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

Report Briefing for the U.S. Fish and Wildlife Service

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Board on Life Sciences
Board on Agriculture and Natural Resources
<http://nas-sites.org/dels/studies/wolf-taxonomy-study/>

Committee on Assessing the Taxonomic Status of the Red Wolf and the Mexican Gray Wolf

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The Questions Asked of the Committee

Statement of Task

At the request of the U.S. Fish and Wildlife Service (FWS), the National Academies of Sciences, Engineering, and Medicine will appoint an ad hoc committee to conduct an independent analysis of scientific literature to answer the following two questions:

- 1. Is the red wolf a taxonomically valid species?**
- 2. Is the Mexican gray wolf a taxonomically valid subspecies?**

The committee will summarize the relevant science about the red wolf and Mexican gray wolf, including research on the animals' evolutionary history and genetic diversity. The committee will deliver its findings and conclusions in a brief report divided into two sections, one for the red wolf and one for the Mexican gray wolf.

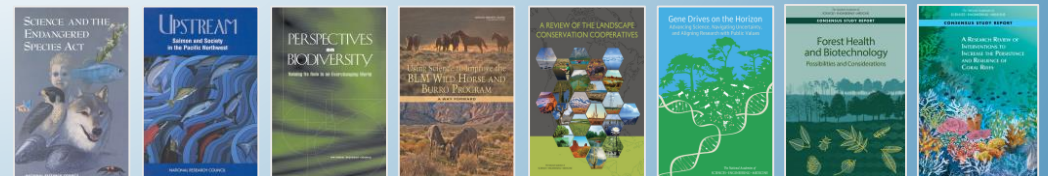
Why ask the National Academies of Sciences, Engineering, and Medicine?

Congressional Mandate

As part of the March 29, 2018, appropriations bills, the U.S. Congress directed the U.S. Fish and Wildlife Service to obtain an independent assessment of the taxonomic validity of the red wolf, *Canis rufus*, and the Mexican gray wolf, *Canis lupus baileyi*.

Mission of the National Academies

- Provide nonpartisan, objective guidance for decision makers on pressing issues.
- Marshal the energy and intellect of the nation's critical thinkers to respond to policy challenges with science, engineering, and medicine at their core.



Outline

- 1. Why is it sometimes challenging to answer questions about taxonomy?**
2. What guiding principles can be used to answer questions about wolf taxonomy?
3. Is the Mexican gray wolf a valid subspecies?
4. Is the red wolf a valid species?
5. Questions & answers

Why is it sometimes challenging to answer questions about taxonomy?

1. **Multiple species and subspecies concepts.**
2. **Life is dynamic.** A species is not a fixed entity – the relationship among the members of the same species is only a snapshot of a moment in time.
3. **Populations are dynamic.** Different populations of the same species can be in different stages in the process of species formation or dissolution.
4. **Hybridization can be part of a species' history.** Hybridization is far more common in the evolutionary history of many species than previously recognized.
5. **Data interpretation.** Two factors that create considerable challenges when interpreting data on genetic distinctions between groups: (a) rapid, recent radiations and, (b) past hybridization and introgression.

A brief taxonomic history of wolves in North America

- **First *Canis*.** Fossil evidence indicates that the ancestor of the genus *Canis* was a jackal-sized animal that lived in North America as early as 40 million years ago (Merriam, 1911; Wang et al. 2008).
- **First wolf.** The earliest undisputed occurrence of a “wolf” in North America was the medium-sized *Canis edwardii*, which appeared about 3 million years ago (Nowak, 1979).
- **Three wolf lineages.** Scientists have recognized three historic North American lineages of wolves *Canis dirus* (dire wolf), *Canis lupus* (gray wolf), and *Canis rufus* (red wolf).

Why is it sometimes challenging to answer questions about taxonomy of **wolves**?

Since the discovery of the dire wolf, the gray wolf, and the red wolf, scientists have been revising their conclusions about how many species are recognized in each lineage and about the relationship among the various populations of wolves (Chambers et al. 2012). **Why?**

1. The proliferation of descendants from *C. edwardii* or an animal like it occurred very rapidly, which makes it difficult to trace those lineages accurately.
2. Some species of wolves have hybridized with other species, which make delineating species challenging (Nowak, 2002).
3. The present-day geographic ranges of wolves have changed dramatically because of predator control and habitat alteration, which makes it difficult to reconstruct their historic distributions (Hinton et al., 2017).

Outline

1. Why is it sometimes challenging to answer questions about taxonomy?
- 2. What guiding principles can be used to answer questions about wolf taxonomy?**
3. Is the Mexican gray wolf a valid subspecies?
4. Is the red wolf a valid species?
5. Questions & Answers

What guiding principles can be used to answer questions about wolf taxonomy?

- 1. Multiple species concepts have common elements in some level of reproductive isolation and phylogenetic continuity**
- 2. Complete genetic separation and absence of admixture is not a strict criterion for determining taxonomic status**
- 3. Combining morphological, genomic, and ecological data can provide a more complete picture of the taxonomy and evolutionary history of species and subspecies.**

Strong support for the validity of a taxonomic designation of a *species* may include the following types of data:

- **Morphological, paleontological, or fossil evidence** that the taxon under consideration is evolving independently or that specimens possess a phenotype that is distinct from other defined species.
- **Evidence of genetic or genomic distinctiveness.** If hybridization with other defined species is also detected, it must be clear that introgression does not substantially affect the discreteness of the taxon under consideration.
- **Ecological or behavioral data** that indicated adaptive differences and reproductive incompatibilities separating the taxon under consideration from other closely related species. Relevant differences may be ecological, behavioral, or physiological.

Strong support for the validity of a taxonomic designation of a ***subspecies*** may include the following types of data:

- **Morphological, paleontological, or fossil evidence** of a *geographically isolated* and historically separate lineage within the species to which it belongs.
- **Genetic or genomic evidence of distinctness** based on data from multiple independently inherited genetic loci, with *no evidence of reproductive isolation* from other populations of the same species in regions of range overlap.
- **Ecological, behavioral, or physiological characters** that provide evidence of adaptive differences between the lineage and other groups belonging to the same species.

Outline

1. Why is it sometimes challenging to answer questions about taxonomy?
2. Are there guiding principles that can be used to answer questions about wolf taxonomy?
- 3. Is the Mexican gray wolf a valid subspecies?**
4. Is the red wolf a valid species?
5. Questions & Answers

Is the Mexican Gray Wolf (*Canis lupus baileyi*) a valid taxonomic subspecies?

Question 1: Is there evidence for distinctiveness of Mexican gray wolves from other north American *Canis* populations?

Question 2: Is there evidence for continuity between the historic Mexican gray wolf lineage and the present managed population?



SOURCE: U.S. Fish and Wildlife Service.



Much-Abbreviated Background

Mexican gray wolves were extirpated from the wild in the United States in the mid-1970s. Then 20 years ago they were reintroduced, amidst much controversy, into a small portion of their former range.

Controversies



- **Determining the historic range.**
- **Disagreement about definition of a subspecies.**
- **Hybridization with other canids.**

Question 1: Is there evidence for distinctiveness of Mexican gray wolves from other North American *Canis* populations?



The Committee's Findings:

Morphological Evidence

- The Mexican gray wolf has, from its discovery, been considered a distinct wolf. Its size, morphology, and coloration pattern distinguish it from other North American wolves.

Genetic Evidence

- The Mexican gray wolf is genetically distinct—it is the most genetically distinct subspecies of gray wolf in North America. There is no evidence that Mexican gray wolf genomes include introgression from domestic dogs and no evidence of recent hybridization with coyotes. Mexican gray wolves have 8 private nuclear alleles and a mtDNA haplotype found in no other wolf.

Behavioral Ecology

- Extant wild Mexican gray wolves behave similarly to other North American gray wolves within the confines of the human-constricted Mexican gray wolf recovery area; their wild behavior prior to their 1970 extirpation in the wild is unknown. The Mexican gray wolf represents a smaller form of the gray wolf, which inhabits more arid ecosystems (Nowak, 1995). At present, Mexican gray wolves are behaviorally and ecologically distinct.

Question 2: Is there evidence for continuity between the historic Mexican gray wolf lineage and the present managed population?



The Committee's Findings:

Morphology and Paleontology

- There is morphological continuity between historic and extant Mexican gray wolf lineages.

Genetics

- The analysis of ancient DNA reinforces the conclusion that the historic population of Mexican gray wolf represents a distinct evolutionary lineage of gray wolf. Furthermore, the extant Mexican gray wolves are direct descendants from the last remaining wild Mexican gray wolves. The known history of the extant Mexican gray wolves suggests that there is continuity between them and the historic lineage.

Behavioral Ecology (reapplied finding from Question 1)

- Extant wild Mexican gray wolves behave similarly to other North American gray wolves within the confines of the human-constricted Mexican gray wolf recovery area; their wild behavior prior to their 1970 extirpation in the wild is unknown. The Mexican gray wolf represents a smaller form of the gray wolf, which inhabits more arid ecosystems (Nowak, 1995) and, as such, is ecologically distinct.



Is the Mexican gray wolf (*Canis lupus baileyi*) a valid taxonomic subspecies? **Yes.**

Synthesis of Findings

Mexican gray wolves are distinct from other North American gray wolves morphologically, paleontologically, genetically, genomically, behaviorally, and ecologically.

Conclusion

The Mexican gray wolf is a valid taxonomic subspecies of the gray wolf, *Canis lupus*, with its current classification of *Canis lupus baileyi*.

Outline

1. Why is it sometimes challenging to answer questions about taxonomy?
2. What guiding principles can be used to answer questions about wolf taxonomy?
3. Is the Mexican gray wolf a valid subspecies?
- 4. Is the red wolf a valid species?**
5. Questions & Answers

Is the red wolf (*Canis rufus*) a valid taxonomic species?

Question 1: Is there evidence that the historic population of red wolves was a distinct lineage?

Question 2: Is there evidence for distinctiveness of contemporary red wolf populations from gray wolves and coyotes?

Question 3: Is there evidence for continuity between the historic red wolf population and contemporary managed populations?



SOURCE: U.S. Fish and Wildlife Service.



Much-Abbreviated Background

- During the 20th century, red wolf populations were driven to very low numbers by predator eradication programs and by habitat loss.
- A few remaining animals were captured from Texas and Louisiana before the red wolf was declared to be extinct in the wild, and used to establish a breeding program.
- The descendants of this breeding program were reintroduced in North Carolina.



Controversies

- **Genetic identity of the founders.**
- **Ancestry and hybridization.**

Question 1: Is there evidence that the historic population of red wolves was a distinct lineage?



The Committee's Findings:

Morphology and Paleontology

- Fossil evidence suggests that at least five subspecies of *Canis lupus* were present in North America after 1 million years ago. The earliest fossils attributed to *Canis rufus* were found in Florida and dated at 10,000 years ago.
- Fossil evidence indicates that *Canis latrans* (coyotes) arose in North America and spread across the continent but that it disappeared from the eastern North America approximately 10,000 years ago and returned in the 1900s.

Question 1: Is there evidence that the historic population of red wolves was a distinct lineage?



The Committee's Findings:

Morphology and Paleontology (continued)

- Based on the limited set of specimens available for analysis, prior to contact with modern coyotes, populations of *Canis rufus* could be morphologically distinguished from *Canis lupus* using canonical discriminant analysis. Although conclusions from studies based on skull morphology differ as to whether *Canis rufus* represented a subspecies of *Canis lupus* or a distinct species, an analysis of the anatomy of the cerebellum supports the recognition of *Canis rufus* as a historically distinct species.

Question 1: Is there evidence that the historic population of red wolves was a distinct lineage?



The Committee's Findings (continued):

Genetics and Genomics

- North American canid species are genetically very similar to each other and have substantial amounts of shared genetic variation.
- The mtDNA haplotypes from historic wolf-like canids (previous to the recent sympatry with coyotes) in the eastern United States cluster within the coyote clade.

Question 2: Is there evidence for distinctiveness of contemporary red wolf populations from gray wolves and coyotes?



The Committee's Findings:

Morphology and Paleontology

- The contemporary population of red wolves in North Carolina is morphologically distinguishable from sympatric coyotes and red wolf–coyote hybrids.

Ecology and Behavior

- Red wolves have a social organization and reproductive behavior that is more similar to gray wolves than to coyotes, and when mates are available they exhibit assortative mating.

Question 2: Is there evidence for distinctiveness of contemporary red wolf populations from gray wolves and coyotes?



The Committee's Findings (continued):

Genetics

- The red wolf population shows evidence of past genetic contributions from populations related to gray wolves, coyotes, or both.
- The red wolf is genetically more closely related to coyotes than to western gray wolves.
- 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.
- The red wolf has some degree of genetic ancestry not found in reference populations of western gray wolves or coyotes.

Question 3: Is there evidence for continuity between the historic red wolf population and contemporary managed populations?



The Committee's Findings:

Morphology and Paleontology

- Morphological analyses suggest cohesiveness among red wolf specimens from the end of the Pleistocene to the early 1900s, but it remains unclear if this continuity is shared with the extant captive and managed populations

Question 3: Is there evidence for continuity between the historic red wolf population and contemporary managed populations?



The Committee's Findings:

Ecology and Behavior

- The reported social behaviors of the natural and restored populations are very similar.
- The diet of the red wolves in the restored population includes a greater consumption of deer than the natural population. However, this may be a function of prey availability and body size. Both red wolves and coyotes in North Carolina consume a similar diet in terms of the types of prey, but they differ in the proportions of deer, rabbits, and other small mammals in their diets and in their seasonal consumption of these prey types.

Question 3: Is there evidence for continuity between the historic red wolf population and contemporary managed populations?



The Committee's Findings (continued):

Genetics

- Genetic continuity between the managed red wolf population and the historic wolf in the eastern United States cannot be firmly established without genomic data from ancient specimens. However, the patterns of genetic variability in contemporary population 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 red wolf has some degree of genetic ancestry not found in reference populations of western gray wolves or coyotes.

Is the red wolf (*Canis rufus*) a valid taxonomic species?



Lets do some synthesis of the findings...

The four possible taxonomic options for the red wolf are:

1. it is a distinct species of wolf (*Canis rufus*)
2. it is a subspecies of gray wolves
3. it is a subspecies of coyotes, or
4. it is a group of recently admixed individuals belonging to neither wolves nor coyotes.



Taxonomic Option 4: No.

~~The red wolf is a group of recently admixed individuals belonging to neither wolves nor coyotes.~~

This option can be rejected for three main reasons:

1. the estimates of deep divergent DNA in red wolves (vonHoldt et al. 2016);
2. the estimates of an admixture time mostly predating the coyote expansion (even if the red wolf is considered a hybrid species between gray wolf and coyote) (from vonHoldt et al. 2011), and
3. 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 (Heppenheimer et al. 2018).



Taxonomic Option 3. No.

~~The red wolf is a subspecies of coyote.~~

This option is not tenable.

There are substantial morphological and behavioral differences between coyotes and red wolves. Furthermore, prezygotic isolation mechanisms, possibly driven by size differences, are at least partially maintained between red wolves and coyotes.



Taxonomic Option 2. No.

~~The red wolf is a subspecies of gray wolves.~~

This option is inappropriate.

Red wolves, historically and presently, show genetic evidence of being more closely related to coyotes than to gray wolves.

Taxonomic Option 1. Plausible



The red wolf is a distinct species of wolf (*Canis rufus*)

- The available evidence from morphology, behavior (especially the partial maintenance of pre-zygotic isolating mechanisms), and ecology, combined with genetic evidence of a relatively deep divergence and the maintenance of some unique genetic ancestry, suggest that the most appropriate taxonomic designation for red wolves is as a distinct species that possibly has had historical admixture.
- The time scales of divergence and the amount of introgression since divergence can affect taxonomic considerations. However, even a recently emerged species can be recognized as such if it is ecologically, functionally, and reproductively separated from other species.
- 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 might also represent much of the historic red wolf genome spread into fragments in different individuals.
- Analysis of genomic DNA from historic red wolf specimens could help clarify whether there is continuity between historic and extant red wolves. More precise genetic analyses might also help determine the exact proportion of the red wolf genome that has been replaced by recent admixture.

Is the red wolf (*Canis rufus*) a valid taxonomic species?



Conclusion

1. Available evidence suggests that the historic 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 historic red wolves.
4. Although additional genomic evidence from historic specimens could change this assessment, evidence available at present supports species status (*Canis rufus*) for the extant red wolf.

Recap of the Committee's Conclusions

Mexican gray wolf

Canis lupus baileyi



- The Mexican gray wolf is a valid taxonomic subspecies of the gray wolf, *Canis lupus*, with its current classification of *Canis lupus baileyi*.

Red wolf

Canis rufus



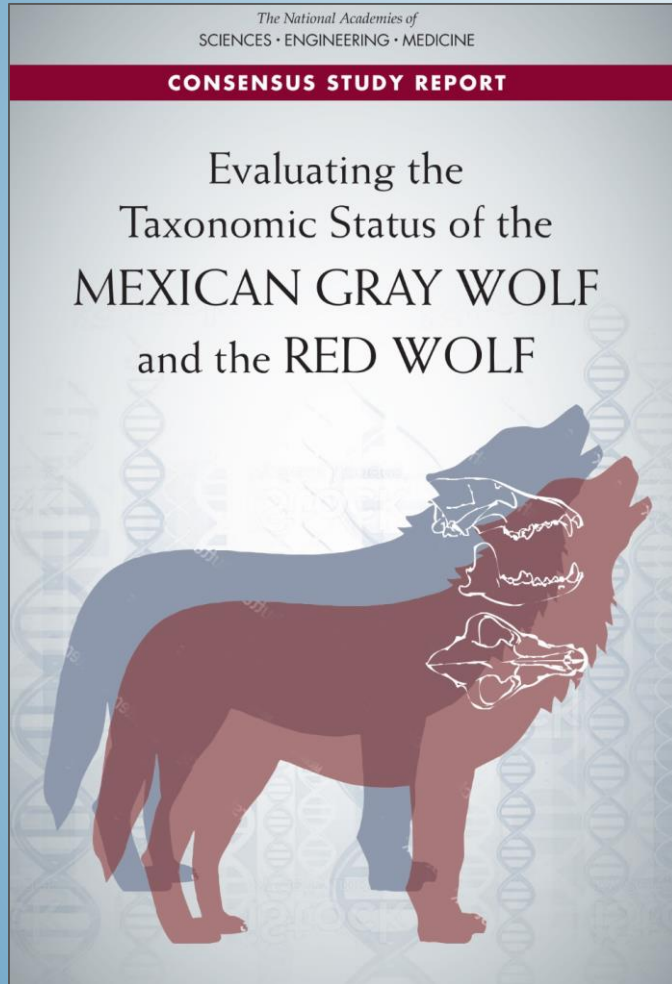
- Available evidence at present support species status (*Canis rufus*) for the extant red wolf.

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- Invited Speakers
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- Committee members

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Where to Find Information about the Report



Visit <http://nas-sites.org/dels/studies/wolf-taxonomy-study/> to access:

- PDF of the report for free download
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