

Framework for Identifying Greater Sage-grouse Conservation Units and Potential Distinct Population Segments

This document provides the framework for identifying conservation units of the Greater Sage-grouse (*Centrocercus urophasianus*) and evaluating those conservation units under the 1996 Distinct Population Segment (DPS) Policy (USFWS and NMFS 1996). The purpose of providing this framework is to ensure that decisions regarding identification and evaluation of potential DPSs are transparent, reasoned, and take into account the specific life history, population ecology, and genetic makeup of greater sage-grouse. The framework consists of two parts. **Part 1** explains our framework for identifying conservation units using information from studies of Greater sage-grouse movement ecology and genetic connectivity. **Part 2** provides a species-specific framework for formally evaluating the discreteness and significance of the conservation units as potential DPSs identified in Part 1.

Part 1 – Framework for Identifying Conservation Units

A central tenet of conservation biology is the conservation of genetic diversity and adaptive differences within a species or subspecies. Identifying intraspecific units is critical in developing effective strategies for the conservation of genetic resources and the adaptive potential of a species. Implementers of the Endangered Species Act (ESA) recognized this need when they developed the DPS Policy. The stated purpose of the Services' DPS policy is to allow USFWS and NOAA to protect and conserve species and the ecosystems upon which they depend before large-scale decline occurs that necessitates listing a species or subspecies throughout its entire range. The preamble to the policy articulates the Service's interpretation of the ESA to support the interrelated goals of **(1) conserving genetic resources** and **(2) maintaining natural systems and biodiversity over a representative portion of their historic occurrence**. Thus, the DPS policy embraces a dual purpose, to recognize both of these intentions, without focusing on either to the exclusion of the other. These principles guided our framework for identification of conservation units that we would then evaluate to determine whether they met the more specific criteria in the DPS policy.

Greater Sage-grouse Populations

As a first step toward identification of conservation units we sought to identify discrete populations of Greater Sage-grouse because populations are the primary units of evolution (Mayr 1963) and thus are useful units for evaluating genetic variation across a species' range. Connelly et al. (2003) defined a breeding population as a group of sage-grouse associated with 1 or more occupied leks in the same geographic area separated from other leks by >20km. Subsequently, Connelly et al. (2004) identified 41 "relatively discrete" populations, defining those populations as concentration areas of leks separated from the nearest adjacent concentration of leks by at least 30km and /or separated by unsuitable habitat such as mountain ranges, desert, or large areas of cropland (Fig. 1). As Connelly et al. (2004) noted, many of these populations are physically isolated, while others are connected by narrow corridors of sagebrush habitat.

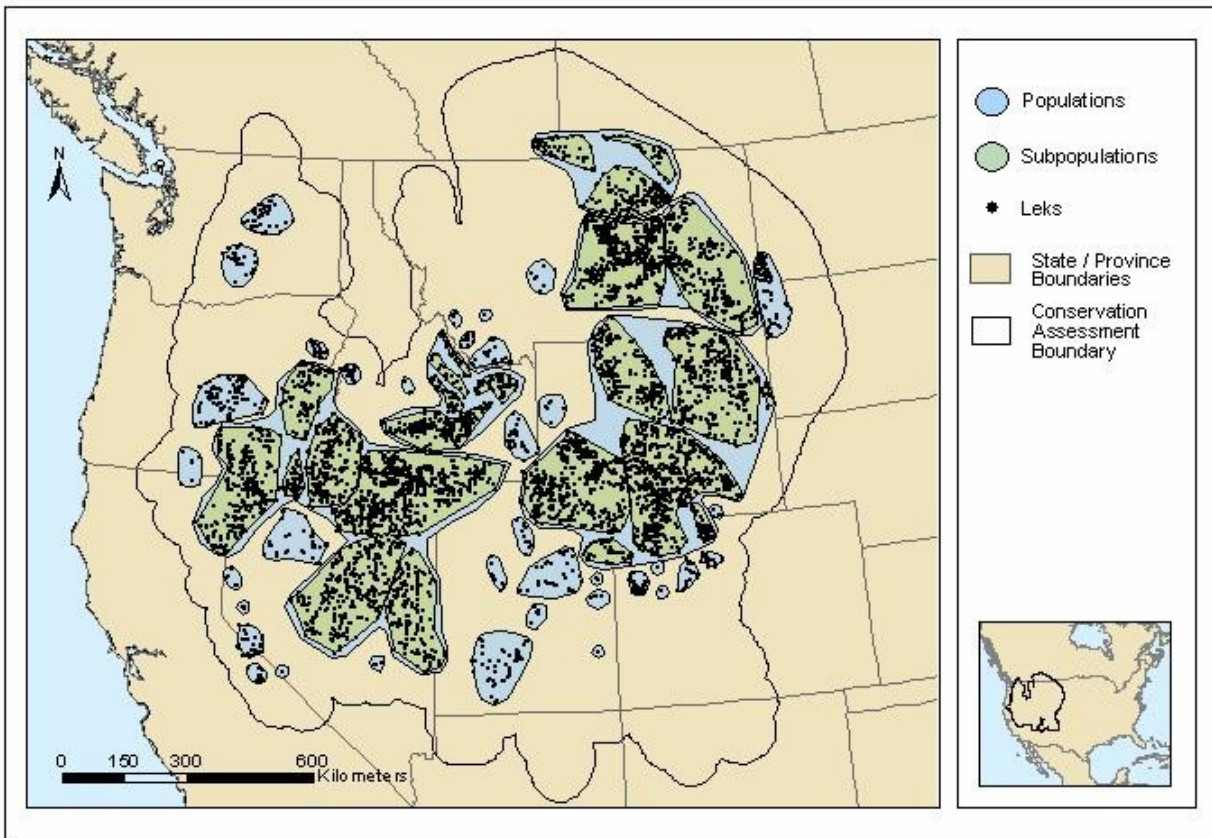


Figure 1. Populations and subpopulations of sage-grouse as identified by Connelly et al. (2004), Fig. 6.37.

Although each of these populations may be somewhat separated demographically, movement has been documented between some of the populations identified by Connelly et al. (2004). Thus, we decided to evaluate how best to group populations where there may be some dispersal or genetic connectivity to define conservation units that captured the geographic and genetic breadth of the species. This framework proposes that four pieces of information are essential to inform this grouping: (1) genetic information, (2) greater Sage density, (3) Greater Sage-grouse movement ecology and population connectivity, and (4) anthropogenic barriers to dispersal.

Greater Sage-grouse Genetics

Ideally, we would look to the genetic makeup of each of these potentially discrete populations to evaluate levels of gene flow and genetic uniqueness. Unfortunately, genetic data are not available for all 41 populations identified by Connelly et al. (2004). Nevertheless, a range-wide evaluation of greater

sage-grouse population genetics using multiple-loci was available that included samples from many of these populations (Oyler-McCance et al. 2005).

Oyler-McCance et al. (2005) analyzed both mitochondrial DNA (mtDNA) and microsatellite DNA. mtDNA is maternally inherited without recombination, making it a more conserved marker that is useful for identifying species, subspecies, and conservation units (Wan et al. 2004). Microsatellites, short tandem repeats in nuclear DNA, are subjected to recombination and evolve orders of magnitude faster than mtDNA. Thus, microsatellites provide a powerful tool for analyzing recent gene flow (Wan et al. 2004).

Oyler-McCance et al. (2005) grouped populations into genetic clusters based on microsatellites using a model-based clustering analysis without regard to geographic location (Fig 2). Their analysis revealed that populations were structured geographically with a positive correlation between genetic distance and geographical distance ($r = 0.4312$, $P=0.00001$). The results suggest that gene flow is limited to the movement of individuals between neighboring populations and it is unlikely that individuals move across large portions of the range.

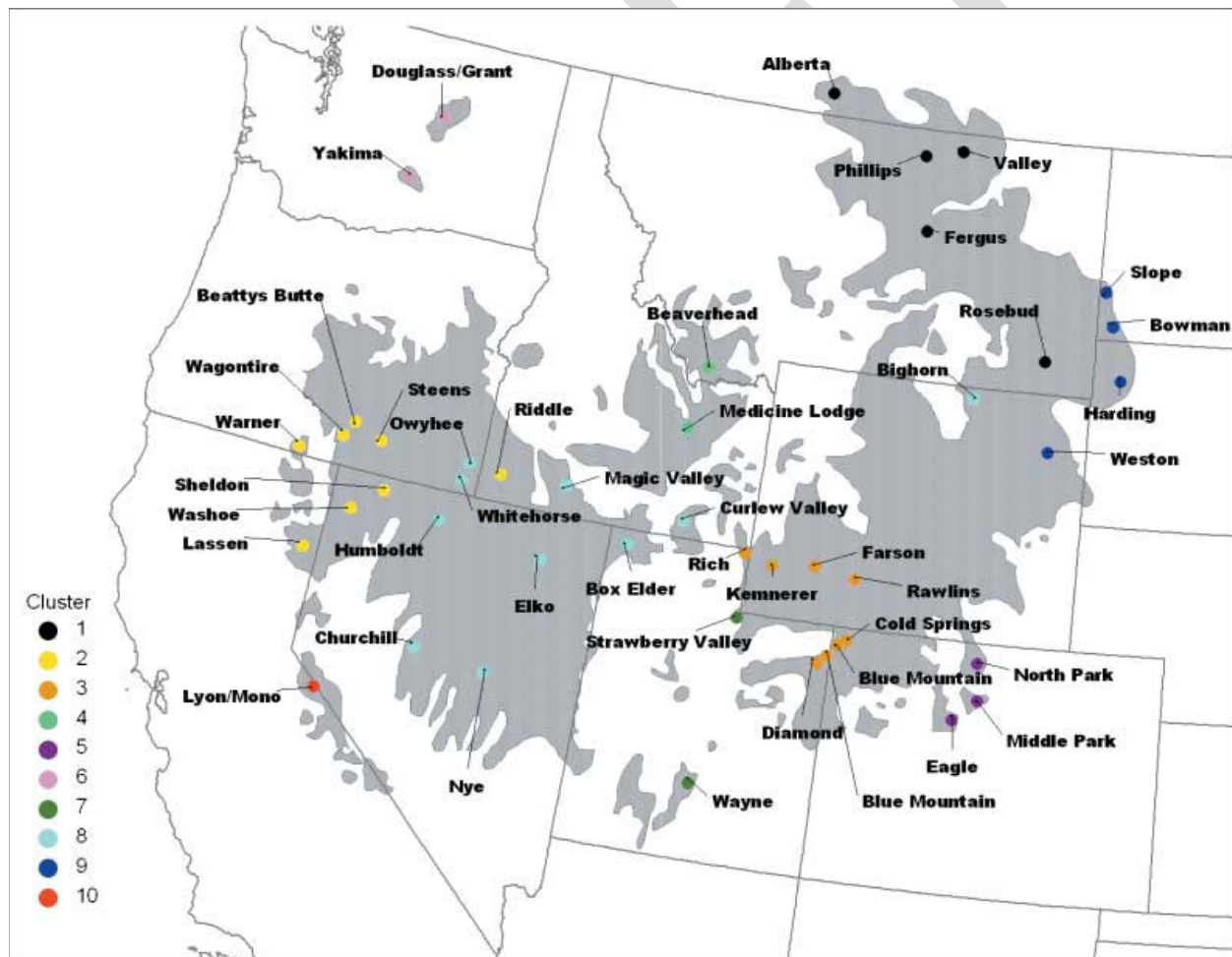


Figure 2: Genetic clusters from Oyler McCance et al. (2005).

Oyler-McCance et al. (2005) also evaluated patterns of mtDNA across the species' range and found that, consistent with the nuclear DNA, a gradual shift across the range in the percentage of individuals in each clade. That information was used to map the distribution of the most common haplotypes to help us identify appropriate conservation units (Fig 3).

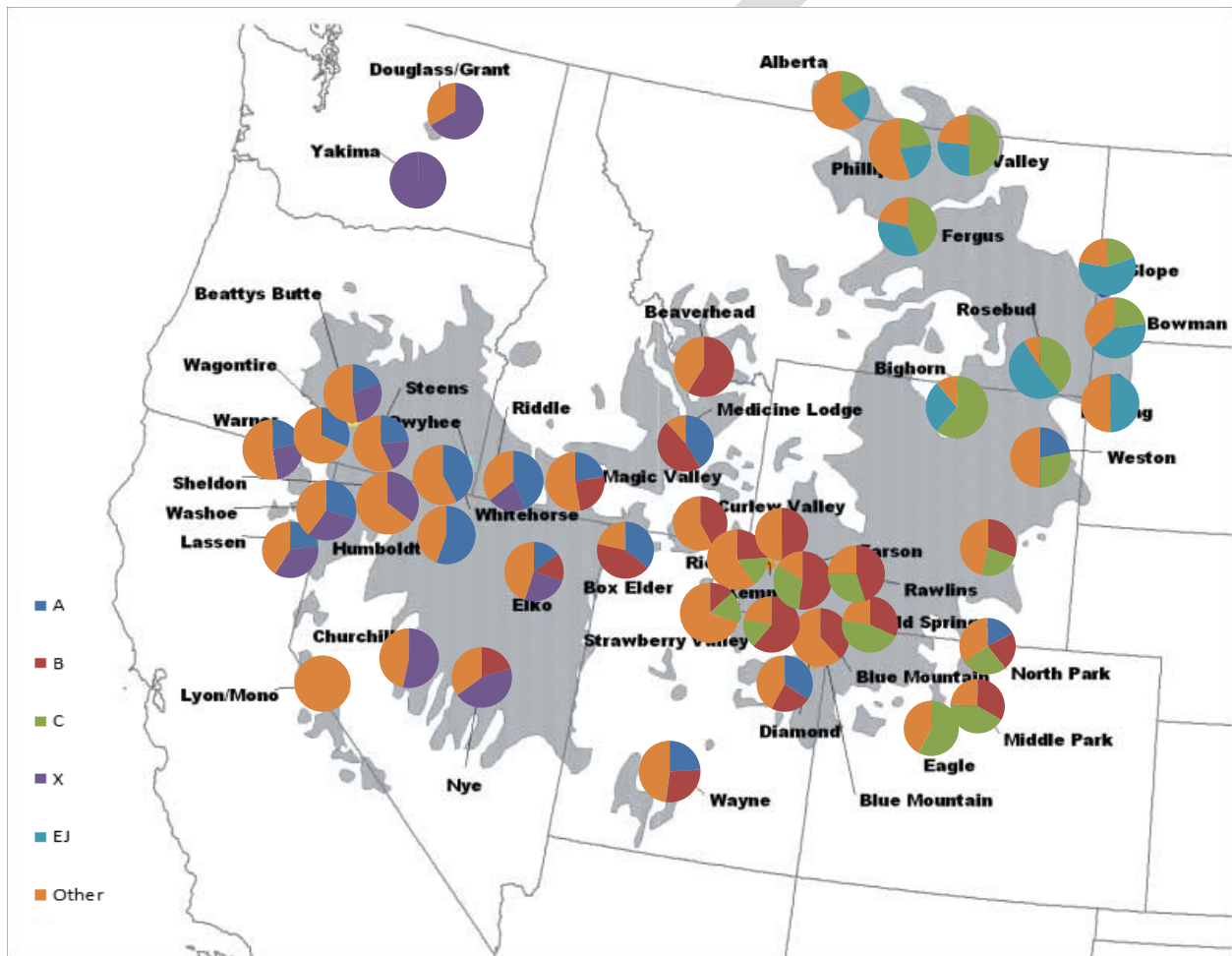


Figure 3: Distribution of the most common mtDNA haplotypes , derived from Oyler-McCance et al. (2005). NOTE: Orange represents *numerous* other uncommon, and in some cases globally unique, haplotypes.

The genetic data (both microsatellite markers and mtDNA) provide strong support for separating out the Bi-State population as an independent conservation unit (Oyler-McCance et al. 2005), as detailed in our 2013 proposal to list that DPS (78 FR 64358). The data also suggest genetic differences across the range,

such that identification of conservation units may be useful for sustaining genetic diversity and geographic distribution (Figs. 2, 3).

Greater Sage-grouse Density

Sage-grouse have a non-uniform distribution across the landscape (Fig 4), and the patterns of sage-grouse density may be informative when determining appropriate conservation units.

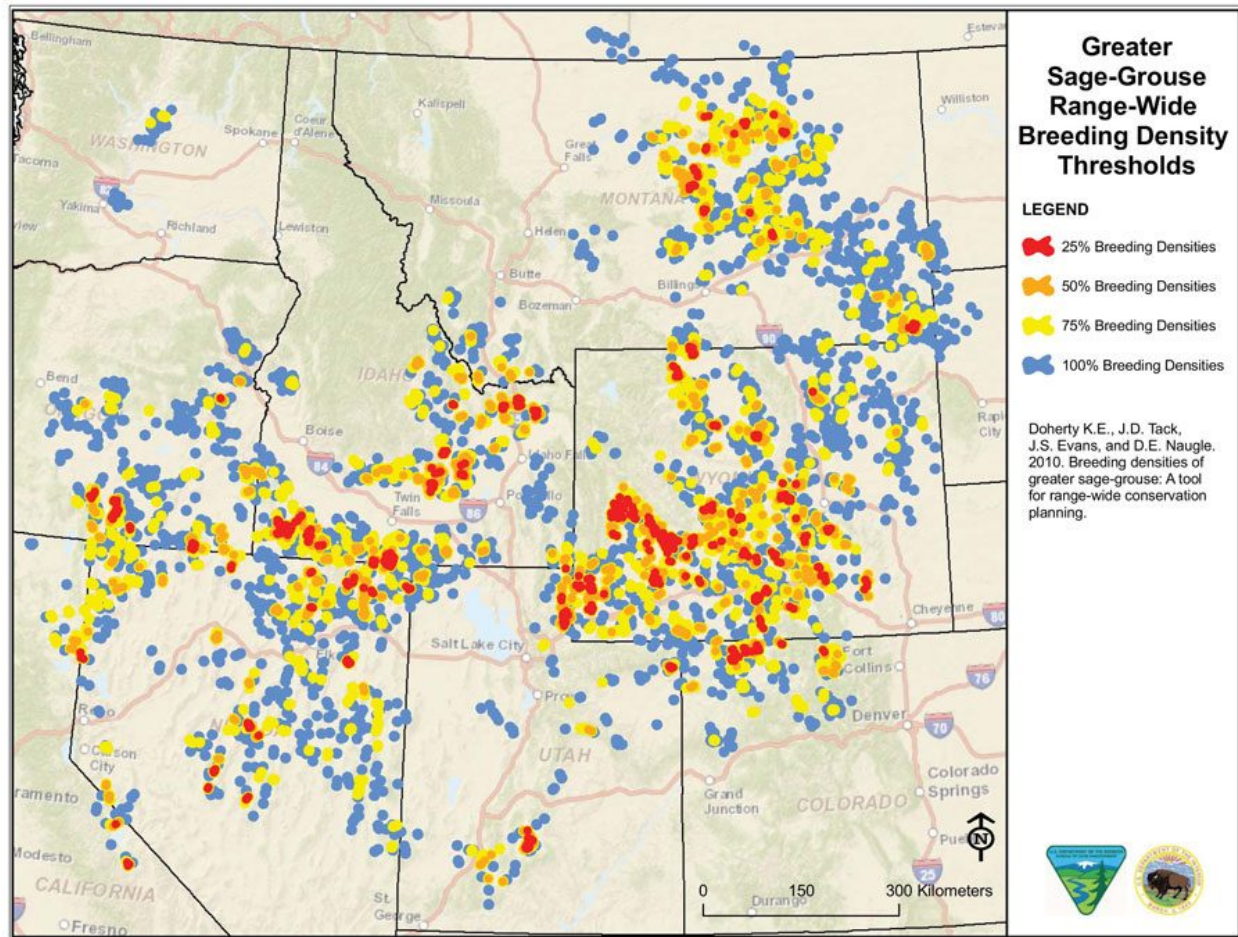


Figure 4. Greater Sage-grouse rangewide breeding densities from Doherty et al. 2010.

Greater Sage-grouse Movement Ecology

Dispersal. Greater Sage-grouse exhibit strong site fidelity (Connelly et al. 2004). Unfortunately, there is little published information regarding dispersal of Greater Sage-grouse. Dunn and Braun (1985) reported a dispersal distance from hatching site to breeding site of a median of 8.8 km for females and 7.4 km for males (Dunn and Braun 1985) in Colorado. Dispersal appears to be discrete from brood breakup (Browers and Flake 1985), and the relatively few movements described seem to be rather

gradual and sporadic (Dunn and Braun 1986). Aside from Dunn and Braun (1985), we could not find any other published dispersal distances.

Seasonal Movements. Greater Sage-grouse have similar habitat requirements across their range but the distances traveled to obtain habitat resources are highly variable between different Sage-grouse groupings (Tack 2010). While populations from Connelley et al. (2004) provide a useful starting point, the use of 30 km as a break point and the identification of potential barriers to movement is somewhat subjective. Movements of individual sage-grouse >30 km and movement across suspected physical barriers have been documented, suggesting that there might be significant gene flow between apparently distinct populations. For example, long-distance movements between seasonal ranges have been reported in the literature : 80 km (Dalke et al. 1963), 82 km (Connelly et al. 1988), 122 km (Tack 2010), and up to 161 km during severe winter conditions (Patterson 1952; p. 189). One hen in northwestern Wyoming moved 96 km from the lek on which she bred to her nesting location (Holloran and Anderson 2005). It is unclear whether these long-distance movements made under adverse conditions are typical, or an anomaly. The movement reported by Patterson (1952) was made during a particularly severe winter to an area that provided exposed sagebrush for cover and food. While this may not be the “typical” migration distance for that particular population, it demonstrates that sage-grouse will move long distances to secure seasonal habitat requirements.

Sage-grouse have large home ranges (>600 km²), which reflect the seasonal movement distances (Connelly et al. 2011). We found no information resolving the published low dispersal distances with seasonal movements and large home ranges. While adult sage-grouse rarely abandon their site fidelity we found no information on how frequently juvenile birds move independently from adults, potentially contributing to dispersal. Using distances to determine potential conservation units is therefore problematic.

Bush et al. (2011) found that natural features, such as rivers, do not generally preclude sage-grouse movement. This is consistent with observations in Wyoming of Sage-grouse moving long distances across very rough (mountainous) terrain when making seasonal movements (WGFD Snake River LWG annual report 2014), and the occurrence of sage-grouse in the Bi-State DPS at elevations of >10,000 feet.

Anthropogenic Barriers to Dispersal

Range reduction, habitat fragmentation and the resulting isolation reduces connectivity between populations (Knick and Hanser 2011; Fig. 5). Dispersal of sage-grouse in Montana was limited by habitat fragmentation resulting from human activities (in this case, conversion of sagebrush to agricultural lands) vs. natural features (Bush et al. 2011). Knick et al. (2011) concluded that human land use is a dominant stressor in sagebrush ecosystems, and must be considered in conservation efforts for sage-grouse.



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and Hanser (2011) reported that sage-grouse avoided available suitable habitats when those habitats occurred in proximity to oil and gas wells and power lines, indicating that effects of the human footprint on sage-grouse are both direct and indirect. Many studies have demonstrated a decline in sage-grouse due to the presence of agricultural conversion, energy development, urbanization, and infrastructure development. Unfortunately, none of these studies provide precise information as to the amount of which development results in the loss of connectivity between sage-grouse populations.

Integrating Genetic and Disturbance Data for Delineating Conservation Units

Based on the above information, we propose delineating conservation units using genetic information, information on sage-grouse distribution and density, as well as the distribution and density of anthropogenic disturbances within sage-grouse habitats. Available genetic data provide a window into population connectivity over many sage-grouse generations. In some cases, especially with mtDNA, genetic information may reflect historical patterns of gene flow that are no longer accurate. This occurs when anthropogenic disturbances have either reinforced barriers to gene flow or have created novel barriers that have severely reduced or eliminated gene flow. Therefore, it is important to look at both factors when evaluating appropriate conservation units. We provide two examples below to demonstrate how these factors could be considered together.

Example 1: NE Portion of the Range

The northeastern portion of the greater sage-grouse range (Alberta, eastern Montana, North and South Dakota and northeastern Wyoming) contains two complete microsatellite genetic clusters and one instance of a third cluster, as defined by Oyler-McCance et al. (2005; Fig. 2). Examination of mtDNA haplotype data (Oyler-McCance et al. 2005, Figure 3) suggests that these clusters share a large proportion of common mtDNA haplotypes, meaning they are descended from common lineages. Comparison of these birds with the next closest genetic cluster (central and southwestern Wyoming, Fig. 3) demonstrates a shift in mtDNA haplotype frequency, and suggests a possible historical barrier to gene flow.

Northeastern Wyoming and southeastern Montana have experienced significant energy development and loss of sagebrush due to agricultural conversion. This area is also projected to sustain continued development pressure from energy development (Fig. 6). Numerous authors have found that these sources of habitat fragmentation limit sage-grouse movement (Bush et al. 2011; Knick and Hanser 2011). It is likely that development in this area is reducing gene flow across this boundary. More detailed genetic information (currently being collected and analyzed) will be useful in determining the extent to which gene flow is already restricted in this area and the most appropriate boundaries for particular conservation units.

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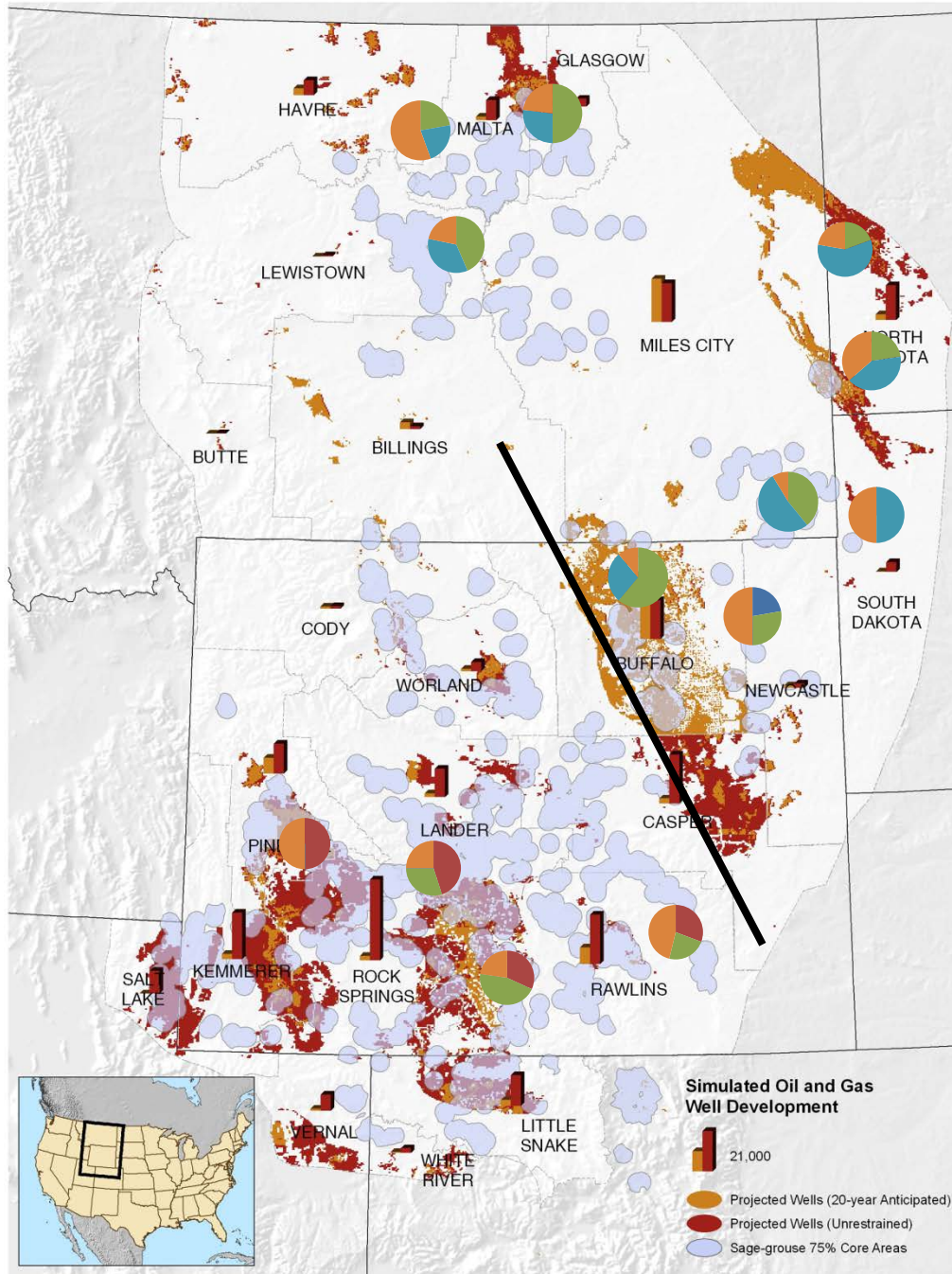


Figure 6. Oil and gas well development from Copeland et al. 2009, with greater sage-grouse common mtDNA haplotypes from Oyler-McCance et al. 2005 and 75% breeding density from Doherty et al. 2010. Black line represents a likely barrier to dispersal from habitat loss and fragmentation associated with oil and gas development.

Example 2. Snake River Plain

Agricultural development along the Snake River Plain has produced a gap in sage-grouse population connectivity (Fig. 7). This gap in connectivity is reflected in the microsatellite data which shows that populations north of the Snake River Plain form their own genetic cluster, suggesting limited recent gene flow. mtDNA analyses show that the most common haplotypes present both north and south of this barrier are similar. This suggests historically (prior to agricultural development) these areas were likely connected, with recent loss of gene flow. Regardless of historical connectivity, these areas appear to now be functionally independent.



Figure 7. Overlay of genetic cluster information (Oyler-McCance et al. 2005) with habitat connectivity analyses (Knick and Hanser 2011) for the Snake River area. The black line indicates the Snake River Plain where agricultural development has created a relatively wide barrier to gene flow over the last century.

Part 2 – Species-specific Criteria for Evaluating Potential DPSs

Discreteness Criteria

According to the 1996 DPS Policy, a population segment of a vertebrate species may be considered discrete if it satisfies either one of the following conditions:

1. It is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may provide evidence of this separation.
2. It is delimited by international governmental boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of section 4(a)(1)(D) of the Act.

We chose not to consider the second criteria for further analyses based on the following information. Recent data demonstrate that most birds in Canada winter in northern Montana, thereby reflecting the continuity of this population that is not supported by a political boundary (Tack et al. 2010). This is supported by the genetic information presented by Bush et al. (2011) who concluded that Canada and Montana are part of one genetic grouping. There are very few remaining sage-grouse in Canada (approx. 135) and the connection to habitats in the United States is important to managing these individuals. Canada lists the greater sage-grouse as endangered under their Species At Risk Act (SARA), and is currently taking active steps to conserve their habitats. Additionally, Greater Sage-grouse in Canada were considered in the 2010 range-wide finding and not segregated on the basis of this boundary.

We separated the components identified in the first criterion of the DPS policy, examining physical, physiological, ecological or behavioral factors independently. Those analyses follow.

Table 1. Framework for evaluating greater sage-grouse population discreteness.

Discreteness	Species-specific criteria
Physical Separation	Physical separation can be established by one or more of the following factors: <ul style="list-style-type: none"> • Demographically independent populations (as evidenced by population trend or movement data); • Major anthropogenic barrier(s) between populations; • Evidence of restricted gene flow (e.g., unique nuclear genetic cluster or private common mtDNA haplotype from Oyler-McCance et al. 2005); or, • Published connectivity analyses showing a significant break in population or habitat connectivity.
Ecological Factors	Not applicable. We are not aware of ecological factors causing sympatric discreteness.
Physiological and Behavioral Factors	None found (Shroeder 2008; Taylor and Young 2006). Latitudinal differences in size were attributed to environmental differences, vs. genetic differences.

Physical Separation

Genetic analyses indicate that greater sage-grouse move within population areas, but do not engage in large range-wide movements (Oyler-McCance et al. 2005). Although published information regarding actual dispersal distance (defined as movements between place of hatch to place of breeding) is very limited, seasonal movement data suggest birds are capable of moving large distances (up to 161 km), and that sage-grouse have large home range sizes ($>600 \text{ km}^2$). Movement does not appear restricted by natural topographic features, but it is limited by large areas of anthropogenic disturbances and wildfire. Physical separation of sage-grouse should therefore be determined by habitat fragmentation from key factors identified in the literature (e.g. energy development) and as supported by the connectivity analyses conducted by Knick and Hanser (2011).

Ecological Separation

We interpret ecological separation to mean individuals that occur within the same general area (i.e., they are not physically separate) but that do not interbreed due to ecological factors (e.g., differences in diet which may affect morphology or mate selection). We are not aware of ecological separation in greater Sage-grouse anywhere in the range.

Physiological and Behavioral Factors

We could find little evidence supporting physiological differences among Greater Sage-grouse populations. An unpublished study by Schroeder (2008), conducted for the Service, compared a variety

of common physical measurements made by researchers who captured birds for other research purposes. The goal of Schroeder's comparisons was to examine data with reference to variation associated with the region, population, and/or previously established genetic characteristics. The study was limited by the variation anticipated with differences individual sampling (e.g. not all researchers measured sage-grouse toe length to the same location on each bird). The most significant finding was a regional difference in body mass. Sage-grouse from Washington and northern Colorado to Alberta were larger than Sage-grouse in Idaho, Nevada, Oregon and California (Schroeder 2008). The author cautions that the results may be biased by a lack of data from birds in smaller populations, but hypothesized that the results are more likely the result of environmental, not genetic factors. No other significant differences were detected that were independent of body size (i.e. larger Sage-grouse had longer wing and tail lengths). Strutting behavior on leks, a key component of mate selection, is the only behavioral data available. Schroeder (2008) noted regional variation in the strut rate of sage-grouse, but the data were not sufficient to determine if the variation reflected population-level effects or resulted from some other undefined variation. The only published comparison of behavioral data found no significant differences in strut rate, nor acoustical signals for sage-grouse outside the already designated Bi-state DPS (Taylor and Young 2006). We found no other published information regarding differences across the species' range in behavior. Thus, there is no information to suggest that breeding populations of sage-grouse are discrete due to physiological or behavioral barriers.

Significance Criteria

If a population segment is considered discrete under one or more of the above conditions, its biological and ecological significance will then be considered in light of Congressional guidance (see Senate Report 151, 96th Congress, 1st Session) that the authority to list DPS's be used “* * * sparingly” while encouraging the conservation of genetic diversity. In carrying out this examination, the Services will consider available scientific evidence of the discrete population segment's importance to the taxon to which it belongs. This consideration may include, but is not limited to, the following:

1. Persistence of the discrete population segment in an ecological setting unusual or unique for the taxon,
2. Evidence that loss of the discrete population segment would result in a significant gap in the range of a taxon,
3. Evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range, or
4. Evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics.

Criteria #3 does not apply to sage-grouse, so we only evaluated 1, 2, and 4.

Table 2. Framework for evaluating greater sage-grouse population significance.

Significance	Species-specific criteria
Unique or Unusual Ecological Setting	The conditions where the unit is found are so different from the rest of the range that it is likely that adaptive divergence has taken place or is in the process of taking place.
Significant Gap in the Range	Loss of the unit would mean loss from an entire North American Level III ecoregion.
Marked genetic differences	Majority of mtDNA haplotypes in the unit are globally unique; or, Published peer reviewed paper indicates that the unit has marked genetic differences.

NOTE: THIS IS CURRENTLY A PLACEHOLDER – WE’LL NEED A LOT MORE INTERNAL DISCUSSION TO DEVELOP THESE CRITERIA.

Unique or Unusual Ecological Setting

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Significant Gap in the Range

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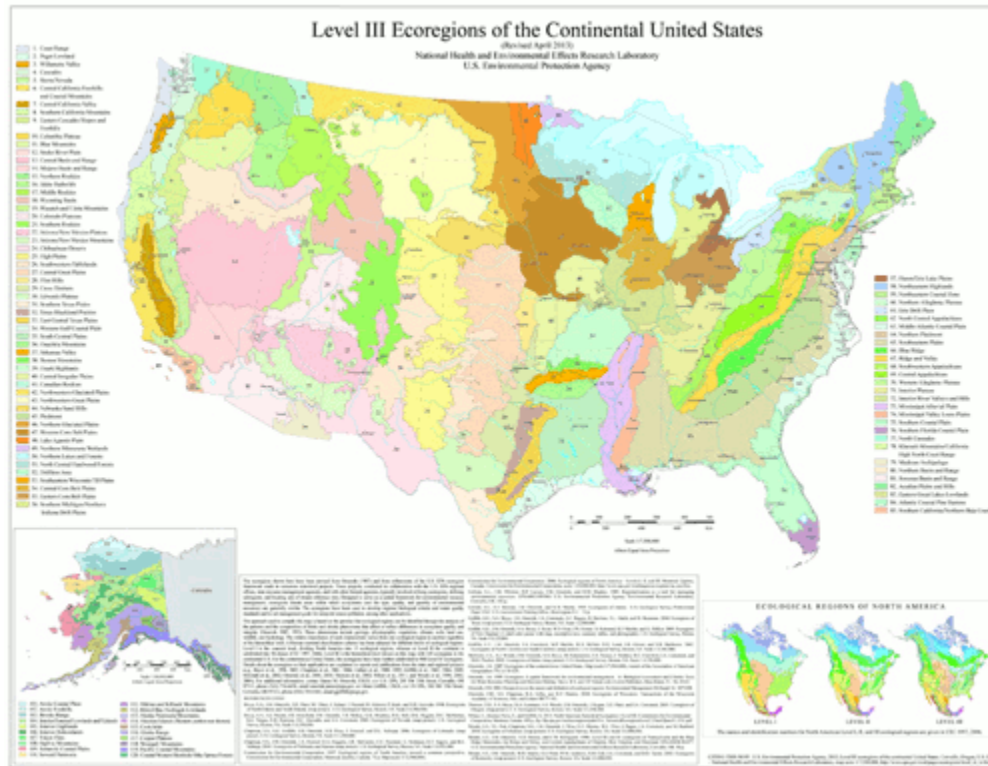


Figure xx. Level III ecoregions of the U.S. [need a better map here – would be good to overlay sage-grouse range with these ecoregions].

Marked Genetic Differences

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