

# Captive breeding and the reintroduction of Mexican and red wolves

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## Abstract

Mexican and red wolves were both faced with extinction in the wild until captive populations were established more than two decades ago. These captive populations have been successfully managed genetically to minimize mean kinship and retain genetic variation. Descendants of these animals were subsequently used to start reintroduced populations, which now number about 40–50 Mexican wolves in Arizona and New Mexico and about 100 red wolves in North Carolina. The original captive Mexican wolf population was descended from three founders. Merging this lineage with two other captive lineages, each with two founders, has been successfully carried out in the captive population and is in progress in the reintroduced population. This effort has resulted in increased fitness of cross-lineage wolves, or genetic rescue, in both the captive and reintroduced populations. A number of coyote-red wolf hybrid litters were observed in the late 1990s in the reintroduced red wolf population. Intensive identification and management efforts appear to have resulted in the elimination of this threat. However, population reintroductions of both Mexican and red wolves appear to have reached numbers well below the generally recommended number for recovery and there is no current effort to re-establish other populations.

*Keywords:* ancestry, *Canis lupus baileyi*, *Canis rufus*, genetic rescue, hybridization, inbreeding depression

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## Introduction

Captive breeding programs have been established for a number of endangered species to save them from extinction, to provide a population from which to reintroduce the species into the wild, and to supplement an endangered or reintroduced wild population. Documenting the successes, failures, and difficulties of these efforts in captive populations and reintroductions is important so that future programs to prevent extinction can benefit from these experiences. Here we discuss some aspects of the captive breeding, reintroduction, and the beginnings of recovery in two endangered North American wolf taxa, the Mexican (*Canis lupus baileyi*) and red (*C. rufus*) wolves, focusing primarily on the Mexican wolf.

There are some parallels in the recovery efforts for these two taxa; for example, the last surviving wild animals

were captured to start the captive populations for both Mexican and red wolves about the same time because of their imminent extinction in the wild (Hedrick *et al.* 1997; Phillips *et al.* 2003). Also, all of the individuals in the reintroduced populations of Mexican and red wolves are descended from captive populations established from these last wild animals. However, critical to the Mexican wolf program is that the original captive population was descended from only three individuals and inbreeding became the main genetic problem. On the other hand, the captive red wolf population was established with more founders and the main genetic problem in the reintroduced red wolf population became introgression from coyotes.

The grey wolf (*C. lupus*) was distributed throughout most of North America, except for the southeastern United States, which was inhabited by the red wolf. Eradication programs, starting in the late nineteenth century, resulted in extirpation of grey wolves from most of their original range within the United States except Alaska and some

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**Table 1** Summary of pedigree and molecular genetic data for the three Mexican wolf lineages before they were merged (Hedrick *et al.* 1997)

Source	Measure	Lineage		
		McBride	Ghost Ranch	Aragón
Pedigree	Number of founders	3	2	2
	Inbreeding coefficient	0.184	0.608	0.263
	Number of alleles surviving	5.41	2.02	3.44
	Number alive	91	18	9
Microsatellite loci	Number of alleles	2.50	1.55	1.50
	Proportion of loci polymorphic	0.90	0.45	0.45
	Heterozygosity (observed)	0.457	0.128	0.255
	Frequency of unique alleles	0.337	0.148	0.110
	Genetic distance to other lineages	0.356	0.274	0.236

wolves in Minnesota (Mech & Boitani 2003). The remaining wolves were declared endangered by the US Fish and Wildlife Service (USFWS), and the Mexican grey wolf subspecies (*C. lupus baileyi*) was listed as endangered in 1976 (see Leonard *et al.* 2005 for genetic analysis of historical specimens). Mexican wolves were apparently extirpated from the United States and greatly reduced in Mexico by 1970 (Brown 1983), and there is no reliable evidence of wild Mexican wolves in Mexico for the last two decades. In a similar time period, the red wolf was eliminated from most of its range. By the 1960s, the remaining small number of wolves was confined to marginal habitats of Louisiana and Texas and listed as endangered by the USFWS in 1967.

Below we first discuss the captive and reintroduced population of Mexican wolves, focusing on the merging of the three lineages that comprise the ancestry of contemporary Mexican wolves. We will then discuss the recent finding of lowered fitness of animals descended only from the original captive lineage along with increased fitness of animals with ancestry from two or more lineages, or genetic rescue (Tallmon *et al.* 2004). Finally, we will more briefly discuss the red wolf captive and reintroduced populations, partly because some of the relevant genetic analysis is either unpublished or has not been undertaken.

## Mexican wolf

### *Captive population*

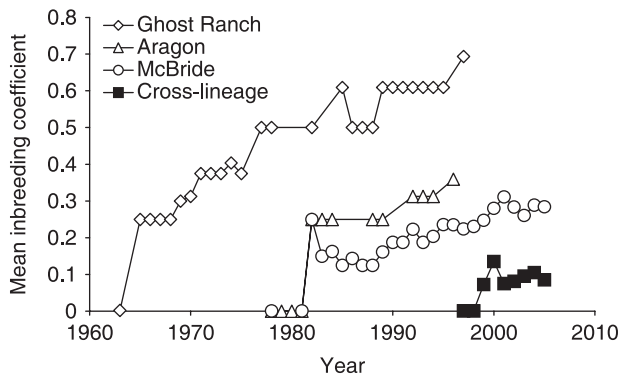
Because Mexican wolves were facing extinction in the wild, a captive population was initiated from animals captured in Mexico between 1977 and 1980 and taken to the United States. However, this captive population, now known as the McBride lineage (originally known as the Certified lineage), was descended from only three founder animals – one female and two males (Hedrick *et al.* 1997). The captive McBride lineage has been managed genetically

and demographically under a Species Survival Plan (SSP) (Siminski 2006). The genetic goals of this intensive management plan are to minimize mean kinship and inbreeding levels, and to retain genetic variation in the captive population (Ballou & Lacy 1995).

Two other captive putative Mexican wolf lineages, known as the Ghost Ranch and Aragón lineages, were evaluated using microsatellite loci and closely clustered with the McBride lineage (Garcia-Moreno *et al.* 1996; Hedrick *et al.* 1997). As a result of this molecular examination, and information indicating that the three lineages descended from independent founders, the Aragón and Ghost Ranch lineages were incorporated into the managed captive population, starting in 1995.

Based on pedigree information, the McBride lineage had more founders, a lower inbreeding coefficient, and a greater number of alleles surviving than the Ghost Ranch and Aragón lineages (Table 1). The lower inbreeding coefficient for the McBride lineage was the result of both more founders and the intensive management in the McBride lineage to maintain genetic variation and minimize inbreeding. The differences, predicted from pedigree information, were consistent with the values observed for the microsatellite loci; that is, the McBride lineage had more microsatellite alleles, more polymorphic loci, and higher heterozygosity than the Ghost Ranch and Aragón lineages (Table 1).

As a result, the Genetics Committee of the Mexican Wolf Recovery Team recommended that the combined population with ancestry from the three captive lineages should at minimum consist of 10% Ghost Ranch and 10% Aragón, with the remainder from the McBride lineage (Hedrick *et al.* 1997). During the process of constituting this population, they recommended that factors such as morphology, behaviour, physiology, juvenile survival, and reproduction be monitored. They also recommended that the upper limit of ancestry from Ghost Ranch and Aragón lineages

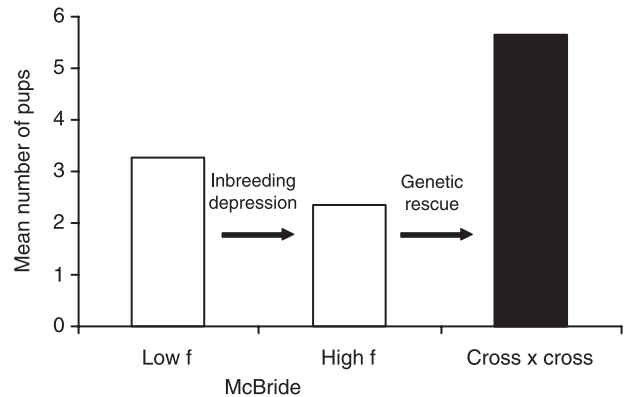


**Fig. 1** The mean inbreeding coefficient for newborn captive Mexican wolves over time calculated from pedigree information. Inbreeding coefficients ( $f$ ) are given separately for the three original lineages, McBride, Ghost Ranch, and Aragón, and the combined cross-lineage population.

should not exceed 25% each because of the more thoroughly documented history, intensive management for inbreeding avoidance, higher number of founders, and greater genetic variation in the McBride lineage.

To illustrate the impact of combining the three captive lineages, Fig. 1 gives the inbreeding coefficients for newborn wolves each year for the three lineages and the combined cross-lineage wolves. As discussed above, the Ghost Ranch and Aragón lineages had the highest inbreeding coefficients (the inbreeding coefficient for Aragón may have actually been higher than given here because of some undocumented early history). After the first few years, the McBride lineage gradually increased in mean inbreeding coefficient to over 0.25. On the other hand, the initial crosses between lineages had an inbreeding coefficient of 0.0 because the founders from the different lineages were assumed to be unrelated. Over the past few years the cross-lineage wolves have only gradually accumulated inbreeding and, as of 2005, their mean inbreeding coefficient is only 0.085, still far below the inbreeding levels that had been reached within the three lineages. As of 2006, the ancestry of the captive wolves is 72.7% McBride, 14.8% Ghost Ranch, and 12.5% Aragón (Siminski 2006), which has progressed somewhat beyond the initial ancestry goal because there has been no negative evidence from the merging of the lineages and important positive effects, as discussed below.

One of the major obstacles inhibiting recovery of endangered species with very small population sizes is inbreeding depression; that is, lower fitness of progeny from matings of relatives than for progeny from unrelated parents (Hedrick & Kalinowski 2000). In captive wolves, inbreeding has been documented to cause decreased growth rate, lower survival and reproduction, and blindness in Scandinavian wolves (Laikre & Ryman 1991; Laikre *et al.* 1993). In wild wolves, inbreeding depression



**Fig. 2** The mean number of pups in litters from the McBride lineage with either a low or high inbreeding coefficient ( $f$ ; open bar) and in litters from cross-lineage by cross-lineage wolves (closed bar; after Fredrickson *et al.* 2007). A decline in number of pups from low to high  $f$  indicates inbreeding depression, while an increase in the number of pups from the McBride wolves with high inbreeding to cross-lineage wolves indicates genetic rescue.

and detrimental genetic effects have been shown in Scandinavian wolves (Vilà *et al.* 2003; Liberg *et al.* 2005) and a high incidence of skeletal malformations in the wolves on Isle Royale in Lake Superior has been observed (J. Räikkönen, personal communication). This is in contrast to the belief by some wolf experts that inbreeding in the wild has purged many of the deleterious genetic variants from wolf populations.

To quantify the impact of inbreeding on fitness in captive Mexican wolves, Kalinowski *et al.* (1999) examined juvenile survival and litter size in the captive population. Although they did not find any significant inbreeding depression, they suggested that their results 'be used conservatively and with healthy circumspection.' For example, the captive breeding goal of minimizing mean kinship (Ballou & Lacy 1995) results in very low levels of inbreeding and/or only a few levels of inbreeding, and, as a result, quite low statistical power to detect inbreeding depression (Kalinowski & Hedrick 1999). Subsequently, however, Fredrickson & Hedrick (2002) found that historic wild wolves had larger body sizes than captive McBride lineage wolves with little or no inbreeding, and that within captive McBride lineage wolves, an increase in inbreeding further reduced body size.

Recently, Fredrickson *et al.* (2007) have examined the effects of inbreeding on litter size, probability of birth, and juvenile survival in the captive Mexican wolf population. The effects of litter size and probability of birth are combined in Fig. 2 as the mean number of pups for wolves in the McBride lineage with low and high levels of inbreeding and for cross-lineage wolves. There is a statistically non-significant decline between the McBride wolves with low and high inbreeding levels, suggesting little or no inbreeding depression.

**Table 2** The nine packs of the reintroduced Mexican wolf population as of late 2006, ranked by the inbreeding coefficient of their progeny, with the inbreeding coefficient ( $f$ ) and proportion of ancestry from the McBride (M), Ghost Ranch (G), and Aragón (A) lineages for the alpha male, alpha female, and progeny from the alpha pair

Pack	Alpha male				Alpha female				Progeny			
	$f$	M	G	A	$f$	M	G	A	$f$	M	G	A
Hawk's Nest	0.281	1.0	0.0	0.0	0.25	1.0	0.0	0.0	0.348	1.0	0.0	0.0
Luna	0.25	1.0	0.0	0.0	0.25	1.0	0.0	0.0	0.289	1.0	0.0	0.0
San Mateo	0.281	1.0	0.0	0.0	0.289	1.0	0.0	0.0	0.279	1.0	0.0	0.0
Rim	0.123	0.75	0.25	0.0	0.281	1.0	0.0	0.0	0.202	0.88	0.12	0.0
Saddle	0.133	0.62	0.12	0.25	0.289	1.0	0.0	0.0	0.154	0.81	0.06	0.12
Meridian	0.059	0.5	0.25	0.25	0.059*	0.5	0.25	0.25	0.136	0.5	0.25	0.25
Middle Fork	0.082	0.62	0.25	0.12	0.125	0.75	0.0	0.25	0.135	0.68	0.12	0.18
Bluestem	0.25*	1.0	0.0	0.0	0.0	0.5	0.5	0.0	0.123	0.75	0.25	0.0
Aspen	0.0	0.5	0.5	0.0	0.125	0.75	0.0	0.25	0.082	0.62	0.25	0.12
Mean	0.162	0.778	0.153	0.069	0.160	0.833	0.111	0.056	0.194	0.806	0.132	0.062

\*Deceased.

On the other hand, the cross-lineage wolves had a significantly higher number of pups than the contemporaneous high inbreeding group. This recovery in fitness in crosses between lineages indicates genetic rescue (Tallmon *et al.* 2004) of the captive Mexican wolf population. This pattern can be explained by assuming that some detrimental variants had reached high levels in the McBride lineage so that inbreeding did not result in a decrease in number of pups. When the McBride wolves were crossed to the other lineages, these detrimental variants were covered up by dominant normal variants from the other lineages and resulted in an overall increase in the number of pups. However, some inbreeding from McBride ancestry has recently occurred in the cross-lineage wolves and resulted in a decline in fitness, or inbreeding depression (Fredrickson *et al.* 2007).

#### Reintroduced population

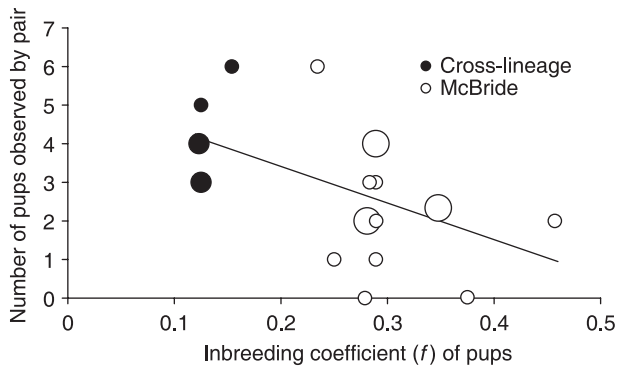
The reintroduced population of Mexican wolves was initiated in 1998 with wolves having only the original McBride lineage ancestry. Starting in 2000, wolves with ancestry from more than one lineage have been released. As of late 2006, there were about 40–50 wolves in the reintroduced population, a number that has not changed, or declined, for the past several years. The ancestry of the alpha wolves in nine packs was known (one other pack has been recently identified but the ancestry of the alpha wolves is not yet known).

Table 2 gives for these nine packs the inbreeding coefficient of the alpha wolves and their progeny and the proportion of ancestry from the McBride, Ghost Ranch, and Aragón lineages. First, notice that there are three packs (Hawk's Nest, Luna, and San Mateo) in which both parents are entirely descended from the McBride lineage and are highly inbred. Progeny from the Hawk's Nest pack have

the extremely high inbreeding coefficient of 0.348. On the other hand, there are four packs (Saddle, Meridian, Middle Fork and Aspen) in which there is ancestry from all three lineages. Progeny produced from these packs have much lower inbreeding coefficients, ranging from 0.082 to 0.154. Unfortunately, the alpha female from the Meridian pack, the only alpha female with ancestry from all three lineages, was killed in 2006.

Second, the average proportions of ancestry from progeny from the McBride, Ghost Ranch, and Aragón lineages over all packs are 0.806, 0.132, and 0.062, respectively. In other words, as given in the recommendations for combining the lineages (Hedrick *et al.* 1997), about 80% of the ancestry is from the original McBride. However, there is about twice as much ancestry from the Ghost Ranch lineage as from the Aragón lineage. An important goal is to have the ancestry from all the lineages spread throughout a number of animals in the populations. At this point, much of the ancestry from the Ghost Ranch and Aragón lineages resides in only a few individuals so that the population is quite vulnerable to loss of this ancestry if these individuals are lost and/or do not contribute to the population. Finally, merging of the three lineages in the reintroduced population is much easier when the numbers are small than when the numbers are large. This occurs simply because the reintroduced population was initiated with only McBride lineage wolves and to reach the ancestry goals for Ghost Ranch and Aragón lineages requires a larger number of wolves from the captive population as the population grows.

It is more difficult to obtain data on reproduction in wild wolves than in captive wolves because the first measurement of reproduction is when the pups emerge from the den at around 10 weeks of age. The number of pups observed at this time is the result of a combination of the probability of birth, litter size, and survival from birth



**Fig. 3** The maximum number of progeny observed in litters in the reintroduced population as a function of the inbreeding coefficient ( $f$ ) of the progeny. Open and closed circles indicate McBride and cross-lineage wolves and the three circle sizes indicate one, two, or three litters (after Fredrickson *et al.* 2007).

to emergence from the den. Figure 3 gives the data for reproduction in the reintroduced population, as a function of the inbreeding coefficient of the progeny. The cross-lineage wolves (indicated by closed circles) have a lower inbreeding coefficient and a higher number of pups than the highly inbred McBride wolves. In other words, as in the captive population, there appears to be genetic rescue for reproduction in the reintroduced population. This is also consistent with the observation that the mean litter size for wild-conceived and wild-born pups during the first five years of the reintroduction program was about  $1/3-1/2$  that observed in other grey wolf populations (IFT 2005).

Although these genetic considerations are important in the recovery of the reintroduced Mexican wolf, management policies and actions have had quite detrimental effects on the reintroduced population (Povilitis *et al.* 2006). First, the reintroduced population is limited in range and animals leaving this recovery area are generally caught or killed. Second, introduction of captive wolves with no previous wild experience is limited to a small area in Arizona and not permitted in New Mexico, which contains some of the best wolf habitat. The cumulative effects of wolf removals due to boundary issues and livestock depredations caused the overall removal/mortality rate (64%) to exceed that predicted (47%) for the reintroduced population in the first five years (IFT 2005).

Further, since 2003 management of the reintroduced population has been controlled by an interagency committee headed by the Arizona Game and Fish Department, an agency that initially opposed the reintroduction of Mexican wolves. This committee appears to be strongly influenced by political considerations, mainly in response to the livestock industry, and acts independently of the Mexican Wolf Recovery Team (PWH is a member of this team, which has not met since 2004). In recent years, death (mainly due to human causes) and removal rates due to

management actions in the wild population approved by this committee have been extremely high (AMOC 2005; Povilitis *et al.* 2006). For recruitment to compensate for these losses, the recruitment rate also needs to be quite high. Because there have been few new introductions recently (only one new pair with two pups was introduced in 2006, the alpha female and one pup have since died, and no new introductions are planned for 2007) in combination with the increased impact from genetic factors in McBride wolves on recruitment as we have shown, persistence of the reintroduced population is in question. Capra (2006) has suggested that the policies of this committee are in keeping with the 'slow death' approach the present political administration appears to be advocating in conservation.

## Red wolf

### *Captive population*

The USFWS initiated a captive breeding program for red wolves to prevent extinction of the species by capturing over 400 wild canids from the remaining red wolf distribution beginning in 1973 (Phillips *et al.* 2003). Because of the large number of coyotes and red wolf-coyote hybrids in the area of the last wild red wolves, only 43 of these animals were initially believed to be red wolves. Ultimately only 14 of these animals became the founders of the captive population (Phillips *et al.* 2003) and questions have been raised about the purity and genetic uniqueness of these individuals (e.g. Roy *et al.* 1994). Genetic data have been collected from the 14 founders (Miller *et al.* 2003) and analyses to assess the ancestry of the founders and their relationship to other canids are ongoing (L. Waits, personal communication).

The red wolf has also been managed under a SSP (Waddell 2006). As of 2006, there are approximately 200 animals in captivity in facilities around the United States, the mean inbreeding coefficient is 0.063, and there is ancestry from 12 of the initial 14 founders. Management efforts have somewhat equalized the ancestral contributions from the 12 founders to approach 1/12 each but two founders each still have about 15% of the ancestry and two others each have about 2% of the ancestry. Kalinowski *et al.* (1999) also examined survival and litter size in the captive red wolf population and found no significant effects of inbreeding although there was low statistical power (Kalinowski & Hedrick 1999).

### *Reintroduced population*

The first red wolves were reintroduced into northeastern North Carolina in 1987 into an area believed to be uninhabited by coyotes (many details of this reintroduction are given by Phillips *et al.* 2003). However, by the early 1990s,

coyotes began to colonize the reintroduction area and pairings between red wolves and coyotes were observed (Phillips *et al.* 2003). As a result, introgression of coyote ancestry into the reintroduced population came to be considered the greatest biological threat (Kelly *et al.* 1999; Allendorf *et al.* 2001; Miller *et al.* 2003).

Management goals were developed to identify and then either remove or sterilize animals within the reintroduction area that appeared to have coyote ancestry. A theoretical examination of the dynamics of coyote hybridization demonstrated that without such management the reintroduced population would be overwhelmed by coyote introgression, but with management and/or with positive-assortative mating between red wolves and strong territorial interactions, the reintroduced population could maintain its red wolf ancestry (Fredrickson & Hedrick 2006). A recent genetic study (L. Waits, personal communication) of specimens from the reintroduction area has identified the hybridization events over the history of the reintroduced population. Overall, it appears that management actions have resulted in low overall hybridization and introgression of coyote ancestry into the reintroduced population. The number of wolves in the reintroduced population reached about 100 several years ago and does not appear to have increased recently. Inbreeding and inbreeding depression have not been examined in the reintroduced population of red wolves.

## Conclusions

The programs to establish captive populations of Mexican and red wolves and to use these animals to subsequently establish reintroduced populations have had mixed success. The captive populations have been well managed and have only slowly accumulated inbreeding and lost genetic variation. However, the Mexican wolf captive population was started from only three founders and, as a result, was subsequently expanded to include two other lineages with two founders each to provide more genetic variation and reduce problems with inbreeding. Progress to combine these lineages has gone well in the captive population and examination of reproductive and survival data show evidence of increased values, or genetic rescue from this effort. In the reintroduced population, the Aragón lineage is somewhat underrepresented but there also appears to be an increase in reproduction in cross-lineage wolves.

However, USFWS self-imposed rules greatly limit the range of the reintroduced Mexican wolf population and only allow reintroduction into a limited area. Also because of management decisions, there have been few recent releases of captive wolves and many removals of wild wolves. The reintroduced population of Mexican wolves has been severely impacted by these actions and has not

increased in the past few years. If more cross-lineage wolves were released into the reintroduced population to increase reproduction and management were more favourable for wolf population growth, the numbers in the reintroduced population could increase substantially thereby increasing the probability of long-term persistence.

The reintroduced red wolf population reached a crisis in the late 1990s when a large number of coyote-red wolf litters were observed. The intensive management subsequently instituted appears to have identified and eliminated coyote ancestry from the population. On the other hand, at this point there has not been an effort to examine inbreeding depression in the reintroduced population and to evaluate in detail the founder representation and genetic constitution of this population (PWH is a former member of the Red Wolf Recovery Team and strongly advocated these actions without success).

In addition, both the reintroduced Mexican and red populations are well below the minimum census numbers advocated for long-term recovery. A majority of the Mexican Wolf Recovery Team members recommended a minimum census number of 250 (or an effective population size of 100) and population viability analysis carried out for the red wolf recommended a census number of 220 (Phillips *et al.* 2003). Further, for both taxa, three independent reintroduced populations of these sizes have been recommended for recovery and long-term persistence. At present, there does not appear to be, for either the Mexican or red wolves, an effort to either increase the census number or to establish more than one reintroduced population for each taxa. As a result, these recovery programs, which have overcome a number of obstacles and achieved reasonable short-term success, may be faced with further difficult times in the future. A common thread obvious from both of these recovery efforts is the importance of genetic management and the consequent need for close collaboration between agency managers and academics with conservation genetic expertise. Optimistically, the recovery efforts for these two species can be used as a model of what to do, and what not to do, in the conservation genetics of other highly managed, endangered species.

USFWS recently estimated there was a minimum of 59 Mexican wolves present in the reintroduced population at the end of 2006. During the first four months of 2007, there were significant changes in the population, including the replacement of two alpha males and the deaths of two other alpha males. In addition, two new packs were discovered, a permanent removal order was issued for the Saddle pack in response to cattle predation, and a pair of previously wild wolves were translocated into New Mexico. Given these changes, the proportion of McBride lineage ancestry in the progeny is expected to increase to 0.838, the Ghost Ranch ancestry to decrease to 0.094, and Aragón ancestry to remain about the same at 0.069.

## Acknowledgements

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P.W. Hedrick and R.J. Fredrickson are both interested in evolution, genetics and ecology as they relate to conservation.

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