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Hybridization: the Double-edged Threat

by Ron Nowak

This article explores the use of morphology and geographical evidence
to assess possible hybridization events in the history of North American canids.

[Ed. - we plan to post the figures on-line soon!]

The wolves of North America are under a severe new threat from an influential group; not the lumber companies, fur trappers, or stockmen, but the zoologists, or at least some among them who are keen to publish claims that wolf populations have hybridized with other species. These scientists are unwittingly playing into the hands of certain commercial interests, which will seize upon any suggestion that a species is no longer taxonomically valid, in order to argue that conservation efforts are not warranted and that the species and its habitat may be exploited.

The last few years have seen the widespread promulgation of various interesting but controversial notions. These include proposals that a vast wolf (*Canis lupus*)-coyote (*C.latrans*) hybrid zone has engulfed central North America, that the arctic wolf (*C.lupus arctos*) has been substantially altered through genetic introgression from the domestic dog (*C.familiaris*), and that the southeastern red wolf (*C.rufus*) is nothing more than a hybrid of the grey wolf and coyote. None of these ideas has been accepted by the scientific community, but some are being related as fact in the media and are being turned against the wolf. Formal petitions to remove both the grey and red wolf from the List of Endangered and Threatened Wildlife were received and extensively reviewed by the U.S. Fish and Wildlife Service, although eventually these were denied (Henry, 1992; Refsnider, 1990).

The above is not intended to downplay concern that hybridization, induced by human disruption of natural populations and their environment, is a serious problem to wildlife and plants (Rieseberg, 1991; Williams & Nowak, 1992). My own research (Nowak, 1979) indicates that the near disappearance of the red wolf was indeed caused in large part by interbreeding with the coyote. The grey wolf and coyote have also apparently hybridized in southeastern Canada, where the small subspecies *C.lupus lycaon* now occupies a restricted range and could be jeopardized by genetic swamping. There has been a recent proliferation of commercially bred wolf-dog hybrids, some of which are being turned loose into areas where wolves occur naturally.

Based on an analysis of mitochondrial DNA, Wayne and Jenks (1991) went well beyond the long-recognized view that the red wolf and coyote had interbred. They suggested that *C.rufus* actually originated as a hybrid and had never been a valid species or subspecies. Their study was simultaneously utilized by Gittleman and Pimm (1991) to criticize efforts being made to reintroduce

the red wolf in the wild. These papers were immediately challenged, both on the basis of genetics (Dowling *et al.*, 1992a; 1992b) and paleontology and morphology (Nowak, 1992).

Examination of fossil and modern skulls (Nowak, 1979; 1992; in press; Nowak *et al.*, in press) indicates that *C.rufus* has existed in southeastern North America, in much the same form as now, for at least 700,000 years. *C.lupus* did not even arise until much later and never penetrated far into the southeast. *C.latrans* did not enter the southeast during this entire period, except for a brief incursion about 10,000 years ago and again within the last few decades. Hybridization between *C.rufus* and *C.latrans* began about 100 years ago in central Texas and subsequently spread through much of the former range of the red wolf. *C.lupus* was also present in Texas at that time, but was completely distinct from the other two species and the hybrids. A small population of *C.rufus* on the Texas coast evidently escaped substantive interbreeding; a few individuals from this group were taken into captivity and served as the founding stock for current reintroduction efforts.

The proponents of hybrid origin for the red wolf have largely ignored the above evidence, claiming that large grey wolf and coyote populations must somehow have moved into the southeast and interbred to form the red wolf. Since mitochondrial DNA analysis has revealed little basis for taxonomic division of wolf populations in most of North America, they have argued that it would be unlikely for a separate species to exist in the southeast, especially since there were no barriers to prevent the entry of the large and mobile grey wolf. They have even suggested that instead of using the captive red wolf population for current reintroduction efforts in the southeast, it would be better to bring in grey wolves from Canada, Alaska, or Mexico (Jenks & Wayne, 1992).

In the attempt to prove hybrid origin for the red wolf, both Jenks & Wayne (1992) and Wayne (1992) have published a composite of two figures from my own work (Nowak, 1979: 22, 32). Each of the figures depicts the same graphical distribution of large samples of known skulls of female *C.lupus*, female *C.latrans*, and *C.familiaris*, based on a canonical analysis of 15 measurements. One of the figures also shows the graphical positions of 52 female *C.rufus*, and the other figure shows the positions of 5 suspected female hybrids of *C.lupus* and *C.latrans* from southeastern Canada. The composite figure indicates that most of the suspected hybrids fall within the graphical range of *C.rufus* (which itself is largely between the ranges of *C.lupus* and *C.latrans*), and thus was used to argue that the red wolf is essentially the same thing as a grey wolf–coyote hybrid.

The composite figure, as utilized by Jenks & Wayne (1992) and Wayne (1992), demonstrates a misunderstanding of both phylogenetics and multistatistical procedures. The two original figures were based on a procedure that was not intended to distinguish red wolves and grey wolf–coyote hybrids, but to show how individuals of each group compared to three known samples, including the domestic dog. Considering that *C.rufus* is a primitive wolf, representing a stage in the evolution of *Canis* intermediate to *C.latrans* and *C.lupus*, its position on the graph is not surprising. Likewise, hybrids of the grey wolf and coyote could reasonably be expected to fall between their parent species.

In order to illustrate the principle, I carried out a new canonical discriminant analysis of 10 skull

measurements (those numbered 1, 2, 4, 5, 6, 8, 11, 12, 14, and 15 in Nowak 1979), using the Statistical Analysis System (SAS Institute, 1987). Three known groups were examined: 18 female *C.latrans* from eastern Wyoming, 20 female *C.lupus* from Minnesota (18) and Isle Royale (2), and 20 domestic dogs. The wolf and coyote samples were chosen based on their geographical proximity to the areas of interest and their lack of any morphological evidence of hybridization; there was no selectivity and all available specimens were used. The dog sample, however, was selected to achieve a size range comparable to that of the two wild species, and was taken from a larger series already chosen so as to avoid extremes of domestication. In addition, 9 female red wolves collected in southeastern Missouri in 1923–1925 were compared as individuals to the three known groups. The red wolf sample comprises all available females taken before 1930 in the area and was chosen because: (1)the presence of a distinguishable sympatric coyote population in the same area of Missouri (Nowak, 1979) demonstrates that red wolf–coyote hybridization was not then a factor; and (2)this red wolf sample is the one closest to the area of suspected grey wolf–coyote hybridization. Also compared as individuals were the same 5 suspected female grey wolf–coyote hybrids from southeastern Canada that are discussed above.

Graphical results (Fig.1) show the three known samples – *C.latrans*, *C.lupus*, and *C.familiaris* – to be distinct from one another. The groups of individual red wolves and suspected hybrids are separate from the three known samples but are both distributed between the limits of grey wolf and coyote and overlap one another extensively. The analysis thus yields the same result as shown in the composite prepared by Jenks & Wayne (1992) and Wayne (1992). However, I then did a second analysis, in which the sample of domestic dogs was eliminated and the samples of red wolves and suspected hybrids were entered as independent groups. Graphical results (Fig.2) still show complete distinction of the grey wolf and coyote, but now the red wolf and the suspected grey wolf–coyote hybrids also form distinct clusters. I do not claim that larger samples of red wolves and hybrids would not overlap, but multistatistical analysis does show that the two do not have identical characteristics.

The publications of Wayne and Jenks followed closely on reports of another "hybrid zone" in the Great Lakes region, said to involve the spread of coyote mitochondrial DNA to 62% of grey wolves in Minnesota and to 100% of those on Isle Royale (Lehman *et al.*, 1991). As usually understood, a hybrid zone refers to an area where the ranges of two related species meet, interbreeding occurs, and a new population is produced that bridges the morphological, behavioural, and ecological gap between the parent species. In fact, nothing of the sort has developed in Minnesota or Isle Royale, where observations by field personnel and analysis of specimens indicate no change in the original characters of *C.lupus* (Nowak, 1991; 1992).

Isle Royale is of particular interest because if the students of the mitochondrial DNA approach had been provided only blood or tissue samples from the area, and had no other knowledge of the situation there, they would have concluded that the island is occupied solely by a population of coyotes. Actually, the only wild *Canis* on Isle Royale are packs of grey wolves, the main prey of which is moose. Skulls taken over the years (and loaned to me through the kindness of Durward L.

Allen and John A. Vucetich, Jr.) show no hint of an approach to the coyote in size or other characters; indeed the wolves of Isle Royale may be getting larger. Considering dental size, perhaps a more conservative expression of relationship than is over-all skull size and proportion, the Isle Royale animals have not changed at all. The five available skulls of male wolves, collected on Isle Royale through 1971, have upper carnassials (fourth premolar teeth) nearly identical in size to those of the five available males collected from 1980 to 1991 (Fig.3).

A recent reduction in size has been claimed for *C.lupus arctos*, a subspecies found on most of the Canadian Arctic islands, not because of hybridization with the coyote, but through introgression from escaped sled dogs (Clutton-Brock, Kitchener & Lynch, 1994). Skulls in a series taken between 1930-1950 and after 1950 reportedly averaged smaller size than those taken before 1930. However, the pre-1930 sample consists only of five specimens, four being known males and one a probable male. The two subsequent series have somewhat more specimens, but contain both sexes. Since the males of any given population of *Canis* are significantly larger than the females (Nowak, 1979), it is likely that a series consisting predominantly of males will have larger average measurements than will series with a normal sex ratio.

In any case, I have examined most of the same collections and have not observed a reduction in size over time or any other indication of substantive dog introgression. One of the most useful characters in distinguishing the skull of a large dog from that of a wolf is the relatively tiny and well-spaced teeth of the former. The conservative dentition has not kept up with the bones of the skull in the development of large breeds of *C.familiaris*. The most useful individual teeth are the carnassials. *C.lupus arctos* has especially huge carnassials, and series of available specimens of males only demonstrate no decline in size over the years (Fig.3).

In addition to a size reduction, Clutton-Brock, Kitchener & Lynch (1994) referred to the relatively broad rostra and crowded teeth of the more recent Arctic wolves as characters suggesting introgression from dogs. I would note also that both *C.familiaris* and *C.lupus arctos* commonly share a relatively broad frontal shield (forehead). However, I do not think that these characters indicate genetic relationship. The same features show up in various other wolf populations, and reach extreme development in a series of skulls taken in the 1950s on Banks Island, where *arctos* apparently spread following extirpation of the original population. The Banks Island skulls maintain a very large carnassial (Fig.3) and show no particular evidence of dog hybridization. A series of male *C.lupus albus* from the Taymyr Peninsula of northwestern Siberia have the same basic characters (Nowak, in press).

Broad rostra, broad frontal shields, crowded teeth, huge carnassials, and certain other features of modern Arctic wolves are also characteristic of some late Pleistocene *C.lupus* from the tar pits of southern California and from the Yukon (Nowak, 1979). The commonality of characters suggests phylogenetic affinity between these Ice Age wolves and those now found in northern Eurasia, on Banks Island, and in the Canadian high Arctic (Fig.4). Another interpretation would be that the various populations are not related, but all underwent a similar phenotypic response to environmental conditions. The least likely alternative is that hybridization with the domestic dog

occurred in all these times and places and affected wolf populations in the same way.

According to Mengel (1971), hybrids of *C.familiaris* and *C.lupus* breed annually, like wild wolves, but the timing is shifted so that on average the hybrids breed approximately three months earlier. Therefore, the offspring of hybrids are born during the winter and would have little chance of survival in the wild. If Mengel's views are correct, the Arctic would be the last place on earth where we would expect introgression from dogs into a wild wolf population.

Although Mengelµs position is based on limited experimentation, it is supported by abundant circumstantial evidence from throughout North America. Walker & Frison (1982) found canid remains at archaeological sites indicating that prehistoric Amerindians of the western United States, like modern Eskimos, had crossed their large dogs with wolves. There also have been a handful of documented instances in which wild wolves apparently mated of their own volition with domestic dogs and produced offspring (Young & Goldman, 1944). However, there is no evidence of gene flow in the other direction.

Following analyses of hundreds of wolf skulls from North America (Nowak, 1979; in press), I reported fewer than 10 that seemed to represent wolf–dog hybridization. Much of my study centered on large collections from the western United States assembled in the early 20th century, when the region was filling up with humans and dogs and when wolf populations were in severe decline. If ever there was a set of conditions that might be expected to foster wolf–dog hybridization and introgression, it existed then, and yet there is no evidence that such a process developed.

Wolves have continued to live in close proximity with people and dogs throughout western Canada and Alaska, but without any hint of size reduction or other signs of introgression. Of particular note is the Peace River district of Alberta, where wolves occur regularly on the fringe of agricultural development. Specimens recently taken there are consistently large in all measurements and, indeed, include the largest skulls of *C.lupus* ever reported (Gunson & Nowak, 1979). Likewise, specimens from the wolf population now expanding southward into the western United States are all large and fully wolflike (Nowak, 1983; in press).

The view that wolf and dog are the same species has recently gained popularity and was accepted in Wilson & Reeder (1993). I still recognize the two as separate species, especially considering the ease with which adult skulls can be distinguished and the extreme rarity of natural interbreeding. The two have shared a vast part of North America for centuries, and it might have become difficult for wolves to pair with their own kind as their numbers dwindled, as their range was fragmented, and as individuals were forced to disperse into settled country. That the wolf has remained completely distinctive under such conditions is something for which canid conservationists should be grateful.

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