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COMMENT

Problems with the claim of ecotype and taxon status of the wolf in the Great Lakes regionMATTHEW A. CRONIN* and
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Koblmuller *et al.* (2009) analysed molecular genetic data of the wolf in the Great Lakes (GL) region of the USA and concluded that the animal was a unique ecotype of grey wolf and that genetic data supported the population as a discrete wolf taxon. However, some of the literature that the researchers used to support their position actually did not, and additional confusion arises from indefinite use of terminology. Herein, we discuss the problems with designation of a wolf population as a taxon or ecotype without proper definition and assessment of criteria.

Koblmuller *et al.* (2009) wrote 'The GL wolf is morphologically distinct from both western grey wolves (*Canis lupus*) and coyotes (*Canis latrans*) (Nowak 2002)'. However, Nowak (2002) did not draw this conclusion nor did his plots of the first and second canonical variables show this (Nowak 2002: Figures 6 and 8). Nowak's (2002: Figure 8) could be interpreted as indicating either overlap between western *C. lupus* and wolves from Michigan or a continuum between the two types. Furthermore, similar analyses by Nowak (2009: Figures 15.1 and 15.2) show complete overlap between Minnesota wolves and western wolves and partial overlap between Michigan wolves and Minnesota and western wolves. Regardless, skull morphology (size and dimensions) is influenced by genetics and environment. Morphological variation is not a definitive indicator of phylogenetic ancestry (and hence taxonomy) or local adaptation (and hence ecotype status) without controlled experimentation. Morphology may indicate ancestry (and be useful in taxonomy—e.g. domestic animal breeds differ in morphology because of ancestry) or environment (and

reflect ecology—e.g. nutrition will influence body size), but these factors must be empirically assessed.

A second discrepancy is found in the Note at the end of Koblmuller *et al.* (2009) stating 'Additional genetic analyses of the GL wolf was recently published by Wheeldon & White (2009) which further supports the conclusions presented here'. On the contrary, Wheeldon & White (2009) concluded that the genetic makeup of historic (*c.* 100 years ago) and extant wolves of the GL region resulted from hybridization between grey wolves (*C. lupus*) and eastern wolves (*Canis lycaon*), whereas Koblmuller *et al.* (2009) reported that the wolf of the GL region has experienced a high degree of ancient and recent hybridization with western grey wolves and coyotes (*Canis latrans*, see also Leonard & Wayne 2008). The genetic data (and mitochondrial DNA, mtDNA, data in particular,) used in these analyses are complicated, and the discrepancy of interpretations arises to some extent from assignment of mtDNA haplotypes to named taxa. Koblmuller *et al.* (2009) found some recent wolves of the GL region had mtDNA haplotypes that occurred in a mtDNA clade with mtDNA haplotypes of western grey wolves, and others had mtDNA haplotypes that occurred in a mtDNA clade with mtDNA haplotypes of coyotes. Historic wolves of the GL region had only mtDNA haplotypes that occurred in an mtDNA clade with mtDNA haplotypes of coyotes. However, Wheeldon & White (2009) reported some of the same coyote clade mtDNA haplotypes (i.e. C1 and C13) in historic wolves of the GL region that they interpreted as *C. lycaon* haplotypes of New World origin. These haplotypes and others were identified by Leonard & Wayne (2008) in wolves of the GL region. Leonard & Wayne (2008) recognized mtDNA haplotypes of historic wolves in the GL region as 'genetically distinct', with an average mtDNA control-region sequence divergence about 6% different from coyotes and 19% different from grey wolves, and they referred to them as the 'GL wolf'. However, Koblmuller *et al.* (2009: Fig. 2) found that historic GL-wolf mtDNA haplotypes cluster in phylogenetic analysis with coyote mtDNA haplotypes, not as a distinct monophyletic group. Wheeldon & White (2009) considered historic mtDNA haplotypes in wolves of the GL region as *C. lycaon*.

These mtDNA analyses were appropriate and the authors (Leonard & Wayne 2008; Koblmuller *et al.* 2009; Wheeldon & White 2009) considered legitimate hypotheses to explain the patterns observed. However, the relationships are not definitive, as evidenced by the different interpretations. It is very important to note that it is not uncommon for mtDNA phylogenetic relationships to be different from the overall relationships of species or populations. For example, there are paraphyletic mtDNA phylogenies between distinct species: mule deer/blacktailed

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deer *Odocoileus hemionus* and white-tailed deer *Odocoileus virginianus* (Cronin *et al.* 1988) and grizzly/brown bears *Ursus arctos*, and polar bears *Ursus maritimus* (Cronin *et al.* 1991). The point is that mtDNA and other molecular patterns can help understand current and historic processes, but do not necessarily reflect species and population status. The use of molecular markers other than mtDNA (as Koblmüller *et al.* 2009 and Wheeldon & White 2009 did) helps to overcome this limitation. We note that the mtDNA and Y-chromosome DNA sequence data and microsatellite DNA allele frequencies analysed by Koblmüller *et al.* (2009) were not accessible in these studies, and should be made available for other workers to assess the results and replicate analyses.

A third problem with the Koblmüller's *et al.* (2009) study is undefined terminology and unclear application of taxonomy. Koblmüller *et al.* (2009) used the terms 'ecotype', 'species and subspecies', 'unique population', 'wolf-like canid', 'discrete wolf taxon', 'population integrity', 'morphologically distinct' and 'hybridization and introgression' without clear definitions or criteria. We recognize that authors must use terms to communicate effectively, and some terms' meanings are assumed to be self evident. We also recognize that Koblmüller *et al.* (2009) and other authors on wolf taxonomy acknowledged the potential problems of interpreting historical and extant patterns of molecular variation (limited samples, lineage sorting, ancient and current hybridization, uncertain use of species and subspecies designations). However, clear and consistent definition of terminology is necessary for formal taxonomic designation or quantification of population status for legal and regulatory implications (e.g. endangered species status of wolves of the GL region). Full discussion and definition of these terms is beyond the scope of this article (see Cronin 2006, 2007), but a few comments are warranted.

With regard to the taxonomic names and origins of the wolf of the GL region, Koblmüller *et al.* (2009) discussed alternative origins (Kyle *et al.* 2006) considering their molecular data:

It is a small subspecies (*C. l. lycaon*) of *C. lupus* (perhaps from *C. lupus* × *Canis rufus* hybridization).

It is a distinct species (*C. lycaon*).

It is a hybrid between *C. lupus* and *C. latrans*.

Regarding subspecies status, it is widely acknowledged that designation of subspecies is quite subjective and many currently named subspecies have not been rigorously assessed (e.g. Wilson & Brown 1953; Mayr 1970; Cronin 1993, 2006, 2007; Zink 2004 and references therein). Also, because there is not a consensus on the species status of *C. lycaon* and *C. rufus* (e.g. Schwartz & Vucetich 2009) interbreeding between the various *C. lupus*, *C. rufus* and *C. lycaon* populations could be considered as either mixing of differentiated groups or simply gene flow among *C. lupus* populations, albeit complicated by potential gene flow with *C. latrans*. We suggest that for North American *Canis* it is wise to avoid typological thinking and designation of formal taxonomic names to what are essentially geographic populations with varying levels of past and

present gene flow. In this context, it is important to use the terms 'hybridization and introgression' carefully to differentiate interbreeding between groups differentiated with definitive criteria from simple gene flow over geography.

Koblmüller *et al.*'s (2009) consideration of the wolf of the GL region as both a 'unique population or ecotype' and a 'taxon' is also problematic because of the lack of definition and criteria. One definition of ecotypes is populations with convergent morphological, demographic and behavioural adaptations to similar ecological conditions (Cronin *et al.* 2005). This is a reasonable ecological designation, although adaptation has not actually been demonstrated in the case of the wolf of the GL region. The morphological differences between the GL wolves and other wolves could be due to either local adaptation (supporting an ecotype designation) or hybridization with coyotes (not supporting an ecotype designation unless the hybrids subsequently adapt to local conditions). The important point is that ecotypes are designated based on ecological criteria, not phylogenetic criteria, and therefore are not taxonomic units.

However, Koblmüller *et al.* (2009) also describe molecular data that support recognition of the wolves of the GL region as a 'discrete wolf taxon' (without naming the taxonomic level or name). Taxonomy is based on phylogenetic relationships, so members of a taxon share more recent common ancestry with each other than with other taxa. Because of gene flow and recent common ancestral populations, phylogenetic relationships at, and below, the species level are seldom definitive. Considering the mixed ancestry of the extant wolves of the GL region including historic GL wolves, other wolves, and coyotes, it is not surprising these wolves have a gene pool different from other wild canids. In addition, there is apparent contradiction by Koblmüller *et al.* (2009) in that they call the wolves of the GL region a discrete taxon but note there is likely recent and ongoing interbreeding with coyotes and other wolves. If they are discrete, there would not be continued gene flow with other groups. Regardless, one could call the wolves of the GL region a taxon (based on ancestry and phylogeny) or an ecotype (based on local adaptation) but the term applied needs definition and assessment of clear criteria. We suggest that the wolves in the GL region can simply be called a wolf population with mixed ancestry. Continuing research on the patterns and processes occurring in the complex mix of canids in the GL region may allow more definitive identification of taxon or ecotype status.

This view allows more focus on the population's ecological and demographic status and does not prevent management and conservation (e.g. the Endangered Species Act can consider distinct population segments in addition to species and subspecies). As discussed by Schwartz & Vucetich (2009), Koblmüller *et al.* (2009) used the term population integrity without clear definition. Integrity could refer to taxonomic 'purity' or individual and population fitness. It is generally acknowledged that the GL wolf population is fit, with abundant genetic variation. However, molecular genetic data indicate the wolf of the GL region is not taxonomically 'pure' as there is evidence of past and ongoing

gene flow among various proposed species and subspecies (Leonard & Wayne 2008; Wheeldon & White 2009). We suggest maintaining a fit wolf population is an important management consideration, regardless of ancestry and molecular genetic patterns (see Schwartz & Vucetich 2009; Wheeldon & White 2009). Designation of the population as a species, subspecies, taxon, or ecotype will remain largely subjective without rigorous use of definitions and assessment of measurable criteria for each term.

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