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## Letter to the Editor

### Wolf Subspecies: Reply to Weckworth et al. and Fredrickson et al.

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Colleagues disagree with statements in our discussion (Cronin et al. 2015) regarding subspecies taxonomy of wolves (*Canis lupus*) in southeast Alaska (Weckworth et al. 2015) and the southwest United States (Fredrickson et al. 2015). Following the presentation of results of single nucleotide polymorphism (SNP) variation in several populations of wolves in North America, we discussed other genetic data and stated that the results “do not support a subspecies designation of wolves in southeast Alaska” (*C. l. ligoni*) and that designation of a Mexican wolf (*C. l. baileyi*) subspecies “is of questionable validity.” Fredrickson et al. and Weckworth et al. provide information and insights that support the Mexican wolf subspecies designation and the southeast Alaska subspecies designation, respectively. We and they discuss the same data, so this is essentially a “lumper-splitter” (e.g., Mayr 1982, p. 240) disagreement over subspecies, and whether a degree of genetic differentiation, or strict phylogenetic independence, is needed for subspecies designation. Because subspecies and taxonomy in general, may not be the focus of many readers of the *Journal of Heredity* who work in agriculture, medicine, and conservation, we provide insights from the literature to explain the concepts relevant to our thinking on this topic. This is important because of the potential for misconceptions of classic principles and literature of evolutionary biology (Karl et al. 2012).

#### Taxonomic Considerations

It is important to first recognize that the contrasting views of Cronin et al., Weckworth et al., and Fredrickson et al. (and references therein) exemplify the long-standing uncertainty and lack of consensus on animal subspecies in general. This has been the case since the classic critique of subspecies by Wilson and Brown (1953), who were convinced that the subspecies concept was “the most critical and disorderly area of modern systematic theory...,” and that “...the subspecies trinomial ... in its assumed function as a formal means of

registering geographic variation within the species it tends to be both illusory and superfluous.”

Consider these insights on subspecies by other prominent evolutionary biologists:

Mayr (1970): “This concept of the subspecies is fallacious. Species are not composites of uniform subtypes-subspecies-but consist of an almost infinite number of local populations, each in turn (in sexual species) consisting of genetically different individuals... The better the geographic variation of a species is known, the more difficult it becomes to delimit subspecies and the more obvious it becomes that many such delimitations are quite arbitrary.”

Vanzolini (1992, p. 189): “... present applications of the subspecies concept are uneven, frequently undocumented, and lead to no improvement of either evolutionary theory or practical taxonomy.”

Futuyma (1998): “No criteria specify how different populations should be to warrant designation as subspecies, so some systematists have argued that the practice of naming subspecies should be abandoned.”

Ehrlich (2000, p. 49, 291): “Widespread species thus can be divided into any number of different sets of ‘subspecies’ simply by selecting different characteristics on which to base them,” ... “As is the case with other species, geographic variation in human beings does not allow *Homo sapiens* to be divided into natural evolutionary units. That basic point...has subsequently been demonstrated in a variety of organisms... and use of the subspecies (or race) concept has essentially disappeared from the mainstream evolutionary literature.”

Zink (2004): “Mitochondrial DNA sequence data reveal that 97% of ...avian subspecies lack the population genetic structure indicative of a distinct evolutionary unit....A massive reorganization of classifications is required so that the lowest ranks, be they species or subspecies, reflect evolutionary diversity. Until such reorganization is accomplished, the subspecies rank will continue to hinder progress in taxonomy, evolutionary studies and...conservation.”

Awise (2000, p. 308): "In intermediate situations (and also in hybrid settings), educated nomenclatural judgments will remain necessary at species and subspecies levels."

Recognizing there is a "subspecies problem," Ryder (1986) suggested a category, evolutionarily significant units (ESU), to supplant subjective subspecies and help conservation of important intraspecific groups. However, the subsequent proliferation of terms, all referring to intraspecific populations, led to considerable redundancy, lack of consistency, and the same subjectivity of subspecies (see Cronin 2006). Regarding ESU, Awise (2000) notes:

"Any such empirical suggestion is arbitrary to some extent because there can be no clean line of demarcation along the continuum of possible magnitudes of population genetic differentiation or inferred temporal depths of population separation. Consider, for example, the criteria noted above that were intended to answer 'how much difference is enough?' for ESU qualification. Under any such guidelines, uncertainties remain: How many or what fraction of nuclear loci must show significant allele frequency differences for populations to warrant ESU designation?; How many or what fraction of individuals who carry heterotypic mtDNA lineages would disqualify a population from ESU status?; What magnitude of nucleotide sequence divergence between mtDNA clades is necessary for ESU recognition? Any universal definition that demarcates ESU status from non-ESU status is arbitrary to some extent and fails to concede that some situations truly are intermediate."

So regardless of terminology, we are left with the reality that intraspecific groups (e.g., subspecies, populations, ESU, distinct population segments-DPS etc.) are genealogically indefinite because of gene flow and recent common ancestry. However, subspecies, unlike other named population units, have the *distinction of being part of the formal taxonomic system*. In this regard, the key point to consider, as we note in our discussion (Cronin et al. 2015), is that biological taxonomy (i.e., classification of organisms) is based on phylogeny (i.e., genealogy) as noted by Darwin (1859, p. 391):

"All the ... rules and aids and difficulties in classification may be explained, ...on the view that the Natural System is founded on descent with modification;-that the characters ...are those which have been inherited from a common parent, *all true classification being genealogical*;-that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not...the mere putting together and separating objects more or less alike." (Our emphasis).

This is a critical point. As part of the formal taxonomic system, subspecies are genealogical units (i.e., phylogenetic units) as defined by Awise and Ball (1990):

"Subspecies are groups of actually or potentially interbreeding populations, phylogenetically distinguishable from, but reproductively compatible with other such groups. Importantly, the evidence for phylogenetic distinction must normally come from the concordant distributions of multiple, independent, genetically based traits."

Agricultural genetics readers of this journal will recognize that recognized plant varieties and animal breeds with distinct pedigrees fit this definition. However, subspecies of wild species do not have documented pedigrees, resulting in uncertainty of genealogy. It is the unique position of subspecies in the taxonomic system, as groups that are reproductively compatible, that results in indefinite phylogenetic relationships among them.

## Wolf Subspecies

With regard to wolves in southeast Alaska, Weckworth et al. wrote that we assert wolves in southeast Alaska are not a subspecies, and that we concluded our SNP data do not support a subspecies designation of wolves in southeast Alaska. This is not entirely accurate. We referred to our SNP data and other data for microsatellite DNA and mitochondrial DNA (mtDNA) to state that: "These results indicate that wolves in southeast Alaska are not a genetically isolated or monophyletic population, and do not support a subspecies designation of wolves in southeast Alaska." Weckworth et al. also make several points about subspecies subjectivity and criteria, and we refer the reader to the previous section for this topic.

Briefly, mtDNA haplotypes of wolves in southeast Alaska (summarized by Chambers et al. 2012) are not monophyletic and some haplotypes in southeast Alaska wolves also occur in other regions. One haplotype (*lu38*) is shared by wolves in southeast Alaska, coastal and interior British Columbia, interior Alaska, the Northwest Territories Canada, and historical samples from Kansas and Nebraska (Table 5 of Chambers et al. 2012). Regarding our SNP data, allele frequencies vary among wolves from different parts of southeast Alaska and wolves in adjacent regions (British Columbia-BC, interior Alaska) and the northern U.S. Rocky Mountains (that are derived from BC and adjacent Alberta populations, Table 1). There are relatively small  $F_{st}$  values between the northern southeast Alaska mainland and these other regions, intermediate  $F_{st}$  between the southern southeast Alaska mainland and these other regions, and large  $F_{st}$  between the southeast Alaska islands and these other regions. The range of  $F_{st}$  values within southeast Alaska encompasses the range of  $F_{st}$  between southeast Alaska and these other regions. These data (like the mtDNA data) could reflect genetic drift and/or recent colonization and gene flow between other regions and parts of southeast Alaska, particularly the northern mainland.

With regard to the Mexican wolf subspecies, there are 2 reasons why we think this subspecies designation is questionable: There is not unequivocal phylogenetic distinction of Mexican wolves, and the extant animals may not represent enough of the native population to properly assess taxonomy. Fredrickson et al. contend that the "near-monophyly" of mtDNA justifies the subspecies status of Mexican wolves. Perhaps, but the lack of complete monophyly and shared haplotypes with other regions do not support phylogenetic distinctiveness, and thus do not support subspecies status in our view. One's view of subspecies depends on how rigorous one is with regard to the criterion of phylogenetic distinctiveness. Fredrickson et al. also state that the founding of extant Mexican wolves from only 7 animals is not relevant to whether Mexican wolves are a subspecies. We agree. However, we think it is relevant that the founding population of 7 wolves probably does not represent enough of the (exterminated) native populations to adequately characterize their genetic variation and potential phylogenetic distinctiveness (i.e., subspecies status). Use of historical samples provides insights (Leonard et al. 2005), but sampling is still limited. Fredrickson et al. also note there may have been a zone of intergradation of Mexican wolves and wolves to the north, and without characterizing this zone and the rest of the Mexican wolf's native range we cannot be definitive about phylogenetic distinctiveness.

With regard to the issue of dog (*Canis familiaris*) ancestry in extant Mexican wolves, we cited others who reported the possibility of dog ancestry in the captive animals, and we acknowledged this may be improbable or of small genetic importance to the extant population. However, the potential for dog (or coyote, *Canis latrans*) ancestry in the extant population is relevant to assessing subspecies status and deserves mention.

**Table 1.**  $F_{st}$  values for SNP data for wolf populations in southeast Alaska (SeAk), interior Alaska (IntAk), Idaho (Id), Montana (Mt), Wyoming (Wy), and British Columbia (BC). Idaho, Montana, and Wyoming comprise the northern Rocky Mountains (NRM). Data from Cronin et al. (2015)

		BC	IntAk	Id	Wy	Mt	SeAk1A	SeAk1B	SeAk1C	SeAk1D	SeAk2	SeAk3
Southern SeAk mainland	SeAk1A <sup>1</sup>	0.1373	0.1793	0.1549	0.1643	0.1886						
Southern SeAk mainland	SeAk1B <sup>1</sup>	0.1021	0.1458	0.1136	0.1286	0.1491	0.0394					
Northern SeAk mainland	SeAk1C <sup>1</sup>	0.0638	0.0929	0.0741	0.0872	0.1025	0.1018	0.0621				
Northern SeAk mainland	SeAk1D <sup>1</sup>	0.0607	0.0740	0.0430	0.0785	0.0954	0.2106	0.1596	0.0912			
SeAk Islands	SeAk2 <sup>1</sup>	0.1849	0.2247	0.2101	0.2188	0.2441	0.1239	0.1139	0.1226	0.2811		
SeAk Islands	SeAk3 <sup>1</sup>	0.1681	0.2106	0.1935	0.2033	0.2267	0.0797	0.0344	0.1219	0.2462	0.1140	
Southern southeast AK mainland intermediate $F_{st}$ from BC, IntAK, NRM							Fst = 0.10-0.19					
Northern southeast AK mainland small $F_{st}$ from BC, IntAK, NRM							Fst = 0.04-0.10					
Southeast AK Islands large $F_{st}$ from BC, IntAK, NRM							Fst = 0.17-0.24					
Within southeast AK small to large $F_{st}$							Fst = 0.03-0.28					

<sup>1</sup>number indicates Alaska Game Management Unit-GMU

In both southeast Alaska wolves and Mexican wolves, there is not mtDNA monophyly and haplotypes are shared with other regions. In the case of Mexican wolves, we have limited ability to characterize the exterminated native populations. In the case of southeast Alaska wolves, allele frequencies in southeast Alaska and adjacent regions might reflect recent common ancestry and gene flow. Weckworth et al. and Fredrickson et al. support subspecies designations and we feel the data do not support subspecies designations. Of course, neither view is right or wrong in an absolute sense, considering the subspecies issues described above.

## Practical Considerations

Haig et al. (2006) noted:

“Among taxonomists, definitions of subspecies are a source of considerable disagreement...the scientific community has some level of comfort with the subjective nature of subspecies classification...”

It may be appropriate for taxonomists to accept subjectivity and agree to disagree on subspecies designations. However, when there are legal and regulatory implications, such as with the US endangered species act (ESA), scientists should not be comfortable with subjectivity. The ESA defines species as “species, subspecies, and distinct population segments” and the wolf in southeast Alaska and the Mexican wolf are being considered as endangered subspecies. The ESA also mandates use of the best available science. The question is: Who decides on subspecies designations in such cases? Given the general uncertainty of subspecies and the increasing number of subspecies designations that are not supported by genetic data (see Cronin et al. 2015; Zink 2015) we propose that consideration of subspecies for the ESA is not warranted. Perhaps the recognition that population variation can be meaningfully characterized without subspecies designations (e.g., Wilson and Brown 1953; Ryder 1986; Cronin et al. 2015; Fredrickson et al. 2015; Weckworth et al. 2015) can lead to such a change.

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