Rethinking Conservation Goals for North America's Gray Wolves

By: Kevin Carpenter

Abstract

Gray wolves (*Canis lupis*) were extirpated from the continental United States in the early 1900's. During the 1970's wolves began dispersing into Montana and they were immediately placed under the protection of the Endangered Species Act. Reintroduction areas were established for the wolves in the Northern Rocky Mountains, West of the Great Lakes, and in the Southwest. Between 2008 and 2013 wolf populations across the country we systematically removed from the Endangered Species Act, now only the Southwestern Mexican gray wolf remains protected. The threshold which determined the removal, or delisting, of gray wolves from the act was arbitrarily contrived. When determining the protection status of these wolves ecological services and issues with long term persistence should be considered. Gray wolf introduction promotes tree growth and recruitment providing an essential role as a buffer against climate change. Wolves are also at risk after they were delisted both from interactions with humans and genetic isolation. New areas for reintroduction were suggested for the still protected Mexican gray wolf in suitable areas of the southwest where connected metapopulations could be established. Grey wolves were once found nationwide, therefore the goal of gray wolf conservation should be to promote a large range for wolves which extends across the nations. This could restore the historic gene flow dynamics which gray wolves had in the U.S and provide extensive biological carbon sequestration.

Introduction

Globally, gray wolves (*Canis lupis*) have been removed from almost a third of their original territories (Ripple et al., 2014). The United States once held a contiguous population of gray wolves (Fig.1b), but due to human expansion and habitat fragmentation, the gray wolf became nationally extirpated in early 1900s (Leonard et al., 2005). In 2012, the continental United States was home to about 5,400 gray wolves (USFWS,) as a result of reintroduction programs and years of legal protection under the Endangered Species Act. Even though these methods have shown success, the current population of grey wolves does not compare to the historic value. Leonard et al. (2005) estimated that the original population size of U.S gray wolves' was about 380,000 individuals. Therefore, conservation efforts have only restored 1.42% of the grey wolves, and their range has yet to reach its previous nation-wide extent.

Figure 1. (from Bergstrom et al., 2009)
Total range of gray wolves in the United States as of 2009 (a) and of the estimated original range (b).

Wolves from Canada dispersed back into parts of Montana during the 1970's and policy makers saw an opportunity to reestablish this iconic species. They were given sanctuary under the Endangered Species Act in 1973 and subsequent reintroductions were planned to repopulate grey wolves in the northwestern United States (Bergstrom et al., 2009). These programs have given rise to three distinct regional populations; the Northern Rocky Mountain, the Western Great Lakes, and the Southwestern populations (Fig.1a). The Northern Rocky Mountain wolf population is the largest and grew the fastest as part of the Yellowstone National Park reintroductions of 1995-1996 (Smith et al., 2003). The success seen in the Northern Rocky Mountain region led to policy changes which named this area a Distinct Population Segment (DPS). This meant the gray wolf population had reached the size and growth goals set during the original reintroduction (Bergstrom et al., 2009). The establishment of the DPS opened discussion about the future protection of gray wolves under the Endangered Species Act. Minimum recovery for the Northern Rocky Mountain wolves was set at a total population of 300 individuals over the entire 250,000 square kilometer range. That equates to 0.0012 wolves per square kilometer which is only 1.2% of the wolf density found around British Columbia which is just north of the Northern Rocky Mountain DPS (Ripple et al., 2012). A delisting attempt in 2008 failed (Bergstrom et al. 2009) and the recovery goal was arbitrarily formulated to be 15 packs and 150 individuals within the three states which form the DPS. After a year, the states which comprised the Rocky Mountain DPS, and some in the Western Great Lakes DPS, began delisting wolves. Those in Yellowstone were protected though as they were within a nation park boundary (Bergstrom et al., 2009). A ruling which was proposed on June 13th 2013 would nationally delisted gray wolves from the endangered species act (Federal Register, 2013), except for the Mexican gray wolf subspecies in the southwest. Biological arguments for delisting have not proved to be strong. There are many concerns about population dynamics which were not considered during the pre-planning of the first gray wolf introductions. The recovery goals were said to be based on opinions from the recovery team which were then validated by a questionnaire sent to biologists in 1992 instead of being based on peer reviewed data or theoretical population models (Bergstrom et al., 2009).

Environmental Benefits Provided by Reintroduced Grey Wolves

Gray wolves, similar to many other large terrestrial carnivores, are a keystone predator which has a disproportionate influence on the regulation of ecosystem processes (Ripple et al., 2014). Part of this influence comes from their top-down control of prey species, such as cervids (deer). Density of North American and Eurasian cervid species are six times higher in areas where wolves have been extirpated (Ripple et al., 2012). Some suggest that human hunting can replace this form of natural control, but wolf predation and human hunting do not follow similar patterns. Lethal control of cervids is provided in the form of permit required hunting seasons, such as the Gardiner Lake Elk Hunt. It is held annually in Yellowstone National Park and lasts only about 30 days (Wright et al., 2006). Wolves hunt year round and tend to target weaker members of the population such as calves and older adults. The average age adult elks killed by wolves in Yellowstone National Park was 14 years between 1995 and 2001 (Smith et al., 2003). These wolves are providing a greater amount of population control without negatively effecting the overall fitness of the elk population. Anthropogenic harvest targets adult females to increase their impact on elk recruitment as a compensatory measure for not harvesting year round. Wright et al. (2006) found hunters had a greater reproductive impact than the wolves over a 30 day period, but as previously stated, wolves hunt throughout the year. Therefore, their effect on overall recruitment is greater than that of human control efforts. It is also possible that gray wolves can hunt in areas which are inaccessible to humans during their allotted harvest time (Ripple et al., 2014). The Yellowstone elk population was greater than 15,000 individuals before the reintroduction of gray wolves, but by 2010 their population decreased to about 6,100 (Ripple and Beschta, 2011). The gray wolf provides natural population control for species at a magnitude which humans cannot compete with. The ecological services provided by the gray wolf's trophic influence are not always direct. Predators induce behavioral changes in their prey species when they are reintroduced to an ecosystem. Prey species

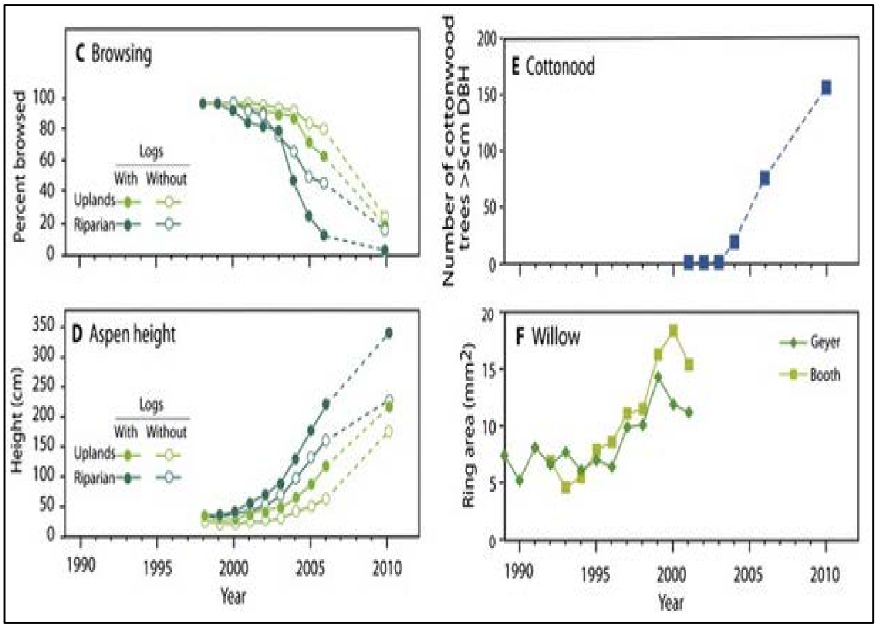

Figure 2. (modified from Ripple and Beschta, 2011)
Response of vegetation to indirect facilitation by the reintroduction of wolves to Yellowstone National Park. Browsing (C) is measured in percent aspen leaders browsed. Aspen height (D) was measured during springtime before their summer growth period. (E) is a graphical representation of Cottonwood recruitment. Geyer and Booth (F) refer to species of willow found within the park. All graphs are representative of data collected from the northern range of Yellowstone National Park

must increase their vigilance and avoid impediments to escape while foraging to avoid the risk of predation (Wirsing and Ripple, 2010). Elks within gray wolf territories will avoid riparian areas where the number of potential impediments (such as deep channels, fallen logs, incised banks) are high (Wirsing and Ripple, 2010). The behavioral changes, in addition to a decrease in the elk population, facilitate the recruitment and growth of plant species within the gray wolf's reintroduced range (Fig.2). Deciduous trees within Yellowstone National Park were declining as a result of uninhibited browsing by elks up until the reintroduction of wolves between 1995-1996 (Ripple and Beschta, 2011). From 1998 to 2010 the height of aspens grew over 500% from less than 40 cm to an average of 265 cm (Fig.2D). Riparian areas had a higher rate of deciduous plant recruitment than the upland areas due to an increased risk of predation associated with natural escape barriers, as described previously (Ripple and Beschta, 2011). Rising plant biomass, as a result of indirect trophic interactions with grey wolves, also provides a buffer against climate. Increasing tree size, and subsequently leaf density, will aid in regional carbon sequestration.

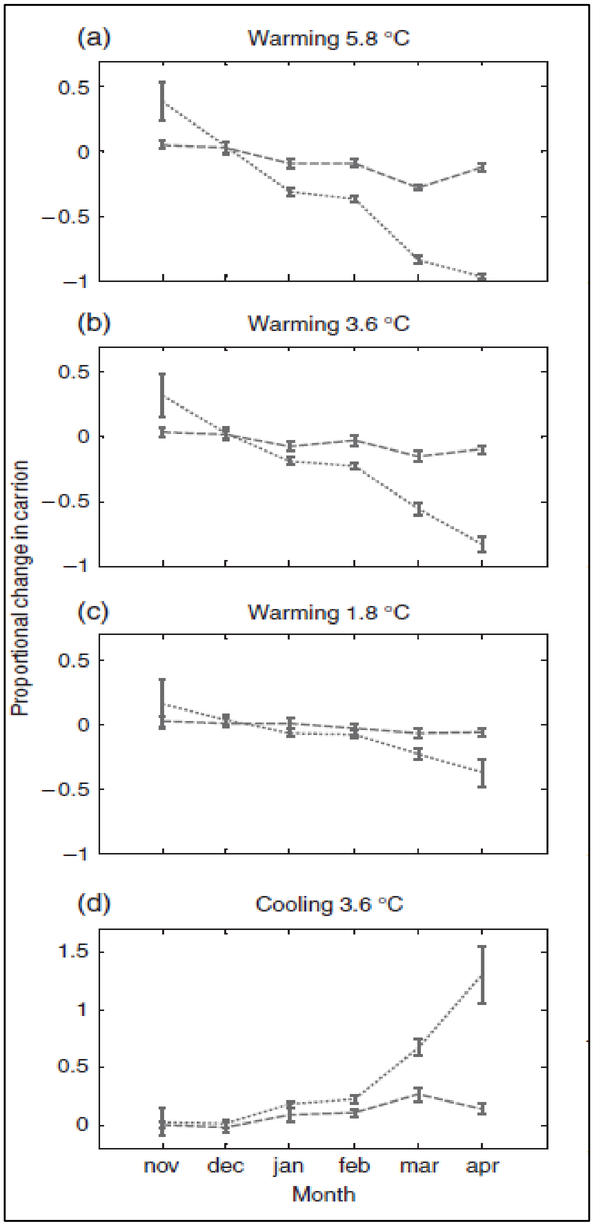

Figure 3. (modified from Wilmer and Post, 2006) Models (a-d) represent proportional change in average carrion availability from 2000-2100under four different simulated climate change scenarios. Dotted lines represent simulations without wolves and dashed lines have wolves present. All scenarios with wolves show more moderate changes in carrion than those without.

Wolves can indirectly provide ecological benefits to entire animal guilds within their ecosystem. Predation in post-reintroduction areas increases carcass meat availability for scavenger consumption. There are about ten different species which feed off wolf kills in Yellowstone

National Park alone (Smith et al., 2003). Winter carcass biomass in the absence of wolves is controlled by climate conditions, and highly dependent on deep snow accumulation in the winter. Moving through deep snow is an energetically costly task for animals and weaker individuals will be highly vulnerable to predation (Wilmers et al., 2003).

The availability of carcasses is predicted to decrease as the effects of climate change increase mean global temperature (Wilmers and Post, 2006). Wilmers and Post (2006) simulated four century long climate change scenarios based on the 2001 IPCC predictions and modeled the changes in carcass abundance with wolves in the ecosystem and without them in it. In all warming scenarios, and one cooling scenario, wolf presence buffered against changes in carrion availability (Fig.3). Proportional changes in the carrion available for scavengers are more extreme when the simulated temperature was higher. The most current IPCC report states that even if all emission production was to immediately stop the globe would still raise about 2ºC above the pre-industrial average (Collins et al., 2013). Grey wolf population stability can be useful in providing natural mitigation against the biotic and abiotic effects of climate change on a regional level.

The ecological regulations described previously are only a few examples of the gray wolf's influence. Beavers, bison, and other small mammal species all experienced forms of indirect trophic facilitation after wolf reintroduction (Ripple and Beschta, 2011; Smith et al., 2003). Even though most of this section discussed wolves in the Northern Rocky Mountain DPS, similar ecological effects were seen by the experimental wolf colony established on Isle Royale, Michigan (Smith et al., 2003). These environmental services, and their potential loss, should have some degree considered when determining the legal protection this species receives. The delisting of the Northern Rocky Mountain and Western Great Lake wolves allows states to legalize human wolf harvest. The threat of gray wolf extirpation from their reintroduced regions could result in ecosystem wide regime changes due to an irruption of herbivorous species in the absence of predators compounded with a shifting global climate.

Threats to Long-term Gray Wolf Persistence

The grey wolf is a large, intelligent, carnivorous species weighing an average 33 kilograms, or ~73 pounds (Ripple et al., 2014). Many people find the idea of purposefully aiding the reestablishment of a species with dangerous potential unnerving. These sentiments are particularly strong among citizens in pastoral communities. Generally, people like the idea of repopulating gray wolves in the United States, but conversely they also support lethal controls and hunting when there is a perceived potential for human/wolf conflict (Treves and Bruskotter, 2012). Once the Northern Rocky Mountain gray wolves were delisted humans began acting on their fears without any fear of repercussion. During the 2012-2013 hunting season, a buffer zone against hunting outside Yellowstone National Park was dissolved and people could hunt wolves who wandered directly outside the park boundaries without any limitations (Eisenburg, 2014). As stated before, people who rely on pastoral farming tend to react strongly to the presence of wolves near their communities. These fears are unsubstantiated in scientific findings. A study on the causes of livestock mortality in Idaho in 2001 showed that wolves were the cause of 0.005% of livestock deaths (Bergstrom et al., 2009). Additionally, 60% of all sheep deaths were a result of coyote predation. Coyotes are a mesopredator, and their abundance is affected by gray wolf presence due to interspecific competition for food and territory, often resulting in Coyote mortality (Smith et al., 2003). This is not the only beneficial service gray wolves provide to farmers. Wolves preferably hunt prey which is weak, old, and sick. Wolf presence reduces the number of sick cervids, which subsequently decreases the likelihood that livestock will be exposed to infection (Ripple et al., 2014). This data highly suggests that the presence of wolves will positively impact livestock health. Even so, Stronen et al. (2007) conducted a survey on farmer's attitudes towards gray wolf presence, and 60% of those who perceived the wolf presence as too high were also extremely concerned about their cattle being infected by wild elk. Such conflicting desires provide blind public support for getting rid of a species which is beneficial to them.

Even if gray wolves were given their nationally endangered status again, scientists and wildlife managers would still have concerns about their long term success. Gene flow between different populations increases the overall genetic diversity of the species and reduces the potential for inbreeding depression. Minimal focus was placed on the importance of genetic diversity during the original planning of the gray wolf reintroductions (Bergstrom et al., 2009). Concerns over genetic diversity are particularly important to the Northern

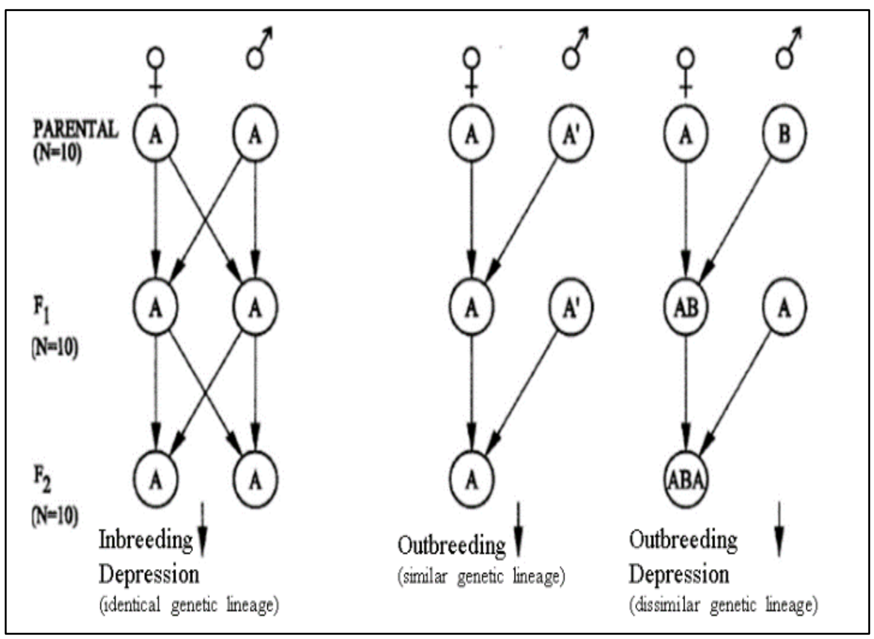

Figure 4. (modified from Luna and Hawkins, 2004)
This graphic displays the three types of gene flow interactions discussed in this paper. Inbreeding depression (left) is the reduction in fitness due reproduction between individuals who are genetically identical, thereby increasing the prevalence of potentially harmful recessive alleles (allele A). Natural outbreeding (middle) allows for new alleles (allele A') to interact with recessive alleles and potentially overwrite them to help increase offspring survivability. Outbreeding depression (right) introduces novel alleles (allele B), which may not be suitable for the offspring's given environment.

Rocky Mountain DPS and the Southwestern population. The alpine terrain which covers the Northern Rocky Mountain wolf range provides many natural obstacles for dispersal, and subsequently gene flow. U.S Fish and Wildlife suggested human assisted migrations as a way to prevent inbreeding depression (Bergstrom et al., 2009). Artificial selection of individuals for dispersal could see an outbreeding depression. Outbreeding depression occurs by breeding two individuals who are locally adapted to different environments which in turn produce offspring that have inherited traits, while beneficial in one location, are maladaptive in the other (Frankham et al., 2011). A natural migrator would be have adaptations which allow for greater habitat plasticity, and thus would not produce offspring which are poorly adapted to the local habitat. The Southwestern population is in much greater need of gene flow as it is only comprised of 109 individuals (USFWS, 2015) and these individuals are a locally adapted subpopulation. Leonard et al. (2004) analyzed the genetic history of extant wolves and suggests that it is possible to establish healthy gene flow among the Mexican gray wolf population. They suggest reintroducing another group of Mexican gray wolves or a mixed group of the Mexican subspecies and Canadian wolves to mimic historic genetic gradation. The Canadian wolves would be introduced to a montane environment and the

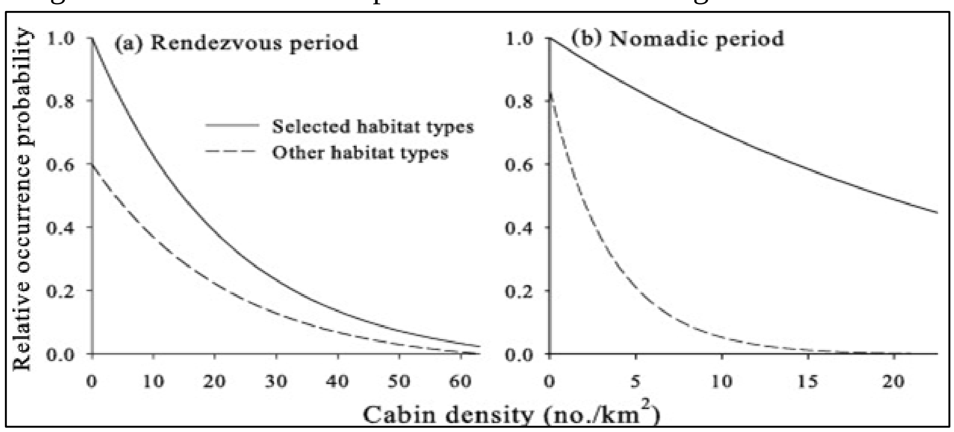

Figure 5. (modified from Lesmires et al., 2012)
Graphic representation of gray wolf habitat selection (relative occurrence probability) in a boreal forest region in Quebec. Rendezvous period refers to the period between July and mid-September/November when pack members regularly meet at rendezvous points. Nomadic period refers to the period between late November and mid-April when the pack moves together but do not regularly meet at set rendezvous points. Selected habitats refer to the preferred habitat types determined by telemetry collar data. Gray wolves were less prone to avoid human settlements during the nomadic period due to decreased human encounter risk during winter.

Mexican wolves in an arid one within dispersal range. Simulated population models of Mexican gray wolves show that the probability of extinction becomes zero in just two generations given that there are three subpopulations, each has >150 members, and there are multiple migrants per generation (Carrol et al., 2014). If the gray wolf regains its protected status wildlife management must considered new reintroduction areas to strengthen the genetic viability of the species on a national level.

The reintroduction of more subpopulations requires new suitable habitat area. Wolf packs require large territories, in the Northern Rocky Mountain region territory size varies from 100 to 200 square miles. Wolves have been known to inhabit smaller territories, but usually they are never smaller than twenty square miles (Eisenburg, 2014). Wolves, in general, prefer to avoid direct interaction with humans. The probability wolves would use a given habitat is dependent on the time of year (which affects pack behavior) and the density of human housing (Fig.5). As the density of human settlements increased so did gray wolf avoidance. Humans, although a strong deterrent to dispersal and habitat selection, are not the strongest factor influencing how wolves choose what habitats to colonize. Geffen et al. (2004) studied allele frequencies in different populations of gray wolves to determine if variation in genes correlated with distinct environmental variables such as climate, habitat type, and vegetation. Genetic variability between gray wolf populations was most significantly correlated with climatic factors. They hypothesized that young wolves are climatically imprinted to their local habitat. This behavioral ecotyping would then direct the dispersal of young gray wolves towards familiar habitats which will increase their chance of survival. Translocating species can be difficult if they find their new territory to be unsuitable. Bradley et al. (2005) studied gray wolf translocations as a non-lethal control method in the Northern Rocky Mountain DPS. While the motivation for the movement of these individuals was to reduce human conflict, wildlife managers used these individuals to establish new packs and to promote artificial dispersal. Released adult wolves showed strong homing behavior and they would pass through potentially dangerous territory in an attempt to go back to their pre-release location (Bradley et al., 2005).Individuals who migrate out of the area increase their risk of potential mortality.

Long term population persistence of grey wolves in the continental United States will rely on the ingenuity of wildlife managers to overcome these barriers to success. Many of the solutions to overcome these problems require expansion of wolf protection and wolf territory. Unfortunately, federal lawmakers had no intention of allowing wolves to disperse any more than their originally allotted range (Bergstrom et al., 2009). Human development planning has already begun in sensitive gray wolf reserves, such as Yellowstone National Park. By 2028, road development within Yellowstone will reduce the overall carrying capacity of gray wolves by 49-66% (Carroll et al., 2003). Sightings of wolves have become increasingly rare in Yellowstone. Between 2010 and 2013 Yellowstone National Parks wolf sighting index (measure of the change in amount of annual wolf sightings) dropped from 44% to 4% (Eisenburg., 2014).

Conservation Outlook for Gray Wolfs

Gray wolves in the Northern Rocky Mountain and Western Great Lakes DPS only occupied ~30% of their range when their protection under the Endangered Species Act was revoked (Bergstrom et al., 2009). The original goals of the gray wolf conservation program were set without considering ecological influence, genetic connectivity, or benefits to livestock. There is a growing body of evidence which suggest that losing apex predators causes environmental changes which rival anthropogenic climate change (Power et al., 2011). To be more specific, losing gray wolves again will effectively increase our carbon footprint in the same manner as fossil fuels. It is difficult to understand the degree to which gray wolf extirpation affects climate conditions as this is an understudied subject (Powers et al., 2011). Even so, through understanding gray wolf trophic interactions, it can be theorized that the extirpation of wolves would result in a net carbon loss for the ecosystem when herbivores over-browse and kill many individual plants (Fig.6). All the carbon from these plants will be released into the atmosphere once they begin to decay.

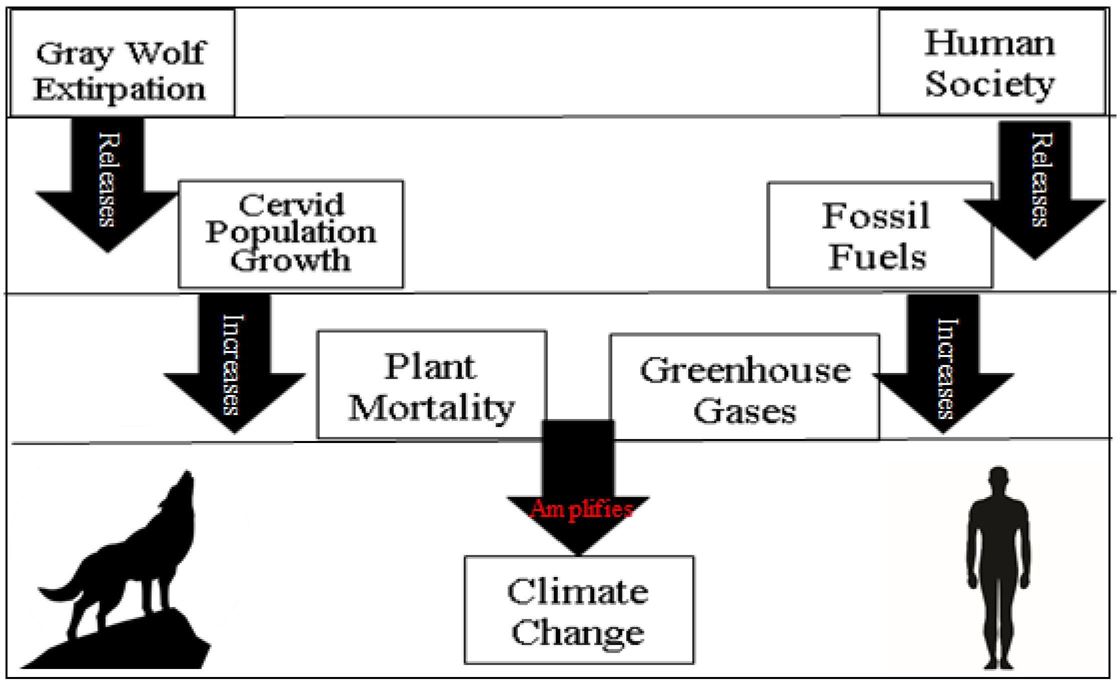

Figure 6 (original)
Concept map showing the analogous relationship that human induced climate change has with climate change influenced by wolf extirpation. In both scenarios it is direct carbon consumptions which drives the process towards climate change.

While suitable reservoirs for new wolf reintroductions have been rare in the United States and Canada (Fritts and Carbyn, 1995) they are not impossible to find. Sneed (2001) suggests that gray wolves be introduced to the Grand Canyon Ecoregion. The three proposed areas within Arizona would hold between 230 and 374 individual wolves based on the availability of prey species. Carroll et al. (2003) focused on an area within the Southern Rocky Mountain Ecoregion.

Instead of identifying separate reservoirs they provide three options for wolf reintroduction, two of which involve the establishment of multiple nearby subpopulations which would could be migrated between to help maintain gene flow. An area called the Blue Range in southwestern Arizona is highly connected to both the Southern Rockies and the Grand Canyon (Carroll et al., 2014). This whole area of the southwest, if properly planned, could form a large metapopulation network to promote recovery of the Mexican gray wolf.

Before conservation efforts begin promoting Mexican gray wolf populations there must be adequate changes to the recovery criteria so as to avoid what happened with their northern conspecifics. Carroll et al. (2014) simulated the probability of endangerment versus population size within three proposed areas for Mexican gray wolf reintroduction (Blue Range, Grand Canyon, and Southern Rocky Mountains). They found that establishing a population between 150 and 250 individuals would result in the wolves' probability of endangerment decreasing below 50%. Therefore, the species would not be classified as "threatened" anymore. This threshold is based on scientific findings unlike the northern wolves, but it could be advantageous for Mexican grey wolves to retain their endangered status even if their population rises above that amount. Gray wolves are a species which ranged across the entire continental United States from north to south. If we are going to restore wolf populations in this region to an ecologically substantive level then there should be a metapopulation network which effectively runs the same distance. Such a suggestion might seem like an excessive measure, but globally keystone predators are disappearing and the effects on the ecosystem are more pervasive than previously thought. Only 7% of reintroduction studies done in the 15 years between 1990 and 2005 focused on ecosystem level effects (Seddon et al., 2007). Trans-national reestablishment of grey wolves in the United States can be used to study novel regional scale changes in trophic cascades.

References

Bergstrom, B. J., Vignieri, S., Sheffield, S. R., Sechrest, W., & Carlson, A. A. (2009). The northern rocky mountain gray wolf is not yet recovered. *Bioscience, 59*(11), 991-999.

Bradley, E. H., Pletscher, D. H., Bangs, E. E., Kunkel, K. E., Smith, D. W., Mack, C. M., ... & Jimenez, M. D. (2005). Evaluating wolf translocation as a nonlethal method to reduce livestock conflicts in the northwestern United States. *Conservation Biology*, 19(5), 1498-1508.

Carroll, C., Fredrickson, R. J., & LACY, R. C. (2014). Developing metapopulation connectivity criteria from genetic and habitat data to recover the endangered mexican wolf. *Conservation Biology*, 28(1), 76-86. doi:10.1111/cobi.12156

Carroll, C., Phillips, M. K., Schumaker, N. H., & Smith, D. W. (2003). Impacts of landscape change on wolf restoration success: Planning a reintroduction program based on static and dynamic spatial models. *Conservation Biology*, 17(2), 536-548. doi:10.1046/j.1523-1739.2003.01552.x

Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W.J. Gutowski, T. Johns, G. Krinner, M. Shongwe, C. Tebaldi, A.J. Weaver and M. Wehner, 2013: Long-term Climate Change: Projections, Commitments and Irreversibility. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Eisenberg, C., SpringerLink (Online service), & SpringerLINK ebooks - English/International Collection. (2014). *The carnivore way coexisting with and conserving north america's predators*. Washington, DC: Island Press/Center for Resource Economics.

Frankham, R., Ballou, J. D., Eldridge, M. D. B., Lacy, R. C., Ralls, K., Dudash, M. R., & Fenster, C. B. (2011). Predicting the probability of outbreeding depression. *Conservation Biology*, 25(3), 465-475. doi:10.1111/j.1523-1739.2011.01662.x

Federal Register, 78 Fed. Reg. 35664 (2013) (to be codified at 50 C.F.R. pt. 17).

Fritts, S. H., & Carbyn, L. N. (1995). Population viability, nature reserves, and the outlook for gray wolf conservation in north america. *Restoration Ecology, 3*(1), 26-38.

Geffen, E., Anderson, M. J., & Wayne, R. K. (2004). Climate and habitat barriers to dispersal in the highly mobile grey wolf. *Molecular Ecology*,13(8), 2481-2490. doi:10.1111/j.1365-294X.2004.02244.x

Leonard, J., Vila, C., & Wayne, R. (2005). Legacy lost: Genetic variability and population size of extirpated US grey wolves (canis lupus). *Molecular Ecology, 14*(1), 9-17.

Lesmerises, F., Dussault, C., & St-Laurent, M. (2012). Wolf habitat selection is shaped by human activities in a highly managed boreal forest. *Forest Ecology and Management, 276*(0), 125-131.

Luna, M. G., & Hawkins, B. A. (2004). Effects of inbreeding versus outbreeding in Nasonia vitripennis (Hymenoptera: Pteromalidae). *Environmental entomology*, 33(3), 765-775.

Power, M. E., Scheffer, M., Brashares, J. S., Estes, J. A., & Terborgh, J. (2011). Trophic downgrading of planet earth. *Science*, 333(6040), 301-306. doi:10.1126/science.1205106

Ripple, W. J., & Beschta, R. L. (2012). Large predators limit herbivore densities in northern forest ecosystems. *European Journal of Wildlife Research*,58(4), 733-742. doi:10.1007/s10344-012-0623-5

Ripple, W. J., & Beschta, R. L. (2012). Trophic cascades in yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation, 145*(1), 205-213.

Ripple, W., Estes, J., Beschta, R., Wilmers, C., Ritchie, E., Hebblewhite, M., . . . Zoologiska institutionen. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343(6167), 151-151. doi:10.1126/science.1241484

Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the science of reintroduction biology; desarrollando la ciencia de biología de la reintroducción. *Conservation Biology, 21*(2), 303-312.

Sneed, P. G. (2001). The feasibility of gray wolf reintroduction to the grand canyon ecoregion. *Endangered Species Update, 18*(4), 153-158.

Stronen, A. V., Brook, R. K., Paquet, P. C., & Mclachlan, S. (2007). Farmer attitudes toward wolves: Implications for the role of predators in managing disease. *Biological Conservation*, 135(1), 1-10. doi:10.1016/j.biocon.2006.09.012

Treves, A., & Bruskotter, J. T. (2011). Gray wolf conservation at a crossroads. *Bioscience, 61*(8), 584-585.

[USFWS] U.S Fish and Wildlife Service. *Grey Wolf (Canis lupis) Current Population in the United States* [Fact sheet]. (2013, August 20). Retrieved 3 8, 2015, from http://www.fws.gov/midwest/wolf/aboutwolves/WolfPopUS.htm

Wilmers, C. C., Crabtree, R. L., Smith, D. W., Murphy, K. M., & Getz, W. M. (2003). Trophic facilitation by introduced top predators: Grey wolf subsidies to scavengers in yellowstone national park. *Journal of Animal Ecology, 72*(6), 909-916.

Wirsing, A. J., & Ripple, W. J. (2011; 2010). A comparison of shark and wolf research reveals similar behavioral responses by prey. *Frontiers in Ecology and the Environment*, 9(6), 335-341. doi:10.1890/090226

Wright, G. J., Peterson, R. O., Smith, D. W., & Lemke, T. O. (2006). Selection of northern yellowstone elk by gray wolves and hunters. *Journal of Wildlife Management*, 70(4), 1070-1078. doi:10.2193/0022-541X(2006)70[1070:SONYEB]2.0.CO;2