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Use of cranial characters in taxonomy of the Minnesota wolf (*Canis* sp.)

L. David Mech, Ronald M. Nowak, and Sanford Weisberg

Abstract: Minnesota wolves (*Canis* sp.) sometimes are reported to have affinity to a small, narrow-skulled eastern form (*Canis lupus lycaon* Schreber, 1775) and sometimes to a larger, broader western form (*Canis lupus nubilus* Say, 1823). We found that pre-1950 Minnesota wolf skulls were similar in size to those of wolves from southeastern Ontario and smaller than those of western wolves. However, Minnesota wolf skulls during 1970–1976 showed a shift to the larger, western form. Although Minnesota skull measurements after 1976 were unavailable, rostral ratios from 1969 through 1999 were consistent with hybridization between the smaller eastern wolf and the western form. Our findings help resolve the different taxonomic interpretations of Minnesota skull morphology and are consistent with molecular evidence of recent hybridization or intergradation of the two forms of wolves in Minnesota. Together these data indicate that eastern- and western-type wolves historically mixed and hybridized in Minnesota and continue to do so. Our findings are relevant to a recent government proposal to delist wolves from the endangered species list in Minnesota and surrounding states.

Résumé : On associe les loups (*Canis* sp.) du Minnesota quelquefois avec une forme de l'est de petite taille et à crâne étroit (*Canis lupus lycaon* Schreber, 1775) et d'autres fois à une forme de l'ouest (*Canis lupus nubilus* Say, 1823) plus grande et à crâne plus large. Nous observons que les crânes de loups du Minnesota récoltés avant 1950 sont de taille semblable à ceux de loups du sud-est de l'Ontario et plus petits que ceux des loups de l'ouest. Cependant, les crânes de loups du Minnesota durant la période de 1970–1976 montrent un déplacement de taille vers la forme plus grande de l'ouest. Bien qu'aucune mesure de crânes du Minnesota ne soit disponible après 1976, les rapports des rostres de 1969 jusqu'à la fin de 1999 sont compatibles avec une hybridation entre le loup plus petit de l'est et la forme de l'ouest. Nos données aident à résoudre les différences d'interprétation taxonomique de la morphologie des crânes du Minnesota et concordent avec les preuves moléculaires d'une hybridation récente ou d'une intégration des deux formes de loups du Minnesota. Conjointement, ces données indiquent que les loups des types est et ouest se sont mêlés et hybridés dans le passé au Minnesota et continuent de le faire. Nos résultats sont pertinents compte tenu d'une proposition gouvernementale récente de retirer les loups de la liste des espèces en péril au Minnesota et dans les états adjacents.

[Traduit par la Rédaction]

Introduction

The wolf in Minnesota (MN) and surrounding Great Lakes states has been on the US government's endangered species list since 1967 and was legally protected by the Endangered Species Act of 1973 (Mech 2010). The population has since reached recovery size, so the US Fish and Wildlife Service has proposed delisting the animal. However, the preliminary proposal to delist the wolf in the Great Lakes states recognizes two species of wolves there (*Canis lupus* L., 1758 and *Canis lycaon* Schreber, 1775) (USFWS 2011), a conclusion that is in dispute (vonHoldt et al. 2011). We studied wolf skull measurements that shed further light on the question.

Originally, Goldman (1944) considered the smaller gray wolf subspecies *Canis lupus lycaon* Schreber, 1775 to occupy much of eastern Canada and the United States, and the larger subspecies *Canis lupus nubilus* Say, 1823 to occur

over a large region immediately to the west. He referred all specimens of Minnesota (MN) wolves to *C. l. lycaon*, except for one taken at Crookston, near the North Dakota border, which he assigned to *C. l. nubilus*. Goldman (1944) noted that the skull of *C. l. lycaon* is similar to that of *C. l. nubilus* but smaller, with a much narrower rostrum and also that specimens from eastern MN and Michigan had characteristics intermediate to *C. l. lycaon* and *C. l. nubilus*.

Subsequent assessors of morphology have tended to shift the boundary between the larger and the smaller forms eastward as far as southeastern Ontario. They sometimes have referred all wolves in MN and adjacent western Ontario to *nubilus* (Standfield 1970; Mech and Frenzel 1971; Kolenosky and Standfield 1975; Skeel and Carbyn 1977; Schmitz and Kolenosky 1985; Nowak 1995, 2002, 2003, 2009). However, the latest specimens examined by these studies were from 1976.

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Meanwhile, molecular genetics studies of wolves in the region began with 1989 specimens. Those studies disagree about the identity of these wolves. Some have suggested that *C. l. lycaon* is an entirely separate species which they call *C. lycaon*. They believe that *C. lycaon* is more closely related to *Canis latrans* Say, 1823 (coyotes) than to *C. lupus*, and that MN is part of a zone where *C. lycaon* and *C. lupus* hybridize (Wilson et al. 2000, 2009; Kyle et al. 2006; Wheelodon and White 2009; Fain et al. 2010; Stronen et al. 2010; Wheelodon et al. 2010). In contrast, other genetic studies have concluded that many MN wolves and most wolves to the east have hybridized with *C. latrans* (Lehman et al. 1991; Leonard and Wayne 2008; Koblmüller et al. 2009; vonHoldt et al. 2011).

Because the proper name of the wolf in MN is in dispute, we will use the term “eastern wolves” throughout this manuscript to mean either *C. l. lycaon* or *C. lycaon*. So far, genetic studies have not resolved this controversy, and there have been no recent morphological studies to shed light on the identity of the wolves in this area (Mech 2010). In addition, extensive reduction of the MN wolf population by the 1960s, probable repopulation by larger western-type wolves from Ontario (Mech and Frenzel 1971; Van Ballenberghe 1977), and information about ear lengths (Mech 2011) have complicated determination of the taxonomic identity of MN wolves.

To shed further light on the question of MN wolf identity, we examined collections of skulls of adult wolves (Nowak 1979) from across the range where wolf genetic identity is in question. We used two types of skull measurements: (1) standard *Canis* male skull dimensions (Nowak 1995) and (2) the lengths and widths of rostra as an indicator of relative pointedness (Goldman 1944). We hypothesized that skulls from the eastern part of the wolf range in question would be smaller and the rostra more pointed than those of wolves farther west. This hypothesis is in keeping with the claim that eastern wolves differ from wolves farther west (Goldman 1944; Nowak 1995; Wilson et al. 2000, 2009), and with body-mass data. Body mass of most recently examined MN wolves approximates that of wolves in Riding Mountain National Park, Manitoba, about 500 km northwest of the central point of the MN wolf population (Mech and Paul 2008). The greatest difference in body mass among MN wolves is between those of extreme northeastern MN that were collected during 1969–1972, which weighed the least (Van Ballenberghe 1977), and those from farther west, taken mostly during 1978–2006 (Mech and Paul 2008).

Based on the above information and a review of MN wolf-population history (Mech 2010), we hypothesized that (i) skull dimensions and rostral shape of MN wolves would be intermediate to those of wolves from Algonquin Park in eastern Canada and wolves from the western US because of the hybridization shown by genetics; (ii) traits of wolves collected from northeastern MN before 1950 would be more similar to those collected from Algonquin Park than would those of wolves collected from 1970 to 1976 because of the apparent influx of western wolves in the late 1960s mentioned above; and (iii) traits of wolf skulls in MN collected from 1970 to 1976 would be more similar to those of skulls from the western US. Our findings should contribute to a better understanding of the varying taxonomic views of wolves in eastern North America and of the complex genetic

and morphological information about the identity of MN wolves.

Materials and methods

Skulls

We measured four series of skulls of male wolves ≥ 1 -year-old (following convention; Nowak 1979), including three series used by Nowak (2009): 27 *C. l. nubilus* collected prior to 1930 in the western states of Idaho, Kansas, Montana, Nebraska, Oklahoma, North Dakota, South Dakota, and Wyoming; 23 collected during 1970–1976 in northern MN; 12 collected before 1950 from northeastern MN; and 20 eastern wolves collected during 1964–1965 in Algonquin Provincial Park, southeastern Ontario (Table 1). We considered the sample from the western states to represent the wolf population originally occupying areas west and north of MN (Nowak 1995: Fig. 20) and the Algonquin sample to represent the eastern wolves inhabiting southeastern Canada (Nowak 1995: Fig. 20; Wilson et al. 2000, 2009). Because our pre-1950 skull sample from MN was collected from the northeastern MN counties of Cook, Lake, and St. Louis where Mech and Paul (2008) documented that body mass of wolves was lighter than farther west in MN, we separated 11 specimens from these counties from the 1970–1976 sample for an appropriate comparison with the pre-1950 skulls. Consequently, the skulls in column 4 of Table 1 are a subset of the skulls in column 3. In the analyses, we contrasted the size of the 11 skulls from northeastern MN with the 12 remaining skulls in our 1970–1976 MN sample.

Our first assessment involved 10 measurements of cranial and dental features (Table 1): (1) greatest length of skull; (2) zygomatic width; (3) alveolar length from P1 to M2; (4) maximum width of rostrum across outer sides of P4; (5) palatal width between alveoli of P1; (6) width of frontal shield; (7) height from alveolus of M1 to most ventral point of orbit; (8) depth of jugal; (9) crown length of P4; and (10) greatest crown width of M2 (illustrations of these measurements were presented by Nowak 1995).

For the analysis of the 10 cranial and dental features, we used one-way multivariate analysis of variance (MANOVA) of these 10 features with group membership as the predictor. Because of the high dimension of responses, we also replaced the 10 cranial measurements by their first few principal components based on centered and scaled data (correlation matrix), and repeated the analysis. We did follow-up analysis comparing between pairs of the four groups, either based on the principal components or on each of the 10 individual response variables using the “linear hypothesis” function in the “car” package in R (Fox and Weisberg 2011). Results of all these separate analyses were similar, so we report here only the analysis based on the first principal component.

Rostra

A second assessment involved rostral ratios derived by dividing width (between bases of upper canines) by length (from distalmost end of palate end to outer edges of middle incisors) of a series of skulls different from those used for the above 10 measurements. We made the rostral measurements on skulls from 15 wolves collected in northern MN

Table 1. Means (SE) of 10 measurements of skulls from adult male wolves (*Canis* sp.).

Measure ^a (mm)	1964–1965, Algonquin Park (20)	<1950, NE Minnesota (12)	1970–1976		
			Minnesota (23)	NE Minnesota (11 ^b)	<1930, western US (27)
Greatest length	245.10 (1.40)	248.42 (1.49)	256.30 (1.52)	256.45 (2.77)	256.85 (1.29)
Zygomatic width	132.23 (0.89)	135.00 (1.35)	140.13 (1.39)	141.00 (2.17)	139.50 (0.77)
Alveolar length	82.54 (0.52)	84.10 (0.69)	86.25 (0.59)	87.17 (0.78)	86.24 (0.53)
Greatest skull breadth ^c	76.20 (0.55)	79.13 (0.86)	81.82 (0.78)	82.41 (1.16)	82.34 (0.49)
Palatal width	27.05 (0.34)	30.03 (0.70)	31.97 (0.40)	32.01 (0.64)	31.86 (0.34)
Frontal shield	60.69 (0.83)	60.86 (0.89)	64.30 (1.02)	65.61(1.41)	64.57 (0.75)
Tooth row-orbit height	37.27 (0.52)	37.37 (0.67)	39.46 (0.46)	39.50 (0.59)	39.84 (0.33)
Jugal depth	17.20 (0.22)	18.40 (0.34)	20.00 (0.24)	20.26 (0.34)	19.67 (0.22)
Upper carnassial	24.51 (0.19)	25.08 (0.35)	25.09 (0.18)	25.01 (0.25)	25.70 (0.23)
Upper M2	14.32 (0.19)	13.85 (0.23)	14.20 (0.13)	14.07 (0.20)	13.39 (0.13)

Note: Dates and locations of specimen collections are listed in the column headings followed by sample size in parentheses. For every row in this table, the overall *F* test of equality of means in the groups has a significance level of ≤ 0.002 , regardless of whether the 1970–1976 NE Minnesota wolves are treated as a separate group or if they are combined with the other 1970–1976 Minnesota wolves.

^aSame as in Nowak (1995: 377 and Fig. 3).

^bA subset of the 1970–1976 MN sample in column 3.

^cBetween outer sides of P4.

from 1937 to 1959, on 53 skulls collected in northeastern MN from 1969 to 1999, and on 20 skulls from Idaho, Montana, Nebraska, Oklahoma, South Dakota, and Wyoming collected during 1894–1921 (Table 2). For a series of 20 Algonquin Park skulls collected during 1960–1971, we used the means of the same measurements made independently by three cooperators working with our directions to calculate the ratios.

For the rostral measurements, we analyzed the bivariate (width, length) data by looking first at the within-sample covariance matrices and testing for common principal components (Flury 1988). Follow-up analysis was done using analysis of variance and Tukey's HSD. Computations were done with R (R Development Core Team 2011) using the package *cpcbp* (Bolker and Phillips 2011).

Results

Skulls

Based on the MANOVA, the four group means of the original skull measurements differ (Pillai trace = 1.14, approximate $F_{[30,213]} = 4.36$, $P = 1.0 \times 10^{-9}$). To lessen the effect of assumptions on this test, we also computed a permutation test based on 10 000 simulations, with the resulting significance level ≤ 0.0001 . We repeated this same procedure with the 10 measurements replaced by the first *k* principal components ($k = 1, 2, 3, 4, 5$) based on centered and scaled data, and equivalent results. The first principal component accounted for about 56% of the variation in the 10 measurements and the first 5 measurements accounted for 88% of the variation.

We obtained the Pillai statistics for comparing all possible pairs of groups, applied to the original 10 measurements, and to the first few principal components (Table 3). Tests of both all 10 traits and the first principal component gave similar results except for the comparison of MN 1970–1976 skulls to western US skulls. In the test using all 10 traits, the difference between these two populations is due to only one of the variables, greatest crown width of M2. If this one variable

is removed, the value of *F* decreases to 1.31 and the corresponding significance level is 0.247 before Bonferroni correction (multiplication by 6). We conclude that we have no evidence that these two populations differ, apart from one trait and that the other pairs of groups all differ.

Rostra

For the analysis of rostral ratios, we have measurements on length and width of the rostrum. The aspect of these data of primary interest is pointedness of the rostrum, measured by the ratio width/length. Assuming the rostrum has an approximately circular cross-section, the variable width²/length should be proportional to the volume of the rostrum, and for purpose of display of the data, we have plotted log(pointedness) versus log(volume) in Fig. 1, separately for each of the four samples. The ellipses shown in Fig. 1 give 95% confidence regions for the within-group means; these vary in size because of the differences in sample size between the four groups. The lines drawn on the plot correspond to the principal components of the estimated within-group covariance matrices. In all the samples apart from pre-1950 MN, the first principal component, corresponding to the longer of the two lines, is a combination of log(pointedness) and log(volume), whereas for the pre-1950 MN sample, the first principal component is nearly parallel to the log(volume) axis; thus, log(pointedness) and log(volume) are more nearly independent.

Following the suggestion of a reviewer, we applied the methodology and software provided by McCoy et al. (2006) to test for a common principal component for the four groups. One common principal component is equivalent to proportionality of the covariance matrices for the groups. The test owing to Flury (1988) was performed for both the original data (log(width) and log(length)) and for the data transformed to log(pointedness) and log(volume), and we report here the tests based on the original data because this seems to be most common in the literature. In both cases, the tests suggest no common principal component ($\chi^2_{[3]} = 15.52$, $P = 0.001$; the low *P* corresponds to a lack of fit of the common principal component model). However if the pre-1950 MN sample

Table 2. Series of adult male wolf (*Canis* sp.) skull rostral ratios^a (width/length).

<i>N</i>	Location	Dates	Mean (SD) rostral ratios	Range	Source
20	Algonquin Park	1960–1971	0.214 (0.012)	0.194–0.246	Trent University, Ontario
15	NE Minnesota ^a	1937–1959	0.231 (0.005) ^b	0.220–0.239	University of Minnesota ^c
53	NE Minnesota	1969–1999	0.233 (0.012) ^b	0.206–0.258	University of Minnesota and present study
20	Western US ^d	1894–1921	0.244 (0.011)	0.225–0.266	National Museum of Natural History

^aIncludes two from northwestern Minnesota.

^bAlthough means of these two samples are similar, a bootstrap test of their variances indicates that even considering their disparate sample sizes, the later sample is significantly more variable.

^cBell Museum of Natural History.

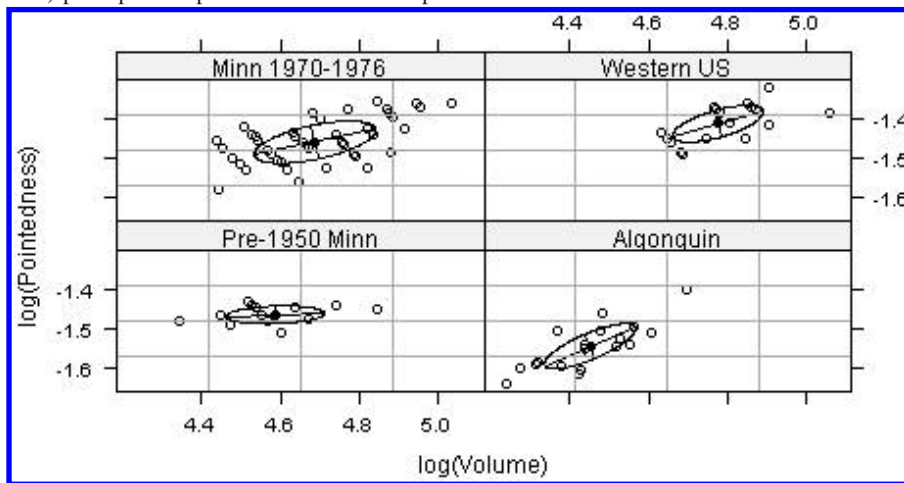
^dIncludes specimens from Wyoming, Idaho, Montana, Oklahoma, South Dakota, and Nebraska.

Table 3. Summary of MANOVA and two-sample *t* tests comparing skull measurements from four samples of wolf (*Canis* sp.) skulls.

Population 1	Population 2	Comparison based on 10 traits		Comparison based on first principal component	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Algonquin	MN 1975–1976	10.68	<0.0001	55.66	<0.0001
Algonquin	Northeastern MN pre-1950	3.08	<0.0001	6.69	0.069
Algonquin	Western US	12.46	<0.0001	65.21	<0.0001
MN 1970–1976	Northeastern MN pre-1950	2.67	0.048	14.08	0.0020
MN 1970–1976	Western US	3.91	0.0018	0.124	1.000
Northeastern MN pre-1950	Western US	2.77	9.0367	17.17	0.0005

Note: Traits are listed in Table 1. All specimens from Minnesota collected during 1970–1976 were combined in this analysis. *P* values have been multiplied by 6 to use the Bonferroni inequality to correct for multiple testing.

Fig. 1. Plot of log(pointedness) versus log(volume) for four samples of wolf (*Canis* sp.) rostra. Ellipses are 95% confidence intervals for the mean of each sample. The differing sizes of the ellipses are caused by differing sample sizes. The crossed lines within each ellipse are the first (longer) and second (shorter) principal component axes of the sample covariance matrices.



is excluded, a common principal component is plausible ($\chi^2_{[2]} = 5.42, P = 0.07$). The data support the hypothesis that the covariance matrix and hence the distribution of (log (width), log(length)) in the pre-1950 MN sample is different from the distribution in the other three samples.

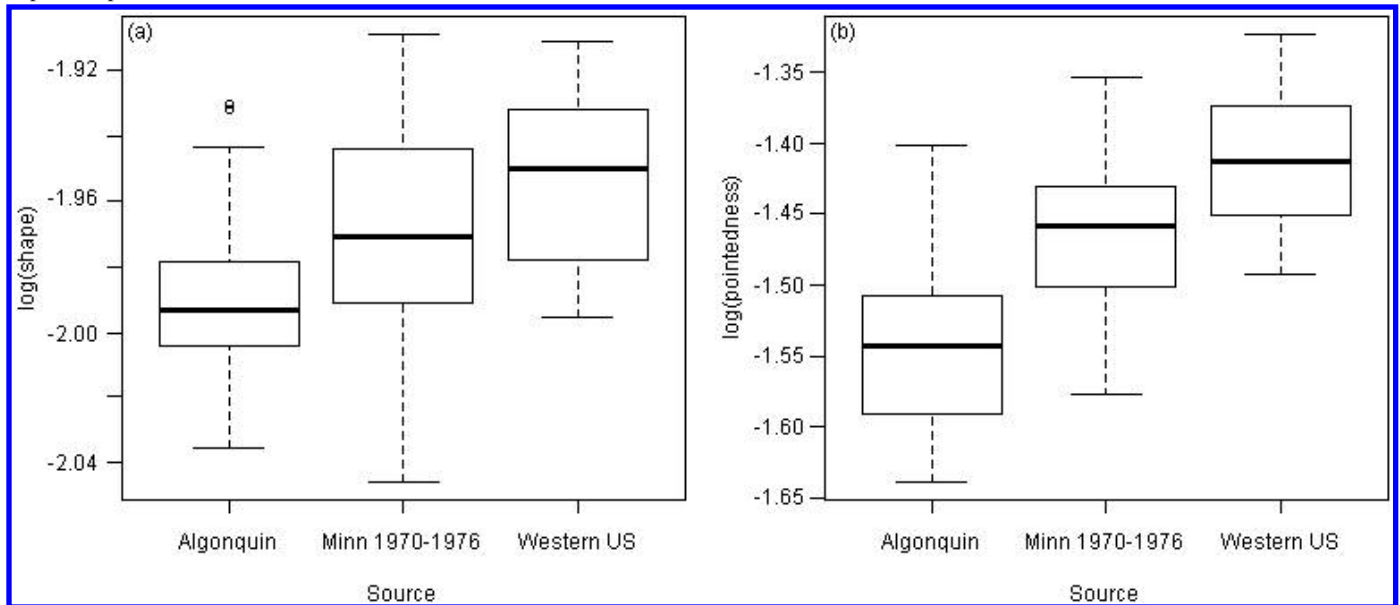
For the three samples that are consistent with the hypothesis of common principal components, we computed a one-way analysis of variance (ANOVA) on both the second principal vector (which we call log(shape), equal to approximately $0.36 \cdot \log(\text{width}) - 0.93 \cdot \log(\text{length})$), which is the same as Burnaby’s back-projection method (Burnaby 1966; McCoy et al. 2006) (Fig. 2a), and for the log of the rostral

ratio (equal to $\log(\text{width}) - \log(\text{length})$) for the three samples excluding pre-1950 MN, as summarized in Fig. 2b. In both cases, the 1969–1999 MN wolf rostra are intermediate between the other two samples; using Tukey’s HSD, the 1969–1999 MN sample is not distinguishable from the western US ($P = 0.07$), whereas for log(pointedness), all three groups (Algonquin, 1969–1999 Minnesota, and western) differ significantly (all *P* values <0.01).

Discussion

Our data support our hypotheses; they also document a shift in the composition of wolves in MN over time. The

Fig. 2. Parallel boxplots of (a) rostral log(shape), the second principal factor from common principal component analysis, and (b) rostral log(pointedness) = log(length/width). Data for the pre-1950 Minnesota sample are omitted because these data do not share a common first principal component. For data sources see Table 2.



overall dimensions of the skulls from northeastern MN collected before 1950 and the sample collected during 1970–1976 indicated that the earlier sample was more similar to the eastern wolf sample, whereas our later sample was almost identical to western wolves. The rostral data suggests that the pre-1950 MN sample was different from the others, but the relationship of more recent MN rostra (1969–1999) to the rostra of eastern and western wolves shows signs of hybridization. This finding probably reflects changes that occurred after 1976 and accords with the genetic data and with information based on ear lengths (Mech 2011).

Our findings about the pre-1950 northeastern MN wolf sample accord with the genetic findings of early eastern wolf influence in MN (Wheeldon and White 2009) and might indicate predominately eastern wolf content in the population at that time. From 1970 through 1976, however, our results indicate that this population was influenced to the point that wolf skull dimensions became almost identical to those of western wolves, at least through 1976. This finding offers an explanation of why the MN wolf population was classified predominantly as *C. l. lycaon* by an early authority (Goldman 1944) but as *C. l. nubilus* by Nowak (1995). A change in composition of MN wolves in the late 1960s was suggested by Mech and Frenzel (1971) and by Van Ballenberghe (1977); Mech (2010) hypothesized that the original wolf population in most of MN consisted predominantly of *lycaon* or of hybrids with high-content *lycaon*. Furthermore, as the original population declined drastically into the 1960s because of human persecution (Fuller et al. 1992), *nubilus*-like wolves immigrated from the north and northwest. Since 1976, however, apparently eastern wolf influence has begun to increase as evidenced by our rostral measurements and recent wolf ear lengths (Mech 2011)

Genetic findings about MN wolves since 1988 indicate that they currently form a homogeneous population of eastern and western hybrids (Wheeldon et al. 2010) or at least a mixture of hybrids and some of each parent species (Fain et al.

2010). The wolf that is listed on the US Endangered Species list is *C. lupus*. At the time of that listing (1978), *C. l. lycaon* was regarded as a mere subspecies. The claim that *lycaon* is a full species, which is still controversial (see above), could greatly complicate the proposed delisting of the wolf population of the western Great Lakes area. Our analysis documents that regardless of the final conclusion about the taxonomic identity of that population, it had historically been a dynamic mixture of eastern- and western-type wolves before, during, and after placement on the Endangered Species List. In that respect, the current biologically recovered population can best be considered a reasonable semblance of what the once-endangered population was.

Other challenges exist in trying to resolve the morphological and genetic data for MN wolves. Genetic samples are lacking from key areas, such as Cook County in the extreme northeastern MN, where even in the early 1970s, there were indications that wolves there were more similar to wolves of eastern Canada (Mech 2009, 2010). In addition, recent specimens do not allow for analysis of former temporal shifts, yet all genetic specimens have been collected since 1988, except for two from central MN taken about 1900 (Wheeldon and White 2009) and one from east-central MN taken in 1892 (Koblmüller et al. 2009).

The fact that our 1970–1976 skulls, which are so similar to those of western wolves, contrast with the genetic findings of hybridization, requires explanation. Those skulls were collected before 1977, but the recent genetic specimens discussed above are all from wolves sampled after 1988. Possibly most of the current hybridization occurred after 1976. This hybridization could have occurred between the western-type (*nubilus*) wolves represented by our 1970–1976 skull sample and higher content eastern wolves that might have remained in areas not represented by our skull sample, or that might have immigrated from Ontario east of MN since 1976. Examination of MN wolf skulls taken after 1976, as well as additional morphological and genetic assess-

ments of historical and modern specimens, are needed to help explain this dilemma and to further determine the taxonomic history and present taxonomic status of MN wolves.

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