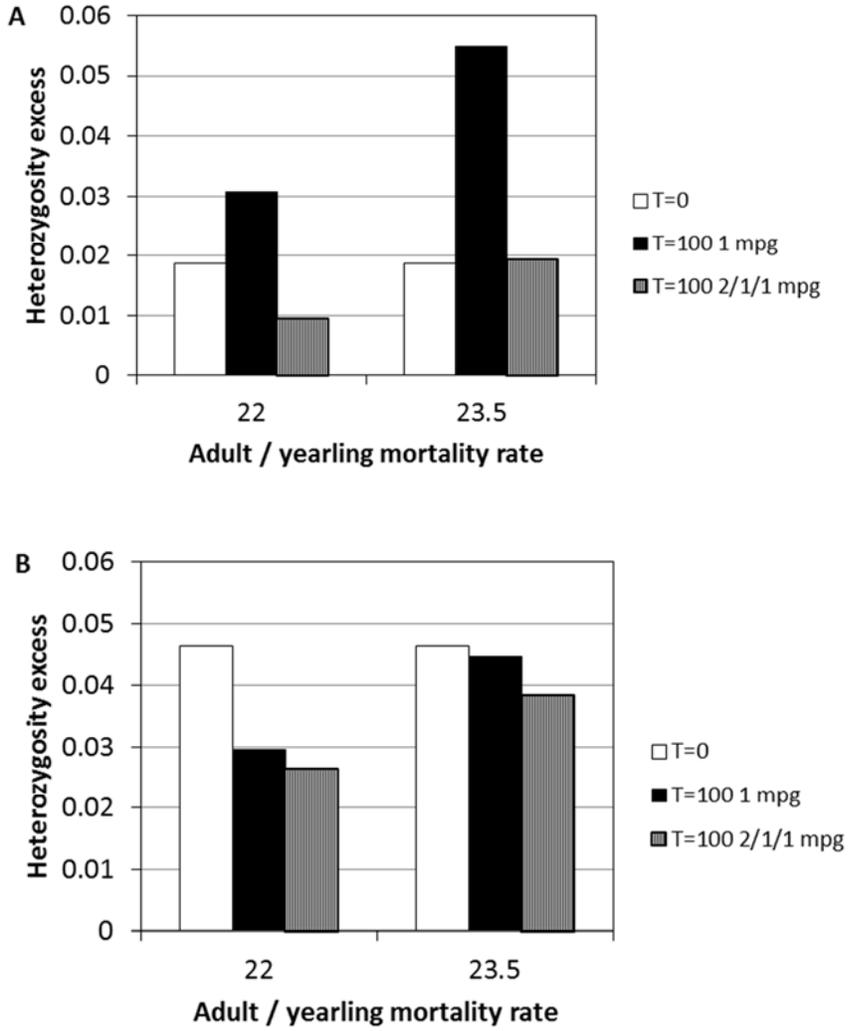


Figure 18. Mean heterozygosity excesses for the 3x250 + Sonora scenario: A) BRP; and B) Sonora.



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Figure 19. Subpopulation extinction rates for 3x250+Sonora scenario: A) 22% annual mortality; and B) 23.5% annual mortality.

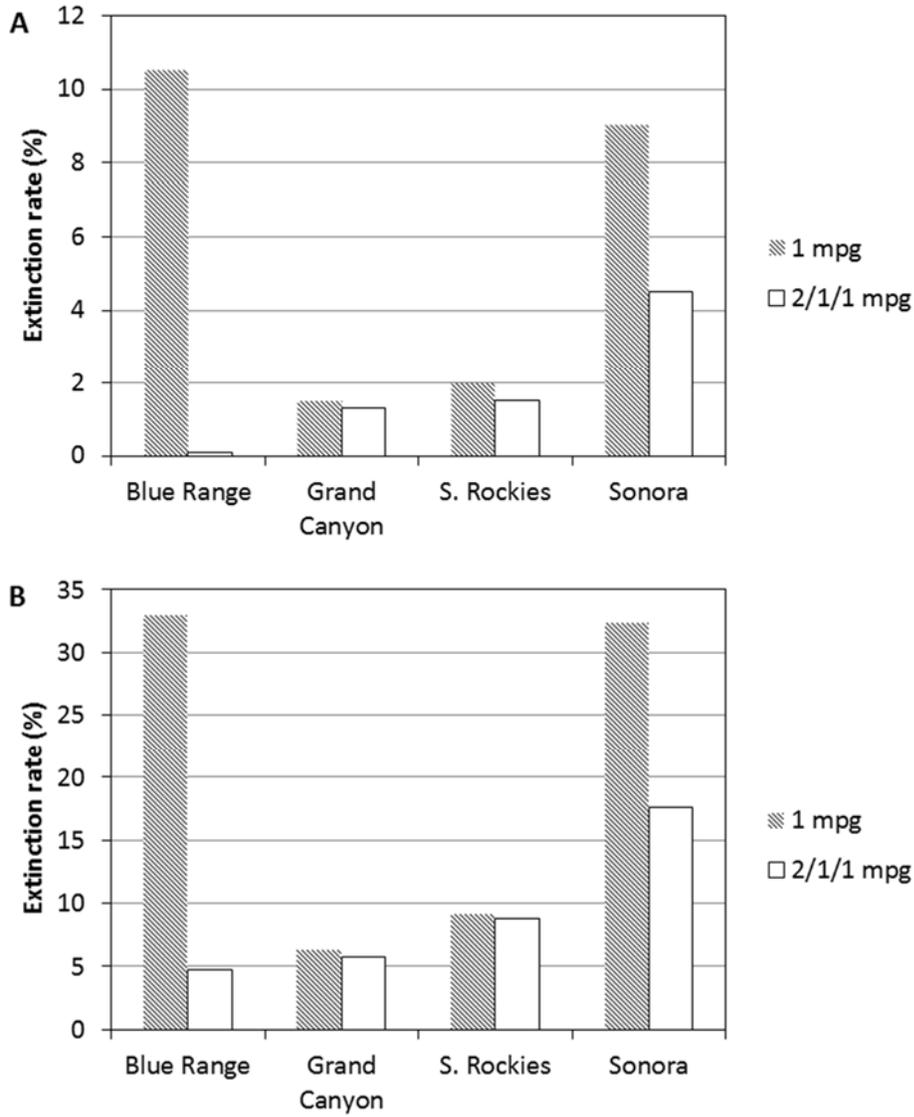


Figure 20. Mean metapopulation sizes at year 100 for the BRP+2MX100, 3x250+Sonora, and the 3x250 scenarios.

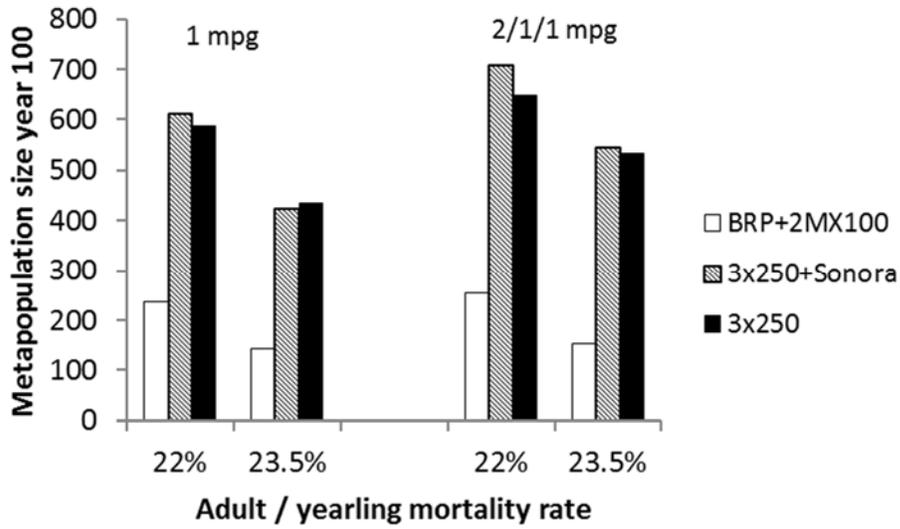


Figure 21. Total number of population extinctions for the BRP+2MX100, 3x250+Sonora, and the 3x250 scenarios.

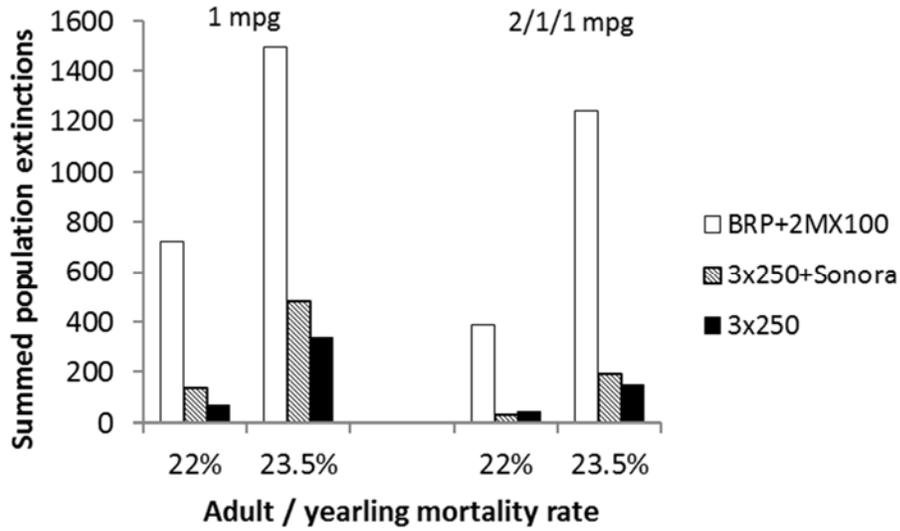


Figure 22. Mean census population sizes over time among extant iterations for the BRP + 2MX100 scenario: A) BRP with 22% adult mortality; B) BRP with 23.5% adult mortality; C) Sonora with 22% adult mortality; D) Sonora with 23.5% adult mortality; E) Durango with 22% adult mortality; and F) Durango with 23.5% adult mortality.

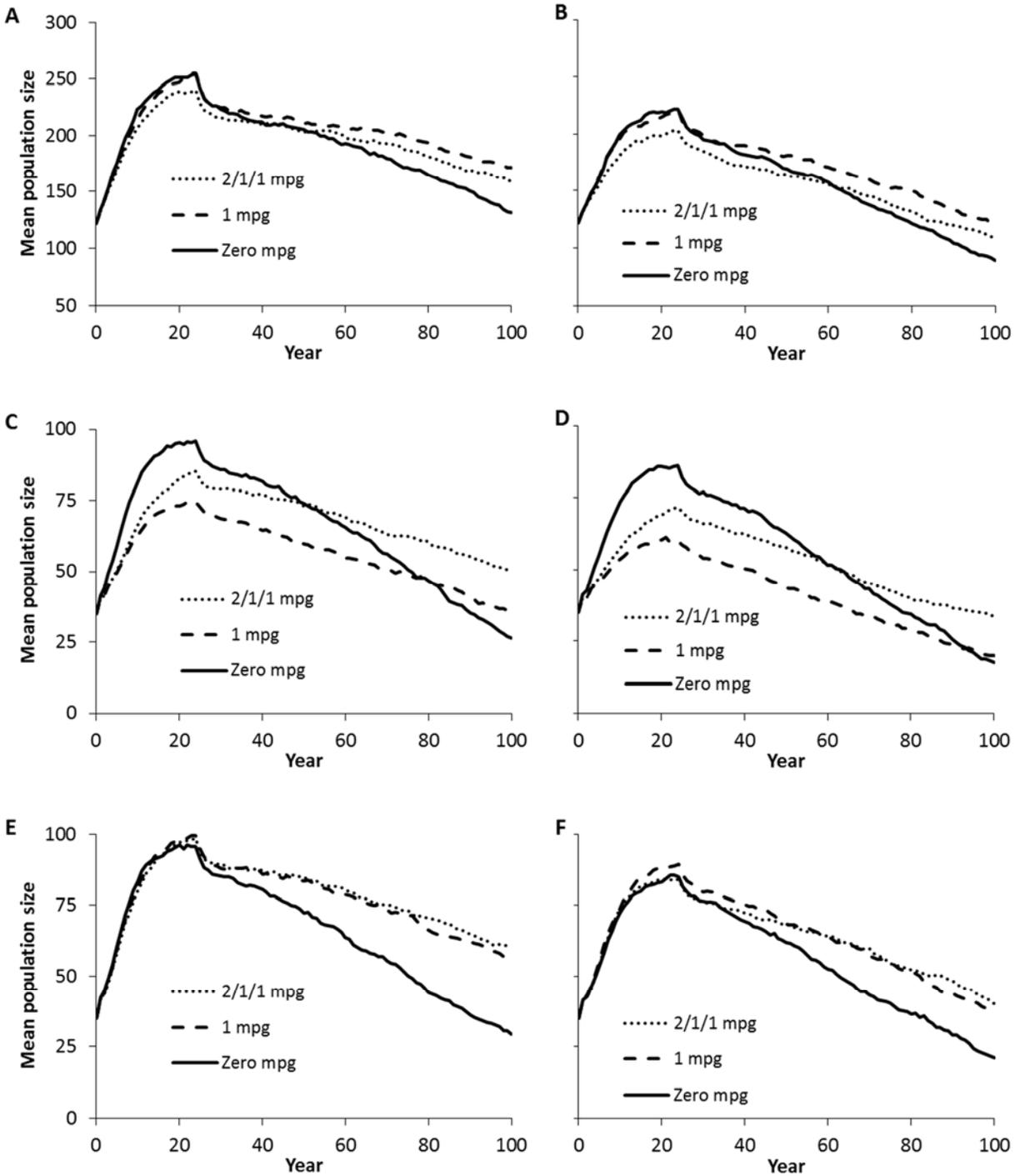


Figure 23. Mean expected heterozygosity over time for the BRP + 2MX100 scenario: A) BRP with 22% adult mortality; B) BRP with 23.5% adult mortality; C) Sonora with 22% adult mortality; D) Sonora with 23.5% adult mortality; E) Durango with 22% adult mortality; and F) Durango with 23.5% adult mortality.

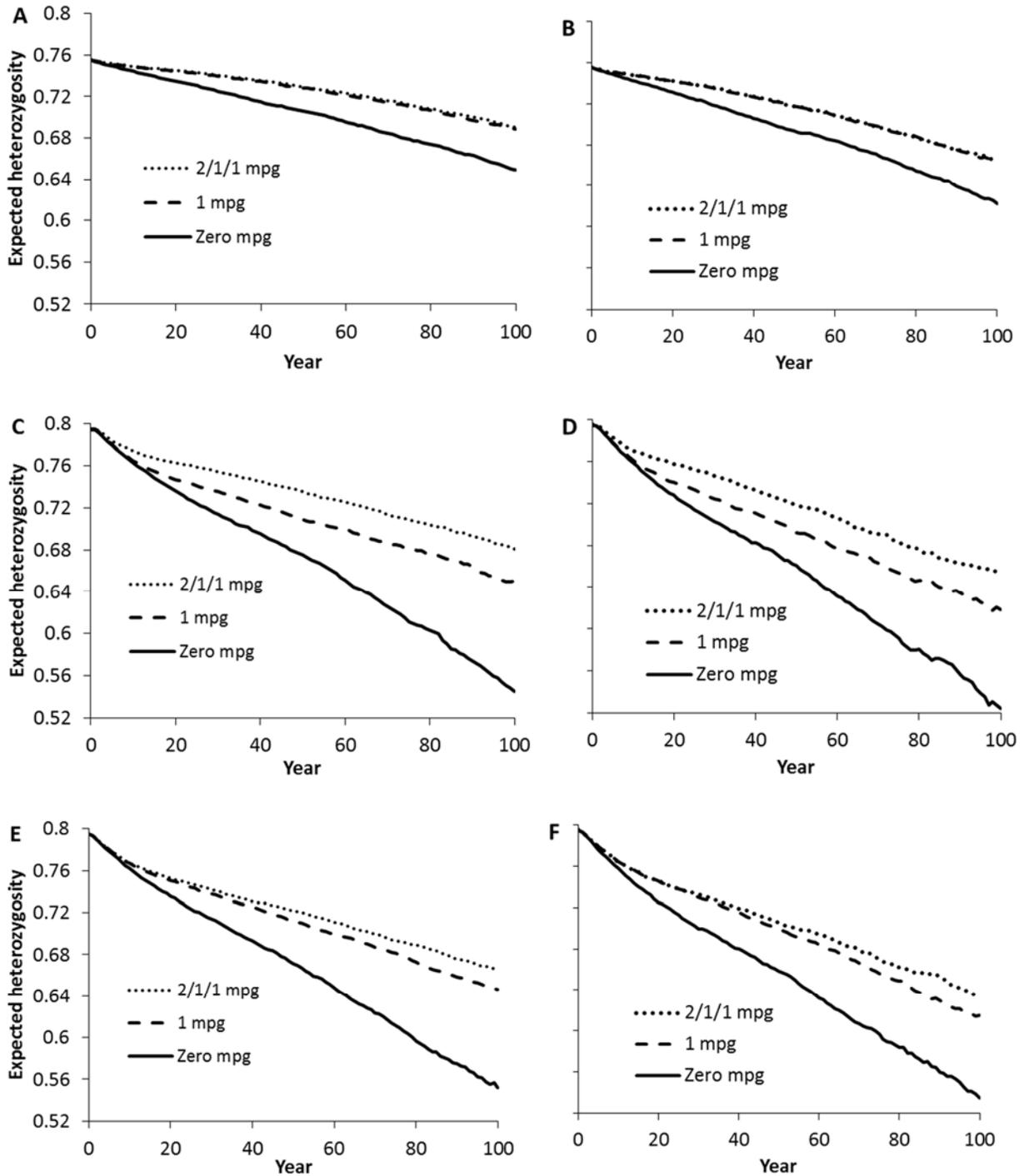


Figure 24. Mean heterozygosity excesses for the BRP + 2MX100 scenario: A) BRP; B) Sonora; C) Durango.

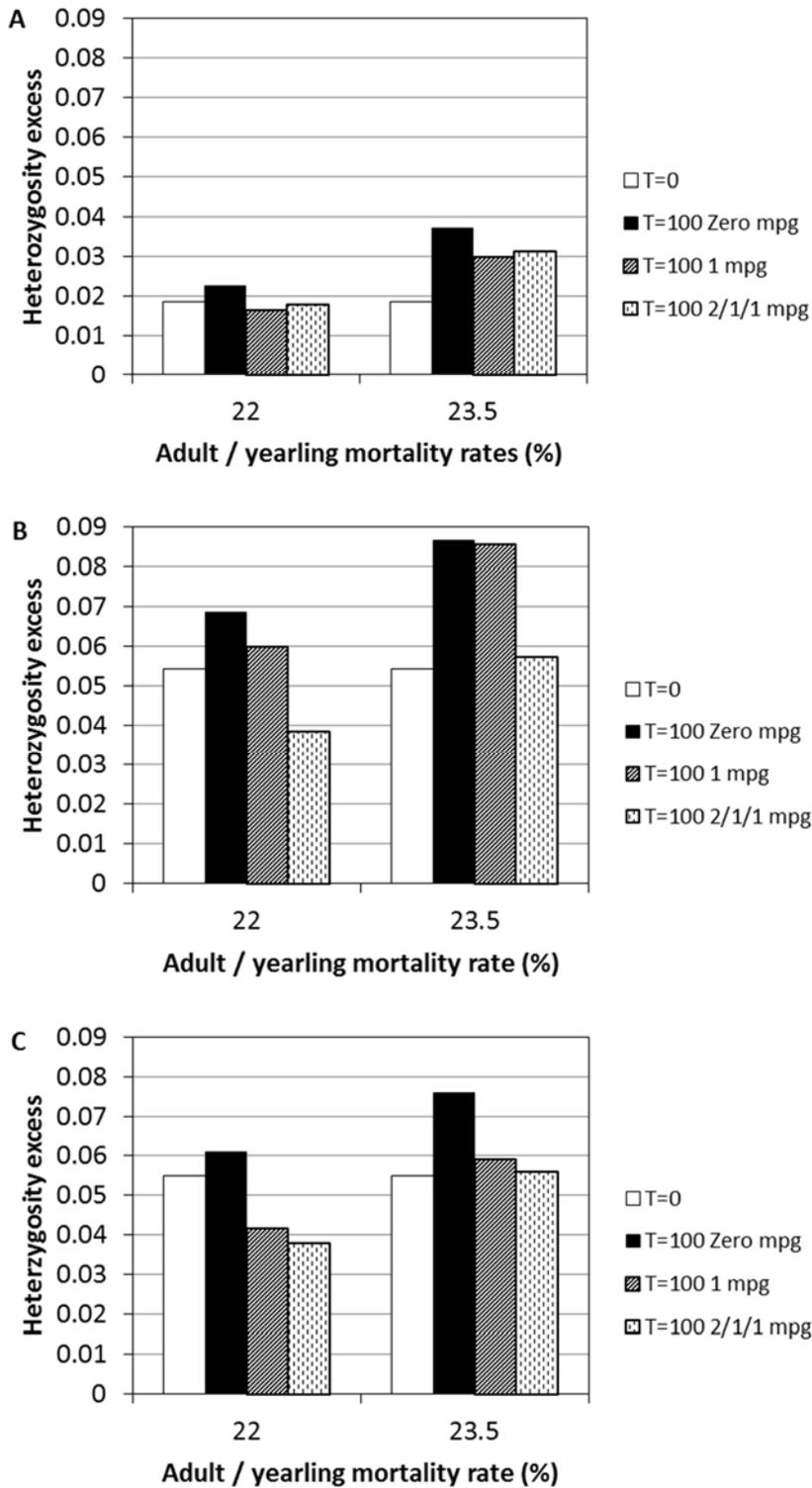


Figure 25. Subpopulation extinction rates for the BRP + 2MX100 scenario: A) 22% adult mortality; and B) 23.5% adult mortality.

