

In response to your request to review publications on sage-grouse to evaluate whether the Gunnison sage-grouse is a listable entity, I have reviewed the following literature:

American Ornithological Union, 1998, Checklist of North American Birds, 7<sup>th</sup> ed., p. 119.  
American Ornithological Union, 2000, [Checklist Supplement] *The Auk* 117:847-858.  
Hupp and Braun, 1991, *Wilson Bulletin* 103:255-261.  
Kahn, et al., 1999, *The Auk* 116:819-824.  
Oyler-McCance et al., 1999, *Molecular Ecology* 8:1457-1465.  
Oyler-McCance et al., 2005, *Journal of Wildlife Management* 69:630-637.  
Young et al., 1994, *Animal Behavior* 47:1353-1362.  
Young et al., 2000, *Wilson Bulletin* 112:445-453.

In this review, I follow the recommendations of Young et al. (2000) in using the common name Gunnison sage-grouse for populations known under the scientific name *Centrocercus mimimus*, and sage-grouse for populations known as *Centrocercus urophasianus*.

The most striking evidence bearing on the taxonomic standing of Gunnison sage-grouse is the unique reproductive display behavior exhibited by Gunnison males. Young et al.'s (1994) data from their comparison of behavior between sage-grouse from Mono, California, and Jackson, Colorado, is strong evidence that these behaviors are highly conserved across the range of the sage-grouse. The reasonable interpretation is that there is strong selection maintaining the constancy of display behavior across the range of the species. In contrast, the display behavior (including associated plumage differences) of Gunnison sage-grouse is strikingly different (despite being geographically closer to Jackson than is Mono) and indicates population history separate from sage-grouse. This is taxonomically important because of the role of female choice in these lek breeding systems; reproductive isolation to the point of species formation can rapidly arise when there are changes in display behavior. It is therefore not surprising that Young et al. (2000, citing Young's 1994 PhD dissertation, which I have not seen) report that females of sage-grouse from Colorado and Gunnison sage-grouse "avoid playbacks of male courtship vocalizations that differed from the vocalization of their local population." The importance of these types of changes in breeding behavior to formation of species is well-documented; there are many more studies on this process in various organisms than the few cited in these papers. The data on the divergence in courtship display between sage-grouse and Gunnison sage-grouse is convincingly presented by Young et al. (1994).

The mitochondrial DNA (mtDNA) data of Kahn et al. and Oyler-McCance et al. do not show the kind of fixed haplotype differences or the "reciprocal monophyly" that some recent workers would demand for recognition of separate species, but they do show that sage-grouse and Gunnison sage-grouse have led separate evolutionary histories and not interacted reproductively for some time. One haplotype is nearly fixed in Gunnison sage-grouse, but is also present—usually at low frequencies—in sage-grouse samples. Another interesting feature is the G haplotype found only in Gunnison sage-grouse, and at a low frequency. The suggestion by the authors that it arose after the split between Gunnison sage-grouse and sage grouse is reasonable, and is further evidence that there has not been recent reproductive interaction that would have allowed G to spread to sage-grouse populations. I was pleased to see Oyler-McCance et al.'s (1999) use of analysis of molecular variance (AMOVA) to analyze the mtDNA data. This

method partitions the genetic variance into components that represent different groupings of population and is a good way to test the correspondence of genetic variation with various hypotheses of geographic and/or geographic structure. They found that 65% of the total variance was accounted for by the level of classification separating sage-grouse from Gunnison sage-grouse. This is a large component and indicates significant genetic difference despite the lack of fixed haplotype differences between sage-grouse and Gunnison sage grouse.

As I mentioned in the previous paragraph, mtDNA haplotypes do not show reciprocal monophyly between sage-grouse and Gunnison sage-grouse. I do not believe that this, or any other single criterion, should be used as the sole standard for recognizing species. This is a one-dimensional criterion, and species formation is a multi-dimensional process. Reciprocal monophyly is time-dependent on a time scale that is generally much longer than for achieving reproductive isolation, which can take place especially rapidly (on an evolutionary time scale) with species with the kind of complex mating and recognition behavior seen in these birds. It also appears to me that the broader phylogenetic criterion of species being distinguished by diagnosable differences is met here by the behavioral and size differences between sage-grouse and Gunnison sage grouse.

Valid criticisms of mtDNA sequences as population markers are that they are inherited as a single locus, and they may provide a misleading picture if there is sex-biased dispersal. These disadvantages (there are certain positive advantages as well) can be addressed by combining mtDNA with analysis of nuclear gene markers. The microsatellite DNA loci used in the Oyler-McCance et al. studies are just such nuclear markers. Although I would prefer to have seen the allele frequency tables of the microsatellite data published in these papers so I could directly examine the differences locus-by-locus, it appears that some journals discourage this. Nevertheless, the analysis and presentation of the microsatellite data by different tree-building methods in the 1999 paper give a consistent picture separating Gunnison sage-grouse from sage-grouse.

From the standpoint of the formal procedures of taxonomy, the formal description of the species by Young et al. (2000) fully satisfies the requirements of the International Code of Zoological Nomenclature, and provides a convincing review of the supporting evidence.

The 1998 AOU Checklist account of the sage-grouse included a note that the Gunnison Basin populations represented an unnamed species. From this it appears that the authors of that portion of the Checklist were already convinced of the species-level validity of Gunnison sage-grouse, which they formally recognized in the revised Supplement to the Checklist published in *The Auk* (AOU 2000). Interestingly, they attribute the scientific name of the Gunnison sage-grouse, to Bradbury and Vehrencamp, who apparently used the name and provided enough of a description to have (mostly likely inadvertently; I have not seen their book) effectively described the species in their 1998 book, *Principles of Animal Communication*. Nevertheless, the Young et al. (2000) description still provides an essential service by including a detailed description, identifying supporting evidence, and designating type material. The views of the AOU's Committee on Classification and Nomenclature, as published in the Checklist and its Supplements, deserve careful consideration, as they express a philosophy that taxonomic changes will not be recognized unless "substantial and convincing evidence is published." Pertinent to the issue of

Gunnison sage-grouse, the Committee identified in the 2000 Supplement includes genetic expertise.

In summary, there is significant discontinuity between sage-grouse and Gunnison sage-grouse in behavior, plumage, size, and genetic composition. I do not believe that the genetic data and the behavioral/plumage differences are incompatible; because sexual selection can accelerate evolution of secondary sexual characteristics so that the behavior has simply evolved at a greater rate than genetic processes leading to genetic monophyly or fixation. The documented differences are sufficient to satisfy the discreteness criterion of our DPS policy, and in my view are of taxonomic significance. Because the type of differences seen involve reproductive behavior and reproductive isolation, I believe that species-level recognition of Gunnison sage-grouse is well supported. In direct response to your question, I believe that the Gunnison sage-grouse is a listable entity in the sense that it meets the definition of "species" under the Endangered Species Act.