

Genetics of Mexican wolves: assessment of possible hybridization with other canids

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Abstract

This study assessed whether living Mexican wolves (*Canis lupus baileyi*) are hybrids resulting from breeding of native wolves and domestic dogs of Native American origin. Previous genetic studies of Mexican wolves had concluded that hybridization with dogs has been negligible to nonexistent. However, those studies compared Mexican wolves and European dog breeds rather than dogs of Native American origin (i.e. brought by native people who crossed the Bering Land Bridge approximately 12,000 - 14,000 years ago). In our analysis we combined three data sets of 172,000 single nucleotide polymorphisms per data set (SNP, Fitak 2014; Cronin et al. 2015; and Shannon et al. 2015). Our results were consistent with previous studies: living Mexican wolves are not derived from hybridization with Native American dogs. The results also did not indicate recent hybridization between Mexican wolves and coyotes. However, one wolf-dog hybrid was detected in wolves from Idaho. Our study used captive-reared Mexican wolves, therefore future analyses of wild-born wolves and dogs living in the same areas are needed to determine if hybridization is occurring in the wild population of Mexican wolves in Mexico, New Mexico and Arizona.

Introduction

The objective of this study was to test the hypothesis that living Mexican wolves are derived from interbreeding of native wolves and domestic dogs of Native American origin. Recent studies on the genetics of wolves and dogs have shown that dogs were derived from domesticated wolves in Eurasia approximately 15,000 to 32,000 years ago (Savolainen et al. 2002; Ardalan et al. 2011; Brown et al. 2011; Ding et al. 2012; Pang et al. 2009; Skoglund et al. 2011; Thalmann et al. 2013; Shannon et al. 2015; Wang et al. 2016; Fan et al. 2016). Dogs spread across Eurasia and Africa, dogs also accompanied human colonization of North America over the Bering Land Bridge and have been found in numerous archaeological sites in North and South America (Colton 1970; Brothwell et al. 1979; Morey and Wiant 1992; Lupo et al. 1994; Leonard et al. 2002; Goebel et al.

2008; Vellanoweth et al. 2008; Castroviejo-Fisher et al. 2011; Aush et al. 2013). The archaeology and anthropology literature documents that Native American dogs also hybridized with wolves, in the wild and in captivity by Native Americans, although the frequency of such hybridization is unknown (Audubon and Bachman 1851; Elder and Hayden 1977; Walker and Frison 1982). One culture in Mexico even produced wolf-dog hybrids for ceremonial purposes (Valadez et al. 2002). Therefore, to fully test whether the captive Mexican wolf population has evidence of hybridization with dogs, genetic comparisons must include descendants of the lineage of dogs derived from those brought to North America by native people, rather than only European dog breeds (van Asch et al. 2013).

Past genetic studies compared Mexican wolves and European dog breeds (i.e. Garcia-Moreno et al. 2003; Fitak 2014; Cronin et al. 2015) and did not include Native American dogs. This is a significant data gap because domestic dogs of Native Americans had a longer period of possible contact with wolves (beginning 12,000 to 14,000 years ago), and therefore, may have been more likely to hybridize with Mexican wolves than dogs of European origin (beginning less than 500 years ago with European colonization).

Regardless of the potential source, hybridization between domestic dogs and wolves is a wildlife management issue in North America and Eurasia because of the potential to dilute the native wolf gene pool, introduce undesirable wolf-dog hybrid behaviors, and compromise wild population recovery programs (Vila et al. 2003; Fabrini et al. 2014; Lescureux et al. 2014; Lorenzini et al. 2014; see Heffelfinger et al. 2017 for a comprehensive review of Mexican wolf population history and taxonomy).

However, an unexpected consequence of hybridization with dogs can be the introduction of genes that can enhance wolf survival, through natural selection. For example, black coat color was likely introduced into wolves through hybridization with Pre-Columbian Native American dogs (Anderson et al. 2009, Fan et al. 2016). The gene for black coats has spread across North American wolves because it is linked to immune function that results in greater longevity.

A second hybridization concern involves wolves and coyotes. Wolves and coyotes share a recent common ancestor during the Pleistocene (Ice Ages) in North America and their subsequent occupation of the same ranges may result in some level of hybridization. Indeed, evidence of historic and recent hybridization comes from mitochondrial DNA (mtDNA) sequences, y-chromosome, SNPs and whole genome sequences (WGS, Leonard et al. 2005; Hailer and Leonard 2008; von Holdt et al. 2016). However, land use changes following European colonization of North America have favored the spread of coyotes while wolf populations have declined, resulting in substantial levels of hybridization between these two species in some areas (e.g. Eastern North America.) This same process also resulted in hybridization with domestic dogs, contributing to three-species hybrids in some populations (von Holdt et al. 2011; 2016).

Reporting on the proportion of coyote ancestry in extant North American wolves (i.e. from both ancient and recent hybridization), from their analysis of WGS data, von Holdt

et al. (2016) found that,

"all North American wolves and coyotes have significant amounts of coyote ancestry (Table S1). In addition, we detect a strong geographic cline in the proportion of coyote ancestry across North American canids: Alaskan and Yellowstone wolves have 8 to 8.5% coyote ancestry, Great Lakes wolves have 21.7 to 23.9% coyote ancestry, Algonquin wolves have at least 32.5 to 35.5% coyote ancestry, and Quebec sequences have more than 50% coyote ancestry (Fig. 3)."

The Mexican wolf in their study had a coyote ancestry of approximately 11% (see Figure 3 in von Holdt et al. 2016). The significance of these results, as well as those of previous authors, is that wolf-coyote hybridization occurs naturally, and the process can be accelerated in human-dominated landscapes that favor coyotes. Similarly, while wolf-dog hybridization occurs, albeit at low frequency, it too can be accelerated in human-dominated landscapes where domestic dogs greatly outnumber wolves (Leonard et al. 2005; Muñoz-Fuentes et al. 2010; Fabrini et al. 2014; Lorenzini et al. 2014). Two cases of Mexican wolf females breeding with domestic dogs have been detected and potential hybrids of unknown origin observed (USFWS 2005, 2012; Cart 2011). Similarly, gray wolves recolonizing Vancouver Island, Canada have been documented as having a dog mtDNA that could only have come from hybridization (Muñoz-Fuentes et al. 2010). Therefore, this issue and the results reported here raise an important question for the future Mexican wolf population: is recovery in the wild possible without ongoing intensive monitoring and management to limit hybridization, perhaps in perpetuity (i.e. Gese and Terletzky 2015; Gese et al. 2015)?

Methods

We obtained three SNP data sets genotyped on Illumina 172,000 (172k) Canine HD arrays: Fitak (2014); Cronin et al. (2015); and Shannon et al. (2015). The data sets utilized by Cronin et al. (2014) and Shannon et al. (2015) were publicly available via the Dryad database, while the data set produced by Fitak (2014) was kindly provided by the University of Arizona. After initial merging and preliminary analysis we discovered compatibility issues between the data sets (i.e., triallelic loci and undocumented sequence "flips"). Compounding these issues, we discovered that all three studies had inadequately documented their methods, including: genome assembly used, allele coding scheme, manifest file, and steps taken during data manipulations to make the data compatible with other data sets.

After receiving clarifications from authors, the data sets were successfully merged. A subset of the same animals shared among the data sets had genotypes that matched, validating the compatibility among data sets and allowing analyses to proceed (Reed et al. 2015). Similar issues to those described above were reported by Zuvich et al. (2011) for human SNP data being merged from different genotyping centers after being released using different file formats.

The merged data set included: Mexican wolves, wolves from interior Alaska, southeastern Alaska, British Columbia, and the introduced Northern Rocky Mountain

population in the Yellowstone National Park area (Idaho, Montana, and Wyoming); arctic dogs (Alaskan village, Alaskan malamute, Siberian husky, samoyed, Greenland sledge); American village dogs (Mexican village dogs and Carolina dogs); east Asian dogs (akita, chow-chow, shar-pei, shiba inu), and European dogs (Labrador retrievers, Irish wolfhounds, cocker spaniels, beagles, border collies, English bulldogs, and poodles).

The three genotype data sets were merged in the PLINK1.9 program and SNP loci with genotyping rates <90% or with MAF <1%, and samples with >5% missing data were deleted. In addition, Mexican wolves related greater than 25% (i.e., close relatives) were removed (--rel-cutoff) and then Hardy-Wienberg equilibrium pruning was done using a .0001 mid p-value as the cutoff. After this data quality control, a total 96,947 SNPs and 523 samples remained for analysis (designated the HWE dataset). We prepared a second data set, pruning the Mexican wolf population subset further for linkage disequilibrium using the independent pairwise command in PLINK with a window size of 50kb, step size of 10kb, pairwise r^2 threshold of 0.5, which produced a final data set of 9,278 SNPs (HWE+LD dataset).

We conducted a PCA analysis and calculated population pairwise F_{ST} in the program, SVS (Golden Helix). Population admixture testing was completed using fastSTRUCTURE, ADMIXTURE, and LEA. Analysis runs for both the simple and logistic prior options in fastSTRUCTURE were used. The values of K ranged from 1-15 for ADMIXTURE and LEA and fastSTRUCTURE using a simple prior for both datasets, and 1-9 for fastSTRUCTURE using the logistic prior for both datasets. The optimal K value range was settled to be between k=5-12 based both on prior knowledge of the populations used in this study, but as well based on the chooseK.py program provided with the fastSTRUCTURE package.

Additionally, error checking was done in ADMIXTURE by using 10 fold cross validation (--cv=10) and in LEA using 10 repetitions at each K of the analysis and selecting the model with minimal cross-entropy from those 10.

Results and discussion

Results obtained from F_{ST} PCA, LEA, STRUCTURE, and ADMIXTURE were broadly consistent with previous studies (Table 1, Figures 1 and 2). The captive Mexican wolf samples were divergent from other wolves as well as coyotes and dogs of European, East Asian, and North American descent (von Holdt et al. 2010, 2016; Cronin et al. 2015; Fan et al. 2016). With the exception of one recent, but previously undetected, apparent wolf-dog hybrid in Idaho (Figure 1, data from Cronin et al. 2015), the genetic signal of admixture from hybridization with North American and East Asian dogs was minimal, and similar to that described by Fitak (2014). Consequently, our results do not support the hypothesis that the living captive population of Mexican wolves was derived from individuals of appreciable mixed wolf-dog (or coyote-dog) ancestry.

As the sample of Mexican wolves was drawn from the captive population (and released captives), our results do not extend to the wild population, specifically animals conceived and born in the wild. Previous research and monitoring of the Mexican wolf population indicate that hybridization with dogs and coyotes may remain an issue. Ongoing monitoring will be necessary to identify hybridization in the wild Mexican wolf population and the effort required for that sampling can be expected to increase proportionally if their numbers increase.

Our results, and those done previously, show the Mexican wolf population as divergent from other North American wolves. While this has been frequently attributed to Mexican wolves being part of a unique, ancient lineage of North American wolves (Wayne et al. 1992; Vilá et al. 1999; von Holdt et al. 2011; Fan et al. 2016), it is primarily due to simple differentiation of the gene pools in a small, isolated population (i.e., a population bottleneck, genetic drift and inbreeding). This can be stated as an alternative hypothesis: the observed divergence of Mexican wolves from other North American wolf populations could be the result of our inability to sample the historic intervening populations between the Mexican wolf and northern gray wolves (due to their extirpation in the first half of the 20th century), and the strong genetic drift from the population bottleneck and lineage selection in captivity. As wolves were completely exterminated throughout the rest of the western USA, there is no way of knowing the full extent of genetic variation that once existed. However, Leonard et al.'s (2005) mtDNA analyses of historic specimens gave a glimpse into the high levels of genetic variation that once existed in the extirpated populations.

Additionally, the remnant Mexican wolf population was subject to, and has the genetic signal of, one of the most severe, recent genetic bottlenecks in conservation history (Pilot et al. 2013). It was founded from just seven remaining individuals separated into three lineages, subsequently inbred in captivity, and then lineages cross-bred to attempt a genetic rescue (Hedrick et al. 1997, 2001; Hedrick and Kalinowski 2000; Hedrick and Fredrickson 2001; Hedrick and Fredrickson 2008). From SNP and whole genome sequence data, it has the least heterozygosity of any wolf population in North America, long runs of homozygosity, high linkage disequilibrium, and 18 of 38 autosomes were reported as virtually invariant (von Holdt et al. 2011; Fan et al. 2016). Because genetic drift is one of the primary drivers of population genetic divergence, it is reasonable to consider that genetic drift could have been a contributing factor to the current, observed genetic divergence of Mexican wolves compared to other wolves.

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Table __. Population pairwise F_{ST} values. Above diagonal from HWE pruned data (96,947 SNPs), below diagonal from HWE + LD pruned data (9,278 SNPs).

Population	Coyote	Dog-Arctic	Dog-EAsia	Dog-Euro	Dog-NA	Wolf-BC	Wolf-Yel	Wolf-IntAK	Wolf-NM	Wolf-SEAK
Coyote	-	0.310	0.307	0.302	0.335	0.261	0.255	0.279	0.381	0.342
Dog-Arctic	0.317	-	0.093	0.102	0.073	0.237	0.242	0.249	0.344	0.316
Dog-EAsia	0.310	0.096	-	0.120	0.093	0.229	0.234	0.240	0.346	0.314
Dog-Euro	0.305	0.103	0.118	-	0.019	0.240	0.246	0.251	0.331	0.314
Dog-NA	0.325	0.071	0.090	0.019	-	0.246	0.254	0.261	0.372	0.343
Wolf-BC	0.260	0.211	0.202	0.209	0.197	-	0.023	0.053	0.257	0.127
Wolf-Yel	0.254	0.211	0.202	0.211	0.199	0.024	-	0.056	0.253	0.147
Wolf-IntAK	0.276	0.222	0.214	0.223	0.212	0.053	0.057	-	0.272	0.165
Wolf-NM	0.328	0.259	0.260	0.245	0.239	0.227	0.227	0.239	-	0.324
Wolf-SEAK	0.338	0.288	0.283	0.282	0.287	0.125	0.144	0.165	0.297	-

Figure 1. Graph of first 2 coordinate axes of principal components analysis (PCA) of coyote, wolf, and dog individual genetic distances for 96,947 (SNP) loci. The potential wolf-dog hybrid individual was from Idaho.

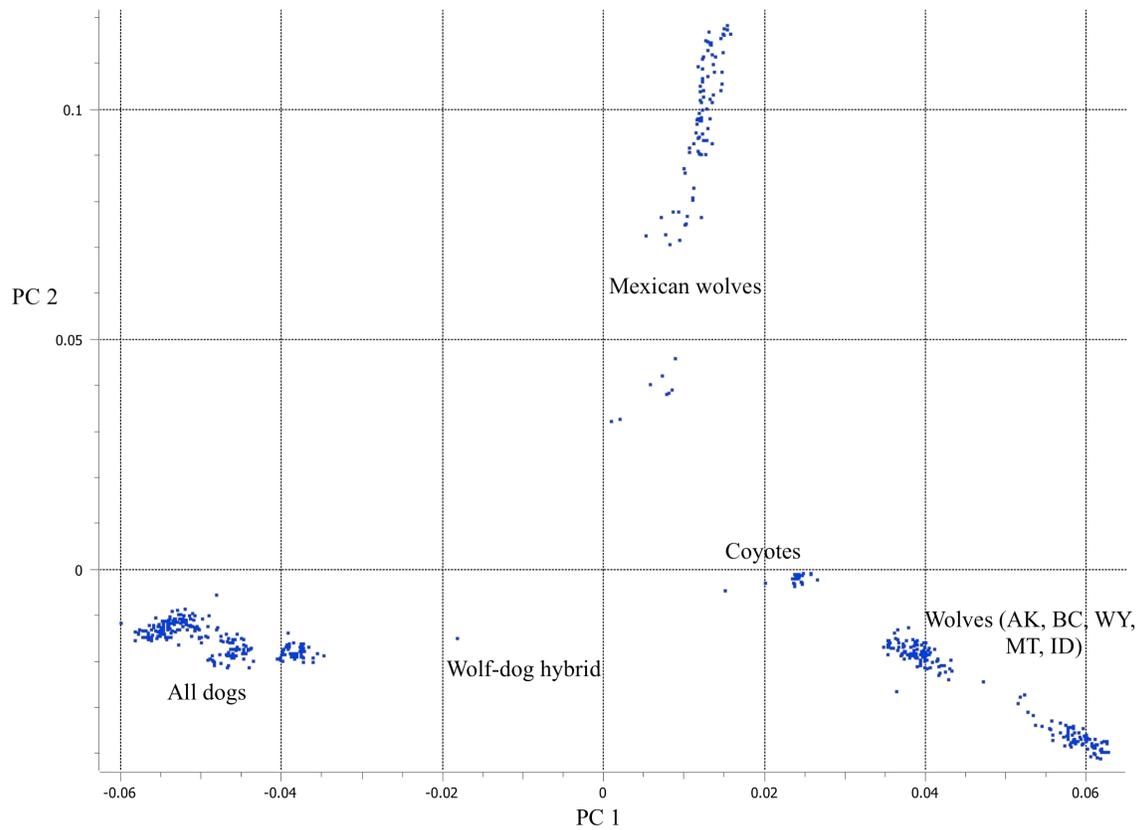


Figure 2. Histogram of ADMIXTURE analysis for $K = 8$, using HWE + LD pruned data (9,278 SNPs) for 523 wolves, coyotes, and dogs. Similar results were obtained using fastSTRUCTURE and LEA for both data sets.

