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DISTRIBUTION OF SAGE-GROUSE IN NORTH AMERICA

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Abstract. We revised distribution maps of potential presettlement habitat and current populations for Greater Sage-Grouse (*Centrocercus urophasianus*) and Gunnison Sage-Grouse (*C. minimus*) in North America. The revised map of potential presettlement habitat included some areas omitted from previously published maps such as the San Luis Valley of Colorado and Jackson area of Wyoming. Areas excluded from the revised maps were those dominated by barren, alpine, and forest habitats. The resulting presettlement distribution of potential habitat for Greater Sage-Grouse encompassed 1 200 483 km², with the species' current range 668 412 km². The distribution of potential Gunnison Sage-Grouse habitat encompassed 46 521 km², with the current range 4787 km². The dramatic differences between the potential presettlement and current distributions appear related to habitat alteration and degradation, including the adverse effects of cultivation, fragmentation, reduction of sagebrush and native herbaceous cover, development, introduction and expansion of invasive plant species, encroachment by trees, and issues related to livestock grazing.

Key words: *Centrocercus minimus*, *Centrocercus urophasianus*, distribution, Greater Sage-Grouse, Gunnison Sage-Grouse, habitat change.

Distribución de *Centrocercus* spp. en América del Norte

Resumen. Revisamos los mapas de distribución potencial precolombino y de poblaciones actuales de *Centrocercus urophasianus* y *C. minimus* en América del Norte. El mapa modificado de hábitat potencial precolombino incluyó algunas áreas omitidas de mapas anteriormente publicados, como el Valle San Luis de Colorado y el área de Jackson, Wyoming. Las áreas excluidas de los mapas modificados fueron las dominadas por hábitats forestales, alpinos y estériles. La distribución precolombina resultante para *C. urophasianus* abarcó 1 200 483 km², con un territorio actual de 668 412 km². La distribución de hábitat potencial para *C. minimus* abarcó 46 521 km², con un territorio actual de 4787 km². Estos contrastes tan marcados parecen estar relacionados con la modificación y degradación del

hábitat, incluyendo los efectos nocivos de la agricultura, la fragmentación de hábitat, la disminución de *Artemisia* spp. y otras coberturas herbáceas nativas, el desarrollo, la introducción y la expansión de especies de plantas invasoras, la invasión de árboles y cuestiones relacionadas con pastoreo de ganado.

INTRODUCTION

Accurate mapping of a species' distribution is extremely important, particularly in an age where satellite imagery and habitat maps can be linked with management scenarios involving issues of population viability, land-use planning, and habitat quality, quantity, and distribution (Wisdom, Rowland, et al. 2002, Wisdom, Wales, et al. 2002). These possibilities are complicated by variation in types of distributions. For example, some maps are not available at a scale adequate for specific management concerns. Furthermore, the distribution for most species is not constant. Some species may acquire range or become extirpated in areas, with the contractions and expansions resulting in an altered current distribution.

Leopold (1931:163) suggested that "The original distribution of the . . . species is of more than academic import. Without it we can not distinguish acquired range from original range. This is essential in diagnosing the behavior of populations, and in appraising the opportunities for management." Obtaining detailed information on past and current distribution is an important consideration for Greater Sage-Grouse (*Centrocercus urophasianus*) and Gunnison Sage-Grouse (*C. minimus*). This is especially true because recent trends suggest sage-grouse populations are declining in most portions of their range and the area occupied is shrinking (Connelly and Braun 1997, Braun 1998). Both species are being considered for federal listing under the Endangered Species Act in the United States; the Greater Sage-Grouse was listed as an endangered species in Canada in 1988 (Aldridge and Brigham 2003).

The general distribution of sage-grouse is clearly associated with distribution of sagebrush (*Artemisia* spp.), and in particular, big sagebrush (*A. tridentata*). This relationship has been shown in numerous descriptions of sage-grouse range including reports by Bendire (1892), Judd (1905), Girard (1937), McClanahan (1940), Patterson (1952), Aldrich and Duvall (1955), Aldrich (1963), Wallestad (1975), Johnsgard (1973, 1983, 2002), Connelly and Braun (1997), Braun (1998), Schroeder et al. (1999), Young et

al. (2000), and Benedict et al. (2003). Unfortunately, distribution maps for sage-grouse are usually shown at a scale that makes coordination with localized management efforts difficult.

Lack of precision in earlier mapping efforts is one reason uninhabited areas were included in the known distribution and areas of current or historical occupation were omitted. For example, forested or alpine habitats in numerous mountain ranges were included in earlier distribution maps, even though they do not support sage-grouse. These areas included the upper slopes of the Lemhi Range in Idaho, Bighorn Mountains in Wyoming, and Uinta Mountains in Utah. Some areas with historical or current records of sage-grouse were excluded, such as the San Luis Valley of Colorado and Jackson area of Wyoming.

Early maps are not available in formats that can be linked with other databases, such as those based on satellite imagery. This resulted in differences in interpretation, particularly with reference to distribution lines. This is especially true for sage-grouse distribution near the borders of states, such as between Utah and Arizona. For example, Girard (1937) and Patterson (1952) considered northern Arizona to be part of the past distribution of sage-grouse because of the association of sage-grouse and sagebrush habitats throughout the West. Patterson (1952) showed sage-grouse on the northern Arizona state line in two places (northwestern and northeastern borders). Although Aldrich and Duvall (1955) showed the same boundaries for both past and current distributions, and in the same areas (on the Utah-Arizona border), Aldrich's 1963 publication shows the line extending 5–10 km south of the Utah-Arizona border on the western edge. This confusion was illustrated by Johnsgard (1983) when he referred to the historical distribution as including 14 or 15 states, with the fifteenth being Arizona.

Our primary goal was to produce a 1:2 000 000 scale digital map of the current distribution of sage-grouse and their potential habitat prior to occupation by people of European descent. Potential sage-grouse habitat was evaluated based on past interpretations of sage-

grouse distribution (e.g., Aldrich and Duvall 1955), recovery locations for museum specimens, locations for published observations, information on habitat use, and the distribution of general habitat types. Information such as the distribution of general habitat types (e.g., Kuchler 1985) was not available when earlier distribution maps were produced. The digital map produced will provide a foundation for future conservation efforts and research on the distribution of sage-grouse and their habitats (Knick et al. 2003).

METHODS

Previous publications have used “original” (Connelly and Braun 1997), “past” (Aldrich and Duvall 1955) and “historical” (Johnsgard 1983) to describe the early distribution of sage-grouse; however, these names are difficult to interpret. Consequently, we used the term “presettlement” to define the period prior to 1800, before rapid settlement by people of European descent, particularly in Nevada, Oregon, and Utah (Miller and Eddleman 2001). Nevertheless, many changes associated with settlement occurred in portions of the sage-grouse distribution prior to 1800 (perhaps as early as the 1600s in some areas; Simpson 1964, Bandelier 1966); these included the introduction and expansion of livestock grazing by cattle, horses, sheep, and goats.

There are few references documenting sage-grouse during the 1800s. We reviewed the journals of Meriwether Lewis, William Clark, and their sergeants which described their 1803–1806 expedition from St. Louis, Missouri, to the west coast of Oregon and return (transcribed by Moulton 1987, 1988; summarized by Zwickel and Schroeder 2003). We also reviewed publications that provided information about early observations of sage-grouse, especially those prior to 1850 (Swainson and Richardson 1831, Stansbury 1852, Frémont 1887, Thwaites 1978, Johnson 1984).

We considered 1167 records of museum specimens. We were cautious in our interpretations because of potential inaccuracies in recorded locations and the ability of individual sage-grouse to travel long distances (Connelly et al. 1988). A portion of these museum records ($n = 166$) had locations that were unknown or too imprecise to be plotted. We also considered 138 published observations of sage-grouse, including those mentioned by Bent (1932) or mapped by

Aldrich and Duvall (1955). We concentrated our efforts on published observations outside the current distribution. Because many published observations and museum specimens were poorly documented, we primarily considered these data in terms of their generalities.

Current distribution was evaluated within each state and province using annual counts of males on known display sites (leks) and searches for new or previously unidentified lek sites (Jenni and Hartzler 1978, Autenrieth et al. 1982). Additional surveys included brood routes, harvest questionnaires, check stations, and wing collections (Connelly et al. 2000). Radio-telemetry research in most states and provinces helped identify patterns of habitat use, movement capabilities, and specific breeding, brood-rearing, late-summer, and winter areas. In some states Landsat data were used to estimate the current distribution of sage-grouse, based on the combination of information on habitat distribution and known populations.

Data were compiled separately for each state and province and subsequently integrated into a North American map. Because population monitoring has been ongoing for at least 30 years in many states and provinces, the extirpation of many populations was documented with data rather than assumptions about changes in habitat availability. Although data used for evaluating the current distribution were collected over many years, the current distribution is believed to represent the approximate distribution in the year 2000.

We considered the current distribution to have been within the potential presettlement distribution of habitat. The presettlement distribution of potential sage-grouse habitat was based, in part, on the descriptions of the sage-grouse distribution presented by Bendire (1892), Girard (1937), McClanahan (1940), Patterson (1952), and Aldrich and Duvall (1955). Aldrich and Duvall's (1955) assessment was the most thorough and has provided the foundation for most distribution maps since 1955.

We modified the perimeter of Aldrich and Duvall's (1955) map with the aid of habitat maps, especially that of Kuchler (1985), but also other interpretations such as Brown and Lowe (1980), Jacobson and Snyder (2000), and Miller and Eddleman (2001). Presettlement distribution of potential habitat was evaluated in light of information on seasonal habitat use (Schroeder et al.

1999, Connelly et al. 2000), movement capabilities (Connelly et al. 1988), and locations for published observations and museum specimens. Using Kuchler's (1985) map we identified seven core habitats that supported most sage-grouse including (1) sagebrush steppe, (2) Great Basin sagebrush, (3) wheatgrass (*Agropyron spicatum*)-needlegrass (*Stipa* spp.) shrubsteppe, (4) grama (*Bouteloua* spp.)-needlegrass-wheatgrass, (5) wheatgrass-needlegrass, (6) wheatgrass-bluegrass (*Poa* spp.), and (7) fescue (*Festuca* spp.)-wheatgrass. Although Kuchler's habitat map indicates some of these core habitats are not dominated by sagebrush, a key component of sage-grouse habitat, data from portions of these regions (e.g., Daubenmire 1970, Brown and Lowe 1980, Jacobson and Snyder 2000) indicates that sagebrush may be locally abundant within definable portions of an otherwise grass-dominated habitat type. Consequently, our map of presettlement habitat included only sagebrush-dominated portions of three core habitat types (wheatgrass-needlegrass, wheatgrass-bluegrass, fescue-wheatgrass). An additional core habitat, Great Basin sagebrush, was not mapped in lower-elevation areas along the Colorado River, Little Colorado River, and Chinle Creek in Arizona due to the apparent absence of sagebrush (partly illustrated by Brown and Lowe 1980). The other three core habitats were mapped more completely.

Comparison of Kuchler's (1985) map with known information on sage-grouse abundance and habitat use illustrated the existence of several secondary habitats, in which suitability varies due to tree abundance, sagebrush type and density, and connectivity and proximity to core habitats (Connelly et al. 2000, Miller and Eddleman 2001). Secondary habitats include (1) foothills prairie, (2) saltbush (*Atriplex* spp.)-greasewood (*Sarcobatus vermiculatus*), (3) juniper (*Juniperus* spp.)-pinyon (*Pinus edulis*) woodland, (4) grama-galleta (*Hilaria* spp.) steppe, (5) grama-buffalo grass (*Buchloe dactyloides*), and (6) desert. Secondary habitats were mapped locally in specific situations: (1) currently occupied areas, (2) areas clearly occupied in the past, or (3) areas within 10 km of core habitats. Habitats without known use by sage-grouse were excluded from the presettlement distribution of potential habitat, even if there were scattered observations or recoveries of sage-grouse. The differentiation between Gun-

nison and Greater Sage-Grouse in transition zones in Utah and Colorado was addressed in earlier research and was included in these maps (Young et al. 2000).

The initial draft of the current distribution for sage-grouse in North America was produced from numerous hand-drawn state or province-specific maps, and in the case of Washington state, a GIS database prepared at a 1:10 000 scale. These maps were transferred to 1:2 000 000 scale U.S. Geological Survey maps along with a hand-drawn approximation of potential habitat. These maps were digitized and placed in a GIS database in Arc/INFO (ESRI 1998). Biologists from states and provinces were provided opportunities to comment on drafts of the maps. We incorporated many recommended changes including digital data from California, Colorado, Montana, Nevada, Utah, and Wyoming. Because each state and province provided distribution and habitat data at inconsistent scales (<1 ha to >1000 ha resolution), we made compromises to maintain continuity of distribution lines crossing state and provincial boundaries. In some cases, these compromises resulted in localized reductions in the precision of established habitat maps. The final 1:2 000 000 scale maps will be available on web sites such as the USGS Sagebrush and Grassland Ecosystem Map Assessment Project (U.S. Geological Survey 2001). The 1:2 000 000 scale maps were reduced for this paper.

RESULTS

GREATER SAGE-GROUSE

Presettlement distribution of potential habitat. Potential habitat, estimated to be 1 200 483 km² in area, is closely associated with the distribution of museum specimens and published observations in most areas (Fig. 1). The revised map excludes many areas included in earlier maps (e.g., Aldrich 1963, Johnsgard 1983). These exclusions include forested, alpine, and barren habitats that probably never supported sage-grouse. Portions of the Bighorn, Hawley, Uinta, Wasatch, San Pitch, Tushar, and Escalante Mountains; the Lemhi, Lost River, and Sawtooth Ranges; the Markagunt, Paunsaugunt, and Aquarius Plateaus; the White Cloud Peaks, and some of the sparsely vegetated areas near the Great Salt Lake were excluded.

The revised map also excluded more of the grassland-dominated habitats in central North

and South Dakota as well as the Palouse Prairie in southeastern Washington than earlier maps have. Most museum specimens and early observations of sage-grouse in the Dakotas were from an area that is either currently occupied or close to an area that is occupied (Fig. 1, 2). Furthermore, Johnson and Knue (1989) reported sage-grouse remains at only 2 of 29 American Indian villages where Sharp-tailed Grouse (*Tympanuchus phasianellus*) remains were found in North Dakota. Hence, the distribution of potential pre-settlement habitat in this region is limited to southwestern North Dakota, western South Dakota (except for forested portions of the Black Hills), and northwestern Nebraska (Fig. 1).

Despite the map revisions, there are still published observations and museum specimens outside the established distribution. Records are particularly evident in the grasslands of Alberta, Colorado, Nebraska, North Dakota, Saskatchewan, and South Dakota (Fig. 1). The history and reliability of these records is uncertain. Meriwether Lewis (Moulton 1987:258) observed his first sage-grouse on 5 June 1805 while traveling near the confluence of the Missouri and Marias Rivers (present-day Loma, Montana): "I saw a flock of the mountain cock, or a large species of heath hen with a long pointed tail which the Indians informed us were common to the Rocky Mountains." On 2 March 1806, William Clark added that "the first of those fowls which we met with was on the Missouri below and in the neighbourhood of the Rocky Mountains" (Moulton 1988:370). Members of the expedition did not observe sage-grouse in central or eastern Montana, or in the Dakotas (Zwickel and Schroeder 2003). The quote from Lewis implies that Mandan Indians considered sage-grouse to be common close to the Rocky Mountains. This observation was reinforced 25 years later by Swainson and Richardson (1831:359) when they reported that sage-grouse "do not exist on the banks of the river Missouri; nor have they been seen in any place east of the Rocky Mountains." Sage-grouse also were observed prior to 1843 on the Yellowstone River, but not along the Missouri (Audubon 1960).

Coues (1874:402) considered sage-grouse to overlap the distribution of "various species of *Artemisia* or wild sage, upon which it chiefly feeds," primarily in central and southern Montana, southwestern North Dakota, and western South Dakota. He did not consider sage-grouse

to be present along the northern edge of Montana and did not observe them near Fort Stevenson, North Dakota, along the Missouri River. In contrast to earlier accounts, Bendire (1892) suggested the area of sage-grouse occupation included most of Montana and western North Dakota, stretching about 50 km north of the U.S.–Canadian border along the upper tributaries of the Missouri River. An examination of museum specimens and published observations supports the past occurrence of sage-grouse up to 240 km north of the U.S.–Canadian border (Fig. 1); however specimens and observations more than 100 km north of the border are all more recent than 1945.

In 1834 John Townsend wrote: "We first met with this noble bird on the plains, about two days' journey east of Green River [Wyoming], in flocks, or packs, of fifteen or twenty" (Thwaites 1978). In 1843 John Frémont referred to the Green River "as the Seeds-kedée-agie, or Prairie Hen (*tetrao urophasianus*) River. . . on which this bird is still very abundant" (Frémont 1887:199). In 1849 in the same general area, Howard Stansbury observed that sage-grouse "were seen in great numbers, and the men shot as many as we could conveniently carry" (Stansbury 1852:70). Field (1857) stated that sage-grouse were supported by vast expanses of sagebrush, particularly in southwestern Wyoming. We could not locate published early observations of sage-grouse in eastern portions of Wyoming, within their current range (Fig. 2).

There are ambiguities in the presettlement distribution of habitat. Dates and locations of observations following 1805 (Moulton 1987) support the possibility of a northward and eastward transition in distribution. However, data regarding the presettlement distribution of sagebrush throughout the region are limited. Additionally, sage-grouse are known to use alternate species of sagebrush such as silver sagebrush (*Artemisia cana*) in Alberta, Saskatchewan, and the Dakotas (Sealy 1963, Aldridge and Brigham 2002, 2003, Smith 2003). It is possible that Lewis (Moulton 1987) and others might not have observed sage-grouse because of low densities along their primary travel corridors. Periodic fluctuations in the abundance of sage-grouse (or cycles, Rich 1985) may also have had an impact. Because of these considerations, we constrained eastern portions of the presettlement range to areas of known occupation and did not expand

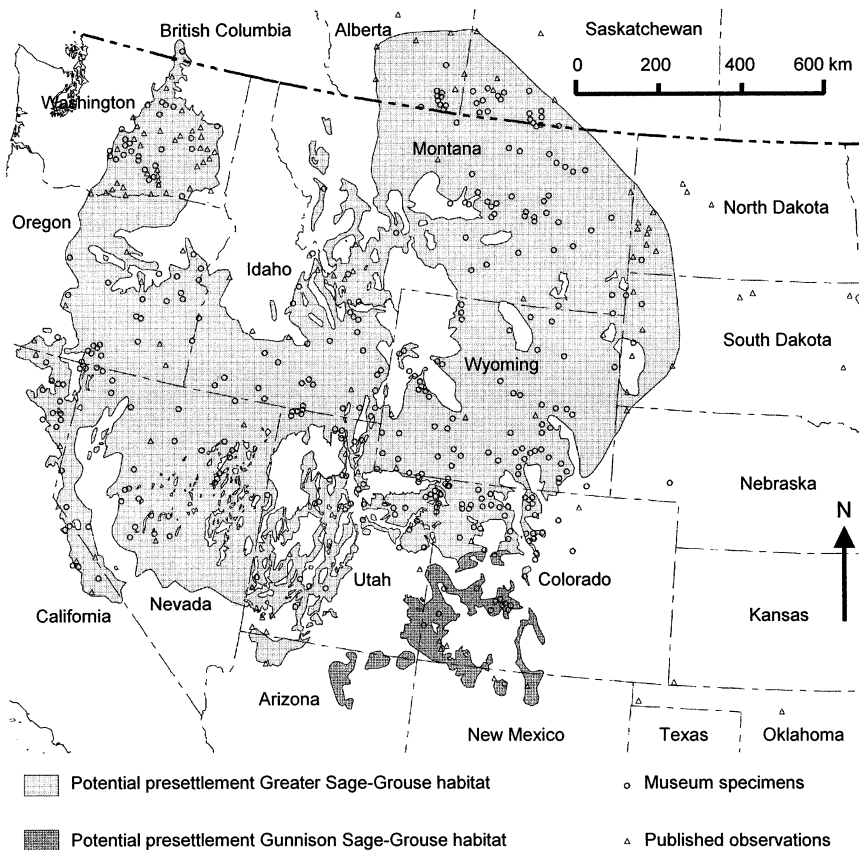


FIGURE 1. Presettlement distributions of potential habitat for Greater and Gunnison Sage-Grouse in North America in relation to estimated locations for 358 museum specimens and 126 published observations. The sample does not include 830 additional specimens and observations for which locations were either too imprecise to be mapped or were within 10 km of locations already mapped. The published observations are from Peale (1848), Stansbury (1852), Wheeler (1874), Goss (1886), Bendire (1892), Frémont (1887), Royal Historical Society (1914), Nice (1931), Bent (1932), Girard (1937), Huey (1939), Behle (1943), Patterson (1952), Aldrich and Duvall (1955), Yocom (1956), Christensen and Johnson (1964), Rogers (1964), Simpson (1964), Bandelier (1966), Cassin (1978), Thwaites (1978), Johnson (1984), Johnson and Knue (1989), Thompson and Ely (1989), Braun (1995), Roy (1996), Schroeder et al. (2000), Beck et al. (2003), Smith (2003), and Zwickel and Schroeder (2003).

them to include all observations and specimens (Fig. 1).

The presettlement distribution of potential habitat was expanded to include areas excluded from earlier maps. For example, sage-grouse currently occur in the valley around Jackson, Wyoming (Fig. 2), and presumably would have been there in the past (Fig. 1). Aldrich and Duvall (1955) also showed an area of historical occupation by sage-grouse along the Bitterroot Valley in southwestern Montana, whereas Aldrich's revised map in 1963 did not include this area. This was in a region where Lewis and Clark observed many grouse (mostly Blue

Grouse [*Dendragapus obscurus*] and sharp-tailed grouse; Zwickel and Schroeder 2003), but apparently no sage-grouse. One specimen apparently collected near Missoula, Montana, in 1900 (Fig. 1) provides evidence of a presettlement population inhabiting the region's foothills prairie habitat (Kuchler 1985). In 1942, sage-grouse were translocated to the Bitterroot Valley, an effort that was ultimately unsuccessful in establishing (or reestablishing) a population (Reese and Connelly 1997).

The southernmost observation of a sage-grouse is from an area west of Mt. Trumbull in 1937, approximately 65 km south of the Utah-



FIGURE 2. Current distribution of Greater and Gunnison Sage-Grouse in North America around the year 2000.

Arizona border (Huey 1939, Fig. 1). Phillips et al. (1964) considered the range of sage-grouse in Arizona to be hypothetical. The history of sage-grouse in southern Utah (Griner 1939, Lords 1951, Beck et al. 2003), and by extension northern Arizona, is poorly understood, due to the small number of travelers and early changes in habitat associated with settlement (Brown and Lowe 1980, Miller and Eddleman 2001). Rasmussen (1941:267) suggested that livestock grazing in northern Arizona was so severe in the 1870s and 1880s that the habitat was permanently altered: "Like most lowland sagebrush areas in the Great Basin, the associated grass species have almost all been destroyed by indiscriminate and unregulated grazing." Recent history has shown populations continuing to recede northward. For example, two recently extirpated leks in southern Utah were only 30 km north of the Arizona-Utah border (N. L. McKee, pers. comm.). In addition, sage-grouse have been ex-

tirpated from formerly occupied areas in the southwestern corner of Utah (Fig. 1, 2).

Current distribution. We estimated the area of current occupation of Greater Sage-Grouse to be 668 412 km² (Fig. 2), or approximately 56% of the presettlement distribution of potential habitat. We did not quantify the respective distributions of the eastern and western subspecies (*C. u. urophasianus* and *C. u. phaios*, Aldrich 1946) because of the lack of a clear dividing line (Aldrich and Duvall 1955) and the lack of genetic differentiation (Benedict et al. 2003).

Although the apparent decline in area of occupation appears to be related to habitat conversion and degradation (Braun 1998), specific explanations and observations appear to be regional in nature. For example, in 1805 Lewis and Clark observed sage-grouse on both sides of the continental divide near Lemhi Pass in Idaho and Montana (Zwicker and Schroeder 2003); an area still occupied (Fig. 2). In contrast, Lewis and

Clark in 1805 (Zwickel and Schroeder 2003), Douglas in 1826 (Royal Historical Society 1914), and Peale (1848) and Cassin (1978) in 1841 observed many sage-grouse along the Columbia River in southern Washington, an area where they are now absent.

The largest changes in sage-grouse distribution are in northern Oregon, Washington, and southern British Columbia (Fig. 2), mostly related to habitat conversion (Yocom 1956, Crawford 1982, Schroeder et al. 2000). Population isolation and declines are primary reasons why sage-grouse in the area have been labeled a "distinct population segment" for consideration as a threatened or endangered species by the U.S. Fish and Wildlife Service (Warren 2001). In British Columbia, Canada, sage-grouse were first recorded in 1864 near Osoyoos Lake, extirpated about 1918, translocated back into the area in 1958, and re-extirpated about 1966 (Campbell et al. 1989). A similar translocation effort into Sherman and Umatilla Counties of northern Oregon also was unsuccessful (Reese and Connelly 1997).

Greater Sage-Grouse have also declined in southern portions of the range and in arid areas. For example, habitat along the Snake River likely supported sage-grouse in the past, but is almost completely unoccupied at present (Bean 1941, Autenrieth 1981; Fig. 2). Observations during the mid-1800s indicated that many of the well-traveled areas close to the Snake River were dominated by sagebrush and little grass (Vale 1975). These areas are the lowest elevation and driest, and are the most likely to be developed or converted (Bunting et al. 2002). The only museum specimens collected <25 km from the Snake River were three specimens west of American Falls and another near Wilder, Idaho; all were collected in 1933 or earlier (Fig. 1). This suggests that sage-grouse were extirpated close to the Snake River relatively early, perhaps prior to 1900. In addition, populations are apparently continuing to recede from the Snake River and its tributaries (since Autenrieth 1981), indicating this may be a long-term trend.

The current distribution (Fig. 2) indicates that remaining populations of sage-grouse are increasingly isolated, often requiring translocations for support (Musil et al. 1993, Reese and Connelly 1997). Not only is the current range substantially smaller than the presettlement distribution of potential habitat (Fig. 1), but the cur-

rent range is smaller than it was 40 years ago (Aldrich 1963). In many areas, sage-grouse are found only along higher slopes and ridges, separated from adjacent populations by unoccupied valleys.

GUNNISON SAGE-GROUSE

Presettlement distribution of potential habitat.

Potential habitat for the Gunnison Sage-Grouse includes 46 521 km² distributed in central and southwestern Colorado, southeastern Utah, northwestern New Mexico, and northeastern Arizona (Fig. 1, Young et al. 2000). Regional journals in 1849 (Simpson 1964) and 1880–1882 (Bandelier 1966) did not mention sage-grouse but noted the prevalence of agriculture and the long history of settlement. After traveling between Santa Fe, New Mexico, and Fort Defiance, Arizona, in 1849, Simpson (1964:108) stated "a more wretched country for game of every kind I have never seen than that we have been traversing since we left Santa Fe." Neither Simpson (1964) nor Bandelier (1966) spent much time in potential sage-grouse habitat.

Aldrich and Duvall (1955) included southeastern Utah, southwestern Colorado, and north-central New Mexico in the past distribution; Young et al. (2000) also included the northeastern corner of Arizona. Regardless of the exact presettlement distribution line, sage-grouse populations appear to be receding from the southern portions of their previously occupied range. Sage-grouse in Colorado were found within 35 km of Arizona as recently as 1961 (Rogers 1964); they are currently more than 70 km away (Fig. 2). The only museum specimen from New Mexico was collected in 1874 near Tierra Amarilla (Bailey 1928), and the last known Gunnison Sage-Grouse in New Mexico occupied the Tres Piedras area until 1908 (Bailey 1928) and the Chama area until 1912 (Ligon 1961). The Chama birds were along the Continental Divide, the highest-elevation sagebrush habitat in the area. Much of the potential sage-grouse habitat in New Mexico was considered marginal, but may have been occupied to the Arizona state line in the past (Ligon 1927, 1961). There are no published observations of sage-grouse in northeastern Arizona, or the area south of the San Juan River.

Current distribution. The overall area for the current distribution of Gunnison Sage-Grouse was estimated to be 4787 km² (Fig. 2), or ap-

proximately 10% of the potential presettlement habitat (Fig. 1). Brown and Davis (1995) mentioned regional extirpations of sage-grouse as part of a long-term trend in the northward contraction of species formerly found in the southwestern United States and northwestern Mexico. This possibility is supported by the distribution of early sage-grouse specimens in New Mexico, including four sites in the southwestern corner, most of which have been dated to the Holocene or late Pleistocene. Specimens have been found in Hidalgo, San Juan, Dona Ana, Bernalillo, and Grant Counties (Howard and Miller 1933, Howard 1962, Rea 1980, Harris 1985, 1989).

More than 400 Greater Sage-Grouse were captured in Wyoming, South Dakota, Washington, and Nevada between 1933 and 1969 and released in New Mexico, mostly in the Tres Piedras area, but also in Rio Arriba County (Ligon 1961, Reese and Connelly 1997). Although birds were observed as recently as 1989, the translocation ultimately was unsuccessful. In 1976, 48 Greater Sage-Grouse were translocated from Wayne to San Juan County, Utah, in the former range of Gunnison Sage-Grouse. Although the population persisted for many years, it now appears to be extirpated. It is not clear if the lack of success in these translocations was due to habitat considerations or the incorrect placement of Greater Sage-Grouse within the distribution of Gunnison Sage-Grouse.

The core of the current distribution is near Gunnison, Colorado (Fig. 2; Braun 1995, Young et al. 2000). Although there are small, scattered populations to the west of Gunnison, including two on the Utah border, they are all at risk of extirpation (Braun 1995, Beck et al. 2003). In 1971–1972 and 2000–2002, 71–81 Gunnison Sage-Grouse were translocated between Gunnison and Saguache Counties, Colorado. Remaining populations in the region appear to be continuing to decline (Young et al. 2000).

MISCELLANEOUS CONSIDERATIONS

Sage-grouse were observed in southwestern Kansas during the 1870s (Goss 1883, 1886), west of Wilburton, Kansas, in the early 1930s, near Waynoka, Oklahoma, in 1902 (Tate 1923), and north of Beaver Creek in Cimarron County, Oklahoma, in 1910–1920 (Tate 1923, Fig. 1). The Beaver Creek observations were within 20 km of Texas, the northeastern tip of New Mexico, and the southeastern tip of Colorado. Nice

(1931) reported that a specimen was collected in the region; however its existence has not been verified. Tate (1923:43) observed these sage-grouse “strutting about, the sacs on their necks inflated and tails erect. . . hissing and buzzing.” Although the details associated with this description are ambiguous and do not fit the stereotypical descriptions of either sage-grouse species (Schroeder et al. 1999), these birds were hypothesized to be Gunnison Sage-Grouse due to their proximity to the established distribution (Young et al. 2000). Tate (1923) also differentiated between sage-grouse and the two other grouse species present in the region, Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) and Sharp-tailed Grouse, perhaps supporting the validity of the observations.

The past presence of sage-grouse in southwestern Kansas–western Oklahoma has been considered hypothetical (Thompson and Ely 1989), and observations have been attributed to erratic wanderings or mistaken identities (Applegate 2001). However, the number of distinct observations (at least five) and the fact that observations were in the same general area (Fig. 1) supports the possibility that sage-grouse may have been resident in this area. However, their relationship with specific habitat types in the region is not clear. Sand sagebrush (*A. filifolia*) is the dominant shrub species in the region, but has an extensive distribution that includes many areas where sage-grouse have not been observed; in particular, the adjacent areas of eastern Colorado and the panhandle of Texas. Because of these contradictions, we did not attempt to define a presettlement distribution for potential sage-grouse habitat in regions dominated by sand sagebrush (Fig. 1).

DISCUSSION

Although our maps represent the presettlement distribution of potential habitat and the current distribution of sage-grouse, a distribution is dynamic due to factors such as habitat conversion or degradation, alteration of fire frequency, and climate change (Miller and Eddleman 2001). Some of these factors may explain changes in distribution (Brown and Davis 1995). Potential deficiencies with mapping are exacerbated by inaccuracies in habitat data and differences in the timing of landscape alteration. For example, changes associated with settlement began in the southwestern United States as early as the

1600s, while widespread settlement in northern areas did not commence until the mid-1800s.

Another challenge with mapping is that habitat types can be difficult to define consistently over large regions. Although Girard (1937) and Patterson (1952) argued that the past distribution of sage-grouse was defined by the presence of sagebrush-dominated habitats, the quantity of sagebrush in a given habitat type is not always known or consistent. For example, some grassland habitats (fescue-wheatgrass, wheatgrass-needlegrass, wheatgrass-bluegrass, grama-needlegrass-wheatgrass; Kuchler 1985) may have a large component of sagebrush in some regions and virtually none in others. In addition, sagebrush-dominated habitat types may lack sagebrush in some areas, perhaps due to recent fires. Similar factors may influence the suitability of habitats with regard to trees such as juniper and pinyon pine (Connelly et al. 2000, Miller and Eddleman 2001, Oyler-McCance et al. 2001). Habitats characterized by an open tree canopy may support sage-grouse when the canopy is reduced, whereas habitats dominated by sagebrush may cease to support sage-grouse when the density and height of trees is increased; changes in the frequency of fire may have a fundamental influence in these processes (Miller and Eddleman 2001).

A lack of data may make it difficult to know whether there is an absence of birds or whether there is inadequate documentation of existing birds. It is possible that Lewis and Clark (Moulton 1986, 1987), Swainson and Richardson (1831), and Audubon (1960) failed to observe sage-grouse along the Missouri River, even though they were present. At the least, if sage-grouse did occupy the Missouri watershed in eastern Montana and western North Dakota, their densities must have been low in areas visited by early explorers. A similar issue applies to southern portions of the distribution. The 1912 extirpation of sage-grouse in New Mexico (Ligon 1961) suggests that changes in distribution occurred too early for adequate documentation. Future examinations of regional habitat and habitat change should provide more insight into long-term changes in the distribution of sage-grouse.

The locations of some observations and museum specimens were outside the perimeter we delineated for the presettlement distribution of potential habitat. There have been numerous ob-

servations of sage-grouse in areas outside big sagebrush-dominated habitats, particularly in Colorado, Kansas, Nebraska, Oklahoma, and the Dakotas. Because of these observations, and the large area involved, our distribution of potential habitat may be a conservative estimate of the total amount of area occupied in the past.

The area currently occupied by sage-grouse is clearly smaller than would likely have been occupied in presettlement times. Declines in distribution have been noted throughout the twentieth century (Hornaday 1916, Locke 1932, McClanahan 1940, Aldrich and Duvall 1955, Connelly and Braun 1997). The primary causes for the declines appear to be habitat degradation and conversion, including the adverse affects of cultivation, dams, fragmentation, reduction of sagebrush and herbaceous cover, resource extraction, power lines, fences, expansion of invasive plant species, changes in the fire regime, and issues related to the timing and intensity of livestock grazing (Connelly and Braun 1997, Braun 1998). Declining densities within core populations may also reduce the occupation of peripheral habitats. Hence, the declining distribution may reflect degraded conditions within the currently occupied range.

We believe these distribution maps are more accurate than earlier maps and that they allow digital comparisons of distribution with other spatial characteristics such as land ownership, habitat type, range condition, and fire frequency. They also eliminate habitats that are clearly not occupied by sage-grouse, such as forests. The acquisition of new information and reinterpretation of existing information will allow these maps to be periodically evaluated and refined. Important considerations for future efforts should be differentiation among areas of varying population density and seasonal suitability. This differentiation will improve the understanding of spatial and demographic characteristics of sage-grouse populations that are important in evaluations of population viability.

These digital maps will offer opportunities that were previously impractical. First, they will permit detailed examinations of habitat characteristics, topography, weather, history, and management within the current distribution of sage-grouse and within the presettlement distribution of potential habitat. Consequently, hypotheses concerning the effects of habitat alteration can be examined in relation to observed changes in

population distribution. Second, these maps can be used in evaluations of alternate habitat management strategies (Wisdom, Rowland, et al. 2002, Wisdom, Wales et al. 2002). Third, they can provide a foundation for addressing information needs (Knick et al. 2003). Finally, they will aid the production of a rangewide assessment of the status and viability of sage-grouse in North America.

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