

A Perspective on the Genetic Composition of Eastern Coyotes

Steven M. Chambers*

Abstract - Way et al. (2010) define a “coywolf” population in the northeastern United States and eastern Canada that originated through hybridization between *Canis lycaon* (Eastern Wolf) and *Canis latrans* (Coyote), but they maintain that it is now genetically uniform and only minimally influenced by either parental species. An alternative interpretation of available data is that this northeastern Coyote population is genetically diverse, substantially more Coyote than Eastern Wolf in its genetic composition, and part of a larger population of Coyotes that interbreeds with a hybrid Coyote/Eastern Wolf population in southern Ontario and western Coyotes in western New York and Pennsylvania.

Introduction

A series of recent papers have provided extensive information on the genetic characteristics of populations of the genus *Canis* in eastern Canada and the northeastern United States (Wilson et al. 2000, 2003, 2009; Grewal et al. 2004; Koblmüller et al. 2009; Kyle et al. 2006; Leonard and Wayne 2007; Rutledge et al., in press; Wheeldon and White 2009). A primary interest of these studies has been the interbreeding between *Canis latrans* Say (Coyote) and *Canis lycaon* Schreber (Eastern Wolf; also has been referred to as Great Lakes wolf), which is considered by some authors (e.g., Nowak 2009) to be a subspecies of *Canis lupus* L. (Gray Wolf), or the result of previous hybridization between Coyotes and Gray Wolves (Lehman et al. 1991). Way et al. (2010) have now extended this series of investigations to include a population of Coyotes in eastern Massachusetts. Way et al. (2010) conclude that, although the Coyote population of the northeastern United States is of hybrid (Eastern Wolf x Coyote) origin, it is relatively uniform in its genetic composition, and is morphologically and genetically distinct from other *Canis*, including Eastern Wolf. They define the range of this population as “east of longitude 80° including New England, New York, New Jersey, Pennsylvania, Ontario, and Quebec,” and propose the vernacular name “coywolf” to reflect its hybrid origin and distinctiveness. A close examination of the genetic data and analysis of Way et al. (2010) and of another recent study that included northeastern Coyotes (Kays et al. 2010a) suggests an alternative genetic characterization of northeastern Coyotes.

Nuclear Microsatellite DNA Variation

The case of Way et al. (2010) for the distinctiveness of the northeastern Coyote population is based largely on two different analyses of nuclear

*Division of Ecological Services, US Fish and Wildlife Service, PO Box 1306, Albuquerque, NM 87103; steve_chambers@fws.gov.

microsatellite DNA variation: STRUCTURE and factorial correspondence analysis. STRUCTURE (Pritchard et al. 2000) is a model-based method for analyzing multi-locus genetic data to identify population clusters or cryptic population structure. The method is very widely applied to microsatellite DNA data. Pritchard et al. (2000) warn that clusters identified by their method may not correspond to “real”, biological populations if individuals have mixed ancestry, or where populations are continuous and exhibit isolation by distance. Schwartz and McKelvey (2009) have further explored the problem of sampling continuous distributions and confirmed that clusters identified by STRUCTURE can sometimes be artifacts of sampling and have no biological meaning. Unfortunately, both hybridization and continuous distribution are evident in the Coyote population of eastern North America, so caution is required before accepting the discreteness of units identified by STRUCTURE.

A close examination of the results of the STRUCTURE analysis (Fig. 2 in Way et al. 2010) reveals that rather than isolation of northeastern Coyotes from Eastern Wolves from southern Ontario, they are genetically connected across the Frontenac Axis where individuals with both Coyote and Eastern Wolf genetic markers are common. This pattern was detected and described in earlier studies (Grewal et al. 2004, Wilson et al. 2009). The abrupt-appearing discontinuity between northeastern Coyotes and “western” Coyotes (from Ohio, North Carolina, and Texas) in Way et al. (2010) can be attributed to sampling pattern: the Coyotes are represented by widely spaced samples from a continuous population. These are the conditions that Pritchard et al. (2000) and Schwartz and McKelvey (2009) warn can lead to recognition of artifacts of sampling as biological clusters.

The factorial correspondence analysis (Fig. 3 in Way et al. 2010) portrays variation among individuals at the 8 microsatellite DNA loci. Visual examination of pattern in these scatter plots can be challenging, but drawing polygons that enclose the area occupied by a particular symbol can be helpful in comparing groupings of the data. In this case, the area occupied by symbols for northeastern Coyotes overlaps with and is transitional between other Coyotes (from Ohio, North Carolina, and Texas) and the Algonquin Provincial Park, ON, population of Eastern Wolves. About 1/3 of the polygon occupied by northeastern Coyotes overlaps with Eastern Wolves, and 1/3 overlaps with the polygon occupied by the pooled sample of Coyotes from Ohio, North Carolina, and Texas. The microsatellite data therefore favor an interpretation of the northeastern Coyote population as a genetic bridge between Coyotes and the Eastern Wolves, rather than as a population that is genetically distinct from and “minimally influenced” by Coyotes and Eastern Wolves.

Mitochondrial DNA Variation

Another recent study of northeastern Coyotes presented information from control region sequences of mitochondrial DNA (mtDNA) (Kays et

al. 2010a). They found that about 1/3 of the Coyotes in the northeast (New England, southern Quebec, New Jersey, and eastern portions of Pennsylvania and New York) had Eastern Wolf haplotypes. This result is consistent with the finding of Way et al. (2010) that 21 of the 67 (31%) Massachusetts Coyotes had the C1 haplotype, which is considered a marker for Eastern Wolves (Wilson et al. 2000). Fewer Eastern Wolf haplotypes were found in Coyotes from western portions of Pennsylvania and New York, and Coyotes from Ohio had only Coyote haplotypes. Kays et al. (2010a) interpret these results as indicating two routes for Coyotes in a recent invasion of the eastern United States: (1) Coyotes invading north of the Great Lakes encountered Eastern Wolves and incorporated Eastern Wolf mtDNA haplotypes into their population as a result of hybridization, and (2) Coyotes invading south of the Great Lakes show no Eastern Wolf influence because Eastern Wolves had been extirpated from that pathway prior to the time of the Coyote immigration. While agreeing with Kays et al. (2010a) about the contribution of Eastern Wolf introgression to northeastern Coyotes, Wheeldon et al. (2010) propose that the pathway that led to contact with Eastern Wolves in southern Ontario was through the lower peninsula of Michigan rather than from Minnesota and north of the Great Lakes. Kays et al. (2010b) responded with new mtDNA data that indicate the presence of northeastern Coyote mtDNA haplotypes in Coyotes from Minnesota and the upper peninsula of Michigan. Kays et al. (2010b) provide additional support for a northern route from museum records of pre-1940 Coyote presence in Minnesota, the upper peninsula of Michigan, and Ontario, which is consistent with Nowak's (1979:15) finding, based on historical reports, that eastward Coyote expansion was more rapid through a northern route.

Genetic Composition of the Eastern Coyote Population

Way et al. (2010:10) argue that the "uniform genetic makeup" and minimal genetic influence from other *Canis* of the northeastern Coyote population indicate that it is an "emerging new species" that should be recognized on a par with other species of North American *Canis*. The genetic composition of the northeastern Coyote population does not support this interpretation.

The northeastern Coyote population defined by Way et al. (2010) has a genetic composition that is about 1/3 Eastern Wolf in both mtDNA sequences (Kays et al. 2010a, Way et al. 2010) and nuclear microsatellite variation (Way et al. 2010). Its genetic composition is therefore predominantly Coyote, but there has been substantial introgression from Eastern Wolves. It is therefore not a genetically uniform population. Because mtDNA does not recombine and is maternally inherited, individuals have either the mtDNA of one species or the other. We cannot discern with mtDNA alone the extent of hybrid ancestry of any given individual. The nuclear microsatellite DNA does provide some information on the ancestry of individuals with respect to the two species. Both STRUCTURE and factorial correspondence analysis of Way et al. (2010:Figs. 2 and 3) indicate that some northeastern Coyotes

have a microsatellite DNA composition similar to Eastern Wolves, but many show no Eastern Wolf influence. The northeastern Coyote population is therefore not uniform, but highly variable with respect to the relative contributions of the two species to the ancestry of individuals.

The northeastern Coyote population defined by Way et al. (2010) is also not separate, disjunct, or discrete with respect to other canids. There is geographic and genetic continuity of northeastern Coyotes and the hybrid Coyote/Eastern Wolf population of southern Ontario (Grewal et al. 2004, Kays et al. 2010a, Wilson et al. 2009). The pattern of mtDNA variation in Coyotes south of the Great Lakes is strongly suggestive of continuity, with Eastern Wolf influence decreasing in western New York and Pennsylvania, and absent from a sample of 30 Coyotes from Ohio (Kays et al. 2010a). Coyotes continued their invasion from the northeast down the Appalachian Mountains to the south (Nowak 1979:16), so similar genetic continuity from north to south is also likely.

An alternative interpretation and description of the genetic composition of Coyotes in eastern North America is that the northeastern Coyote population defined by Way et al. (2010) is part of a larger population of Coyotes in eastern North America. It hybridizes (or hybridized) with Eastern Wolves in southern Quebec and Ontario. The only discernable pattern is a decrease in genetic influence of Eastern Wolves from eastern New York and Pennsylvania to Ohio. Overall, the Coyote population of eastern North America is diverse, with influence of Eastern Wolf introgression probably decreasing from east to west and north to south. This interpretation is consistent with behavioral and morphometric studies that suggest the influence of Eastern Wolf hybridization on northeastern Coyotes, but primarily group them with other Coyotes (Lawrence and Bossert 1969, Nowak 1979, Silver and Silver 1969).

Schwartz and Vucetich (2009) have made recommendations on the resolution of questions about defining populations and taxa of *Canis* in the Great Lakes region. These include geographic sampling that does not leave gaps that can lead to misinterpretation of genetic discontinuities, and the use of a variety of genetic markers to more comprehensively characterize patterns of geographic variation. Reporting of genetic information on a finer scale (Schwartz and McKelvey 2009) is needed to confirm possible genetic discontinuities that might indicate separation of populations. Finer-scale sampling of information from diverse genetic markers (mtDNA, Y-chromosome haplotypes, and microsatellites) can provide a better understanding of the relative contributions of different species to the ancestry of the northeastern Coyote population and its relationship to other Coyotes.

Vernacular Names and Nomenclature

The name “coywolf” was coined by Way et al. (2010) to apply to the population that they defined in the northeastern United States and eastern Canada. If common or vernacular names are deemed advantageous for some purpose, they should accurately describe some attribute of the population to

which they are applied. In this case, coywolf implies a group that is as much or more Eastern Wolf than Coyote, which is not supported by the available genetic information. The canids in this area should be referred to as Coyotes. If a more restrictive name is required, I suggest “northeastern Coyote”, but users should recognize that these animals are only a part of a larger Coyote population that extends to the west and south.

Vernacular names can cause unnecessary confusion and controversy when applied in biological situations that are already complex and contentious, such as those involving North American canids (e.g., the exchange on use of the term “Great Lakes wolf” [Kays et al. 2010b, Wheeldon et al. 2010]). Coining and application of vernacular names to any convenient group of populations should be discouraged, unless they apply to taxa that have been, or are in the final stages of being, formally described as species or subspecies. Otherwise, these names can misleadingly imply that such names have taxonomic standing that is not justified. Even when vernacular names are objectively descriptive and may have some practical use, it must be recognized that they have no standing under the International Code of Zoological Nomenclature (ICZN 1999).

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