Biological Conservation 203 (2016) 151–159

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Discussion

Genetic management and setting recovery goals for Mexican wolves (*Canis lupus baileyi*) in the wild

Larisa E. Harding[a,*], Jim Heffelfinger[a], David Paetkau[b], Esther Rubin[a], Jeff Dolphin[a], Anis Aoude[a,1]

[a] Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, AZ 85086, USA
[b] Wildlife Genetics International, P. O. Box 274, Nelson, British Columbia V1L 5P9, Canada

ARTICLE INFO

Article history:
Received 6 June 2016
Received in revised form 9 September 2016
Accepted 17 September 2016
Available online 24 September 2016

ABSTRACT

Mexican wolf recovery planning has spanned >3 decades, yet federal and state planners have not reached consensus on how to structure recovery efforts with the remaining inbred founder lineages to maximize genetic diversity while balancing many other demographic and social considerations. The US Fish and Wildlife Service and state wildlife agencies are working to draft a revised recovery plan specific to the Mexican wolf that will appropriately incorporate genetic concerns in recovery criteria that can be implemented on a human-dominated landscape. Inbreeding effects, where present in the remaining lineages, are stochastic and unpredictable in a management context. Despite these effects, population growth in Mexican wolves the past 5 years rivals the rate observed in Yellowstone wolves during the last decade. While small populations risk extinction via inbreeding depression, there are often larger, more imminent threats of demographics, mortality, or habitat loss that may impact success of recovery efforts. Releasing captive-reared wolves is problematic and often creates conflict in local human communities, but fostering of captive-born wolves into wild wolf packs is a viable means of increasing genetic diversity and decreasing habituated wolf-human conflict. There are many alternative ways to estimate the number of wolves per population needed to recover the Mexican wolf. Efforts should thus be made to provide for sufficient genetic diversity, but not at the expense of more immediate factors that influence successful recovery.

1. Introduction

The current Mexican wolf (*Canis lupus baileyi*) population traces its ancestry to 7 founders used to establish a captive breeding program now consisting of 245 wolves in 53 institutions in the U.S. and Mexico. Mexican wolves were presumed extinct in the wild by 1980 due to control efforts resulting from conflicts with livestock production (Brown, 2002). Between 1970 and 1980, five wild animals were captured in Arizona and Mexico and added to a few animals already in captivity as founders of the new captive population (see Hedrick et al., 1997 for comprehensive history of pedigree). In 1998, the first 11 captive-raised Mexican wolves were released into the Blue Range wolf recovery area of Arizona (Fig. 1). None of the original founders were still alive, but management of the resulting captive population and selection of their offspring for release were carefully planned to maximize genetic diversity of the new wild population. Subsequent collaboration with Mexico also resulted in the release of captive wolves in northern Mexico beginning in 2011. At last official count in 2016, 21 Mexican wolves are living in the wild in Mexico, including 3 consecutive litters totaling 15 wild-born pups (C. Lopez-Gonzales, Universidad Autonoma de Queretaro, personal communication).

As with many attempts to recover populations in the wild, this undertaking has faced formidable social, demographic, mortality and habitat security challenges. Among its many challenges, the Mexican wolf recovery program has struggled to establish and update a species recovery and management plan that has the support of both state and federal agencies involved, even though recovery planning has spanned >3 decades. The original Mexican Wolf Recovery Team was formed in 1979 with representatives from Mexico, Arizona, and New Mexico, the US Fish and Wildlife Service (USFWS), and other subject matter experts. This team wrote the 1982 Mexican Wolf Recovery Plan, which was then signed by representatives from the United States and Mexico. A second Mexican wolf recovery team was assembled in the mid-1990s to update and revise the original recovery plan, but no final draft resulted from that effort. In 1998, an Interagency Management Plan was

* Corresponding author.
E-mail addresses: lharding@azgfd.gov (L.E. Harding), jheffelfinger@azgfd.gov (J. Heffelfinger), dpaetkau@wildlifegenetics.ca (D. Paetkau), erubin@azgfd.gov (E. Rubin), jdolphin@azgfd.gov (J. Dolphin), Anis.Aoude@dfw.wa.gov (A. Aoude).
[1] Present address: Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, WA 98501-1091, USA.

http://dx.doi.org/10.1016/j.biocon.2016.09.018
0006-3207/

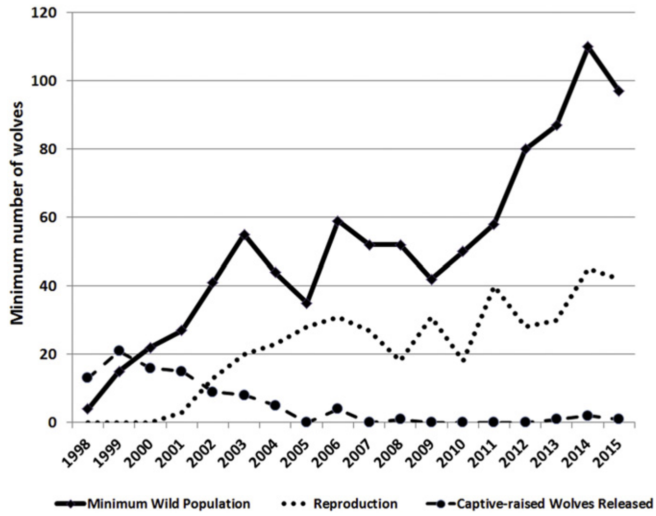

Fig. 1. Mexican wolf population growth, reproduction (i.e. annual observed increase in population from pup production), and number of captive wolves released, Arizona and New Mexico, 1998–2015.

developed to facilitate and guide the first release of Mexican wolves into the wild that year. In 2003, the USFWS reclassified the gray wolf (*C. lupus*) in North America, creating three Distinct Population Segments, and convened a third recovery team to develop a new recovery plan for Mexican wolves in the Southwestern Distinct Population Segment (SWDPS). Recovery planning for the Mexican wolf was again put on hold in January 2005 when a court ruling vacated the SWDPS designation. In 2010, the USFWS began the fourth iteration of recovery planning for the Mexican wolf and chartered a recovery team to revise the 1982 Mexican Wolf Recovery Plan to include achievable and measureable recovery criteria to result in the wolf's eventual delisting. The work of this team came to a halt in early 2013 without a revised draft recovery plan.

In 2015, the USFWS revised the list of Endangered and Threatened Wildlife to remove the Mexican wolf from the general listing under all gray wolves and list it separately as a subspecies (USFWS, 2015a). The taxonomic status of the Mexican wolf as a valid subspecies has been generally supported by morphologic and genetic data (Bogan and Mehlhop, 1983; Nowak, 2003; vonHoldt et al., 2011; USFWS, 2015a; but see Cronin et al., 2015a, b). Regardless of any disagreement over infraspecific taxonomy, the Mexican wolf is now listed as a subspecies under the Endangered Species Act and there is a legal obligation to work towards recovery of this subspecies. Currently, the USFWS is undertaking a renewed effort to revise the draft plan by incorporating input gathered during a series of ongoing Mexican wolf recovery planning workshops of state wildlife agencies (i.e. Arizona, New Mexico, Colorado, Utah), Mexico, and others with wolf recovery experience.

Controversy over the recovery program has often been extreme and has involved numerous lawsuits, disagreements over state and federal recovery objectives, and negative local attitudes. After three failed attempts to revise the original recovery plan, uncertainty and mistrust among stakeholders has produced multiple lawsuits (e.g. 6 filed since November 2014, J. Odenkirk, Arizona Assistant Attorney General, personal communication) and compromised public support for the recovery effort. Significant contention has revolved around questions primarily related to the location and number of wolves that should be allowed on the landscape. It has become increasingly evident that recovery of Mexican wolves will need to consider and weigh both the social concerns voiced by local communities and the numbers of wolves required for sustainable populations in the wild.

The demographic history of the modern population dictates a need to consider the relative and absolute importance of inbreeding effects as recovery planning and actions seek to increase genetic diversity and fitness in wild wolves. Yet genetic recovery and wolf numbers must be strategically balanced against social pressures and concerns from local communities that can strongly impact recovery success. Here we seek to briefly discuss genetic and demographic considerations for maintaining and increasing the genetic diversity present in the original founders and their progeny in the wild population and the extent to which genetic considerations should set recovery criteria.

2. Small populations and inbreeding effects

Wherever population numbers are dramatically reduced, genetic diversity is lost, and populations with few remaining founders, like the Mexican wolf, may suffer inbreeding depression as deleterious alleles are exposed in a homozygous state (Hartl and Clark, 2007). Such effects are stochastic and dependent on the number and character of deleterious alleles in the genomes of subsequent generations, on how those alleles relate to success in the local environment, and on how variation is lost as alleles are sampled from one generation to establish the next (i.e. random genetic drift). The genetic considerations of inbreeding are relevant to Mexican wolf recovery because the founding population included only 7 animals. Initially, the captive population arising from these founders displayed little evidence of inbreeding depression (Kalinowski et al., 1999). Yet in the first several years of recovery efforts, inbreeding effects were suggested in a few recruitment-related variables among the most highly inbred individuals and lineages (i.e. sperm motility in Asa et al., 2007; captive litter size in Fredrickson et al., 2007), as was observed in two other extremely inbred populations of gray wolves (both founded by a single pair of wolves) that manifest skeletal abnormalities (Räikkönen et al., 2009) or lowered fitness (Vilà et al., 2003). However, more outbred individuals and lineage crosses of Mexican wolves performed similarly to gray wolves that were not highly inbred (Asa et al., 2007; Fredrickson et al., 2007). Recent growth of the wild Mexican wolf population, increased pup production, and larger litter sizes (Figs. 1, 2) also suggest inbreeding effects do not unduly compromise recovery efforts in Mexican wolves.

Even when inbreeding effects are substantial, the magnitude and timing of manifested effects vary unpredictably among species and populations within species (Hundertmark, 2009; Räikkönen et al., 2009, and references therein). This indirect connection between inbreeding depression and persistence in wild populations is exemplified by many translocated animal populations that are thriving demographically (Table 1). For instance, the white-tailed deer (*Odocoileus virginianus*) population in Finland began with 4 individuals during the 20th century, but now supports an annual harvest of 25,000 individuals (Heffelfinger, 2011). North American elk (*Cervus elaphus*) in some areas (e.g. in Pennsylvania and California) and bison (*Bison bison*) have rather low modern

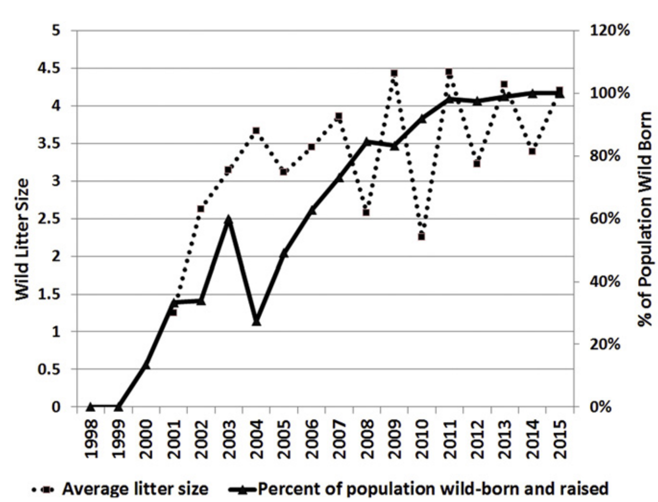

Fig. 2. Increase in average litter size and percent of wild-born individuals in Mexican wolf population, 1998–2015.

Table 1
Examples of mammal populations with small number of founders (Incr. = increasing).

Country	Species	Population low point	Population currently	Status	Reference
Finland	White-tailed deer	4 (1934) 4 (1937) 4 (1948) 100 (1960–70s)	25,000 harvested annually	Stable	Heffelfinger (2011)
New Zealand	White-tailed deer	4 (1901) 19 (1905)	1500 + harvested annually	Stable	Heffelfinger (2011)
France-Haute Isl.	Mouflon	2	Peaked @ 700; now 200–600	Fluctuating	Kaeuffer et al. (2007)
KwaZulu-Natal province, South Africa	African wild dogs	20 (1980s)	257 (by 2011)	Stable	Spiering et al. (2011)
USA-Santa Rosa Island	Kaibab mule deer	30	4000–6000	Increasing until NPS removal	Heffelfinger (2013)
USA-Tiburon Isl.	Bighorn sheep	20	500	Stable/incr.	Wilder et al. (2014)
USA-Arizona	Rocky Mtn elk	<300	Sustains hunting take of > 9000/year	Stable/incr.	Carmony et al. (2010)
USA	Black-footed ferret	18	>1500	Stable	Miller et al. (1996)
USA-Alaska, Prince William Sound	Sitka black-tailed deer	8 (1916) + 16 (1917–1932)		Stable/incr.	Paul (2009)
USA-Alaska, Kodiak Island	Sitka black-tailed deer	9 (1934)		Stable/incr.	Paul (2009)
USA-Alaska, Baranof Island	Mountain goat	18 (1923)		Stable/incr.	Paul (2009)
USA-Alaska, Kodiak Island	Mountain goat	17 (1952–1953)		Stable/incr.	Paul (2009)
USA-Alaska, Revillagigedo Island (Swan Lake)	Mountain goat	17 (1983)	~250	Stable	Paul (2009)
USA-Alaska, Revillagigedo Island (Deer Mtn)	Mountain goat	15 (1991)	~120	Stable	Paul (2009)
USA-Alaska, Copper River Delta	Moose	~24 (1949–1958)		Stable/incr.	Paul (2009)
USA-Alaska, Berners Bay	Moose	16 (1958) + 11 (1960)	~100	Stable	Paul (2009)
USA-Alaska, Kalgin Island	Moose	2 (1957) + 3 (1958) + 1 (1959)	179 (2003)	Fluctuating (due to severe winters)	Paul (2009)
USA-Alaska, Adak Island	Caribou	10 (1958) + 14 (1959)	Projected to grow to 5000	Irruptive (due to overgrazing)	Paul (2009)
USA-Alaska, Afognak Island	Elk	8 (1929)	Peaked 1400		Paul (2009)
USA-Alaska	Plains bison	23 (1928)	~900 in 4 herds	Stable	www.adfg.alaska.gov (2016)
USA	Bison (on several NP, NWR)	<100 (~1880s)	20,000 +	Stable/incr.	Hedrick (2009; see also Table 5 therein)
USA-California	Tule elk	<30 (1895)	3800 (in 2007)	Stable	J. Hobbs, in Phillips et al. (2012)
USA-Isle Royale, MI	Moose	Arrived early 1900s	1250	Stable/incr.	Vucetich and Peterson (2015)

genetic variability, suggestive of past bottleneck events, yet their historically broad distributions point to flexible ecologies that have permitted small populations of animals to thrive in a variety of environmental conditions across their respective ranges (Hedrick, 2009; Broughton et al., 2012). These species exhibit little to no negative demographic effects from inbreeding, perhaps because sufficient gene flow occurred between herds or because historical bottlenecks allowed natural selection to purge deleterious alleles and decrease detrimental genetic loads associated with the effects of inbreeding (Glémin, 2003).

The capacity to withstand genetic bottlenecks cannot be generalized across species, but there are also accounts of wolf populations recovering from low numbers (Table 2). A well-known example in the USA is the reintroduction of wolves to the Yellowstone ecosystem, where a founding population of 31 individuals in 1995 rapidly expanded to a current population of over 500, largely successful because the population was augmented naturally by migrants from Canada and Idaho (vonHoldt et al., 2008; J. Gude, Montana Fish, Wildlife, and Parks, personal communication). Likewise, wolves on Isle Royale provide a more extreme example of resilience in the face of isolation and inbreeding. This island population was founded by 2 individuals, joined later by a third, and grew and persisted in near isolation without intentional augmentation for 60 years, with an average population of about 25. Given the extremely small founding population, it is unsurprising that the recent population exhibits skeletal and genetic characteristics consistent with inbreeding depression (Räikkönen et al., 2009). Although the population has now dwindled to a few wolves (Table 2; Vucetich and Peterson, 2015), and its relevancy to recovery efforts here is questionable because no wolf recovery program would intentionally limit recovery efforts to a single pair of wolves, the wolves on Isle Royale did well for several decades. They hunted large prey (moose, *Alces americanus*) and lived as long and had similar demographic parameters to outbred populations of wolves elsewhere (Mech and Cronin, 2010; Mech and Fieberg, 2014).

Another example, which approximates the population size of the Mexican wolf, is the recovery of gray wolves in Scandinavia. After a period of growth from 3 founders, recovery stalled because of poor pup survival. However, the addition of 2 more breeding animals coincided with a remarkable turnaround (Ingvarsson, 2002; Vilà et al., 2003), and the population now exceeds 400. The Mexican wolf population is now thriving similarly. In the wild in Arizona and New Mexico, Mexican wolves have a 5-year mean (2010–2014) of 41.7% in the observed population increase from pup production (Fig. 1) and 30.5% annual recruitment of pups to 31 December (AZGFD, unpublished results). Annual censuses demonstrate that the population has been growing by an average 20% annually for 5 years (Fig. 1), a similar trajectory to that of Yellowstone wolves during their first 10 years. Additionally, average number of pups observed per breeding female in the wild from May through September (termed "litter size") has increased (Fig. 2) concurrently with the transition to a 100% wild born population. Also encouraging is the fact that observed litter size has been above the 1998–2014 mean of 3.3 pups in 6 of the last 9 years (Fig. 2).

Still, as with many other conservation efforts (e.g. Caro and Laurenson, 1994; Caughley, 1994; Spiering et al., 2011), actions to restore this species during the last 30 years have demonstrated that small populations face multiple challenges in recovery. While genetic factors often impact population growth and persistence, the greatest

Table 2
Persistence of wolf populations with few founders (Incr. = increasing).

Country	Population low point	Population currently	Status	Reference
Italy (Apennines)	100 (1973; isolated for 100–200 years)	~1500	Incr.	Mech and Boitani (2003:326), Salvatori and Linnell (2005), L. Boitani (2015, pers. comm.)
Greenland		20–100 (2003)		Mech and Boitani (2003:322)
Croatia/Slovenia	50 (1990)	260–300 (2005–08)	Stable/Incr.	Gomerčić et al., 2010
Scandinavia (Sweden, Norway)	2 founders (1980s), +1 (~1990), +2 (2008)	460 (winter 2014/15)	Stable/Incr.	Hagenblad et al. (2009), Liberg et al. (2012); Swedish monitoring program
French Alps	Migrants from Italy	~300	Stable/Incr.	L. Boitani (2015, pers. comm.), BBC News Clip on 10/13/15 (www.bbc.com/news/science-environment-34510869); Fritts and Carbyn (1995)
Israel		91–159 in Negev Desert	Stable	Hefner and Geffen (1999)
Poland	Reduced to ~100 after WWII	~600–700	Stable/Incr.	Mech and Boitani (2003), http://www.wolvesandhumans.org/how_to_help_pages/wolf_research_poland.htm
Spain	"Few packs in 1960s"	>2000	Stable/Incr.	Mech and Boitani (2003)
Brandenburg, Germany	Extirpated 19th century; 2 founders 2007	~75–90 wolves (2012)	Incr.	Ministerium für Umwelt, Gesundheit und Verbraucherschutz Brandenburg (2012)
NW Montana[a, b]	Approx. 30 in 1990	~315 (2006)	Incr.	Sime et al. (2007)
Yellowstone NP[b]	31 (1995) + 10 (1996; only 2 of 10 reproduced)	510 minimum count in Greater Yellowstone Area (2014)	Incr.	USFWS (2007), vonHoldt et al. (2008), Justin Gude (pers. comm.)
Central Idaho[b]	20 (1996)	719 minimum count in 2014	Incr.	Justin Gude (pers. comm.)
Isle Royale, MI[c]	2–3 (founded 1949)	Reached ~50 animals; now <5	Declining	Mech and Cronin (2010), Vucetich and Peterson (2015)
Mainland Michigan	Estimated ~6 (1973)	687+ (2010/11)	Stable/Incr.	Fuller et al. (2003), Michigan DNR (http://www.michigan.gov/dnr)
Kenai Peninsula, AK	Founded 1960	150–180	Stable	Fritts and Carbyn (1995)
Wisconsin	14 (1985)	782–824 (2011)	Stable/Incr.	Wisconsin DNR (http://dnr.wi.gov)
Minnesota	450–700	~2450	Stable	Minnesota DNR (http://www.dnr.state.mn.us)
Riding Mountain Ntl Park, Canada	30 (1996/97)	Reached 113 (2011/12); now ~69 (2013/14)	Stable	Fritts and Carbyn (1995), Parks Canada (http://www.pc.gc.ca)

[a] The Magic Pack started with 2 in 1981 from animals collared in British Columbia in 1979. The pair denned in NW MT and first had 5 pups in 1982. The minimum count in 2014 in NW MT was 428 animals.
[b] Areas share immigrating wolves moving between these populations and Canada, so all population growth cannot be exclusively attributed to the founding populations.
[c] Isle Royale represents an extreme case, with no intentional translocation and little natural immigration into the population for ~50 years, yet population has persisted >60 years.

threats to populations are frequently something other than inbreeding depression (Gilpin and Soulé, 1986; Lande, 1988; Caro and Laurenson, 1994; Mech and Cronin, 2010). This was illustrated in Mexican wolves when wild population growth stalled from 2005 to 2009 because of necessary removals and illegal poaching of released wolves (Wayne and Hedrick, 2010). Likewise, inbreeding depression (as manifest in lowered pup survival and recruitment) is generally assumed greater in the wild than in captivity (e.g. Kalinowski et al., 1999; Hedrick and Kalinowski, 2000). Yet pup survival in highly inbred red wolves (*Canis rufus*) was higher in the wild (Brzeski et al., 2014), indicating that environmental factors in the wild abated the stress of captivity (caused by e.g. potential disease transmission or crowding stress in captive conditions) and also impacted population viability in the short-term more than did the direct genetic effects of inbreeding.

These observations and others (Tables 1, 2) show the potential for populations to persist in the face of genetic challenges, and also indicate that genetic effects, although important, may not be the overriding factors that determine population viability. We acknowledge the challenge with such anecdotes is that they provide no sense of how often similar circumstances lead to undocumented population extinctions. While the anecdotes demonstrate the potential for persistence, at least in the short term, they do not speak to the probability or the durability of recovery.

In extreme cases, low genetic diversity in a species has been 'rescued' by genetic contributions from immigrant conspecifics (Ingvarsson, 2002; Vilà et al., 2003) or other subspecies, as occurred in the Florida panther (Johnson et al., 2010). However, this type of intervention may introduce maladapted traits and cause detrimental effects through outbreeding depression (Lynch, 1991; Edmands, 1999). The Mexican wolf is currently increasing in abundance and lacks any apparent demographic or physical signs of inbreeding, so we suggest that this level of intervention is not warranted at this time. As Mexican wolves and their conspecifics recovering elsewhere continue to expand, contact will undoubtedly occur, but ideally not before the Mexican wolf is recovered sufficiently that its genetic and taxonomic integrity can be preserved.

The recovery of small populations is therefore most often a game of probabilities of survival, influenced by population history and genetic load (Flather et al., 2011). Against this background, we review a few primary tools that are available to increase genetic diversity and direct management actions in the recovery of the Mexican wolf.

3. Release of captive adults

An intuitive course of action, which has been suggested by conservation groups (e.g. letter to USDI Secretary Sally Jewel, dated October 8, 2015), is to release more adult wolves from the captive population. While this strategy has the potential to increase genetic diversity in the wild population, we believe that this benefit is outweighed by more immediate, non-genetic challenges.

Captive-raised wolves released to the wild frequently get into conflicts (Wayne and Hedrick, 2010; Appendix 1); 56 of 90 confirmed nuisance incidents from 1998 to 2012 (Table 3) were caused by captive–raised or –conditioned wolves. Mexican wolf recovery efforts stalled for several years (~2003–2009, Fig. 1), primarily because of high wolf mortality and removal from the wild in response to depredation claims and boundary violations, illegal killing, and road kills (Wayne and Hedrick, 2010). In 9 cases where captive–raised or –conditioned wolves

Table 3
Wolf nuisance reports investigated by the Interagency Field Team (IFT), 1998–2012.

Interagency Field Team investigated wolf nuisance reports	Arizona	New Mexico	White Mountain Apache Tribe	San Carlos Apache Reservation	Total
Total for each jurisdiction	74	58	2	3	137
Confirmed nuisance wolf incident	40	45	2	3	90
Incidents involving domestic dogs	21	11	2	3	37
Domestic dog fatalities	0	4	0	0	4
Incidents involving captive-reared, released wolves	33	20	2	1	56

were released to the wild, 8 failed to produce offspring that lived > 1 year (Appendix 1). Consequently, wolves that spent more than just a few months in captivity have rarely contributed new genetic material to the wild population. Captive–raised or –conditioned animals may also unduly jeopardize recovery efforts as their actions reduce public support and complicate joint federal and state recovery coordination. We therefore see the potential for the release of large numbers of naïve captive-born wolves to do more harm than good.

In 2010, the available data suggested that a cessation of captive releases would leave the population with an unsustainable load of adult mortality (Wayne and Hedrick, 2010). However, the cessation of captive releases between 2009 and 2012, and the resulting decrease of captive-born animals in the wild (Fig. 3), was followed by a sharp increase in population size (Figs. 1, 3), reduced conflicts with domestic dogs, and no clear evidence of decline in litter size (Fig. 2) or an increase in depredation (Fig. 4). These observations could be due to factors other than fewer captive releases, but clearly the trends remain favorable despite fewer captive releases. It appears in hindsight that by limiting introductions to appropriately conditioned captive wolves, and by maintaining a savvy wild-born population, mortality has been moderated, freeing the population to expand more rapidly than during the early years of recovery (20% per year over the past 5 years).

4. Fostering

Recovering rare species using captive-reared animals is challenging. Wildlife reared in captivity often lack the skills required to survive in the wild. To circumvent these challenges, wildlife managers have used fostering as a valuable tool in releasing captive-bred animals into the wild. Fostering is the act of placing newly born young or eggs, often produced in captivity, with wild or wild-adapted parents of the same species while they are rearing young of their own. Fostering has been successfully used in a variety of species, including marsupials (e.g. Taggart et al., 2010) and many birds (Fyfe and Armbruster, 1977; Walton, 1977; Armbruster, 1978; Burnham et al., 1978; Engel and Isaacs, 1982). It also provides a mechanism for introducing underrepresented genomes into a wild population (Scharis and Amundin, 2015).

Successful fostering efforts in other large mammalian carnivores demonstrate that this technique should be considered whenever using captive-reared wildlife for species recovery, particularly for species having complex social structures and extended learning periods. For example, 79% of orphaned black bear (*Ursus americanus*) cubs placed in foster natal dens emerged from the den with mothers who subsequently cared for them (Alt, 1984; Alt and Beecham, 1984). Kitchen and Knowlton (2006) demonstrated that coyote (*Canis latrans*) pups could be added to litters with no evidence that surviving foster pups were at any disadvantage in weight gain or dominance status to the natal pups. Fostering was also used in efforts to recover the critically endangered red wolf, with a total of 21 captive- or wild-born red wolf pups fostered between 2002 and 2013 (Brzeski et al., 2014). Subsequent efforts also reported a 93% success rate with pups fostered from captivity into wild red wolf dens (David Rabons, Former Red Wolf Coordinator, personal communication, 2014). Likewise, gray wolves in Scandinavia showed successful fostering in 4 litters (Scharis and Amundin, 2015). Four females with litters of their own accepted additional foster pups introduced to the den between the ages of 2–8 days, and there was no significant difference between survival rate of the foster pups and natal pups. With as many as 9 pups per litter, the foster pups successfully competed with biological pups during nursing, even when they were 8 days younger. Scharis and Amundin (2015) recommended fostering pups at least 4–6 days of age to introduce new founder genes into wild wolf populations, and their study illustrated the efficacy of fostering in gray wolves to increase genetic variation in recovering endangered species.

Against this backdrop, the Mexican wolf Interagency Field Team (IFT) conducted a fostering operation in 2014 with 2 wild-born litters in Arizona. The Coronado Pack, a mated adult pair, was released in

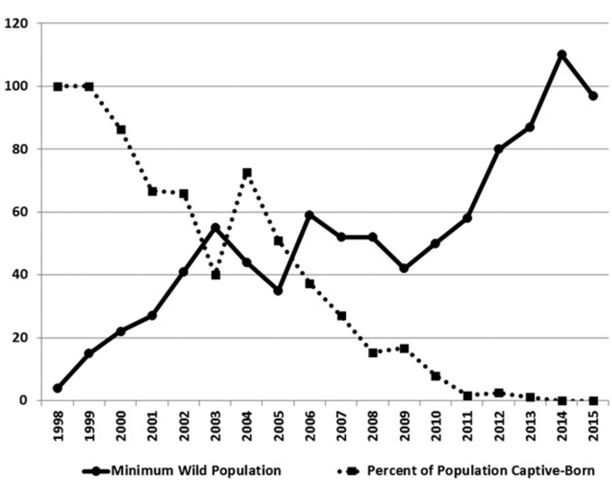

Fig. 3. Percent of Mexican wolf wild population comprised of captive-born individuals and overall wild population growth in Arizona and New Mexico, 1998–2015.

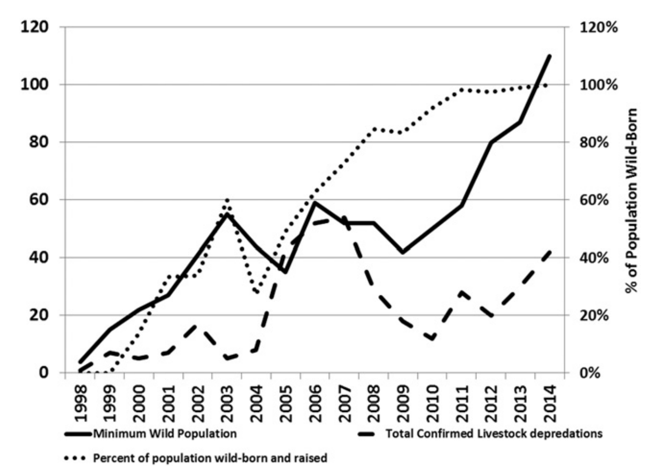

Fig. 4. Relationships of wild Mexican wolf population to confirmed livestock depredations, 1998–2014.

April, but split up 3 days later. The female (F1126, Appendix 1) whelped a litter of 6 pups in early May, and the IFT trapped her, located her litter, and removed one female and one male pup for fostering with pups of similar age in the Dark Canyon Pack (DCP). At the end of June, both fostered pups and the 3 biological pups in the DCP were documented on camera, indicating the fostering effort was successful. Both fostered pups were still alive and healthy during surveys in January 2015 and the male pup has since paired with a female from a neighboring pack.

Given this history of successful fostering in many mammal species, including critically endangered canids, fostering should be an active part of the recovery of endangered Mexican wolves. Strategic breeding, translocation, and fostering efforts in the captive and wild populations can mitigate many of the effects of inbreeding depression and produce new animals with greater genetic variation (e.g. Ingvarsson, 2002; Vilà et al., 2003; Tallmon et al., 2004; Hedrick, 2005; Fredrickson et al., 2007; Wayne and Hedrick, 2010; Adams et al., 2011; Fredrickson, 2011).

5. Setting recovery targets

There is ongoing discussion in the literature about what number of animals is appropriate for recovery. In reality, there is "no single 'magic' population size that guarantees persistence of populations" (Thomas, 1990). Yet to deal with the complexity and stochasticity surrounding inbreeding effects, the conservation genetics tradition offers the '50/500' rule. This suggests that the genetic effective population size (N_E; the size of a randomly mating model population subject to same genetic drift as the actual population) should be maintained above 50 at all times, and above 500 over the long term (Franklin, 1980; Soulé, 1980). Theoretically, these values would moderate the power of random drift to fix deleterious alleles in the short term, while maintaining immunological diversity and a base of variation on which selection could act over the long term (Gillespie, 2004).

However, the 50/500 numbers are far from being a universal threshold of success. In arriving at 50, Soulé (1980) observed that breeders of domestic animals tolerate N_E in the range of 17 to 25 (i.e. 2–3% loss of heterozygosity per generation), but stating that he preferred to be more conservative, picked an N_E of 50, or 1% loss per generation. On the other hand, Lande (1995) argued that 5000 would be a more appropriate N_E for the maintenance of adaptive potential, a value that many species would fail to achieve without human aid. In short, these numbers are convenient reference points, and provide a framework for discussion, but are not thresholds beyond which a population's fate turns from promising to dire (Fritts and Carbyn, 1995).

It is appropriate to desire that a population be free of immediate genetic threats before being considered 'recovered', and the temptation is to reference the generic '50/500 rule' for guidance. In keeping with this guideline, Wayne and Hedrick (2010:18) recommended for Mexican wolf recovery that for the "…*recovery of Mexican wolves three populations, each simultaneously having 250 animals for 8 years (approximately two generations) is the minimum necessity*". The resultant current draft recovery criteria for Mexican wolves are consequently based on an N_E of 50, which is offered as a minimum number for each population before Mexican wolves are no longer regarded as endangered (Hedrick and Fredrickson, 2008; Wayne and Hedrick, 2010; USFWS 2013, unpublished report). If N_E of 50 is to be maintained in each population, the rule for the draft recovery criteria stipulates a minimum of 250 wolves needed in each censused population (N_C) because the ratio of N_E/N_C was assumed to be ~0.20 based on published estimates and modeling conducted on Scandinavian wolves (Forslund, 2009; Bruford, 2015). Under these guidelines, long-term persistence of Mexican wolves will require 2500 wolves (500/0.20) in each of 3 populations unless there is sufficient genetic exchange. While this is much less than the thousands or 100s of thousands suggested for N_E (e.g. Thomas, 1990; Lande, 1995; Traill et al., 2010), this 50/500 rule for genetic fitness is subjective (Flather et al., 2011) and may only be within the right order of magnitude (Fritts and Carbyn, 1995, and references therein).

There are several weaknesses in Wayne and Hedrick's (2010) recommendation. First, as stated above, the number 50 was selected as an approximation, arbitrarily halving the rate of genetic loss that is broadly acceptable in domestic animals. The actual genetic vulnerability of a given population depends on, among other things, its history, because selection has an opportunity to purge deleterious alleles as populations contract (Glémin, 2003). Such history may explain why many ungulates seem able to routinely withstand severe genetic bottlenecks (Table 1).

Second, the choice is not between "good" (≤1% loss of heterozygosity per generation) and "bad" (>1%), but rather a decision along a continuous scale. We also have no way of knowing what specific 'gene × environment' challenges will be faced by Mexican wolves (e.g. will particular deleterious alleles that get fixed in Mexican wolves be especially problematic in their native, but now highly altered, environments?). There are no quantitative data to show that inbreeding depression would unduly impact Mexican wolves at 1% loss per generation ($N_E = 50$), 1.5% ($N_E < 33$), 3% per generation ($N_E = 17$), or at any other specific threshold.

Identification of a minimum viable population (MVP; Soulé, 1987) size also needs to consider a population's connection to other populations (Wolf et al., 2015), because networks of small populations, connected as parts of larger metapopulations, may have much different viability than those existing in isolation. As an example, Vortex population models (USFWS 2013, unpublished report) show that 2 connected populations of 250 wolves perform similarly to the 3 populations of 250 wolves recommended by Wayne and Hedrick (2010). The amount of gene flow between populations affects population persistence more strongly when population size is small (i.e. <300 individuals; USFWS, 2015b). Yet having high connectivity between 2 or 3 populations increases N_E and reduces the number of wolves needed for recovery in each subpopulation (Soulé, 1987; Fritts and Carbyn, 1995). There is also considerable disagreement about whether this guideline can be generalized across different taxa or used to examine extinction risk (Flather et al., 2011) because it is based on general theoretical principles (Shaffer, 1981).

The ratio between N_C and N_E is another notoriously difficult parameter to estimate. In real populations, the calculation of N_E is complicated by factors like fluctuating population sizes, social dynamics, spatial dispersion, overlapping generations, and gene flow. For example, Harris and Allendorf (1989) evaluated 9 ways to calculate the ratio of N_E/N_C and the results varied widely using the same dataset. The literature suggests gray wolf populations have N_E/N_C ratios of 0.20 to 0.40 (Aspi et al., 2006; Liberg et al., 2005; vonHoldt et al., 2008), with 2 recent studies producing an estimated N_E of 0.29 and 0.40 of N_C (Aspi et al., 2006; vonHoldt et al., 2008). By contrast, information from the wild population in 2011 suggested the ratio might be as low as 0.10 (J. Oakleaf, USFWS, personal communication). Assuming that these ranges of values capture a point of true biological relevance to the Mexican wolf, the appropriate target for population size might be 63 (25/0.4) or 500 (50/0.1).

The N_E (and N_E/N_C ratio) deemed necessary for the recovery of the Mexican wolf is critically important to the scientific defensibility of the recovery criteria, yet there is demonstrated support for a range of population sizes that could be used as valid recovery criteria. Certainly, discussions on the minimum number of wolves necessary for population survival have not coalesced, and estimates range widely from theoretical models to empirical considerations (Fritts and Carbyn, 1995; Musiani et al., 2009). Based on the range of scientifically defensible possibilities, it would be misleading to offer up a single number as the minimum population size and N_E needed to recover Mexican wolves. Nevertheless, until the recovery plan can be revised, the 2015 Final Rule for the experimental 10j population proposes 300–325 animals as a total number of Mexican wolves needed for population recovery (USFWS, 2015b).

6. Population viability analyses

A common criticism of MVP estimates is that they fail to account for the high natural resilience of small wolf populations (e.g. Fritts and Carbyn, 1995; Mech and Cronin, 2010). Population viability analyses (PVAs) are theoretical models implemented to examine the viability of a population under certain management or environmental conditions. A great deal of emphasis was originally placed on using PVAs to identify MVPs, by assessing the risk of extinction of populations of various sizes, or to indicate the urgency of recovery efforts (Shaffer, 1981; Gilpin and Soulé, 1986). However, direct applications of PVAs are limited, and many researchers have provided recommendations for their appropriate use (Beissinger and Westphal, 1998; Ellner et al., 2002; Reed et al., 2002; Wolf et al., 2015). In particular, Reed et al. (2002) concluded that although PVAs are a powerful tool in conservation biology, these assessments should not be used to determine minimum population size or the specific probability of reaching extinction. Rather, PVAs are most appropriate for comparing the relative effects of potential management actions on population growth or persistence. Moreover, the outcome of a PVA, in terms of absolute risk of extinction, is driven by the demographic parameters entered into the model, and there is great uncertainty in these values (Ellner et al., 2002) because they often change with fluctuating population sizes and environmental conditions.

The most effective use of PVAs is to compare relative, not absolute, risk under various management scenarios (Beissinger and Westphal, 1998; Reed et al., 2002). Absolute extinction probabilities from PVA (e.g. in Mexican wolves, the Vortex model) should not discount alternative recovery scenarios. In addition, a PVA should include sufficient detail and a systematic sensitivity analysis to identify those parameters driving population viability and the range of uncertainty around the risk assessment (Ellner et al., 2002; Reed et al., 2002). In the case of recovery planning, PVAs should be based on empirical data and used to identify parameters to incorporate into the recovery criteria rather than justifying a desired population size or the number of effective migrants/generation.

7. Conclusions

The genetic guidelines for preventing inbreeding depression are uncertain and basing explicit recovery goals on such guidelines stretches them beyond their scientific underpinnings, and beyond the spirit in which they were first proffered. As important as genetic considerations are, they are not the only factors that might affect the success of a recovery process (Hedrick and Fredrickson, 2008; Mech and Cronin, 2010; Johnson et al., 2011). For instance, political controversy has been an impediment to Mexican wolf recovery and undermined public support for the recovery program, as illustrated by the observation that of the 124 documented Mexican wolf mortalities from 1998 to 2015, 66 (53%) were attributed to illegal shooting and trapping (USFWS, 2014). This underscores the need to develop a legally-sufficient, science-based Mexican wolf recovery plan that recognizes that not all challenges are biological. We recommend a more practically minded approach in which recovery goals are developed with reference to the available resources (human and habitat; Meffe and Carroll, 1994), and then reviewed from the perspective of inbreeding depression. We suggest that the intensity of monitoring can be adjusted to ensure that severe inbreeding effects are detected before they threaten population stability, providing an opportunity to modify management if needed. If problematic inbreeding depression arises in a given population, we note that even a low rate of movement between populations, whether natural or human assisted (e.g. through fostering or adult migration) can be used to raise the N_E of any individual population to near that of the metapopulation as a whole. Given the availability of these powerful and flexible tools for managing inbreeding depression, recovery targets should emphasize practical considerations that are likely to immediately impact success, rather than an inexact genetic rule of thumb.

Appendix 1

Fates of 13 adult Mexican wolves in wild population that spent ≥4 months as captive animals, 2008–2015. Fate unknown animals are considered non-contributing to the wild wolf population. F, female; M, male, *captive–raised/conditioned; +wild–raised/conditioned; ^potential genetic contributors = produced pups that have survived >1 year.

Individual(s)	Fate(s)
M1039+ F836*	Pair released 2008 as Moonshine Pack in Arizona, but split up. Male went to New Mexico; now fate unknown; female was illegally shot.
F1105*	Translocated 2009 to New Mexico to pair with male in local pack, but effort failed; illegally shot near a residence.
M1054*	Translocated 2011 to Arizona to pair with female in local pack, but effort failed. Removed to captivity for nuisance issues.
F1106*	Translocated 2011 to New Mexico; lethally removed for nuisance issues.
M1133*	Released 2013 in Arizona to pair with Bluestem Pack female, but effort failed. Removed to captivity for nuisance issues.
M1249+^ F1126*^ M1051*	Released 2014 as Coronado Pack, but split up. M1249 became breeder in Diamond Pack. F1126 later captured with pups; 2 pups fostered into the Dark Canyon Pack; one pup is now 2 years old; other is fate unknown. F1126 and her 4 remaining pups were paired with M1051 and translocated. F1126 is now dead, and M1051 and 4 pups are fate unknown.
M1290+^ F1218*	Released 2014 as Hoodoo Pack, but split up. Male paired with an uncollared female to form new Hoodoo Pack. F1218 was illegally shot.
F1305+ M1130*	Released as Rim Pack 2015, but split up. Female was illegally shot, and male was lethally removed for nuisance issues.

Acknowledgements

We thank Luigi Boitani for providing current population estimates for wolves in Italy and France. We also thank L. David Mech, Matthew Kauffman, Matthew A. Cronin, Terry L. Bowyer, Justin Gude, and Randall W. DeYoung, and three anonymous reviewers for their reviews and discussions of this material. Funding for this project and the captive wolf recovery program in Arizona comes from USFWS Section 6 funds (AZ E-5-27 F16AP00022), the USFWS Cooperative Endangered Species Conservation Fund (AZ E-5-27 F16AC00814), Wildlife Restoration Funds (FW-100-P) from The Federal Aid in Wildlife Restoration Act, and a Rocky Mountain Elk Foundation PAC Grant (AZ140343) to the Arizona Game and Fish Department.

References

Adams, J.R., Vucetich, L.M., Hedrick, P.W., Petersen, R.O., Vucetich, J.A., 2011. Genomic sweep and potential genetic rescue during limiting environmental conditions in an isolated wolf population. Proc. R. Soc. B. http://dx.doi.org/10.1098/rspb.2011.0261 (Published online 30 March 2011).
Alt, G.L., 1984. Cub adoption in black bear. J. Mammal. 65, 511–512.
Alt, G.L., Beecham, J.J., 1984. Reintroduction of orphaned black bear cubs into the wild. Wildl. Soc. Bull. 12, 169–174.
Armbruster, H.J., 1978. In: Schaeffer, P.P., Ehlers, S.M. (Eds.), Current peregrine falcon populations in Canada and raptor management programs. Proceedings of the National Audubon Symposium on the Current Status of Peregrine Falcon Populations in North America. National Audubon Society, Tiburon, CA USA, pp. 47–54.
Asa, C., Miller, P., Agnew, M., Rebolledo, J.A.R., Lindsey, S.L., Callahan, M., Bauman, K., 2007. Relationship of inbreeding with sperm quality and reproductive success in Mexican wolves. Anim. Conserv. 10, 326–331.
Aspi, J., Roininen, E., Ruokonen, M., Kojola, I., Vilà, C., 2006. Genetic diversity, population structure, effective population size and demographic history of the Finnish wolf population. Mol. Ecol. 15, 1561–1576.
Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. J. Wildl. Manag. 62, 821–841.
Bogan, M.A., Mehlhop, P., 1983. Systematic relationships of gray wolves (*Canis lupus*) in southwestern North America. Occasional Papers No. 1. Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM.
Broughton, J.M., Beck, R.K., Coltrain, J.B., O'Rourke, D.H., Rogers, A.R., 2012. A late Holocene population bottleneck in California tule elk (*Cervus elaphus nannodes*): provisional support from ancient DNA. J. Archeol. Method Theory. http://dx.doi.org/10.1007/s10816-012-9167-y.
Brown, D.E., 2002. The Wolf of the Southwest: The Making of an Endangered Species. High-Lonesome Books, Silver City, New Mexico, USA.
Bruford, M.W., 2015. Additional population viability analysis of the Scandinavian wolf population. Report 6639 to Swedish Environmental Protection Agency, Stockholm, Sweden.

Brzeski, K.E., Rabon, D.R., Chamberlain, M.J., Waits, L.P., Taylor, S.S., 2014. Inbreeding and inbreeding depression in endangered red wolves (*Canis rufus*). Mol. Ecol. 23, 4241–4255.
Burnham, W.A., Craig, J., Enderson, J.H., Heinrich, W.R., 1978. Artificial increase in reproduction of wild peregrine falcons. J. Wildl. Manag. 42, 625–628.
Carmony, N.B., Brown, D.B., Heffelfinger, J.R., 2010. Arizona's elk restorations. In: Glinski, R., Aubuchon, D., Keebler, B. (Eds.), Arizona Wildlife Trophies. Arizona Wildlife Federation, Phoenix, AZ, USA, pp. 73–86.
Caro, T.M., Laurenson, M.K., 1994. Ecological and genetic factors in conservation: a cautionary tale. Science 263, 485–486.
Caughley, G.J., 1994. Directions in conservation biology. J. Anim. Ecol. 63, 215–244.
Cronin, M.A., Cánovas, A., Bannasch, D.L., Oberbauer, A.M., Medrano, J.F., 2015a. Single nucleotide polymorphism (SNP) variation of wolves (*Canis lupus*) in southeast Alaska and comparison with wolves, dogs, and coyotes in North America. J. Hered. 106, 26–36.
Cronin, M.A., Cánovas, A., Bannasch, D.L., Oberbauer, A.M., Medrano, J.F., 2015b. Wolf subspecies: reply to Weckworth et al. and Fredrickson et al. J. Hered. http://dx.doi.org/10.1093/jhered/esv029.
Edmands, S., 1999. Heterosis and outbreeding depression in interpopulational crosses spanning a wide range of divergence. Evolution 53, 1757–1768.
Ellner, S.P., Fieberg, J., Ludwig, D., Wilcox, C., 2002. Precision of population viability analysis. Conserv. Biol. 16, 258–261.
Engel, J.M., Isaacs, F.B., 1982. Bald Eagle Translocation Techniques. USDI Fish and Wildlife Service, Twin Cities, MN, USA.
Flather, C.H., Hayward, G.D., Beissinger, S.R., Stephens, P.A., 2011. Minimum viable populations: is there a "magic number" for conservation practitioners? Trends Ecol. Evol. 26, 307–316.
Forslund, P., 2009. Modeling growth and inbreeding in the Scandinavian wolf population. Report to the Swedish Environmental Protection Agency. Environmental Protection Agency, Stockholm Included in Appendix 1 of the Swedish Environmental Protection Agency's report Dnr 429–8585-08 Nv. (in Swedish).
Franklin, I.R., 1980. Evolutionary change in small populations. In: Soulé, M.E., Wilcox, B.A. (Eds.), Conservation Biology: An Evolutionary Ecological Perspective. Sinauer Associates, Sunderland, MA, USA, pp. 135–140.
Fredrickson, R.J., 2011. Genetic re-rescue prospects for the Mexican wolf captive population. Final Report Prepared for the Mexican Wolf Species Survival Plan. University of Montana, Missoula, MT, USA.
Fredrickson, R.J., Siminski, P., Woolf, M., Hedrick, P.W., 2007. Genetic rescue and inbreeding depression in Mexican wolves. Proc. R. Soc. B 274, 2365–2371.
Fritts, S.H., Carbyn, L.N., 1995. Population viability, nature reserves, and the outlook for gray wolf conservation in North America. Restor. Ecol. 3, 26–38.
Fuller, T.K., Mech, L.D., Cochrane, J.F., 2003. Wolf population dynamics. In: Mech, L.D., Boitani, L. (Eds.), Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, IL, USA, pp. 161–191.
Fyfe, R.W., Armbruster, H.I., 1977. Raptor research and management in Canada. In: Chancellor, R.D. (Ed.), World Conference on Birds of Prey: Report of Proceedings. International Council for Bird Preservation, Vienna, Austria, pp. 282–293.
Gillespie, J.H., 2004. Population Genetics: A Concise Guide. 2nd ed. The Johns Hopkins University Press, Baltimore, MD, USA.
Gilpin, M.E., Soulé, M.E., 1986. Minimum viable populations: processes of species extinction. In: Soulé, M.E (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA, USA, pp. 19–34.
Glémin, S., 2003. How are deleterious mutations purged? Drift versus nonrandom mating. Evolution 57, 2678–2687.
Gomerčić, T., Sindičić, M., Galov, A., Arbanasić, H., Kusak, J., Kocijan, I., Đuras Gomerčić, M., Huber, Đ., 2010. High genetic variability of the grey wolf (*Canis lupus* L.) population from Croatia as revealed by mitochondrial DNA control region sequences. Zool. Stud. 49 (6), 816–823.
Hagenblad, J., Olsson, M., Parker, H.G., Ostrander, E.A., Ellegren, H., 2009. Population genomics of the inbred Scandinavian wolf. Mol. Ecol. 18, 1341–1351.
Harris, R.B., Allendorf, F.W., 1989. Genetically effective population size of large mammals: an assessment of estimators. Conserv. Biol. 3, 181–191.
Hartl, D.L., Clark, A.G., 2007. Principles of Population Genetics. 4th edition. Sinauer Associates, Sunderland, MA, USA.
Hedrick, P.W., 2005. Genetic restoration" a more comprehensive perspective than "genetic rescue". Trends Ecol. Evol. 20, 109.
Hedrick, P.W., 2009. Conservation genetics and North American bison (*Bison bison*). J. Hered. 100, 411–420.
Hedrick, P.W., Fredrickson, R.J., 2008. Captive breeding and the reintroduction of Mexican and red wolves. Mol. Ecol. 17, 344–350.
Hedrick, P.W., Kalinowski, S.T., 2000. Inbreeding depression in conservation biology. Annu. Rev. Ecol. Syst. 31, 139–162.
Hedrick, P.W., Miller, P.S., Geffen, E., Wayne, R.K., 1997. Genetic evaluation of the three captive Mexican wolf lineages. Zoo Biol. 16, 47–69.
Heffelfinger, J.R., 2011. Chapter 1: taxonomy, evolutionary history, and distribution. In: Hewitt, D.G. (Ed.), Biology and Management of White-tailed Deer. CRC Press, Boca Raton, FL, USA, pp. 3–39.
Heffelfinger, J.R., 2013. Kaibab Plateau: land of the giants. Mule Deer Retrospective. Falcon Press, Helena, MT, USA, pp. 182–285.
Hefner, R., Geffen, E., 1999. Group size and home range of the Arabian wolf (*Canis lupus*) in southern Israel. J. Mammal. 80, 611–619.
Hundertmark, K.J., 2009. Reduced genetic diversity in two introduced and isolated moose populations in Alaska. Alces 45, 137–142.
Ingvarsson, P.K., 2002. Lone wolf to the rescue. Nature 420, 472.
Johnson, W.E., Onorato, D.P., Roelke, M.E., Land, E.D., Cunningham, M., Belden, R.C., McBride, R., Jansen, D., Lotz, M., Shindle, D., Howard, J., Wildt, D.E., Penfold, L.M., Hostetler, J.A., Oli, M.K., O'Brien, S.J., 2010. Genetic restoration of the Florida panther. Science 329, 1641–1645.
Johnson, H.E., Mills, L.S., Wehausen, J.D., Stephenson, T.R., Luikart, G., 2011. Translating effects of inbreeding depression on component vital rates to overall population growth in endangered bighorn sheep. Conserv. Biol. 25, 1240–1249.
Kaeuffer, R., Coltman, D.W., Chapuis, J.L., Pontier, D., Réale, D., 2007. Unexpected heterozygosity in an island mouflon population founded by a single pair of individuals. Proc. R. Soc. Lond. Ser. B Biol. Sci. 274, 527–533.
Kalinowski, S.T., Hedrick, P.W., Miller, P.S., 1999. No inbreeding depression observed in Mexican and red wolf captive breeding programs. Conserv. Biol. 13, 1371–1377.
Kitchen, A.M., Knowlton, F., 2006. Cross-fostering in coyotes: evaluation of a potential conservation and research tool for canids. Biol. Conserv. 129, 221–225.
Lande, R., 1988. Genetics and demography in biological conservation. Science 241, 1455–1460.
Lande, R., 1995. Mutation and conservation. Conserv. Biol. 9, 782–791.
Liberg, O., Andrén, H., Pedersen, H.C., Sand, H., Sejberg, D., Wabakken, P., Kesson, M., Bensch, S., 2005. Severe inbreeding depression in a wild wolf (*Canis lupus*) population. Biol. Lett. 1, 17–20.
Liberg, O., Aronson, Å., Sand, H., Wabakken, P., Maartmann, E., Svensson, L., Åkesson, M., 2012. Monitoring of wolves in Scandinavia. Hystrix 23, 29–34.
Lynch, M., 1991. The genetic interpretation of inbreeding depression and outbreeding depression. Evolution 45, 622–629.
Mech, L.D., Boitani, L. (Eds.), 2003. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, IL, USA.
Mech, L.D., Cronin, M.A., 2010. Letter to the editor: Isle Royale study affirms ability of wolves to persist. Biol. Conserv. 143, 535–536.
Mech, L.D., Fieberg, J., 2014. Growth rates and variances of unexploited wolf populations in dynamic equilibria. Wildl. Soc. Bull. 39, 41–48.
Meffe, G.K., Carroll, C.R., 1994. Principles of Conservation Biology. Sinauer Associates, Sunderland, MA, USA.
Miller, B., Reading, R.P., Forrest, S., 1996. Prairie Night: Black-footed Ferrets and the Recovery of Endangered Species. Smithsonian Institution Press, Washington.
Ministerium für Umwelt, Gesundheit und Verbraucherschutz Brandenburg, 2012r. Managementplan für den Wolf in Brandenburg 2013–2017.
Musiani, M., Boitani, L., Paquet, P.C., 2009. A New Era for Wolves and People: Wolf Recovery, Human Attitudes, and Policy. University of Calgary Press, Calgary, Canada.
Nowak, R.M., 2003. Wolf evolution and taxonomy. In: Mech, L.D., Boitani, L. (Eds.), Wolves: Behavior, Ecology and Conservation. University of Chicago Press, Chicago, pp. 239–258.
Paul, T.W., 2009. Game Transplants in Alaska. Technical Bulletin #4. 2nd edition. Alaska Department of Fish and Game, Juneau, AK, USA.
Phillips, J., Phillips, R., Srinivasan, N., Aso, D., Lao, W., Cornely, P., 2012. Safe Passage for Coyote Valley: A Wildlife Linkage for the Highway 101 Corridor. Kirsch Center for Environmental Studies, De Anza College, Cupertino, CA, USA.
Räikkönen, J., Vucetich, J.A., Peterson, R.O., Nelson, M.P., 2009. Congenital bone deformities and the inbred wolves (*Canis lupus*) of Isle Royale. Biol. Conserv. 142, 1025–1031.
Reed, J.M., Mills, L.S., Dunning, J.B., Menges, E.S., Mckelvey, K.S., Frye, R., Beissinger, S.R., Anstett, M., Miller, P., 2002. Emerging issues in population viability analysis. Conserv. Biol. 16, 7–19.
Salvatori, V., Linnell, J.D.C., 2005. Pg. 12, in report on the conservation status and threats for wolf (*Canis lupus*) in Europe. Convention of the Conservation of European Wildlife and Natural Habitats. Council of Europe.
Scharis, I., Amundin, M., 2015. Cross-fostering in gray wolves (*Canis lupus lupus*). Zoo Biol. 34, 217–222.
Shaffer, M.L., 1981. Minimum population sizes for species conservation. Bioscience 31, 131–134.
Sime, C.A., Asher, V., Bradley, L., Laudon, K., Ross, M., Trapp, J., Atkinson, M., Handegard, L., Steuber, J., 2007. Montana Gray Wolf Conservation and Management 2006 Annual Report. Montana Fish, Wildlife & Parks, Helena, MT, USA.
Soulé, M.E., 1980. Thresholds for survival: maintaining fitness and evolutionary potential. In: Soulé, M.E., Wilcox, B.A. (Eds.), Conservation Biology: An Evolutionary Ecological Perspective. Sinauer Associates, Sunderland, MA, USA, pp. 151–169.
Soulé, M.E., 1987. Where do we go from here? In: Soulé, M.E (Ed.), Viable Populations in Conservation. Cambridge University Press, pp. 175–183
Spiering, P.A., Gunther, M.S., Somers, M.J., Wildt, D.E., Walters, M., Wilson, A.S., Maldonado, J.E., 2011. Inbreeding, heterozygosity and fitness in a reintroduced population of endangered African wild dogs (*Lycaon pictus*). Conserv. Genet. 12, 401–412.
Taggart, D., Schultz, D., Fletcher, T., Friend, A., Smith, I., Breed, W., Temple-Smith, P., 2010. Cross-fostering and short-term pouch young isolation in macropodid marsupials: implications for conservation and species management. In: Coulson, G., Eldridge, M. (Eds.), Macropods: The Biology of Kangaroos, Wallabies, and Rat-kangaroos. CSIRO Publishing, Australia, pp. 263–276.
Tallmon, D.A., Luikart, G., Waples, R., 2004. The alluring simplicity and complex reality of genetic rescue. Trends Ecol. Evol. 19, 489–496.
Thomas, C.D., 1990. What do real population dynamics tell us about minimum viable population sizes? Conserv. Biol. 4, 324–327.
Traill, L.W., Brook, B.W., Frankham, R.R., Bradshaw, C.J.A., 2010. Pragmatic population viability targets in a rapidly changing world. Biol. Conserv. 143, 28–34.
USFWS, 2007. Endangered and threatened wildlife and plants; designating the northern Rocky Mountain population of gray wolf as a distinct population segment and removing this distinct population segment from the federal list of endangered and threatened wildlife; proposed rule. Federal Register 72. US Fish and Wildlife Service, Department of the Interior, pp. 6106–6139.
USFWS, 2014. Mexican Wolf Recovery Program: Progress Report #17. US Fish and Wildlife Service, Albuquerque, NM, USA.

USFWS, 2015a. Endangered and Threatened Wildlife and Plants; Endangered Status for the Mexican Wolf (80 FR 2488-2512) 2015 Final Rule. Federal Register, US Fish and Wildlife Service, Albuquerque, NM, USA.

USFWS, 2015b. Final Rule for Revision to the Regulations for the Nonessential Experimental Population of the Mexican Wolf (*Canis lupus baileyi*) (80 FR 2512) 2015 Final Rule. Federal Register, US Fish and Wildlife Service, Albuquerque, NM, USA.

Vilà, C., Sundqvist, A.K., Flagstad, Ø., Seddon, J., Björnerfeldt, S., Kojola, I., Casulli, A., Sand, H., Wabakken, P., Ellegren, H., 2003. Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. Proc. R. Soc. Lond. B 270, 91–97.

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

vonHoldt, B.M., Pollinger, J.P., Earl, D.A., Knowles, J.C., Boyko, A.R., Parker, H., Geffen, E., Pilot, M., Jedrzejewski, W., Jedrzejewska, B., Sidorovich, V., Greco, C., Randi, E., Musiani, M., Kays, R., Bustamonte, C.D., Ostrander, E.A., Novembre, J., Wayne, R.K., 2011. A genome-wide perspective on the evolutionary history of enigmatic wolf-like canids. Genome Res. 21, 1294–1305.

Vucetich, J.A., Peterson, R.O., 2015. Ecological Studies of Wolves on Isle Royale: Annual Report 2014–15. Michigan Technological University, Houghton, MI, USA.

Walton, B.J., 1977. Development of techniques for raptor management, with emphasis on the peregrine falcon. California Department of Fish and Game Adm. Rep. 77–4.

Wayne, R.K., Hedrick, P.W., 2010. Genetics and wolf conservation in the American West: lessons and challenges. Heredity 107, 16–19.

Wilder, B.T., Betancourt, J.L., Epps, C.W., Crowhurst, R.S., Mead, J.I., Ezcurraet, E., 2014. Local extinction and unintentional rewilding of bighorn sheep (*Ovis canadensis*) on a desert island. PLoS ONE 9 (3), e91358. http://dx.doi.org/10.1371/journal.pone.0091358.

Wolf, S., Hartl, B., Carroll, C., Neel, M.C., Greenwald, D.N., 2015. Beyond PVA: why recovery under the Endangered Species Act is more than population viability. Bioscience 65, 200–207.