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Declining populations of greater sage-grouse: where and why

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Abstract: Scientists have been predicting the extinction of greater sage-grouse (*Centrocercus urophasianus*) since 1916, and sage-grouse populations have declined relentlessly during the last century despite attempts to reverse the decline. In this review paper, we examined the scientific literature to evaluate hypotheses about why sage-grouse populations have declined. There is little support for the hypotheses that the decline is due to overhunting, parasites, food shortages, or collisions with power lines or fences. West Nile Virus (WNV) reduced sage-grouse up to 25% when the virus first reached the West during 2002, but sage-grouse have developed resistance to the virus since then, rendering the virus less virulent. Golden eagles (*Aquila chrysaetos*), great horned owls (*Bufo virginianus*), and coyotes (*Canis latrans*) kill many adult sage-grouse, but populations of these predators have not increased during the last century, so predation by these predators probably have not contributed to the decline. In contrast, common ravens (*Corvus corax*) have become more numerous in the West, and nesting success of sage-grouse is higher in areas where raven numbers are low or have decreased. Sage-grouse broods often forage in wet meadows that are interspersed among the sagebrush (*Artemisia* spp.), but many of these wet areas have converted into pastures and alfalfa fields. Local populations of sage-grouse have collapsed when sagebrush habitat is eliminated due to fire, development, or conversion to pasture or farmland. Areas where sage-grouse have been extirpated are along the periphery of the sage-grouse's range, have more people, have less sagebrush, and have lost much of the sagebrush that once existed there. Hence, the decline of sage-grouse populations can be attributed, at least in part, to the loss of large stands of sagebrush, but just why large stands are important is unclear.

Key words: common ravens, diseases, extinction, habitat fragmentation, habitat loss, hunting, parasites, predators, sagebrush, sage-grouse

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are a sagebrush (*Artemisia* spp.) obligate species and do not occur in areas devoid of sagebrush. Many people consider sage-grouse to be a keystone species of the sagebrush-steppe ecosystem and believe that the health of this ecosystem can be determined by changes in sage-grouse populations. Sage-grouse currently occupy a little more than half of the range they had prior to American settlement (hereafter referred to as before settlement) of the West (Schroeder et al. 1999, 2004; Connelly et al. 2011). This decline in sage-grouse populations has been occurring without interruption since the 1800s (Conover and Roberts 2017). In fact, the first scientific paper predicting the extinction of the species was published a century ago (Hornaday 1916, Conover and Roberts 2017). Since then, numerous hypotheses have been proposed to explain the declining numbers of sage-grouse including overhunting, diseases, parasites, habitat loss, food shortages, and predation (Braun 1998, Connelly et al. 2004, Schroeder et al. 2004, Connelly et al. 2011). In this paper, we examine factors that might have contributed to the century-long decline in sage-grouse numbers and determine where populations of sage-grouse have declined.

Hunting

Compared to most gamebirds, sage-grouse have low reproductive rates, high survival rates for adults outside of the breeding season, and long life spans (Table 1). While some sage-grouse are shot each year during the fall hunting season, U.S. states and Canadian provinces adjust the timing and length of the hunting season so that hunting will not have an adverse impact on local sage-grouse populations. In most states and provinces, <15% of sage-grouse are killed annually by hunters (Reese and Connelly 2011). Hunting mortality is normally compensatory (i.e., hunting merely replaces another type of mortality) and is believed not to impact the sage-grouse populations in the subsequent spring. Johnson and Braun (1999) tested this with sage-grouse in Colorado and reported that some hunting mortality may be additive to winter mortality. More recently, Sedinger et al. (2010) found no support for an additive effect of hunter harvest in either Colorado or Nevada.

Two experimental studies have assessed the impact of hunting mortality on sage-grouse populations: one in Nevada (Zunino 1987) and one in Idaho (Connelly et al. 2000*a*). Both reported that population growth was slower in hunted areas than in areas with no or little hunting. Other studies have looked at correlations between counts of adult sage-grouse on leks (hereafter called lek counts) and various levels of hunting pressure; these studies reached the conclusion that hunting does not impact most sage-grouse populations (Reese and Connelly 2011). One benefit of allowing the hunting of sage-grouse is that this activity creates a group of stakeholders in each state who are interested in maintaining healthy populations of sage-grouse (Conover 2002).

Predators

Golden eagles (*Aquila chrysaetos*), great horned owls (*Bufo virginianus*), red foxes (*Vulpes vulpes*), and coyotes (*Canis latrans*) kill many adult sage-grouse. The Bald and Golden Eagle Protection Act of 1940 provides special protection for eagles. No studies have examined whether removing eagles will increase sage-grouse numbers, and it is unlikely that state or federal permission can be obtained to kill or relocate eagles depredating sage-grouse (Conover and Roberts 2017). The impact of great horned owls on sage-grouse numbers have not been studied; it is also unknown if removing owls will increase sage-grouse numbers. Efforts to remove red foxes or coyotes have failed to reduce mortality rates of adult sage-grouse; these same efforts have produced inconsistent results on decreasing nest depredation (Baxter et al. 2007, 2013; Orning 2013; Dinkins et al. 2016). More success in reducing depredation of sage-grouse nests has been obtained by removing common ravens (*Corvus corax*; Coates et al. 2007; Coates and Delehanty 2010; Dinkins et al. 2016; also see Bradley et al. 2013). It is unclear if an increase in the reproduction rate will result in more adult sage-grouse (Conover and Roberts 2017).

Parasites and diseases

Sage-grouse serve as host to many parasites, but these parasites rarely kill sage-grouse or produce noticeable changes in the reproductive success of infected birds (Connelly et al. 2004, Christiansen and Tate 2011). Occasionally, a sage-grouse has so many ticks that the infestation impairs the bird's health (Parker et al. 1932, Boyce 1990, Gibson 1990). Internal parasites, such as tapeworms (e.g., *Raillietina centocerci*) and micro-parasites (e.g., *Leukocytozoon lovati*) are found in some sage-grouse, but infected birds are usually in good physical condition and have normal reproductive success (Parker et al. 1932, Thorne 1969, Honess 1982, Gibson 1990).

Few diseases, except West Nile Virus (WNV), are serious enough to impact sage-grouse populations (Christiansen and Tate 2011). WNV is an African virus that reached North America during 1999 when the virus was first detected in New York City (Conover and Vail 2015). Four years later, the virus had swept across the North American continent (Figure 1). The virus can infect humans and caused 1,400 human deaths in the United States by 2013. Birds, especially passerines, are the reservoir host for WNV, which is usually transmitted by mosquitoes that had previously fed on infected birds. For this reason, mosquito control is often implemented once a WNV outbreak poses a threat to humans.

In sagebrush-steppe ecosystem, the primary vector of WNV is the mosquito *Culex tarsalis* (Walker and Naugle 2011). This mosquito lays its eggs in warm, standing water, including puddles and water-filled hoof prints left in wet areas; the warm water allows the larva to mature quickly. Adult mosquitos feed on many avian and mammalian species. Sage-grouse are a reservoir host for WNV, and the virus can spread rapidly within a sage-grouse flock. WNV has killed large numbers of sage-grouse, especially in newly infected areas. When WNV first invaded the West during 2002, it reduced survival rates of sage-grouse by 25% in some areas (Naugle et al. 2004, Moynahan et al. 2006). Disease outbreaks continue to occur

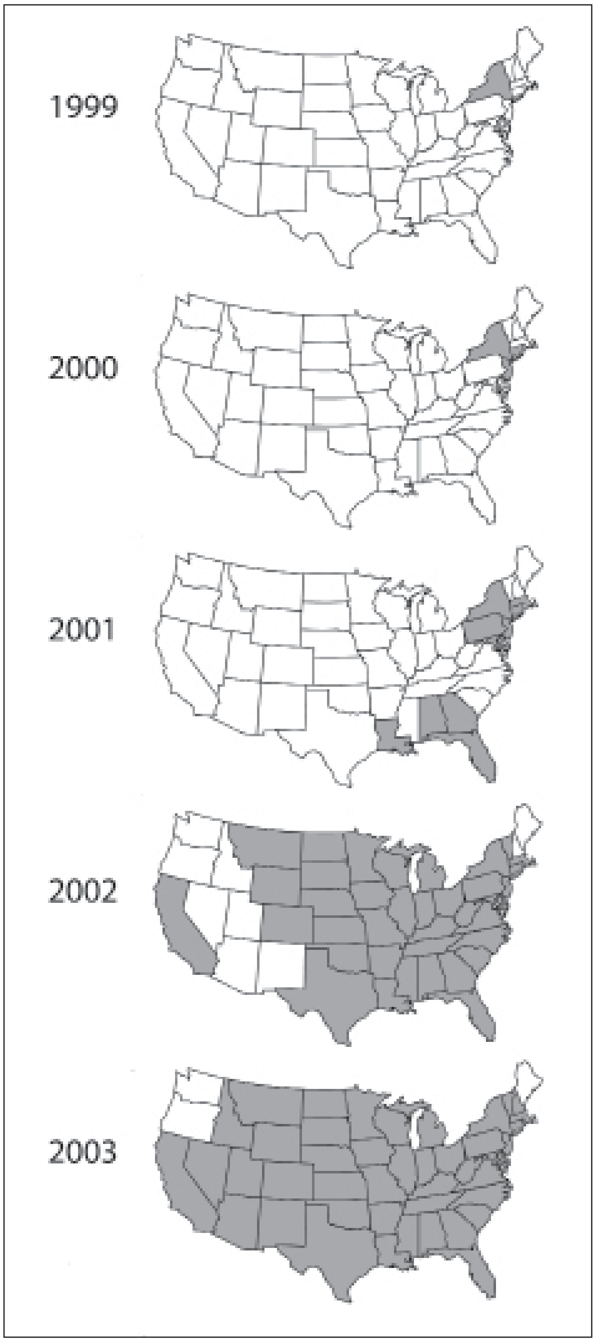

Figure 1. Maps showing the spread of human cases of West Nile Fever and West Nile Virus across the United States (dark areas). From CDC West Nile Virus annuals maps and data.

in sage-grouse populations, but resistance to the virus has increased in sage-grouse over time, reducing the impact of the virus on sage-grouse; nevertheless, it still causes fatalities in sage-grouse (Conover and Vail 2015).

Loss of sagebrush habitat

Availability of sagebrush for winter habitat is often cited as a primary limiting factor for the decline in sage-grouse populations (Patterson 1952, Eng and Schladweiler 1972, Beck 1977, Heath et al. 1997, Moynahan et al. 2006). In Wyoming, more sagebrush on a landscape scale (4 km^2) resulted in greater use of the area by sage-grouse during winter (Doherty et al. 2008). Removal of sagebrush on the winter range is detrimental to sage-grouse populations (Higby 1969, Pyrah 1972).

Winter habitat for sage-grouse is particularly important when sagebrush is buried by deep snow (Beck 1977). During such times, sage-grouse may move to wind-swept ridges or areas with taller sagebrush. When deep snow buried most of the sagebrush on Deseret Ranch in Utah, sage-grouse became concentrated in the few patches where sagebrush still extended above the snow (Danvir 2002). These areas also drew the attention of golden eagles, resulting in a higher number of sage-grouse mortalities. Danvir (2002) noted that sagebrush plants tall enough to protrude above the snow were often limited to draws. Sage-grouse using these draws were especially vulnerable to golden eagle attacks because sage-grouse could not see approaching eagles until the eagles crested the draw's brow.

The importance of sagebrush to sage-grouse has been documented by noting the reduction in sage-grouse numbers following large wildfires (Fischer et al. 1996, Connelly et al. 2000*b*, Nelle et al. 2000). Wildfire is a natural disturbance within sagebrush ecosystems, and the fire interval before settlement was 17–100 years (Wright and Bailey 1982). After settlement, the frequency and intensity of fires in sagebrush ecosystems changed. Initially, fire frequency decreased because of overgrazing by livestock during the late 1800s and early 1900s (Miller and Rose 1999). More recently, wildfire frequency has increased above historic levels due to the invasion of sagebrush areas by cheatgrass (*Bromus tectorum*), a fire-adapted annual plant. Once these plants die during summer, they become fire prone (Baker 2006). While fires that eliminate sagebrush over large areas are detrimental to sage-grouse (Connelly et al. 2000*b*, Byrne 2002, Blomberg et al. 2012), managed fires, which create a mosaic of small burned patches surrounded by large areas of sagebrush, can be beneficial for sage-grouse. Such a phenomenon occurs because small burned areas create better habitats and

Table 1. Estimates of survival rates (S) of greater sage-grouse during the non-breeding season. Principal cause of mortality is reported for the first row of a study only, and is listed again if different than already stated. Only studies reporting a survival estimate for hens or all sex classes were used in this review (WNV = West Nile virus).

Reference	Sex	Age class	Year(s)	Month(s)	State	N	S	SE	Principal cause of mortality
Fall Only									
Blomberg et al. 2013	Both	All	2008–2012	Aug–Oct	NV	173	0.79	0.03	Mammal predators
Hausleitner 2003	Hens	Adults	2001–2002	Sep–Nov	CO	35	0.89	0.06	Mammal predation
Hausleitner 2003	Hens	Juveniles	2001–2002	Sep–Nov	CO	27	0.95	0.04	
Hausleitner 2003	Hens	Adults	2002–2003	Sep–Nov	CO	59	0.90	0.05	
Hausleitner 2003	Hens	Juveniles	2002–2003	Sep–Nov	CO	18	0.87	0.09	
Heath et al. 1997	Both	N/A	1995–1996	Sep–Nov	WY, ID	?	0.80		Bobcats, mammals
Wik 2002	Hens	Adults	1999–2000	Sep–Nov	ID, NV	15	0.74		Hunters, predators
Wik 2002	Hens	Adults	2000–2001	Sep–Nov	ID, NV	35	0.83		
Wik 2002	Hens	Adults	2001	Sep–Nov	ID, NV	33	0.86		
Wik 2002	Hens	Subadults	1999–2000	Sep–Nov	ID, NV	6	0.40		
Wik 2002	Hens	Subadults	2000–2001	Sep–Nov	ID, NV	8	0.69		
Wik 2002	Hens	Subadults	2001	Sep–Nov	ID, NV	9	0.67		
Moynahan et al. 2006	Hens	N/A	2002	Sep–Oct	MT	83	0.92	0.03	Not stated
Moynahan et al. 2006	Hens	N/A	2003	Sep–Oct	MT	64	0.89	0.04	WNV, harsh winters
Fall and Winter									
Wik 2002	Hens	Adults	1999–2000	Dec–Feb	ID, NV	10	1.00		Hunters, predators
Wik 2002	Hens	Adults	2000–2001	Dec–Feb	ID, NV	28	0.88		
Wik 2002	Hens	Subadults	1999–2000	Dec–Feb	ID, NV	3	0.87		
Wik 2002	Hens	Subadults	2000–2001	Dec–Feb	ID, NV	4	1.00		
Moynahan et al. 2006	Hens	N/A	2002	Nov–Apr	MT	69	0.99	0.01	Not stated
Moynahan et al. 2006	Hens	N/A	2003	Nov–Apr	MT	64	0.91	0.02	WNV, harsh winters
Hausleitner 2003	Hens	Adults	2001–2002	Nov–Mar	CO	35	0.96	0.04	Mammal predators

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Hausleitner 2003	Hens	Juveniles	2001–2002	Nov–Mar	CO	27	0.90	0.06	
Hausleitner 2003	Hens	Adults	2002–2003	Nov–Mar	CO	59	0.82	0.07	
Hausleitner 2003	Hens	Juveniles	2002–2003	Nov–Mar	CO	18	1.00	0.0	
Anthony and Willis 2008	Both	All	1990–1991	Oct–Feb	OR	131	0.46	0.06	Harsh winters
Anthony and Willis 2008	Both	All	1991–1992	Oct–Feb	OR	131	0.45	0.07	
Walker 2008[a]	Hens	Adults	2003	Sep–Apr	WY	23	0.85–1.0		Predators
Walker 2008[a]	Hens	Adults	2004	Sep–Apr	WY	46	0.9–1.0		
Walker 2008[a]	Hens	Adults	2005	Sep–Apr	WY	63	0.6–0.8		
Walker 2008[a]	Hens	Adults	2006	Sep–Apr	WY	40	0.85–0.9		
Baxter et al. 2013[b]	Both	All	1998–2011	Sep–Mar	UT	53	0.96		Not stated
Beck et al. 2006	Both	Juveniles	1997–1999	Sep–Mar	ID	14	0.64	0.13	Predators
Beck et al. 2006[c]	Both	Juveniles	1997–1999	Sep–Mar	ID	42	0.86	0.06	

[a] Exact estimates not reported
[b] Translocated individuals included
[c] Different study site with lower elevation and increased disturbance from previously listed

increased food for sage-grouse broods (Klebenow 1970, Sime 1991, Pyle and Crawford 1996, Thacker 2010). This increase in food production, however, does not always result in larger sage-grouse populations (Harniss and Murray 1973, Pyle and Crawford 1996).

Roads, power lines, homes, petroleum wells, and other forms of human development result in the replacement of sagebrush with grass and forbs (Biondini et al. 1985, Hansen et al. 2016). Summer and fall foods may be more abundant in sagebrush-edge habitat that is adjacent to roads or oil developments than in a continuous sagebrush landscape. Yet, sage-grouse avoided sagebrush edges for nesting in Alberta (Aldridge and Boyce 2007). A likely explanation is that such areas are dangerous for sage-grouse because both people and predators are more likely to occur along habitat edges than in the middle of a large stand of sagebrush. Large undisturbed areas of sagebrush are becoming less common as more roads, power lines, and petroleum pipelines are built in the West.

While sagebrush habitat is arid, it is interspersed with small swales and wet meadows where forbs remain green during the dry summer and fall. Historically, large numbers of sage-grouse hens and their broods used these areas in mid- to late summer to feed on the abundant forbs and insects (Connelly et al. 2011). Many wet meadows have been converted into pastures or alfalfa fields. These areas, and even irrigated lawns, are used by sage-grouse broods during the summer and fall, but it is unlikely that sage-grouse forage in these areas as much as they did in the wet meadows that preceded them (Gates 1983, Connelly et al. 1988). Lack of suitable brood-rearing habitat may be a limiting factor for some sage-grouse populations (Aldridge 2000, Robinson 2007, Smith 2009).

There is an interaction between avian predators and sage-grouse habitat. When seeking sites for their nests and broods, sage-grouse avoid areas where they see avian predators (Dinkins et al. 2012, 2014, 2016; Mabray and Conover 2015). Consequently, sage-grouse may avoid areas that otherwise

Table 2. Summary of seasonal diets of greater sage-grouse (N = number of birds sampled, % of sagebrush in the diet = % diet).

Reference	Year(s)	Month(s)	Site	*N*	Primary food	% diet	Notes
Barnett and Crawford 1994	1990–1991	Mar–Apr	OR	42	Sagebrush	62[a]	
Gregg et al. 2008	2002–2003	Mar–Apr	OR	75	Sagebrush	69[a]	
Patterson 1952	1948–1950	Nov–Mar	WY	N/A	Sagebrush	100[b]	
Remington and Braun 1985	1980–1982	Jan–Apr	CO	40	Sagebrush	90[c]	Diet noted from feeding locations
Wallestad and Eng 1975	1953–1973	Oct–Nov	MT	34	Sagebrush	88[a]	
Welch et al. 1988	1984	Feb	UT	5	Sagebrush	N/A	Diet noted from feeding locations

[a] Relative dry weight
[b] Percent volume
[c] Percent browsed plants

would be optimal habitat. This results in sage-grouse nests and broods becoming clustered together, making them easier for predators to locate (Conover 2007).

Reduction in foods for chicks

Sage-grouse populations are sensitive to changes in juvenile survival, which in turn is impacted by predator densities and food availability. Forbs and arthropods are the primary food items of sage-grouse chicks that are <10 weeks old (Drut et al. 1994). In an experimental feeding study, sage-grouse chicks <3 weeks old were unable to survive without insects in their diet; older chicks survived but grew slower without them (Johnson and Boyce 1990).

Sage-grouse chicks typically forage in the small open areas between sagebrush plants rather than in large meadows (Connelly et al. 2011), perhaps because small openings offer better protection from predators. In these openings, availability of forbs, such as common yarrow (*Achillea millefolium*), common dandelion (*Taraxacum officinale*), slender phlox (*Phlox gracilis*), common salsify (*Trapogon dubius*), and lupine (*Lupinus* spp.) are important for sage-grouse broods (Klebenow 1969, Gregg and Crawford 2009).

Reduction of food for adults

During winter, sage-grouse diets consist primarily of sagebrush leaves (Table 2; Patterson 1952, Wallestad and Eng 1975). Sage-grouse consume leaves from a variety of sagebrush species including Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), alkali sagebrush (*A. longiloba*), and black sagebrush (*A. nova*; Wallestad and Eng 1975, Remington and Braun 1985, Welch et al. 1988). Some investigators have reported that sage-grouse prefer Wyoming big sagebrush (Table 2), while others noted preferences for mountain big sagebrush (*A. tridentata vaseyana*; Hupp 1987, Welch et al. 1988) and black sagebrush (Thacker 2010, Wing 2014).

Wintering habitat for sage-grouse consists of dense stands of sagebrush (Eng and Schladweiler 1972, Beck 1977, Moynahan et al. 2006, Doherty et al. 2008). Because of the plethora of sagebrush leaves in these areas, starvation should not be a problem for adult sage-grouse unless only a small proportion of sagebrush leaves are nutritious or nontoxic (e.g., have low levels of monoterpenes; Table 3). Wing (2014) and Wing and Messmer (2016) tested this by chemically analyzing leaves from sagebrush plants where they had just observed a sage-grouse eating leaves, leaves from unbrowsed plants, and leaves from randomly selected sagebrush plants. They found that there were no differences in nutrients or toxic monoterpenes among leaves from browsed, unbrowsed, and randomly selected sagebrush. These results indicate that a high proportion of sage-grouse leaves are palatable to sage-grouse

Table 3. Protein and calcium (Ca) and phosphorus (P) content (% dry matter) of sagebrush species and subspecies fed on by greater sage-grouse.

Reference	Year	Month(s)	Location	Food item	Protein	Ca	P
Welch et al. 1988[a]	1984	Feb	UT	Basin big sagebrush	15		0.22
Barnett and Crawford 1994	1990–1991	Mar–Apr	OR	Big sagebrush	16	0.7	0.25
Patterson 1952	1950	?	WY	Black sagebrush	10		
Barnett and Crawford 1994	1990–1991	Mar–Apr	OR	Low sagebrush	14	0.4	0.21
Gregg et al. 2008	2002	Mar–Apr	OR	Low sagebrush	16	0.5	0.29
Gregg et al. 2008	2003	Mar–Apr	OR	Low sagebrush	12	0.4	0.23
Myers 1992[b]	1987–1990	Apr–May	CO	Mountain big sagebrush	10		
Remington and Braun1985[c]	1981–1982	Jan–Apr	CO	Mountain big sagebrush	11		
Welch et al. 1988[a]	1984	Feb	UT	Mountain big sagebrush	9		0.18
Myers 1992[b]	1987–1990	Apr–May	CO	Wyoming big sagebrush	12		
Remington and Braun 1985[c]	1981–1982	Jan–Apr	CO	Wyoming big sagebrush	14		
Welch et al. 1988[a]	1984	Feb	UT	Wyoming big sagebrush	12		0.2

[a] Average of reported values
[b] Unfertilized values, fertilization increased protein content by 30–52%
[c] Exact values not provided

and that starvation should not be a problem for adult sage-grouse.

Oil and gas development

Oil and gas development, including the construction of well pads and roads, can make sagebrush habitat unsuitable for sage-grouse. In Alberta, sage-grouse abandoned leks that were near energy development sites (Aldridge 1998). In Wyoming, female sage-grouse captured on leks disturbed by petroleum development initiated fewer nests and had lower nest-initiation rates than hens captured on undisturbed leks (Lyon 2000, Holloran et al. 2010). Annual survival rates for male and female sage-grouse living near energy developments were lower than for sage-grouse living farther away. Fortunately, the adverse impacts of petroleum development on sage-grouse may be ephemeral. In Colorado, sage-grouse were initially displaced by oil development and coal-mining activities, but sage-grouse numbers returned to pre-disturbance levels once the activities ceased (Braun 1987, Remington and Braun 1991). There also is an interaction effect between WNV and petroleum development because WNV infection rates among sage-grouse are higher in areas where petroleum activity created ponds that support mosquito larva (Walker 2008).

Livestock grazing

The sagebrush-steppe ecosystem evolved while being grazed by several large mammalian species including pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), and bison (*Bison bison*). Following settlement, bison herds were replaced by herds of cattle and bands of sheep. Researchers are still debating how this change in herbivore species has impacted the sagebrush-steppe ecosystem, but there is scant evidence that it caused the decline of sage-grouse populations.

Grazing by domestic livestock can either improve or degrade sagebrush habitat, depending upon grazing intensity and season of use (Braun 1987, Connelly and Braun 1997, Beck and Mitchell 2000, Crawford et al. 2004). Sage-grouse prefer to nest in areas where there is grass cover, and sage-grouse nest sites are more successful in such areas (Wakkinen 1990, Gregg 1991, Gregg et al. 1994, Delong et al. 1995, Sveum et al. 1998). Grazing by livestock or wild herbivores can be so intense that it reduces the understory of grass and forbs beneath sagebrush and exposes sage-grouse nests to predators (Braun 1987, Dobkin 1995). But grazing can also improve foraging habitat of sage-grouse chicks because chick survival is higher in areas where short grass is dominant. Furthermore, sage-grouse broods avoid areas with dense, tall grass (Gregg and Crawford 2009). This avoidance may result because tall grass limits the ability of hens to detect approaching predators in time to warn their chicks to hide. In Utah, Guttery (2011) found that forbs and grasses were more abundant after intense grazing and that sage-grouse broods spent more time foraging in plots that have been intensely grazed than in ungrazed plots.

Fences and power lines

Every year, some sage-grouse are killed when they fly into fences and power lines. Stevens et al. (2012) surveyed 130 km of fence lines in Idaho during the spring of 2009 and 2010 and detected evidence of 86 sage-grouse collisions. Elsewhere in Idaho, 2 of 56 juvenile sage-grouse that were radio-tagged died after flying into a power line (Beck et al. 2006). However, collisions with fences and power lines are not a common source of mortality among sage-grouse. The number of radio-tagged sage-grouse killed by flying into a fence or power line was 0 of 50 sage-grouse in Utah (J. Reinhart, personal communication), 0 of 123 in Utah (Wing 2014), 0 of 69 in Wyoming (Orning 2013), 2 of 427 in Wyoming (J. Dinkins and C. Kirol, personal communication), and 1 of 117 in Idaho (Connolly et al. 2000*a*). If these data from radio-tagged birds are averaged together, 0.6% of sage-grouse are killed annually by flying into fences and power lines. Hence, it is unlikely that collisions with fences or power lines are responsible for the decrease in grouse populations, but habitat fragmentation caused by power lines may have an adverse impact on sage-grouse (Hansen et al. 2016).

Where have sage-grouse populations declined?

Sage-grouse populations in North America have declined throughout the last century. Currently, sage-grouse inhabit <60% of their range prior to settlement (Schroeder et al. 2004, Connelly et al. 2011). Several authors have tried to understand what accounts for this range contraction. Aldridge et al. (2008) used records from historical publications and museum specimens to locate 40,000 sites where sage-grouse were known to occur in the past. The authors divided the sites into 2 groups: sites where sage-grouse still occupied (hereafter, occupied sites) and sites where they had been extirpated (extirpated sites). The authors discovered that extirpated sites were more likely than occupied sites to be close to the edge of the former range of sage-grouse, and where sagebrush habitat had declined, human population had increased and more land had been converted to farmland.

Wisdom et al. (2011) examined 22 variables in occupied sites and extirpated sites. Occupied sites differed from extirpated sites in that the former contained almost twice as much sagebrush cover, were higher in elevation, farther from transmission lines or radio transmission towers, and had a higher proportion of land owned by government agencies. Of these 5 variables, sagebrush cover was the best predictor of sites where sage-grouse still occupied (Wisdom et al. 2011). In extirpated areas, the percent cover of sagebrush was less than 27% compared to >50% in occupied areas.

Hess and Beck (2012) examined the persistence of sage-grouse leks in the Bighorn Basin of Wyoming over a 30-year period. They found 144 active leks and 39 abandoned ones. Leks were more likely to be abandoned if the land around them had been burned by a wildfire, had sagebrush that were short in stature, or if petroleum wells were nearby (Hess and Beck 2012). In the Powder River Basin of Wyoming, Walker et al. (2007) reported that leks were less likely to be abandoned where a large proportion of the area within 6.4 km of a lek was in sagebrush (Walker et al. 2007).

Schroeder et al. (2000) describe differences between sites occupied by sage-grouse and extirpated sites with the historic sage-grouse range in Washington state. Their analysis indicated that occupied sites had a higher proportion of land in sagebrush-steppe, more land enrolled in the U.S. Department of Agriculture (USDA) Conservation Reserve Program, and less farmland. Aldridge et al. (2008) and Wisdom et al. (2011) analyzed the decline of sage-grouse across their historical and current range and consistently found that loss of sagebrush stands was correlated with declining populations of sage-grouse.

Management implications

Sage-grouse populations have declined due to a combination of diseases, predators, and loss of sagebrush habitat. West Nile Virus has killed large numbers of adult sage-grouse, especially in newly infected areas. When WNV first invaded the West during 2002, it reduced survival rates of sage-grouse by 25% in some areas. Historically, mortality rates on adults were offset by reproduction, but this is no longer true in some places because a high proportion of sage-grouse nests and broods are depredated by common ravens and badgers (*Taxidea taxus*; Conover and Roberts 2017). Nest success can be improved by reducing raven numbers (Conover and Roberts 2017). Where sagebrush was eliminated due to wildfire or development, sage-grouse have disappeared. This loss of sagebrush is exacerbated because sage-grouse avoid suitable sagebrush habitat when avian predators are abundant (Dinkins et al. 2012, 2014, 2016; Mabray and Conover 2015). More effort must be expended to protect large stands of sagebrush.

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