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Source: *Conservation Biology*, Vol. 12, No. 3 (Jun., 1998), pp. 726-729

Published by: [Wiley](#) for [Society for Conservation Biology](#)

Stable URL: <http://www.jstor.org/stable/2387258>

Accessed: 28/05/2013 17:29

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Origin of the Red Wolf: Response to Nowak and Federoff and Gardener

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The discussion by Nowak and Federoff distills to seven issues pertinent to Roy et al. (1996) to which we would like to respond. We feel, however, that none of the issues they raised are consequential, and we stand by our conclusions.

First, Nowak and Federoff criticize our contention that Nowak (1979) argued that the red wolf was ancestral to modern coyotes and gray wolves. Our interpretation was based on Fig. 55 in his treatise, duplicated here as Fig. 1, and the statement from their text (p. 87) that "*C. rufus* [the red wolf] represents a primitive line of wolves that has undergone less change than *C. lupus* [the gray wolf], and has thus retained more characters found in the ancestral stock from which both wolves and coyotes arose." We interpreted this to mean that the red wolf lineage diverged first from the same ancestral stock that later gave rise to coyotes and gray wolves (Fig. 1). This apparently was not what Nowak intended, and we apologize. In view of the paucity and fragmentary nature of the canid fossil record (e.g., Nowak 1979; Kurtén & Anderson 1980), we believe that such evidence alone cannot adequately support any single view of Pleistocene canid phylogeny, a conclusion clearly supported by all the alternative connections in Nowak's figure (Fig. 1). We disagree strongly with the statement by Nowak and Federoff that "If the red wolf did not exist, we would have to invent it." The phylogenetic transition between coyote and gray wolf, if it occurred, could have progressed rapidly such that intermediate forms would not be preserved or even recognizable as a distinct species.

The issue of whether the red wolf was ancestral to either coyote or gray wolf is a red herring; it is simply not relevant. The essential dichotomy, the focus of our paper, concerns whether the red wolf has an *ancient* origin or was formed *recently* by hybridization between gray wolves and coyotes. We state that "the evolutionary

paradigm for the red wolf embraced by the U.S. Fish and Wildlife Service (USFWS) postulates that the red wolf is a native species of the American South, originating in the early Pleistocene, and is ancestral to modern coyotes and gray wolves." The origin of the red wolf in the early Pleistocene (Nowak 1979) alone predicts that it should have unique, "diagnosable" molecular markers, as do species such as the coyote and the gray wolf that appeared at about the same time (Fig. 1). The red wolf has no diagnosable mitochondrial or microsatellite markers (although even the Mexican gray wolf subspecies does); instead it has characteristics otherwise found in gray wolves or coyotes consistent with a hybrid origin. Therefore, we stand by the dichotomy presented in our paper.

Second, Nowak and Federoff assert that we claim that only our genetic studies reveal hybridization before 1940. We are well aware that Nowak and others (Table 1) documented limited hybridization before 1940, but he viewed hybridization as much more widespread after 1940 and used a set of pre-1930 red wolves to establish the unadulterated phenotype of the red wolf from the southcentral United States (pp. 30–33 and Fig. 15 in Nowak 1979). We followed his approach, although our sample was more limited by the availability of pelts, because of concern by us and the USFWS that the founders of the captive red wolf population captured in the early 1970s were too thoroughly hybridized with coyotes for diagnostic markers to be found. Our presumption was that if Nowak had used pre-1930 red wolves as representing phenotypically unmodified samples, we would stand a much greater chance of finding unique genetic markers in samples from approximately the same time period. We found none; genetically, the historic and recent red wolves were extremely similar, suggesting that they were derived from a common gene pool.

Third, Nowak and Federoff provide supposed examples of carelessness. The group of 16 "pre-1940" wolves did include a single 1943 specimen. The comment about the map being outdated, however, we dispute. The map we used is derived from Carbyn (1987), who summa-

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Paper submitted November 19, 1997; revised manuscript accepted February 18, 1998.

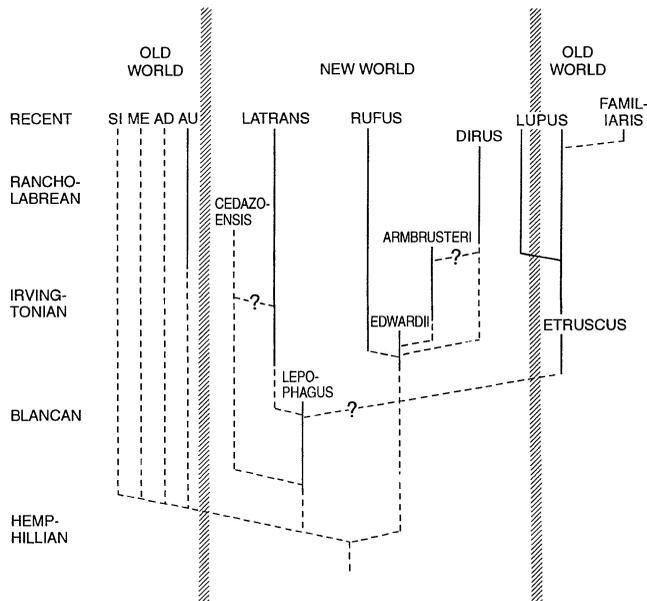


Figure 1. Phylogeny of species in the genus *Canis* from Nowak (1979). Dashed lines indicate possible lineages lacking fossil evidence. Species names are placed at the latest known occurrence. Horizontal and vertical distances are not to scale and do not indicate degree of affinity. Abbreviations: SI, *C. simensis*; ME, *C. mesomelas*; AD, *C. adustus*; and AU, *C. aureus*. Question marks show alternative lineages.

rized objectively Nowak's (1979) data and other historical records. Subsequent publications by Nowak were published in a symposium volume (1995) or gray literature (Nowak 1992; Nowak & Federoff 1996) and were produced subsequent to our original article (Wayne & Jenks 1991). We do not have much confidence in these reports because they did not undergo rigorous peer review and because of the problem in distinguishing gray wolf-coyote hybrids from genuine red wolves or southern gray wolves (Wayne 1992). Lawrence and Bossert (1975) did a multivariate analysis similar to Nowak's and concluded that the early pre-1930 population of red wolves in Arkansas were no more than subspecifically distinct from gray wolves and differed less from Northern gray wolves than did an Old World subspecies of gray wolf. "It is noteworthy, also, that the Arkansas *gregoryi* [southcentral subspecies of red wolf], supposedly belonging to a different species, is even less distant from *lycaon* [a gray wolf subspecies inhabiting the Great Lakes region], and the generalized *lupus* than is *pallipes* [the gray wolf from India]" (Lawrence & Bossert 1975:84).

The remark about the divergence of the Ethiopian wolf is puzzling. In both Roy et al. (1996:1421) and Gottelli et al. (1994:309) and in a review publication derived from these results (Wayne 1996), we make the same statement that the Ethiopian wolf diverged from gray wolves in the late Pleistocene based on the fossil record of the gray

Table 1. Review of literature that presents new data, new analysis, or explicit statements about red wolf systematics.

Hypotheses*	Reference
D	Audubon & Bachman 1851
D	Goldman 1937
D, H	Young & Goldman 1944
D, H, HS	McCarley 1962
D, H, HS	Lawrence & Bossert 1967
D, H	Paradiso 1968
D, H	Pimlott & Joslin 1968
D, HS	Mech 1970
D	Atkins & Dillon 1971
D, H	Paradiso & Nowak 1972
D, H	Gipson et al. 1974
D, H, HS	Lawrence & Bossert 1975
D, H	Riley & McBride 1975
D, H	Elder & Hayden 1977
D, H, HS	Van Gelder 1978
D, H, HS	Nowak 1979
D, H	Ferrell et al. 1980
D, H, HS	Wayne & Jenks 1991
D, H, HS	Dowling et al. 1992a
D, H, HS	Dowling et al. 1992b
D, H, HS	Phillips & Henry 1992
D, H, HS	Wayne 1992
D, H, HS	Roy et al. 1994
D, H, HS	Wayne & Gittleman 1995
D, H, HS	Roy et al. 1996

*Three general hypotheses have been suggested for the origin of the red wolf in the southcentral United States, the area sampled by Roy et al. (1996): D, it has not hybridized and/or is fully distinguishable from closely related North American *Canis*; H, it is a distinct species or subspecies that hybridized with gray wolves, coyotes or both, at least in a significant portion of its range; or HS, it is possibly a hybrid species derived from hybridization between gray wolves and coyotes.

wolf in Europe (Kurtén 1968). This is probably a more conservative procedure than using the genetic divergence between Ethiopian wolves and gray wolves and the fossil divergence time of the coyote and gray wolf to determine a divergence date. Genetic divergence and fossil divergence dates often do not agree exactly, reflecting the inherent sampling problems in both fossil and genetic analyses. This issue is another red herring. Because the gray wolf, coyote, and Ethiopian wolf have similar levels of sequence divergence from one another, the red wolf, originating in the early Pleistocene, should be at least as divergent and contain diagnostic characters as do the other three species of wolflike canid.

Fourth, Nowak and Federoff claim that our samples were drawn from less than a quarter of the historic red wolf population. The important consideration is that the founders of the living red wolves were drawn from part of this sampled area. Our results show that wolves from throughout this region were highly modified by hybridization with coyotes and gray wolves. Historic populations of east coast red wolves may have had unique genetic markers or may simply have been gray wolf-coyote hybrids or a southern population of gray wolves (e.g., Lawrence & Bossert 1967). These alternatives cannot be discriminated by

Nowak's previous morphologic analysis because coyote-gray wolf hybrids may be morphologically indistinguishable from "true" red wolves (Wayne 1992). A study focusing on diagnosable characters is needed (Wayne 1992). Unfortunately, molecular analyses of ancient red wolves from archeological sites on the east coast might not be feasible because the procedure is technically difficult, expensive, and without guarantee of success.

Fifth, Nowak and Federoff criticize our reference to the red wolf subspecies as extinct. This again is a semantic issue. The genetic evidence indicates that the founders of the captive red wolf population have no diagnostic markers that might be expected of a distinct subspecies, such as the Mexican gray wolf, and were highly modified by the acknowledged hybridization with coyotes. Consequently, the red wolf subspecies in an unadulterated form does not exist. As we suggested, however, even though modified, the captive population represents the only living repository of genes from this now extinct subspecies and may merit conservation as such (Roy et al. 1996).

Sixth, Nowak and Federoff suggest that our scenario of hybridization is not consistent with historical data and the presence of distinct southeastern red wolves. We maintain that historical records and Nowak's deduction of range limits and movements are dubious. The fossil record of both red wolves and gray wolves in the American southeast is sparse (Nowak 1979). In Nowak's treatise, gray wolves are shown as being found within the supposed range of red wolves (Fig. 51 in Nowak 1979). Our greatest concern is that deductions concerning species origin based on morphologic similarity are clouded by hybridization originally between gray wolves (or a distinct subspecies of gray wolf) and coyotes (Table 1). With the disappearance of gray wolves, such hybrids became predominantly coyote-like. East coast red wolves that are considered distinct may merely be a population of small gray wolves that hybridized less with the expanding wave of coyotes. The process of hybridization can be extremely rapid and could have effects that remain even after gray wolves have disappeared. For example, although coyotes entered Ontario only about 50 years ago, morphologically intermediate canids thought to be hybrids are common (Kolenosky & Standfield 1975; Schmitz & Kolenosky 1985). The appearance of a large, wolflike canid in New England, where gray wolves are extinct, is thought to be due to the migration of wolf-coyote hybrids from the Great Lakes region (Hilton 1978). This suggests that both species need not be present for hybrids to predominate.

We believe that the issue of range expansion and hybridization cannot be determined without the addition of new, discrete character data and cladistic analysis. As argued previously (Wayne 1992), the proponents of the theory of the red wolf as a species need to find diagnosable traits unique to red wolves, whether on the east coast or elsewhere. Despite the proliferation of letters in response to our publications, symposium chapters, and

gray literature discussions, no new discrete character data have appeared. In fact, the USFWS funded the additional genetic analysis of red wolves in the hope that we would find new diagnosable characters. We did not.

Finally, Nowak and Federoff lament that time and money have been spent responding to the issue of taxonomic status rather than saving the red wolf. We are proponents of the conservation effort for the red wolf and maintain that such efforts should not hinge on the taxonomic issue (e.g., Wayne & Jenks 1991; Wayne & Gittleman 1995). The conservation of the red wolf could be defended as both a hybrid species or as an ancient primitive wolf: "Species that are believed to be of hybrid origin would retain or maintain eligibility for threatened or endangered status if they have developed outside of confinement, are self-sustaining, naturally occurring taxonomic species and meet the criteria for threatened or endangered species under the Act [the U.S. Endangered Species Act]" (Frampton & Foster 1996).

The Florida puma is a hybrid population that owes its hybrid status to the introduction of South American pumas by the USFWS (O'Brien et al. 1990). Hybrids appear more fit, and a program has been developed to introduce pumas from Texas on a regular basis (Hedrick 1995). Consequently, we agree with Nowak and Federoff that the central concern should be how to prevent extinction from hybridization in the wild and that USFWS efforts should be turned toward dealing with this problem rather than spending time and money on a campaign to defeat the hybrid hypothesis with inconclusive and problematic data. We believe that the intransigence of the proponents of the red wolf species hypothesis is focusing research in inappropriate directions. We have acknowledged that our data are not conclusive and have allowed for a variety of alternative explanations, including a separate subspecies hypothesis (e.g., Wayne & Jenks 1991; Roy et al. 1996). The genetic evidence is strong enough that the proponents of the hypothesis of the red wolf as a separate species should allow for other possibilities for its origin. The USFWS should concentrate on the issue of conservation and on whether the red wolf is self-sustaining in the wild given the near certainty of overwhelming hybridization with coyotes.

In another response to Roy et al. (1996), Gardner expresses concern about the species status of one of the red wolves used in our analysis. One supposed red wolf typed by us was later reported to R.K.W as a coyote. We regret the misidentification and inclusion of this specimen, for which R.K.W takes responsibility. In any case, the sample was difficult to analyze and subsequently was not typed for mtDNA variation (Roy et al. 1996); also only 2 of 10 microsatellite loci were scored (locus 200, score C:D; locus 172, score A:I). At locus 200, frequencies change at allele C from 0.269 to 0.250, at allele D from 0.269 to 0.250, at allele E from 0.115 to 0.125, and at allele F from 0.346 to 0.375. At locus 172, fre-

quencies change at allele A from 0.300 to 0.286, at allele C from 0.033 to 0.000, at allele D from 0.067 to 0.071, at allele I from 0.067 to 0.071, at allele H from 0.233 to 0.250, at allele I from 0.267 to 0.250, and at allele J from 0.033 to 0.071. Therefore, the mistaken identity of 1 of 16 historic red wolves typed in only 2 of 10 loci had negligible effects and does not affect our overall results.

Authors' Note

We discovered three typographical errors in Appendix 1 of Roy et al. 1996: the frequency for the N allele (0.050) under locus 200 should be moved under locus 213, the frequency for the M allele under locus 377 should be 0.038 rather than 0.308 as printed, and there is no C allele at locus 172.

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