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Validity of the Red Wolf: Response to Roy et al.

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"Red wolf" is a name commonly given to a kind of wild *Canis* historically found from central Texas to the Atlantic (Fig. 1). Since first recorded in colonial times, it has been treated variously as a full species or as a subspecies of the Holarctic gray wolf. Current technical names would be *C. rufus* if a species and *C. lupus rufus* if a subspecies. McCarley (1962) found that the red wolf had hybridized extensively with the coyote (*C. latrans*). That factor, together with human persecution and environmental disruption, brought the red wolf to the point of extinction. It was classified as endangered in 1967.

The recent paper by Roy et al. (1996) is one of a series (Wayne & Jenks 1991; Jenks & Wayne 1992; Wayne 1992, 1993, 1995; Roy et al. 1994*a*, 1994*b*; Wayne & Gittleman 1995; Wayne et al. 1995) suggesting, through analysis of mitochondrial and nuclear DNA, that the red wolf is not a valid species or subspecies, but instead originated as a hybrid of *C. lupus* and *C. latrans*. Although this hypothesis has achieved limited support (Brownlow 1996), it has been challenged by other genetic authorities (Dowling et al. 1992*a*, 1992*b*; Cronin 1993).

That there has been introgressive hybridization of the red wolf and coyote is not in dispute. Its occurrence has long been recognized by all who have looked into the issue and is a major reason that the red wolf is endangered. It would not be unexpected to find that genetic material from one species has spread through the other.

Nevertheless, to accept this process of hybridization and the consequent decline of the red wolf within the last century is very different from accepting that the red wolf had a hybrid origin hundreds or thousands of years ago. It requires some effort to comprehend the fundamental difference between the two positions. One argues that the red wolf is an ancient component of its ecosystem but has nearly disappeared, in part because of a process (hybridization) induced and perhaps controllable by humans. This interpretation demands priority work to save the animal. The other position holds that the red wolf is a modern creation of a process brought on by human environmental modification, and hence that the animal is nothing more than an artifact that can be discarded. The salvation of the red wolf may hinge upon the effort made to grasp this distinction.

A recovery program, led by the U.S. Fish and Wildlife Service pursuant to the U.S. Endangered Species Act, has involved location and breeding of animals as close as possible to the original red wolf. The program has helped restore a viable wolf population along the coast of North Carolina (Nowak et al. 1995; Morse 1996). This reintroduction of a large predator sparked opposition from certain interests (Gilbreath & Phillips 1996). A bill to cut off funding nearly passed the U.S. Senate in August 1995 (Chafee 1995), and a lawsuit aimed at stopping the project is now in progress.

Arguments against the systematic validity of the red wolf have been used by those opposing reintroduction. In responding, recovery personnel have spent resources that might have been better used for conservation. Stating such is not an attempt to dissuade healthy criticism and debate. Published questioning of the validity of established taxa, however, especially already controversial endangered species, should be done with care and full consideration of the consequences. Such consideration has not always been given in recent advocacy of hybrid origin for the red wolf.

Roy et al. (1996) asserted repeatedly that Nowak (1979) argued that the red wolf is ancestral to both the coyote and gray wolf. This alleged position was worked into a central target, the "ancient origin hypothesis," against which Roy et al. directed much attention. Nowak (1979), in fact, never took such a position; instead he suggested that the red wolf, and the entire wolf line, is descended from an early coyote-like population. He referred to some evidence that the wolf line may have originated independently but never hinted that any wolf gave rise to the coyote. Examination of more recent work (Nowak 1992, 1995; Nowak et al. 1995; Nowak & Federoff 1996) would have revealed a prevailing view that the red wolf

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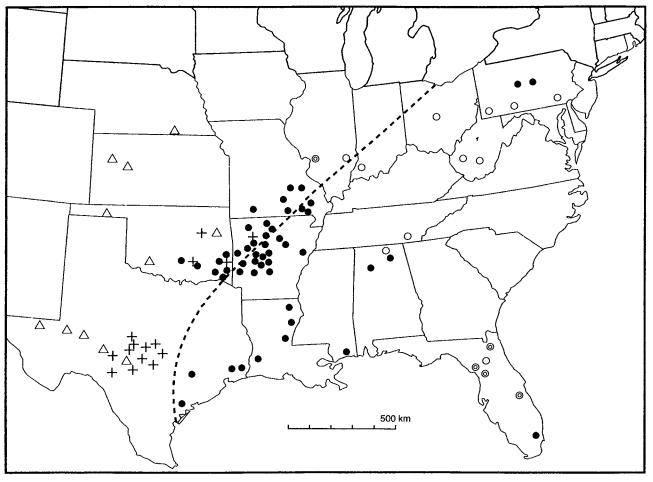

Figure 1. Localities of specimens collected before 1930 (except for the Mississippi record, which is 1931) in the southeastern United States and adjacent areas (adapted from Nowak and Federoff 1996). Triangles, C. lupus nubilus*; dots, complete adult specimens of* C. rufus*; open circles, fragmentary archeological mandibular remains or complete immature specimens in the size range of* C. rufus*; double circles, Pleistocene fossil mandibular remains in the size range of* C. rufus*; crosses, specimens evidently representing hybridization of* C. rufus *and* C. latrans*; dashed line, eastern limits of the range of* C. latrans *during this period. In historical time and up to 1930, no specimens of* C. latrans *or any wild* Canis *(other than as shown above) are known from the region east of the dashed line and south of New York.*

is a primitive species or subspecies, representing part of the phylogenetic transition from coyote to gray wolf. Ironically, even if those challenging the validity of the known red wolf were totally correct, another such taxon would be needed to cover this gap in canid evolution. It might be said that if the red wolf did not exist we would have to invent it.

Roy et al. (1996) also indicated that only their new genetic studies reveal hybridization prior to 1940. In fact, Nowak (1979) devoted extensive attention to the presence of a red wolf–coyote hybrid population in central Texas in the period 1890–1920 and discussed hybridization in Missouri, Oklahoma, and Arkansas between 1920 and 1940. Various other morphological investigators were aware of apparent hybrids dating long before 1940 (Goldman 1944; Lawrence & Bossert 1967, 1975).

Other examples of carelessness by Roy et al. (1996) include a reference to "16 pre-1940 red wolves captured between 1915–1943," the use of a long-outdated map of the range of the red wolf, and a statement that the Ethiopian wolf (*C. simensis*) diverged from the gray wolf in the late Pleistocene. This last statement contradicts other genetic work (Wayne 1993; Gottelli et al. 1994; Roy et al. 1994*a*; Wayne et al. 1995) indicating that the Ethiopian wolf is no more closely related to the gray wolf than is the coyote. There is general agreement that the coyote and wolf lines separated at least a million years ago in the late Pliocene or early Pleistocene (Nowak 1979; Kurten & Anderson 1980; Vila et al. 1997).

Roy et al. (1996) drew their samples from specimens collected from 1915 to 1943 in a small region of southern Missouri, eastern Oklahoma, Arkansas, and northern Louisiana. That region may represent less than a quarter of the original range of the red wolf, which extended eastward to Pennsylvania and Florida (Nowak & Federoff 1996). That region, west of the Mississippi, was also the most likely part of the red wolf's range to have been affected through introgression from the coyote, especially by the twentieth century. The much larger and earlier populations to the east may have presented a different genetic picture. As demonstrated by Nowak and Federoff (1996), all available early morphological material from east of the Mississippi consistently demonstrates the presence of a small wolf, with no coyote influence. This material is also statistically very similar to pre-1930 series from just west of the Mississippi in Louisiana and Missouri, where Roy et al. obtained their samples.

Roy et al. (1996) did acknowledge this possibility and that the red wolf may have been a distinct subspecies. They indicated, however, that such a subspecies would now be extinct. Why could this subspecies not have persisted, even to this day, modified to some extent through recent hybridization with the coyote? Roy et al. (1996) readily accepted that the small gray wolf of southeastern Canada (*C. lupus lycaon*) has hybridized with the coyote, and that its current genotype has been extensively influenced by the latter species (Lehman et al. 1991; Wilson et al. 1996). Nonetheless, they did not question the validity of *lycaon* as a wolf, and there has been no substantive challenge to conservation efforts to assist that subspecies. Why could the same not apply to *rufus*? Why is it any less a wolf? Allele frequency data presented by Roy et al. (1996, Table 3, Fig. 3) actually suggest an affinity between *rufus* and *lycaon*. Indeed, these data are analogous to morphological analyses (Nowak 1979) showing the two taxa as occupying a position intermediate to other *C. lupus* and *C. latrans*.

Although they acknowledge that their analysis cannot readily deduce the precise timing of hybridization or the true origin of the red wolf, Roy et al. (1996) suggest two scenarios to explain the origin and fate of the red wolf. In the first, "settlers who arrived in the early 1700s" destroyed forests, thereby allowing coyotes to spread through the southeast and hybridize with presumptive gray wolves already present. In the early 1700s, however, settlement was limited to a strip along the Atlantic coast and to a few points on the Gulf coast. Forest destruction there would not have affected the coyote populations then restricted to prairies far to the west and

north. Not until the mid to late 1800s did substantive habitat disturbance reach the eastern fringe of the coyote's range. Even as late as the 1920s, there is no evidence of a natural movement of the coyote east of a line roughly from San Antonio to St. Louis (Fig. 1). The subsequent spread of the coyote and of its hybridization with the red wolf is well documented (Nowak 1979; Hill et al. 1987).

In the second scenario, the gray wolf and coyote hybridized in the southcentral United States as long ago as the Pleistocene. It is incongruous, however, to suggest that such a process took place in a region where neither species was known to have been present, while at the same time hybridization never developed anywhere in western North America, where both species occurred together in abundance for many thousands of years.

Moreover, if gray wolf–coyote hybridization had begun hundreds or thousands of years ago and progressed to the point of producing a new intermediate population, two outcomes could be postulated. First, the new population could have become reproductively isolated from the two parental species. This essentially would mean speciation through hybridization, a phenomenon evidently rare in animals and now unknown in higher vertebrates.

The second possibility would have been extensive backcrossing and a total blending of the new population with both parental species. All available material, however, including fossils, archaeological fragments, and museum specimens from the nineteenth and early twentieth centuries, shows a sharp distinction between the wolf of the southeast and the most proximal populations of the gray wolf. There was complete distinction between the southeastern wolf and coyote, except in a few limited areas where hybridization evidently had begun by the early twentieth century (Nowak 1979, 1995; Nowak & Federoff 1996).

Roy et al. (1996) suggest that red wolf conservation would be justified in the event of their second but not their first scenario. Whether they would be supportive if an alternative view prevailed is not clear, but it is encouraging that they recognize the potential value of saving the red wolf. Their concluding warnings with respect to the continued danger posed by hybridization to reintroduction should be carefully heeded. We hope that all parties who have investigated this complex issue will yet reach a consensus, thus allowing the systematic controversy to be put aside in favor of progress toward conservation. (Note: The views presented are those of the authors and do not necessarily reflect those of any U.S. Government Agency.)

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