REVIEW / SYNTHÈSE

What is the taxonomic identity of Minnesota wolves?

L.D. Mech

Abstract: The taxonomic identity of the historical and current wolf (*Canis lupus* L., 1758 or *Canis lycaon* Schreber, 1775 or their hybrids) population in Minnesota (MN) and the Great Lakes region has been, and continues to be, controversial. So too does its legal status under the U.S. Endangered Species Act. This review summarizes the morphological and genetic information about that population and concludes that historically the MN population consisted of a gray wolf (*C. lupus*) in the west and an eastern type (*Canis lupus lycaon* or *C. lycaon*) in the east with intergrades or hybrids between the two in most of the state. After extirpation in much of its original MN range, the now-recovered population was infused with gray wolves from Ontario but still consists of hybrid *lycaon* × gray wolves, probably with higher content gray wolves in the west and higher content *lycaon* in the east but with most wolves morphologically appearing to be gray wolves. Because the current Wisconsin and Michigan wolf population was derived from MN wolves, they would be primarily hybrids as well. Future research should seek to relate genetic data with morphological measurements in MN wolves. In addition, attempts to breed coyotes (*Canis latrans* Say, 1823) with gray wolves in captivity would shed considerable light on the controversy over the origin and taxonomic identity of the newly proposed *C. lycaon*.

Résumé : L'identité taxonomique des populations passée et actuelle de loups (*Canis lupus* L., 1758 ou *Canis lycaon* Schreber, 1775 ou leurs hybrides) au Minnesota (MN) et dans la région des Grands Lacs a été et continue d'être controversée. Il en va de même de leur statut légal vis-à-vis la loi américaine sur les espèces menacées. La présente rétrospective résume les renseignements morphologiques et génétiques sur la population du MN et conclut que la population historique de loups comprenait des loups gris (*C. lupus*) dans l'ouest et un forme différente (*Canis lupus lycaon* ou *C. lycaon*) dans l'est avec des formes de transition ou des hybrides entre les deux sur la majeure partie de l'état. Après son extirpation sur une grande proportion de son aire de répartition originale au MN, la population maintenant restaurée a été infiltrée par des loups gris en provenance de l'Ontario, mais est toujours constituée d'hybrides des loups *lycaon* × gris, probablement avec une prédominance de loups gris dans l'ouest et de *lycaon* dans l'est, bien que la plupart des loups ressemblent morphologiquement à des loups gris. Parce que les populations actuelles de loups du Wisconsin et du Michigan sont dérivées des loups du MN, elles sont aussi probablement en majorité des hybrides. Les recherches futures devraient viser à relier les données génétiques aux mesures morphologiques chez les loups du MN. De plus, des tentatives pour accoupler des coyotes (*Canis latrans* Say, 1823) avec des loups gris en captivité devraient apporter un important éclairage sur la controverse au sujet de l'origine et de l'identité taxonomique du taxon nouvellement proposé *C. lycaon*.

[Traduit par la Rédaction]

Introduction

Minnesota (MN) bears the distinction of being the only 1 of the 48 contiguous United States (U.S.) to have harbored a substantial popula-tion of wolves (*Canis lupus* L., 1758 or *Canis lycaon* Schreber, 1775 or their hybrids) when the animal was placed on the federal endangered species list. Although wolves originally inhabited all the contiguous 48 U.S. (Young and Goldman 1944), by 1969 they remained there only in Isle Royale National Park in Lake Superior, and in part of MN (Mech 1970). In MN the wolf population has long been and remains the subject of much uncertainty and controversy, both scientific and conservation-oriented. This controversy has recently been fed by the field of conservation genetics (e.g., Lehman et al. 1991 vs. Wilson et al. 2000; Leonard and Wayne 2008 vs. Mech 2009 and Wheeldon and White 2009). Therefore, for an appropriate assessment and interpretation of past and future morphologic and genetic data, and for designing future studies, a review of the population's history and of what is known so far is in order.

Under classical taxonomy, two subspecies of wolves originally were recognized in MN (Young and Goldman 1944), but in 1995 they were lumped into one (Nowak 1995). Wolves were placed on the federal endangered species list in

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1967 and were fully protected by the Endangered Species Act of 1973. They were downlisted in MN to threatened in 1978, removed from the list in 2007, restored by a lawsuit to the list in 2008, delisted again in 2009, and relisted once more as a result of a lawsuit.

The genetic identity of the MN wolves has also been in dispute (cf. Lehman et al. 1991; Wayne and Vila 2003; Leonard and Wayne 2008; and Koblmüller et al. 2009 with Wilson et al. 2000, 2009; Kyle et al. 2006; and Wheeldon and White 2009). Whether the MN wolves that were recently delisted and then relisted were genetically the wolves that were originally listed on the federal endangered species list has even been questioned and debated (cf. Leonard and Wayne 2008 and Koblmüller et al. 2009 vs. Mech 2009; Wheeldon and White 2009; and Wheeldon 2009).

After federal protection, MN wolves spread into Wisconsin (WI) and Michigan (MI) complementing the Canadian wolves north of the Great Lakes. Thus the wolf population in the Great Lakes region (GLR) has now biologically recovered from its federal endangered status, with some 4000 animals inhabiting much of MN, WI, and MI (Mech 2009). However, when they occupied only MN and nearby Isle Royale National Park, wolf numbers had been as low as 750 (Fuller et al. 1992).

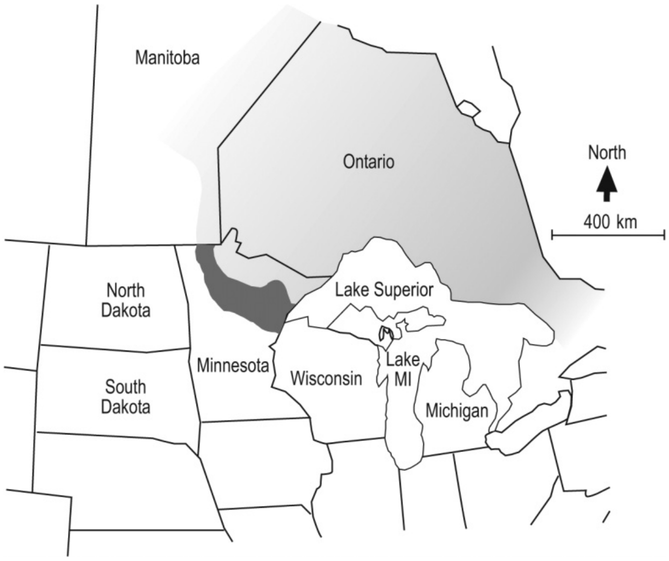
With all these critical changes and biological uncertainties, the wolves of MN and the entire GLR are now the subject of ongoing genetic and taxonomic research in an attempt to establish their identity (Fain et al. 2010; T.J. Wheeldon, B.R. Patterson, and B.N. White, submitted for publication[2]). Kyle et al. (2006), Wheeldon and White (2009), and Wheeldon (2009) have reviewed and summarized the taxonomic and genetic aspects of wolf identity in the GLR, but as mentioned above, Koblmüller et al. (2009) stated "At present, there still is no general consensus about which species of wolf-like canid currently inhabits the Great Lakes region…", and Schwartz and Vucetich (2009) wrote that the Koblmüller et al. (2009) paper "will not be the end to the eastern canid controversy". All of these studies seemed to have ignored Cronin's (1993) caution, and the axiom of Pamilo and Nei (1988) that "gene trees may not equal species trees".

This review focuses on MN, for recent WI and MI specimens merely reflect colonization of those states by current MN wolves. Furthermore, the MN wolf population must be considered in the total context of its adjacent population in Canada because it is a southern extension of wolf populations in Ontario and eastern Manitoba. That connection has never been disrupted, although for a few decades wolf movement between southeastern Manitoba and MN was probably minimal (see below). In extreme northeastern MN, however, where the wolf population remained the most intact of any in the state (Stenlund 1955), connection remained strong with Ontario wolves both to the north and east (Fig. 1).

History of Minnesota wolf population

Within MN, wolves were extirpated from the south, central, and extreme northwestern portions of the state by about 1945, although precise information about the remaining range, while important to any genetic assessment of the original population, is unknown. Surber (1932) stated that wolves were fairly common in the northern third of the state, but Swanson et al. (1945) characterized MN wolf range as north of Lake Superior and "a strip perhaps 75 miles [120 km] westward". This assessment suggests that wolves only persisted in the extreme northeastern part of MN. In northwestern MN just south of the Manitoba–Ontario border, wolves were mostly absent from about 1900 to the mid-1930s but began repopulating since then (Fritts and Mech 1981). By the early 1950s, when state bounty records became precise enough to indicate wolf distribution, the primary wolf range was considered the full northern tier of counties from the Manitoba border to MN's northeastern border with Ontario, although some wolves even lived as far as 175 km southeast of there (Stenlund 1955). Thus one might conclude that the nadir of MN wolf range and numbers occurred sometime between 1900 and the 1950s. In any case, since the early 1950s, MN wolves have been increasing (Fuller et al. 1992), and they now occupy the northern 40% of the state (Fig. 2).

Fig. 1. Range of wolves (*Canis lupus* or *Canis lycaon* or their hybrids) in Minnesota (Stenlund 1955) and adjacent Canada during the low point in their history. Ranges in Manitoba based on Webb (1970) and in Ontario based on Clarke (1970). Light gray area represents primary wolf range, whereas dark gray area represents peripheral range.



When assessing the taxonomic and genetic identity of the MN wolves, the original (presettlement) population and the current populations must be considered separately. The original population would have been mixing with immigrants from Manitoba and western Ontario in the northwest; from North Dakota and South Dakota (which would have been receiving immigrants from Manitoba) in the west; from Iowa and Illinois in the south; from Wisconsin in the southeast and east; and from Ontario from the northeast and north (Fig. 1).

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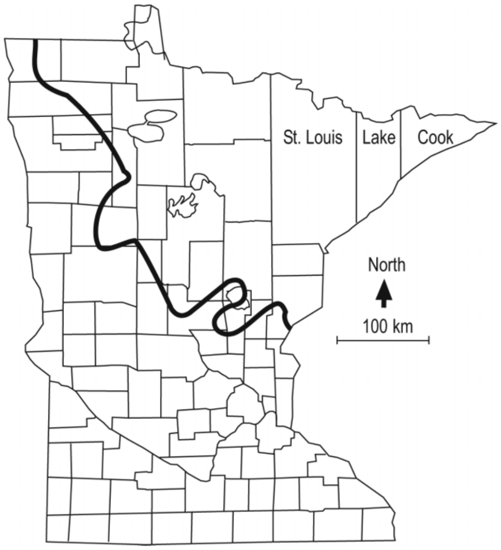
[2] T.J. Wheeldon, B.R. Patterson, and B.N. White. Sympatric wolf and coyote population of the western Great Lakes region are reproductively isolated. Submitted for publication.

Fig. 2. Current Minnesota wolf (*Canis lupus* or *Canis lycaon* or their hybrids) range based on Erb and DonCarlos (2009).



As wolves were exterminated throughout most of the 48 contiguous U.S. and from parts of southern Canada, the only populations remaining adjacent to MN were those in south-central and southwestern Ontario (Clarke 1970) and southeastern Manitoba (Webb 1970) (Fig. 1). Thus as wolves recovered in MN during the 1950s, 1960s, and 1970s, the primary immigrants to western MN would have been from southeastern Manitoba and southwestern Ontario, and those farther east would have been those from south-central Ontario (Fig. 1). Because the highest density of wolves and the least disrupted part of the MN wolf population was that of northeastern MN located against the Lake Superior shore (Fuller et al. 1992), dispersers southward and westward from this population would also have contributed to the repopulation of the rest of the state (Mech and Frenzel 1971; Gese and Mech 1991; Mech et al. 1995). In northwestern MN, depending on how many wolves remained there during its population bottleneck, the resident wolves could have contributed to the recent population there and possibly farther east and south and to WI and MI. Nevertheless, because of the above unknowns and because of the historical turbulence in the population, the genetic distribution and proportions of the current northwestern and north-central MN wolves may or may not reflect those of the original population.

The northeastern MN population has never been extirpated and continuously enjoyed the potential of immigration from the east and north by Ontario wolves, so it has had the greatest chance of remaining genetically the same for the longest time. Furthermore, the current WI and MI wolves probably reflect mostly the traits of the northeastern MN population because chances are best that most of the wolves available to emigrate from MN to WI and then from WI to MI would have been from northeastern MN (Mech et al. 1995).

Minnesota wolf taxonomy based on morphology

Classical wolf taxonomy has long been based on skin and skull morphology. These characteristics are, of course, genetically based. While skull measurements can conceivably also be influenced by nutrition, large enough samples can dilute such an environmental effect. Skin color would not be so influenced. The type of genes affecting morphology, however, are not the same as those commonly used in current molecular genetic assessments. Rather the latter are chosen for their practical and theoretical advantages (Wayne and Vila 2003). Thus the degree to which morphological traits should reflect molecular genetic findings in wolves remains relatively unexplored (but see Kays et al. 2010).

The classical subspecific designations of North American wolves recognized in MN are *Canis lupus lycaon* Schreber, 1775 (the eastern timber wolf), and a gray wolf, *Canis lupus nubilis* Say, 1823 (the Great Plains wolf), with the border between them roughly paralleling MN's western border but about 65 km eastward and extending southward to beyond the state border (Fig. 3A) (Young and Goldman 1944). More recently Wilson et al. (2000) proposed that *C. l. lycaon* should be a separate species, *C. lycaon*, but that designation has not been universally accepted (see below). Thus in this paper, I will use the terminology "*lycaon*" to mean either *C. l. lycaon* or *C. lycaon*, and "gray wolf" to mean all other wolves. (To the south, there were no major divisions recognized for many kilometres, and no genetic assessments have been made immediately south of MN, so no more attention need be paid to areas to the south.)

Young and Goldman (1944) acknowledged that *lycaon* in the GLR graded toward gray wolves, and the precision of the line between the two in MN has been questioned because of traits of some northeastern MN wolves thought to be more characteristic of the larger gray wolves to the northwest and north (Mech and Frenzel 1971; Van Ballenberghe 1977; Mech and Paul 2008). It is also notable that although Young and Goldman (1944) attributed the Ontario wolves north of MN and Lake Superior up to Hudson Bay as *lycaon*, these workers examined no Ontario skulls north of the Lake Superior shore.

In 1995, Nowak revised the classical North American wolf subspecies designations and lumped all MN wolves into one subspecies that extended from the Pacific coast to the eastern border of Michigan, with *lycaon* occurring east of there to the Atlantic coast. However, his analysis of MN skulls was based on specimens collected from 1970 through 1975 after apparent immigration of gray wolves probably from northern Ontario (see below), so his conclusion would not necessarily apply to the original MN wolves (L.D. Mech and R.M. Nowak, submitted for publication[3]). Koblmüller et al. (2009) stated that Nowak (2002) found the GLR wolf to be "morphologically distinct" from gray wolves, but the only data in Nowak (2002) that might support this conclusion is based on male skulls from MI, and the canonical distribution of those skulls appears to be on a continuum with that of gray wolves, not distinct. Furthermore, Nowak's (2009: 15.1, 15.2) later analysis indicates a high degree of

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[3] L.D. Mech and R.M. Nowak. Use of cranial characters in Minnesota wolf taxonomy. Submitted for publication.

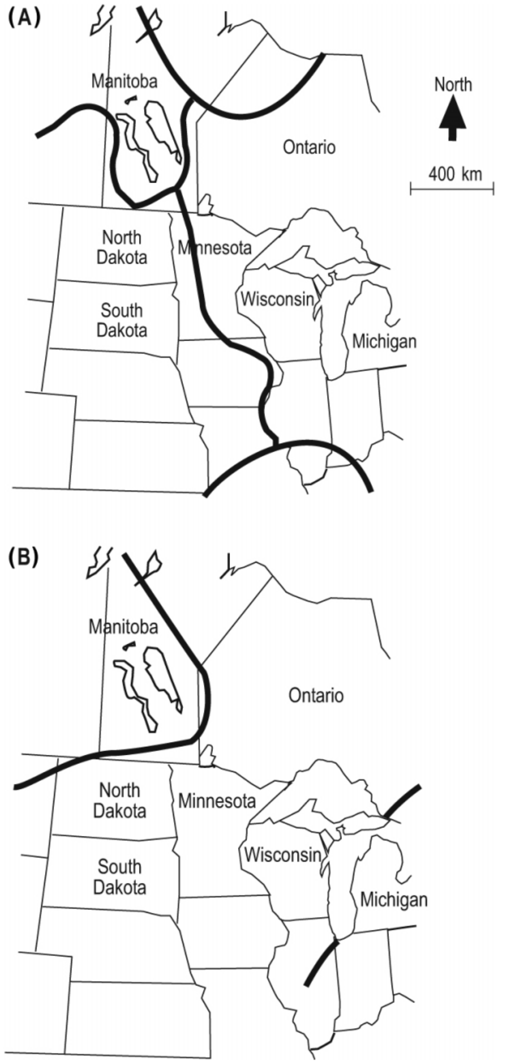


Fig. 3. (A) Dividing lines among subspecies of wolves (*Canis lupus* or *Canis lycaon* or their hybrids) recognized until 1995, based on Young and Goldman (1944). Northern area = *Canis lupus griseoalbus* Baird, 1858; northwest = *Canis lupus hudsonicus* Goldman, 1941; west = *Canis lupus nubilus*; east = *Canis lupus lycaon*; south = *Canis rufus* Audubon and Bachman, 1851. (B) Dividing lines among subspecies of wolves recognized after 1995 (Nowak 1995). Central area = *C. l. nubilus*; northwest = *Canis lupus occidentalis* Richardson, 1829; eastern = *C. l. lycaon*.

overlap between MN wolves and gray wolves. Thus the Koblmüller et al. (2009) interpretation of the Nowak findings that GLR wolves are morphologically distinct appears incorrect.

Nowak (1995) recognized another separate gray wolf subspecies in southeastern Manitoba within dispersal distance of northwestern MN (Fig. 3B). Because wolf movement between MN and Manitoba and vice versa has been documented (Fritts and Mech 1981; Fritts 1983; T. Davis, personal communication), it is reasonable to think that original and current northwestern MN wolves are genetically related to this type of wolf as well as to those to the west. Similarly, Skeel and Carbyn (1977) suggested that the wolves just north of MN resembled those farther west. Schmitz and Kolenosky (1985), however, found that the skulls of Ontario wolves just north and northeast of MN more closely resembled those of *lycaon* than of MN wolves or of those west of MN, although the body measurements of those Ontario wolves were more similar to those of MN wolves.

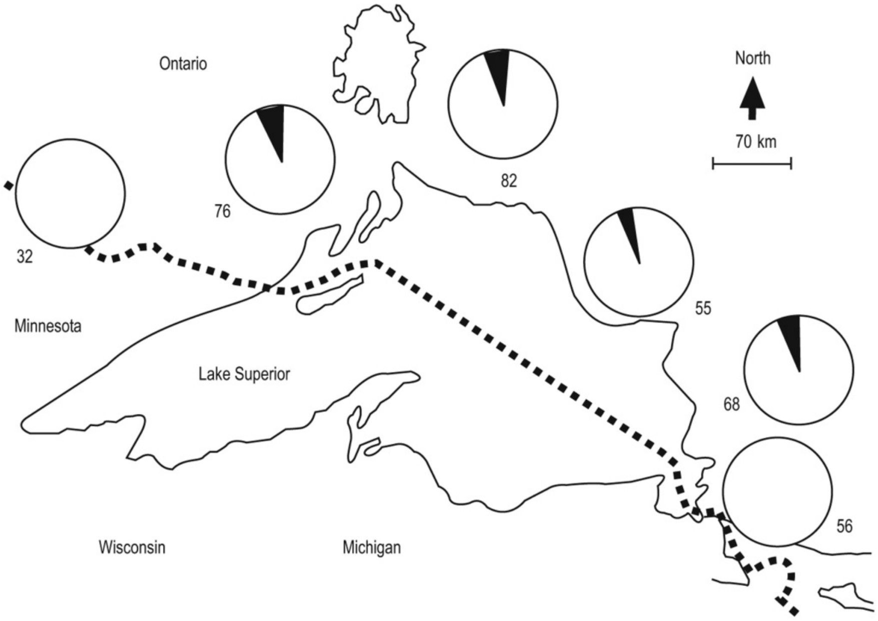
The physical characteristics of *lycaon* vs. gray wolves follow (Young and Goldman 1944; Kolenosky and Standfield 1975): (1) *lycaon* wolves have lower body mass than gray wolves; (2) *lycaon* wolves have longer ears; (3) *lycaon* wolves tend to be mottled gray, whereas gray wolves can vary from black to white, although most of them are also gray; and (4) *lycaon* wolves have a narrower rostrum than gray wolves. Hybrids would probably have intermediate characteristics. Recently, Mech and Paul (2008) found body masses of recent wolves in northeastern MN similar to those in eastern Ontario and those in northwestern MN similar to those in Manitoba, with a significant east–west increase in size, and L.D. Mech and R.M. Nowak (submitted for publication)[3] found that 10 standard mean skull dimensions of 12 pre-1950 northeastern MN wolves approximate those of Algonquin Park wolves, whereas the same dimensions of 1970 to 1975 wolves from both northeastern MN and northern MN approximated those of gray wolves. These findings support the Young and Goldman (1944) conclusion, including the hybridization hypothesis, but they suggest that between 1950 and 1970 gray wolves have had more of an influence across the state.

Although Young and Goldman (1944) thought the *lycaon* wolf extended northward to the Hudson Bay area (about 52°N latitude), Kolenosky and Standfield (1975); Schmitz and Kolenosky (1985), and Nowak (1995) all set its north boundary at about 50°N latitude. Those workers found that north of there wolves share the above characteristics of gray wolves. For example, a sample of 14 male wolf skulls from western Ontario showed the same mean dimensions as those of *C. l. nubilus* (Nowak 1995: Table 1). Thus in this paper, reference to gray wolves include those north of about 50°N latitude, as well as those west of MN.

The presence of black wolves in various parts of MN and the GLR might also give some indication of temporal and spatial distribution of gray wolf genes because that color phase is not unusual for gray wolves, while it is much rarer in *lycaon* wolves north of the Great Lakes. Kolenosky and Standfield (1975) documented that about 5% of wolves in Ontario inhabiting the area north of Lake Superior, including within 80 km of MN, between 1957 and 1975 were black (Fig. 4), while none of >500 wolves immediately north of Lake Huron and Lake Ontario was black.

In MN, it appears that black wolves have appeared more recently, or at least their incidence has increased. Stenlund (1955) made no mention of black wolves in the Superior National Forest of northeastern MN based on his studies during 1948–1952, although he recorded observations of 318 wolves, described several packs, and gave masses of 144 wolves. Three conservation officers who aerially hunted or trapped wolves before 1960 in the same area indicated that out of a total of 580 wolves taken, only 4 (<1%) were black (Mech and Frenzel 1971). Wholesale persecution of the wolf in Minnesota ended in 1965 with the repeal of the bounty on wolves, so wolves began proliferating in the state, no doubt some immigrating from Canada to the north. By

Fig. 4. Distribution of black wolves (*Canis lupus* or *Canis lycaon* or their hybrids) north of Minnesota, based on Kolenosky and Standfield (1975). The numbers represent sample sizes, and the black areas represent proportions of black wolves. The centers of the circles represent the centers of where the samples were taken.



1967–1969 incidence of black wolves in the same area had increased to 3.6% (11 of 309 sightings; $\chi^2_{[1]} = 10.01$, $P \leq 0.01$) (Mech and Frenzel 1971). At least since about 1980 when large numbers of wolves were sampled across MN (Mech and Paul 2008), black wolves have been found throughout at least the eastern 75% of MN wolf range. They also occur in low percentages throughout current WI and MI wolf range.

Thus morphological information indicates that historically MN wolves were probably primarily *lycaon* in the east, *lycaon* × gray wolf hybrids farther west, and primarily gray wolves in western MN, as Young and Goldman (1944) stated. Probably WI and MI wolves were primarily *lycaon* with some hybrids, and within a narrow strip along the north shore of Lake Superior the wolves tended to be of high-content *lycaon* wolves. North of there they probably were gray wolves (Kolenosky and Standfield 1975; Nowak 1995).

In the current MN wolf population, body mass (Mech and Paul 2008), the occurrence of black animals (Mech and Frenzel 1971), and skull dimensions (L.D. Mech and R.M. Nowak, submitted for publication)[3] suggest more gray wolf influence (Nowak 1995), although body mass difference alone in recent wolves suggests higher content gray wolves in the west and higher content *lycaon* in the east (Mech and Paul 2008).

Molecular genetics of Minnesota wolves

As the field of molecular genetics emerged in the 1980s, geneticists began to assess mostly recent MN wolves. Based on mitochondrial DNA (mtDNA), they found two main classes of mtDNA haplotypes, one shared by wolves in Alaska and northwestern Canada (Old World or gray wolves) and one shared by wolves of eastern Ontario and Quebec that was similar to that of coyote (*Canis latrans* Say, 1823) (Lehman et al. 1991). They concluded that the coyote-like mtDNA in MN and eastern Canadian wolves resulted from gray wolf hybridization with coyotes. In a follow-up genetic assessment of these wolves and of other wolves from the GLR, including historic specimens from WI, MI, eastern Ontario, New York, and Quebec, Leonard and Wayne (2008) found three mtDNA haplotypes, Old World (gray wolf), coyote-like, and "Great Lakes" wolf, although Koblmüller et al. (2009) referred to the same mtDNA specimens simply as either wolf-like or coyote-like.

Meanwhile, Wilson et al. (2000) compared microsatellite data and mtDNA haplotypes of wolves from southeastern Ontario, Quebec, Manitoba, and MN, as well as from coyotes, and concluded that the coyote-like mtDNA haplotypes that Lehman et al. (1991) had identified in MN wolves actually were from a species of wolf that had evolved, along with the coyote, in North America, a species they called *Canis lycaon*, the eastern wolf, or New World wolf. Further assessments and opinions supported this viewpoint (Kyle et al. 2006; Murray and Waits 2007; Wheeldon 2009; Wilson et al. 2009, Fain et al. 2010), and Wheeldon and White (2009) showed that the mtDNA haplotypes that Leonard and Wayne (2008) attributed to Great Lakes wolves (i.e., *C1* and *C3*) and to coyotes (i.e., *C13*) were the same as those of *lycaon*. Although Koblmüller et al. (2009) stated that the Wheeldon and White (2009) analysis supported their conclusions, a close reading of Wheeldon and White (2009), and personal communication with them, indicates that they do not agree (Cronin and Mech 2009).

Wheeldon (2009), based on mtDNA, Y intron, and 12 microsatellite loci analyses of 404 GLR wolves and coyotes, concluded that the GLR wolf population was composed of a homogeneous population of *lupus* × *lycaon* hybrids. However, Fain et al. (2010), using Y chromosome, autosomal, and mtDNA haplotypes of 42 recent MN wolves and a total of 124 GLR wolves, concluded that the current population consists of *C. lupus*, *C. lycaon*, and their hybrids. Thus, although there is not agreement on the genetic identity of the MN and GLR wolves, there is agreement that they consist of a population with the genetics of gray wolves, as well as with the genetics of either *lycaon* (Wilson et al. 2000) or *latrans* (Lehman et al. 1991), and that the two genotypes hybridize as Lehman et al. (1991), Wilson et al. (2000), and Mech and Federoff (2002) suspected.

Because none of the genetic samples from any of the studies so far have been collected randomly from the GLR wolf range and thus are subject to spatial bias (Schwartz and McKelvey 2009), it is difficult to assess the meanings of the proportions and distributions of the two genotypes. Nevertheless, some general information about these matters might be gleaned from examining the results of these studies. Because of the above-mentioned disagreement between the two genetic schools over whether the non-*lupus* genes are *latrans* or *lycaon*, I will refer to them as "non-gray wolf" in the following discussion. Leonard and Wayne (2008) found that all mtDNA haplotypes of 12 GLR wolves about 100 years old from WI and MI, not including any from MN, were non-gray wolf. Similarly, Wheeldon and White (2009) learned that two historic samples from central MN and one from WI also were non-gray wolf. We then might generalize from these studies that originally in MN and to the east, at least some wolves generally possessed *lycaon*-like or *latrans*-like haplotypes, rather than those of gray wolves.

As for the recent population, Lehman et al. (1991) reported that 55 (62%) of 88 wolf specimens taken in 1988 from across northern MN except the extreme northeast (Cook County) (Fig. 2) showed non-gray wolf mtDNA haplotypes, including 31 (74%) in 42 wolves from northeastern MN (Lake and St. Louis counties). Wheeldon (2009) also found 71% of 49 specimens collected during 2005 (n = 1) to 2007 (n = 52) from across MN wolf range (except Cook and Lake counties and only one specimen from St. Louis County all in northeastern MN) showed non-gray wolf mtDNA haplotypes. His proportion of non-gray wolf haplotypes decreased from 75% in the eastern quarter of his MN and adjacent Ontario study area to 67% in the western quarter, although the difference was not significant. Wheeldon's (2009) MN sample was also shown via FCA analysis of microsatellite genotypes to be at the south end of a cline of admixture grading through Manitoba into the gray wolves of the Northwest Territories.

Koblmüller et al. (2009) using the Lehman et al. (1991) MN specimens and others from WI and MI concluded that "the Great Lakes area appears to be a zone of limited hybridization between gray wolves, GL wolves and coyotes", based on their analysis of maternally, paternally, and biparentally inherited genetic markers. However, they also concluded that GL wolves should be considered gray wolves. This conclusion disagrees with the genetic findings of Wilson et al. (2000, 2009), Kyle et al. (2006), Wheeldon and White (2009), Wheeldon (2009), and Fain et al. (2010). This conclusion also fails to distinguish any difference between wolves of northeastern and northwestern MN despite body-mass differences (Mech and Paul 2008), but it is supported by recent skull measurements (L.D. Mech and R.M. Nowak, submitted for publication).[3]

Taxonomic synthesis?

No one has attempted to correlate GLR wolf genetics with morphology. The original subspecies designations (Young and Goldman 1944) were based subjectively on body size, coat color, and skull size, and shape of historical specimens. Nowak's (1995) revision was based on statistical discrimination of multiple skull measurements of recent wolves. The genetic assessments were based strictly on molecular methods of genetic segments that do not code for phenotype. Mech and Paul (2008) proposed that because both the taxonomic descriptions and the mtDNA haplotype assessments recognized two types of wolves over an east–west dimension, a correlation might be found between morphology and genetics in the current MN population. They hypothesized that the two types had hybridized in MN (Mech and Federoff 2002; Kyle et al. 2006), but that the purest of each type would inhabit the extreme ends of the MN wolf range so that there might be an east–west cline in morphology as Young and Goldman (1944) reported. Mech and Paul (2008) did find such a cline in body mass, with recent wolves of *lycaon* mass in extreme northeastern MN (Cook County; Fig. 2).

The degree to which historical and current extreme northeastern MN wolves harbor *lycaon* wolf genes depends considerably on the historical and current identities of the wolves immediately north of Lake Superior in both northeastern MN and Ontario. This population has not been very thoroughly assessed genetically. As discussed above, Young and Goldman (1944) considered the historical population as *C. l. lycaon*; Nowak (1995, 2009) as *C. l. nubilus*; and Kolenosky and Standfield (1975) and Schmitz and Kolenosky (1985) as *C. l. lycaon* (Boreal type), which is closer to a gray wolf than to *lycaon.* Young and Goldman (1944) considered the wolves north of Lake Superior as *lycaon*, although they only examined specimens from along the shore itself and eastward. Nevertheless their work does suggest that the range of *lycaon* extended from southeastern Canada along the north shore of Lake Superior into MN. However, because the north side of Lake Superior projects strongly northward, its north shore just northeast of Minnesota (Fig. 1) also falls into the Boreal type of *C. l. lycaon* zone of Kolenosky and Standfield (1975). Thus gray-like wolves from that zone dispersing southward would be funneled toward northeastern MN, leading to the possibility that some mixed with that population. Lehman et al. (1991) considered recent specimens from northeastern MN as gray wolf × coyote hybrids; and Wheeldon (2009) as gray wolf × *lycaon* hybrids, although Wheeldon examined only a few specimens from there, and neither study examined specimens from Cook County.

Here the wolf population on Isle Royale also gains relevance. Isle Royale, some 25 km south of the northwest shore of Lake Superior was colonized about 1949 (Mech 1966), and the mtDNA haplotype of its wolves was non-gray wolf as found along the northwest shore of Lake Superior northeast of MN (Wayne et al. 1991). This finding dates wolves with coyote or *lycaon* mtDNA as having inhabited the north shore of Lake Superior in 1949.

The hypothesis that *lycaon* and gray wolf types have hybridized in MN and that there should be clinal variation across MN should apply to both the original and current MN wolf populations. This is because the original population would have included the Great Plains gray wolf subspecies in the west and the *lycaon* eastern timber wolf in the east under the Young and Goldman (1944) interpretation or would at least have been receiving dispersers from the gray wolf, *C. occidentalis*, subspecies from only 75 km to the northwest (Fig. 3A). Under the Nowak (1995) interpretation it would have included *C. l. nubilus* from the north and *lycaon* from the east (Fig. 3B). Since map lines between different wolf types are not meant to be taken literally, and given the wolf's extensive dispersal movements of >1000 km straight line (Wabakken et al. 2007), the overlapping and (or) blending of wolf types is expected unless physical or ecological barriers exist.

However, also because of potential long-range dispersal from each of the pure *lycaon* and pure gray wolf populations, occasional pure or high-content *lycaon* or gray wolves from each direction probably lived interspersed with the mixed population in the middle or even far into the ranges of the purer wolves to the east and west. A documented example of an isolated gray wolf population embedded in a *lycaon* × gray wolf hybrid population survives in Pukaskwa National Park along the north shore of Lake Superior. It is surrounded on three sides by *lycaon* × gray wolf hybrids based on recent specimens (Grewal 2001; Kyle et al. 2006). Historically it might have been surrounded by *lycaon* wolves (Young and Goldman 1944).

As wolves were exterminated from the south and west in MN toward the north and east, this original distribution would have been disrupted to some unknown degree. Because the main intact part of the MN population survived in northeastern MN and was continuous with the Ontario wolves, it is reasonable to assume that the type of wolves there would be the highest content *lycaon* wolves in MN even though high-content gray wolves might be found there (Mech and Frenzel 1971). This conclusion does not conflict with the findings of Nowak (2009) that generally MN wolves are morphologically gray because Nowak's MN sample consisted of specimens from 1970 to 1975 after putative gray wolves immigrated there (L.D. Mech and R.M. Nowak, submitted for publication).[3] Nowak's (2009) sample from 1970 to 1975 included only one wolf from MN's eastern-most county, Cook County (Fig. 2), which is where wolves of the lowest body mass were found in 1969–1972 (Van Ballenberghe 1977; Mech and Paul 2008), and where presumably the highest content *lycaon* wolves in MN would have survived.

Wheeldon (2009) using mtDNA haplotypes, Y-intron sequences, and 12 microsatellite loci in a large sample of GLR wolves concluded that his sample is "part of a large homogeneous wolf population extending across Michigan, Wisconsin, Minnesota, and northwestern [more aptly southwestern] Ontario" and that that population is composed of hybrids between *lycaon* and gray wolves. He also suggested that no pure *lycaon* wolves (which tend to hybridize with coyotes in the east and gray wolves to the north and west; Wilson et al. 2000) exist. Fain et al. (2010), also using all three types of genetic markers, concluded that "the recovered WGL [western Great Lakes] population was comprised of *C. lupus*, *C. lycaon*, and their hybrids".

Whatever the proportion of *lycaon*-like and gray-wolf-like animals currently found in MN, however, that should not be taken as necessarily representing the proportion in the original population, as would also be true of WI and MI wolves.

Conclusion

This review of both the available morphological and genetic evidence suggests that the original MN wolves were primarily *lycaon* in eastern MN, gray wolf in western MN, and hybrid *lycaon* × gray in between as Young and Goldman (1944) wrote. The degree of original genetic purity in the east or west remains unknown. Since about 1970, an increasing number of wolves with the larger skulls and wider rostra of gray wolf types have immigrated from Canada (L.D. Mech and R.M. Nowak, submitted for publication).[3] Thus the population since then may contain a higher degree of gray wolf genes than originally, thus explaining Nowak's (1995) revision of MN wolf taxonomy. Probably higher content *lycaon* and gray wolves still occupy the eastern and western ends of the MN wolf range. Most of the current MN population, however, probably consists of hybrids with the proportion and distribution of *lycaon* and gray wolf genes variable, not necessarily the same as in the original population, and with highest content *lycaon* in the east and gray wolf in the west. Morphologically most MN wolves, especially those in the western half of the state, appear to be gray wolves.

To better assess the relative purity of the original and current wolves in northwestern and northeastern MN, two approaches will be necessary. One is to examine the genetics of as many historic specimens as possible from each area. The second is to assess both mtDNA and microsatellites of large samples of recent animals from both areas as Wheeldon (2009), Koblmüller et al. (2009), and Fain et al. (2010) did for the GLR, but also to distribute the sample evenly across wolf range while taking several morphological measurements of the same wolves. This approach would help relate wolf morphology to genetics and presumably better help determine the taxonomic identity of the wolves throughout MN.

As for whether the *lycaon*-like wolf haplotypes found in GLR wolves by various workers are better interpreted as belonging to coyotes (Lehman et al. 1991; Koblmüller et al. 2009) or to a New World eastern wolf, *C. lycaon* (Wilson et al. 2000, 2009; Wheeldon and White 2009; Fain et al. 2010), this review adds little. The coyote interpretation depends on the claim that gray wolves interbreed with coyotes. The *C. lycaon* interpretation depends on the claim that there is little or no definitive evidence to that effect. Of some relevance is the fact that no author reporting on wolf morphology has reported specimens in MN, MI, or WI that they suspected were wolf × coyote hybrids, nor has any such specimen been found in museums. Although Koblmüller et al. (2009) report that their evidence suggests "intensive recent and ongoing hybridization" between GL wolves and coyotes, no recent specimen of such a hybrid has been reported either, nor do the GLR wolves show any coyote trait. This fact is true despite the 2000–3000 wolves that have been examined during 1970–2008 (Mech and Paul 2008; Beyer et al. 2009; Wydeven et al. 2009; and others).

In addition wolves are well known to kill coyotes (Paquet 1992; Berger and Gese 2007) and apparently exterminated them on Isle Royale (Mech 1966). The one exception is a report of wolves and coyotes traveling together, although no hybrids were known to have resulted from them (Thiel 2006).

The only genetic data that might document a gray wolf hybridizing with a western coyote was the statement by Koblmüller et al. (2009) that a western coyote haplotype (*la28*) was "exclusively shared between GL wolves and western coyotes". However, that finding did not appear to be documented in that paper's figures or tables, and it does not rule out the possibility that *la28* could also be found in eastern coyotes not sampled by the study.

Further adding to the confusion is that, although Leonard and Wayne (2008) consider the GL wolves "genetically distinct" and Koblmüller et al. (2009) consider the same specimens as an "ecotype of gray wolves", the latter lumps the GL haplotypes into the coyote clade (Cronin and Mech 2009).

It is true that the wolf in eastern Canada that the Wilson et al. (2000) school considered a coyote-related separate species does hybridize with coyotes in the wild in southeastern Ontario (Kolenosky and Standfield 1975) and in captivity (Kolenosky 1971). The Wilson et al. (2000) school explained that wolf × coyote hybridization as possible because the *lycaon* is more closely related to coyotes. The fact that coyote × *lycaon* hybridization was documented in the east long before genetic assessments were made (Standfield 1970; Kolenosky and Standfield 1975) lends evidence against recent coyote × gray wolf hybridization because that has never been reported. Furthermore, the hybridization in captivity involved a female wolf and a male coyote, whereas the genetic evidence for wolf × coyote hybridization suggested it resulted only from male wolves and female coyotes (Lehman et al. 1991).

Because the two competing interpretations seem to depend on whether evidence is found of coyotes hybridizing with gray wolves, it appears that both interpretations will remain competitive until such hybrids are found or captive-bred or until most wolf geneticists favor one interpretation. For both the historical and recent MN wolf populations, in general, however, the existing morphological data currently seem better explained by Wilson et al. (2000, 2009); Kyle et al. (2006); Wheeldon and White (2009); Wheeldon (2009); and Fain et al. (2010).

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