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Source: *Conservation Biology*, Vol. 10, No. 2 (Apr., 1996), pp. 390-396
Published by: Wiley for Society for Conservation Biology
Stable URL: http://www.jstor.org/stable/2386855
Accessed: 24/06/2013 16:30

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Molecular Taxonomy and the Conservation of the Red Wolf and Other Endangered Carnivores

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Abstract: *Recent publications have reaffirmed that the red wolf (*Canis rufus*) is a hybrid of the coyote and the gray wolf. Besides the implications these results will likely have for future conservation efforts and allotment of resources through the Endangered Species Act for recovery of the red wolf, it is likely that broader consequences will be felt throughout the conservation community as species come under the scrutiny of a more powerful means of taxonomic identification. As molecular technology is refined in its ability to resolve taxonomic histories and uncertainties, it is likely that hybridization event(s) will be recognized in more species. This may be of particular importance for large carnivores, whose small population sizes make them susceptible to hybridization episodes with closely related, sympatric species. Because of negative perceptions, powerful antipredator advocates, conservation and resource constraints, and an enigmatic hybrid policy within the Endangered Species Act, how red-wolf taxonomy is decided by the U.S. Fish and Wildlife Service may affect the future of large carnivores in general.*

Taxonomía molecular y la conservación del lobo colorado y otras especies de carnívoros en peligro

Resumen: *Publicaciones recientes han reafirmado el estado taxonómico del lobo colorado (*Canis rufus*), identificándolo como un híbrido entre coyote y lobo gris. Además de las consecuencias que estos resultados tendrán sobre los esfuerzos de conservación futuros y sobre la alocación de recursos, a través del Acta de Especies en Peligro, para la recuperación del lobo colorado, es probable que se establescan consecuencias más amplias a lo largo y ancho de la comunidad conservacionista a medida que más especies caigan bajo el escrutinio de métodos poderosos de identificación taxonómica. Es probable que, a medida que la tecnología molecular es refinada en su habilidad para resolver historias y dudas taxonómicas, se reconozcan eventos de hibridación en más especies. Esto puede ser particularmente importante para los grandes carnívoros, cuyos tamaños poblacionales pequeños los hacen susceptibles a episodios de hibridación con especies simpátricas estrechamente relacionadas. Debido a percepciones negativas, a los poderosos partidarios anti de predadores, a las limitaciones de la conservación y los recursos y a una enigmática e híbrida política dentro del Acta de Especies en Peligro, la forma en que el Servición de Pesca y Vida Silvestre resuelva la Taxonomía del lobo colorado podría afectar el futuro de los grandes carnívoros en general.*

Introduction

Two recently published articles (Wayne & Jenks 1991; Roy et al. 1994*a*, 1994*b*) have provided data further questioning the species status of the red wolf (*Canis rufus*), adding fuel to the continuing debate over its taxonomic position within the Canidae. The results of these studies, all molecular-genetic in form, indicate unambiguously the hybrid nature of this southern canid, emphasizing its genetic similarities to an ever-expanding coyote (*Canis latrans*) population. They also have the potential of placing a strain on a reintroduction program that has been referred to by the U.S. government as one of the "most significant success stories" of the Endangered Species Act (ESA) (U.S. Fish and Wildlife Service 1994) because an obscure "hybrid policy" (O'Brien &

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Paper submitted January 23, 1995; revised manuscript accepted April 20, 1995.

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Mayr 1991; Littell 1992:21) will now likely be called upon in an effort to delist the red wolf (Gittleman & Pimm 1991; Rennie 1991). The consequences of this case may be greater than currently understood because, as populations get smaller due to natural or anthropic factors, not only does the likelihood of hybridization among certain groups of animals increase, but the benefits of hybridization also increase, often adding outside alleles to an already depauperate genetic base. Given the ESA's history of last-minute listings and science's often last-minute, crisis-oriented conservation efforts (Soulé 1985), more populations may come to the point where hybridization is a viable option for population survival (Cohn 1987; Parker 1990; Lehman et al. 1991). Furthermore, to combat the demographic and genetic effects that small population size and subsequent inbreeding can produce (O'Brien et al. 1985; Fergus 1991; Packer et al. 1991), the deliberate introduction of outside genetic material of closely related species or subspecies may be utilized by conservation officials as a last-ditch effort to prevent species extinction (Avise 1989; Avise & Nelson 1989).

As molecular-genetic technology becomes more sophisticated, allowing researchers to further resolve the taxonomic identities of species of uncertain origins, it is likely that many species and populations will display genetic material indicating hybridization at some point in the recent or distant past. Many of these animals will have been historically considered conservation focal points and standard bearers (O'Brien et al. 1990; Lehman et al. 1991), and in our subsequent efforts to appropriate efficiently and effectively the limited funds provided by the ESA, these historically popular species may then be ignored. Carnivores, with historically low numbers—made even smaller by years of direct and indirect persecution by humans—due to their top trophic position, potentially have an increased likelihood to interbreed cross-specifically during times of demographic stress. These factors, combined with likely calls for delistment by those who perceive predators as a threat, have the potential to change significantly how we approach carnivore conservation. Using the red wolf as an example, I discuss the potential consequences that the combined effects of carnivore natural history, public attitudes toward carnivores, limited resources for conservation efforts, destructive human activities, and superior taxonomic identification technology may have upon future carnivore conservation efforts. I focus on carnivores in particular but will discuss other taxa for illustrative purposes. The definition of "species" within the ESA and used by conservationists and those in decision-making positions is of obvious consequence to the current topic. But the role of the definition has been well-documented elsewhere (O'Brien & Mayr 1991; Jenks & Wayne 1992; Hill 1993), and I will not comment upon it here.

The Red Wolf: Conservation and Controversy

Recognized as *Canis niger* as early as 1791 and first identified scientifically in 1851 (Nowak 1979; Cohn 1987), the red wolf (*Canis rufus*) historically ranged throughout the southeastern United States into Texas and southern Illinois (Nowak 1979; Peek et al. 1991; Phillips 1991*b*) and was considered abundant throughout the western part of its range through the first half of this century (Peek et al. 1991). Perhaps numbering in the hundreds of thousands (Parker 1984), the red wolf, like the closely related gray wolf (*Canis lupus*), was subject to the persecution and loss of habitat that accompanied the movement of European settlers west, until by the 1930s it had been extirpated east of the Mississippi (Nowak 1979; Cohn 1987; Peek et al. 1991). The small population that remained in the 1960s in the coastal areas of southerneastern Texas and southwestern Louisiana was subjected to further stress in the forms of heavy parasite loads and hybridization with an expanding coyote (*Canis latrans*) population, a closely related canid more adaptable to human landscape alterations. Declared an endangered species in 1967 under the ESA, the red wolf numbered fewer than 100 by the time it received priority conservation measures under the 1973 ESA (U.S. Fish and Wildlife Service 1994). In the mid-1970s all remaining red wolves were captured for captive breeding purposes before the species was lost to hybridization. By 1980 the red wolf was considered extinct in the wild (Cohn 1987; Meese 1989).

Only 40 out of 400 wolves trapped were considered "pure" enough for breeding purposes (Cauley in Cohn 1987; Jenks & Wayne 1992), and the remaining animals were destroyed because of infiltration of coyote genetic material. Of the 40 only 14 individuals eventually made up the founding population (Cohn 1987; U.S. Fish and Wildlife Service 1994). By 1984 the captive population numbered no more than 50 animals (Parker 1984). In July 1986 the U.S. Fish and Wildlife Service (USFWS) proposed reintroduction of the red wolf into the recently obtained Alligator River National Wildlife Refuge (ARNWR) in coastal North Carolina (U.S. Fish and Wildlife Service 1986*a*), and in November of that same year four pairs were flown and released into the refuge under an "experimental" status that permits limited "taking" of the wolves under conditions approved by the USFWS (Parker & Phillips 1991). In 1990 the Great Smoky Mountains National Park was considered as a second release site (Parker 1990). By the end of 1993 the red wolf population had grown to 233–247 individuals with 46–60 animals in the wild and 187 in captive breeding programs around the country (U.S. Fish and Wildlife Service 1994). Despite local fears that the wolf would harm livestock and domestic animals (U.S. Fish and Wildlife Service 1984, 1986*a, b*; Kellert 1986; Cohn 1987; Meese 1989; Rees 1989*a, b*; Phillips 1991*b*), through the use of

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extensive public education and outreach programs, the reintroduction has been considered exemplary by both conservationists and USFWS and now serves as a model for other reintroduction programs (Phillips 1991*a*, 1991*b*; U.S. Fish and Wildlife Service 1986*b*, 1994).

Considered by some to be the only wolf to have evolved in North America (Nowak 1979, 1992), the red wolf is of size and stature almost exactly between that of coyotes and gray wolves (Nowak 1979, 1992; Wayne 1992), a fact that had persuaded some (e.g., Goldman 1944) of its potential to hybridize with these two animals. It was, however, still considered a viable species. Not until the early 1990s did molecular data establish absolutely the hybrid nature of the red wolf (Wayne & Jenks 1991), putting into question its species status. But several authors cite anatomical (Nowak 1979, 1992), behavioral, and ecologic (Phillips & Henry 1992) factors in their support of the viable species status of the red wolf. Nowak (1979) combined skeletal and dental measurements with data from the fossil record to conclude that not only is the red wolf a viable species but it is perhaps the ancestral stock from which both the coyote and gray wolf emerged. Likewise, Phillips and Henry (1992) note distinctive wolf-like predatory and social behaviors within the North Carolina red wolf population, thereby refuting challenges to a red wolf–coyote hybrid hypothesis.

Recent molecular analysis, however, may have established beyond a doubt the hybrid nature of the red wolf (Wayne & Jenks 1991; Roy et al. 1994*a*, 1994*b*). Using mtDNA analysis from several extant gray wolves, coyotes, and red wolves, as well as from several museum specimens of red wolf, Wayne and Jenks (1991) concluded that "the red wolf is entirely a hybrid form or a distinct taxon that hybridized with coyotes and gray wolves over much of its previous geographical range." In particular, they note the unquestionable presence and influence of coyote genetic material within the red-wolf genome. The study sparked controversy as many called for the immediate delistment of the red wolf from the ESA, stating that the funds allotted for its reintroduction (roughly $160,000 per year for the ARNWR population; Phillips 1991*b*) might be better spent upon other, less questionable and more recognizable species (Gittleman & Pimm 1991; Rennie 1991). Likewise, despite any indication that the red wolf was a threat to livestock, the study was adopted by the American Sheep Industry in their petition to the Secretary of the Interior to delist the red wolf from the ESA (Phillips & Henry 1992). The USFWS denied the petition, remarking that it did not provide substantial enough evidence to warrant delisting (Henry 1992). On the other hand, many researchers rallied in defense of the red wolf, noting the potential bias in Wayne and Jenks's study and its analysis of mtDNA only (Dowling et al. 1992*a*, 1992*b*; Nowak 1992; Phillips & Henry 1992), what Avise (1989) has controversially referred to as "molecular chauvinism." Further research was called for before any conclusions on red-wolf taxonomy would be considered. In their recent analysis of microsatellite loci in coyotes and gray and red wolves, it appears that Roy et al. (1994*a*) have provided this missing information, further confirming the red wolf's hybrid nature.

Molecular Taxonomy and Endangered Species Conservation

As molecular techniques used in the resolution of taxonomic histories and events become more refined, their role in the conservation of flora and fauna threatened with extinction will most certainly become of increasing importance. May (1990) notes the overwhelming importance of taxonomy and systematics in conservation endeavors, referring to these disciplines as "bricks" from which biological science is constructed. Methods such as polymerase chain reaction (PCR) and other DNA analyses irrefutably identify and clarify relationships among species, often widely separated both taxonomically and geographically, including extinct taxa that exist only within museum collections (Arnheim et al. 1990; Roy et al. 1994*b*). Daughtery et al. (1990), studying allozyme differentiation between subpopulations of the tuatara (*Sphenodon punctatus*), including live and museum specimens, discovered that the population actually consisted of two species and a single, possibly extinct, subspecies. Faulty taxonomy applied to *S. punctatus* historically by national and international conservationists and decision makers resulted in little to no international protection and the possible extinction of several subspecies. Only current molecular and genetic techniques could have resolved the taxonomic identities within *S. punctatus*, and they have therefore been fundamental in the establishment of appropriate conservation efforts. Avise (1989) provides further arguments for the use of molecular techniques in the conservation of endangered species.

It is extremely likely that as more species are scrutinized through molecular means the identification of hybrid events in the distant or recent past will be discovered. Hybridization occurs through many media, both natural and anthropic. Combined with introductions of often dominant domestic and/or game species (Courtenay 1978), however, the continuing increase in habitat loss and the resultant fragmenting of populations have the potential to increase significantly the likelihood of hybridization. This may be of particular importance for closely related, sympatric carnivores with small population sizes that are the result of ecologic and anthropic factors. Lehman et al. (1991) have discovered the introgression of coyote DNA into gray-wolf populations in

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the northern United States that have been reduced in number to the point that Allee effects (the inability to find an appropriate mate) have now become apparent. Similarly, as red-wolf populations decreased to extremely low numbers in the southern United States, hybridization with coyotes was facilitated when appropriate mates could not be located (Parker 1990; Jenks & Wayne 1992). Domestic pets also have a profound effect, exemplified by two recently published studies. Gottelli et al. (1994), researching the causal factors behind the endangerment of the Ethiopian wolf (*Canis simensis*, considered by many to be the world's most endangered canid) have discovered a dangerous influx of genetic material from the domestic dog (*Canis familiaris*). Combined with continued habitat loss and reduction in population size, the hybridization of the Ethiopian wolf may take it beyond conservation's rescue. Similarly, declining populations of the European wildcat (*Felis silvestris*) in Britain are being inundated by genetic material from local house cats (Hubbard et al. 1992), potentially compromising any future conservation efforts. Instances of hybridization due to the combined effects of habitat degradation and the intentional introduction of a more competitive species by, generally, short-sighted enthusiasts has led to the possible endangerment of several trout species in the southwest (Dowling & Childs 1992) and northwest (Leary et al. 1993) United States.

To combat the extreme demographic (Allee) and genetic effects produced by small population size, researchers may be faced with the dilemma of either allowing the introduction of genetic material from outside the (sub)species, thereby compromising the species-specific "purity" of the endangered population, or allowing the species to run its course to possible extinction. Small population size often results in inbreeding between closely related individuals, which then in many instances manifests itself in reduced fitness throughout the population as a whole. Unchecked, this loss of fitness has the potential to cause population extinction. Large felids in particular appear to be at risk due to loss of fitness. Packer et al. (1991), studying a naturally isolated and increasingly inbred population of lions in the Ngorongoro crater in Tanzania, have discovered significant levels of abnormal sperm throughout the male population. Similar findings have been recorded for the African cheetah (*Acinonyx jubatus*), which appears to have undergone an extreme population bottleneck several thousand years ago (O'Brien et al. 1985, 1987). Although the likelihood of hybridization in these two cases is absent (the Ngorongoro lion population is not a subspecies of African lion; the cheetah is the only species within its genus and therefore cannot naturally breed outside of the species), they clearly illustrate the natural demographic and genetic risks large carnivores face in the wild. These risks are only compounded by human activities that further marginalize and fragment carnivore populations.

The endangered Florida panther (*Felis concolor coryi*) was found to have a remarkably high amount of abnormal sperm throughout its male population (O'Brien et al. 1990; Fergus 1991). Considered a subspecies of the North American cougar, loss of habitat in the wake of increasing development has fragmented the Florida panther population to a remnant of no more than 50 individuals in the wild areas south of Lake Okeechobee. In a population of such small size the sperm abnormalities discovered by O'Brien et al. are not surprising. In addition to these abnormalities, however, the researchers also discovered genetic material within the population that was not local in origin. It has since been discovered that panthers from South America were released in the Everglades by the U.S. Park Service in the 1950s and 1960s in an effort to boost population size and decrease the likelihood of genetic defects due to small population size (O'Brien & Mayr 1991; Fergus 1991). South American genetic material is now found in roughly 50% of the population (O'Brien et al. in Fergus 1991; U.S. Fish and Wildlife Service 1991). But with potentially detrimental genetic factors now found throughout the male population due to small population size and inbreeding, O'Brien and Mayr (1991) suggest that this influx of new genetic material may be of benefit to the population in combatting potentially detrimental effects through the addition of new alleles.

Demographic factors resulting from small population size and the subsequent efforts at conservation through hybridization are perhaps nowhere better illustrated than in the case of the Dusky Seaside Sparrow (*Ammodramus maratimus nigrescens*) of Florida's Atlantic Coast. Considered by many to be a melanistic subspecies of the more common Seaside Sparrow (*Ammodramus maratimus*) (O'Brien & Mayr 1991; Bean 1993), the Dusky Seaside Sparrow underwent severe population decline during the 1950s and 1960s because of severe loss of habitat. By 1980 only five individuals remained, all males. In a last-ditch effort to save the species, these individuals were brought into captivity and a breeding program was established with females of the morphologically similar Scott's Seaside Sparrow (*Ammodramus maratimus peninsulae*) from Florida's gulf coast (Avise & Nelson 1989; O'Brien & Mayr 1991; Bean 1993). The intentional hybridization subsequently denied the Dusky Seaside Sparrow protection under the ESA, and conservation efforts were eventually halted. The last male died on 16 June 1987 and the subspecies were pronounced extinct. But post-mortem molecular data indicated that *A. m. nigrescens* was virtually identical genetically to the more common Seaside Sparrow of the Atlantic coast and clearly distinct from the gulf coast subspecies with which it was bred, factors unknown at the time (Avise 1989; Avise & Nelson 1989).

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Perception of Carnivores

Historically, carnivores have been perceived as evil, deplorable creatures in need of subordination or eradication (Lopez 1978; Kellert 1980, 1986). Wolves, in particular, have been the subject of often misguided hatred in this country (and around the world), exemplified by our rigorous and successful efforts at eradication in the lower 48 states during the nineteenth and early twentieth centuries (Lopez 1978; Kellert 1986). But as public attitudes toward predators have evolved to encompass a more naturalistic and humanistic character (Kellert 1980, 1986), many of these species have become veritable icons in this country's conservation movement. The bald eagle, grizzly bear, and gray wolf all currently serve as powerful symbols in our efforts to conserve this country's endangered fauna (Kellert 1986, 1994). Furthermore, they are now considered by many conservationists as "umbrella" species, whose large habitat requirements encompass the ranges and ecological requirements of many more, smaller species; conservation of the one promotes conservation of the whole. Nevertheless, because of their predatory nature and expansive habitat requirements, conservation of these animals is often considered to run opposite many interests, particularly the economically and politically powerful development and livestock industries. As molecular techniques are applied to more of these predatory animals and the identification of hybridization events is further resolved, these interests are further armed with data that may legally benefit their causes under an enigmatic "hybrid policy" of the ESA (O'Brien and Mayr 1991; Littell 1992:21). Industry support of the hybrid policy, combined with the negative perceptions that the public, in general, attaches to the term "hybird" (often mistaking it to mean "mongrel" or "interbreed"; U.S. Fish and Wildlife Service 1991), may be of great consequence to future conservation efforts. This has been illustrated in the case of the red wolf, which, upon publication of its likely hybrid nature (Wayne & Jenks 1991), was petitioned for delistment from the ESA by the American Sheep Industry (Phillips & Henry 1992). It is likely that recent publications by Roy et al. (1994*a*, 1994*b*), further questioning the red wolf's taxonomic identity, will result in renewed efforts to delist the animal. Similarly, removal of the gray wolf from the ESA was soon sought by farm bureaus from Wyoming, Montana, and Idaho following the publication by Lehman et al. (1991) of wolf-coyote hybridization data in the northern U.S. (O'Brien & Mayr 1991). O'Brien et al. (in Fergus 1991) express fear that development interests will seek delistment of the Florida panther now that its hybridization with South American cougars has been identified.

Calls for delistment come from within the scientific community as well, as scientists remind us of the limited funds available for species conservation. Gittleman and Pimm (1991) and Rennie (1991) were quick to point this out following Wayne and Jenks's (1991) conclusion of coyote–red wolf hybridization. Indeed, the article by Gittleman and Pimm was published in the same edition as the study by Wayne and Jenks.

The Hybrid Policy of the Endangered Species Act

Although the Endangered Species Act has no formal policy on hybrids, historical legislation dealing with hybrid animals appears to have been species-specific in nature (Appenzeller 1989; Henry 1992; Bean 1993). In the case of the Dusky Seaside Sparrow, the intentional hybridization with Scott's Seaside Sparrow resulted in its exemption from any federal conservation funding (Steinhart 1986; O'Brien & Mayr 1991; Bean 1993). According to the USFWS, "once the Dusky had been contaminated with whatever genes, the biological entity that was there is no more; . . .the subspecies was extinct biologically, in our view" (in Steinhart 1986). In a not altogether different case, however, the USFWS ruled in favor of the red wolf after it had been petitioned for delistment by the American Sheep Industry (Henry 1992; Phillips & Henry 1992). Whether or not this is a case of taxonomic prejudice remains to be seen. The two cases have been compared within both biological (O'Brien & Mayr 1991) and legal (Hill 1993) frameworks. The conclusions of these respective studies, however, are very different. Whereas O'Brien and Mayr (1991) call for the redefinition, clarification, and subsequent consistent implementation of the ESA's hybrid policy, Hill (1993) suggests the redefinition of "species" as applied by the ESA.

Conclusion

As molecular techniques with greater capabilities of taxonomic resolution are produced and employed in our efforts to define conservation priorities, it is likely that many more species will be identified as having experienced a hybridization event(s) in their recent or distant past. This may be of particular importance to large carnivores whose numbers have been constrained by both ecological and anthropic factors. As a consequence of the Allee effects that accompany reduced population size, the potential of hybridizing events increases with increased effort to ensure gene flow and avoid extinction. These fundamental demographic factors are often overlooked in our efforts to define conservation foci on a genetic level (Lande 1988). Future studies of the genetic makeup of large carnivores may put further strain on conservation efforts if these animals, like the red wolf and the Florida panther, are found to contain genetic material of a nonspecific origin. In the hands of interests

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that oppose carnivore conservation, such data can be an awesome legal weapon. Furthermore, it adds additional constraints to the conservation measures necessary to save those species and subspecies undergoing severe genetic and/or demographic effects because of human activities (U.S. Fish and Wildlife Service 1991). As the hybrid policy is now interpreted, once the Dusky Seaside Sparrow consisted only of males all conservation measures were effectively for naught and the bird was allowed to go extinct. Similarly, without genetic exchange from an outside source, the sperm abnormalities throughout the male Florida panther population may eventually render this species extinct (O'Brien & Mayr 1991; U.S. Fish and Wildlife Service 1991).

To deny conservation resources and efforts to these species or populations based upon recent or distant hybrid events produces not only ecological arguments (the loss of these species may lead to the loss of those organisms falling underneath their respective "umbrellas") but also adds further to the ethical argument of our approach to endangered species conservation in general. In the case of most large carnivores in the U.S., population decline and fragmentation has resulted from human activities. We are becoming increasingly responsible for the fact that many species and populations are in the otherwise unlikely and precarious position of mating with closely related yet more abundant species in order to further genetic contribution and secure population survival, thereby reducing species-specific "purity." We are also responsible for the need to introduce outside genetic material to allow population (species) persistence. Some argue that these are plausible grounds to discontinue conservation efforts (e.g., Jenks & Wayne 1992; but the authors do express concern over this situation). Other state that, all else failing, flexibility should be permited in such situations to a certain extent (U.S. Fish and Wildlife Service 1991).

The questions raised by these issues are numerous and controversial. By depriving, through our activities, many of these species of the chance to locate suitable mates and habitat, thereby increasing the likelihood (necessity) of hybridization, is it then just to consider these species effectively extinct? Furthermore, are we in a position to confront the onslaught of legal and scientific controversy that will likely accompany the increasing revelations of hybrid identities? Finally, how prepared are we to accept the inevitable hybrids that will be identified by increased scrutiny through molecular technology? The revelation of genetic histories may be likened to the opening of Pandora's Box: discoveries and surprises both great and terrible likely await us. These are extremely important questions that must be debated and answered among the scientific and legislative community responsible for the management and conservation of endangered species.

The red wolf appears to have been confirmed as a hybrid (Wayne & Jenks 1991; Roy et al. 1994*a*, 1994*b*), and its taxonomic status will most likely once again be confronted and decided upon by the U.S. Fish and Wildlife Service. It will likely constitute a landmark decision and, for many more species waiting in the wings, may make the difference between survival and extinction.

Acknowledgments

I thank Stephen Kellert, Tim Clark, and Dwight Barry of the Yale School of Forestry and Environmental Studies for their help during the early stages of this manuscript. I also thank Russell Lande and two anonymous reviewers for their insight and helpful comments and suggestions.

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