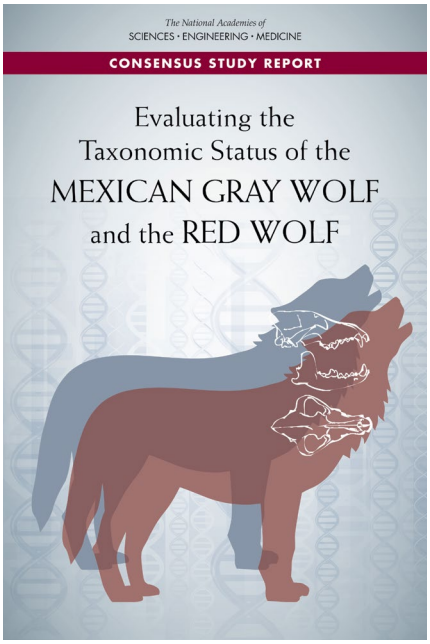
Consensus Study Report
HIGHLIGHTS
March 2019

Evaluating the Taxonomic Status of the Mexican Gray Wolf and the Red Wolf



Taxonomy—the scientific study of biological classification—enables scientists to name and group living organisms. However, because species are dynamic and not fixed entities, taxonomic designations are often debated. At any given time, different populations can be in different stages in the process of species formation or dissolution. In many cases, hybridization (i.e., mating with other species and producing offspring) may be introducing genes from one species to another.

In 2018, Congress directed the U.S. Fish and Wildlife Service (FWS) to obtain an independent assessment of the taxonomic status of the red wolf and the Mexican gray wolf. Currently, FWS considers the red wolf a valid taxonomic species and the Mexican gray wolf a valid taxonomic subspecies. Both wolves are listed as endangered under the U.S. Endangered Species Act. This report assesses the taxonomic status of the Mexican gray wolf and the red wolf based on an evaluation of multiple types of data, including morphological and paleontological evidence, evidence of genetic and genomic distinctiveness, and ecological and behavioral evidence.

For every organism, from the tallest tree to the noisiest cricket to the tiniest microorganism, there is a name. Naming living things is a hallmark of human communication: they allow people to explore, classify, and interpret the world around them. Not all communities name organisms the same way, however. For example, a puma, a mountain lion, and a cougar are common names for the same animal. Moreover, names carry with them an implicit grouping of objects. Recognizing the implication of names and the importance of standardized naming conventions, scientists strive to develop clear rules for naming and grouping living organisms.

Taxonomy is the scientific study of biological classification. Modern taxonomy uses the evolutionary relationships among lineages to draw this classification. Members of a species, the fundamental unit of taxonomy and evolution, share a common evolutionary history and a common evolutionary path to the future. Yet, it can be difficult to determine whether the evolutionary history or future of a population is sufficiently distinct to designate it as a unique species. As a result, the precise taxonomic status of an organism may be highly debated. This is the current case with the Mexican gray wolf (*Canis lupus baileyi*) and the red wolf (*Canis rufus*).

GUIDING PRINCIPLES

Determining the taxonomic status of the Mexican gray wolf and the red wolf requires an understanding of the contemporary meanings of species and subspecies. While there are many modern species concepts, all share the goal of identifying groups of organisms whose mutual reproductive compatibility sustains genetic continuity across time and space.

Increasingly, genomic data reveal that gene flow among taxonomic groups through hybridization[1] is a common feature of the evolutionary history of many widely accepted species, including wolves. The complete genetic separation and absence of admixture[2] is no longer a strict criterion for determining taxonomic status. Thus, a variety of approaches are needed for assessing whether a given group of organisms constitutes a distinct, independently evolving lineage. Combining multiple data types and tools, such as morphology, behavioral traits and ecological roles, and genetic and genomic data, can provide a

1 The mating and production of offspring from different species.
2 The formation of novel genetic combinations through the hybridization of genetically distinct groups.

more complete picture of the taxonomy and evolutionary history of species and subspecies, generally, and of wolves specifically.

USING GENETICS AND GENOMICS TO DISCERN TAXONOMY

Ecological, morphological (e.g., data on animal size), and behavioral data can all be of use in identifying lineages. But challenges can arise when data of different types suggest different conclusions. Modern genetic data and analytical tools can help to address these challenges. Key insights on population history can emerge through an analysis of genomic data from ancient samples collected using paleontological or archaeological approaches combined with genomic data from modern populations that inhabit the same locations. Assembling data can be challenging, however. For North American canids, for example, while multiple whole-genome sequences are available from a large set of modern individuals, data from older samples are comparatively sparse.

THE TAXONOMIC STATUS OF THE MEXICAN GRAY WOLF

Gray wolves often disperse over long distances across a variety of environments. This behavior has been used to argue that the subspecies of North American gray wolves generally, and the subspecific status of the Mexican gray wolf in particular, cannot be justified biologically. The designation of the Mexican gray wolf as a subspecies has also been questioned on other grounds, specifically whether they are sufficiently distinct, morphologically and genetically, to justify that status. In addition, some scientists have suggested that the extant Mexican gray wolf population, derived from individuals from three captive lineages, includes ancestry from dogs or coyotes due to previous admixture.

Whether the Mexican gray wolf is a valid subspecies hinges on the strength of available evidence to answer two questions:

1. Is there evidence for distinctiveness of Mexican gray wolves from other North American *Canis* populations?
2. Is there evidence for genetic continuity between the historical Mexican gray wolf lineage and the present managed population?

Distinctiveness of Mexican Gray Wolves from Other North American *Canis* Populations

From its discovery, the Mexican gray wolf has been considered behaviorally, ecologically, and physically distinct. For example, the Mexican gray wolf represents a smaller form of the gray wolf and inhabits a more arid ecosystem than the gray wolf. Its morphology and coloration also distinguish the Mexican gray wolf from other North American wolves. The genetic evidence published to date also overwhelmingly supports the Mexican gray wolf being a subspecies of the gray wolf. According to a large number of studies (using mitochondrial DNA sequencing and microsatellite loci as well as studies using next-generation sequencing and genomic technologies), this subspecies has been determined to be the most genetically divergent wolf in North America. There is no evidence that Mexican gray wolves are derived from a hybridization with dogs and no evidence for any recent hybridization with coyotes.

Continuity Between the Historical Mexican Gray Wolf Lineage and the Present Managed Populations

While differences in allele frequencies and DNA sequences alone do not demonstrate the distinctiveness of a lineage, the analysis of ancient DNA reinforces the conclusion that the historical population of Mexican gray wolf represents a distinct evolutionary lineage of gray wolf. Studies that have used ancient DNA taken from historical museum specimens in combination with modern DNA samples have also determined that the Mexican gray wolf lineage likely resulted from one of the earliest waves of colonization of *Canis lupus* into the New World. Additionally, the known history of the extant Mexican gray wolves suggests that there is continuity between them and the historical lineage.

Synthesis of Findings and Conclusion

Mexican gray wolves are distinct from other North American gray wolves morphologically, paleontologically, genetically, genomically, behaviorally, and ecologically. Thus, the Mexican gray wolf is a valid taxonomic subspecies of the gray wolf, *Canis lupus*, with its current classification of *Canis lupus baileyi*.

Mexican gray wolf

THE TAXONOMIC STATUS OF THE RED WOLF

During the 20th century, red wolf populations were nearly eradicated. A few remaining specimens with red wolf morphology were captured and used to establish a breeding program. The breeding program descendants were reintroduced in North Carolina and are now a managed population in the wild. Ever since, there has been substantial controversy regarding the species status of the red wolf. This is because the individuals that were used to inaugurate the breeding program were captured from a region where there had already been substantial admixture between eastward-expanding coyotes and the local gray wolves or red wolves.

Whether the red wolf is a valid species hinges on the strength of the evidence to answer three questions:

1. Is there evidence that the historical population of red wolves was a distinct lineage?
2. Is there evidence for distinctiveness of contemporary red wolf populations from gray wolves and coyotes?
3. Is there evidence for continuity between the historical red wolf population and contemporary managed populations?

Distinctiveness of the Historical Population of Red Wolves

The paleontological record of canids in the eastern United States indicates the presence of a canid during the last 10,000 years that was slightly smaller than gray wolves and substantially larger than coyotes. The specimens of this canid show aspects of cranial morphology distinct from both coyotes and gray wolves. The earliest specimen of this canid, found in Florida, is dated at about 10,000 years ago, when coyotes had disappeared from what is now eastern North America. Coyotes returned to this region in the 1900s, long after extant red wolves had been described as a separate species from gray wolves.

Distinctiveness of Contemporary Red Wolf Populations from Gray Wolves and Coyotes

The extant red wolf population carries genetic ancestry divergent from coyotes that dates back 55,000 to 117,000 years ago. The red wolf is also genetically more closely related to coyotes than to western gray wolves. However, it carries some genetic ancestry not found in reference populations of western gray wolves or coyotes. This is reinforced by the genetic analyses of the Galveston Island population of wolves, which shares private alleles with the North Carolina red wolves. The red wolf has coyote-like mitochondrial DNA, which indicates some degree of past historical admixture. However, the genetic evidence is not compatible with the suggestion that the extant red wolves are products of recent hybridization between gray wolves and coyotes.

Red wolf

The timing of the admixture between red wolves and other canids is still unresolved, but red wolves have divergent genetic ancestry that predates European colonization[3].

Red wolves have a social organization and reproductive behavior that are more similar to those of gray wolves than to coyotes, and when mates are available, red wolves exhibit positive assortative mating.

Continuity Between the Historical Red Wolf Population and Contemporary Managed Populations

Genetic continuity between the managed red wolf population and the historical wolf in the eastern United States cannot be firmly established without genomic data from ancient specimens. However, the patterns of genetic variability are compatible with the hypothesis that the red wolf shares a fraction of its genetic history with a canid distinct from modern reference coyotes and gray wolves.

The social behavior of the restored populations is very similar to that reported for the natural population. For example, the requirement of larger home ranges for wolves compared to coyotes is consistent between the original natural population and the extant managed population in North Carolina. The diet of the red wolves in the restored population also includes a greater consumption of deer than the natural population, but this may be a function of prey availability and body size.

Synthesis of Findings

The four possible taxonomic options for the red wolf are:

1. **It is a distinct species of wolf (*Canis rufus*)**
   Plausible. The available evidence suggests that the most appropriate taxonomic designation for red wolves is as a distinct species that possibly has historical admixture.

3 Evidence suggests that admixture in red wolves took place prior to the 1500s (before significant European colonization of what is now the eastern United States), and so is not the result of human-induced ecological changes.

2. **It is a subspecies of gray wolves**
   Seems inappropriate. Red wolves, historically and presently, show genetic evidence of being more closely related to coyotes than to gray wolves.

3. **It is a subspecies of coyotes**
   Not tenable. There are substantial morphological and behavioral differences between coyotes and red wolves.

4. **It is a group of recently admixed individuals belonging to neither wolves nor coyotes**
   Can be rejected due to the estimates of deep divergent DNA in red wolves; the estimates of an admixture time mostly predating coyotes expansion; and the presence of unique alleles in red wolves that are also found in a population of wolves on Galveston Island but not found with other reference populations.

The time scales of divergence and the amount of introgression (gene transfer through hybridization) since divergence can affect taxonomic considerations. Red wolves have a deep divergence from coyotes, although the extant red wolf seems to trace a large proportion of its genome to relatively recent admixture with coyotes. The genomes of extant red wolves may also represent much of the historical red wolf genome spread into fragments in different individuals.

Genomic DNA from historical red wolf specimens could help clarify the issue regarding continuity between historical and extant red wolves. And, more precise genetic analyses might help determine the exact proportion of the red wolf genome that has been replaced by recent admixture.

Conclusions

1. Available evidence suggests that the historical red wolves constituted a taxonomically valid species.
2. Extant red wolves are distinct from the extant gray wolves and coyotes.
3. Available evidence is compatible with the hypothesis that extant red wolves trace some of their ancestry from the historical red wolves.
4. Although additional genomic evidence from historical specimens could change this assessment, evidence available at present supports species status (*Canis rufus*) for the extant red wolf.

COMMITTEE ON ASSESSING THE TAXONOMIC STATUS OF THE RED WOLF AND THE MEXICAN GRAY WOLF

Joseph Travis (*Chair*), Florida State University; **Fred W. Allendorf,** University of Montana; **Diane K. Boyd,** Montana Department of Fish, Wildlife, and Parks; **Liliana Cortés-Ortiz,** University of Michigan; **Lori S. Eggert,** University of Missouri; **Diane Genereux,** Broad Institute, Massachusetts Institute of Technology, Harvard University; **Michael Lynch (NAS),** Arizona State University; **Jesús E. Maldonado,** Smithsonian Conservation Biology Institute, National Zoological Park; **Rasmus Nielsen,** University of California, Berkeley. Staff from the National Academies of Sciences, Engineering, and Medicine: **Keegan Sawyer** (Study Director), **Camilla Ables** (Senior Program Officer), and **Jenna Briscoe** (Research Assistant).

For More Information . . . This Consensus Study Report Highlights was prepared by the National Academies of Sciences, Engineering, and Medicine based on the Consensus Study Report *Evaluating the Taxonomic Status of the Mexican Gray Wolf and the Red Wolf* (2019). The study was sponsored by the U.S. Fish and Wildlife Service. Any opinions, findings, conclusions, or recommendations expressed in this publication do not necessarily reflect the views of any organization or agency that provided support for the project. Copies of the Consensus Study Report are available from the National Academies Press, (800) 624-6242; http://www.nap.edu or via the Board on Life Sciences web page at http://www.nationalacademies.org/bls.

Division on Earth and Life Studies

The National Academies of
SCIENCES • ENGINEERING • MEDICINE

The nation turns to the National Academies of Sciences, Engineering, and Medicine for independent, objective advice on issues that affect people's lives worldwide.
www.national-academies.org