The Effects of Management Practices on Grassland Birds—Greater Sage-Grouse (*Centrocercus urophasianus*)

Chapter B of

The Effects of Management Practices on Grassland Birds

Professional Paper 1842–B

U.S. Department of the Interior
U.S. Geological Survey

Cover. Greater Sage-Grouse. Photograph by Tom Koerner, U.S. Fish and Wildlife Service.
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The Effects of Management Practices on Grassland Birds—Greater Sage-Grouse (*Centrocercus urophasianus*)

By Mary M. Rowland[1]

Chapter B of

The Effects of Management Practices on Grassland Birds

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U.S. Department of the Interior
U.S. Geological Survey

U.S. Department of the Interior
DAVID BERNHARDT, Secretary

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Conversion Factors

International System of Units to U.S. customary units

Multiply	By	To obtain
	Length	
centimeter (cm)	0.3937	inch (in.)
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
	Area	
square meter (m^2)	0.0002471	acre
hectare (ha)	2.471	acre
square kilometer (km^2)	247.1	acre
square centimeter (cm^2)	0.001076	square foot (ft^2)
square meter (m^2)	10.76	square foot (ft^2)
square centimeter (cm^2)	0.1550	square inch (ft^2)
hectare (ha)	0.003861	square mile (mi^2)
square kilometer (km^2)	0.3861	square mile (mi^2)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as

$$°F = (1.8 \times °C) + 32.$$

Abbreviations

CBM	coal-bed methane
CRP	Conservation Reserve Program
n	sample size number
NWR	National Wildlife Refuge
SE	standard error
SGCA	Sage-Grouse Conservation Area
SMZ	Sage-Grouse Management Zone
spp.	species (applies to two or more species within the genus)
ssp.	subspecies
WNV	West Nile virus

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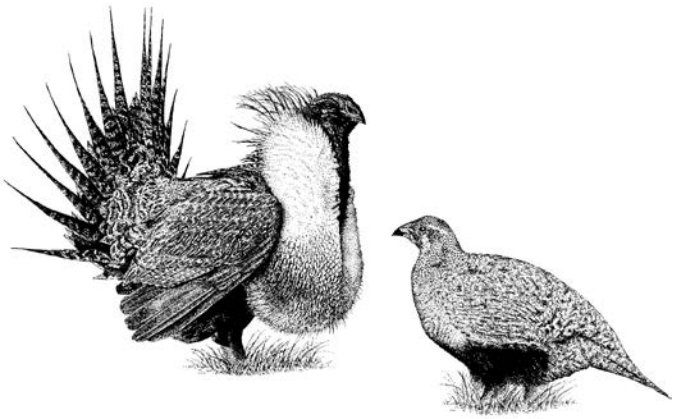
The Effects of Management Practices on Grassland Birds—Greater Sage-Grouse (*Centrocercus urophasianus*)

By Mary M. Rowland[1]

Capsule Statement

Keys to Greater Sage-Grouse (*Centrocercus urophasianus*) management are maintenance of expansive stands of sagebrush (*Artemisia* species [spp.]), especially varieties of big sagebrush (*Artemisia tridentata*) with abundant forbs in the understory, particularly during spring; undisturbed and somewhat open sites for leks; and healthy perennial grass and forb stands intermixed with sagebrush for brood rearing. Within suitable habitats, areas should have 15–25 percent canopy cover of sagebrush 30–80 centimeters (cm) tall for nesting and 10–25 percent canopy cover 40–80 cm tall for brood rearing (Connelly and others, 2000b). In winter habitats, shrubs should be exposed 25–35 cm above snow and have 10–30 percent canopy cover exposed above snow. In nesting and brood-rearing habitats, the understory should have at least 15 percent cover of grasses and at least 10 percent cover of forbs greater than or equal to (>) 18 cm tall. Greater Sage-Grouse have been reported to use habitats with 5–110 cm average vegetation height, 5–160 cm visual obstruction reading, 3–51 percent grass cover, 3–20 percent forb cover, 3–69 percent shrub cover, 7–63 percent sagebrush cover, 14–51 percent bare ground, and 0–18 percent litter cover. The descriptions of key vegetation characteristics are provided in table B1 (after the "References" section).

Unless otherwise noted, this account refers to habitat requirements and environmental factors affecting Greater Sage-Grouse but not Gunnison Sage-Grouse (*Centrocercus minimus*). Habitats used by Gunnison Sage-Grouse are generally similar to habitats used by Greater Sage-Grouse, but some differences have been reported (Young and others, 2000; Aldridge and others, 2012). The Greater Sage-Grouse is a game bird and is hunted throughout most of its current range (Reese and Connelly, 2011). This account does not address harvest or its effects on populations; rather, this account focuses on the effects of habitat management. Vernacular and scientific names of plants and animals follow the Integrated Taxonomic Information System (https://www.itis.gov).



Male and female Greater Sage-Grouse. Illustration by Darrell Pruett, used with permission.

Breeding Range

Since European settlement, the range of Greater Sage-Grouse has been substantially reduced (Connelly and Braun, 1997; Braun, 1998; Schroeder and others, 1999, 2004; Connelly and others, 2011b). Sage-grouse have a disjunct year-round range within suitable sagebrush habitats from central Washington through southern Idaho and most of Montana, to extreme southeastern Alberta and southwestern Saskatchewan, Canada; south to the southwestern corner of North Dakota, western South Dakota, most of Wyoming, western Colorado, and portions of Utah; and west to Nevada, extreme eastern California, and eastern Oregon (fig. B1; Connelly and others, 2004; Schroeder and others, 1999, 2004). The species has been extirpated from Arizona, British Columbia, Kansas, Nebraska, and Oklahoma (Schroeder and others, 1999, 2004; Garton and others, 2011). The current and historical distributions of the Greater Sage-Grouse in the United States and southern Canada, based on data from the U.S. Geological Survey (2014a, 2014b, 2016), are shown in figure B1 (not all geographic places mentioned in report are shown on figure).

[1]U.S. Forest Service.

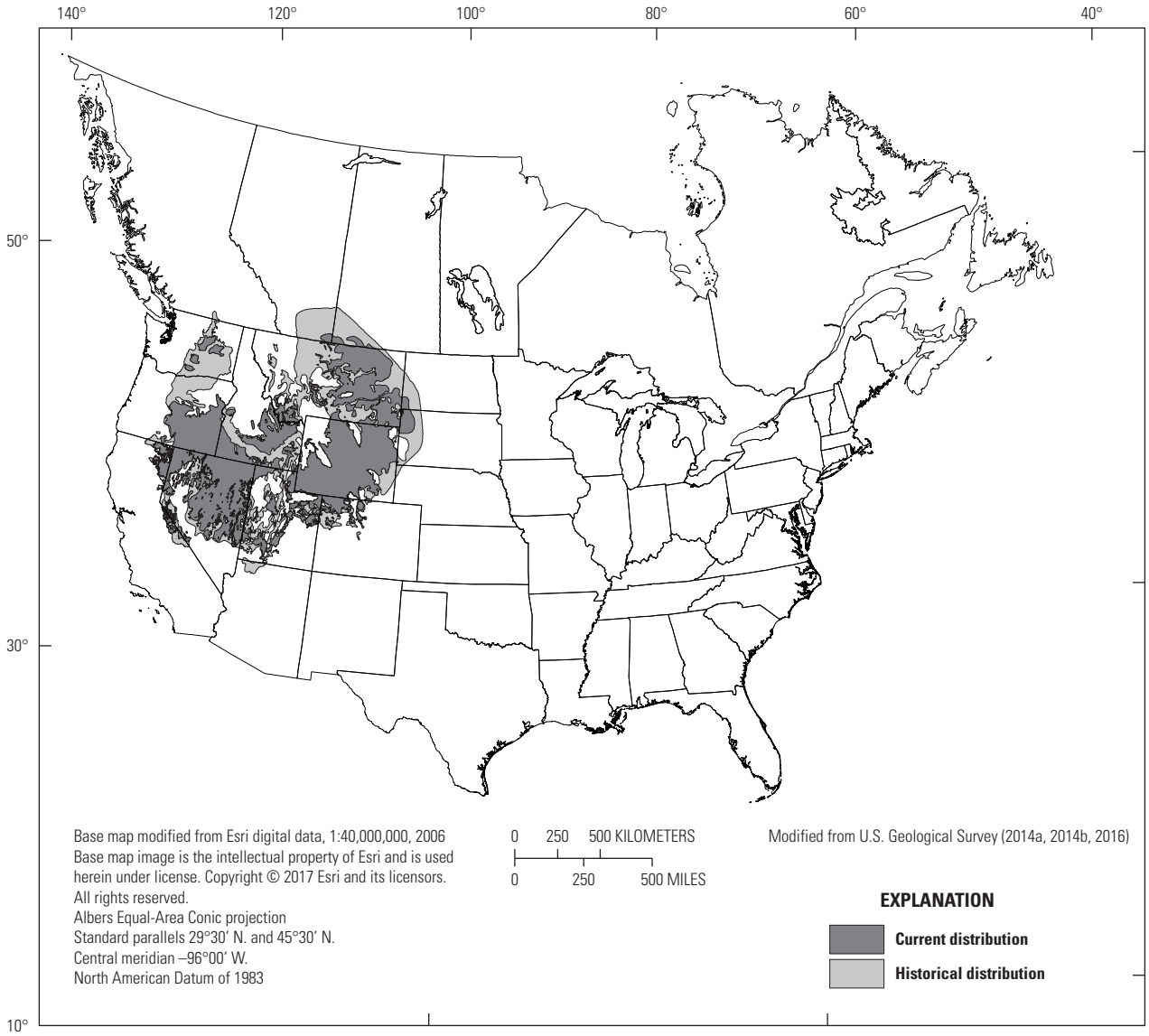


Figure B1. The current and historical distributions of Greater Sage-Grouse (*Centrocercus urophasianus*) in the United States and Canada. (Data from U.S. Geological Survey, 2014a, 2014b, 2016)

Suitable Habitat

Greater Sage-Grouse are widely distributed in sagebrush habitats throughout the western United States and are considered a sagebrush-obligate species because of their year-round dependence on sagebrush communities (Patterson, 1952; Braun and others, 1976; Braun and Beck, 1996; Paige and Ritter, 1999; Schroeder and others, 1999; Connelly and others, 2004). Although most closely allied with larger varieties of sagebrush (big sagebrush, threetip sagebrush [*Artemisia tripartita*], and silver sagebrush [*Artemisia cana*]), sage-grouse also use a variety of other native habitats, especially outside the breeding season, including sagebrush species of low stature (for example, low sagebrush [*Artemisia arbuscula*] and black sagebrush [*Artemisia nova*]), antelope bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothamnus* spp.), riparian and upland meadows, and sagebrush grasslands (Patterson, 1952; Dalke and others, 1963; Wallestad, 1971; Nisbet and others, 1983; Klebenow, 1985; Connelly and others, 1991, 2011c; Gregg and others, 1993; Musil and others, 1994; Braun, 1995; Apa, 1998; Sveum and others, 1998; Schroeder and others, 1999; Aldridge and Brigham, 2002; Crawford and Davis, 2002; Danvir, 2002).

Despite their reliance on sagebrush habitats, Greater Sage-Grouse also use human-modified habitats, such as croplands, when these habitats are adjacent to sagebrush (Schroeder and others, 1999). Sage-grouse have been reported in crested wheatgrass (*Agropyron cristatum*) seedings, alfalfa (*Medicago sativa*) fields, and irrigated and dry cropland (for example, wheat [*Triticum* spp.] and barley [*Hordeum* spp.]

fields) (Batterson and Morse, 1948; Patterson, 1952; Leach and Browning, 1958; Gill, 1965; Wallestad, 1971; Beck, 1977; Gates, 1981; Hulet and others, 1986; Willis, 1991; Leonard and others, 2000; Connelly and others, 2011c).

The species also has been reported in Conservation Reserve Program (CRP) grassland fields in western South Dakota and eastern Montana (Igl, 2009). Unlike CRP fields in the Midwest, CRP fields in Washington commonly are on lands that were historically sagebrush steppe (Schroeder and Vander Haegen, 2011). In a radio-telemetry study investigating use of CRP fields by sage-grouse hens (sample size number [*n*] = 89) in Washington, nest success was similar in CRP fields (45 percent) and shrubsteppe habitats (39 percent) (Schroeder and Vander Haegen, 2011). Moreover, the proportion of nests in CRP increased during the study (1992–97) as sagebrush shrubs became better established in CRP fields. For populations of sage-grouse in Washington, CRP lands seemed to increase in importance as nesting, brood-rearing, and winter habitat for sage-grouse concomitant with increasing shrub cover (Stinson and others, 2004; Schroeder and Vander Haegen, 2006). The benefits of these lands were further demonstrated by a reversal of population declines in north-central Washington in 1992–2007 following CRP establishment (Schroeder and Vander Haegen, 2011). Gunnison Sage-Grouse (*n*=13) used CRP lands in Utah for nesting, brood-rearing, and summer habitat, but not in greater proportion than their availability (Lupis and others, 2006). However, Gunnison Sage-Grouse avoided CRP lands in the study area when cattle were present, a result of an emergency drought declaration.

The overall value of CRP lands to sage-grouse remains unknown (Connelly and others, 2004; Knick and others, 2011). However, CRP lands in Washington are essential to sage-grouse conservation in that State because CRP lands provide shrub cover similar to the surrounding sagebrush (Schroeder and Vander Haegen, 2011). The removal of CRP in Washington would likely result in substantial population declines, as realized in 2016 after the conversion of large amounts of CRP to crops (Schroeder and others, 2016). Additionally, CRP lands in Washington provide connectivity among fragmented sagebrush habitats (Schroeder and Vander Haegen, 2011).

Specific characteristics of habitats used by sage-grouse differ throughout the year. During the breeding season, males display on leks that are characterized by low, sparse vegetation or bare ground (Patterson, 1952; Gill, 1965; Klebenow, 1985). Nesting habitats include moderate sagebrush cover, typically ranging from 15 to 25 percent (Connelly and others, 2000b); nests are most commonly placed beneath a sagebrush shrub (Patterson, 1952; Petersen, 1980; Drut and others, 1994a; Gregg and others, 1994). Herbaceous understories composed of native grasses and forbs are a key component of nesting and brood-rearing habitats (Wallestad, 1970; Klott and Lindzey, 1990; Connelly and others, 1991; Drut and others, 1994a; DeLong and others, 1995; Hagen and others, 2007; Gregg and others, 2008). During winter, foraging sage-grouse rely on sagebrush exposed above snow (Batterson and Morse, 1948; Patterson, 1952; Schroeder and others, 1999).

Formal guidelines for managing habitat for sage-grouse were first published in the 1970s (Braun and others, 1977) and subsequently updated by Connelly and others (2000b). The more recent guidelines (Connelly and others, 2000b) suggested maintaining a diversity of habitats for sage-grouse during different seasonal-use periods (for example, breeding, brood rearing, and wintering). Specifically, Connelly and others (2000b) indicated that canopy cover of sagebrush in arid and mesic sites should be maintained as follows: 15–25 percent in breeding habitat, 10–25 percent in brood-rearing habitat, and 10–30 percent in wintering habitat (canopy cover in winter refers to the portion of sagebrush exposed above snow). The recommended percentages of grass-forb cover during breeding are >15 percent in arid sites, but >25 percent in mesic sites; during brood rearing, grass-forb cover should exceed 15 percent in mesic and arid sites (Connelly and others, 2000b). (Cover of grasses and forbs for wintering habitats is irrelevant, because of the nearly complete reliance of sage-grouse upon sagebrush during this winter period.)

Recommendations for sagebrush height also are provided in the guidelines for the following habitats: breeding and brood rearing (40–80 cm for mesic sites or 30–80 cm for arid sites) and winter (25–35 cm exposed above snow) (Connelly and others, 2000b). The recommended height of grasses and forbs in mesic and arid breeding habitats (greater than [>] 18 cm) has recently (Gibson and others, 2016b) been acknowledged as the average height measured at nest fate, not nest initiation. Therefore, residual grass height at the time of nest-site selection is shorter, but no universal average has been identified. In brood-rearing habitat, grass and forb height can be variable; and, in winter, height is not applicable. At least 80 percent of breeding and winter habitats and 40 percent of brood-rearing habitats should be maintained within these prescribed conditions. Hagen and others (2007) led a meta-analysis of sage-grouse nesting (*n*=24) and brood-rearing (*n*=8) studies and concluded that sagebrush canopy cover and grass height were greater at nest sites than at random sites. By contrast, vegetation in brood-rearing sites had less sagebrush cover and greater grass and forb cover than random sites (Hagen and others, 2007). Sagebrush cover within the range of sage-grouse in Canada is generally less than that in the southern portions of the species' range (Aldridge and Brigham, 2002), suggesting that the guidelines may be adapted to local conditions when used at the northern edge of the range.

Traditionally, managers have monitored the status of sage-grouse populations through counts of males on leks and, to a lesser extent, numbers of birds seen along routes driven during summer ("brood counts") and hunter harvest data (for example, Batterson and Morse, 1948; Patterson, 1952; Beck and others, 1975; Jenni and Hartzler, 1978; Emmons and Braun, 1984; Willis and others, 1993; Braun and Beck, 1996; Schroeder and others, 1999; Connelly and others, 2003b; Walsh and others, 2004; Johnson and Rowland, 2007). Connelly and others (2003b) described standardized techniques for monitoring sage-grouse habitats and populations. The Western

Association of Fish and Wildlife Agencies funded work to estimate actual population numbers compared to trends (Nielson and others, 2015), but that methodology has not been applied by all States. Stiver and others (2015) provided a comprehensive, multi-scaled approach for monitoring sage-grouse habitat. Specific information on habitats used during various seasons (for example, courtship activities [lekking], nesting, brood rearing, and foraging) appears in the following sections.

Lek Sites

Male sage-grouse require fairly open areas during the breeding season for displaying (Scott, 1942; Patterson, 1952; Dalke and others, 1963; Klebenow, 1973, 1985; Autenrieth, 1981; Connelly and others, 1981; Schroeder and others, 1999). Such sites are typically adjacent to sagebrush that provides nesting habitat, protection from avian predators, and support short, sparse vegetation, if any at all (Scott, 1942; Petersen, 1980; Autenrieth, 1981; Klebenow, 1985; Connelly and others, 2004; Dinkins and others, 2012). Flat or gently sloping terrain is a common characteristic of leks (Rogers, 1964), as is the location of leks in valley bottoms or draws (Patterson, 1952; Rogers, 1964). Leks can be formed opportunistically within or adjacent to nesting habitat (Connelly and others, 2000a), and no evidence exists indicating that suitable habitat for leks is limiting for sage-grouse (Schroeder and others, 1999).

Of 10 leks surveyed in Mono County, California, 6 were in meadows, although meadows composed only 9 percent of the available sagebrush-meadow habitat (Gibson, 1996). Habitat type did not seem to be the primary factor in lek location; however, female dispersal traffic (patterns of movement between wintering and nesting areas) seemed to most strongly affect lek location (Bradbury and others, 1989a; Gibson, 1996). In addition to open areas for displaying males and moving hens, protection from raptors is a factor in lek location (Bradbury and others, 1989b). Aspbury and Gibson (2004) evaluated visibility of leks (n=7) in Mono County, California, from the perspective of Golden Eagles (*Aquila chrysaetos*) (flying and perched), sage-grouse hens searching for leks, and lekking males searching for eagles. Results of the evaluation determined that leks were in areas that diminished long-range visibility from ground observers but were in areas that enhanced short-range visibility. Aspbury and Gibson (2004) hypothesized that displaying males, thus, use topography to increase their visibility to hens while forcing eagles to monitor leks from the air, where eagles are more visible to male sage-grouse.

In Nevada and Utah, 41 leks were preferentially established in black sagebrush habitats (based on use compared to availability) (Nisbet and others, 1983). Environmental variables beyond vegetation type that were included in a lek preference model were slope (less than [<] 10 percent), precipitation (>25 cm), distance to nearest water source (less than or equal to [<] 2,000 meters [m]), and sites with no predicted encroachment by pinyon-juniper woodlands. Such encroachment is one of the key stressors of sagebrush habitats (Connelly and others, 2011b; Miller and others, 2011, 2017).

In North Park, Colo., mating areas (arenas) within three leks had an average sagebrush canopy cover of only 7.3 percent and a mean vegetation height of 5.3 cm; sagebrush species present included big sagebrush, alkali sagebrush (*Artemisia arbuscula* ssp. [subspecies] *longiloba*), and black sagebrush (Petersen, 1980). Rogers (1964) reviewed characteristics of 120 leks throughout Colorado during 1953–61 and determined that, on average, one-half were in sagebrush; 54 percent were on gentle slopes; 55 percent were in bottoms; only 5 percent were within 200 m of a building; and although 42 percent were >1.6 kilometers (km) from an improved road, 26 percent were within 100 m of a county or State highway. During daytime, male sage-grouse in northeastern Utah used areas near leks that had comparatively greater canopy cover (mean of 31 percent) and taller shrubs (mean of 53 cm) than did nearby nonuse areas (Ellis and others, 1989).

Sage-grouse establish leks not only in native habitats but also in altered or disturbed environments (Schroeder and others, 1999; Connelly and others, 2011c). Leks have been found on airstrips, firing ranges, gravel pits, sheep bedding grounds, cultivated fields, burned sagebrush, plowed fields, cleared roadsides or roadbeds, and actively occupied ant mounds (Batterson and Morse, 1948; Patterson, 1952; Dalke and others, 1963; Rogers, 1964; Klebenow, 1973; Giezentanner and Clark, 1974; Autenrieth, 1981; Connelly and others, 1981; Gates, 1985; Hofmann, 1991).

Leks commonly are in complexes, with satellite leks on the periphery that may not be used in every year, depending on population size or weather (Dalke and others, 1963; Rogers, 1964; Wiley, 1978). In a study of 31 leks in Idaho, mean interlek distance (that is, distance between nearest-neighbor leks) was about 1.6 km (Wakkinen and others, 1992). Of 13 leks examined in the Upper Snake River Plains in Idaho, 10 were in threetip sagebrush habitat (Klebenow, 1969). For two of these leks, interlek distance was 0.8 km, and for eight others, interlek distance was 2.4 km. In Wyoming, lek density of 29 leks within a water-reclamation project area averaged 6.8 leks per 100 square kilometers (km^2), compared with 8.4 leks per 100 km^2 for 18 leks in nearby, undeveloped sagebrush habitats (Patterson, 1950). Similar lek densities were reported in Oregon; 4.3 leks per 100 km^2 were at Hart Mountain National Antelope Refuge and 4.7 leks per 100 km^2 were at Jackass Creek (Willis and others, 1993).

Lek and nesting habitat may be selected in part based on nutritional needs. In a low sagebrush community in the Great Basin, forbs were an important component of the diet of preincubating sage-grouse hens (Gregg and others, 2008). Although low sagebrush was the most common diet item, forbs had higher levels of crude protein, calcium, and phosphorus. Nest-site selection also has been linked to early chick survival, suggesting that hen selection of nesting habitat is based on its quality as early brood-rearing habitat (compared to nest survival), which includes diverse food availability (Gibson and others, 2016a).

Nesting Habitat

Greater Sage-Grouse nest in a variety of sagebrush-dominated cover types, but most nests are under sagebrush (Rasmussen and Griner, 1938; Patterson, 1952; Gill, 1965; Wallestad and Pyrah, 1974; Petersen, 1980; Wakkinen, 1990; Connelly and others, 1991, 2011c; Drut and others, 1994a; Gregg and others, 1994; Sveum and others, 1998; Schroeder and others, 1999; Lowe and others, 2009; Hansen and others, 2016). Other shrubs used for nesting cover include bitterbrush, greasewood (*Sarcobatus vermiculatus*), horsebrush (*Tetradymia* spp.), mountain mahogany (*Cercocarpus* spp.), rabbitbrush, shadscale (*Atriplex confertifolia*), snowberry (*Symphoricarpos* spp.), and western juniper (*Juniperus occidentalis*) (Patterson, 1952; Klebenow, 1969; Wakkinen, 1990; Connelly and others, 1991; Crawford and Davis, 2002; Lowe and others, 2009), and nests also have been observed under basin wildrye (*Leymus cinereus*) (Wakkinen, 1990; Crawford and Davis, 2002; Foster, 2016). Nests have been found on sites with large (mean=41 percent, *n*=22) percentages of bare ground within a large-scale burn in Oregon (Foster, 2016) or even on bare ground devoid of cover (Patterson, 1952). However, nests established in areas of low or no cover are typically unsuccessful.

Sage-grouse nest locations are consistently described in the literature as being placed under larger, taller shrubs with obstructing cover and within shrub patches (compared to random sites) (Wallestad and Pyrah, 1974; Connelly and others, 2011c). Nesting habitat generally has more sagebrush cover and taller sagebrush when compared to available habitats (Connelly and others, 2011c). In addition, suitable nesting sites contain a healthy understory of native grasses and forbs that provide (1) cover for concealment of the nest and hen from predators, (2) herbaceous forage for prelaying and nesting hens, and (3) insects as prey for chicks and hens. Gibson and others (2016a) suggested that nest-site selection is based on the ability of an area to provide early brood-rearing habitats rather than improving nesting success. Connelly and others (2011c), in summarizing several studies, reported that mean sagebrush canopy cover at nest sites ranged from 15 to 50 percent, and mean sagebrush height ranged from 36 to 79 cm. A meta-analysis of vegetation characteristics at nest and brood-rearing sites drawn from 19 studies by Hagen and others (2007) reported similar values, with mean sagebrush canopy cover at nests of 21.5 percent. In addition to sagebrush canopy cover, evidence of selection was found for grass height at nests, which averaged 19.8 cm at the time when hens and broods leave the nest. However, grass height at the time of nest selection is likely much shorter simply because of plant phenology (that is, plants are shorter 30–40 days before egg hatch; Gibson and others, 2016b).

In central Oregon, nests were most common in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*); however, the percentage of nests in this type was similar to the availability of the type (Hanf and others, 1994). Although mountain shrub types (mountain big sagebrush-antelope bitterbrush) and native grasslands were less commonly used, sage-grouse seemed to select these types for nesting; that is, use exceeded availability. In southeastern Oregon, Drut and others (1994a) found that 72 percent of 18 nests were in big sagebrush. In another study in southeastern Oregon, Gregg and others (1994) found that 94 percent of 124 nests of radio-marked hens were under sagebrush in an area where sagebrush composed 87 percent of the shrubs.

Sveum and others (1998) evaluated nesting habitat selection at the Yakima Training Center in Washington, which contained some of the most intact sage-grouse habitat remaining in the State. Most first nest attempts (64 percent of 72) were in the big sagebrush-bunchgrass cover type. This type was preferred (use exceeded availability) in 1 of 2 years of study. Sage-grouse nested in scabland sagebrush (*Artemisia rigida*)-bluegrass (*Poa* spp.) and grassland-cover types less than expected in both years. Sage-grouse had no preference (that is, use was proportional to availability) for nesting in big sagebrush-bunchgrass that had reduced shrub cover and increased bare ground resulting from military training activities, or in riparian cover types (for example, ephemeral streams and wet areas). Shrub cover at nest sites averaged 51 percent (1992; *n*=35) and 59 percent (1993; *n*=58), compared with 6–7 percent at random sites (*n*=60 and 30 sites for 1992 and 1993, respectively). Shrub height was greater (59 and 63 cm) at nest sites than at random sites (15 and 13 cm in 1992 and 1993, respectively). Nest sites also had less cover of short (<18 cm) grasses, greater vertical cover height, less bare ground, and more litter than random sites (Sveum and others, 1998).

In an Idaho study, 216 nest bushes were taller and larger than big sagebrush shrubs in 40-square meter (m^2) plots surrounding the nests (Autenrieth, 1981). Mean height of nest bushes ranged from 58.2 to 79.3 cm, compared with 30.2 to 54.9 cm in the plots. Mean diameter of nest bushes ranged from 93.9 to 109.7 cm, compared with 42.7 to 61.0 cm for other sagebrush shrubs in the plots. Mean canopy cover of big sagebrush in the surrounding plots ranged from 23.4 to 38.1 percent. Distance from nests to water varied from 530 to 2,257 m. Patterson (1952) recorded more than 200 sage-grouse nests in an 11-year period in the Eden Valley-Pacific Creek area in western Wyoming. Height of cover at nest sites ranged from 0 to 102 cm, with a mean of 36 cm; nests were most commonly placed beneath “short sagebrush of medium density, such as is found on drier sites, in preference to the dense, tall sagebrush found along watercourses…” (Patterson, 1952, p. 114). Although the specific taxa of sagebrush were not mentioned, this area is an arid Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) site, thus, accounting for the relatively shorter stature of nesting shrubs compared to those reported for Washington and Idaho.

In the Green River Valley in Wyoming, Lyon (2000) evaluated a suite of variables at 50 nests. In comparison with independent, random sites (*n*=63), nest sites had taller average live sagebrush (32.7 compared with 27.6 cm), more grass cover (10.6 compared with 5.4 percent), more forb cover (8.2 compared with 4.3 percent), and taller nest bushes

(44.4 compared with 21.4 cm). Nest sites also had greater total herbaceous cover and less bare ground than random locations (Lyon, 2000).

Dinkins and others (2016) evaluated nest-site selection (*n*=928) and success (*n*=924) at three micro-habitat scales (1, 2.5, and 5 m) during 2008–14 in core areas established in Wyoming to reduce human disturbance near sage-grouse. Sage-grouse selected sites with greater sagebrush height and cover and visual obstruction; for example, for each 10 percent increase in shrub cover (1-m scale), the relative probability of nest selection increased 48 percent. Hansen and others (2016) measured nest-site selection and survival at three scales in south-central Wyoming to obtain data before proposed wind-energy development. The comparison of nest sites (*n*=109) to paired, available sites (*n*=545), indicated strong selection for sites with increased visual obstruction from 22.9 to 45 cm at all scales (Hansen and others, 2016). Increasing canopy cover of sagebrush was positively associated with probability of selection at the nest-patch (5-m radius) and nest-bowl scales. Nest survival (*n*=128) was positively associated with grass height at the nest area (30-m radius) and nest-patch scales and was negatively correlated with drought. Hansen and others (2016) recommended maintaining grass height above 15 cm, especially during drought years. This value can be adjusted for plant phenology of the surrounding grasses to assess the adequacy of nesting habitat at the time of nest-site selection (Gibson and others, 2016b).

Of 61 sage-grouse nests evaluated at the Sheldon National Wildlife Refuge (NWR) in Nevada, 41 percent were in mountain big sagebrush, 31 percent were in mountain shrub (including mountain big sagebrush, antelope bitterbrush, bluegrass, and needlegrass [*Stipa* spp.]), and 13 percent were in low sagebrush cover types (Crawford and Davis, 2002). Neither cover type, medium-height (40–80 cm) shrub cover, nor total forb cover were related to nest success, and age of hen was not related to type of cover used for nesting. Compared to random sites, nest sites had greater amounts of tall (that is, >18 cm) residual grass cover and greater cover of medium-height shrubs (Crawford and Davis, 2002).

Moynahan and others (2007) monitored 287 sage-grouse nests in Phillips County, Mont., and found that grass canopy cover was the only management-related attribute related to nest survival (daily survival rate) in their model. However, the grass effect varied by year, and the range of values for grass cover during the 3 years of their study was small (from 22.0 to 24.7 percent). In Wyoming, an evaluation of 529 nests during 2003–07 indicated strong and positive effects of increasing grass height on nest survival, despite a range of values across years and study areas (from 11.4 to 29.2 cm; Doherty and others, 2014).

In North Park, Colo., Petersen (1980) studied breeding biology of sage-grouse hens; mean sagebrush canopy cover at 35 nest sites was 24 percent (range from 9.4 to 52.6 percent), and mean sagebrush height was 32 cm (range from 11.1 to 59.8 cm), with no differences between nest sites used by adult hens compared to nest sites used by yearling hens. Mean shrub canopy height (range from 27 to 76 cm) at nests was 52.3 cm, but only 32.3 cm in surrounding areas (range from 11.1 to 59.8 cm). Roost sites were in areas with shorter (mean height of 7.6 cm) sagebrush than were nests. Slope at nest sites was gentle, with 85 percent of nests on slopes of <12 percent (Peterson, 1980). Gill (1965), also working in North Park, located 92 percent of 117 nests under sagebrush; mean height of cover at the nest was 43 cm; nests were typically on flat ground, with a mean slope of 2 percent.

In south-central Idaho, Klott and others (1993) found four sage-grouse nests in Wyoming big sagebrush, two in low sagebrush, and one each in mountain big sagebrush and crested wheatgrass. No nests were found in quaking aspen (*Populus tremuloides*), mountain mahogany, mountain shrub, or meadow habitat types. In the Upper Snake River Plains of southeastern Idaho, sage-grouse nested primarily in threetip sagebrush (Klebenow, 1969). Mean height of shrubs under which sage-grouse nested was 43 cm (*n*=87 nests), whereas mean height of threetip sagebrush in the study area was only 20 cm (sample sizes not given). Mean total shrub cover near nest sites was 18.4 percent, compared with 14.4 percent in the threetip sagebrush community overall. Although big sagebrush density and crown cover were greater near nests than in the general area, sage-grouse nests were not found in big sagebrush stands with cover exceeding 25 percent. Bitterbrush provided all or part of the nesting shrub cover for 29 percent of the nests. Klebenow (1969) used stepwise discriminant function analysis to distinguish between nest sites and the surrounding habitat in the threetip sagebrush community; however, a satisfactory model could not be developed with the data collected. In Idaho high desert dominated by threetip sagebrush, sage-grouse selected big sagebrush more than expected and threetip sagebrush less than expected for nesting cover based on the abundance of the species; sage-grouse had greater nest success in big sagebrush (*n*=47; Lowe and others, 2009).

For sage-grouse in a xeric Wyoming big sagebrush community in southeastern Idaho, Wakkinen (1990) also attempted to build a logistic-regression model to discriminate between nest and nonnest sites. The resulting model, however, had poor classification accuracy. Two variables, grass height and nest-bush area, were significant; sage-grouse nest locations (*n*=49) had taller grasses (mean of 18.2 cm compared with 15.3 cm) and larger shrubs (mean area of 11,108 square centimeters compared with 9,384 square centimeters) than random plots (*n*=70) (Wakkinen, 1990). Of the 42 nests used in developing the model, 55 percent were under Wyoming big sagebrush and 29 percent were beneath threetip sagebrush. The area within a 20-m radius of each nest was characterized as follows: 21.5 percent mean canopy cover of sagebrush and 43.9 (1988) and 46.9 cm (1987) mean height of sagebrush. Mean height of nest bushes was 70.6 cm (Wakkinen, 1990). In central Idaho, translocated sage-grouse nested in sites (*n*=6) with greater horizontal cover (86 percent) than random sites (67 percent; *n*=7); mean shrub height at nests was 51 cm (Musil and others, 1994).

At the eastern edge of their range in North Dakota, sage-grouse placed nests in shorter shrubs compared to available shrubs, selecting grazed areas where shrub density was greater, but shrub height was on average shorter than in nongrazed areas (Herman-Brunson and others, 2009). Nest survival was positively associated with grass height and shrub cover, and successful nests were found under shorter shrubs (*n*=29) (Herman-Brunson and others, 2009).

Predation is a key source of mortality of sage-grouse and, thus, may drive local nest selection. In Wyoming, densities of a suite of common avian predators (for example, Golden Eagles, Black-billed Magpies [*Pica hudsonia*]) were lower around sage-grouse nests than at random locations, indicating predator avoidance by sage-grouse through strategic placement of nests (Dinkins and others, 2012). In a study of sage-grouse nesting in Utah and southwest Wyoming, Conover and others (2010) found that sage-grouse seemed to place nests to reduce risk of predation by visual predators (for example, Common Raven [*Corvus corax*]), but not olfactory predators (for example, American badger [*Taxidea taxus*]). Depredation was the primary cause of nest failure in a study of sage-grouse nests (*n*=71) in northern Nevada where habitat quality was degraded and Common Ravens were the most frequent nest predator (Lockyer and others, 2013). Several studies have investigated sage-grouse nest location in relation to leks to address the hypothesis that hens nest midway between leks to avoid high predation rates commonly associated with leks (Bergerud, 1988). Connelly and others (2000b) reported that mean distance between nests and nearest leks ranged from 1.1 to 6.2 km; however, nests have been observed more than 20 km from the nearest lek.

Current guidelines for sage-grouse recommend protecting breeding habitat within 3.2 km of the lek for nonmigratory populations and within 18 km of the lek for migratory populations (Connelly and others, 2000b). In Idaho, Wakkinen (1990) reported that 37 nests were farther from leks compared to distances midway between nearest-neighbor leks (that is, one-half the interlek distance; *n*=31). In addition, distances from nests to the nearest lek were no different than distances from random points to the nearest lek. In another Idaho study, distance from nests to the nearest lek was greatly variable; in two sites, >95 percent of 193 nests were within 3.2 km of the nearest lek, whereas in one site, only 52 percent of 62 nests were within 6.4 km (Autenrieth, 1981). Autenrieth (1981) suggested that nests were placed closer to leks when nesting cover around leks was good. In southeastern Alberta, mean distance from nest (*n*=27) to lek of capture was 4.7 km for hens, and 59 percent of nests were >3.2 km (considered to be the standard site-protection distance) from the lek (Aldridge and Brigham, 2001). During 1994–2003, Holloran and Anderson (2005) used radio-marked sage-grouse hens to investigate nest locations in relation to leks in central and southwestern Wyoming. Mean distance from the lek of capture to the nest (*n*=437) was 4.7 km (range of 282 m to 27.4 km), and 45 percent and 64 percent of all nests were within 3 or 5 km of a lek, respectively. Results indicated no difference in mean lek-to-nest distance between successful and unsuccessful nests and no relation between lek-to-nest distance and lek size. In a study in North Dakota at the eastern edge of the range of Greater Sage-Grouse, 68 and 86 percent of nests were within 3.2 and 5 km of a lek, respectively (Herman-Brunson and others, 2009). The average distance (plus [+] standard error [SE]) from nests to the lek at which a hen was captured was 4.9 plus or minus (±) 4.1 km and to the nearest lek was 2.7±2.4 km. Average distance to nearest lek did not differ between adults and yearlings. Similar to Wyoming, results indicated no differences in these distances between successful and unsuccessful nests (Herman-Brunson and others, 2009).

The effects of vegetation at or surrounding nest sites are unclear. At the Yakima Training Center in Washington, nest success did not seem to differ among cover types (for example, big sagebrush-bunchgrass compared to grassland), and nests placed under big sagebrush shrubs were not more successful than nests placed under other shrub species (Sveum and others, 1998). Wakkinen (1990) also found no differences in vegetation characteristics between 24 successful and 16 unsuccessful nests in southeastern Idaho. Based on 165 nests in Idaho, Autenrieth (1981) reported that neither height nor canopy cover of nest bushes differed between successful and unsuccessful nests. In contrast, nest success in Montana was significantly related to vegetation characteristics (Wallestad and Pyrah, 1974). The 31 successful nests were in areas of higher sagebrush density than the 10 unsuccessful nests, and canopy cover of sagebrush was greater (27 percent) in stands with successful nests than in stands with unsuccessful nests (20 percent). However, neither mean height of sagebrush plants covering nests nor mean height of the tallest sagebrush plants covering nests differed between successful and unsuccessful nests. Nest success of yearling and adult sage-grouse in southeastern Idaho (*n*=84) was significantly greater under sagebrush shrubs (53 percent) than under other vegetation (for example, bitterbrush, rabbitbrush; 22 percent) (Connelly and others, 1991). Gibson and others (2016a) reported that the amount of sagebrush and residual grass height did not improve nesting success of birds in Nevada.

In the westernmost part of their range (Mono County, California), sage-grouse hens selected nest sites with greater shrub cover than nearby nonnest sites, but residual grass cover and height did not differ between nest and nonnest sites (Kolada and others, 2009b). In the same study area, nest survival (*n*=95) increased with increasing cover of shrubs other than sagebrush, rather than with sagebrush or residual grass cover (Kolada and others, 2009a).

In Oregon, Gregg and others (1994) investigated habitat at 124 sage-grouse nests and found that 18 nondepredated nests were in areas of greater medium-height (40–80 cm) shrub cover (41 percent) than depredated nests (29 percent) or random sites (8 percent). Cover of tall (>18 cm) grasses also was greater at nondepredated nest sites (18 percent) than at depredated nests (5 percent) or random sites (3 percent). A study of predation rates of 330 artificial nests within mountain big sagebrush and low sagebrush communities in Oregon

revealed that nests in sites with relatively less cover of tall grasses and medium-height (40–80 cm) shrubs (mean cover = 5 percent and 29 percent, respectively) were more likely to be depredated than were nests in sites of greater cover (mean cover = 18 percent and 41 percent, respectively, for nests not depredated) (DeLong and others, 1995). In contrast, Ritchie and others (1994) found greater predation rates in Utah on artificial nests in untreated sagebrush sites with greater cover compared to sites that had been treated (that is, disked or sprayed and planted with crested wheatgrass) 25 years before the study (27 percent mean shrub cover in untreated sites compared with 17 percent in treated; 21 percent mean herbaceous cover in untreated compared with 18 percent in treated). Predation rates were not significantly correlated with shrub cover but were positively correlated with increasing horizontal cover, herbaceous cover, and maximum shrub height.

In Alberta, where sagebrush cover is generally less than that in more southern portions of the species' range, sage-grouse nested in sites that had nearly twice the canopy cover of silver sagebrush than random sites (Aldridge and Brigham, 2002). Vegetation characteristics at 14 successful nests differed from 15 unsuccessful nests; for example, successful nests were in areas with less grass cover (33.8 percent compared with 48.9 percent) but taller grasses (31.6 cm compared with 24.4 cm) than unsuccessful nests (Aldridge and Brigham, 2002).

Using 238 artificial nests placed around 8 sage-grouse leks in southeastern Alberta, Watters and others (2002) studied predation rates in relation to predator type and vegetation characteristics. In the best-fit model, with a correct classification of 65.4 percent, successful nests were associated with greater forb cover (11.1 percent compared with 8.2 percent at depredated nests), greater sagebrush cover (26.5 percent compared with 24.9 percent), and fewer sagebrush plants (3.1 compared with 3.4 plants around the nest) (Watters and others, 2002).

Density of sage-grouse nests varies across the range of the species, from 3.8 to 55.6 nests per km^2 (Schroeder and others, 1999). Nest densities averaged 16.2 nests per km^2 during two breeding seasons within big sagebrush habitats in Wyoming (Patterson, 1952). In southeastern Idaho, Klebenow (1969) found 3.8 nests per km^2 in a big sagebrush-threetip sagebrush site; however, nests were not evenly distributed across the study area, and in some areas, nest density reached 24.7 nests per km^2. In North Park, Colo., nest density was estimated at 12.4 nests per km^2 (Gill, 1965). In the most productive nesting habitat in the Strawberry Valley in Utah, Rasmussen and Griner (1938) found 36 nests per km^2. This habitat was composed of newly disturbed (for example, from burning or flooding) sites in which big sagebrush or black sagebrush had recovered so that >50 percent of total cover was in sagebrush, and shrubs were >45 cm tall. True nest densities are unknown because it is unlikely that all nests will be found in any given area.

Brood-Rearing Habitat

Brood-rearing habitats are divided into early and late stages. Sage-grouse hens will rear their chicks for the first 2–3 weeks (sometimes longer) near the nest. This early brood-rearing habitat is, therefore, characterized similarly to nesting habitat—a sagebrush overstory and healthy herbaceous understory containing an abundance of insects (Connelly and others, 2011c; Gibson and others, 2016a). Brood-rearing habitats for sage-grouse are typically mosaics of upland sagebrush and other habitats (for example, wet meadows, riparian areas) that together provide abundant insects and forbs for hens and chicks (Dalke and others, 1963; Schroeder and others, 1999; Connelly and others, 2000b, 2004; Thompson and others, 2006; Atamian and others, 2010). In Hart Mountain National Antelope Refuge and Jackass Creek in southeastern Oregon, sage-grouse broods (n=18) were most common in low sagebrush during early brood rearing (first 6 weeks posthatch), but then moved to sites dominated by big sagebrush (7–12 weeks after hatching) (Drut and others, 1994a). Following brood breakup in August, sage-grouse used meadows and lake beds more frequently than during the brood-rearing period. During early brood rearing at Jackass Creek, forb cover at sites used by broods (n=83) was 10–14 percent and exceeded forb cover at random sites (n=176); however, no pattern was evident during late brood rearing. Broods at Hart Mountain used forb cover in relation to its availability during early brood rearing (n=87) but selected sites with greater forb cover (19–27 percent) during the late brood-rearing period (n=39) (Drut and others, 1994a).

At Sheldon NWR in Nevada, sage-grouse broods generally remained in upland habitats (primarily low sagebrush), with 92 percent of all brood locations (n=244) in upland sites during two summers (1978 and 1980) (Klebenow, 1985). During the intervening summer (1979), however, rainfall was scarce, and sage-grouse used meadows more than upland sites (64 percent of locations in meadows compared with 36 percent in upland sites; n=150), which were abandoned by broods by late summer (Klebenow, 1985). Brood habitat in uplands (n=86 brood locations) differed from that in wet meadows (n=33). Upland brood sites had greater canopy cover of sagebrush (mean of 25 compared with 0 percent), less grass cover (15 compared with 57 percent), and less forb cover (10 compared with 38 percent). Meadows encroached upon by tall sagebrush were seldom used by sage-grouse during brood rearing; no sage-grouse were in areas with a mean shrub height of 140 cm and >40 percent canopy cover. Instead, most broods were in meadows with relatively shorter shrubs (60 cm) and greater dominance of grass and forb cover (Klebenow, 1985).

In a subsequent study during 1998–2000 at Sheldon NWR, broods used primarily low sagebrush for the first few weeks after hatching, moving to big sagebrush (mountain or

Wyoming) or mountain shrub communities by 3 weeks post-hatch (Crawford and Davis, 2002). Key brood habitats were low sagebrush (40 percent of 392 brood locations), a 10-year old burn in a mountain big sagebrush site (19 percent), mountain shrub (16 percent), and mountain big sagebrush (13 percent). Vegetation characteristics (for example, tall grass cover and forbs consumed by hens) were different between brood locations and random sites; however, these differences varied among cover types. For example, in the low sagebrush cover type, cover of forbs eaten by hens and chicks was less (about 5.7 percent) at brood locations (*n*=51) than at random sites (*n*=30; 10.2 and 8.2 percent for hens and chicks, respectively), but tall grass cover was greater (4.4 percent at brood locations compared with 1.4 percent at random sites). In contrast, cover of forbs used by hens and chicks in the burn was greater at brood locations (6.7 and 5.2 percent; *n*=12) than at random sites (2.3 and 3.4 percent, respectively; *n*=20), but tall grass cover was less (18.3 percent at brood locations compared with 26.2 percent at random sites). Of the five cover types that had significant differences, cover of forbs eaten by hens and chicks was greater at brood locations than at random sites in four types (all but low sagebrush). Vegetation characteristics were not different between early and late brood-rearing habitats (Crawford and Davis, 2002).

Summer habitat use by hens with and without broods was studied at Cold Spring Mountain, Colo. (Dunn and Braun, 1986). Sites used by sage-grouse differed from random sites; horizontal cover and habitat interspersion (as measured by distance to a different cover type or edge) were two key variables in discriminating summer habitats. Habitat use did not differ between juvenile and adult females. Mean canopy cover of sagebrush at 84 juvenile sage-grouse locations was 24 percent compared with 16 percent at random locations. Mean sagebrush height at sage-grouse locations was 28 cm, and forb ground cover was 5 percent. Dunn and Braun (1986) recommended managing for homogeneous sagebrush stands with regard to shrub size and density, which are in turn juxtaposed with other cover types (for example, meadows, aspen [*Populus* spp.] stands).

Wallestad (1971) measured vegetation at 511 brood locations in a big sagebrush-grassland-dominated site in central Montana. Some, but not all, broods moved from big sagebrush to greasewood bottoms and alfalfa fields in August, returning to sagebrush by early September. Mean sagebrush cover at brood locations varied during the summer, reflecting these shifts; average cover was 14 percent in June, decreasing to 10 percent in August, and increasing to 21 percent in September. Shifts in distribution seemed to be tied to changes in food availability. Forb canopy cover averaged 27 percent and 17 percent in the two summers of the study; a dominant forb was yellow sweetclover (*Melilotus officinalis*). Mean canopy cover of grasses at brood locations was 47–51 percent. Mean height of shrubs, primarily big sagebrush, at brood locations was 18 cm in June but increased to 25 cm by August (Wallestad, 1971).

In southeastern Idaho, sage-grouse broods (*n*=98) commonly were in big sagebrush (83 percent of broods), whereas sage-grouse hens nested primarily in threetip sagebrush (Klebenow, 1969). Mean big sagebrush crown cover at brood locations was 8.5 percent, significantly less than in the surrounding area (14.3 percent). Broods seemed to avoid sites with dense (for example, 40 percent) big sagebrush cover and few forbs. In the development of a predictive model for brood habitat using discriminant function analysis, several variables were useful in distinguishing brood habitat. Compared to the available big sagebrush habitat, broods used areas with lower density of big sagebrush plants and greater frequency of the following three forbs: yarrow (*Achillea millefolium*) (23.5 percent), tailcup lupine (*Lupinus caudatus*) (18.3 percent), and common dandelion (*Taraxacum officinale*) (12.0 percent) (Klebenow, 1969).

Autenrieth (1981) summarized brood-rearing studies in Idaho and noted that, when broods do not migrate to upland habitats during summer, the broods rely on springs and wet meadows for succulent forbs. Livestock commonly graze these sites, so that when precipitation is scarce, adequate access to succulent forbs for sage-grouse can be difficult. Key forbs for sage-grouse in Idaho include common dandelion, prickly lettuce (*Lactuca serriola*), common salsify (*Tragopogon* spp.), western yarrow (*Achillea millefolium*), alfalfa, and sweetclover (*Melilotus* spp.) (Autenrieth, 1981).

Bunnell and others (2004) used logistic regression to identify habitat variables in Strawberry Valley, Utah, that discriminated among nest, brood, and adult (that is, adult male and broodless or nonnesting female sage-grouse) sites. Brood sites (*n*=30) had greater forb diversity (mean=3.0 compared with 2.7 species per 0.25 m^2) and shorter sagebrush (37.6 cm compared with 54.1 cm) than adult sites (*n*=64). Neither sagebrush nor forb canopy cover was significant in discriminating between brood and adult sites, but shrub species composition did differ between brood and adult sites (Bunnell and others, 2004).

In a landscape-scale analysis of sage-grouse occurrence and fitness in southeastern Alberta, Aldridge and Boyce (2007) found that broods selected mesic habitats and large patches of high productivity, heterogeneous sagebrush, while avoiding cultivated croplands, human developments, and areas with high densities of oil wells. Aldridge and Boyce (2007) modeled source and sink habitats for sage-grouse broods within the 1,100-km^2 study area and reported that 90 percent of all source brood-rearing habitats were within about 10 km of all active leks. Only 5 percent of available habitat was considered source habitat for brood rearing. Moreover, three-fourths of available habitat was characterized as sink (high risk) habitat for broods (Aldridge and Boyce, 2007). Lyon (2000) examined sage-grouse ecology in a natural-gas field development in western Wyoming. Early brood-rearing use sites had greater total herbaceous cover than did available habitats, whereas density of live sagebrush, total shrub canopy cover,

live sagebrush canopy cover, litter, and bare ground were less at used sites than at available sites. Near Savery, Wyoming, sage-grouse broods used primarily sagebrush-grass (*n*=26) and sagebrush-bitterbrush (*n*=21) habitats (Klott and Lindzey, 1990). Sage-grouse broods used sagebrush-bitterbrush habitats more, and mountain shrub less, than expected based on availability. Overall, broods were in sites with shorter shrubs and lower shrub canopy cover than the surrounding habitat. Total shrub cover for all brood locations during the 2-year study averaged 29.6 percent, whereas shrub cover at random sites averaged 45.8 percent. Mean sagebrush cover at brood sites was 16.9 percent, mean grass cover was 22.2 percent, and mean forb cover was 16.6 percent. Discriminant function analysis suggested that the following two variables were significant in classifying sage-grouse brood habitat: perennial herbaceous species and mountain snowberry (*Symphoricarpos oreophilus*)-desert madwort (*Alyssum desertorum*) presence. Functions based on these two variables correctly classified 68 percent (1985) and 73 percent (1986) of the sites (Klott and Lindzey, 1990).

Holloran (1999) also examined sage-grouse habitat use in Wyoming and found that early brood-rearing habitat was characterized by lower shrub cover and greater total herbaceous and forb cover than in available habitats. Late brood-rearing habitat, and that used by broodless hens and males, was associated with greater forb cover and less residual grass cover than in available habitats. Atamian and others (2010) examined brood-rearing habitat of Greater Sage-Grouse in east-central Nevada and found strong selection for certain land-cover types (for example, moist sites with riparian shrubs or montane sagebrush); late brood-rearing habitat supporting successful broods composed <3 percent of the study area, and the authors concluded that late brood-rearing habitat may limit sage-grouse populations in this area.

The beginning of late brood-rearing season is characterized by the senescence of herbaceous vegetation in upland habitats, which corresponds with a shift in diets of sage-grouse chicks from insects to forbs (Connelly and others, 2011c). During summer, sage-grouse will use a variety of more mesic habitats with substantial forb production, including riparian areas, wet meadows, and irrigated crops; the intensity of use is dependent on seasonal moisture patterns (Johnson, 1987; Schroeder and others, 1999; Connelly and others, 2000b, 2011c). Movements of broods to late-summer habitats are tremendously variable and related to availability of succulent forbs. Movements are commonly to higher elevations and can be short (for example, 5 km) or more than 80 km (Connelly and others, 2011c). In Idaho, Fischer (1994) reported that when moisture in forbs was below about 60 percent, summer migration ensued; Fischer (1994) suggested there might be a threshold for moisture content that triggers movement to areas with more succulent forage. Results from a study in Utah indicated a similar relation with increased use of meadows during dry summers (Danvir, 2002). In central Montana, sage-grouse broods shifted from sagebrush grasslands to alfalfa fields and greasewood bottoms as forbs at higher elevations became desiccated (Wallestad, 1971). In Idaho, sage-grouse formed large flocks near water and green meadows as plants senesced during summer (Dalke and others, 1963). In southeastern Idaho, broods moved to higher elevations during both summers of study, presumably in response to food availability (Klebenow, 1969). A shift to sites with bitterbrush, associated with more mesic conditions, also was noted as the summer progressed; in June, 38 percent of 98 broods were in the bitterbrush vegetation type, increasing to 53 percent in July. In Saskatchewan, meadows were used more than expected based on abundance (23–33 percent compared with 16 percent of available vegetation) (Kerwin, 1971).

Sage-grouse may not always shift habitats during their brood-rearing season. Within silver sagebrush habitats in Alberta, Aldridge and Brigham (2002) found no difference between early (<7 weeks old) and late (7–12 weeks old) brood habitats. Overall, brood-rearing sites (*n*=91) were characterized by sagebrush canopy cover nearly twice that of random sites (*n*=91; 8.7 percent compared with 4.5 percent). These differences also were seen at brood sites (1-m^2 plot at the brood location) and at 7.5- and 15-m scales. In addition, height of sagebrush and palatable forbs was significantly greater at brood-use locations than at random sites (Aldridge and Brigham, 2002). In Montana, areas used by broods of <6 weeks of age had lower densities and less crown canopy coverage of big sagebrush than areas used by older broods and adults (Martin, 1965).

Broodless hens may exhibit different seasonal habitat use patterns than hens with broods. In Oregon, Gregg and others (1993) found that broodless hens moved to meadows earlier in the summer (early July) than did hens with broods (early August). During summer, broodless hens selected mountain big sagebrush, low sagebrush-fescue (*Festuca* spp.), and meadow cover types but avoided low sagebrush-bunchgrass cover types. Compared to hens with broods, broodless hens used more low sagebrush-bunchgrass, grassland, and meadow types and less low sagebrush-fescue.

Winter Habitat

During winter, sage-grouse rely almost exclusively on sagebrush for forage (Connelly and others, 2000b). The distribution of sage-grouse in winter commonly is related to snow depth (Patterson, 1952; Dalke and others, 1963; Gill, 1965; Klebenow, 1973, 1985; Beck, 1975, 1977; Danvir, 2002), snow hardness, topography, and vegetation height and cover (Connelly and others, 2011c). At the onset of winter, sage-grouse gradually move to lower elevations, where more sagebrush is exposed above the snow; in migratory populations, this movement may extend up to 160 km (Patterson, 1952). During more severe winters, a large proportion of the sagebrush may be beneath snow and, thus, unavailable for roosting or foraging. Moynahan and others (2006) found that increased mortality of sage-grouse hens during winter in north-central

Montana was associated with deep snows, despite the abundance of high-quality habitat.

In northern Utah, wintering sage-grouse flocks were among increasingly taller sagebrush shrubs as snow depth increased (Danvir, 2002). With deep (>30 cm) snows, sage-grouse selected taller (>56 cm) sagebrush. Regardless of snow depth, the average height of sagebrush extending above the snow was about 25 cm at winter-use sites (*n*=168). In central Montana, sage-grouse selected dense (>20 percent canopy cover) stands of big sagebrush during winter (Eng and Schladweiler, 1972), whereas in central Idaho sage-grouse preferred black sagebrush when these shrubs were available above the snow (Dalke and others, 1963). Sage-grouse in Oregon typically winter in low sagebrush habitats or in a mosaic of low and big sagebrush types, commonly on windswept ridges with less snow (Willis and others, 1993). In a study in central Oregon, 72 percent of winter observations (*n*=103) were in mountain big sagebrush, and sagebrush canopy cover was typically >20 percent at winter-use sites (Hanf and others, 1994). Within these sites, however, sage-grouse tended to use patches with lower (12–17 percent) canopy cover. Sagebrush canopy height ranged from 0.25 to 0.75 m in late winter habitat in Oregon at the western edge of the species' range, and the winter-use area for the 22 radio-collared sage-grouse was 1,480 km^2 (Bruce and others, 2011). Mean daily movement was 425 m, and most locations were on flat (<2 percent) slopes. In southeastern Oregon, sage-grouse used mixed sagebrush (basin big sagebrush [*Artemisia tridentata* ssp. *tridentata*] and other shrubs) and low sagebrush types in winter more than expected in three study areas (Hagen and others 2011), possibly because of the availability of preferred forage despite the lower stature of mixed and low sagebrush vegetation types.

In Utah, Homer and others (1993) used satellite imagery to classify winter habitat of sage-grouse into seven shrub categories. Wintering sage-grouse preferred shrub habitats with medium-to-tall (40–60 cm) shrubs and moderate shrub canopy cover (20–30 percent). Sage-grouse strongly avoided winter habitats characterized by medium (40–49 cm) shrub height with sparse (<14 percent) sagebrush canopy cover (Homer and others, 1993).

In Colorado, female sage-grouse were more likely than males to use dense stands of sagebrush (primarily mountain big sagebrush) during winter (Beck, 1977). Flocks were typically on south- or southwest-facing aspects of gentle slope (generally <5 percent). In northern Utah, wintering sage-grouse flocks also selected flat areas, with 87 percent of the winter locations (*n*=297) on slopes of <5 percent (Danvir, 2002). With deep (>30 cm) snows, however, sage-grouse were most common in draws dominated by tall basin big sagebrush.

Radio-marked sage-grouse (*n*=200) in the Powder River Basin of Montana and Wyoming selected winter habitat based on percent sagebrush cover on the landscape; this relation was strongest at a 4-km^2 scale, at which used sites had >75 percent sagebrush cover (Doherty and others, 2008). Sage-grouse in this study also selected gentle topography during winter, based on a topographic roughness index. Radio-marked sage-grouse (*n*=98) in Wyoming big sagebrush habitat in the Dakotas used winter sites with a greater proportion and density of sagebrush, shorter sagebrush, more vegetation cover, smaller percentages of grass and litter cover, and shorter grass height than random unoccupied sites. Sagebrush cover at use sites was 10.7 and 19.2 percent in North Dakota and South Dakota, respectively. Sagebrush cover and, to a lesser degree, sagebrush height (and their interaction) were the key predictors of winter habitat use by sage-grouse (Swanson and others, 2013).

A landscape-scale study of sage-grouse in southeastern Alberta revealed that wintering sage-grouse selected sites with homogeneous, dense sagebrush cover and gentle topography, while avoiding areas with energy development and two-track trails (Carpenter and others, 2010). Relative probability of selection increased sharply at about 1,200–1,800 m from energy wells. In a northwest Colorado site with oil and gas development, wintering sage-grouse selected sites with intermediate total shrub cover and less heterogeneity in Wyoming big sagebrush cover and total shrub cover (Smith and others, 2014). Moreover, surface disturbance from oil and gas was negatively associated with occurrence of sage-grouse.

Sage-grouse in North Park, Colo., concentrated during winter in seven small areas that totaled only 85 km^2; however, these areas composed only 7 percent of the sagebrush in the study area (Beck, 1977). Eng and Schladweiler (1972) suggested that sagebrush removal in winter habitats, which may compose a small portion of the year-round habitat of sage-grouse, may be especially detrimental because of the long periods that winter habitat may be occupied by sage-grouse. Swenson and others (1987) found marked declines in sage-grouse abundance in Montana when a large percentage (30 percent) of the winter habitat was plowed, primarily for grain production. Maintaining winter habitat for sage-grouse may be of critical importance in areas of energy development (for example, natural gas fields, coal-bed methane [CBM]), especially if several populations converge in a common wintering area (Lyon, 2000; Doherty and others, 2008). Although sage-grouse commonly exhibit strong site fidelity within a season, some migratory populations may respond to fluctuations in environmental conditions by moving to areas with better resources. In a study of sage-grouse fitted with GPS transmitters, Smith (2010) found that when snow cover was exceptionally deep in traditional winter habitat in Montana, a migratory population used flat, windswept sagebrush ridge tops within a patchily forested landscape that had previously not been considered sage-grouse habitat. In contrast to a resident population that had a 58 percent winter survival rate, survival in the migratory population was 100 percent.

Roosting, Foraging, and Loafing Habitat

During winter, sage-grouse may roost in snow burrows or snow forms, apparently for energy conservation (Back and others, 1987). In Montana, roost sites (*n*=17) were in sagebrush with a mean canopy cover of 26 percent (range

9–46 percent) and usually on flat terrain (Eng and Schladweiler, 1972). In central Montana, sage-grouse foraged in big sagebrush with a mean canopy cover of 28 percent (range 6–54 percent; *n*=45), and observations in denser (>20 percent) cover were more common than observations in less dense sagebrush. During the breeding season in Montana, feeding and loafing sites (*n*=110) used by males averaged 32 percent sagebrush canopy cover; no males were observed in areas with <10 percent sagebrush canopy cover, and 79 percent of observations were in sites with 20–50 percent canopy cover (Wallestad and Schladweiler, 1974). In Idaho, resting cover ranged from sagebrush, willow (*Salix* spp.), and tall grass to uncut fields of hay and grain and patches of quaking aspen (Dalke and others, 1963).

In Colorado, winter feeding-loafing sites did not differ from roosting sites in physical characteristics or vegetation (Beck, 1977). Short shrubs characterized roosting sites used by hens during the breeding season in North Park, Colo., where 80 percent of 40 roosting sites were in areas with sagebrush <10 cm tall (Petersen, 1980). Feeding and loafing sites used by hens during this study were typically in sagebrush ranging from 15 to 30 cm in height.

Hausleitner (2003) compared diurnal brood-rearing sites (*n*=92) with summer night roosts (*n*=58) of nonmigratory sage-grouse hens in Colorado. Mean shrub cover was less at night-roost locations (9 percent) compared to brood-rearing sites (22 percent); mean shrub height also was shorter at night roosts (31 cm) than at brood sites (58 cm). Night roosts were in burned shrubsteppe (52 percent), shrubsteppe (38 percent), grassy meadows (7 percent), CRP (2 percent), and riparian (2 percent) cover types (Hausleitner, 2003).

Water Use

Sage-grouse do not seem to be dependent on free-flowing water, although their reliance on water or vegetation associated with water is variable (Schroeder and others, 1999). In Nevada, few leks were far from water; thus, in developing a model for lek preference, Nisbet and others (1983) excluded all areas >2 km from a water source. During a 7-year study in eastern Idaho, sage-grouse gathered in large flocks near water during the fall migration, congregating at water for 10–30 minutes (Dalke and others, 1963). Sage-grouse may remain in irrigated fields during much of the summer (Connelly and Markham, 1983; Gates, 1983; Wakkinen, 1990). At the Idaho National Engineering Laboratory, sage-grouse commonly remained near lawns and ponds during summer, watering at these sources and feeding on succulent vegetation (Connelly and Ball, 1978; Connelly, 1982; Connelly and Markham, 1983), which may be the primary attraction of irrigated lands, rather than access to free water (Connelly and others, 2011c). Any consistent benefits of developed water sources to Greater Sage-Grouse are not apparent. In Oregon, sage-grouse were more abundant in areas where springs had not been developed (for example, by fencing and planting vegetation; Batterson and Morse, 1948). Batterson and Morse (1948) hypothesized that dense vegetation at developed springs, where livestock were excluded by fencing, was unattractive to sage-grouse. Sage-grouse broods in Alberta were closer to water impoundments than random sites, but Aldridge and Boyce (2007) cautioned that the relation among such impoundments, drought conditions, and mesic habitats for brood rearing needs further investigation.

Area Requirements and Landscape Associations

Sage-grouse typically inhabit large, unbroken expanses of sagebrush and are characterized as a landscape-scale species (Patterson, 1952; Wakkinen, 1990; Connelly and others, 2004, 2011c). Although total area requirements for the species are unknown (Schroeder and others, 1999; Connelly and others, 2011c), migratory populations of sage-grouse may use areas exceeding 2,700 km^2 (Connelly and others, 2000b; Leonard and others, 2000). The longest migration recorded for sage-grouse (more than 120 km) was documented for a hen in Saskatchewan, with some individuals in this study using areas as large as 6,700 km^2 (Tack and others, 2011). Currently occupied areas that are most similar to extirpated areas are small, disjunct sites along the periphery of the range (Wisdom and others, 2011). Where large-scale conversion of sagebrush has transpired (for example, to cropland or nonnative grasses), sage-grouse populations have declined (Leonard and others, 2000). In a discriminant function analysis with 22 variables, occupied areas were characterized by greater sagebrush area, higher elevations, a greater distance to transmission lines and cellular towers, and a larger percentage of public lands (Wisdom and others, 2011). Predictive models based on Gunnison Sage-Grouse nest sites in Gunnison Basin (Colorado) indicated that the key predictive landscape-scale factors included the proportion of sagebrush cover >5 percent, mean productivity, and road density (Aldridge and others, 2012). Hess and Beck (2012a), in developing models to predict lek occupancy in the Bighorn Basin of north-central Wyoming, found that certain landscape characteristics (for example, shrub height, oil and gas well density, and area burned by wildfire) performed best within 1.0 km of leks rather than at greater distances (3.2–6.4 km).

Conclusive data are unavailable on minimum patch sizes of sagebrush necessary to support viable populations of sage-grouse (Connelly and others, 2011c), in part because some populations are migratory and others are not; moreover, habitat quality varies widely by location. In a range-wide analysis of Greater Sage-Grouse, Wisdom and others (2011) found that mean sagebrush patch size was nearly 9 times greater in occupied (4,173 hectares [ha]) compared with extirpated (481 ha) range. In Utah, Danvir (2002) observed nesting sage-grouse in Wyoming big sagebrush patches that were >100 m in diameter. In Colorado, the only population of Gunnison Sage-Grouse not “severely reduced” from historical

times (Oyler-McCance and others, 2001, p. 329) was in an area with a low rate of habitat loss (11 percent across 35 years) and >340,000 ha of habitat remaining. In this region, nest sites were positively associated with habitat that contained >10 percent big sagebrush cover and negatively associated with residential development and high-volume paved roads (Aldridge and others, 2012). Sage-grouse in Alberta selected nesting habitat with large patches (1 km^2) of sagebrush cover, but with a heterogeneous distribution of sagebrush within the patches (Aldridge and Boyce, 2007). In Wyoming, Patterson (1952) found that large groups of sage-grouse could range as much as several thousand square kilometers.

Wiley (1978, p. 116) suggested that the "basic unit of sage grouse social organization is a lek covering about two hectares…and has a single mating center some 50 square meters in extent." Klebenow (1973) reported a typical range in lek size from 0.04 to 4.0 ha. Based on work on the Laramie Plains in Wyoming, Scott (1942) reported a range in lek size from 0.4 to 16.0 ha; however, one lek was about 20 ha in size and supported 400 strutting males. Schroeder and others (1999), in summarizing several studies, reported that the average area defended by males on leks ranged from 5 to 100 m^2. Hofmann (1991) reported a mean size of 36 ha for the four largest leks in a study in central Washington.

Several techniques have been used to measure movements of sage-grouse; however, differences in the techniques among studies render comparisons of home-range sizes and movements problematic (Schroeder and others, 1999; Hagen and others, 2001). Moreover, there is high natural variation in home-range sizes for sage-grouse (Connelly and others, 2011a) and in seasonal movements of individuals within and across sites (Fedy and others, 2012). In North Park, Colo., sage-grouse hens (n=19) moved on average 5.4 km from leks to nest sites, whereas yearling females (n=23) moved only 2.3 km (Petersen, 1980). Mean distance moved from nests to summer or late brood-rearing habitats in Wyoming was 8.1 km (n=828), and mean distance moved from summer to winter locations was 17.3 km (n=607) (Fedy and others, 2012). Given the high variability (for example, some sage-grouse did not move, whereas others moved more than 50 km in 1 year), Fedy and others (2012) suggested that populations not be classified as migratory or nonmigratory. Distances moved by sage-grouse hens from leks to nests in central Montana were similar between age classes, with adults moving 2.5 km and yearlings moving 2.8 km (Wallestad and Pyrah, 1974). Danvir (2002) reported comparable data for sage-grouse in Utah, with 77 percent of 17 hens nesting no farther than 3.3 km from the lek where the hens were captured. Hens generally stayed within 5 km of the nest site the remainder of the summer. Sage-grouse may move much longer distances between seasonal ranges, especially if their seasonal habitat needs cannot be met without migrating. In eastern Idaho, the mean distance moved between summer and winter ranges was 48.2 km for 28 hens; this movement involved a decrease in mean elevation of 446 m (Hulet and others, 1986).

Home range sizes of sage-grouse hens vary widely among individuals and seasons (Connelly and others, 2011a). Hausleitner (2003) calculated annual home-range sizes for female sage-grouse in Colorado using a 95 percent fixed kernel estimate. Median home range was 8,574 ha for yearling sage-grouse (n=26) and 6,556 ha for adults (n=43). Home ranges during brood rearing were substantially smaller, with a median home range of 470 ha for yearlings (n=7) and 543 ha (n=22) for adults. Spring home ranges in Idaho for four hens averaged 810 ha (Connelly, 1982). Average summer home-range size for four adult hens with broods was 406 ha, whereas three juvenile sage-grouse, including one hen, had summer ranges averaging 94 ha. In eastern Idaho, home ranges of 28 sage-grouse hens during summer averaged 285 ha but varied widely, from 9 to 710 ha (Hulet and others, 1986). At Hart Mountain National Antelope Refuge in Oregon, home ranges of sage-grouse hens declined from 800 ha during early brood rearing (hatch to 6 weeks posthatch) to 100 ha later in the season (7–12 weeks posthatch) (Drut and others, 1994a). At a less productive site, which contained less forb and tall sagebrush cover, home-range size increased from 2,100 ha during the early period to 5,100 ha during the later period. Drut and others (1994a) suggested that these results were due to differences in forb availability and chick diets between the two sites. In central Montana, sagebrush patches used by broods averaged 86 ha in June and July but diminished to 52 ha later in August and September (Wallestad, 1971). Average summer ranges were 297 ha (from 179 to 821 ha) for 11 radio-marked hens in Idaho that primarily used irrigated cropland (Gates, 1983). Winter ranges for four hens in this same study ranged from 176 to 1,070 ha. In Idaho, Connelly (1982) reported a mean fall home range of 2,246 ha for five sage-grouse hens (from 530 to 5,590 ha).

Regarding movements of males, in Montana 10 of 13 (77 percent) sage-grouse males remained within 1 km of their associated leks during the breeding season; however, movements as much as 1.3 km from the leks were common (Wallestad and Schladweiler, 1974). Daily movements of males (n=18) from leks to day-use areas in Utah were 0.5–0.8 km on average, and core day-use areas (sample size not given) were a minimum of 0.25 km^2 (Ellis and others, 1989). Male sage-grouse in north-central Utah moved on average 8.3 km from leks to summer-use areas (Danvir, 2002). Connelly (1982) reported movements of three male sage-grouse from leks to summer habitats with distances ranging from 42 to 50 km. In Washington, 14 males on the Yakima Training Center dispersed an average maximum distance of 15.5 km from the lek (Hofmann, 1991). Home-range sizes (males and females combined) in this 2-year study were somewhat large, ranging from 25.9 km^2 in summer to 44.2 km^2 in fall. In Idaho, one male used an area of 1,190 ha during winter (Gates, 1983).

During a 2-year study, Beck and others (2006) compared movements and survival of juvenile sage-grouse (n=58) in mountain valley populations compared with lowland populations in Idaho. Sage-grouse in mountain valleys moved farther

from autumn to winter ranges than did lowland sage-grouse (13.0 km compared with 10.8 km) and had somewhat poorer estimated survival rates (survival=0.64 compared with 0.86) from September through March (Beck and others, 2006).

Brood Parasitism by Cowbirds and Other Species

Eggs of the Brown-headed Cowbird (*Molothrus ater*), an obligate brood parasite (Friedmann, 1929), have not been documented in sage-grouse nests (Schroeder and others, 1999; Shaffer and others, 2019). The Greater Sage-Grouse is an unsuitable host of the Brown-headed Cowbird because Greater Sage-Grouse young are precocial and chicks leave the nest immediately after hatching.

Several galliform species, however, are considered facultative nest parasites and are known to parasitize nests of other individuals of their own species and other species in the Order Galliformes (Lyon and Eadie, 1991; Krakauer and Kimball, 2009; Bird and others, 2013). In Alberta, using genetic-based analysis, Bird and others (2013) reported evidence of intraspecific nest parasitism in Greater Sage-Grouse; 9.6 percent of 104 sage-grouse hens had their nests parasitized by another sage-grouse hen. No evidence of interspecific parasitism by a Greater Sage-Grouse hen has been reported (Schroeder and others, 1999; Krakauer and Kimball, 2009); in Nevada, Fearon and Coates (2014) found a sage-grouse nest with two Chukar (*Alectoris chukar*) eggs and eight sage-grouse eggs. Greater Sage-Grouse × Sharp-tailed Grouse (*Tympanuchus phasianellus*) hybrids have been reported in Montana (Eng, 1971), North Dakota (Kohn and Kobriger, 1986), and Alberta (Aldridge and others, 2001). Rensel and White (1988) provided descriptions and measurements of two juvenile Greater Sage-Grouse × Dusky Grouse (*Dendragapus obscurus*) hybrids from Utah.

Breeding-Season Phenology and Site Fidelity

Sage-grouse males begin to arrive on leks in late winter or early spring and may display from January through May, or as late as June (Scott, 1942; Dalke and others, 1963; Rogers, 1964; Wiley, 1978; Autenrieth, 1981; Schroeder and others, 1999). Occasionally, males appear on leks so early that the males display on snow-covered ground (Scott, 1942; Dalke and others, 1963). Most of breeding activity takes place shortly after sunrise, with a smaller peak in breeding activity at dusk and at night, particularly during a full moon (Scott, 1942; Jenni and Hartzler, 1978; Schroeder and others, 1999). Peaks in lek attendance are earlier in the season for adult males than for subadult males, which arrive at the lek later in the season (Dalke and others, 1963; Eng, 1963; Wiley, 1978). Overall, yearling males attend leks less frequently and arrive later than adult males, with yearlings generally remaining on the periphery of the lek and seldom breeding (Jenni and Hartzler, 1978). Walsh and others (2004) found that yearling males (n=9) exhibited no defined peak date in lek attendance, and daily lek attendance rates (19 percent+0.14) were substantially lower than those of adult (n=7) males (42 percent+0.23). Hens occupy leks for a shorter period, typically in March and April, with peak attendance by hens paralleling or preceding that of adult males (Scott, 1942; Dalke and others, 1963; Jenni and Hartzler, 1978; Wiley, 1978; Gibson, 1996).

Sage-grouse typically exhibit strong fidelity to leks (Scott, 1942; Connelly and others, 2011a). Some leks have been occupied for decades (Dalke and others, 1963; Wiley, 1978); one lek in Wyoming was used for at least 28 years (Wiley, 1978). In Idaho, Dalke and others (1963) found that when populations were relatively large, both primary leks and smaller leks were used, but during population lows, smaller, satellite leks were abandoned. Male sage-grouse may move between leks during the breeding season, though dominant males are less likely to do so (Dalke and others, 1963). The percentage of male sage-grouse returning to the leks on which the males were banded also is highly variable. In Idaho, this percentage ranged from 5 to 21 percent for 3 years (Dalke and others, 1963). Genetic recaptures identified 39 individuals that attended the same lek, 5 years apart, confirming fidelity to leks in sage-grouse, although longer dispersal events were recorded (Cross and others, 2017).

Nesting hens typically exhibit nest-area fidelity, commonly nesting within 1 km of previous nesting areas (Berry and Eng, 1985; Schroeder and others, 1999; Connelly and others, 2011a); two hens returned to nest within 70 m of their former nesting sites (Patterson, 1952). A similar fidelity was noted for Gunnison Sage-Grouse, with an average distance of 455 m between current and previous years' nests (Young, 1994). New nests may be near (that is, within meters) old nests, but nest bowls themselves apparently are not reused (Patterson, 1952; Schroeder and others, 1999). In north-central Washington, distance between nests in consecutive years averaged 1.6 km for 35 successful (that is, one or more eggs hatched) hens and averaged 5.2 km for 52 unsuccessful hens (Schroeder and Robb, 2003).

Fischer and others (1993) investigated the relation between nest fate and nest-site fidelity of radio-marked sage-grouse hens (n=32; monitored for two consecutive years) in southeastern Idaho. Median distance moved between consecutive-year nests was not associated with nest success in the prior year (median=937 m [n=9] for hens unsuccessful the prior year compared with 506 m [n=13] for hens nesting successfully the prior year). However, the power of test to detect a difference between distance moved for unsuccessful hens compared with successful hens was low (<0.30). Distance moved was also unrelated to subsequent nest success, similar to findings of Holloran and Anderson (2005) in Wyoming. Nest placement in relation to the nearest lek was highly directional, that is, nonrandom, with a smaller median

angle between consecutive-year nests and the nearest lek than the angle between a random point and the nests (Fischer and others, 1993). A long-term (1994–2003) study of nesting in Wyoming found that median distance between consecutive-year nests was 415 m (Holloran and Anderson, 2005). These distances were similar between adult hens (391 m; *n*=5) and yearlings (541 m; *n*=28). In Montana, Moynahan and others (2007) reported a median distance of 600 m between first nests in successive years (*n*=52). Fidelity to winter areas among years has not been well studied, although some evidence of winter area fidelity has been demonstrated in Washington (Schroeder and others, 1999) and Wyoming (Berry and Eng, 1985).

Breeding dates differ among locations, ranging from early to late March in Washington to mid- to late April in Montana and Wyoming, and annual variation in weather can cause delays in nest initiation (Schroeder and others, 1999). Incubation of eggs begins about 3 weeks after copulation, with young hatching from early April to late July. Yearling hens may initiate nesting later than adults (Schroeder, 1997; Herman-Brunson and others, 2009). Renesting is common in some populations but rare in others; the likelihood of renesting after loss of a first clutch ranged from 5 to 87 percent in 16 studies reviewed by Schroeder and others (1999). Adults are more likely to renest than are yearlings (Patterson, 1952; Petersen, 1980; Schroeder and others, 1999; Gregg and others, 2006; Moynahan and others, 2007). Renesting by sage-grouse in Washington was a major contributor to overall nest success, with 87 percent of 69 hens laying a second clutch (Schroeder, 1997). At the Yakima Training Center in Washington, Sveum and others (1998) found that 28 and 23 percent of hens renested during the 2 years of their study (*n*=29 and 47 hens in 1992 and 1993, respectively). On the Sheldon NWR in Nevada, 25 percent of 36 hens renested, with 56 percent of the 9 being successful (Crawford and Davis, 2002). Moynahan and others (2007) reported that 43 of 258 sage-grouse nests evaluated in north-central Montana were renests and that renests had higher survival than did first nests. Locations of renesting attempts in this study also were near the first nests (median distance=0.58 km). Mean renesting probability was greater for adults (0.43) than yearlings (0.19) and also differed across years (Moynahan and others 2007). A renesting rate of 36 percent (*n*=14) was reported for sage-grouse in Alberta (Aldridge and Brigham, 2001). In a subsequent study in Alberta, nest success was similar between initial (*n*=77) and second (*n*=34) nesting attempts (Aldridge and Boyce, 2007). In the Great Basin of northwestern Nevada and southeastern Oregon, 34 percent of hens (*n*=143) renested, and the occurrence of renesting varied by date of nest initiation, nest loss period, and total plasma protein (Gregg and others, 2006). Hens that renested were more likely to initiate nests earlier in the nesting season, lose nests earlier during incubation, and have higher total plasma protein levels than hens with unsuccessful nests that did not renest. The inadequate protein for egg development may have accounted for some variation in renesting rates (Gregg and others, 2006). In contrast, renesting attempts by Gunnison Sage-Grouse in Colorado were infrequent, with only 1 of 30 hens renesting (Young, 1994). Young (1994) postulated that later hatching dates for Gunnison Sage-Grouse and more severe winter weather could leave inadequate time or resources for hens to renest.

Species' Response to Management

Habitats used by Greater Sage-Grouse have been widely altered by land-management practices during the last 150 years (Patterson, 1950; Kufeld, 1968; Braun, 1987; Drut, 1994; Connelly and Braun, 1997; Schroeder and others, 1999, 2004; Miller and Eddleman, 2000; Wisdom and others, 2000, 2002a; Knick and others, 2003; Miller and others, 2011; Beck and others, 2012). By 1974, about 10–12 percent of the 40 million ha of sagebrush rangelands in North America had been treated to provide forage for livestock (Vale, 1974). Overall, >80 percent of sagebrush rangelands have been altered in some way by human activities (West, 1999). Nearly all sagebrush ecosystems on public lands have been impacted by human activities past and present (Knick and others, 2003). In Washington, Dobler (1994) estimated that >60 percent of the native sagebrush steppe had been converted for human use by 1994. In Colorado, Kufeld (1968) reported that >1,000 km^2 of sagebrush on Federal lands had been treated by 1966, primarily to increase livestock forage. Most of this area had been sprayed, although 21 percent had been plowed.

During 1997–2007, lek trends were evaluated across the historical range of sage-grouse in relation to agricultural land, and results indicated that trends were higher for leks that had no agriculture within either 5 or 18 km (Johnson and others, 2011). Moreover, trends in lek counts tended to decrease sharply with increasing percentage of agricultural land from 0 to about 2.5 percent cover within 5 km and to about 1.5 percent cover within 18 km; declines were minimal at higher levels. In North Dakota and South Dakota, Smith and others (2005) found no relation between percentage of tilled land surrounding leks and lek size (counts of males on active leks). However, inactive leks did have a larger percentage of tilled lands within 4 km than did active leks in North Dakota. In addition, percentage of tilled land was greater around random points than around active leks. However, similar comparisons for leks in South Dakota revealed no significant relationship. From the 1970s to late 1990s, the percentage of tilled land surrounding leks (active and currently inactive leks) did not increase, indicating that if the amount of tilled land was a factor in lek abandonment, this effect had transpired before the 1970s. Leonard and others (2000) found a negative association between mean numbers of males per lek and total agricultural area during a 17-year period for sage-grouse populations in the Upper Snake River Plain in Idaho; nearly 30,000 ha of sagebrush in the study area were converted to cropland during 1975–92.

Historically, brush control was used widely to eliminate sagebrush, especially during 1960–70 (Barrett and others, 2000). Sagebrush control efforts diminished in the 1970s, primarily because of reduced Federal funding combined with increasing environmental concern (Donoho and Roberson, 1985). Large areas of former sagebrush have been converted to nonnative grasses such as crested wheatgrass; sagebrush on some private lands also has been planted to agricultural crops such as alfalfa, potatoes (*Solanum* spp.), or wheat. Although sage-grouse will use alfalfa fields and other croplands when such lands are adjacent to large patches of native sagebrush, especially during brood rearing (Patterson, 1952; Leach and Browning, 1958; Wallestad, 1971; Gates, 1981; Connelly and others, 1988), application of chemicals to agricultural lands has posed a hazard to sage-grouse populations (Patterson, 1952; Blus and others, 1989). Patterson (1952) also reported substantial losses of sage-grouse, particularly juveniles, from mowing operations in alfalfa fields. Large-scale reclamation projects involving dam construction, plowing, and irrigation impacted rangelands across the West; for example, the 400-km^2 Riverton Project in Wyoming, resulted in extirpation of sage-grouse from the area (Patterson, 1950).

Mechanical removal of sagebrush, although as effective as herbicides or fire in eliminating sagebrush, tends to be applied to smaller patches of habitat (Connelly and others, 2000b). In Montana, results of a study by Swenson and others (1987) indicated that removing (plowing) 16 percent of the sagebrush in a 202-km^2-study area during 1954–84 corresponded to a decline in the population index (number of males on leks in spring) from 241 to 65. No comparable trend was discernable in nearby control plots. Swenson and others (1987) concluded that plowing was a more serious threat to sage-grouse than was herbicide application, primarily because plowed lands tend to be planted to crops, whereas recovery of sagebrush is more likely in sprayed habitats.

Beck and others (2012) reviewed effects of Wyoming big sagebrush treatments on habitat for wildlife and concluded that treating winter or breeding habitats for Greater Sage-Grouse typically had negative effects. Dahlgren and others (2006) compared the effectiveness of two mechanical (Dixie Harrow and Lawson Pasture Aerator) and one chemical (tebuthiuron) treatments compared to no treatment for improving sage-grouse brood-rearing habitat (four replicates per treatment). Treatments were randomly applied in mountain big sagebrush plots (40.5 ha) with >40 percent sagebrush canopy cover pretreatment. Mechanical treatments were more effective in reducing shrub cover than was tebuthiuron. Grass cover did not significantly respond to any of the treatments. However, forb cover was greater posttreatment in plots treated with tebuthiuron (12.0 percent) or Dixie Harrow plots (10.7 percent) compared to control plots (7.8 percent). Brood use was greater in the tebuthiuron plots than in the controls, presumably because of the greater posttreatment forb cover. Regardless of treatment type, sage-grouse use was greatest within 10 m of plot edges, where sagebrush cover was present outside the plot. Dahlgren and others (2006) urged caution when applying treatments such as Dixie Harrow, Lawson Aerator, and tebuthiuron in sites with other sagebrush taxa or in areas with less precipitation. In Colorado, Braun and Beck (1996, p. 429) examined lek counts where >28 percent of the study area, known as “one of the best sage-grouse habitats in Colorado,” was plowed and sprayed with 2,4–D. Initial spraying of >1,600 ha was in 1965, with an additional 500 ha sprayed and 1,460 ha plowed and seeded during the following 5 years. The 5-year mean number of males on active leks declined from 765 (1961–65) to 575 (1971–75). Numbers rebounded by 1976–80, however, and even exceeded pretreatment levels (5-year mean of 1109 males per lek). Braun and Beck (1996) stated that spraying of large (>200 ha) blocks of sagebrush clearly was detrimental and led to lek abandonment and shifts in sage-grouse distribution.

Much of the historical range of sagebrush is at risk of encroachment by woodlands, particularly at higher elevations. Such encroachment impacts not only vegetation, carbon storage, water, and nutrient and energy cycles (Miller and others, 2017), but may also eventually eliminate sagebrush habitat in the understory (West and others, 1979; Miller and others, 1999; Miller and Eddleman, 2000; Crawford and others, 2004; Miller and others, 2011; Severson and others, 2017). Similar processes have been observed with encroachment by Douglas-fir (*Pseudotsuga menziesii*) into mountain big sagebrush communities (Grove and others, 2005). Conditions created by climate change are predicted to result in a 12-percent loss of sagebrush to woodlands for every 1 degree Celsius increase in temperature, (Miller and others, 2011). Sage-grouse habitat may be improved by removing trees. Numbers of male Gunnison Sage-Grouse on treatment leks doubled 2- and 3-years posttreatment after removal of pinyon-juniper trees (*Pinus* spp., *Juniperus* spp.) by cutting and after height reduction of sagebrush and deciduous shrubs by brush-beating (Commons and others, 1999). Sage-grouse avoided pinyon-juniper habitats except during September to November, when sage-grouse were present in sagebrush with scattered pinyon-juniper >2 m tall. In a study of a small population of sage-grouse in southern Utah, mechanical removal of juniper and reseeding of 358 ha of encroached sagebrush resulted in increases in grass and forb abundance the first three growing seasons after tree removal and resulted in selection by sage-grouse for treated sites (Frey and others, 2013). Severson and others (2017) led the most recent comprehensive study on short-term (2–4 years) effects of conifer removal on sage-grouse in the northern Great Basin of California, Nevada, and Oregon. Monitoring of 262 sage-grouse nests during 2010–14 revealed an annual increased relative probability of nesting in newly restored sites of 22 percent; and, during 2011 (before treatment) to 2014 (3 years posttreatment), 29 percent of the marked birds had shifted nesting into mountain big sagebrush communities that had undergone conifer removal. The efficacy of woodland treatments as a restoration tool for sage-grouse is affected by the presence of sage-grouse in adjacent habitats. If sage-grouse are not present, juniper removal may have no effect on increasing sage-grouse populations even if suitable habitat is present (Knick and others, 2014).

Mowing has been used to control sagebrush growth, but research on the effects that mowing has on sage-grouse habitat is limited. In north-central Wyoming, mowed plots did not have adequate sagebrush canopy cover or height for breeding sage-grouse for as many as 9 years posttreatment (Hess and Beck, 2012b). Mowing in mountain big sagebrush in southeastern Oregon to reduce canopy cover and increase understory vegetation did increase herbaceous production compared to control plots but did not lead to increases in perennial forbs or exotic grasses 3 years after treatment (Davies and others, 2012). By contrast, Davies and others (2011) indicated that in Wyoming big sagebrush communities in the same area, mowing did not increase perennial herbaceous vegetation but did increase the risk that exotic annual grasses would increase. Thus, Davis and others (2012) suggested that mowing should not be used in Wyoming big sagebrush sites with intact understories.

In addition to land-management practices that directly remove sagebrush, other practices such as livestock grazing, pesticide application, and prescribed fire may degrade habitats and, thus, affect populations of Greater Sage-Grouse (Connelly and others, 2004; Crawford and others, 2004). Nearly all studies of effects of land-management practices on sage-grouse rely on indices of abundance (for example, lek counts), rather than measures of survival or reproductive success. In addition, the dearth of manipulative studies to elucidate cause-effect relations of land-management practices on sage-grouse has been previously noted (Braun and Beck, 1996; Rowland and Wisdom, 2002; Connelly and others, 2004).

Fire

Prescribed fire has been used not only to remove sagebrush, primarily to enhance livestock forage, but also with the expressed goal of improving habitat conditions for sage-grouse and other wildlife (Klebenow, 1973). Although some studies have demonstrated neutral or even positive effects on sage-grouse habitats from fire (for example, Martin, 1990; Fischer, 1994; Pyle and Crawford, 1996; Crawford and Davis, 2002; Wrobleski and Kauffman, 2003), others have documented population declines and long-term (that is, >5 years) habitat degradation (Connelly and others, 2000a; Nelle and others, 2000; Beck and others, 2009; Baker, 2011). Some short-term benefits, such as increases in annual forbs eaten by sage-grouse during the initial postburn growing season (Wrobleski and Kauffman, 2003), may accrue from prescribed fires; however, this result is not always true (Beck and others, 2009, Rhodes and others, 2010). For example, insects that are key components of a chick's diet may decrease with prescribed fire (Rhodes and others, 2010). Moreover, nesting cover may be reduced and, thus, become less suitable (Wrobleski, 1999; Nelle and others, 2000). However, nesting cover (defined as grass cover and height and litter cover) recovered in 1–2 years after a prescribed fire study in Wyoming big sagebrush habitat in southeastern Idaho (Beck and others, 2009). The use of prescribed fire may also increase the risk of nonnative invasive plants.

A 9-year study in southeastern Idaho examined lek attendance by males in relation to prescribed fire and suggested that declines in breeding populations of sage-grouse were more severe following fire (Connelly and others, 2000a). The study area was a Wyoming big sagebrush-bluebunch wheatgrass (*Pseudoroegneria spicata*) vegetation type, with 23 cm average annual precipitation. Before a 5,000-ha portion was burned, 4 years of pretreatment data were obtained; nearly 60 percent of the sagebrush was eliminated after the prescribed fire treatment, leaving a mosaic of sagebrush and grassland vegetation types. Although declines in lek attendance happened throughout the study in both the treatment (burned) and control (not burned) plots, declines were greater in the burned plot. Following the prescribed fire, the number of active leks declined by 58 percent (that is, from 12 to 5) in the treatment plot and by 35 percent (that is, from 17 to 11) in the control plot. Furthermore, the mean number of males per lek postburn was 6 in the treatment plot compared with 17 in the control plot, whereas these values had been similar in treatment and control plots before treatment. Attendance at the major leks following the fire declined 90 percent in the treatment plot compared with 63 percent in the control plot.

In southeastern Idaho, Nelle and others (2000) examined characteristics of 20 burns of differing ages and sizes in mountain big sagebrush-dominated communities in relation to sage-grouse habitat. Mean size of four wildfires in the study area was 390 ha, whereas the mean size of 12 prescribed fires was 975 ha. Canopy cover of forbs, grasses, and shrubs was measured, along with invertebrate abundance. Nelle and others (2000) concluded that burning conferred no benefits to sage-grouse nesting or brood-rearing habitat and that long-term negative impacts resulted from fires in nesting habitat, because of the lengthy time (>20 years) for the sagebrush canopy to recover to suitable levels for nesting.

Retrospective studies of burns 5–43 years earlier at Hart Mountain and Steens Mountain in southeastern Oregon revealed that key components of sage-grouse habitat used during the breeding period were available in burned areas that ranged from 25 to 35 years postburn (Crawford and McDowell, 1999; McDowell, 2000). Sagebrush cover was the only habitat component "substantially affected" in the long term by burning (McDowell, 2000). During the first 2 years postburn in mountain big sagebrush at Steens Mountain, forage quality (for example, percentages of calcium and crude protein) was generally superior in burned plots than in unburned control plots. The fires in this study covered 619 and 1,352 ha (Crawford and McDowell, 1999; McDowell, 2000).

Wrobleski (1999) evaluated the response of vegetation to prescribed fires in a Wyoming big sagebrush site at Hart Mountain National Antelope Refuge in eastern Oregon. Vegetation was sampled in eight 400-ha plots, of which four were subsequently burned, creating 27 km of burned-unburned edge. Measurements were obtained 1-year postburn; annual forb cover increased in burned compared to control plots, but perennial grass cover decreased. Most pronounced differences were large increases in sagebrush vigor (number of

reproductive and vegetative shoots) along the edge of the burned plots. In addition to forb cover, changes in vegetation morphology, abundance, and phenology in response to prescribed fire were measured for nine forb species known to be selected by sage-grouse (Wrobleski and Kauffman, 2003). Although prescribed fire resulted in increases in number of racemes and flowers in some species (for example, shaggy milkvetch [*Astragalus malacus*]), fire caused reduced crown cover in other species (for example, low pussytoes [*Antennaria dimorpha*]). For seven of the nine species evaluated, prescribed fire had no effect on relative abundance, density, or frequency of occurrence. Phenology of all species was affected by prescribed fire, resulting in an extension of the period of active growth (Wrobleski, 1999; Wrobleski and Kauffman, 2003).

Fischer (1994) investigated effects of a 5,800-ha prescribed fire on sage-grouse habitat in southeastern Idaho. The study area was primarily Wyoming big sagebrush-bluebunch wheatgrass, but threetip sagebrush also was common. During the 3 years after the prescribed fire, 655 sage-grouse were captured and 127 were followed using radio telemetry. Data had been collected on sage-grouse for 3 years before the prescribed fire. Nest success and habitat characteristics did not differ between burned and unburned areas, and no positive response by sage-grouse to the burned habitat was noted. Abundance of Hymenoptera, a major food item in sage-grouse diets, declined significantly following the prescribed fire (Fischer, 1994). At Sheldon NWR in Nevada, however, arthropod abundance did not decline following a wildfire (Crawford and Davis, 2002). In Utah, 80 percent of sage-grouse flocks in burned and reseeded areas were <60 m from sagebrush (Danvir, 2002).

Posttreatment data collected in southeastern Idaho for 10 years following prescribed fire indicated that shrub height and cover necessary for breeding, brood rearing, and winter cover, as well as winter forage, were slow to recover (Beck and others, 2009). In essence, sagebrush structure had not returned to preburn levels 14 years postburn. Moreover, growth of rabbitbrush and horsebrush, shrubs less desirable to sage-grouse, was promoted in the burned area (Beck and others, 2009). Hess and Beck (2012b) evaluated vegetation structure in burned sites for as many as 19 years posttreatment in north-central Wyoming relative to the minimum vegetation structure required for suitable sage-grouse breeding habitat (Connelly and others, 2000b). Burned sites did not meet these guidelines for shrub canopy cover or height.

A model developed to examine relationships among sage-grouse populations, fire, and grazing by domestic sheep suggested that frequent (fire-return interval of 17 years), large (>10 percent of spring-burned area) fires may lead to local extinction of sage-grouse populations (Pedersen and others, 2003). However, smaller burns resulting from fires of lower intensity and frequency, in which sheep grazing was not allowed after burning, may benefit sage-grouse habitats if invasive annual grasses do not encroach into the burned areas (Pedersen and others, 2003).

Coates and others (2015) used a Bayesian approach to estimate effects of wildfire on sage-grouse population rate of change, using long-term (30-year) population, climate, and fire data from the Great Basin. Results indicated that wildfires interact with climate, such that burned areas near leks effectively depress population growth that typically follows greater precipitation. Models indicated long-term (30-year) population declines despite years of good precipitation. In general, fires seem to have negative long-term (30-year) effects on leks. Lek trends from 1997 to 2007 were downward with increasing amounts of area burned within 5 km for the Southern Great Basin and Snake River Plain Sage-Grouse Management Zones (SMZs) and, at larger scales, 18 km and beyond 40 km, for the Great Plains and Southern Great Basin SMZs, respectively (Coates and others, 2015). Fire was not associated with increasing trends on leks for any SMZ (Johnson and others, 2011). Based on 30 years of data from 144 occupied and 39 unoccupied leks in north-central Wyoming, Hess and Beck (2012a) generated lek occupancy models with landscape predictors at various scales. Unoccupied leks had 3.1 times the percentage of wildfires within 1.0 km compared to occupied leks. Smaller-scale studies have been inconclusive. At the U.S. Sheep Experiment Station near Dubois, Idaho, fires (wild and prescribed) apparently caused the abandonment of two active leks, enhanced the creation of one, and had no apparent effect on the fourth (Hulet and others, 1986). Also in Idaho, Fischer (1994) found that, although the number of active leks declined during the 3 years after a prescribed fire, this decline was similar in burned and control areas.

Coupled with outright loss of sage-grouse habitat from fire, altered fire regimes have resulted in severe habitat degradation in sagebrush steppe because of the invasion of cheatgrass (also known as downy brome; [*Bromus tectorum*]) and other exotic vegetation following wildfires (Pellant, 1990; Billings, 1994; Knick, 1999; West, 1999; Connelly and others, 2004; Crawford and others, 2004; Rhodes and others, 2010; Miller and others, 2011). Postfire establishment of invasive plants is most severe in Wyoming big sagebrush communities at lower elevations and is uncommon in cooler, more mesic sites supporting mountain big sagebrush (Miller and Eddleman, 2000; Hemstrom and others, 2002). About one-half of the Sage-Grouse Conservation Area (SGCA, defined as the historical distribution of sage-grouse buffered by 50 km; Miller and others, 2011) is estimated to have a moderate-to-high probability of containing cheatgrass, and losses are projected to accelerate in the future (Meinke and others, 2009; Miller and others, 2011). The widespread presence of cheatgrass, in turn, increases wildfire frequency (Baker, 2011; Davies and others, 2011). The interwoven threats of fire and invasive plants continue to challenge managers charged with minimizing loss and fragmentation of sagebrush; concepts of resistance to invasion and resilience to stress can be used to prioritize management actions to address these threats (Chambers and others, 2014).

Grazing

Livestock have been grazed throughout virtually the entire range of the sage-grouse (Braun, 1998; Connelly and others, 2004; Knick, 2011, Knick and others, 2011; Boyd and others, 2014); thus, the effect of livestock grazing on sage-grouse habitat is perhaps the most pervasive of any land-management practice. Reference sites within the sagebrush ecosystem that have been protected from livestock grazing are unavailable, which confounds the evaluation of grazing effects (Knick and others, 2011). Effects of livestock grazing on vegetation species composition and structure in the sagebrush community have been well documented (Vale, 1974; Owens and Norton, 1992; Fleischner, 1994; West, 1999; Belsky and Gelbard, 2000; Jones, 2000; Anderson and Inouye, 2001). Grazing can exacerbate the dominance of cheatgrass in sagebrush systems (Reisner and others, 2013). However, because of a paucity of appropriate grazing data, few empirical studies report the responses of sage-grouse to grazing, and experimental research on effects of livestock on sage-grouse is lacking (noted by Braun, 1987; Guthery, 1996; Beck and Mitchell, 2000; Connelly and others, 2000b; Rowland and Wisdom, 2002; Adams and others, 2004; Crawford and others, 2004; Knick and others, 2011). Evaluating effects of livestock grazing on sagebrush at large scales is also difficult due to the lack of sufficiently large control areas (Knick and others, 2011). However, inability to test for grazing effects does not warrant concluding that grazing does not impact sagebrush and sage-grouse (Knick and others, 2011). Monroe and others (2017) led the first large-scale assessment of potential effects of cattle grazing on sage-grouse populations using public grazing records and lek count data (n=743) from 2004 to 2014 in Wyoming. Results of the assessment determined that grazing impacts could be positive or negative, depending on timing and level of grazing. Early grazing seemed to negatively impact growth of cool-season grasses, whereas similar levels of grazing late in the season had some positive effects on population growth rates.

No published studies on the effects of livestock grazing on sage-grouse were manipulative experiments in which cause-effect relations could be measured. Instead, many studies imply negative effects of livestock grazing on sage-grouse by noting that grazing systems must be designed such that adequate herbaceous and shrub cover for nesting or brood rearing are maintained (for example, Gregg and others, 1994; DeLong and others, 1995; Sveum and others, 1998). For example, DeLong and others (1995) found that predation rates on sage-grouse nests in Oregon were negatively related to percentage cover of tall grass and medium-height shrubs and suggested that practices such as livestock grazing that remove grass cover may negatively affect nesting sage-grouse. Interactions of livestock grazing with other factors, such as wildfire, are complex and not widely studied.

Beck and Mitchell (2000) summarized potential effects of livestock grazing on sage-grouse habitats and cited only four references that provide empirical evidence of direct negative effects of livestock grazing on sage-grouse. Of 161 nests examined in Utah, 2 were trampled by livestock (1 by sheep, 1 by cattle), and 5 nests were deserted because of disturbance by livestock (Rasmussen and Griner, 1938). In Nevada, sage-grouse habitat in wet meadows was degraded through overgrazing by domestic livestock and altered system hydrology (Oakleaf, 1971; Klebenow, 1985; as reported by Beck and Mitchell, 2000). Klebenow (1982) examined sage-grouse habitat use in relation to grazing at the Sheldon NWR in Nevada, where sheep and cattle had grazed for >130 years. Dominant sagebrush species at the refuge were low sagebrush, mountain big sagebrush, and Wyoming big sagebrush. Grasses included Sandberg and Cusick's bluegrass (respectively, *Poa secunda*, *Poa cusickii*) in wet meadows and Sandberg bluegrass and mat muhly (*Muhlenbergia richardsonis*) in dry meadows. A rest-rotation grazing system was implemented in 1980 on most of the refuge, where season-long grazing was historically; a smaller portion had previously been managed under deferred rotation. Meadows heavily grazed by livestock (for example, with few forbs and grasses and dense shrubs present) were avoided by sage-grouse, with the exception of use for free water when available. (No explicit definitions were provided for light, moderate, or heavy grazing.) Some positive effects of livestock grazing were noted (Klebenow, 1982). When cattle were introduced into a meadow with residual grass, sage-grouse initially preferred the grazed openings, which had an effective cover height (sensu Robel and others, 1970a) of 5–15 cm, compared with 30–50 cm in the lightly grazed surrounding areas. Sage-grouse avoided dense, ungrazed basin wildrye meadows but were observed in adjacent wildrye that was grazed (Klebenow, 1982). Throughout the summer, one 40-ha meadow that was lightly grazed by cattle (41 yearling heifers, 60 days in June–August) was used by sage-grouse and had more sage-grouse (n=100) than any other meadow on the refuge. Effective cover height in the meadow did not decrease below 5 cm during the summer (Klebenow, 1982).

Danvir (2002) reported two instances of nest abandonment related to livestock grazing in northern Utah during 7 years of observations; one was caused by cattle, the other by sheep. Sage-grouse behavior on leks did not seem to be altered by the presence of grazing cattle. In Idaho, sheep grazing did not seem to disrupt use of leks by sage-grouse (Hulet, 1983). Autenrieth (1981), however, cautioned against grazing sheep in sage-grouse winter habitat. Autenrieth (1981) also suggested that livestock use of meadows occupied by sage-grouse, as well as livestock drives in sage-grouse habitat, could be detrimental to sage-grouse. In Wyoming, nesting densities of sage-grouse were considerably lower (10 nests per 100 ha) in areas heavily grazed by domestic sheep compared to adjacent sites with moderate grazing (28 nests per 100 ha) (Patterson, 1952). Nest desertion caused by migrant bands of sheep also was documented.

Heath and others (1998) compared sage-grouse nesting and breeding success at three ranches with different grazing operations and levels of predator control in Wyoming. Results of the comparison indicated that, despite heavier livestock

use (removal of >50 percent of annual herbaceous production and grazing by sheep and cattle) and predator control on one ranch, nesting and breeding success of sage-grouse did not differ substantially among the three sites. Chick survival to 21 days was, however, greater on the ranch with lighter grazing, suggesting that predator control did not fully compensate for the greater reductions in herbaceous production. Further, hens were documented leaving the more heavily grazed ranch to nest elsewhere but returning to that ranch to rear broods (Heath and others, 1998). In a similar study, Holloran (1999) examined sage-grouse habitat use and productivity in relation to grazing management strategies at four ranches in southeastern Wyoming. Results indicated no differences in nest success, brood survival, or numbers of chicks fledged among the ranches. Some differences in habitat use by sage-grouse were found among the ranches; however, these differences could not be ascribed to differences in grazing pressure but were ascribed to differences in soil types and precipitation patterns. Above-average precipitation during the study, however, may have obscured any potential differences in habitat suitability for sage-grouse among sites. None of these studies used control plots or replication.

Research on upland meadows in Nevada indicated that pastures under a rest-rotation system provided better production of forb species eaten by sage-grouse than did pastures that were not rested, but sage-grouse also used a pasture not grazed by cattle for 10 years (Neel, 1980). The results suggested that light grazing in meadows might enhance habitat for sage-grouse. Evans (1986, as reported in Beck and Mitchell, 2000) also found that grazing by cattle in upland meadows in Nevada stimulated production of forb species used by sage-grouse. Coates and others (2016) found that ravens, a common nest predator, selected sites near sage-grouse leks in Idaho and that the odds of raven occurrence increased 46 percent when livestock were present.

Boyd and others (2014) modeled effects of livestock grazing and fire on sage-grouse habitat using state and transition models and concluded that carefully managed grazing at moderate intensities can be compatible with maintaining ecosystem function in sagebrush communities. Results of the model also concluded that prescribed grazing can be used to reduce fine fuels in areas subject to invasion by exotic annuals, but that caution must be exercised in breeding and brood-rearing habitats (Boyd and others, 2014).

Although little research has been focused on impacts of free-roaming equids (horses and burros) in the sagebrush ecosystem, areas managed for these large grazers overlap with an estimated 18 percent (119,703 km^2) of the current range of sage-grouse (Beever and Aldridge, 2011). Equids affect ecosystem structure and function, from lowered and more fragmented shrub cover to compacted soils and lower vegetation diversity compared to sites with no equids (Beever and Aldridge, 2011). In a study of feral horse impacts in Nevada, Davies and others (2014) compared five grazed and ungrazed sites in mountain big sagebrush. Results of the comparation indicated a two-fold decrease in shrub density in grazed exclosures as well as greater soil penetration resistance and lower soil aggregate stability.

Application of Pesticides and Herbicides

Until the 1980s, herbicides such as 2,4–D were the most common method of eliminating large blocks of sagebrush (Connelly and others, 2000b). Lands after treatment generally were planted with crested wheatgrass or other nonnative perennial grasses for livestock forage. Application of herbicides affects all seasonal ranges of sage-grouse, and the effects of herbicides have been widely reported compared to other land-management practices (for example, Gill, 1965; Martin, 1970; Carr, 1967; Klebenow, 1970; Pyrah, 1970; Rowland and Wisdom, 2002). Although most of these studies reported negative effects of herbicide application within sage-grouse habitats, some reported positive effects, such as increased production of forb species eaten by sage-grouse (for example, Autenrieth, 1969).

Spraying of herbicides primarily degrades habitat for sage-grouse through fragmentation, that is, by removing shrubs used as nesting cover. Spraying of herbicides also eliminates forbs that provide food and cover. Long-term (30-year) studies in North Park, Colo., revealed that applying 2,4–D resulted in reduced cover of sagebrush, fewer sagebrush plants and forbs, and lek abandonment (Braun and Beck, 1996). Production of sage-grouse, as measured by percentage young in the harvest and chicks per hen, declined in the 5 years following treatment but rebounded by 15 years posttreatment (Braun and Beck, 1996). Hens with broods avoided sprayed blocks while moving toward traditional brood-rearing habitats (Carr, 1967; Carr and Glover, 1971). However, spraying did not seem to affect behavior on leks, use of leks, nesting success, use of sagebrush for nests, brood production, or brood survival (Carr, 1967). In another study in North Park, Colo., in which nearly 200 flocks (>5,000 birds) were observed for 2 winters, only 4 flocks were in altered (by spraying with 2,4–D, plowing, burning, or seeding) sagebrush habitats, although >30 percent of the 1,250 km^2 of sagebrush-dominated lands in the study area had been treated (Beck, 1977). Applications of imazapic in mowed Wyoming big sagebrush reduced invasive cheatgrass and nonnative forbs by 67 percent and 80 percent, respectively, but applications of imazapic also reduced native forbs by 84 percent (Baker and others, 2009).

In Montana, 693 ha of big sagebrush in a 777-ha study area were strip-sprayed with 2,4–D in 1 year; 3 years of subsequent study revealed nearly complete mortality (97 percent) of sagebrush in sprayed areas (Martin, 1965, 1970). Only 4 percent of 415 observations of sage-grouse were in sprayed strips. Shifts in sage-grouse distribution were attributed to differences in vegetation composition. Compared to sprayed strips, unsprayed strips had a greater ratio of forbs to grasses (40:60 compared with 20:80 in sprayed strips) and more live sagebrush, as well as more abundant forbs (Martin, 1970). In southeastern Idaho, spraying of >1,300 ha of threetip and big

sagebrush seemed to effectively eliminate nesting in sprayed areas for at least 5 years posttreatment (Klebenow, 1970). In sites with broods and in sites with no recorded broods, sprayed plots also had less basal area of forbs and lower crown cover of big and threetip sagebrush than control plots.

Application of pesticides, commonly for grasshopper (Acrididae) control, may affect sage-grouse by decreasing available prey (Eng, 1952; Patterson, 1952; Johnson, 1987; Connelly and Blus, 1991). Sage-grouse chicks require insects for survival during the first few weeks of life, and the quantity of insects available is related to both survival and growth of chicks (Johnson and Boyce, 1990). Pesticides also poison birds through ingestion of contaminated insects or plant materials treated as bait (for example, for rodent control). Mortality rates directly attributable to organophosphate pesticides, which are no longer legally used, were 16 percent of 73 sage-grouse in Idaho (Blus and others, 1989; Connelly and Blus, 1991). All deaths were of juvenile sage-grouse that died in alfalfa or potato fields. A single die-off of 70 sage-grouse in an alfalfa field also was reported (Connelly and Blus, 1991). In Wyoming, spraying with malathion in June for grasshopper control seemed to reduce brood sizes in one area but not in another (Johnson, 1987).

In Wyoming, >1.7 million ha were treated with toxaphene and chlordane (applied as baited bran) for grasshopper control during 1949–50 (Post, 1951a; Patterson, 1952). In the following 2 years, 45 sage-grouse mortalities were recorded on 16 baited 40-ha plots (Post, 1951a). Of these 45 mortalities, pesticide poisoning was the suspected cause of 11 deaths. Other deaths, however, were indirectly related to toxemia from ingestion of baited grain; sage-grouse also were killed by automobiles and a mowing machine, and all birds had symptoms of toxemia. Subsequent grasshopper control in Wyoming involved spraying of the pesticide Aldrin, which is more toxic than either toxaphene or chlordane (Post, 1951b). No differences were determined in bird mortality between unsprayed and sprayed plots, and no sage-grouse mortalities were observed during the single field season.

Energy and Urban Development

Resource extraction for energy development has been widespread and rapidly increasing throughout the sagebrush ecosystem (Scott and Zimmerman, 1984; Braun, 1987, 1998; Braun and others, 2002; Leu and Hanser, 2011; Naugle and others, 2011), with a tripling of the number of wells to more than 33,000 in the eastern portion of the species range by 2007 (Naugle and others, 2011). The issue is of particular concern because much of the development has been completed or is planned for areas containing some of the most intact sagebrush habitats and robust sage-grouse populations remaining in North America (Naugle and others, 2011).

Results of a survey of 51 surface coal mines in the northwestern United States in the 1980s indicated that sage-grouse were present on 27 mines; baseline biological data were collected on sage-grouse at most of these sites (Scott and Zimmerman, 1984). In Colorado, numbers of males on two leks within 2 km of surface coal mines declined drastically, to near zero, with some resurgence after mining activity was sharply curtailed (Braun, 1986; Remington and Braun, 1991). Overall population trends, however, were similar between the control area and mining area during a 17-year period (Remington and Braun, 1991).

Impacts of coal-mine and oil and gas development on sage-grouse are short (for example, 2–30 years) and long term (for example, permanent) (Braun, 1987, 1998; Braun and others, 2002; Aldridge and Boyce, 2007; Doherty and others, 2008). Braun (1987) noted that initial stages of oil-field development (for example, site preparation, drilling, and road construction) led to decreased numbers of sage-grouse in North Park, Colo. Although populations were sometimes reestablished with time, permanent, negative impacts on sage-grouse populations could transpire because of the construction of refineries, pumping stations, and other facilities associated with mineral development (Braun, 1987).

Aldridge and Boyce (2007) investigated occurrence of sage-grouse nests (n=113) during 2001–04 in southeastern Alberta; about one-third of the study area was affected by oil and gas activity. Results from the investigation indicated that nesting sage-grouse strongly avoided areas with high proportions of anthropogenic edge (for example, cropland, roads, oil wells).

Energy development also has been associated with lek abandonment and declines in recruitment, survival, and abundance of sage-grouse. In southwestern Wyoming, abundance of male sage-grouse at heavily impacted leks (leks with more than 15 wells within 5 km) declined by 51 percent (Holloran, 2005). Recruitment was lower for juvenile males in gas fields, where yearling males avoid leks. In the same study area, yearling females avoided nesting within 950 m of natural gas infrastructure (Holloran and others, 2010). Sage-grouse yearlings of both sexes that were reared in areas with such infrastructure had poorer annual survival compared to yearlings reared in areas with no infrastructure (Holloran and others, 2010). Unoccupied leks in north-central Wyoming had 10.3 times the number of oil and gas wells in a 1-km radius compared to occupied leks, and the presence of wells was the most influential predictor of lek absence (Hess and Beck, 2012a). Sage-grouse in Colorado were not displaced from an active oil field; but of the 11 active leks that remained, 73 percent were on the field's periphery and 82 percent were out of sight of active wells or powerlines (Braun and others, 2002).

During 1984–2008, the results of an analysis of active leks across Wyoming indicated a decrease of 2.5 percent per year in lek attendance by males; attendance was negatively associated with oil and gas well density, with effects most pronounced at the largest spatial scale (6,400 m; Green and others, 2017). Oil and gas development in Alberta, where sage-grouse have declined 66–92 percent during a 3-decade period to <100 individuals, has resulted in the abandonment of at least 4 lek complexes (Aldridge, 1998; Braun and others,

2002). Long-term declines in males per lek since the mid-1980s were correlated with increases in oil-related activities, and more than 1,500 wells have been drilled in the Province (Braun and others, 2002). In a comprehensive analysis of 814 leks in Wyoming in relation to oil and gas development during 1991–2011, numbers of male sage-grouse declined 24 percent with a 3.6-fold increase in well density across the State (Gregory and Beck, 2014). Gregory and Beck (2014) reported a 1–4-year time lag between oil and gas development density and lek decline, although not all leks declined with increasing well density. Harju and others (2010) also documented time-lag effects of 2–10 years for impacts of oil and gas development on lek attendance by sage-grouse and negative associations of lek attendance with adjacent oil and gas wells in five of seven study areas. Doherty and others (2010a) used counts of males from all active (n=1,190) and inactive (n=154) leks in Wyoming during 1997–2007 to determine impacts of five levels of energy development. Although declines varied spatially, the abundance of males on leks and the probability of a lek persisting decreased with increasing well density.

Johnson and others (2011) related trends in lek counts to a suite of environmental and anthropogenic features in the SGCA during 1997–2007. Results indicated that leks farther from the nearest oil and gas well had more positive trends than did closer leks; this relation was even more pronounced for producing wells. Also, when well numbers within 5 km of a lek exceeded 10, lek trends were negatively related to the number of wells. At a broader scale (within 18 km of a lek), this negative relation was observed when at least 160 active wells were within 18 km (Johnson and others, 2011). Future oil and gas developments are predicted to impact as much as 3.7 million ha of sagebrush habitat in the next 20 years, resulting in a 7–19 percent decline from the estimated 2007 sage-grouse population (Copeland and others, 2009).

The development of CBM also is of concern for sage-grouse (Braun and others, 2002; Connelly and others, 2004; Walker and others, 2007a; Doherty and others, 2008; Naugle and others, 2011). In the Powder River Basin of southeastern Montana and northeastern Wyoming, which supports critical regional populations of sage-grouse, about 35,000 wells were drilled between the early 1990s and 2007 (Naugle and others, 2011). In addition, 10,000 km of overhead powerlines were constructed in an area >11,650 km^2 for extraction of CBM gas in the Wyoming portion of the Basin (Braun and others, 2002). The development area supported a large proportion of the leks in northeastern Wyoming and was considered year-round habitat for the species. Researchers determined that (1) fewer males were present per lek when leks were <0.4 km from a well compared to outside this zone, (2) sage-grouse populations associated with leks within 0.4 km of a powerline had slower rates of growth than populations farther away, and (3) sage-grouse numbers were consistently lower in areas <1.6 km from a CBM facility (Braun and others, 2002). In a subsequent study of sage-grouse in the Powder River Basin, Walker and others (2007a) reported that leks in CBM fields had 46 percent fewer males per active lek than did leks outside the well fields. Moreover, the percentage of leks remaining active since 1997 was much lower in CBM fields; only 38 percent (n=26) were active by 2005, compared with 84 percent (n=250) of leks outside CBM fields. Lek persistence was also negatively associated with distance to, and proportion of, powerlines in this CBM field (Walker and others, 2007a). Results from the study indicated that current stipulations requiring no CBM development within 0.4 km of leks on Federal lands were inadequate for lek persistence, and that seasonal restrictions on well-related activities do not address the loss of sagebrush habitat and effects of infrastructure associated with well-field development (Walker and others, 2007a). Doherty and others (2008) modeled winter habitat use by sage-grouse in the Powder River Basin in 2005–06 and found strong avoidance of CBM wells in otherwise suitable habitat. CBM development also is underway in other portions of the range of sage-grouse, including southwestern Wyoming, Utah, Montana, and Colorado.

Creation of artificial leks to replace those destroyed during coal-mining operations has yielded mixed results; such an attempt was somewhat successful in Montana (Eng and others, 1979; Phillips and others, 1986) but not in Wyoming (Tate and others, 1979). If suitable habitat for nesting hens has been permanently destroyed through mining or other disturbances, leks will not become reestablished in these areas. Noise associated with oil wells near Walden, Colo., was believed to be responsible for the abandonment of a lek that historically had supported 1,000 birds (Rogers, 1964). Simulated noise associated with gas drilling and roads resulted in a 29 percent and 73 percent decrease in male abundance at leks, respectively, and intermittent noise had a greater impact than continuous noise (Blickley and others, 2012a). Lyon and Anderson (2003) found that, although sage-grouse nest success was similar on disturbed leks (within 3 km of natural gas development) and undisturbed leks (>3 km from natural gas development or within 3 km from gas development but isolated from roads and well pads) in Wyoming, hens captured on disturbed leks had poorer nest initiation rates and moved twice as far to nest as hens on undisturbed leks. Also, hens from disturbed leks nested in areas with taller live sagebrush (36 compared with 30 cm) and greater total shrub cover (41 compared with 33 percent) than did hens from undisturbed leks (Lyon, 2000).

Urbanization, including development of exurban sites, also affects sage-grouse habitat through associated transportation networks, outright loss of habitat in developed areas, fragmentation, and human disturbance leading to decreased habitat use (Knick and others, 2011). Nearly 20 percent (457,193 km^2) of the SGCA is affected by urbanization (Knick and others, 2011). Leks in the SGCA during 1997–2007 were seldom within 5 km of developed lands (urban, suburban, interstate and State highways), and trends were negatively related to the percentage of developed lands, especially within 18 km of the lek (Johnson and others, 2011). Most nest abandonment by sage-grouse is related in some way to human disturbance (Schroeder and others, 1999). In Idaho, sage-grouse

populations that occupy somewhat xeric habitats near human populations or that occupy fragmented habitats may be subject to overharvesting because of hunting (Connelly and others, 2003a). Disturbance from military activity also may displace sage-grouse, although population-level effects are not known (Hofmann, 1991). In Washington, Schroeder and others (2000) suggested that sage-grouse may have persisted in a military training facility because of the absence or restriction of livestock grazing on the training grounds. Resource subsidies in developed areas also benefit potential predators of sage-grouse eggs and chicks, such as Common Ravens (Coates and others, 2016). In Wyoming, higher than expected raven densities were detected at locations near sage-grouse nests and broods, and raven occupancy was negatively related to sage-grouse nest success (Bui and others, 2010).

Structures associated with energy development and rural expansion, such as fences, roads, and powerlines, may fragment habitats for sage-grouse (Braun, 1998; Connelly and others, 2000b; Braun and others, 2002; Aldridge and Boyce, 2007; Johnson and others, 2011; Leu and Hanser, 2011; Wisdom and others, 2011). Johnson and others (2011) found that relations between short-term (1997–2007) trends of lek counts in the SGCA and roads depended on road type. For example, trends were downward in relation to the length of interstate highways within 5 km, and trends were positively associated with distance to nearest highway (interstate, other Federal, and State highways combined). However, no association was indicated between lek trends and secondary roads (Johnson and others, 2011). Vehicle traffic on roads, along with the increased access that roads provide to recreational users of rangelands, may lead to increased disturbance of sage-grouse on leks or during nesting or brood rearing (Braun, 1998). In Wyoming, hens that were successful at nesting in a natural gas field placed their nests farther from roads than did unsuccessful hens (Lyon and Anderson, 2003). Road densities in the interior Columbia Basin were higher in the extirpated range of the sage-grouse than in the species' occupied range (Wisdom and others, 2002b). The pattern of higher road densities in the species' extirpated range also coincided with less habitat, higher human population densities, increased agricultural development, and greater likelihood of invasion by exotic plants, suggesting a synergy of effects (Wisdom and others, 2002b).

Direct mortality may result from collisions of sage-grouse with powerlines (Beck and others, 2006), fencing (Call and Maser, 1985; Danvir, 2002), and vehicles (Post, 1951a; Patterson, 1952; Stinson and others, 2004; Aldridge and Boyce, 2007). In Wyoming, sage-grouse were most susceptible to death from collisions during summer (June–August), when movements of hens with broods increased and sage-grouse were attracted to moister roadside vegetation (Patterson, 1952).

Powerlines and communication towers may not only increase habitat fragmentation but also provide perches for avian predators of sage-grouse (Ellis, 1984; Braun, 1998; Lammers and Collopy, 2007; Walker and others, 2007a; Wisdom and others, 2011). Although the magnitude of such effects on sage-grouse habitats and populations is unknown, sage-grouse use has been determined to increase as distance from powerlines increases (Braun, 1998). Short-term (1997–2007) trends in lek counts, particularly in some SMZs, were lower in proximity to communication towers, although these trends could be due to human activity associated with the towers rather than the towers themselves (Johnson and others, 2011). In the same analysis, powerlines were unrelated to lek trends; however, powerlines may have impacted lek trends before sage-grouse surveys, specifically when the lines were erected. Disturbance from raptors, particularly Golden Eagles, may disrupt strutting males on leks (Rogers, 1964; Ellis, 1984); thus, structures that provide perches for raptors may increase such disturbance or even mortality of grouse. Common Ravens also benefit from powerline towers as perches and nesting or roost sites (Leu and others, 2008). Positive associations between raven abundance and nest failure were determined in a study of sage-grouse in Nevada (Coates and Delehanty, 2010). In Nevada, concern for sage-grouse prompted research on effectiveness of perch deterrents on towers associated with a new, high-voltage powerline (Lammers and Collopy, 2007). Results of the research indicated that although raptors spent less time perching on the deterrents compared to other perching substrates and had a lower probability of perching on the deterrents than on other perches, the design did not completely prevent use by avian predators (Lammers and Collopy, 2007).

Impacts of wind-energy development on sage-grouse are not yet widely studied but can include direct mortality from turbines and indirect effects of infrastructure, such as powerlines and roads, used to develop wind energy (Knick and others, 2011). Three recent studies in Wyoming examined effects of wind energy on sage-grouse. Results from a study of survival of nests, broods, and sage-grouse hens (n=95, 31, 116, respectively) near a wind-energy facility indicated decreased survival of nests and broods, but not hens (LeBeau and others, 2014). For every 1-km increase in distance from the nearest turbine, the risk of nest or brood failure declined 7.1 percent and 38.1 percent, respectively (LeBeau and others, 2014). In a second study, results indicated that male lek attendance did not decline on leks >1.5 km from wind turbines in Wyoming, although the hypothesis of the presence of wind turbines having no effect could not be ruled out (Type II error; LeBeau and others, 2017a). In the third study, results indicated that the relative probability of sage-grouse hens (n=346) selecting summer and brood-rearing habitat declined as the percentage of surface area impacted by infrastructure associated with wind-energy development increased (LeBeau and others, 2017b).

One stressor to sage-grouse that emerged rapidly was the spread of West Nile virus (WNV; Connelly and others, 2004; Naugle and others, 2004, 2005; Walker and others, 2004, 2007b; McLean, 2006; Moynahan and others, 2006; Kilpatrick and others, 2007; Walker and Naugle, 2011). The virus has been documented as a source of mortality in sage-grouse

populations in Alberta, California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, Saskatchewan, South Dakota, Utah, Washington, and Wyoming (Walker and Naugle, 2011). The WNV complicates conservation of sage-grouse; the species has demonstrated little resistance to WNV and few management options are available to contain the spread of WNV (Walker and Naugle, 2011). All evidence indicates that Greater Sage-Grouse are highly susceptible to WNV; sampling of 363 sage-grouse in 2003 and 2004 produced no evidence of antibody production (Naugle and others, 2005). Clark and others (2006) injected live WNV in vaccinated and unvaccinated sage-grouse (n=14) and confirmed the high susceptibility of sage-grouse to WNV; all sage-grouse died within 6 days of injection. In the Powder River Basin in northeastern Wyoming, substantial declines in males per lek were documented in a site with WNV present (change in mean number of males= −91 percent) compared to two sites without the disease (change in mean number of males= +10.7 percent; Naugle and others, 2004). Furthermore, late-summer survival estimates between pre-WNV and post-WNV years declined by 25.3 percent in four sites across the eastern one-half of the species' range (Naugle and others, 2004). Sage-grouse were monitored for WNV in 12 sites across the current range of sage-grouse in 2004 (Naugle and others, 2005). Results indicated that survival of hens in sites with confirmed WNV mortalities was 10 percent lower than in sites without confirmed WNV mortalities (0.86 compared with 0.96). However, 10.3 and 1.8 percent of newly captured females in 2005 and 2006, respectively, tested seropositive for neutralizing antibodies to WNV; the first evidence of survival of infected Greater Sage-Grouse (Naugle and others, 2005). A recent survey of sage-grouse across a large portion of the Great Basin in Nevada found that all samples (n=31) tested negative for the virus or antibodies (Sinai and others, 2017).

Taylor and others (2013) examined the separate and interacting effects of oil and gas development and outbreaks of WNV on Greater Sage-Grouse in northeastern Wyoming. In a non-outbreak year, the number of males counted declined by 61 percent with the drilling of 3.1 wells per km^2 in a previously undeveloped landscape. Outbreak years in the absence of energy development led to similar declines in total counts and were associated with a near doubling of the lek inactivity rate (proportion of leks with the last count=0). When outbreak years were combined with well drilling (densities of 3.1 leks per km^2), the lek inactivity rate quadrupled compared to sites with neither outbreaks nor energy development (Taylor and others, 2013).

Human-created water sources, such as ponds associated with CBM development, can facilitate spread of the virus by providing habitat for larval mosquitoes (Culicidae) that serve as vectors of WNV. Such ponds and associated WNV are thought to have contributed to the extirpation of a sage-grouse population in northeastern Wyoming (Walker and others, 2004; Walker, 2008). The extraction of CBM is typically accompanied by the pumping of large quantities of water (Bureau of Land Management, 2003). In some natural-gas fields, such as the Powder River Basin, the primary method for water disposal is through direct surface discharge, including into impoundments (Bureau of Land Management, 2003). Potential mosquito larval habitats associated with CBM development increased by 75 percent between 1999 and 2004 in the Powder River Basin (Zou and others, 2006). Other human-created water sources, such as stock ponds, irrigated croplands, and watering tanks for livestock, may also provide habitat for mosquito vectors. Although several genera of mosquitos as well as other insects are vectors of WNV in sagebrush habitat, the widespread mosquito (*Culex tarsalis)* is the dominant vector. *Culex tarsalis* prefers standing water with submerged vegetation, on which the female mosquito deposits its eggs (reviewed in Walker and Naugle, 2011). The species that serve as primary reservoirs for WNV in western North America and the bird species that are primary amplifying hosts are unknown, but sage-grouse may serve as "competent" vectors (Walker and Naugle, 2011). Regardless of the source of WNV, the addition of surface water in arid environments during late summer may affect abundance and distribution of vector populations and of reservoir hosts for the disease. The role of local water sources in the spread of the virus, however, is unclear (Naugle and others, 2004; Walker and others, 2004).

Translocation

Translocations of sage-grouse generally have been unsuccessful (Toepfer and others, 1990; Reese and Connelly, 1997; Schroeder and others, 1999; Connelly and others, 2000b; Baxter and others, 2008), and further research on the effectiveness of translocating sage-grouse is needed (Reese and Connelly, 1997; Rowland and Wisdom, 2002). During the 1930s, 200 sage-grouse were trapped in Wyoming and were reintroduced into New Mexico, where sage-grouse had been extirpated (Allred, 1946; Campbell, 1953). Presumably, the sage-grouse that historically occupied this region were Gunnison and not Greater Sage-Grouse (Young and others, 2000). The transplants eventually failed, and sage-grouse are no longer in New Mexico. Other efforts to translocate sage-grouse failed in British Columbia, Montana, and Oregon (Toepfer and others, 1990). Patterson (1952) reported that despite massive removals from live-trapping and hunting of >13,000 sage-grouse from the Eden Valley in Wyoming, most transplanted birds, especially adults, returned from release sites to the area of capture. Many of the birds were released 30–60 km from Eden Valley, and two transplanted sage-grouse moved more than 200 km to return to Eden Valley. In contrast, Musil and others (1993) evaluated the translocation of nearly 200 sage-grouse during 2 years from southeastern to central Idaho (about 140 km) and reported that dispersal of birds away from the release site was not a problem. In addition, the translocated birds established five new leks in the release site, nested successfully, and persisted for the first 3 years following release. Consequently, Musil and others (1993) concluded that translocation into suitable habitats was a feasible method for supplementing or reestablishing populations of sage-grouse.

More recently, Baxter and others (2008) reported the successful translocation within 3 years (2003–05) of adult sage-grouse hens (*n*=137) from source populations elsewhere in Utah to a release site in Strawberry Valley, Utah. Habitat was not lacking in the release site, though the resident population was estimated to be only 150 birds in 1998 (Baxter and others, 2008). Nest success of translocated hens was 67 percent, and peak attendance of males at the only active lek in the study area in 2006 was 135, nearly 4 times the mean peak count of males during the 6 years prior (36). During 1998–2010, survival rates were 1.51 times higher for resident compared to translocated sage-grouse. Translocated yearling females had the poorest survival rate (0.47; Baxter and others, 2013).

Reese and Connelly (1997) reviewed reports of 56 attempts to translocate sage-grouse, involving >7,200 individuals, and found that only 5 percent of attempts were successful. Successful translocations typically involved (1) reproductively active birds captured on leks during March or April, (2) rapid transportation and release of birds, and (3) release into isolated areas of suitable habitat surrounded by inhospitable habitat (Reese and Connelly, 1997). Reese and Connelly (1997) recommended that (1) translocated sage-grouse should be intensively monitored, (2) the technique should be considered experimental only, and (3) translocations should not be relied upon to reestablish extirpated populations. Reese and Connelly (1997), Toepfer and others (1990), and Baxter and others (2008) provided recommendations and criteria for translocations of sage-grouse. A benefit of translocations may be the maintenance of genetic diversity in small populations, particularly when dispersal corridors are lacking (Schroeder and others, 1999). Based on results of a range-wide genetic survey of Greater Sage-Grouse, Oyler-McCance and others (2005) recommended that translocations be made to nearby, rather than distant, populations to preserve any effects of local adaptations.

Management Recommendations from the Literature

Native sagebrush habitats have undergone drastic declines in quantity and quality in the last century (Hann and others, 1997; West, 1999; Miller and Eddleman, 2000; Miller and others, 2011; Pyke, 2011), with concomitant declines in populations of Greater Sage-Grouse and Gunnison Sage-Grouse (Connelly and Braun, 1997; Braun, 1998; Leonard and others, 2000; Oyler-McCance and others, 2001; Beck and others, 2003; Garton and others, 2011; U.S. Fish and Wildlife Service, 2013). Threats to sage-grouse populations and habitats range from invasive annual grasses and elimination of sagebrush to grazing by livestock and feral equids and differ in importance across the range of the species (U.S. Fish and Wildlife Service, 2013). Despite these challenges, Greater Sage-Grouse populations remain widespread, and few anthropogenic impacts exist in core areas. Based on a comprehensive, long-term (1965–2007) dataset of >75,000 lek counts, Garton and others (2011) estimated the minimum range-wide sage-grouse population in 2007 to be 88,816 males on 5,042 leks. Nielson and others (2015), however, detected recent declines in sage-grouse breeding populations across the species' current range; range-wide declines in lek counts were more severe between 2005 and 2015 compared to declines between 1965 and 2015.

Restoration of sage-grouse habitats will require substantial effort to counter past and future losses and the current downward trend in habitat quality (Bureau of Land Management, 2001; Bunting and others, 2002; Hemstrom and others, 2002; Wisdom and others, 2002a; Connelly and others, 2004; Shaw and others, 2005; Miller and others, 2011; U.S. Fish and Wildlife Service, 2013). Protecting intact sagebrush grasslands while restoring additional habitat is critical to meeting the needs of the Greater Sage-Grouse (Connelly and others, 2011b; Wisdom and others, 2011). Such efforts will be particularly challenging and require long-term management because of the number of years (>20 years) required to establish sagebrush communities, high failure rates in restoring native perennial grass communities, drought conditions predicted under climate change, and current challenges posed by increased frequency of fires and the expanding distribution of invasive annual grasses (Miller and others, 2011; Arkle and others, 2014).

Several publications provide explicit management recommendations for sage-grouse habitats (for example, Braun and others, 1977; Paige and Ritter, 1999, p. 9–26; Connelly and others, 2000b; Wisdom and others, 2000; Adams and others, 2004; Knick and Connelly, 2011). A three-part series of restoration handbooks for sagebrush ecosystems, with an emphasis on sage-grouse, describes key concepts and decision tools for prioritizing restoration projects at landscape and site scales (Pyke and others, 2015a, 2015b, 2017). The following recommendations draw in part from these publications.

Maintaining viable sage-grouse populations will require a coordinated, landscape approach (Doherty and others, 2011; Naugle and others, 2011; U.S. Fish and Wildlife Service, 2013; Crist and others, 2017), including strategic planning tools to overlay the best remaining sage-grouse habitats with current and anticipated energy development and prioritize "set-aside" areas (Naugle and others, 2011). Protecting "stronghold" core regions, such as the Wyoming Basin, and maintaining connectivity among core areas (Doherty and others, 2011) as well as among more isolated leks, such as those in the Columbia Basin, are needed to maintain sage-grouse populations (Knick and Hanser, 2011; Wisdom and others, 2011; Crist and others, 2017). The current conservation strategy of Priority Areas for Conservation in each State across the range of Greater Sage-Grouse (U.S. Fish and Wildlife Service, 2013) may benefit populations if adequate linkages are maintained among the priority areas, but management outside priority areas that fails to preserve sage-grouse habitat may ultimately lead to habitat conditions that cannot support populations (Crist and others, 2017). Connectivity of sage-grouse populations is closely

linked to dominant patterns of sagebrush distribution such as cover and fragmentation. The long-term persistence of leks, however, is driven by land-use practices, particularly energy development and fire (Knick and Hanser, 2011). As new stressors become more widespread, such as climate change and wind-power development, the need for landscape-scale planning will become even more critical. Relating information about the vulnerability of landscapes to anthropogenic risks will allow conservation planners to consider aspects of urgency and the probability of success; for example, prioritizing areas with low energy-development potential is recommended in landscape planning, particularly those areas with high biological value, but even those areas with low biological value can help maintain connectivity to core regions of the sage-grouse range (Doherty and others, 2011).

Sage-grouse typically occupy large, unbroken expanses of sagebrush; thus, maintaining, conserving, and restoring large blocks of intact sagebrush are critical for the conservation of this species (Paige and Ritter, 1999; Connelly and others, 2000b; Aldridge and others, 2008), especially areas with a healthy understory of native grasses and forbs, with variable grass and shrub cover and height (Connelly and others, 2011c). Leu and Hanser (2011) recommended that sagebrush habitat be managed at large spatial scales, specifically 4.5–9.0 km, which is the scale at which sage-grouse dispersal and movement have adapted. Doherty and others (2010b) modeled sage-grouse nesting habitat at local and landscape scales and cautioned that treatments to improve nesting habitat (local scale) must be implemented in the proper landscape context. Sage-grouse are a sagebrush-obligate species that respond to landscape-scale effects (Patterson, 1952; Wakkinen, 1990; Paige and Ritter, 1999; Schroeder and others, 1999; Connelly and others, 2000b). Sagebrush-dominated breeding habitats with a healthy herbaceous understory are critical for the survival of sage-grouse populations; Wallestad and Schladweiler (1974) and Connelly and others (2000b) discouraged habitat alterations (including burning, spraying, oil and gas development, and other disturbances) at lek sites and adjacent breeding habitat (as much as 18 km from the lek, depending on migratory status of the population).

Season of use is a key consideration for any habitat management. Based on the current knowledge of the ecology of sage-grouse and their habitats, Connelly and others (2000b) recommended managing breeding habitats that support a sagebrush canopy cover of 15–25 percent and a perennial herbaceous cover height of 18 cm with >15 percent grasses and 10 percent forbs. Note that this height refers to those measured at nest fate, not initiation (Gibson and others, 2016b).

Sage-grouse wintering habitat is typically a small proportion of the year-round home range of sage-grouse but is used for a long period during the annual cycle. In winter, forage and cover are needed to ensure survival. Sagebrush cover is the key component of winter habitat, and more cover may be needed in winter than in the breeding season (Swanson and others, 2013). In most locations, winter habitat has at least 20 percent sagebrush cover.

Migratory populations of sage-grouse may use as many as nine stopover sites on journeys of as much as 240 km from breeding to wintering grounds. Specific migratory routes differ among and even within individuals, but land uses compatible with sage-grouse habitat needs along general migratory corridors are essential considerations in conservation planning (Smith, 2010).

Where sagebrush density has increased beyond that required for cover (for example, cover >35 percent) and understory habitat is of poor quality (minimal cover of native, perennial grasses and forbs), judicious management of sagebrush through burning or mechanical means (for example, chaining, disking) may be appropriate for restoring sagebrush communities (Paige and Ritter, 1999; Connelly and others, 2000b; Danvir, 2002; Pyke, 2011). Such treatments are primarily to increase grass and forb production (Connelly and others, 2000b), although the relation between sagebrush cover and herbaceous vegetation may be weak or nonexistent (Sowell and others, 2011). Early season forbs and locally adapted seed sources will benefit sage-grouse when reseeding is an option in habitat restoration projects. For example, in the Great Basin, early-season, high-nutrient forbs are included in the diets of preincubating hens; forb species in the Cichorieae tribe and plants of the Apiaceae and Fabaceae families are recommended for habitat restoration projects that require reseeding, if seed sources are available (Gregg and others, 2008). Specifically, Gregg and others (2008) recommended planting hawksbeard (*Crepis* spp.), desertparsley (*Lomatium* spp.), mountain dandelion (*Agoseris* spp.), sagebrush buttercup (*Ranunculus glaberrimus*), longleaf phlox (*Phlox longifolia*), bighead clover (*Trifolium macrocephalum*), pussytoes (*Antennaria* spp.), and arcane milkvetch (*Astragalus obscurus*).

Pinyon-juniper encroachment is a key stressor of sagebrush habitats (Connelly and others, 2011b; Miller and others, 2011, 2017), and mechanical removal (for example, via chaining) of pinyon-juniper has been recommended, as long as conservation of woodland-associated wildlife populations is also carefully considered (Commons and others, 1999; Miller and Rose, 1999; Barrett and others, 2000; Connelly and others, 2000b; Holmes and others, 2017). Although prescribed fire also has been recommended to control tree encroachment, Baker (2011) contended that because fire also kills sagebrush, low-impact mechanical measures are more effective at retaining sagebrush communities. Bates and others (2017) concurred in their evaluation of effects of various control treatments in pinyon-juniper woodlands of the Great Basin on forbs used by sage-grouse. Periodical, manual removal of encroaching trees has been recommended for ridge-top winter habitat (Smith, 2010). To control pinyon-juniper, Miller (2014) suggested tailoring management practices to local conditions, such as soils, site disturbance history, sagebrush taxa present, presence of other species of concern, and available moisture.

Invasive, nonnative plants threaten sagebrush habitats and sage-grouse populations; several publications have emphasized the importance of locating and controlling these invasive plants (Billings, 1994; Paige and Ritter, 1999; Connelly and

others, 2000b; Wisdom and others, 2000). The displacement of native sagebrush steppe by cheatgrass is one of the most dramatic changes in western landscapes (Billings, 1994), and restoration will require unprecedented resources (Knick, 1999; Bunting and others, 2002; Hemstrom and others, 2002; Shaw and others, 2005). Chambers and others (2014) provided guidance on prioritizing landscapes for restoration of sage-grouse habitats across multiple scales based on concepts of resistance to invasion of annual grasses and resilience to altered fire regimes.

Plant species composition, topography, and other physical characteristics of sites are factors to consider in habitat management. For example, microsites in drainages may ameliorate effects of wind, especially at low temperatures (Sherfy and Pekins, 1995) and contribute to maintaining energy balance.

Several authors have suggested that prescribed fire in sagebrush steppe should be used with caution, if at all, especially in more arid portions of the sage-grouse range (Fischer, 1994; Connelly and others, 2000a, 2000b; Byrne, 2002; Beck and others, 2009; Rhodes and others, 2010; Knick and others, 2011; Innes, 2016). Given the extensive habitat loss resulting from wildfires and associated increases in invasive plants, prescribed fire has limited utility for improving habitats for sage-grouse (Baker, 2011; Knick and others, 2011). Prescribed fire can be used as a management tool to maintain a mosaic of habitats following the burn and to minimize impacts on native grasses and forbs (Rhodes and others, 2010). Prescribed fire in more mesic sagebrush communities, such as mountain big sagebrush, may increase production of some desirable forbs although prescribed fire may decrease sagebrush cover (Pyle and Crawford, 1996; but see Rhodes and others, 2010). If fire occurs or is prescribed in areas susceptible to invasion by cheatgrass or other nonnative vegetation, active (for example, seeding, planting) and passive (for example, deferred livestock grazing) restoration may need to be continued until the goals for sagebrush restoration are met (Bunting and others, 1987; Beck and Mitchell, 2000). Fires in these areas may be detrimental to sage-grouse habitat and should be suppressed when feasible (Baker, 2011). Beck and Mitchell (2000) recommended that range rehabilitation of burned habitats should emphasize reestablishment of native forbs and shrubs, with less emphasis on grasses. Arkle and others (2014) examined sage-grouse occupancy in >100 postwildfire seeding projects in sagebrush habitats in the Great Basin. Understory guidelines were met at 50 percent of the sampled plots, but none met full guidelines for breeding habitat. Even with active restoration (that is, seeding), sage-grouse were unlikely to use burned areas within 20 years of fire (Arkle and others, 2014).

Although fire is a natural disturbance agent in all sagebrush ecosystems, fire-return intervals differ widely among sagebrush taxa and are difficult to quantify given the large site-to-site variability and poor fire records in shrubland communities (Miller and others, 2011; Innes, 2016). In sagebrush communities that have been invaded by cheatgrass, fire intervals are much shorter (with returns as short as 5–10 years in Wyoming big sagebrush; Innes, 2016), and complete elimination of sagebrush with replacement by annual grasslands has been reported (Billings, 1994; Monsen, 1994; Crawford and others, 2004; Miller and others, 2011). Baker (2011) estimated historical fire intervals to range from more than 200 years in little sagebrush to 200–350 years in Wyoming big sagebrush and 150–300 years in mountain big sagebrush. Given these historical intervals, Baker (2011) concluded that prescribed fire intervals have been far too short, especially given that climate change is expected to increase wildfire frequency.

Livestock grazing has been proposed as a potential alternative to burning or mowing for improving sagebrush habitats (Hess and Beck, 2012b). Grazing intensity may be managed through stocking rates and season of use on all seasonal ranges of sage-grouse to avoid habitat degradation (Paige and Ritter, 1999; Beck and Mitchell, 2000; Wisdom and others, 2000; Adams and others, 2004), especially on recently disturbed sites, such as those sprayed or burned (Braun and others, 1977). This approach, however, requires intensive management and monitoring. In nesting and brood-rearing habitats, grazing can be managed to maintain enough herbaceous understory cover to deter potential nest predators (Connelly and others, 2000b; Hockett, 2002).

Healthy native understories also support insects and forbs that are key components in the diets of prelaying hens and of chicks (Johnson and Boyce, 1990; Barnett and Crawford, 1994; Drut and others, 1994b). Riparian areas and wet meadows used for brood rearing are especially susceptible to grazing by livestock; in these habitats, removal of livestock before the nesting season may be prudent (Beck and Mitchell, 2000; Hockett, 2002). Livestock also have been positively associated with the abundance of synanthropic predators such as Common Ravens; thus, spatially segregating livestock from breeding areas may reduce predation risk on leks (Coates and others, 2016).

Human-created water sources, such as stock ponds, irrigated croplands, and watering tanks for livestock, can facilitate spread of WNV by providing habitat for mosquitoes that serve as vectors of WNV. Development of livestock-watering structures in sage-grouse habitat is not recommended (Connelly and others, 2000b). If water developments are constructed for sage-grouse or other wildlife, proper placement of these developments will ensure that water is available during movement of sage-grouse from spring to summer ranges (Wakkinen, 1990). Eliminating stagnant water from artificial water structures, which provide breeding habitat for mosquitos that spread WNV, is essential for reducing impacts to sage-grouse (Walker and Naugle, 2011), especially in coal-bed natural gas ponds (Zou and others, 2006; Walker and others, 2007b). Connelly and others (2000b) recommended that pipelines from springs be built so that free water is available to maintain the spring and associated wet meadows.

A primary management consideration is avoiding application of herbicides or pesticides in sage-grouse habitats, particularly during nesting or brood-rearing periods (Carr, 1967; Blus and others, 1989; Beck and Mitchell, 2000; Connelly and others, 2000b). Sage-grouse feed on insects during

spring and summer, and chicks rely heavily on insects during the first few weeks of life (Johnson and Boyce, 1990; Drut and others, 1994b; Schroeder and others, 1999). Spraying of herbicides not only eliminates large blocks of sagebrush, leading to increased habitat fragmentation, but also may poison insects and other invertebrates eaten by sage-grouse (Carr, 1967; Johnson, 1987) and reduce native grasses and forbs (Baker and others, 2009). Spraying an herbicide, like imazapic, to reduce cheatgrass may be effective only if spraying is finely targeted (Baker and others, 2009).

Development of mining and other resource-extraction industries, such as oil and gas or CBM, directly eliminates sage-grouse habitat (for example, through road-building, construction of settling ponds, and mine excavation), fragments sagebrush communities, and increases disturbance from vehicles and other associated activities and infrastructure developed to access and service wells (Remington and Braun, 1991; Schroeder and others, 1999; Braun and others, 2002; Lyon and Anderson, 2003; Aldridge and Boyce, 2007; Naugle and others, 2011; Blickley and others, 2012b). Reducing or avoiding such development within sage-grouse habitats has been recommended by several authors (Braun and others, 2002; Lyon and Anderson, 2003; Holloran and others, 2010; Hess and Beck, 2012a). A maximum density of one well within 2 km of leks is suggested to avoid measurable impacts within a year, and no more than six wells within 10 km of leks to minimize delayed impacts (Gregory and Beck, 2014). Manier and others (2014) synthesized information about observed effects of anthropogenic activities and infrastructure on sage-grouse and provided distance ranges for potential conservation buffers in relation to six classes of these features.

Direct mortality has been reported from collisions of sage-grouse with powerlines (Beck and others, 2006). Braun (1998) and Connelly and others (2000b) recommended avoiding powerline construction in sage-grouse habitat, especially within 3 km of seasonal habitats. Transmission corridors also may fragment habitat, foster establishment of invasive plants, and provide pathways for mammalian predators. Increases in predation on sage-grouse may result from increased availability of perches for roosting and nesting by raptors (Ellis, 1984; Braun and others, 2002; Rowland and Wisdom, 2002). If new powerlines are established, their effects may be minimized by locating the powerlines in areas already impacted by other disturbances (Leu and Hanser, 2011).

Sage-grouse are sensitive to anthropogenic disturbances (Lyon and Anderson, 2003; Aldridge, 2005). Minimizing human disturbance, such as vehicle traffic and recreation, may be a fruitful conservation measure in sage-grouse habitats, especially near leks and nesting habitat (Paige and Ritter, 1999; Connelly and others, 2000b; Braun and others, 2002; Lyon and Anderson, 2003). Leks may be abandoned if disturbance exceeds some threshold (Aldridge, 1998; Braun and others, 2002). Most cases of nest abandonment are either directly or indirectly related to human disturbance (Schroeder and others, 1999).

To summarize, “available evidence clearly supports the conclusion that conserving large landscapes with suitable habitat is important for conservation of sage-grouse” (Connelly and others, 2011c, p. 69). Moreover, Connelly and others (2011c, p. 83) cautioned that “failure to protect what is left and fix what is broken will likely result in extirpation of many, if not most, populations of Greater Sage-Grouse.”

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Table B1. Measured values of vegetation structure and composition in Greater Sage-Grouse (*Centrocercus urophasianus*) breeding habitat by study. The parenthetical descriptors following authorship and year in the "Study" column indicate that the vegetation measurements were taken in locations or under conditions specified in the descriptor; no descriptor implies that measurements were taken within the general study area.

[cm, centimeter; %, percent; --, no data; ±, plus or minus; SD, standard deviation; SE, standard error; >, greater than; m, meter]

Study	State or province	Habitat	Management practice or treatment	Vegetation height (cm)	Vegetation height-density (cm)	Grass cover (%)	Forb cover (%)	Shrub cover (%)	Sagebrush cover (%)	Bare ground cover (%)	Litter cover (%)
Aldridge and Brigham, 2002[a] (successful nests)	Alberta	Sagebrush steppe	Grazed	31.6[b]	--	33.8	11.9[c]	2.6	10.9	40.4	--
Aldridge and Brigham, 2002[a] (unsuccessful nests)	Alberta	Sagebrush steppe	Grazed	24.4[b]	--	48.9	7.6[c]	3.4	9.5	29.5	--
Apa, 1998 (nests)	Idaho	Sagebrush steppe, tame grassland	Multiple	69[d]	--	15	--	--	19	--	--
Autenrieth, 1981 (nests)	Idaho	Sagebrush	--	58.2–79.3[d]	--	--	--	--	23.4–38.1	--	--
Bunnell and others, 2004 (nests)	Utah	Sagebrush steppe	--	50.7[d]	--	21.1	11.04	36.3	24.8	--	--
Bunnell and others, 2004 (broods)	Utah	Sagebrush steppe	--	37.1[d]	--	19.9	16.01	33.4	22.9	--	--
Connelly and others, 1991 (nests)	Idaho	Sagebrush	Multiple	19[b]	--	7	--	--	--	--	--
Connelly and others, 1991 (nests)	Idaho	Non-sagebrush	Multiple	23[b]	--	9	--	--	--	--	--
Crawford and Davis, 2002 (successful nests)	Nevada	Sagebrush steppe	Burned	--	--	19.2[e]	13.6	57.9	--	--	--
Crawford and Davis, 2002 (unsuccessful nests)	Nevada	Sagebrush steppe	Burned	--	--	16.8[e]	12.4	53.4	--	--	--
Ellis and others, 1989 (leks)	Utah	Sagebrush	--	53[d]	--	--	--	31	--	--	--
Fischer, 1994 (nests)	Idaho	Sagebrush steppe	Burned	61[d]	--	30	--	--	--	--	--
Foster, 2016 (nest patch)	Oregon	Sagebrush steppe	Intact habitat	34.8[b]	16[f]	28.1	9.5	28.4	--	41.7	3.3
Foster, 2016 (nest patch)	Oregon	Sagebrush steppe	Burnt habitat	66.3[b]	14[f]	30.8	18.4	4.0	--	28.4	0

Table B1. Measured values of vegetation structure and composition in Greater Sage-Grouse (*Centrocercus urophasianus*) breeding habitat by study. The parenthetical descriptors following authorship and year in the "Study" column indicate that the vegetation measurements were taken in locations or under conditions specified in the descriptor; no descriptor implies that measurements were taken within the general study area.—Continued

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Study	State or province	Habitat	Management practice or treatment	Vegetation height (cm)	Vegetation height-density (cm)	Grass cover (%)	Forb cover (%)	Shrub cover (%)	Sagebrush cover (%)	Bare ground cover (%)	Litter cover (%)
Foster, 2016 (nest vicinity)	Oregon	Sagebrush steppe	Intact habitat	--	25[f]	29.8	10.7	39.8	--	31.6	3.6
Foster, 2016 (nest vicinity)	Oregon	Sagebrush steppe	Burnt habitat	--	20[f]	44.5	20.0	7.3	--	14.6	0
Gill, 1965 (nests)	Colorado	Sagebrush	--	43	--	--	--	--	--	--	--
Gregg, 1991 (nests)	Oregon	Sagebrush steppe	--	14[b]	--	9–32	--	--	24	--	--
Gregg and others, 1994 (non-depredated nests)	Oregon	Sagebrush steppe	--	--	--	18[e]	8	--	--	--	--
Gregg and others, 1994 (depredated nests)	Oregon	Sagebrush steppe	--	--	--	5[e]	9	--	--	--	--
Hansen and others, 2016 (nest area)	Wyoming	Multiple	Grazed	13.0[b], 30[d]	9.8[f]	22	9.7	32	26.5	--	--
Hansen and others, 2016 (nest patch)	Wyoming	Multiple	Grazed	13.4[b], 32[d]	10.5[f]	22	9.1	36	30	--	--
Hansen and others, 2016 (nest bowl)	Wyoming	Multiple	Grazed	14.5[b], 45[d]	15.9[f]	18	5.8	69	63	--	--
Hausleitner and others, 2005[g] (nest initiation)	Colorado	Multiple	Multiple	51.9[d]	--	3.5	3.8	--	29.9	15.9	80.5
Hausleitner and others, 2005[g] (egg hatch)	Colorado	Multiple	Multiple	52.7[d]	--	5.5	5.1	--	29.9	14.0	82.1
Heath and others, 1997 (nests)	Wyoming	Sagebrush	--	29[d]	--	9	--	--	24	--	--
Herman-Brunson and others, 2009 (±SD)	North Dakota	Mixed-grass prairie, sagebrush steppe	Grazed	--	--	27.4±13.6	15.4±11.8	9.8±0.4	--	--	12.9±8.3
Hofmann, 1991 (nests)	Washington	Sagebrush steppe	Multiple	--	--	--	--	--	20	--	--
Holloran, 1999	Wyoming	Sagebrush steppe	Grazed	31[d]	--	5	--	--	25	--	--
Holloran and others, 2005 (successful nests)	Wyoming	Sagebrush steppe	--	32.2[d]	--	6	5.3	30.4	--	18.7	17.9

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Study	State or province	Habitat	Management practice or treatment	Vegetation height (cm)	Vegetation height-density (cm)	Grass cover (%)	Forb cover (%)	Shrub cover (%)	Sagebrush cover (%)	Bare ground cover (%)	Litter cover (%)
Holloran and others, 2005 (unsuccessful nests)	Wyoming	Sagebrush steppe	--	31.6[d]	--	6	4.7	30.3	--	22.3	17.6
Keister and Willis, 1986 (nests)	Oregon	Multiple	--	80[d]	--	--	--	--	20	--	--
Klebenow, 1969[g] (nests)	Idaho	Sagebrush steppe	Grazed	43	--	--	--	18.4	--	22.6	61.2
Klebenow, 1982	Idaho	Sagebrush steppe	Grazed	60–110[d]	70–160[f]	38–51	12–16	21–22	--	--	--
Klott and others, 1993 (nests)	Idaho	Multiple	Grazed	15–30[b]	--	--	--	--	15–32	--	--
Kolada and others, 2009b (±SE)	California	Sagebrush steppe	--	--	--	--	6.6±0.7	43.9±1.1	28.8±1.2	--	--
Lyon, 2000 (nests)	Wyoming	Sagebrush steppe	--	32.7[d]	--	10.6	8.2	--	26	--	--
Moynahan and others, 2007 (lek complexes)	Montana	Mixed-grass prairie, sagebrush steppe	--	--	4.6–7.24[f]	22.0–22.47	3.34–6.32	8.75–11.68	--	--	--
Musil and others, 1994 (nests)	Idaho	Sagebrush steppe	--	51[d]	--	--	--	--	--	--	--
Patterson, 1952	Wyoming	Sagebrush steppe	Multiple	36[d]	--	--	--	--	--	--	--
Petersen, 1980 (leks)	Colorado	Multiple	--	5.3[d]	--	10.3	--	--	7.3	--	--
Petersen, 1980 (nests)	Colorado	Multiple	--	52.3[d]	--	--	--	--	23.6	--	--
Popham and Gutiérrez, 2003 (successful nests)	California	Sagebrush steppe	Grazed	22.1[b], 65.5[d]	40.2[f]	14[h]	--	6	13	51	8
Popham and Gutiérrez, 2003 (unsuccessful nests)	California	Sagebrush steppe	Grazed	24.2[b], 49.2[d]	32.5[f]	11[h]	--	5	16	40	11
Rothenmaier, 1979 (leks)	Wyoming	Multiple	Grazed	--	28[f]	--	--	--	22	--	--
Rothenmaier, 1979 (nests)	Wyoming	Multiple	Grazed	--	--	--	--	--	21.6	--	--

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Study	State or province	Habitat	Management practice or treatment	Vegetation height (cm)	Vegetation height-density (cm)	Grass cover (%)	Forb cover (%)	Shrub cover (%)	Sagebrush cover (%)	Bare ground cover (%)	Litter cover (%)
Schroeder, 1995 (nests)	Washington	Sagebrush steppe	--	--	--	51	--	--	20	--	--
Sveum and others, 1998 (nests)	Washington	Sagebrush steppe	--	61[d]	--	32	--	55	19	--	--
Wakkinen, 1990	Idaho	Sagebrush steppe	--	45.4[d]	18.2[f]	6.5	--	--	21.5	--	--
Wakkinen, 1990 (nests)	Idaho	Sagebrush steppe	--	70.6[d]	--	3–10	--	--	22	--	--
Wallestad, 1975 (nests)	Montana	Multiple	Multiple	40[d]	--	--	--	--	27	--	--
Wallestad and Pyrah, 1974 (nests)	Montana	Multiple	Multiple	--	40.4[f]	--	--	--	>15	--	--

[a]Values are averages from 7.5 and 15 m away from the nest.

[b]Grass height.

[c]Palatable forbs only.

[d]Shrub height.

[e]Values represent cover of tall (greater than or equal to 18 cm) grasses at nest sites.

[f]Visual obstruction reading (Robel and others, 1970b).

[g]The sum of the percentages is >100%, based on methods described by the authors.

[h]Perennial grass cover.

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