Supplementary Material S1. Description of Vortex model structure and parameters

1. INTRODUCTION

The Vortex model simulates the effects of deterministic and stochastic factors on wildlife populations (Lacy 2000, Lacy and Pollak 2012). Vortex models population dynamics as discrete, sequential events that are determined for each individual in a population with a probability given by user-specified distributions. Vortex simulates a population by stepping through a series of events that describe an annual cycle of a sexually reproducing, diploid organism: mate selection, reproduction, mortality, dispersal between populations, harvest, supplementation, and incrementing of age by one year. The simulations are iterated to generate the distribution of fates that the population might experience. Vortex tracks the sex, age, and parentage of each individual in the population as demographic events are simulated. Vortex allows tracking of both demographic metrics (population size, time to extinction) and genetic metrics (heterozygosity, allelic diversity, inbreeding coefficient).

In addition to the newly enhanced genetic capabilities of the current version of Vortex (version 10.0; Lacy and Pollak 2012), we increased the types of genetic metrics that can be output from each simulation to allow us to quantify the numbers of effective migrants received per generation (defined here as an individual that produces at least one offspring in the recipient population), the rate of inbreeding accumulation and change in heterozygosity, and effective population size (Ne). We also used the option in Vortex to specify demographic rates as functions of other variables in order to structure the simulation to incorporate several additional aspects of wolf natural history including: 1) density dependent survival senescence for older wolves, 2) 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, 3) inclusion of a density dependent function for the % adult females breeding based on empirical data, and 4) incorporating a mechanism to allow wolf populations to be maintained at densities substantially below carrying capacity.

We parameterized Vortex based on available information from the reintroduced Mexican wolf population and other wolf populations (references given below within sections describing parameters). We performed a global sensitivity analysis that considered effects on persistence of different recovery criteria (parameters for population size and dispersal) in conjunction with variation (e.g., due to uncertainty) in demographic parameters. In order to assess the effects of stochastic and genetic factors within a PVA, it is common to deterministic factors that affect demographic rates (such as overexploitation) will need to be addressed as a first priority, in order for criteria mitigating stochastic and genetic factors to be relevant (Caughley 1994). We therefore selected a baseline set of demographic rates that allowed population persistence (i.e., resulted in a deterministic lambda > 1), in order to evaluate additional threats from stochastic and genetic factors.

2. MORTALITY PARAMETERS

Data on rates of mortality (natural and human-caused) and management removals (due to wolves leaving the boundary of the Blue Range Wolf Recovery Area, nuisance incidents, depredation on cattle, and other factors) from the reintroduced Mexican wolf population in the Blue Range suggest that deterministic lambda (intrinsic population growth rate) has remained below 1 for much of the period since the reintroduction was initiated (USFWS, unpublished data). We therefore used mortality rates from the wolf population in the Greater Yellowstone Ecosystem

(GYE) because mortality rates there (22.9% and 24.4% for nonpups and pups, respectively; Smith et al. 2010) are intermediate among the three NRM core populations, and represent a plausible goal for mortality rates after recovery actions are implemented but before delisting (Smith et al. 2010). Our baseline demographic parameter set resulted in a deterministic lambda of 1.23, which is similar to that used in previous Mexican wolf PVAs (1.20-1.24; Seal 1990, IUCN 1996). We also evaluated the sensitivity of results to alternate mortality rates as part of the sensitivity analysis. In the sensitivity analysis, adult and pup mortality rates were varied by +/-20%, resulting in a range of 18.32-27.48% for adult mortality and 19.52-29.28% for pup mortality.

The simulations incorporated senescence in adult survival beginning at age seven with the rate of senescence being density dependent. The effect of this was that the mean mortality rate began to increase at age seven and the increases accelerated up to age 11.

3. 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 and males = 2 years

3) Maximum age of reproduction = 9 years, implemented via an age restriction on the litter size function.

4) Maximum number litters per year = 1

5) Maximum number progeny per litter = 11

6) Sex ratio = 50/50

7) % adult males in breeding pool = 100 (before consideration of reproductive tenure effects)

Fecundity for wolf populations in the Vortex simulations is a function of litter size and the proportion of adult females in the breeding pool. The function for litter size was based on Frederickson et al. (2007) as described below under “Genetic Effects.” Previous Mexican wolf PVAs have set the parameter for the proportion of adult females in the breeding pool at 50% (Seal 1990) to 60% (IUCN 1996). Vonholdt et al. (2008) 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 baseline scenario. The sensitivity analysis evaluated a range of proportions from 40-60%, with the SD maintained at one-fourth of the mean. Given the addition of reproductive “tenure” to the model (below), the parameter for “proportion of adult females in the breeding pool” includes both current alpha females and those females eligible to enter alpha status if an opening appears (due to death of an alpha or population growth).

Table S1. Matrix of demographic rates used in baseline scenario of Mexican wolf simulations. The rates imply a deterministic growth rate (lambda) of 1.23. However, average growth rate in the stochastic simulations will be less than 1.23 because of stochastic variation in vital rates and episodic disease events.

		1.218	1.218	1.218	1.218	1.218	1.218	1.218	1.218	1.218	0.000
0.756											
	0.771										
		0.771									
			0.771								
				0.771							
					0.771						
						0.771					
							0.745				
								0.708			
									0.488		
										0.000	0.000

Previous Mexican wolf PVAs (Seal 1990, IUCN 1996) did not incorporate density dependence in reproduction. This approach may be considered parsimonious 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.

On the other hand, ignoring density dependence in reproduction may lead to overly pessimistic conclusions regarding viability of small populations. Therefore, we chose to use an ensemble modeling approach which summarizes results from equal numbers of scenarios with and without a density dependent function for reproduction. The presence or absence of density dependent reproduction was then analyzed as a categorical variable in the sensitivity analysis. We developed a density dependent function based on data from Yellowstone National Park (D. Smith and D. Stahler, unpublished data). 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 percentage of adult females breeding with density dependence was again set to 25% of the mean value for each year.

An important aspect of the wolf social system is 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 (Ne) of natural wolf populations.

In the default behavior for long-term monogamous breeders in the Vortex model, pairs remain together for as long as both wolves survive, but Vortex randomly selects the adult females that will breed each year. To alter this model structure, we used individual state variables to incorporate persistent monopolization of breeding opportunities by both male and female “alpha” individuals (see Supplementary Material S4 for more detailed metadata). Once an individual achieves alpha status, it generally retains that status until death or reproductive senescence. If, due to population growth, additional breeding slots were available within a population, the appropriate number of non-alphas entered alpha status.

5. CARRYING CAPACITY, DENSITY DEPENDENT MORTALITY, AND HARVEST THRESHOLDS

All simulations incorporated 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, and few females produce pups after eight years (Fuller et al. 2003). However, in the Blue Range population, 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 Blue Range population 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 incorporated a function into the simulations that causes mortality to increase with age past six years (Table S1).

Based on a previous study (Carroll et al. 2006) which suggests a current carrying capacity substantially above the population goals considered here, 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 1.33 times the targeted population goal. In the sensitivity analysis, this parameter was varied by +/-20% (between 1.066 and 1.6 times the targeted population goal). We set the standard deviation in carrying capacity due to environmental variation (drought, etc.) to 10%.

Vortex uses the carrying capacity (K) parameter to impose a ceiling model of density-dependence on wolf numbers. If wolf numbers are above K at the end of a time step, Vortex randomly kills additional wolves until the population size is equal to K. However, under our baseline scenario, carrying capacity was far enough above the target population size (the delisting criterion being evaluated in the simulation) that populations were primarily affected instead by an additional parameter, the “harvest” function, that also acted to limit wolf numbers below a threshold.

We parameterized the function to “harvest” wolves each year that the population size exceeded the target population size, beginning in year 30. In most iterations, population size had reached or exceeded the population size goal by year 30. When harvest occurred a fraction of the wolves above the target population size were taken, with mortality spread equally across the sexes and between pups and older wolves. This fraction was based on the assumption that harvest would not be perfectly efficient in annually reducing wolf populations to their target population sizes. This fraction was set at 8 so that 1/8 or 12.5% of wolves above the population threshold were harvested per year. The “harvest efficiency” parameter was varied from 6.4 to 9.6 in the sensitivity analysis. Less efficient harvest had the effect of allowing wolf populations to exist further above their targeted population sizes.

Forecasts of persistence over longer time frame (e.g., 100 years) are necessarily contingent on assumptions about management of wolf populations after they are delisted. Delisted populations of many recovered species are expected to continue to increase after removal from the “emergency room” status of federal ESA listing. However, if agencies view wolf populations as negatively affecting other resources (livestock, wild ungulates), they may seek to maintain delisted wolf populations at the lowest level consistent with maintaining recovered status. The population size criterion used here represents the threshold above which populations will be controlled by hunting or other lethal control. In the case of populations with threatened status, the rate of mortality may increase after downlisting to threatened due to regulatory changes permitting “take” of individual wolves e.g., those involved in livestock depredations.

6. DISEASE AND OTHER CATASTROPHIC EVENTS

We parameterized episodic threats based on data from the Yellowstone National Park wolf population which showed distemper outbreaks occurring on average every 5 years, and affecting primarily fecundity rather than survival (Almberg et al. 2009, 2010). Because we did not model additional potential episodic threats such as other diseases (e.g., parvovirus) 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. During the year in which a disease outbreak occurred, the proportion of females breeding was 20% of the baseline value, and survival of all age classes was 95% of the baseline. As part of the sensitivity analysis, we varied the average frequency of disease outbreaks between 4 and 6 years.

7. GENETIC EFFECTS

Previous Vortex wolf PVAs have either not incorporated genetic effects (Ewins et al. (2000)), or used a fraction of the default number of lethal equivalents (3.14 LE) in Vortex. The Mexican wolf PVAS of Seal (1990) and IUCN (1996) set this value at 1.7 and 3.14 LE, respectively. 3.14 LE is a median value obtained in a study of captive populations of 40 mammalian species (Ralls et al. 1988), which likely underestimates inbreeding effects in wild populations (Keller and Waller 2002).

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 Blue Range population 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 reduces semen quality in captive 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. 2006). 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.

In the simulations we incorporated inbreeding effects on litter size using the best model from the Blue Range population (Fredrickson et al. 2007). Under this model, litter size for pairs consisting of two unrelated adults averages 4.8761 pups, and litter size is reduced by an average of minus 0.082327 pups when pup inbreeding coefficient (I) increases by 0.01. The latter value (0.082327) was varied by +/- 20% in sensitivity analysis (from 0.06586 to 0.09789 [these values are shown scaled to 1 I rather than 0.01 I in Table 1]). We did not invoke the default Vortex option of inbreeding depression affecting juvenile survival, because this would be redundant with the observed reduction in litter size that we did model. Although our parameterization of inbreeding effects is more realistic than that used in previous Mexican wolf PVAs, our treatment of inbreeding as an impact only on litter size likely underestimates the overall effects of inbreeding depression among wild Mexican wolves.

8. FOUNDING POPULATIONS

The Blue Range population pedigree was first updated to reflect the results of the January 2013 wolf count. During this count 75 wolves were detected, but one wolf was permanently removed leaving 74 wolves. Based on the results of the count we assumed that by the breeding season there would be three more pairs than that detected on the count and that one of the pair members would be an undetected wolf. The USFWS currently has two pairs together in captivity with intentions of releasing both in 2013. We assumed both would be released before pups are produced. In total, we assumed there would be 79 wolves and 17 pairs in the Blue Range population by the 2013 breeding season. Two of the pairs, however, would have alphas that are post-reproductive (10+ years old) and would not produce pups in the simulations, leaving 15 reproductive pairs in the population.

To "update" the Blue Range population from spring 2013 to spring 2022, we ran a simulation with only the Blue Range population for nine years, using an adult mortality rate of 22.75%. The median population size at year 9 (2012) was 121 wolves, based on 1000 iterations. We next ran single iteration simulations until we got an ending population size close to 121. The simulation we chose had 122 wolves at year 9. From this simulation we used output from Vortex to extract the pedigree as well as the sexes and ages of wolves alive at the end of the simulation. This led to a starting population size of 122 wolves with 21 pairs for the Blue Range in 2022.

We next created new wolves and wolf pairs to found two 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 713 wolves was generated from which founding wolves could be selected. We used the program PMx (Ballou et al. 2010) to select wolves from the pool to create ten pairs for each of the two populations. Individuals chosen for each population were to be minimally related and collectively the wolves in each population were to provide a good representation of the genetic variation in the existing captive population. The result was two new populations that each had better representation of the existing genetic variation than the current captive population. The wolves selected by this process, however, would have required some individual wolves to produce offspring with up to five different mates. This was unrealistic for the captive population. So we revised the pairings such that the individual wolves producing the release wolves would have no more than two mates.

Once the 20 founding pairs were determined, a timetable was developed for when each pair would be released. We assumed 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. Throughout the process of developing the new populations all wolves were produced by natural pairings, i.e. we assumed that artificial insemination and in vitro techniques based on the existing gamete bank would not be used.

9. RANGE OF POPULATION SIZE AND DISPERSAL CRITERIA

All simulations evaluated a metapopulation composed of three populations. Population criteria (target sizes) for the three individual populations in the metapopulation were always equal, and ranged from 50 to 350 individuals in the sensitivity analysis. For context, the recovery criterion for the Northern Rocky Mountains specified three populations of 100 individuals each (FWS 1987). The potential dispersal criteria considered ranged from zero (no evidence of effective dispersal required for delisting) to a maximum of 8.9 census migrants per generation or 2.4 effective migrants per generation. The dispersal recovery criterion is most relevant to monitoring and management when specified in terms of effective rather than census migrants. We therefore determined the expected proportion of effective to census migrants (0.27) from a quantile-quantile regression of simulation output. In our model parameterization, a migrant experiences dispersal mortality of 62.5%. Of the 37.5% of census migrants that reach the recipient population, approximately 72% become breeders and produce pups at some later point in their lives and thus qualify as effective migrants.

The maximum age of wolves considered for dispersal was 4 years old. Effective migrants were wolves that moved to a new population, paired and produced at least one pup. This is a less stringent definition than the meaning of effective migrants commonly used in population genetics, which is an individual that moves to a new population and whose genes are represented in the next generation. The definition used in the simulations, however, would be more easily quantified in future monitoring programs.

We applied the same annual dispersal parameter to both movement directions between populations. Because the connectivity analysis (see below) found that connectivity between the Grand Canyon and the Southern Rockies areas is likely to be much lower than that between the Grand Canyon and the Blue Range population and between Southern Rockies and the Blue

Range population, the three populations were modeled as connected as an archipelago rather than a complete network. This has the effect of the central population (the Blue Range) receiving approximately double the number of migrants as the two outlying populations.

Supplementary Material S2. Description of habitat inputs and connectivity analysis methods used in analysis of potential dispersal rates between subpopulations

We adapted a previously-published model that predicted wolf habitat suitability in the western United States from data on land cover, primary productivity, slope, and human-associated mortality factors (Carroll et al. 2006). We describe below the data from which these factors were derived and how the factors were combined into a composite habitat suitability index.

LAND COVER - Because abundance estimates of ungulate prey show strong inconsistencies across jurisdictional boundaries, we used land cover and a satellite-imagery-derived metric (tasseled-cap greenness; Carroll et al. 2001) as a surrogate for habitat productivity. We derived land cover types from satellite imagery based data sets (Multi-Resolution Land Characteristics (MRLC) for the US and MODIS data for Canada)(Homer et al. 2004). The highest value (10) was assigned to deciduous, evergreen, and mixed forest. A value of 8 was assigned to shrubland, grassland, and transitional types. A value of 5 was assigned to rock and sand types. A value of 1 was assigned to snow cover and less-intensive agricultural types (orchards and pastures). Intensive agricultural and urban habitat was given zero value.

PRODUCTIVITY - Within the broad landcover classes described above, prey productivity, and hence wolf habitat value, can be expected to vary widely depending on site productivity. Crist and Cicone (1984) proposed three ‘‘tasseled-cap’’ indices as a standardized means of representing the three principal axes of variation in the values of the six spectral bands used in

Landsat Thematic Mapper and the later MODIS sensors. One of the tasselled-cap metrics, greenness, has been frequently used as a ‘‘pseudo-habitat’’ variables due to its correlation with ecological factors such as net primary productivity and green phytomass (Cihlar et al. 1991, Merrill et al. 1993, White et al. 1997), and has proved useful in modeling wildlife distributions (Mace et al. 1999, Carroll et al. 2001). We used an equal-area slice to scale greenness values (maximum of March (spring) and July (summer) greenness to account for latitudinal variation in timing of plant growth) derived from MODIS imagery to a range of 1 to 1000.

SLOPE - Because wolves are coursing predators that avoid steep terrain, the model also incorporated the negative effect of slope on prey vulnerability (Carroll et al. 2006). Data on wolf distribution data within 4 study areas across Canada showed a power relationship with slope in a univariate regression (P. Paquet, unpublished data). We used the function [index = power(0.965, <slope value in degrees>)] to derive the slope component of the conceptual model from DEM data at a resolution of 90 m. Under this model, habitat with slope of 20 and 40 degrees would have 0.49 and 0.24 the value, respectively, of similar habitat with slope of 0 degrees. We used a index value (0.965) that differed than that obtained by Paquet (0.931) because the latter value appeared to underpredict habitat suitability in mountainous areas of the US Northern Rocky Mountains, based on current wolf distribution in that region.

HUMAN-ASSOCIATED MORTALITY FACTORS - Roads and human population are negatively associated with wolf survival in diverse habitats (Fuller et al. 2003). Merrill et al. (1999) developed a ‘habitat effectiveness’ metric combining road density, local human population density, and interpolated human population density to represent human-associated mortality factors. We used the equation of Merrill et al. (1999) to derive habitat effectiveness from data on roads (1:100,000 resolution USGS and equivalent Canadian datasets) and human population (1990 census data at census block level resolution).

The final composite metric was derived by multiplication of above factors (land cover, greenness, slope, and habitat effectiveness), and then scaled by division by the maximum value/1000 to produce a metric which ranged in value from 1 to 1000 (Figure S2).We assumed that habitat suitability index values to be proportional to movement cost (the relevant input to Linkage Mapper) and conductance (the relevant input to Circuitscape). Although this is a common assumption in connectivity analyses, results should be seen as hypotheses which can be improved by future development of empirical models based on movement data (Carroll et al. 2012). This latter goal is especially challenging to achieve for species such as the Mexican wolf which are being reintroduced to their former range after extirpation. Therefore, initial connectivity analyses based on conceptual or empirical habitat models have a key role in supporting conservation planning.

The spatial data layer (in the Arcinfo grid format) containing habitat suitability values is converted to an .asc (ASCII) file for input into Circuitscape (McRae et al. 2008). Linkage Mapper (McRae et al. 2011) accepts the grid input format directly. Points representing the population centroids between connectivity is measured were produced for the NRM population by calculating the centroid of all know n packs as of 2004 (USFWS unpubl. data), a date which falls within period in which Vonholdt et al. 2010 dispersal data was collected). For existing and potential populations of Mexican wolf, the point was located at the center of the three core areas of highly suitable habitat identified in Carroll et al. 2006.For detailed description of the algorithms used in Circuitscape and LinkageMapper, see the manual and other publications available at www.circuitscape.org and code.google.com/p/linkage-mapper/ respectively.

Figure S2. Habitat model used as input to analyses of potential wolf population connectivity.

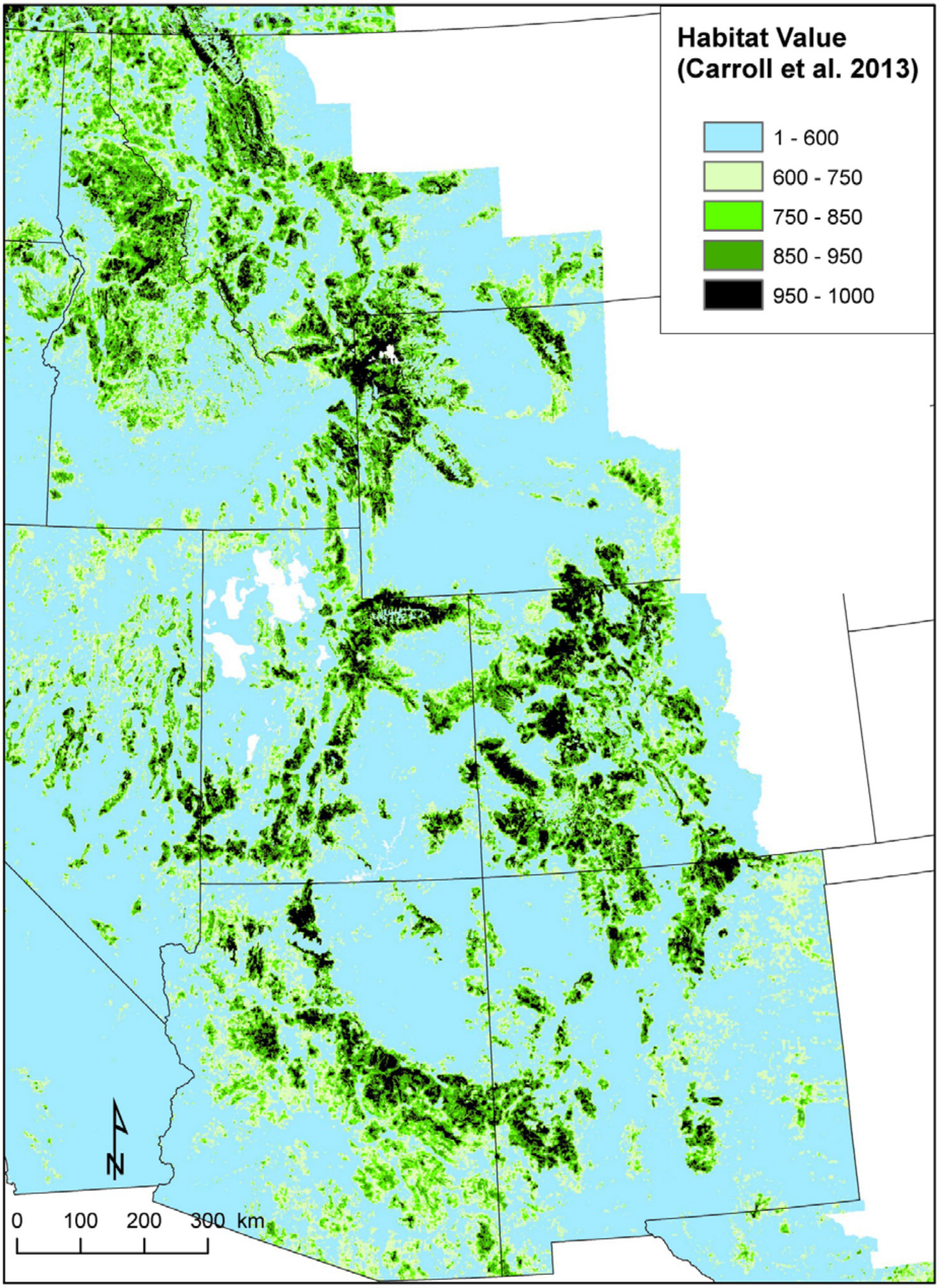
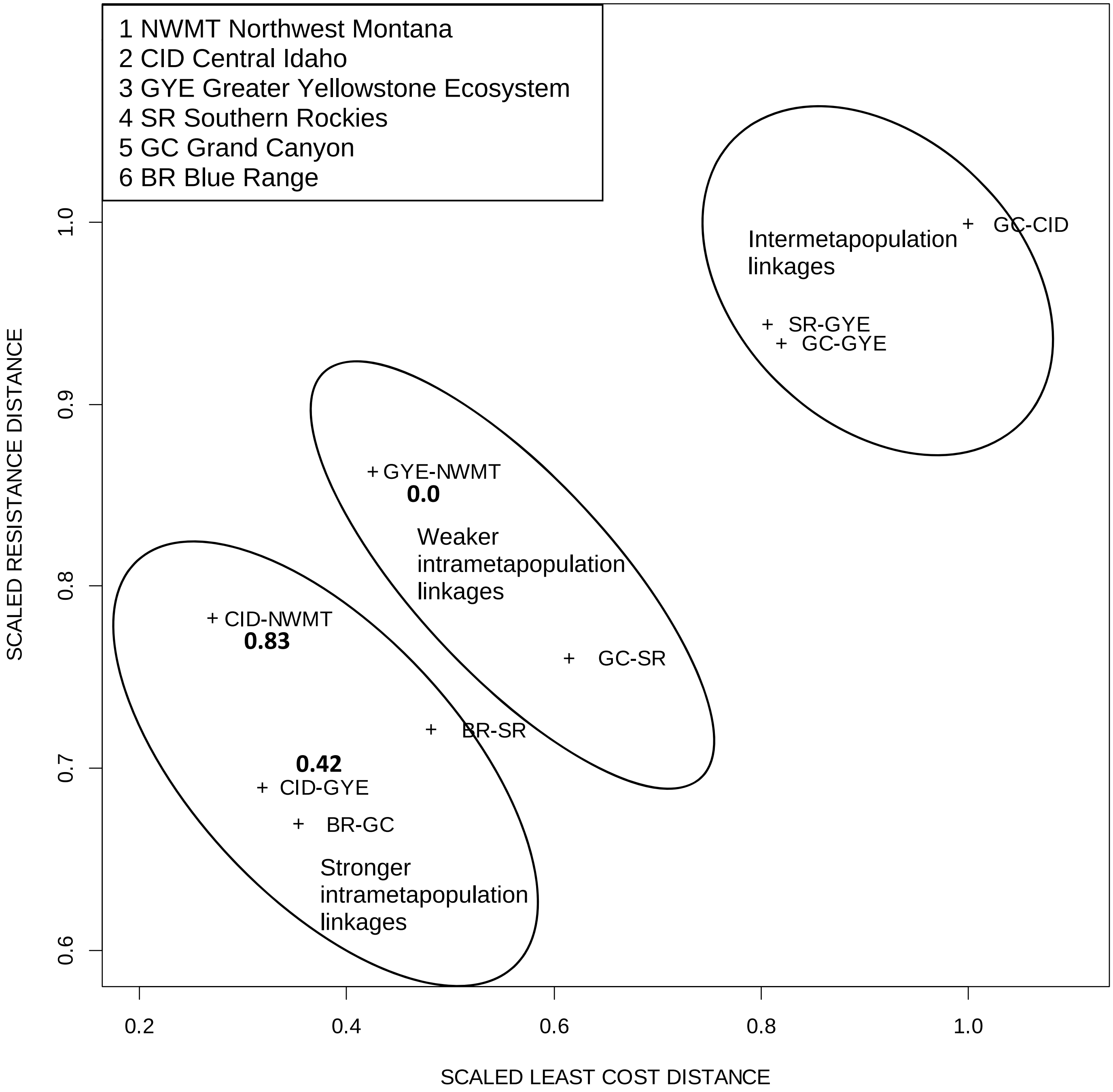


Figure S3. Plot of resistance distance versus least-cost distance between existing or potential wolf population core areas in the western US. The two metrics shown (least cost and resistance distance) are alternate measures of the effective distance for dispersal between two points based on permeability of the intervening habitat. Effective migration rates documented by Vonholdt et al. (2010) for three linkages in Northern Rocky Mountains are shown (boldface).



LITERATURE CITED IN SUPPLEMENTARY MATERIAL

Adams, J. R, L. M. Vucetich, P. W. Hedrick, R. O. Peterson, and J. A. Vucetich. 2011. Genomic sweep and potential genetic rescue during limiting environmental conditions in an isolated wolf population. Proceedings of the Royal Society B

Almberg, E. S., L. D. Mech, D. W. Smith, J. W. Sheldon, and R. L. Crabtree. 2009. A serological survey of infectious disease in Yellowstone National Park's canid community. PLoS ONE 4:e7042.

Almberg, E. S., P. C. Cross, and D. W. Smith. 2010. Persistence of canine distemper virus in the Greater Yellowstone Ecosystem's carnivore community. Ecological Applications 20:2058-2074.

Asa, C., P. Miller, M. Agnew, J. A. R. Rebolledo, S. L. Lindsey, M. Callahan, and K. Bauman. 2007. Relationship of inbreeding with sperm quality and reproductive success in Mexican wolves. Animal Conservation 10:326-331.

Ballou, J.D., R.C. Lacy, and J.P. Pollak. 2010. PMx: software for demographic and genetic analysis and management of pedigreed populations. Chicago Zoological Society, Brookfield, Illinois, USA.

Bensch S, Andren H, Hansson B, et al. 2006. Selection for heterozygosity gives hope to a wild population of inbred wolves. Plos One 1:1-6.

Carroll, C., R. F. Noss, and P. C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications 11:961-980.

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

Caughley, G. 1994. Directions in conservation biology. The Journal of Animal Ecology 63:215-244.

Cihlar, J., L. St.-Laurent, and J. A. Dyer. 1991. Relation between the normalized difference vegetation index and ecological variables. Remote Sensing of the Environment 35:279–298.

Crist, E. P., and R. C. Cicone. 1984. Application of the tasseled cap concept to simulated thematic mapper data. Photogrammetric Engineering and Remote Sensing 50:343–352.

Ewins, P., M. de Almeida, P. Miller and O. Byers, eds. 2000. Population and Habitat Viability Assessment Workshop for the Wolves of Algonquin Park: Final Report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Fredrickson, R. J., P. Siminski, M. Woolf, and P. W. Hedrick. 2007. Genetic rescue and inbreeding depression in Mexican wolves. Proceedings of the Royal Society B 274: 2365-2371.

Fuller T. K.,L. D. Mech, J. F. Cochrane. 2003.Wolf population dynamics. Pages 161–191 in L. D. Mech, L. Boitani, editors. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois.

Homer, C. C. Huang, L. Yang, B. Wylie, and M. Coan. 2004. Development of a 2001 National Landcover Database for the United States. Photogrammetric Engineering and Remote Sensing 70:829-840.

International Union for Conservation of Nature [IUCN]. 1996. Mexican wolf population viability analysis. IUCN Conservation Breeding Specialist Group, Apple Valley, Minnesota, USA.

Keller, L. F., and D. M. Waller. 2002. Inbreeding effects in wild populations. Trends in Ecology and Evolution 17:230–241.

Lacy, R. C., and J. P. Pollak. 2012. Vortex: A stochastic simulation of the extinction process. Version 10.0. Chicago Zoological Society, Brookfield, Illinois, USA. Available from www.vortex10.org, accessed July 2012.

Liberg, O., H. Andren, H. C. Pedersen, H. Sand, D. Sejberg, P. Wabakken, M. Åkesson, and S. Bensch. 2005. Severe inbreeding depression in a wild wolf (Canis lupus) population. Biology Letters, 1, 17-20.

Mace, R. D., J. S. Waller, T. L. Manley, K. Ake, and W. T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat in western Montana. Conservation Biology 13:367–377.

Merrill, E. H., M. K. Bramble-Brodahl, R. W. Marrs, and M. S. Boyce. 1993. Estimation of green herbaceous phytomass from Landsat MSS data in Yellowstone National Park. Journal of Range Management 46:151–157.

Merrill, T., D. J. Mattson, R. G. Wright, and H. B. Quigley. 1999. Defining landscapes suitable for restoration of grizzly bears Ursus arctos in Idaho. Biological Conservation 87:231–248.

Murray, D. L., D. W. Smith, E. E. Bangs, et al. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514–2524.

Räikkönen, J., A. Bignert, P. Mortensen , and B. Fernholm. 2006. Congenital defects in a highly inbred wild wolf population (Canis lupus). Mammalian Biology 71:65–73.

Räikkonen, J., J. A. Vucetich, R. O. Peterson, and M. P. Nelson. 2009. Congenital bone deformities and the inbred wolves (Canis lupus) of Isle Royale. Biological Conservation 142:1025-1031.

Ralls, K., J. D. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. Conservation Biology 2:185-193.

Seal, U. S. 1990. Mexican wolf population viability assessment: Report of workshop, 22-24 October 1990. IUCN Conservation Breeding Specialist Group, Fossil Rim Wildlife Center, Glen Rose, Texas.

Siminski, D. P. 2012. Mexican Wolf, Canis lupus baileyi, international studbook, 2012. The Living Desert, Palm Desert, California, U.S.A. 119pp.

Smith, D.W., E. E. Bangs, C. Mack, et al. 2010. Survival of colonizing wolves in the northern Rocky Mountains of the United States 1982–2004. Journal of Wildlife Management 74:620-634.

U.S. Fish and Wildlife Service [USFWS]. 1982. Mexican wolf recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico. 103 pp.

U.S. Fish and Wildlife Service [USFWS]. 1987. Northern Rocky Mountain wolf recovery plan. Region 6, Denver, Colorado, USA.

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

White, J. D., S. W. Running, R. Nemani, R. E. Keane, and K. C. Ryan. 1997. Measurement and remote sensing of LAI in Rocky Mountain montane ecosystems. Canadian Journal of Forest Research 27:1714–172.