

The Effects of Management Practices on Grassland Birds— Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*)

Chapter C of

The Effects of Management Practices on Grassland Birds



Professional Paper 1842–C

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Chapter C of

The Effects of Management Practices on Grassland Birds

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Contents

| | |
|---|----|
| Acknowledgments | v |
| Capsule Statement..... | 1 |
| Breeding Range..... | 1 |
| Suitable Habitat..... | 3 |
| Lek Sites | 3 |
| Nesting Habitat..... | 5 |
| Brood-Rearing Habitat..... | 7 |
| Roosting Habitat..... | 10 |
| Foraging Habitat—Snow Season | 11 |
| Foraging Habitat—Snow-Free Season | 13 |
| Water Use | 13 |
| Climate | 13 |
| Area Requirements and Landscape Associations | 14 |
| Brood Parasitism by Cowbirds and Other Species | 17 |
| Breeding-Season Phenology and Site Fidelity | 18 |
| Species' Response to Management..... | 20 |
| Fire..... | 20 |
| Grazing..... | 20 |
| Fire and Grazing | 22 |
| Haying | 23 |
| Management Frequency | 23 |
| Planted Cover | 24 |
| Woody Vegetation..... | 24 |
| Habitat and Predator Relationships..... | 25 |
| Effects of Management on Invertebrate Resources | 27 |
| Energy Development and Infrastructure | 27 |
| Translocation | 28 |
| Management Recommendations from the Literature | 29 |
| References..... | 34 |

Figure

- C1. Map showing the current and postsettlement distribution of the Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) and the presettlement boundary of the tallgrass prairie in the United States and Canada2

Table

- C1. Measured values of vegetation structure and composition in Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) breeding habitat by study.....51

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 | |
| hectare (ha) | 2.471 | acre |
| square kilometer (km ²) | 247.1 | acre |
| square meter (m ²) | 10.76 | square foot (ft ²) |
| hectare (ha) | 0.003861 | square mile (mi ²) |
| square kilometer (km ²) | 0.3861 | square mile (mi ²) |
| | Mass | |
| kilogram (kg) | 2.205 | pound (lb) |

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

$$^{\circ}\text{F} = (1.8 \times ^{\circ}\text{C}) + 32$$

Abbreviations

| | |
|-------|---|
| AUM | animal unit month |
| CRP | Conservation Reserve Program |
| IESB | intensive early-season stocking with annual burning |
| mtDNA | mitochondrial deoxyribonucleic acid |
| n.d. | no date |
| SNG | Shenandoah National Grassland |
| spp. | species (applies to two or more species within the genus) |
| VOR | visual obstruction reading |

Acknowledgments

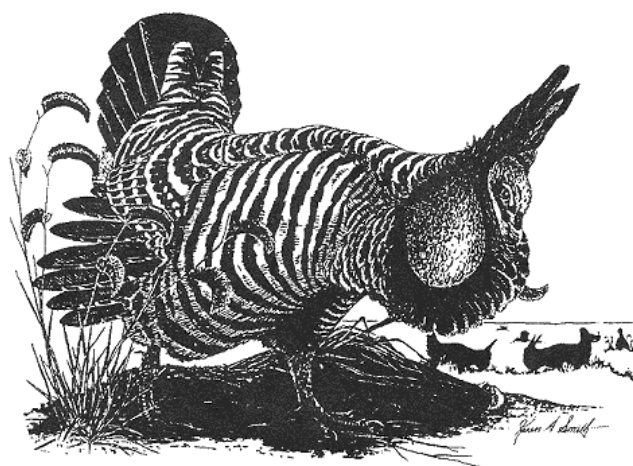
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Capsule Statement

The keys to Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) management are maintaining expansive grasslands; preventing populations of Greater Prairie-Chickens from becoming small and isolated; managing grasslands to maintain proper grassland height, density, and vigor; and reducing woody plant invasion and excessive litter buildup. Within these grasslands, areas should contain short herbaceous cover for lek sites; tall residual grasses for nesting; and disturbed habitats for broods with adequate vegetation regrowth that provides insects for food and cover from predators and weather. South Dakota, Nebraska, Kansas, Minnesota, and Colorado currently (2022) have hunting seasons for Greater Prairie-Chickens (Svedarsky and others, 2000; Johnson and others, 2020). This account does not address population or harvest management but rather focuses on habitat management. Greater Prairie-Chickens have been reported to use habitats with 5–113 centimeter (cm) average vegetation height, 5–40 cm visual obstruction reading (VOR), 18–95 percent grass cover, 1–35 percent forb cover, less than (<) 45 percent litter cover, <5 percent shrub cover, 3–25 percent bare ground, and <12 cm litter depth. The descriptions of key vegetation characteristics are provided in table C1 (after the “References” section). Vernacular and scientific names of plants and animals follow the Integrated Taxonomic Information System (<https://www.itis.gov>).



Greater Prairie-Chicken. Illustration by Karen A. Smith, used with permission.

Breeding Range

Historically, three subspecies of Greater Prairie-Chicken (*Tympanuchus cupido*) occurred in North America: Greater Prairie-Chicken (*T. c. pinnatus*), Attwater’s Prairie-Chicken (*T. c. attwateri*), and Heath Hen (*T. c. cupido*). This account primarily deals with *T. c. pinnatus* and not with the Attwater’s Prairie-Chicken, which breeds only in a localized area in Texas, or with the now extinct Heath Hen, which occurred on the East Coast. For information on the Attwater’s Prairie-Chicken, see Lehmann (1941) and Silvy and others (1999); for information on the Heath Hen, see Gross (1928).

The Greater Prairie-Chicken is a year-round resident that breeds in disjunct populations from eastern North Dakota and western Minnesota; south through central South Dakota, central and southeastern Nebraska, to northeastern Colorado, northern and eastern Kansas, southern Iowa, northern and west-central Missouri, and northeastern Oklahoma; and east to central Wisconsin and south-central Illinois (National Geographic Society, 2011). The subspecies has been extirpated from Alberta, Saskatchewan, Manitoba, Ontario, Michigan,

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2 The Effects of Management Practices on Grassland Birds—Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*)

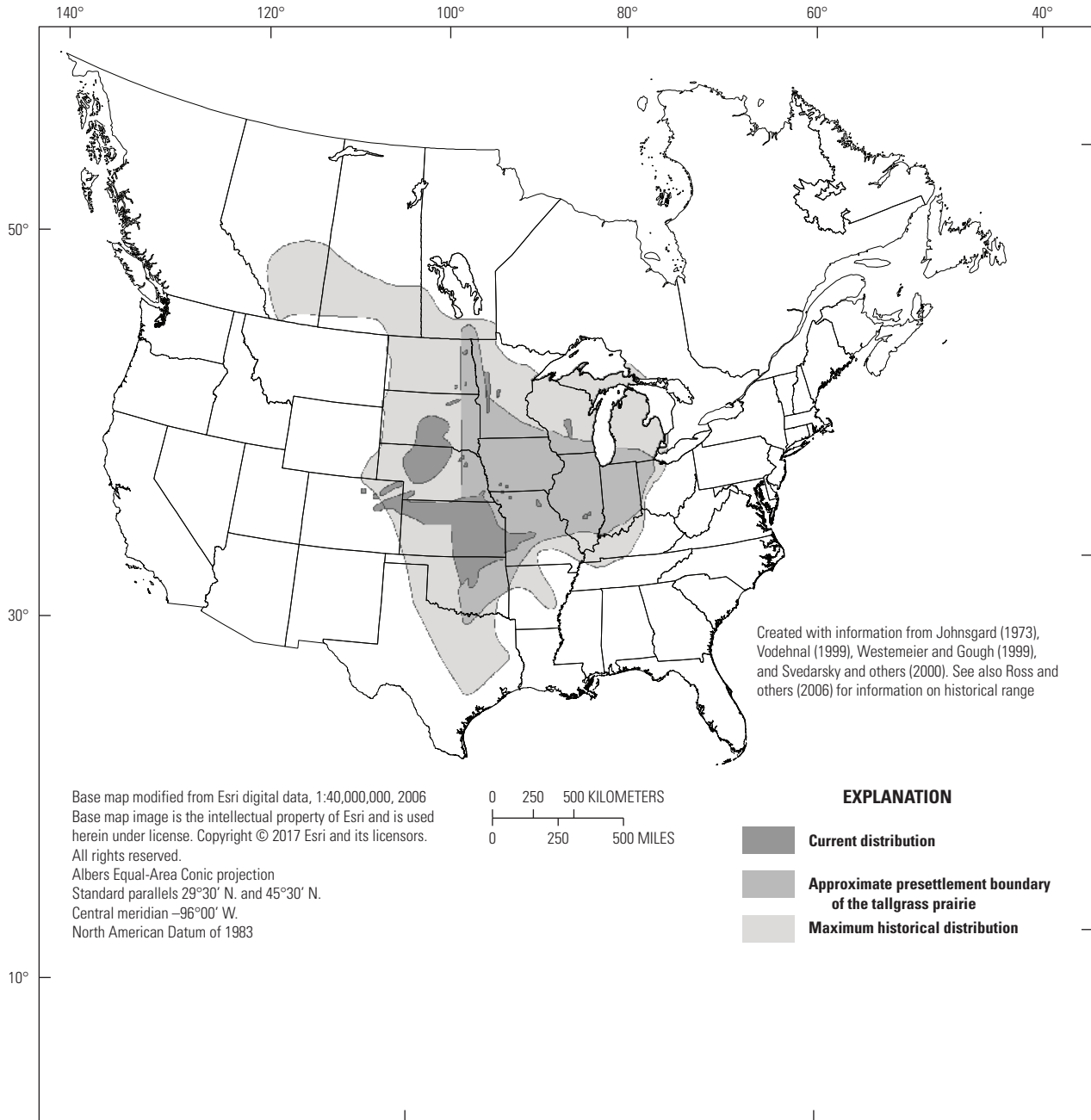


Figure C1. The current and postsettlement distributions of the Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) and the presettlement boundary of the tallgrass prairie in the United States and Canada (Johnsgard, 1973; Vodehnal, 1999; Westemeier and Gough, 1999; Svedarsky and others, 2000).

Indiana, Ohio, Arkansas, Tennessee, Kentucky, Texas, and Wyoming (Hamerstrom and Hamerstrom, 1961; Johnson and others, 2020). The current distribution of the Greater Prairie-Chicken, the approximate presettlement boundary of the tallgrass prairie, and the postsettlement distribution of the Greater Prairie-Chicken (Svedarsky and others, 2000) are shown in figure C1 (not all geographic places mentioned in this report are shown on figure). The species' current distribution is mainly in the tallgrass portion of the grassland biome but extends westward into the mixed-grass prairie, particularly

where land-use changes have supplemented food and cover. The species' distribution at the time of settlement extended into the north-central United States and Canada. Some early publications suggested that the presettlement range of the Greater Prairie-Chicken may have approximated the historical extent of the tallgrass prairie (Hamerstrom and Hamerstrom, 1963; Johnson and Knue, 1989; Westemeier and Gough, 1999; Svedarsky and others, 2000), based on anecdotal evidence from early naturalists (Coues, 1874; Cooke, 1888; Ross and others, 2006) and published and unpublished reports and

museum collections (Houston, 2002). The range expansion of the Greater Prairie-Chicken may have been a response to habitat alterations by European settlers; agricultural development and the presence of grain are thought to have provided favorable conditions for a rapid range expansion in the late 1800s through the early 1900s (Roberts, 1936; Houston, 2002; Ross and others, 2006). However, recent demographic analysis based on provenance data from 238 specimens from museum collections, in addition to genetic analyses of 100 mitochondrial deoxyribonucleic acid (mtDNA) sequences, suggested that the Greater Prairie-Chicken was native to the northern prairies, extending from central Minnesota to Alberta (Ross and others, 2006).

Suitable Habitat

The Greater Prairie-Chicken is a grassland bird. The species evolved in landscapes that consisted of large, open, tall-grass and mixed-grass prairies interspersed with oak (*Quercus* species [spp.]) woodlands, oak savannas, and wooded riparian areas (Johnson and others, 2020). To state that the species is a grassland bird, however, oversimplifies how the species uses its habitats to satisfy its seasonal life-history requirements. The Greater Prairie-Chicken inhabits large, open grasslands, but its habitat requirements may change between life-history stages because of differences in nutritional and energetic needs, behavioral patterns, and resource and cover availability. For example, the species also will use and may, in some cases, require habitats as diverse as shrublands, woodlands, wetlands and wet meadows, and agricultural lands (Svedarsky, 1979; Toepfer, 1988; Johnson and others, 2020). Five Wisconsin studies in the northern portion of the species' range highlight the diverse habitats that Greater Prairie-Chickens will use. Westemeier (1971) suggested that the optimal landscape composition for Greater Prairie-Chickens in Wisconsin had a minimum of 50 percent grassland and a maximum of 25 percent cropland and 25 percent wet meadow, brush, and woodland. Hardy and others (2020) reported that the species selected grassland habitats (for example, remnant prairies, pastures, hayland, and small grain fields) in Wisconsin over other cover types (for example, cranberry [*Vaccinium macrocarpon*] bogs, herbaceous wetlands, cultivated rowcrops, trees and shrubs) during all life-history stages. Gross (1930) considered the extensive grasslands and wet meadows in Wisconsin as requisite habitats to meet the overall needs of the Greater Prairie-Chicken, along with grain farms for areas to forage. Hamerstrom and others (1957) found that Greater Prairie-Chickens were most abundant where there was the greatest amount of perennial grassland cover, especially Kentucky bluegrass (*Poa pratensis*). Toepfer (1988) reported that vegetation within the range of 25–100 cm was a critical habitat component of grasslands and grass/forb habitats that were used by prairie-chickens in Wisconsin for nesting, brood rearing, and roosting.

In the Great Plains portion of the species' range, grasslands are important habitats for Greater Prairie-Chickens throughout the year. In Nebraska, for example, the species occurs primarily in the Sandhills, where tallgrass and mixed-grass prairies are intermixed in the landscape with corn (*Zea mays*) (Blus and Walker, 1966). Hiller and others (2019) reported that female Greater Prairie-Chickens in the Nebraska Sandhills used primarily upland prairie sites during the breeding season; greater than (>) 73 percent of the locations of 31 breeding and 15 nonbreeding females were on the sand prairie cover type and the sands ecological site, which was characterized by rolling grass-covered dunes. In Kansas, Horak (1985) indicated that prairie-chickens will use most areas in tallgrass prairies, ranging from lightly grazed areas for nesting to overgrazed areas for leks. Horak (1985) indicated that an ideal landscape that supports healthy Greater Prairie-Chicken populations consists of 75 percent grassland and 25 percent cropland, with an optimal grassland composition of 70–80 percent grass and 10–20 percent forbs. In northeastern Kansas, shallow range sites (that is, a transition between ridge sides and tops) constituted 16–20 percent of the study area yet accounted for most of the habitat use by Greater Prairie-Chickens in all seasons; these sites were dominated by dropseed (*Sporobolus compositus*), little bluestem (*Schizachyrium scoparium*), and big bluestem (*Andropogon gerardii*) (Robel and others, 1970a). In eastern Kansas, the optimal landscape consisted of at least 50 percent native bluestem grassland interspersed with blackjack oak (*Quercus marilandica*) in some areas and with cropland within 1.6 kilometers (km) (Baker, 1953). In Colorado, the species used cropland in the winter and used sand sagebrush (*Artemisia filifolia*), mixed-grass, and tallgrass areas in late spring and autumn more than expected based on availability (Schroeder and Braun, 1992).

The relationships between a species and its habitat are affected by many factors, such as climate, predation, disease, genetics, and life-history stage. The following sections discuss habitats used for different key aspects of Greater Prairie-Chicken biology: lek sites (mating), nesting, brood rearing, roosting, and foraging.

Lek Sites

Two hypotheses dominate the theoretical understanding of lek-site selection: the hotspot model, in which leks (or booming grounds; that is, areas where male prairie-chickens gather to engage in courtship displays to attract females) form in areas with good nesting cover and many females, and the hotshot theory, in which leks form when many males congregate around a male that is highly preferred by females (Bradbury and Gibson, 1983; Beehler and Foster, 1988; Höglund and Alatalo, 1995; Dastagir and others, 1997). Male Greater Prairie-Chickens maximize the likelihood of encountering and mating with females by selecting leks near good nesting cover (Schroeder and White, 1993; Hovick and others, 2015a). Greater Prairie-Chicken males display in areas of bare ground

or short (<15 cm) cover and at least 2 km from forest patches (Johnson and others, 2020). These frequently are open areas with little residual vegetation where cover has been reduced by burning, mowing, grazing, or cultivation; occasionally, lowland swales are used in areas where snow has flattened the vegetation (Svedarsky, 1979; Hovick and others, 2015a). Furthermore, males usually display on leks where their visibility to females is maximized and where their security from mammalian and avian predators is enhanced (Gibson and others, 2002; Hovick and others, 2015b).

Greater Prairie-Chicken populations often are monitored by counting the numbers of displaying males present at leks (Cannon and Knopf, 1981; Horak and Applegate, 1998; Clifton and Kremetz, 2006). Hamerstrom and others (1957) and Westemeier (1971) suggested that the number of displaying males on a booming ground provides an indication of habitat quality in that locality—a “biological indicator” of sorts; that is, habitats around large booming grounds might be considered more ideal than habitats around small booming grounds. This rationale was used in a landscape ecology study in northwestern Minnesota in which Merrill and others (1999) established broad relationships between landscape characteristics surrounding booming grounds (fewer residential farmsteads, smaller amounts and smaller patches of forests, greater amounts of grasslands enrolled in the Conservation Reserve Program [CRP]) compared to nonbooming ground areas (that is, random points). Comparisons between traditional booming grounds (grounds on which displaying males occurred greater than or equal to ≥ 6 of 11 years) and temporary booming grounds (grounds which were used less than or equal to ≤ 5 of 11 years) indicated that traditional booming grounds were surrounded by less forest and cropland than temporary booming grounds. The traditional booming grounds also were associated with larger patches of grassland, and the shape of forest and grassland patches surrounding traditional booming grounds was more irregular than the shape of grassland and forest patches surrounding temporary booming grounds or random points (Merrill and others, 1999). Niemuth (2000), however, cautioned that the implications of lek attendance, lek type (temporary versus traditional or stable), and lek density to the population ecology of Greater Prairie-Chickens and other prairie grouse need further research. In the Flint Hills and Smoky Hills of Kansas, McNew and others (2011b) reported that counts of prairie-chickens on leks were 30 percent higher when counting prairie-chickens from blinds compared to flush counts (that is, birds were flushed from untrapped leks between 0600 and 0930 hours).

Several studies in the Great Plains have studied broad-scale patterns of habitat use to examine the relationship between lek locations and characteristics of the surrounding landscape or topography (Kirsch and others, 1973; Runia, 2009; Gregory and others, 2011; Hovick and others, 2015b; Londe and others, 2019). In North Dakota, lek sites occurred in or near retired cropland areas (that is, idle grasslands that were enrolled in the Federal Soil Bank or Cropland Adjustment Programs) that were >24 hectares (ha) and were not

found in hayland or heavily grazed pastures without adjacent idle lands (Kirsch and others, 1973). In South Dakota, Runia (2009) investigated land-use factors at multiple scales (400; 800; 1,200; 1,600; 2,000; 2,400; and 3,000 meters [m]) that potentially influence lek locations. The proportion of pastures, CRP grasslands, or a combination of pastures and CRP grasslands was a strong predictor of lek presence at several of the scales. In eastern Kansas, Gregory and others (2011) identified land-cover and geomorphological variables associated with lek sites at three spatial scales (0, 200, and 5,000 m). At the 0-m scale, higher elevations (relative to the surrounding landscape) and areas with an increased distance from urban areas were more likely to be selected as lek sites. At the larger spatial scales, lek occurrence was negatively associated with percent agricultural, urban, and forested areas, and road densities; lek occurrence was weakly and positively associated with percent grassland cover and the total core grassland area within 5 km (Gregory and others, 2011). Hovick and others (2015b) modelled habitat suitability throughout Kansas by overlaying 9 years of Greater Prairie-Chicken lek locations onto seven geographic information system layers that described land cover, topography, and anthropogenic structures to model habitat suitability throughout the State. Elevation was the most influential variable to predict lek locations, explaining three times or more variation than any other variable. The spatial distribution models were improved by adding land cover and anthropogenic structures (that is, transmission lines, roads, and oil and gas structures). Hovick and others (2015b) suggested that the selection of lekking locations that are generally higher than the surrounding landscape is not surprising because selection of these sites allows individuals to detect predators more easily and may provide an acoustic advantage that allows males to be heard over greater distances. In northeastern Oklahoma, lek sites occurred in areas with lower tree cover and lower road densities (Hovick and others, 2015a). As tree cover (defined as the percentage cover of trees in an area within a 2-km radius circle surrounding a lek) increased, the probability of lek-site selection declined exponentially, approaching zero at about 13 percent tree cover. As road densities (that is, length of roads within a 2-km buffer divided by the total area in the 2-km buffer) increased, the probability of lek-site selection declined, dropping below 10 percent when road densities reached 0.0014 m of road per square meter (m^2) (Hovick and others, 2015a). During the lekking period in Oklahoma, female Greater Prairie-Chickens avoided woodlands, showed a neutral response to oil wells and roads, and used grassland patches >13 months postfire more than patches 0–12 months postfire (Londe and others, 2019).

Similar broad-scale patterns of habitat use have been studied in the Midwest (Ammann, 1957; Merrill and others, 1999; Niemuth, 2000, 2005). In Minnesota, traditional leks were surrounded by less forest and cropland and by larger grassland patches than were temporary leks (Merrill and others, 1999). In an agricultural landscape in central Wisconsin, Niemuth (2000) compared land use within 2.4 km of 29 Greater Prairie-Chicken leks and 25 random points to

determine habitats associated with the presence of Greater Prairie-Chickens. Areas around leks had higher proportions of wetlands, grasslands, and shrubs and lower proportions of cropland, hayland, and forests than areas around random points. The differences between leks and random points varied with scale for all cover classes except pasture; the six scales included concentric rings of 0–400; 400–800; 800–1,200; 1,200–1,600; 1,600–2,000; and 2,000–2,400 m from a circle center (Niemuth, 2000). The number of displaying male Greater Prairie-Chickens attending leks was negatively correlated with the proportion of row crops at 800-, 1,200-, and 1,600-m scales and positively correlated with the proportion of grassland at 2,000- and 2,400-m scales (Niemuth, 2000). Also in central Wisconsin, Niemuth (2005) compared landscapes surrounding leks in primary areas (that is, intensively managed grasslands with higher Greater Prairie-Chicken populations) to landscapes surrounding leks in secondary areas (that is, little-managed or nonmanaged areas with reduced Greater Prairie-Chicken populations and low lek attendance). Primary areas had more grasslands, fewer forage crops, forest, and patches (disjunct patches of all land-cover categories), and shorter distances to neighboring leks than secondary areas. In Michigan, 86 percent of leks were within 1.6 km of recently cultivated land (Ammann, 1957).

Disappearance over time of some Greater Prairie-Chicken leks in Wisconsin was attributed to low amounts of grassland in the surrounding landscape (Niemuth, 2003). Although the effect of landscape composition on long-term persistence of Greater Prairie-Chicken populations has not been well studied, studies of Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) may provide insights for the management of Greater Prairie-Chickens. Landscapes around declining Lesser Prairie-Chicken populations experienced greater rates of landscape change compared with populations that were not declining (Woodward and others, 2001). At broader scales, declining populations of Lesser Prairie-Chickens were associated with large amounts of cropland and increased amounts of trees (Fuhlendorf and others, 2002).

Nesting Habitat

Female Greater Prairie-Chicken typically nest in areas with adequate nesting cover and high breeding potential (Drobney and Sparrowe, 1977; Toepfer, 1988; Schroeder, 1991; Schroeder and White, 1993; Matthews and others, 2013; McNew and others, 2013). Females mate with males at lek sites and then select nest sites with favorable microclimates and vegetative cover (Hovick and others, 2014a; Winder and others, 2016; Londe and others, 2021a). Generally, little new vegetation growth has occurred by late April, and as a result, hens typically select nesting cover based on residual vegetation from the previous year (Schwartz, 1945; Baker, 1953; Buhnerkempe and others, 1984; McKee and others, 1998; Emery, 2013; Winder and others, 2016). Optimal nest sites provide concealment from predators, unobstructed escape

routes from predators, and shade and protection from high temperature extremes, intense rains, hailstorms, and flooding. Optimal nest sites also are reasonably close to energy- and protein-rich food resources and provide appropriate cover for chicks.

Female Greater Prairie-Chickens typically select nest sites close to a lek. In southeastern Nebraska, the average distance between the nest and the lek at which a hen was radio-marked was 1.59 km (range 0.17–6.2 km) (Matthews and others, 2013). In north-central Nebraska study, females moved 2–5 km from the leks, where mating had occurred, to nest sites (Anderson, 2012). In northeastern Colorado, female home ranges encompassed >1 lek, the average distance between a nest and the nearest lek was 0.96 km, and the average distance between a nest and the lek where a radio-marked hen was first observed was 3.62 km (Schroeder, 1991). In the Flint Hills and Smoky Hills ecoregions of Kansas, McNew and others (2013) found high spatial variability in nest-site selection. McNew and others (2013) reported an average distance of 1.5 ($n=72$ nests), 1.9 ($n=94$), and 1.5 ($n=133$) km between leks and nests at three study areas. In Minnesota, Toepfer (1988) recorded an average distance of 1.6 km between nest location and the nearest lek.

Greater Prairie-Chickens place nests in a variety of habitats, including native prairie and planted grasslands. In Nebraska, Greater Prairie-Chickens preferred nesting in undisturbed cool- and warm-season CRP grasslands; 75 percent of 90 nests were in CRP fields despite only 28 percent of the available land cover being enrolled in CRP (Matthews and others, 2013). The remainder of the land cover included 46 percent agricultural development (that is, corn, soybean [*Glycine max*], and alfalfa [*Medicago sativa*] production) and 32 percent pastures (that is, grasslands not enrolled in CRP with a history of crop production) and rangelands (that is, grasslands not enrolled in CRP with no history of crop production). Nest sites were farther from woodlands and at higher elevations than random points; nest survival in CRP fields increased with increasing grass and forb coverage and with decreasing litter coverage (Matthews and others, 2013). In the Flint Hills and Smoky Hills of Kansas, McNew and others (2013) examined nest-site selection for 299 nests by using spatially explicit, multiscale models of nesting habitat selection. In the heavily fragmented grasslands of the Smoky Hills, coarse-scale habitat characteristics were more influential for nest-site selection; females selected nest sites in areas dominated by grasslands at larger spatial scales. In the contiguous, unfragmented grasslands of the Flint Hills, local-scale habitat components were more influential; females selected nest sites with higher vertical cover. McNew and others (2013) concluded that the importance of habitat components vary with local environmental conditions of potential nest sites and cautioned that management of grasslands at small spatial scales (for example, individual nest sites) is impractical. In a mixed-grass prairie in Kansas, Fields (2004) found nests of prairie-chickens (Greater Prairie-Chicken and Lesser Prairie-Chicken combined) predominantly in medium- and

tall-statured grasses, such as western wheatgrass (*Pascopyrum smithii*), little bluestem, big bluestem, and switchgrass (*Panicum virgatum*).

In midwestern landscapes, where native grasslands are scarce, Greater Prairie-Chickens will readily nest in tame grasslands. In Minnesota, Svedarsky (1979) reported that Greater Prairie-Chickens preferred nesting in smooth brome (*Bromus inermis*) and redtop (*Agrostis gigantea*). Other habitats were used relative to their availability; these habitats included bluestem, willow (*Salix* spp.), sedge (*Carex* spp.), alfalfa, and sweetclover (*Melilotus* spp.). The leaves of smooth brome and redtop have stems bearing aerial leaves for 25–30 cm of their height rather than at the base of the plant; if maintained in a vigorous condition, these grasses tend to maintain a more vertical position than do native species (for example, switchgrass, Indiangrass [*Sorghastrum nutans*], and big bluestem) and, thus, are better able to withstand flattening by snow. In a Minnesota study area with a variety of native and nonnative cover types, Svedarsky (1988) documented that Greater Prairie-Chickens preferred smooth brome for nesting; 61 percent of 36 nests were found in brome, which constituted only 2.9 percent of the study area. Greater Prairie-Chickens have existed for many years on tame grasslands or “substitute prairie” dominated by Kentucky bluegrass in Wisconsin (Hamerstrom and others, 1957, p. 12) and by redtop and timothy (*Phleum pratense*) in Illinois (Westemeier, 1980). In Wisconsin, 40 nests were observed in a variety of tame hayfields and near woodland edges associated with farms (Gross, 1930). In Michigan, eight nests were found in hayfields: one in sweetclover, three in wildland openings, and one at an airport (Ammann, 1957). Westemeier (1985, p. 35) suggested that, at least in Illinois, brome more closely resembled a species requiring little external maintenance (what he termed a “seed it and leave it” species) than other species used as grass cover on prairie-chicken sanctuaries. During a 29-year study in prairie-chicken sanctuaries (totaling 664 ha in 1982) in Jasper County in southeastern Illinois, nest densities averaged 2.75 per 10 ha in managed cool-season tame grasses (redtop, timothy, and smooth brome) and 1.71 nests per 10 ha in restored native grasses (Westemeier, 1973, 1985; Westemeier and Buhnerkempe, 1983).

Structural characteristics of vegetation, such as height and cover, at Greater Prairie-Chicken nest sites vary across the broad geographical range of the species. For example, vegetation heights at nests were 12.7–27 cm in the Sandhill prairies in Nebraska (Blus and Walker, 1966; Anderson, 2012; Harrison, 2015), 45 cm in sand sagebrush grasslands in Oklahoma (Jones, 1963a), 40–54 cm in the tallgrass prairies in Kansas (McNew and others, 2013), and 4.8–113 cm in multiple habitats in Colorado and Wisconsin (Toepfer, 1988; Westemeier and others, 1995) (table C1). Differences in vegetation height, however, may reflect the use of different sampling techniques (Buhnerkempe and others, 1984). Commonly, “height” is mentioned in the literature, but authors are not always explicit whether that indicates the maximum height of any part of the vegetation, such as flowering stems, or the height of the

vegetative components that conceal a nesting female or her nest. Newell (1987, p. 16) used “height” to indicate maximum height and used effective height as that level below which all dots on a cover board were obscured by vegetation, similar to the 100 percent VOR of Robel and others (1970a). To compare structural features of Greater Prairie-Chicken nesting cover, consistency in terminology and techniques are important. To minimize disturbance to hens, it also is important to measure conditions at the time of nest-site selection or just before egg laying. New growth or activities that remove cover can substantially alter conditions if measurements are taken later in the season.

In the Nebraska Sandhills, nesting cover included some growth from the previous growing season and averaged 12.7 cm (range 9.4–22.9 cm) in height; principal species forming nest canopies included sand lovegrass (*Eragrostis trichodes*), little bluestem, and prairie sandreed (*Calamovilfa longifolia*) (Blus and Walker, 1966). In another study in the Nebraska Sandhills, Powell and others (2020) found that grass height and standing dead vegetation height were lower at Greater Prairie-Chicken nests (43.8 and 47.7 cm, respectively) than at Sharp-tailed Grouse (*Tympanuchus phasianellus*) nests (56.4 and 62.3 cm, respectively). In Kansas, vegetation height was positively associated with nest survival, with females selecting nesting areas that maximized the time since a site had been burned (Hovick and others, 2015c). In a second Kansas study, McNew and others (2013) reported that female prairie-chickens typically placed nests at sites with greater vertical nesting cover; the authors suggested that the optimal range of vertical cover was between 25 and 100 cm. In Illinois, Westemeier (1973) reported that female Greater Prairie-Chickens avoided tall (>1 m), native vegetation. Westemeier (1973) believed that female prairie-chickens were most secure in a setting where they could stand; survey the surrounding area; and readily flush, rather than run, if threatened. Yeatter (1943), Hamerstrom and others (1957), Svedarsky (1979), and Toepfer (1988) also believed that vegetation can become too tall and dense for nesting Greater Prairie-Chickens. In Illinois, Buhnerkempe and others (1984) measured residual vegetation in February and March and found that fields with both successful and unsuccessful nests had a higher maximum vegetative height than fields without nests. In northeastern Colorado, Schroeder and Braun (1992) reported that nests were typically in dense vegetation averaging 59 cm in height.

In a Nebraska study, females selected nest sites with an average VOR of 10.8 cm (Anderson, 2012). Although this was a lower VOR compared to other nesting studies (table C1), it was still higher than what was available in the surrounding landscape (average VOR of random sites was 4.6 cm). In Kansas, McNew and others (2014) suggested that VOR was the main ecological factor driving nest-site selection and nest survival; the probabilities of nest-site selection and nest survival were maximized for VORs between 30 and 70 cm. McNew and others (2013) reported that <2–19 percent of 299 nest sites had VOR readings >50 cm.

Litter usually is not distinguished from “residual vegetation” in the literature, but litter, as used here, is that part of the residual cover that is horizontally oriented and typically older than one growing season. Residual cover is accumulated growth from past years, but usually the vertical growth from the previous year provides most of the concealment cover. Several studies have documented the relationship between high litter cover or residual cover and low nest success. In Nebraska, Matthews and others (2013) reported decreased nest survival when standing dead residual vegetation exceeded 25 percent. In Minnesota, Svedarsky (1979) reported that the amount of litter was inversely related to nest success. In Wisconsin, Broadway (2015) found a negative relationship between daily nest survival rate and residual vegetative cover; daily nest survival fell below 50 percent when residual cover exceeded the maximum threshold of 25 percent. In Missouri, McKee and others (1998) reported that, of several measured nest characteristics, litter cover was the best predictor of nest success in one-variable models. Nests with >25 percent litter coverage failed at twice the rate as nests with <25 percent litter coverage. For two-variable models, grass and forb cover or litter and woody cover correctly predicted Greater Prairie-Chicken nest success 81 percent of the time. Nest success declined when >5 percent woody cover was present at nests, when forb cover was ≤ 5 percent, or when grass cover was ≤ 25 percent (McKee and others, 1998). In Illinois, Buhnerkempe and others (1984) reported that 19 unsuccessful nests were in fields with average litter depth of 5.6 cm and maximum height of 65.5 cm, whereas 15 successful nests were in fields with average litter depth of 4.2 cm and maximum height of 78.7 cm.

An accumulation of litter and a decrease in plant vigor may have contributed to Greater Prairie-Chicken declines on Soil Bank grasslands in North Dakota 5–7 years after seeding (Kirsch and others, 1973). An alternative hypothesis for these declines was associated with elevated predation pressure resulting from an accumulation of litter. For example, predators may have switched to preying upon prairie-chickens or their nests when alternative prey numbers declined or when predator numbers increased (Peterson and Silvy, 1994, 1996). A more complex negative effect may arise when a prey species suffers from the presence of an alternative prey species via shared predators, resulting in a negative reciprocal impact on their populations (Breisjøberget and others, 2018). For example, excessive litter could indirectly reduce prairie-chicken nest success either by enhancing small-mammal populations that attract red foxes (*Vulpes vulpes*) or by providing better conditions for June beetle (*Phyllophaga* spp.) larvae that attract striped skunks (*Mephitis mephitis*) (Svedarsky, 1979). During a 15-year Illinois study, density of small-mammal nests was highest (12.8 per ha) in undisturbed prairie grasses compared to high-mowed (10.5 per ha) or hayed (7.3 per ha) stands (Westemeier and Buhnerkempe, 1983). Westemeier (1988b) reported higher nest densities of prairie voles (*Microtus ochrogaster*) and southern bog lemmings (*Synaptomys cooperi*) in prairie grass (5.13 nests per ha) and lower nest

densities in brome (2.1 nests per ha), and suggested that the lower productivity of Greater Prairie-Chicken nests in planted native stands resulted from an increased attraction to that habitat by mammalian predators.

Brood-Rearing Habitat

Brood-rearing habitat varies geographically and generally differs from nesting habitat. Nesting habitat must be dense enough to conceal the female and provide for predator detection and escape, and may be widely separated from feeding areas because of the greater mobility of females; whereas brood-rearing habitat must accommodate chick movement at ground level, must be accessible from the nest site because chicks have to walk from the nest, and must provide adequate abundance and kinds of insects, concealment from predators, protection from weather factors, and openings for sun exposure and dusting (Svedarsky, 1979, 1988; Johnson and others, 2020). Early reports indicated that Greater Prairie-Chicken broods stayed near the nest for the first few weeks after hatching (Schwartz, 1945; Hamerstrom and Hamerstrom, 1949), advancing the notion of nest-brood habitat (Hamerstrom and others, 1957; Westemeier, 1971; Kirsch, 1974; Drobney and Sparrowe, 1977). The mosaic of diverse grassland habitats and smaller agricultural fields in the 1940s may have better facilitated movements of chicks from nests to brood-rearing areas close to nests (Schwartz, 1945; Hamerstrom and Hamerstrom, 1949) than do contemporary landscapes of large, agricultural fields and crop monocultures with few weeds (Higgins and others, 2002; Nicholls and Altieri, 2013). “Nest-brood habitat” suggests that a given habitat is used for both nesting and brood-rearing, which may be true in some situations (for example, brood locations may reflect nest placement rather than habitat selection; Svedarsky, 1979). For Greater Prairie-Chickens, the term may be used in a general sense. For example, in Minnesota, stands of big bluestem, little bluestem, Indiangrass, and switchgrass might have been termed nest-brood habitat, but specifically, undisturbed stands of big bluestem, little bluestem, Indiangrass, and switchgrass were used as nesting habitat and recently (≤ 1 year) burned, grazed, or hayed stands were used as brood-rearing habitat (Svedarsky, 1979). Jones (1963a, 1963b), working in Oklahoma, was perhaps the first to recognize these differences. Jones (1963b, p. 757) stated that “Nesting took place in areas of exceptionally heavy cover. When hatching was completed, Greater Prairie-Chicken females moved their broods into areas where the vegetation had been disturbed: old fields [that is, idle or neglected arable lands that have naturally reverted back to perennial cover], native shortgrass, or cultivated pastures.”

Females with broods use a variety of native and human-created habitats (Rice and Carter, 1982; Norton, 2005; Matthews, 2009; Norton and others, 2010; Matthews and others, 2013; Broadway, 2015). In a study on the Fort Pierre National Grassland in South Dakota, Rice and Carter (1982, p. 18) pooled brood data from 13 radio-marked Greater

Prairie-Chickens, 9 radio-marked Sharp-tailed Grouse, 1 radio-marked hybrid (*Tympanuchus cupido* × *Tympanuchus phasianellus*), and several incidental observations and noted that “... sweet clover, snowberry [*Symphoricarpos* spp.], and good stands of western wheatgrass and green needlegrass [*Nassella viridula*] were most commonly used for brooding habitat. Some use of vegetation associated with unmowed road ditches and stock dams was recorded. Birds were commonly along drainages and on north-facing slopes.” Quantitative data were not given by Rice and Carter (1982), but the implication was that the heaviest cover available was sought by broods, especially during the hottest part of the day. In central South Dakota, Norton (2005) and Norton and others (2010) conducted a 2-year study on brood habitat use; radio-marked hens with broods preferred stands primarily consisting of western wheatgrass, Japanese brome (*Bromus japonicus*), green needlegrass, and mixed forb-dominated vegetation but avoided smooth brome. In southeastern Nebraska, Matthews and others (2013) reported that the locations of 36 radio-marked brooding hens were distributed among cool-season CRP fields (29 percent of 455 radio locations); rangeland (27 percent); pastureland (20 percent); warm-season CRP fields (11 percent); cropland (7 percent); and a combined category of wetlands, farmsteads, and utility facilities (6 percent). The relative probability of a brooding female selecting a location in a cool-season CRP field or crop field was 1.39 times higher and 2.64 times lower, respectively, than selecting a location in rangeland (Matthews, 2009; Matthews and others, 2013). Females selected areas near crop fields in all land-cover types, although crop fields themselves were avoided; each 100-m increase in distance from cropland predicted a 10 percent decrease in the probability of brood-site selection (Matthews, 2009; Matthews and others, 2013). Factors positively associated with microhabitat selection of brood habitat included the percentage forbs, bare ground, and VOR. The relative probability of selecting a brood location increased as the percent coverage of forbs and bare ground increased; mean use of forbs and bare ground was 33.6 and 24.8 percent, respectively. Selection peaked at 22.5 cm VOR and decreased as VOR diverged from this peak. Selection was negatively associated with the percentage of standing litter (Matthews, 2009; Matthews and others, 2013). In Wisconsin, Broadway (2015) tracked radio-marked hens to investigate juvenile survival; juvenile survival during the brood-rearing period was best explained by the additive positive effects of forb and residual cover (that is, local-level habitat characteristics). The effects were strongest at the beginning of the brood-rearing period and weakened as the brood-rearing period progressed (Broadway, 2015).

Female Greater Prairie-Chickens with broods tend to select disturbed areas, such as recently burned grasslands, pastures, and hayland, over other land covers, if vegetation regrowth is adequate to provide insects and cover from predators and weather factors (Jones, 1963a, 1963b; Svedarsky, 1979; Burger and others, 1989). In Minnesota, Svedarsky (1979) reported that broods moved directly from nests to areas that had been disturbed by burning, grazing, or haying; these

habitats accounted for over 69 percent of 290 brood locations. Studies in other areas in the eastern portion of the range have noted similar patterns of hens with broods moving to disturbed areas (Skinner, 1977; Burger, 1988; Jones, 1988; Toepfer, 1988; Westemeier and others, 1995). This pattern does not indicate, however, that hens cannot raise broods in undisturbed areas. In southeastern Nebraska, Matthews (2009) and Matthews and others (2013) found that females with broods selected undisturbed cool-season grasslands over other land covers. In northwestern Minnesota, Syrowitz (2013) reported higher brood use in undisturbed habitats (>12 months since last disturbance) than in disturbed habitats (0–12 months since last disturbance) despite higher invertebrate biomass in disturbed habitats. Hens with successful broods (that is, hens with at least one chick after 6 weeks) spent 50.9, 27.2, and 21.9 percent of the time with their broods in habitats that had been disturbed >12, 7–12, and 0–6 months prior to use, respectively. Hens with unsuccessful broods (that is, hens that lost all chicks before 6 weeks) spent 53.8, 15.4, and 30.8 percent of their time in habitats that had been disturbed >12, 7–12, and 0–6 months prior to use, respectively. In Wisconsin, grazing bolstered brood survival rates of Greater Prairie-Chickens but had no effect on hen or nest survival (Hardy and others, 2020). In another Wisconsin study, Golner (1997) reported that 77 percent of Greater Prairie-Chicken brood locations were in grass and grass/forb habitats and that broods selected habitats that were infrequently disturbed (4–6 years since the last disturbance) by grazing or burning. Prairie-chicken broods used mowed habitats or habitats treated with herbicides very little, regardless of time since last disturbance (Golner, 1997). Svedarsky and others (1999) observed that hens successfully raised broods in CRP fields in Wisconsin and Minnesota that had not been disturbed for more than 10 years.

In southeastern Nebraska, females with broods selected areas with intermediate topography 11.3 and 21.7 times more than bottom- or high-level (usually hilltops and ridges) topography, respectively; topographical categories were based on the maximum and minimum elevation in a particular field (Matthews, 2009; Matthews and others, 2013). In the Nebraska Sandhills, radio-marked hens with broods selected upland, rolling hill sites that had thicker vegetation with higher VOR (average=7.7 cm), more variable VOR (20.1), and greater litter depth (0.07 cm) than at coupled random locations (average VOR=6.6 cm, average variance=15.6, and average litter depth=0.05 cm) (Anderson and others, 2015).

Lowlands (that is, areas that contain sedges and usually are wet in spring) seem to be important to prairie-chicken hens with broods in grazed areas of the northern Great Plains. Newell and others (1988, p. 26) collected 921 radio locations from 36 Greater Prairie-Chicken hens with broods on the Sheyenne National Grassland (SNG) in southeastern North Dakota and recorded most locations in the lowland community, “with the highest use occurring in June when lowland vegetation was much taller and denser than upland or midland vegetation.” Broods were in native vegetation 70.1 percent of the time, and when there, they used lowlands, midlands, and

uplands 45.5, 26.9, and 23.2 percent of the time, respectively (Newell and others, 1988). Lowland grasslands occur on foot and toe slopes, midland grasslands occur on the back of foot slopes, and upland grasslands occur on the summit and shoulder slopes of the Hummocky Sandhills Habitat Association of the SNG (Manske and Barker, 1988). Lowland, midland, and upland grasslands constituted 13.9, 23.8, and 26.3 percent of the SNG, respectively (Manske, 1980; Manske and Barker, 1981). During all summer months, Newell and others (1988) indicated that over 44 percent of the locations in lowlands had VORs >25 cm. In Minnesota, Svedarsky (1979) reported that lowland habitats (willow and sedge) had positive brood preference ratings if burned or grazed but had negative ratings when undisturbed, suggesting differences in openness at ground level or in insect abundance. Broods may use lowlands because lowlands provide taller cover or because of advantages in predator avoidance. In northwestern Wisconsin, Gratson (1988) reported one-half as many small mammals in lowlands as in uplands and suggested that this may have decreased predation pressure on Sharp-tailed Grouse in lowlands by predators such as red foxes.

The brood-rearing period represents an informative example of the interaction among ecological factors such as nest placement relative to brood-rearing habitat, brood movements, female and chick nutrition, and brood survival (Jones, 1963b; Kobriger, 1965; Horak and Applegate, 1998; Matthews and others, 2011; Anderson, 2012). Brood habitat also must function as secure roosting cover (Bowman and Robel, 1977). Broods, especially young ones with limited mobility, do not move to optimal roosting habitats but rather roost where they happen to be at the end of the day. Alternatively, broods may move to optimal roosting habitat at roosting time. Young chicks typically move about 0.3 km daily, and older chicks typically move 2 km daily (Lehmann, 1941; Johnson and others, 2020). At the SNG in North Dakota, Newell (1987) recorded average movements of 0.47 km from nests to the first intensive-use areas by 20 radio-marked Greater Prairie-Chicken hens with broods. Newell (1987) reported a 12-day-old brood that moved 10.3 km in 8 days. In South Dakota, Rice and Carter (1982, p. 18) related movements to cover height: “During the severe drought of 1976, movement up to 1.6 km in a 24-hour period was not uncommon. In 1978, when vegetation conditions were good, movement by hens was considerably less than previous years as birds were never recorded more than 0.4 km from nest sites.” In Kansas, Viers (1967) and Silvy (1968) each observed a radio-marked Greater Prairie-Chicken hen with a brood that moved 3.2 km from the nest in 6 and 7 days, respectively. In Minnesota, Svedarsky (1979) recorded average minimum movements of about 2 km for nine radio-marked prairie-chicken hens with broods during their first week. Both Svedarsky (1979) and Newell (1987) documented extensive early movements of broods and high brood mortality, prompting them to suggest that brood-rearing habitat, or at least the brood-rearing period, is an important limiting factor for the Greater Prairie-Chicken. Newell and others (1988, p. 30) reported that, “Mortality of chicks was

very high, with only 28.4 percent of the chicks surviving to the end of the summer” and suggested that population declines at the SNG in North Dakota may be, in part, because of poor brood survival.

The nutritional state of brooding hens in relation to habitat may affect brood survival. Prairie-chickens require exogenous nutritional resources for egg laying, and differences in habitat quality at nest sites or access to nutritional subsidies from agriculture could affect variation in the timing of egg laying through effects on female nutritional status (McNew and others, 2011b). Access to protein-rich food resources during the prelaying and laying periods may be as important for grouse as has been shown for waterfowl (Krapu, 1974; Swanson and others, 1974). The nutritional requirements of female prairie grouse during spring and early summer are not as well-known as those for waterfowl, but the two avian groups share some physiological similarities, including body size, egg size, precocial young, and a propensity to renest (at least in the northern parts of the prairie-chicken’s range). Although more definitive research is needed, food plots and agricultural crops may have critical but generally unrecognized importance to egg-laying females as well as to broods. What Hamerstrom (1963, p. 793) reported for Sharp-tailed Grouse broods in Wisconsin may be even more relevant for Greater Prairie-Chicken hens and broods in the northern prairies: “... food patches may have an unappreciated value for summer food. The greens and insects which accompany cultivation may be even more important than the grains which have been planted.” During the dramatic increases in prairie-chicken populations following European settlement, agricultural practices (small pastures, weedy cropland, abundant field edges, poor drainage preventing replanting of some cropland) during early settlement on the northern prairies may have provided brood habitat for prairie-chickens in the breeding season and waste grain and field-stored grains (bundles, shocks) in the winter. In northeast Kansas, Augustine and Sandercock (2011) reported that predation of nests and Greater Prairie-Chicken hens may have been the main factors limiting population viability rather than maternal nutrition and condition. The researchers suggested that they may have failed to detect a relationship between female traits and their eggs or offspring because predation risk, climatic conditions, and other environmental factors had a greater impact on prairie-chicken survival and reproduction than individual variation among females. Morrow and others (2019) recommended additional research to quantify the influence of key maternal nutrient levels on Greater Prairie-Chicken offspring fitness.

Invertebrates are the primary food source for juvenile prairie-chickens, especially during the critical first 2 weeks of life (Jones 1963a, 1963b; Drobney and Sparrowe, 1977; Rumble and others, 1988). In North Dakota, Rumble and others (1988, p. 51) indicated that “arthropod parts” (mostly insects) constituted an average of 84.6 percent of 75 Greater Prairie-Chicken brood droppings collected in June, July, and August at the SNG. In Oklahoma, Jones (1963a, 1963b) reported that insects (mostly beetles [Carabidae, Scarabaeidae,

Chrysomelidae] and grasshoppers [Acrididae]) constituted 97 percent of 14 Greater Prairie-Chicken brood droppings. Forbs in general and legumes in particular are associated with desirable insect quantities and brood-rearing habitats. Jones (1963b, p. 773) wrote that “counts of insects captured in the various habitat types revealed that the vegetation with the greater percentage of forbs consistently had more insects per unit area than did the other vegetational associations...” and that “... the cultivated pasture association was the cover most frequently selected by birds with broods. This cover was dominated by low weeds and annual lespedeza [*Kummerowia stipulacea*].” Legumes also may be consumed directly by prairie-chicken broods. At the SNG in North Dakota, Greater Prairie-Chickens foraged in alfalfa during summer (Manske and Barker, 1988), and alfalfa and sweetclover leaves constituted 7.4 percent of the June diet, second only to arthropods that made up 80.1 percent (Rumble and others, 1988). At Valentine National Wildlife Refuge in Nebraska, Kobriger (1965) noted that one of the reasons that wet meadows were attractive to Sharp-tailed Grouse and Greater Prairie-Chicken broods was the presence of clover and dandelions (*Taraxacum officinale*) for foraging. In Missouri, Drobney and Sparrowe (1977) noted that legumes covered only 1 percent of their study area but accounted for 19 percent of all brood observations. N.J. Silvy (Texas A&M University, College Station, Texas, written commun., [n.d.]) noted that Attwater’s Prairie-Chicken chicks cannot develop properly on a pure diet of insects, but rather “they need some greens” in their diet.

In evaluating reports of brood habitat use, especially concealment cover, the method or circumstances of detection is an important consideration. For example, trained bird dogs (*Canis lupus familiaris*) were used extensively for censuses of gamebirds and their broods in the early 1900s (Wight, 1931; Kendigh, 1944). An observer searching with one or two dogs and giving vocal commands may alert broods at a greater distance so that they then seek heavier cover, if available (Wight, 1931; Hamerstrom and Hamerstrom, 1949; Kellogg and Doster, 1982). However, an observer on foot without a dog may see more broods in open cover, where gamebirds would be more visible and more apt to flush. The former technique could bias observations of brood habitat use toward denser cover, and the latter technique could bias observations of brood habitat use toward open cover. The advent of radio telemetry in the early 1960s (Marshall, 1963) made it possible to document movements and habitat use by hens and broods without directly observing marked animals. Previously, this could not be done, particularly in dense habitats, and thus knowledge of upland game bird ecology and habitat use has greatly increased since the 1960s (Robel and others, 1970a). Judiciously collected radio-telemetry data probably are the least biased because radio telemetry allows researchers to locate animals in areas where incidental observations would be unlikely (for example, in heavy cover where birds are reluctant to flush), or in areas where an observer would not search because of preconceived ideas about which cover types are good habitat (Newell and others, 1988). In following radio-marked broods in Wisconsin,

Toepfer (1988, p. 439) noted that “The consistent use of the taller grasses is probably the main reason why prairie-chicken broods are rarely seen.”

Roosting Habitat

The term “roosting,” as used here, refers only to nighttime activities and does not include day roosts (for information on day roosts, see Hamerstrom and others, 1957; Manske and Barker, 1988; Toepfer, 1988). Furthermore, roosting cover can be separated according to the snow-free season, when birds use vegetation, and the snow season, when birds commonly burrow into snow if sufficient depths are available (Rosenquist, 1996; Johnson and others, 2020). Leopold (1931) noted reports of birds roosting in trees, but some of the reports may have been sightings in the late evening, after which birds moved to the ground to roost. Most, if not all, night roosts are on the ground (Ammann, 1957; Jones, 1963b; Robel and others, 1970a; Drobney and Sparrowe, 1977; Johnson and others, 2020).

Greater Prairie-Chickens spend over one-half of their lives on a roost, especially in the northern parts of their range where winter nights are long (Toepfer, 1988; Toepfer and Eng, 1988). Roosting sites provide protection from weather and avoidance of predators (for example, reducing detection or facilitating escape from predators). Roosting cover is critical year-round, but perhaps more so in the winter when roosting cover is closely tied to food resources. Roosting sites that are near adequate winter food resources will minimize movements and energy demands and decrease exposure to predators (Toepfer, 1988; Toepfer and Eng, 1988). Farther north, food may be more limiting, but food needs to be accessible from night roosts. In Wisconsin, Schmidt (1936, p. 197) suggested that “Food determines what range is habitable in winter, but so does cover, particularly roost cover.” Hamerstrom and others (1957) believed that winter cover was not limiting when the herbaceous vegetation was covered with snow because birds used woody cover, which is fairly abundant in the Wisconsin portion of the Greater Prairie-Chicken range. In a photograph caption, Hamerstrom and others (1957, p. 57) noted that “Here bluegrass is (matted) down, under ten inches [25 cm] of snow, but sedges, quack [quackgrass; *Elymus repens*], timothy and *Muhlenbergia* still give roosting cover.” Using radio-marked birds, Toepfer (1988) reported that 57.1 percent of 175 winter roosts in northwestern Wisconsin were in wetland habitats and that 51.8 percent of 307 locations in central Wisconsin were in wetland-shrub habitats. Roosting habitat may be more limiting than food in more snow-free areas. In Missouri, Burger (1988, p. 88) noted that “...prairie chickens select optimal winter roosting habitat, then make daily feeding movements radiating as far out from this habitat as necessary to meet energetic demands.”

Manske and Barker (1988) identified the following three habitats as winter roosting habitats at the SNG in North Dakota, based on incidental observations of prairie grouse

(Sharp-tailed Grouse and Greater Prairie-Chicken) roosting sites: switchgrass portion of midland community, shelterbelts and other woody vegetation along cropland edges, and snow when it was >30 cm deep in drifts along shelterbelts and the lee side of hummocks. Manske and Barker (1988) recorded no winter night roosting sites in the lowland-grassland habitat type, but their study did not involve radio-marked birds. Toepfer and Eng (1988) followed 20 radio-marked Greater Prairie-Chickens at the SNG. They reported that 64 percent of 525 night locations were in lowland grass communities, 7.4 percent were in midland grass communities (primarily little bluestem), 1.2 percent were in upland grass communities, 6.6 percent were in a mixture of grass and forbs, 13.7 percent were in reed canarygrass (*Phalaris arundinacea*), and 7.1 percent were in quackgrass.

In Minnesota, a combination of grass and forbs was better than only grass for accumulating snow preferred for snow roosting by Greater Prairie-Chickens (Rosenquist, 1996). Several habitats were used for roosting, but areas with forbs, especially alfalfa and goldenrod (*Solidago* spp.), seemed to provide the best snow-burrowing conditions. Undisturbed vegetation that was 26–50 cm tall was used mostly for roosting and loafing (Rosenquist, 1996). CRP lands with smooth brome and alfalfa were used when snow conditions permitted burrowing. Native prairie was rarely used because of snow packing. Willow areas received little direct use by roosting prairie-chickens, although the associated herbaceous vegetation within willow complexes was used because it tended to accumulate snow that provided good snow-burrowing conditions. Birds rarely roosted under willow branches and, on one occasion, a roosting bird was apparently depredated by a coyote (*Canis latrans*) when the prairie-chicken flushed from a snow burrow into willow branches (Rosenquist, 1996). In Wisconsin, Gratson (1988) discussed a possible predator-avoidance strategy of Greater Prairie-Chickens changing roosting sites because predators may return to sites of previous prey captures.

Because lowland and wetland areas tend to have taller vegetation than upland areas, lowlands and wetlands may possess characteristics that are advantageous to roosting Greater Prairie-Chickens in avoiding predators. In Minnesota, Svedarsky (1979) reported that wetland communities accounted for 62.5 percent of the preincubation roosting locations of radio-marked females. Gratson (1988) suggested that canid predators spend comparatively less time hunting small mammals in lowlands in Wisconsin, which may reduce their chances of encountering roosting prairie grouse. He also suggested that there were fewer trees in wetlands that could serve as hunting perches for Great Horned Owls (*Bubo virginianus*), a crepuscular and nocturnal predator. In a second Wisconsin study, cover >50 cm in grass-sedge or shrub wetlands was used for winter roosting (Toepfer, 1988). In Michigan, Ammann (1957, p. 61) observed that “Marshes and bogs are often sought as roosting cover, particularly by prairie chickens, even though these cover types may not serve any other purpose, and the birds may fly a mile [1.61 km] or more from the most-frequented part of the

area to reach them. Generally, prairie chickens seem to be more exacting in their choice of roosting cover. They show a preference for the lowland types if the water level is not so high as to prevent their finding dry spots.”

Greater Prairie-Chickens select roosting habitat, in part, based on the structural characteristics of the vegetation (for example, height and density). At the SNG in North Dakota, Toepfer and Eng (1988) reported that >89 percent of the winter night locations were in cover >25 cm tall and that the average VOR at 32 roosts was 21 cm. In a second study in the SNG, Manske and Barker (1988) did not separate data for roosts by season but determined that the average VORs for night roosts throughout the year was 19 cm (range 15–22 cm). The authors concluded that “15 cm is the minimum level for good night-roost habitat” (Manske and Barker, 1988, p. 18). If one considered the midpoint of a range or an average to indicate “good” roosting habitat, an alternate view would be to average Toepfer and Eng’s (1988) 21 cm for cover types with Manske and Barker’s (1988) overall VOR of 19 cm for roosting sites throughout a year, which would yield 20 cm as a standard of “good” winter roosting cover, at least at the SNG. In Oklahoma, Jones (1963b) reported mean vegetation heights for night roosts (measured above roost) by season: 13 cm in winter, 4 cm in spring, 32 cm in summer, and 5 cm in fall. Jones (1963b), however, did not study radio-marked birds, and thus these values may be biased toward shorter cover because roosting prairie-chickens may be easier to locate in shorter cover than in taller cover. In Colorado, Schroeder and Braun (1992, p. 16) indicated that “Roosting typically occurred in mid and tall vegetation in relatively dense grassland areas in all seasons,” but they presented no quantitative data to support this statement. Toepfer (1988), following radio-marked Greater Prairie-Chickens in Wisconsin, reported that vegetation <25 cm tall was regularly used during the day but not during the night, when about 90 percent of locations were in cover >25 cm tall. The grass and forb cover type (that is, a mixture of 50–75 percent grass and 25–50 percent forbs) was a major cover type used in all seasons in central Wisconsin, followed by the upland grass cover type (Toepfer, 1988). McKee (1995) collected data for all seasons in Missouri and reported an average VOR of about 20 cm (range 10–35 cm) at roosting sites, but no clear pattern of site selection based on VOR was apparent.

Greater Prairie-Chickens often do not use the same roosting sites from one night to the next (Toepfer and Eng, 1988). In the SNG in North Dakota, Toepfer and Eng (1988) determined that the average distance between successive night-roost locations by radio-marked male and female Greater Prairie-Chickens were 949 and 922 m, respectively.

Foraging Habitat—Snow Season

The winter portion (snow season) of the species’ foraging ecology will be discussed separately from the snow-free season. In some years in the southern portion of the species’ range (for example, in Illinois, Kansas, Missouri, and

Oklahoma), the entire year may be snow free. Other than rose (*Rosa* spp.) hips and buds of shrubs and trees, native prairies in the northern portion of the species' range provide meager food resources for Greater Prairie-Chickens under winter snow cover (Hamerstrom and others, 1941). Before the advent of cultivated cereal crops, Greater Prairie-Chickens may have extensively used acorns as winter food (Gross, 1928, 1930; Schmidt, 1936; Johnson and others, 2020). Based on results from an experimental feeding study, Hamerstrom and others (1941, p. 192) concluded that "...browse alone will not carry prairie chickens through the winter. Small numbers may be able to supplement a browse diet with a certain supply of weed seeds, but to have prairie chickens in quantity in the North Central States, winter grains are necessary." Hamerstrom and others (1941) believed that it was unlikely that prairie-chickens evolved with the development of agriculture but rather adapted to it and, by altering their feeding habits, were able to greatly extend their range far north of the original limits. In North Dakota, Monson (1934) observed prairie-chickens feeding in corn fields during the winter and roosting in deep snow in meadows. At the SNG in North Dakota, prairie grouse were observed foraging in corn and sunflower (*Helianthus* spp.) fields and foraging on waste grain spilled along railroad tracks in winter (Manske, 1987; Manske and Barker, 1988). Manske and Barker (1988) noted that Greater Prairie-Chickens pick undigested grain out of cow manure in winter and believed that high-energy winter food is the primary limiting factor for prairie grouse on the SNG. Rumble and others (1988) reported that agricultural crops (corn, sunflowers, and soybeans) constituted 72.0, 61.3, and 65.2 percent of the diet of SNG prairie-chickens in December, January, and February, respectively. In comparison, shrubs constituted 0.2, 0.9, and 2.7 percent of the diet in December, January, and February, respectively. Toepfer and Eng (1988) recorded 3,945 winter-use areas from radio-marked Greater Prairie-Chickens on the SNG in North Dakota and determined that agriculture accounted for 41 percent of the locations, and 70.8 percent of those locations were in harvested corn. Observations of prairie-chickens feeding during the winter in North Dakota indicated that they prefer sunflowers more than soybeans and soybeans more than corn (Toepfer and Eng, 1988). These observations were measured by monitoring radio-marked birds feeding in three adjacent agricultural fields. Before snow cover, birds fed in sunflower fields. Once sunflowers were unavailable because of snow cover, birds shifted to adjacent soybean fields between two harvested corn fields. When additional snow covered the soybeans, prairie-chickens began feeding in harvested corn fields. When snow melted in late winter, birds shifted back to sunflower fields. Kobriger (1965, p. 789) noted that "Prairie chicken populations shrank as corn acreages decreased, and today the eastern and southern Sandhill borders, with both grasslands and corn, support the best prairie chicken populations in Nebraska." In Minnesota CRP and agricultural lands, vegetation that was 0–8 cm tall was used more for feeding than for other needs (Rosenquist, 1996). Schmidt (1936, p. 200) also spoke of the importance of corn in Wisconsin:

"Increase in prairie chicken population and an extension of range resulted from the extensive growing of corn by the early settlers." In Wisconsin, Leopold (1933) listed corn as a staple winter food that was eaten mostly after the first snowfall. In two Missouri studies of fecal droppings collected in winter, agricultural crops constituted at least 68.2 percent (Korschgen, 1962) and 51.9 percent (Toney, 1980) of the Greater Prairie-Chicken diet by volume.

Kirsch (1974) argued that winter food is not limiting for Greater Prairie-Chickens because they use buds and will migrate seasonally when food availability and cover in their breeding areas do not meet their winter needs. However, Hamerstrom and others (1941) demonstrated that Greater Prairie-Chickens cannot live on buds alone, and Burger (1988) reported increased mortality with increased movements. In South Dakota, Over and Thoms (1920) reported that Greater Prairie-Chickens migrated a few kilometers to find suitable winter-feeding areas, including corn fields when snow covered the ground. Toepfer (2003) recorded increased movements and mortality from electrical wire collisions when snow changed food availability. Even if Greater Prairie-Chickens could survive at minimal population levels in the northern portion of the species' range without agricultural winter foods, it would seem prudent for populations to minimize movements that expend energy and increase their exposure to predators. Rosenquist and Toepfer (1995) monitored 224 radio-marked Greater Prairie-Chickens over 5 years in Minnesota and reported that food accessibility was a major factor influencing winter movements. Movements >16 km were common in females moving from nesting to wintering areas, but males generally remained within 6.4 km of their home leks. Small grains and sunflowers were preferred, but standing corn was used when other foods were covered with snow (Rosenquist and Toepfer, 1995).

In the southern portion of the species range, open rangeland can provide an adequate source of food during moderate winters, but during periods of extended snow cover, agricultural fields may be necessary as a supplementary food source (Jones, 1963a; Korschgen, 1962; Horak and Applegate, 1998). In Kansas, Horak and Applegate (1998) indicated that soybeans, corn, sorghum (*Sorghum* spp.), and green winter wheat (*Triticum* spp.) provided winter food for Greater Prairie-Chickens. In Oklahoma, Jones (1956) noted that seeds of prairie forbs and grasses in native tallgrass prairies provided a good source of winter food for Greater and Lesser prairie-chickens. However, management practices, such as herbicide use (Clubine, 2002) that reduces forbs and increases grass composition, will reduce the availability of natural foods and increase the species' reliance on agricultural crops in winter. In Kansas, the species used sorghum fields extensively in winter (Robel and others, 1970a). Schroeder and Braun (1992) reported the species used cropland in winter in Colorado.

Church and others (1989) measured the combustible energy, gross energy, utilization efficiency, assimilated energy, and metabolizable energy from seeds reported to be eaten in the winter by Greater Prairie-Chickens. Church and others (1989) ranked the quality of the seeds as excellent (millet

[*Milium* spp.], soybeans), good (sunflowers, *Lespedeza* spp.), fair (wheat, corn, sorghum), and poor (snowberry, pigweed [*Amaranthus* spp.], switchgrass). However, soybeans are known to contain antinutritional factors (for example, protease inhibitors, hemagglutinins, and allergens) in their raw form (Coates and others 1970; Rocha and others, 2014), and Morrow and others (2019) recommended further research on the consumption of raw soybeans by female prairie-chickens in relation to the smaller brood sizes in Minnesota compared to Nebraska.

Foraging Habitat—Snow-Free Season

Foraging during the snow-free season is defined more by the snow-free period than by calendar dates and generally commences in mid-March and lasts through mid-November in North Dakota, South Dakota, and Minnesota, subject to annual variation. Rumble and others (1988) indicated that diets during the prenesting and incubation periods (April–May) at the SNG in North Dakota were dominated by dandelion flowers, alfalfa, sweetclover, and corn. Rumble and others (1988) also reported that, by June, the diet of adult prairie-chickens included more arthropods, compared to earlier in the breeding season. By August, arthropods constituted nearly 60 percent of the diet. The use of alfalfa and sweetclover increased throughout the spring to 42 percent in June and then declined to 15 percent in August. In Kansas, Baker (1953) reported that cultivated grains were important in winter months, and greens (native and cultivated) were important in other seasons. In the northern Flint Hills and the Smoky Hills of north-central Kansas, Blanco-Fontao and others (2013) used stable isotope analysis to assess seasonal differences in trophic niche breadth and individual specialization between male and female prairie-chickens and between birds in contiguous grasslands and fragmented landscapes. Males and females exhibited similar feeding behaviors during the lekking period in spring. Prairie-chickens living in native prairies exhibited greater annual trophic variability than prairie-chickens in fragmented agricultural-mosaic landscapes. Blanco-Fontao and others (2013) speculated that contiguous native prairies may have provided greater dietary diversity, resulting in greater diversity of feeding strategies. In tallgrass prairies in Oklahoma, habitat selection was influenced by food resources and thermal cover; female prairie-chickens selected areas that had a high abundance and biomass of invertebrates during all parts of the day, primarily in recently (0–12 months) burned patches (Londe and others, 2021a). In Minnesota, Svedarsky (1979) commonly recorded radio-marked females in cultivated fields and in areas with short cover (grazed prairie or sparse vegetation on ridge tops), where dandelions and other plants were the first to green-up. In another Minnesota study, invertebrate abundance and biomass were greater in habitats occupied by Greater Prairie-Chicken hens that successfully fledged at least one chick than in habitats occupied by hens that were unsuccessful in fledging at least one chick or in control sites

(Syrowitz, 2013). Korschgen (1962) completed an intensive food-habit study in Missouri in which he analyzed 5,040 Greater Prairie-Chicken droppings uniformly collected in the eight Missouri counties that overlapped the species' range and with equal representation during all months of the year. Grassland and agricultural habitats were intermixed in the landscape of the study area. Agricultural crops constituted about three-fourths of the diet; corn was the leading food item by volume throughout the year, followed by soybeans, sorghum, and Korean lespedeza (*Kummerowia stipulacea*). Only 26 percent of the annual diet was native plants. Animal foods were generally of low importance, but Korschgen (1962) did not analyze chick droppings; young birds typically feed more heavily on insects than adult birds. Also, soft-bodied insects and larvae are more completely digested and may have been poorly represented in the samples. About 20 years later, in Missouri, Toney (1980) led a year-long study in a landscape dominated by native tallgrass prairie and determined that native plants constituted over twice as much volume as reported by Korschgen (1962). Wild rose was the most important food item by volume and occurrence, followed by corn, sorghum, and wheat. Several native plants were used, depending on availability.

In late summer and fall, Greater Prairie-Chickens commonly shift their foraging to agricultural fields where available (Baker, 1953; Korschgen, 1962; Horak, 1985; Horak and Applegate, 1998). In Kansas, Horak (1985, p. 62) compared Greater Prairie-Chicken food habits in a grassland to food habits in a cultivated area and concluded that “prairie-chickens are not dependent on cultivated crops but will use them when available.” If common methods of conserving and restoring tallgrass prairie continue to threaten plant diversity and promote domination by warm-season grasses (Howe, 1994), the Greater Prairie-Chicken could become more dependent on cultivated crops.

Water Use

Greater Prairie-Chickens generally obtain water from succulent foods and dew on vegetation (Hamerstrom and Hamerstrom, 1968; Horak, 1985; Bidwell and others, 2003). During dry periods, surface water is used (Jones, 1963a, 1963b; Horak, 1985; Bidwell and others, 2003), but even in the driest parts of the range in Colorado, no emphasis has been placed on the need for providing surface water (Schroeder and Braun, 1992).

Climate

Regional climate and local weather conditions may affect behavior, abundance, occurrence, survival, or productivity of Greater Prairie-Chickens. Wilsey and others (2019) compiled avian occurrence data from 40 datasets to project climate vulnerability scores under scenarios in which global mean

temperature increases 1.5, 2, or 3 degrees Celsius (°C). Greater Prairie-Chickens ranked moderate in vulnerability during the breeding season at a 1.5 °C increase, low in vulnerability at a 2 °C increase, and neutral in vulnerability at a 3 °C increase. In North Dakota and South Dakota, Greater Prairie-Chicken occurrence and density were positively associated with the long-term (1981–2010) minimum January temperature and had a quadratic response to long-term (1981–2010) mean annual precipitation (Runia and others, 2021). In the Nebraska Sandhills, female Greater Prairie-Chickens made adjustments to the timing and duration of incubation off-bouts (that is, departures from the nest during incubation) in response to local environmental cues; female Greater Prairie-Chickens had shorter durations away from their nests at higher wind speeds, at nests with less vegetative cover, at lower ambient temperatures, and at nests closer to roads (Hoppe and others, 2019). In another study in the Nebraska Sandhills, Harrison and others (2017) found no evidence of an effect of the Palmer Drought Severity Index on nest survival. In Kansas, Greater Prairie-Chicken abundance was highest following wetter summers, cooler summers, drier winters, and cooler winters (Schindler and others, 2020). In a second Kansas study, Hovick and others (2015c) used 12 covariates to evaluate the effects of management, anthropogenic structures, and local weather on Greater Prairie-Chicken nest survival. Increased solar radiation (that is, fewer clouds and brighter days) decreased the probability of nest survival. In northeastern Oklahoma, Hovick and others (2014a) reported that prairie-chickens constructed nests in cooler environments relative to the surrounding landscape; nest sites had significantly taller vegetation than nonnest sites, and nests that survived were in cooler environments than nests that failed. Nest survival diminished when operative temperatures were >35 °C; operative temperatures incorporate energy flow between an animal and its environment and depend primarily on radiation, wind, humidity, and air temperature (Hovick and others, 2014a). In another Oklahoma study, daily nest survival declined in years with wetter average springs, during extreme precipitation events, and under higher maximum daily temperatures, especially in years with below-average precipitation (Londe and others, 2021b). Greater Prairie-Chickens nested earlier and had smaller clutches for their initial nests and re-nested in years with warmer temperatures prior to the nesting season. Incubation began later in drought years (Londe and others, 2021b).

Area Requirements and Landscape Associations

Male territory sizes within leks vary with male density and dominance status of males on a given lek. Large territories on leks typically are occupied by dominant males (Robel, 1966; Ballard and Robel, 1974; Robel and Ballard, 1974). Territories in the center also tend to be occupied by dominant males (Hamerstrom and Hamerstrom, 1973). For 10 males

on a single booming ground in the Flint Hills in Kansas, the average territory size was 518.4 m² (range 163.8–1,069.2 m²), with more dominant males holding larger territories (Robel, 1966). In a second study in the Flint Hills in Kansas, territory size of 77 males on four leks averaged 406.8 m² (range 107.9–2,078.1 m²) (Nooker and Sandercock, 2008).

The size of home ranges used by male and female Greater Prairie-Chickens may vary with time of year, location, and across studies. Before the advent of radio telemetry in wildlife research in the 1960s, home-range sizes were estimated by researchers based on their field experiences with the species. For example, Mohler (1952) believed fall home ranges in Nebraska were at least 23 square kilometers (km²). In Wisconsin, Grange (1948) suggested that the summer home-range size of Greater Prairie-Chickens was 8.1–20.2 km², whereas Hamerstrom and others (1957) suggested the average summer home-range size was 10.2 km². Radio telemetry has provided more precise home-range estimates and movement information, which is of fundamental importance when evaluating the feasibility of reintroduction projects. Minimum convex polygon estimates of home-range sizes for nine radio-marked females and three radio-marked males in the Flint Hills of Kansas during the 6-month breeding season were 3.95 and 1.53 km², respectively (Augustine and Sandercock, 2011). In the Flint Hills of Oklahoma, Patten and others (2011) estimated that the average annual 95-percent kernel home-range size for 71 radio-marked Greater Prairie-Chickens was 12.03 plus or minus (±) 2.19 km²; females had larger home ranges than males (25.93 and 7.31 km², respectively). In central Wisconsin, Toepfer (1988) determined that average annual home ranges of nine radio-marked males and 12 radio-marked females were 8.6 and 28.8 km², respectively.

The Greater Prairie-Chicken is considered an area-sensitive species that requires large expanses of grassland in somewhat open condition (Hamerstrom and others, 1957; Horak, 1985; Sample and Mossman, 1997; Niemuth, 2000; Ribic and others, 2009). Large-scale loss of grasslands within the species' range has resulted in the fragmentation of grasslands used by Greater Prairie-Chickens into smaller patches that are spatially isolated in an agricultural matrix (Roy and Gregory, 2019). The colonization and persistence of individual populations of Greater Prairie-Chickens can be framed under the metapopulation dynamics concept (Hanski and Gilpin 1997, Hanski and Gaggiotti 2004). Under the metapopulation framework, demographic processes (for example, population growth, movements, and recruitment) may be linked to the level of connectivity among reproductive populations (for example, through natal dispersal and migration leading to gene flow). The metapopulation dynamics concept is particularly relevant to Greater Prairie-Chickens, because isolated breeding populations of prairie-chickens likely differ in abundance and reproductive fitness because of differences in habitat quality, resource availability, landscape composition, and composition of the predator community (Niemuth, 2011). Limited movements among these isolated populations will reduce interchange among subpopulations, resulting

in reductions in gene flow and genetic diversity (Niemuth, 2011). As structural connectivity (that is, the degree to which some landscape elements of interest are contiguous or physically linked; Bélisle, 2005) becomes increasingly diminished through habitat loss and fragmentation, functional connectivity (that is, the degree to which the landscape facilitates or impedes movement of a species among resource patches; Taylor and others, 1993) is impaired through a reduction in Greater Prairie-Chicken movements and impacts on demographics and genetic diversity (Roy and Gregory, 2019). Using a landscape genetic approach to examine impacts of land cover and use on the isolation and genetic structure of Greater Prairie-Chickens, Roy and Gregory (2019) studied the functional connectivity of Greater Prairie-Chicken populations in Minnesota along a planned grassland corridor, a coordinated, multi-agency effort to effectively address the loss and degradation of prairies by creating functional landscapes able to adapt to changing conditions (Minnesota Prairie Plan Working Group, 2011). The most supported hypothesis to explain genetic exchange among Greater Prairie-Chicken leks included landscape and anthropogenic influences (for example, human population density, land use and infrastructure, and human accessibility) (Roy and Gregory, 2019). The composition of the grassland corridor was 24–40 percent grassland and 56–60 percent agriculture, with an average functional isolation among population clusters of 52.9 resistance units (that is, a metric of functional isolation). Areas surrounding the grassland corridor consisted of 18–22 percent grassland and 56–64 percent agriculture, with an average functional isolation among genetic clusters of 93.7 resistance units (Roy and Gregory, 2019). In landscapes lacking functional connectivity, such as in Illinois and Wisconsin, managers have used translocation (see “Translocation” subsection) of individual Greater Prairie-Chickens to maintain populations and genetic diversity (Walk, 2004; Bouzat and others, 2009; Bateson and others, 2014; Mussman and others, 2017; Hardy and others, 2018). In Wisconsin, genetic variation in Greater Prairie-Chicken populations significantly declined between 1951 and the late 1990s, ostensibly because of fragmentation and loss of habitat (Bellinger, 2001; Bellinger and others, 2003).

Hamerstrom and others (1957) indicated that Greater Prairie-Chickens in Wisconsin would use grasslands as small as 10.4 km² but recommended a minimum area of 46.6 km² for sustaining prairie-chickens. Based on knowledge gained from more than 20 years working with radio-marked Greater Prairie-Chickens, Toepfer and others (1990) believed that 16 km² of suitable habitat would be the minimum area needed to sustain a Greater Prairie-Chicken population containing 200–250 males in reintroduction projects. Such a minimum goal was planned for Illinois (Simpson and Esker, 1997). More recent work on movements (Halfmann and others, 2001) and genetic analyses of populations (Westemeier and others, 1998b; Bellinger, 2001; Bellinger and others, 2003; Johnson and others, 2003) suggested that even 16 km² may be too conservative, although the size of the area will depend on

the habitat composition in the surrounding landscape and the proximity to other populations. Kirsch (1974) indicated that 5.2 km² of high-quality habitat was a minimum area needed for prairie-chickens in intensively managed habitats. High-quality habitat was defined as grassland providing residual vegetation averaging about 51 cm in height in the spring and sufficiently dense to completely conceal a nesting female prairie-chicken. Kirsch (1974) based his conclusion largely on the dramatic population response achieved in Illinois by intensively managing 5.3 km² (Westemeier and Vance, 1972) and a similar area (5.5 km²) in Missouri where populations had been maintained for >10 years (D.M. Christisen, pers. commun., [n.d.] in Kirsch, 1974). However, after Kirsch’s (1974) recommendation, both the Illinois (Westemeier and others, 1998a) and Missouri (Mechlin and others, 1999) populations experienced dramatic declines. The Illinois population declined after nearly two decades of high densities (Westemeier and others, 1998a). Westemeier and Gough (1999) suggested a minimum of 6.1 km² for prairie-chickens (for leks, nesting, broodrearing, roosting) in Illinois, assuming management of the area is suitable for prairie-chickens. Niemuth (2000) analyzed land use around booming grounds in central Wisconsin and suggested that agricultural landscapes managed for prairie-chickens should be a minimum of 18 km², should be in close proximity to other Greater Prairie-Chicken populations and habitat, and should contain few trees and at least 15 percent potential nesting cover (that is, grasslands). In the species’ former range in Michigan, Ammann (1957) suggested 10.2 km² as a minimum area requirement for Greater Prairie-Chickens.

Greater Prairie-Chicken movements and area requirements may vary seasonally and by sex. Greater Prairie-Chickens are highly mobile compared to other gallinaceous birds (Walk, 2004), but movement capabilities are limited for Greater Prairie-Chicken hens with dependent broods. Movements also consume energy and potentially expose birds to predation. Hamerstrom and Hamerstrom (1973, p. 28) summarized this relationship best: “With most of the known activities of the birds within a range of two-three miles [3.2–4.8 km], and almost all of them within five miles [8 km], it follows that management practices should also be close together so that all of the annual requirements of the birds can be met within small compass.” Generally, movements are greatest during winter and least during the breeding season. Males usually stay within 1 km of their traditional booming ground, and females usually stay within 1 km of their nest (Toepfer, 1988). Winder and others (2015a) investigated variation in spatial ecology and habitat requirements of female prairie-chickens (Lesser and Greater prairie-chickens combined) across an ecological gradient of different landscapes in Nebraska, Kansas, Oklahoma, and Missouri; larger home ranges were associated with higher amounts of annual precipitation, but home-range size was not related to road density, lek density or spacing, or the availability of prairie habitats. Greater than 95 percent of the monitored females had activity centers within 5 km of leks, which suggested

that conservation efforts can be effectively concentrated near active lek sites (Winder and others, 2015a). In the large, contiguous grasslands of the Oklahoma Flint Hills, average Greater Prairie-Chicken movements were 2–3 times greater in autumn (839 ± 142 m) and winter (845 ± 121 m) than in spring (289 ± 40 m) and summer (391 ± 43 m) (Patten and others, 2011). Females moved more than males in spring, but less than males in summer. Overall, females had larger home ranges than males, moved more frequently between activity centers, and moved greater maximum distances. Patten and others (2011) suggested that this may make females more susceptible to the negative effects of habitat fragmentation. Females are limited during the early-brood period by the mobility of their chicks. In the Flint Hills in Kansas, eight radio-marked females traveled a maximum distance of 3.7 ± 0.7 km from the lek where they were first banded (Augustine and Sandercock, 2011). Vogel (2015) reported distances travelled over the course of a year for 10 adult female Greater Prairie-Chickens tagged with satellite transmitters that were translocated from Nebraska to southern Iowa and northern Missouri. On average, females travelled 364 km, with one bird travelling 3,988 km, between April of the year the birds were translocated to June of the following year. In Missouri, prairie-chickens in contiguous prairie landscapes had fewer adult movements, fewer brood movements, higher survival, and higher nest success compared to birds in landscapes with scattered grasslands intermixed with agricultural lands (Burger, 1988; Ryan and others, 1998). In a second Missouri study, large prairies were more effective than small prairies in attracting females (Jones, 1988).

Greater Prairie-Chicken occurrence, abundance, and nest success may be affected by landscape-level factors, such as the composition and spatial arrangement of surrounding habitats. Runia and others (2021) used information-theoretic methods to identify land cover, topographic, and climate variables that predicted Greater Prairie-Chicken occurrence and density in North Dakota and South Dakota. Greater Prairie-Chicken occurrence and density were positively associated with the percentage of the landscape in herbaceous grassland (including CRP) and negatively associated with the percentage of the landscape classified as developed (roads and buildings) (Runia and others, 2021). The probability of occurrence nearly doubled from 0.10 to 0.19 when the percentage of the landscape in herbaceous grassland increased from 60 to 95 percent; predicted occurrence declined from 0.36 to 0.17 when the percentage of the landscape classified as developed increased from 0.0 to 2.5 percent. Density increased from 0.7 to 1.7 males per 2.56 km^2 when the percentage of the landscape in herbaceous grassland increased from 55 to 95 percent; predicted density of Greater Prairie-Chickens declined from 3.40 to 1.58 males per 2.56 km^2 when the percentage of the landscape classified as developed increased from 0.00 to 2.5 percent (Runia and others, 2021).

In the tallgrass prairies of southeastern North Dakota and northwestern Minnesota, Greater Prairie-Chickens seemed to be highly sensitive to both grassland patch size and landscape

composition (Winter and others, 1998, 1999, 2000, 2001). Of 259 individuals that were detected during a 4-year study, 95 percent occurred in large prairies (>200 ha) that were surrounded by neutral landscapes (landscapes surrounded by little woody vegetation), whereas 5 percent occurred in large prairies surrounded by hostile landscapes (landscapes surrounded by woody vegetation). No individuals occurred in small (<50 ha) prairies.

In the Nebraska Sandhills, the probability of presence of female Greater Prairie-Chickens decreased with increasing distance to the nearest wet meadow, with probabilities >0.5 for distances <470 m and probabilities <0.1 for distances >1,275 m from the nearest wet meadow (Hiller and others, 2019). Female Greater Prairie-Chicken distribution probabilities were greater at moderate distances from agricultural fields; the probability of presence peaked at about 0.65 with a distance of 4.4 km from the nearest agriculture field, with probabilities >0.5 for distances ranging between 1,930 and 6,790 m (Hiller and others, 2019).

In Kansas, Schindler and others (2020) quantified the effects of percent grassland and edge density of grassland patches on Greater Prairie-Chickens at three spatial scales (3, 5, and 10 km) buffered around 16-km survey routes. At the 3- and 5-km spatial scales, Greater Prairie-Chicken abundance initially declined with increasing percent grassland until reaching thresholds of 65.3 and 64.8 percent grassland at the 3- and 5-km spatial scales, respectively (Schindler and others, 2020). At the 10-km spatial scale, Greater Prairie-Chicken abundance initially increased with increasing percent grassland until reaching a threshold of 82.1 percent grassland, after which Greater Prairie-Chicken abundance declined with increasing percent grassland. At the 3-km spatial scale, Greater Prairie-Chicken abundance initially declined with increasing edge density of grassland patches until reaching the threshold of 67.5 m per ha, after which abundance increased with increasing edge density of grassland patches (Schindler and others, 2020). At the 5-km spatial scale, Greater Prairie-Chicken abundance declined with increasing edge density of grassland patches. At the 10-km spatial scale, Greater Prairie-Chicken abundance initially increased with increasing edge density of grassland patches until reaching the threshold point of 38.6 m per ha, after which abundance declined with increasing edge density (Schindler and others, 2020).

Throughout the Kansas Flint Hills, Herse and others (2020) evaluated the role of grassland amount, edge context, and degree of fragmentation on Greater Prairie-Chicken occurrence at spatial scales of 800- and 1,600-m radii from avian point-count survey locations. Greater Prairie-Chicken occurrence was most strongly related to landscape structure within a 1,600-m radius of point-count surveys, responding positively with percentage grassland and negatively with edge density. Although Greater Prairie-Chickens favored expansive grasslands, they often were absent from such grasslands; Herse and others (2020) suggested that their absence may

be, in part, related to the intensity of range management and resulting lack of vegetative cover.

Using data from standardized prairie-chicken surveys in northwestern Minnesota, Adkins and others (2019) evaluated the association between Greater Prairie-Chicken lek density (leks per square kilometer), the number of males at leks, and CRP enrollments in the context of landscape structure and composition. At the landscape scale (41-km² survey blocks), lek density was positively associated with the percent area of CRP grasslands and CRP wetlands, the percent area of grasslands and wetlands with permanent or long-term conservation goals, the contiguity of grasslands (that is, the size and connectivity of grassland patches), and the number of wetland patches in each survey block each year; lek density was negatively associated with the area of other wetlands managed with variable or no continuity in conservation goals and the number of grassland patches in each survey block each year (Adkins and others, 2019). At the lek scale, the number of males per lek was positively associated with the contiguity of grasslands and the percent area of CRP grasslands, other grasslands, CRP wetlands, and shrublands; the number of males per lek was negatively associated with the percent area of other wetlands, forests, and developed areas. Increasing the area of CRP grasslands within a 2-km habitat radius around a lek by 25 percent resulted in a 5 percent increase in males per lek (Adkins and others, 2019).

Adkins and others (2021) also simulated changes in Greater Prairie-Chicken abundance (number of leks or number of males on leks) in response to three land-cover scenarios in northwestern Minnesota: expiration of existing CRP enrollments; random, small-parcel (4,040-m²) addition of CRP grasslands; and strategic large-parcel (80,000-m²) addition of CRP grasslands. Greater Prairie-Chicken abundance was predicted to increase with the large-parcel and small-parcel scenarios, with the greatest increases associated with large-parcel additions (Adkins and others, 2021). Greater Prairie-Chicken abundance declined when grassland landscape contiguity declined with the loss of CRP enrollments. Simulations of strategic, large-parcel additions of CRP grasslands increased Greater Prairie-Chicken abundance more often than random, small-parcel additions of CRP grasslands of the same area that did not increase grassland contiguity. Adkins and others (2021) predicted that the loss of CRP enrollments because of the expiration of CRP contracts at the landscape scale could lead to reductions up to 80 percent of the number of Greater Prairie-Chicken leks per square kilometer within survey blocks (41-km²), which could result in declines in population size and further contraction of the species' range in northwestern Minnesota. In Wisconsin, lek presence was associated with landscapes with large expanses of idle tame grassland and wetland and less forest cover than was available in the landscape; proximity to other populations and associated habitat also was an important predictor of lek presence (Niemuth, 2000, 2003). In addition, the number of males attending leks was positively associated with idle, tame grassland (Niemuth, 2000). In western Wisconsin,

Westemeier (1971, p. ii) sampled landscapes around leks and noted that prairie-chicken populations were "directly related to grassland and marsh acreage."

In managing for the seasonal habitat needs of Greater Prairie-Chickens, important considerations include how habitats are arranged within a landscape and how much of each habitat is needed during different seasons. The concept of ecological patterning has guided Greater Prairie-Chicken management in Wisconsin since the 1950s (Hamerstrom and others, 1957). This concept proposed a network of grassland management units throughout private lands, yet it had not been thoroughly tested against an alternative of larger contiguous blocks of managed habitat. An important evaluation of these alternatives was completed in Missouri (Ryan and others, 1998). Ryan and others (1998) radio-marked Greater Prairie-Chicken hens in two areas. A 112-km² "mosaic landscape" of scattered prairie units constituted 11.9 percent of the landscape, with the remainder consisting of row crops and small grains. The "contiguous prairie landscape" was 52.5 km² and consisted of the same habitat types and amounts as the mosaic landscape but configured differently. Native prairie constituted 15.4 percent of the contiguous prairie landscape, but 75 percent of that was within a 6.5-km² unit. This large block of prairie was managed by rotational burning and haying (Ryan and others, 1998). Over a 27-year period, the Greater Prairie-Chicken population had been somewhat stable in the contiguous area but declined in the mosaic area. Apparent nest success was higher in the contiguous area during 1 of the 2 years (Ryan and others, 1998). Hens with broods in the contiguous area had smaller home ranges and moved less than in the mosaic. Females nested more in agricultural areas of the mosaic landscape, where their nests were more prone to destruction, compared to the contiguous landscape (Ryan and others, 1998).

Brood Parasitism by Cowbirds and Other Species

The Greater Prairie-Chicken is an unsuitable host for the obligate brood parasite, the Brown-headed Cowbird (*Molothrus ater*). Only one study has documented cowbird brood parasitism of a Greater Prairie-Chicken nest (Shaffer and others, 2019); in Minnesota, Svedarsky (1979) recorded two cowbird eggs in a Greater Prairie-Chicken nest containing 11 prairie-chicken eggs. The nest was in an unburned clump of bog birch (*Betula pumila*) and willow that was surrounded by burned brush prairie (Svedarsky, 1979).

Other upland-nesting gamebirds have been reported as interspecific brood parasites of Greater Prairie-Chicken nests. In Nebraska, one of 91 Greater Prairie-Chicken nests was parasitized by a Wild Turkey (*Meleagris gallopavo*); the parasitized nest contained 14 prairie-chicken eggs and 6 turkey eggs (Harrison and others, 2018). One turkey egg hatched after more than 38 days of incubation, but none of the prairie-chicken

eggs hatched. In Texas, Brown (1968) reported that Northern Bobwhite (*Colinus virginianus*) parasitized one of nine Greater Prairie-Chicken nests. In Kansas, Hagen and others (2002) reported no instances of Ring-necked Pheasant (*Phasianus colchicus*) parasitism of Greater Prairie-Chicken nests but reported 4 percent of 75 Lesser Prairie-Chicken nests were parasitized by pheasants. In Minnesota, Carlson (1942) reported single pheasant eggs in two Greater Prairie-Chicken nests. In west-central Minnesota, 42 percent of 19 Greater Prairie-Chicken nests contained Ring-necked Pheasant eggs (Toepfer, 2007). Also in Minnesota, Toepfer and others (2005) reported that 30 percent of 86 prairie-chicken nests were parasitized by pheasants; the incidence of pheasant eggs in prairie-chicken nests increased with the density of crowing male pheasants. In Illinois, Westemeier and others (1998a, 1998b) reported that 11 percent of 676 prairie-chicken nests had been parasitized by Ring-necked Pheasants. Although nest success (≥ 1 host egg hatching) did not differ between parasitized and unparasitized nests, the productivity of prairie-chickens was reduced because of increased embryo mortality, increased nest abandonment, or because hens left their nests earlier because of the shorter incubation period of the pheasant (average of 25 days for prairie-chickens and 23 days for pheasants) (Westemeier and others, 1998b). In five cases, this nest abandonment resulted in nearly full-term prairie-chicken eggs being left in nests after pheasant eggs had hatched. Nest parasitism increased from 2 to 43 percent over a 14-year period and remained high for an additional 4 years (Westemeier and others, 1998b). In another Illinois study, 5 percent of 19 Greater Prairie-Chicken nests were parasitized by Ring-necked Pheasants (Walk and others, 1999).

In Kansas, McNew and others (2011b) and Gregory and others (2018) reported intraspecific parasitism in Greater Prairie-Chicken nests. In three study areas differing in landscape composition and rangeland management in the Flint Hills and Smoky Hills of Kansas, McNew and others (2011b) reported that egg-laying rates of >1 egg per day indicated that intraspecific nest parasitism occurred in 6–15 percent of 67 Greater Prairie-Chicken clutches. Using molecular genetics and parentage analyses of blood samples, Gregory and others (2018) reported no evidence of intraspecific brood parasitism in eight broods at their Southern Flint Hills study area; 0.5 percent parasitism of 18 broods at their Northern Flint Hills study area; and 17 percent parasitism of 29 broods at their Smoky Hills study area, a highly fragmented landscape with 20–30 percent less grassland and 2–4 times higher road density than the other two study areas. Parasitic female prairie-chickens tended to be older females that parasitized nests of yearling females. Parasitic female prairie-chickens only laid parasitically after their initial nesting attempt failed, and all parasitic females re-nested and hatched their own clutches (Gregory and others, 2018). Gregory and others (2018) suggested that intraspecific nest parasitism among female Greater Prairie-Chickens is facultative and a behavioral mechanism used to directly increase fecundity in a risky habitat with low adult survival.

There are no records of interspecific parasitism between Greater Prairie-Chickens and Lesser Prairie-Chickens; however, hybridization between the two species has been reported in a zone of sympatry in the northern portion of the Lesser Prairie-Chicken's range in Kansas (Bain and Farley, 2002; Fields, 2004; McDonald and others, 2012; Oyler-McCance and others, 2016). Hybridization also has been reported between Greater Prairie-Chickens and Sharp-tailed Grouse in a zone of sympatry where the two species' ranges overlap (Johnsgard and Wood, 1968; Augustine and Trauba, 2014; Huschle and Toepfer, 2020). For example, Augustine and Trauba (2014) reported that 8 percent of 75 Greater Prairie-Chickens in Minnesota included individuals of putative mixed genetic makeup (based on morphology) of Greater Prairie-Chicken and Sharp-tailed Grouse following translocation of Greater Prairie-Chickens into the area.

Multiple paternity (that is, females mating with multiple males) has been reported in the Greater Prairie-Chicken (Hess and others, 2012; Gregory and others, 2018) and has been shown to vary with landscape condition (Gregory and others, 2018). Multiple paternity produces broods with greater genetic diversity than paternity with a single partner (Gregory and others, 2018). In Wisconsin, Hess and others (2012) found that 44 percent of 25 broods showed genetic evidence of multiple paternity. In three study sites in the Flint Hills and Smoky Hills in Kansas, 4 percent of 24 chicks (14 percent of 8 broods) in the least-fragmented site (72 percent grassland, 1.41 km per km² road density, and 0.22 km² grassland contagion) were the result of multiple paternity (Gregory and others, 2018). Twenty percent of 179 chicks (38 percent of 29 broods) in the most-fragmented site (38 percent grassland, 0.32 km per km² road density, and 0.38 km² grassland contagion) were the result of multiple paternity (Gregory and others, 2018). Gregory and others (2018) concluded that, when faced with uncertain and unescapable conditions (for example, isolation and fragmentation), female Greater Prairie-Chickens may choose to mate with more than one male to increase the genetic diversity of their brood.

Breeding-Season Phenology and Site Fidelity

Male Greater Prairie-Chickens typically visit booming grounds throughout the year, but regular attendance is most pronounced in the spring (particularly March, April, and May) and less so in late fall (Johnson and others, 2020). Female Greater Prairie-Chickens begin visiting booming grounds from mid-March through May. At three study sites in Kansas, males attended leks between March 2 and May 19, females visited leks from March 20 to April 16, peak male lek attendance was April 9, and peak female lek attendance was April 10 (McNew and others, 2011b). In South Dakota, peak hen visitation occurred on April 8, based on hens captured at leks (Norton, 2005). In Wisconsin, based on 6,014 mornings in a

blind between 1950 and 1969, Hamerstrom and Hamerstrom (1973) reported April 18 as the day for peak hen visitation to a booming ground. At the northern edge of the species' range in Minnesota and Wisconsin, the peak of copulations occurred on April 20 (Hamerstrom and Hamerstrom, 1973; Svedarsky, 1983). At the southern edge of the subspecies' range in Illinois, peak copulation was about 1 week earlier (Westemeier and others, 1998a). However, in Kansas, at a latitude similar to that in Illinois, Robel (1970) observed peak copulation during April 21–30, and McNew and others (2011b) observed copulations between April 3 and May 9.

About 4 days after the first copulation, hens begin laying one egg per day (Johnson and others, 2020). In the northern Great Plains, Greater Prairie-Chicken females begin nesting about the third week in April (Svedarsky, 1979; Newell, 1987); nest initiation typically is earlier in southern portions of the species' range (Westemeier and others, 1998a; McNew, 2010; McNew and others, 2011b; Johnson and others, 2020). In Kansas, McNew and others (2011b) reported active nests from April 1 to July 8, a range of clutch initiations for all clutches from April 1 to May 22, and the mean date of clutch initiation of first and renesting attempts as April 26 and May 24, respectively.

Average clutch size varies from 10 to 14 eggs (Hamerstrom, 1939; Robel, 1970; Svedarsky, 1983; Horak, 1985; Peterson and Silvy, 1996; Augustine and Sandercock, 2011); clutch sizes initiated later in the breeding season typically are smaller (Johnson and others, 2020). In South Dakota, the average clutch size for 27 initial nests was 13.8 eggs and 11.3 eggs for 9 renests (Norton, 2005). In Kansas, the average clutch size was 10.9 eggs for 24 first nests and 10.8 eggs for 6 renests (Augustine and Sandercock, 2011). In Minnesota, the average clutch size of 26 nests was 13.2 eggs (Svedarsky, 1983). Average clutch size was 12 eggs in Illinois (Yeatter, 1943; Vance and Westemeier, 1979) and Wisconsin (Hamerstrom, 1939).

If nests are destroyed, hens may renest at least twice, but the clutch size may decrease in nests that are established later in the summer (Baker, 1953; Robel and Ballard, 1974; Svedarsky, 1979; McNew and others, 2011b). For example, in the Nebraska Sandhills, average clutch size was 10.6 eggs for 76 initial nests, 8 eggs for 23 second nests, 6.5 eggs for three third nests, and 5 eggs for one-fourth nest (Anderson, 2012). The average nest survival (≥ 1 egg hatched) for 127 nests was 28.3 percent.

The incubation period for the Greater Prairie-Chicken ranges from 23 to 25 days (Gross, 1930) but tends to be shorter for renesting attempts initiated later in the year (Svedarsky, 1983; Johnson and others, 2020). In southeastern Nebraska, the average incubation initiation date was May 17, with a renesting average date of June 5, and an average hatch date of June 12 (Matthews and others, 2013). In Kansas, hatch dates were from May 18 to July 8, brood rearing occurred from May 18 to July 22, and juveniles were independent by September 7 at 60 days of age (McNew and others, 2011b). Females that lost first nests late in the season had a lower probability of renesting. Renesting attempts occurred, on

average, 7.8 days after failure of the first nest (McNew and others, 2011b).

Double-brooding by a single female is rare; in Kansas, McNew and White (2012) described the first case of a female Greater Prairie-Chicken successfully renesting after losing her initial brood. McNew and White (2012) suggested that double-brooding may only be possible in areas like the Flint Hills in Kansas, where the breeding season is long and brood loss is high during the pre fledging period, but production of a second brood would be limited to females that lose their first broods early in the breeding season because of the species' long brood-rearing period and high survival rate of juveniles after fledging.

Fidelity to breeding areas has both advantages (for example, maintenance of an established territory, increased knowledge of an area and its predators and competitors) and disadvantages (for example, birds with high philopatric tendencies may continue to occupy low-quality habitats) (Schroeder and Robb, 2003). Based on studies of marked birds, most territorial males that attend a given lek will return daily during the lekking season (Hamerstrom and Hamerstrom, 1973). Individual males also tend to display on the same lek, or at least in the same general area, in subsequent years (Hamerstrom and Hamerstrom, 1949; Robel and Ballard, 1974). In Wisconsin, Toepfer (1988) noted that about 85 percent of the males on a booming ground return from 1 year to the next, suggesting strong site fidelity of males to a lek. In a second Wisconsin study, Hamerstrom and Hamerstrom (1949) banded 52 males; 21 of the marked males were seen in more than one spring, and 15 of the marked males returned to their original booming grounds in subsequent breeding seasons. In a 4-year study in Illinois, translocated male Greater Prairie-Chickens had high lek-site fidelity; 89 percent of 38 males were resident each year at the same lek (Mussman and others, 2017). Although females may develop a temporary attachment to a given lek and even to a particular male on the lek, they may visit other leks after a nest is destroyed to initiate renesting (Robel and others, 1970a; Svedarsky, 1979). In Colorado, Schroeder (1991) reported that 85 percent of 79 radio-marked females visited more than one lek during the breeding season. Females also may develop an attachment to a particular area where they have successfully nested in the past. In Minnesota, Svedarsky (1988) documented two females that nested 4.6 and 29.8 m from their successful nests of the previous year.

Greater Prairie-Chickens may be annual short-distance migrants in portions of their range (Hamerstrom and Hamerstrom, 1949; Ammann, 1957; Svedarsky, 1988; Schroeder and Braun, 1993). Banded individuals have been reported to migrate as much as 12 km in Minnesota (Svedarsky, 1988), 161 km in Wisconsin (Hamerstrom and Hamerstrom, 1949), and 30 km in Michigan (Ammann, 1957). Roberts (1936) summarized several accounts of large flocks of Greater Prairie-Chickens from Minnesota and northern Iowa moving to Missouri for the winter; the movements were presumably more pronounced, especially during severe winters. In recent years, the species is largely nonmigratory, moving only short

distances (<48 km) (Svedarsky and Van Amburg 1996). For example, Schroeder and Braun (1993) reported partial migration in a Greater Prairie-Chicken population in northeastern Colorado; radio-marked birds migrated as much as 40 km between breeding and wintering areas and seemed to display fidelity to both their breeding and wintering sites.

Species' Response to Management

Fire

Throughout the Greater Prairie-Chicken range, fire and grazing are the main management practices that affect vegetation structure and composition on native prairies and shrublands in the Greater Prairie-Chicken range (Bidwell and others, 2003). The synthesis by Shaffer and DeLong (2019) includes a comprehensive review of fire, grazing, and their interaction in North American prairies. Studies that have evaluated the Greater Prairie-Chicken's response to both fire and grazing will be covered in the "Fire and Grazing" subsection, and studies that addressed the species' response to grazing-only will be covered in the "Grazing" subsection.

Although fire has been an evolutionary force that helped shape and maintain the prairie ecosystem for thousands of years (Higgins, 1984; Pyne, 1986), few studies have examined Greater Prairie-Chicken response to fire-only management. Reinking (2005) synthesized avian responses to fire regimes in the tallgrass prairies. The impacts of fire on the Greater Prairie-Chicken and other birds will differ depending on the time of year that a burn occurs and the frequency of burns among years. For example, spring and early summer fires may negatively impact prairie-chickens and other grassland birds because the timing coincides with the nesting season (Reinking, 2005). Prairie-chicken nests may be destroyed or abandoned if the fire occurs during the nesting season (Johnson, 1934; Zimmerman, 1997). Patten and others (2007) suggested that there may be tradeoffs associated with fire; for example, Greater Prairie-Chickens may benefit from an increase in arthropod biomass, but the loss of cover may negatively impact the species. Infrequent fires or the absence of fire may negatively impact prairie-chickens by increasing buildup of residual cover and litter (Westemeier, 1973) or by shifting grasslands to a state of dominance by woody vegetation (Reinking, 2005). In Illinois, Greater Prairie-Chicken nest densities were higher in redbottom-dominated grasslands in the second, third, and fourth nesting seasons after a March or August prescribed fire than in recently burned redbottom grasslands or unburned redbottom grasslands that were seeded ≥ 2 years earlier (Westemeier, 1973).

Current management practices that emphasize annual or near-annual spring burns (Reinking, 2005; Towne and Craine, 2016) have shifted many Kansas and Oklahoma rangelands to structurally homogeneous, grass-dominated habitats, rather than the patchy mosaic of varying structure that once existed

(see "Fire and Grazing" subsection). In Oklahoma tallgrass prairies, Patten and others (2007) reported that lekking male Greater Prairie-Chickens were not affected adversely by spring burns, but females avoided nesting on recently spring-burned patches; only 19 percent of 74 nests were in burned prairie, but no difference in nest success was detected between burned and unburned prairies. Female prairie-chickens preferred burned tallgrass prairies in subsequent nesting attempts, especially after grassland vegetation in May recovered from the burn (Patten and others, 2007).

Grazing

Huss (1996) defined a grazing system (for example, continuous year-long grazing, seasonal grazing, deferred-rotation grazing) as a specialization of grazing management that defines the periods of grazing and nongrazing; Huss (1996) further defined a grazing system as the manipulation of livestock grazing to accomplish a desired result. Grazing systems are not a panacea for solving all problems in grassland management, such as providing adequate residual cover for wildlife. Each grazing system produces different landscape patterns, plant composition, and habitat structure (Bidwell and others, 2003). Shiflet and Heady (1971) and Heady (1974) reviewed published studies on specialized grazing systems and concluded that grazing systems vary from highly successful to highly unsuccessful; the authors emphasized the importance of range-improvement practices that improve both the production of livestock and vegetation. After reviewing numerous studies, Van Poolen and Lacey (1979) concluded that adjustments in animal numbers have a greater effect on herbage production than do grazing systems. Wilson (1986, p. 221) stated, "The total stocking intensity is the most important factor affecting rangeland productivity and stability." No grazing system will provide adequate residual vegetation if the stocking rate is too high. J.D. Kobriger (North Dakota Game and Fish Department [retired], Dickinson, North Dakota, written commun., [n.d.]) had "come to the conclusion that it all boils down to stocking rates. You can abuse any system if you overstock. On the other hand, you can have residual grass left in any system if you monitor it, stock it right, and remove the critters when use gets to a certain point."

In much of their current range, Greater Prairie-Chickens persist on rangelands. Optimizing livestock and Greater Prairie-Chicken production, as well as production of other desirable plant and animal populations, is difficult in many if not all settings. Sidle (2005) discussed the challenges in balancing livestock production and habitat for Greater Prairie-Chickens and Sharp-tailed Grouse on Federal lands. The suitability of grassland habitat for prairie grouse is mostly determined by the amount of residual vegetation (that is, the height and density of vegetation measured in the fall) remaining after livestock grazing (Sidle, 2005). Greater Prairie-Chickens prefer the mosaic of grassland patches (including greater vegetation diversity and an interspersed short grass,

bare ground, and tall grasses and forbs) created by grazing systems that apply light-to-moderate grazing pressure intensity (that is, a measure of stocking rate over a defined period of time) over intensive grazing systems that apply high grazing intensity that reduce grass and shrub cover (Bidwell and others, 2003). Moreover, cattle that graze in current rangelands typically are 30–40 percent larger than the 454-kilogram (kg) standard used in most animal unit month (AUM) allotments on public lands (Scarnecchia, 1985; Uresk, 2010). Larger cattle require more forage, and therefore stocking rates may need to be adjusted to use forage in proportion to the carrying capacity of the rangeland resource. L.L. McDaniel (U.S. Fish and Wildlife Service [retired], Valentine, Nebraska, written commun., [n.d.]) observed that, when annual AUMs were reduced from 50,000 to 10,000 on Valentine National Wildlife Refuge in Nebraska, there was a five-fold increase in booming male Greater Prairie-Chickens.

The substantial increase in Greater Prairie-Chickens on the SNG in North Dakota between 1961 and 1987 was attributed mostly to changes in land management, primarily grazing practices (Kobriger and others, 1988; Manske and others, 1988). When the SNG was managed with season-long grazing (grazed for 8 months in 1940–54 and for 6 months in 1955–67), the population apparently was kept near the threshold of extinction. Pastures grazed season-long had VORs <15 cm (Manske and others, 1988), the minimum necessary to provide adequate concealment cover for nesting or roosting prairie-chickens (Manske and Barker, 1981; Manske and others, 1988). Beginning in 1971, prairie-chicken populations on the SNG increased during a period when grazing management began to switch from season-long grazing to rotational grazing systems, especially a three-pasture twice-over grazing rotation system (sometimes in combination with burning of meadows). Newell (1987) determined that the majority (59.2 percent) of 59 prairie grouse nests on SNG lands were in deferred grazing systems involving a three-pasture rotation (that is, all three pastures were grazed every year with grazing deferred in one pasture each year during the peak growing period from May to mid-September). The deferred pasture typically was used by both brooding and nonbrooding hens more than the other two pastures in the rotation. Nest success was low in pastures that were grazed season-long (that is, grazed during the entire growing season); only one of seven nests successfully hatched (Newell, 1987).

Jensen (1992) reviewed seven studies from North Dakota and South Dakota (Kohn, 1976; Mattise, 1978; Manske and Barker, 1981; Grosz, 1982; Rice and Carter, 1982; Newell and others, 1986; Sedivec and Barker, 1989), each of which evaluated grazing systems relative to providing adequate residual cover for prairie grouse. Jensen (1992) stated that most evidence seemed to support a three-pasture, once-over, deferred grazing system as an optimal means of providing residual cover, a critical element for nesting Greater Prairie-Chickens; that is, all three pastures were grazed every year with grazing deferred in one pasture each year during the peak growing period from May to mid-September. Kobriger and

others (1988) mentioned that Greater Prairie-Chicken populations began to decline in the SNG in North Dakota in the early 1980s. Changes in grazing systems, including the implementation of short-duration, rapid-rotation systems (that is, cattle are moved every 12 days among three pastures); reduction of prescribed fires; and possible changes in crops available for winter food made it difficult to attribute population declines to a single factor. Kobriger and others (1988) suggested that implementing rapid-rotation systems should be delayed until wildlife effects were more thoroughly evaluated. Bidwell and others (2003) stated that rotational grazing, as it is normally applied, with small paddocks, high livestock density, and rapid rotations, does not provide the landscape pattern, habitat structure, or plant community composition preferred by the Greater Prairie-Chicken.

On Fort Pierre National Grassland in South Dakota, Rice and Carter (1982) determined that height and density of ungrazed forage was affected by both the grazing system and the stocking rate of individual allotments. Rest-rotation grazing involved idling some pastures each year, whereas deferred-rotation grazing involved rotationally grazing all pastures once during the growing season but delaying the initiation date. Winter pastures were not grazed during the growing season and received little grazing pressure. When all range sites were combined, forage left ungrazed in rest-rotation systems was significantly greater than forage left ungrazed in deferred-rotation systems because of the forage present in the ungrazed rest-rotation pasture (Rice and Carter, 1982). Although the hectares per AUM for the rest-rotation grazing system were lower than for any other grazing system tested, this system still left more forage ungrazed than the deferred-rotation system. Comparisons between systems showed that winter pastures produced an average of 2.5 prairie-chicken nests and broods per 100 ha, ungrazed rest-rotation pastures produced 2.3 nests and broods per 100 ha, and deferred-rotation systems produced 0.21 nest and broods per 100 ha. Rest-rotation grazing systems were substantially more beneficial to nesting and brooding prairie-chickens than were deferred-rotation systems (Rice and Carter, 1982). Vegetative differences between rest- and deferred-rotation grazing systems reflected the grazing-system design rather than AUM usage. Even when nest counts from grazed pastures of the rest-rotation system were included in the analysis, there were still significantly higher densities of prairie-chicken nests and broods on rest-rotation pastures than on deferred-rotation pastures. Of all grazing systems sampled, deferred-rotation pastures were least preferred by nesting and brooding prairie-chickens (Rice and Carter, 1982). Although the stocking rates of deferred-rotation systems were less than rates for rest-rotation systems, the amount of ungrazed forage was lower. Grazing all pastures each year apparently left insufficient residual vegetation to meet minimum requirements for nesting and brooding prairie-chickens. Nesting use and success, as related to residual cover, were dependent on about 1,121 kg of forage per ha being present no matter which grazing system was sampled (Rice and Carter, 1982).

Fire and Grazing

Managers often use a combination of burning and grazing as a tool in grassland management. The pattern of burning and grazing (for example, the frequency, seasonality, intensity, and extent) as well as the interaction between fire and grazing are important considerations in applying these practices to meet the year-round habitat requirements of Greater Prairie-Chickens and restore habitat for the species (Bidwell and others, 2003). Early European settlers of the tallgrass prairies of the Flint Hills observed that livestock selected forage from burned range more readily than unburned range and that livestock gained weight faster on burned than unburned range (Hensel, 1923; Higgins and others, 1989; Allen and Palmer, 2011). Traditionally, livestock producers in the Flint Hills burned every 2–3 years with season-long stocking and grazing from May to October, which created a mosaic of burned and unburned areas in the region (Robbins and others, 2002). Beginning in the early 1980s, however, rangeland management in the Flint Hills and surrounding areas shifted from season-long grazing to a grazing system that involves intensive early-season stocking with annual burning (often abbreviated as IESB) to improve forage value and use by livestock (Applegate and Horak, 1999; Horton and Wolfe, 1999; Robbins and others, 2002). Under IESB grazing management, most grasslands in the Flint Hills are burned annually in March and April, and livestock are released into pastures between mid-March and mid-May (Robbins and others, 2002). Livestock are released into burned areas as soon as 10 days postburn and remain on the burned pastures for 90–120 days (Robbins and others, 2002). Under season-long stocking conditions, livestock remained on pastures longer but at lower stocking rates, whereas under IESB grazing management, livestock are on pastures for shorter periods but at higher stocking rates (as much as double the rate under season-long conditions) (Robbins and others, 2002). The practice of spring burning and intensive early-season grazing produces a homogeneous vegetation structure (Coppedge and others, 2008), removes nesting and brood-rearing cover for Greater Prairie-Chickens (Svedarsky and others, 2000; Clubine, 2002; Robbins and others, 2002), and has been implicated in the species' population decline (Robbins and others, 2002). In the Flint Hills and Smoky Hills of Kansas, clutch initiation was delayed at the two Flint Hills study sites under the IESB grazing system (specifically, one head of livestock per 0.8 ha for 90 days or one head of livestock per 1.6 ha for 180 days), compared to a third study site in the Smoky Hills that received infrequent burning and had a lower grazing intensity (one head of livestock per >2 ha for 180 days) (McNew and others, 2011b). The authors speculated that burning may have affected the timing of clutch initiation if hens delayed egg-laying until the vegetative cover was sufficient to conceal nests; alternatively, site differences may have reflected differences in food availability or weather. McNew and others (2012b) analyzed the occupancy dynamics of Greater Prairie-Chickens at 112 sites in the Konza Prairie Biological

Station in northeastern Kansas over the course of 28 years and reported a 3.8 percent average annual decline, with an overall decline in occupancy of 40 percent. The probability of local Greater Prairie-Chicken extinction was affected by a weak interaction between grazing and the average frequency of prescribed fires. Sites that were not grazed were 1.8 times more likely to be colonized than sites that were grazed; there was a significant interaction between grazing and the average frequency of fire, which suggested that the effects of fire frequency on local prairie-chicken extinction may have depended on whether a site was grazed or ungrazed. In Oklahoma, Patten and others (2007) suggested that increased or continued extensive spring burning may cause female prairie-chickens to delay nesting attempts until more suitable habitat becomes available.

In response to declining populations of grassland bird species, Fuhlendorf and Engle (2001, 2004) promoted an alternative grazing system, termed patch-burn grazing (or pyric herbivory), for use in the Flint Hills and other mesic grasslands. Patch-burn grazing is a management strategy in which only a portion (for example, one-third) of the landscape is burned annually, and livestock preferentially graze on these burned areas, generating heterogeneity in vegetation structure and composition (Fuhlendorf and Engle, 2001, 2004; Starns and others, 2020). Patch-burn grazing attempts to mimic the historical grazing patterns of native grazers and thus has the potential to create a favorable mosaic of habitat patches and habitat structure across the landscape for Greater Prairie-Chickens, while maintaining high nutritional value for domestic livestock (Fuhlendorf and Engle, 2001). In tall-grass prairies in the Flint Hills of Kansas, McNew and others (2015) reported that sites under the patch-burn grazing system had a higher quality and quantity of Greater Prairie-Chicken nesting sites and subsequent nest survival compared to IESB sites. Nest-site selection and nest survival were both directly related to VOR, which was determined by the fire-return interval of a pasture. In the patch-burn grazing treatment, preferred nest sites were unburned patches that were not grazed by cattle (McNew and others, 2015).

In other studies within the Flint Hills in Kansas and Oklahoma, Winder and others (2017) determined that female Greater Prairie-Chickens that were captured and radio-marked at sites managed with patch-burn grazing selected areas with low stocking rates and high fire frequencies, although they avoided recently burned areas. Winder and others (2018) reported that mortality risk of female prairie-chickens was significantly reduced under patch-burn grazing management compared to IESB grazing management. Females had annual survival estimates that were 35 percent higher on patch-burn pastures than females on IESB pastures (Winder and others, 2018). Females that selected patch-burn pastures were more vulnerable to mammalian predators, whereas females that selected IESB pastures were particularly vulnerable to avian predators (Winder and others, 2018). In the southernmost extent of the Flint Hills in northeastern Oklahoma, Londe and others (2021a) monitored brooding and nonbrooding female

Greater Prairie-Chickens during May–July in a landscape managed under the patch-burn grazing system. Female Greater Prairie-Chickens selected patches 0–12 months postfire that had high abundances and biomasses of invertebrates compared to 13–24 and >24 months postfire patches. Greater Prairie-Chickens further modified their habitat selection within these food-rich patches by selecting patches with greater grass cover and denser vegetation that provided cooler temperatures during the hottest part of the day (Londe and others, 2021a). In northeastern Oklahoma, Hovick and others (2015a) assessed the stability of Greater Prairie-Chicken lek locations in the context of restoring the dynamic disturbance history of fire and grazing through patch-burn grazing. Most (65 percent) leks moved by nearly 1 km on an annual basis in response to shifting vegetation structure within a landscape that has spatial and temporal variability in grassland structure.

Few studies have examined the response of Greater Prairie-Chickens to patch-burn grazing outside of the Flint Hills. In Oklahoma (including areas inside and outside of the Flint Hills) and in Texas, Starns and others (2020) assessed the differences in vegetation structure created by patch-burn grazing compared to fire-only treatments to determine whether patch-burn grazing increased habitat heterogeneity for Lesser and Greater prairie-chickens during their distinct life-history stages. Compared to the fire-only treatment, patch-burn grazing improved those vegetation characteristics deemed critical to Lesser and Greater prairie-chicken reproduction, including higher forb coverage, reduced vegetation height and biomass, and longer intervals in which bare ground was present after fires (Starns and others, 2020). Canopy cover in the patch-burn treatment also maintained adequate canopy cover for prairie-chicken young, whereas canopy cover in the fire-only treatment exceeded the moderate canopy levels (25–60 percent, 20–30 cm tall) recommended for prairie-chicken young within 12 months postfire (Starns and others, 2020). In Missouri, areas of tallgrass prairie that were managed with patch-burn grazing received disproportionately higher use by radio-marked Greater Prairie-Chickens (Jamison and Alleger, 2009). Patch-burn grazing management units constituted 6–9 percent of the landscape but accounted for 34–39 percent of the locations of radio-marked birds. Jamison and Alleger (2009), however, cautioned that their results may have been biased because the areas chosen for treatment with patch-burn grazing were traditionally habitats occupied by prairie-chickens.

Haying

Harvest of grass or legume forage crops for hay or silage may negatively impact local populations of Greater Prairie-Chickens. The presence of hayfields and timing of harvest may have critical implications for the use of ecological patterning (that is, embedding a checkerboard of permanent grassland reserves to provide nesting and brood-rearing cover within the larger, productive agricultural matrix) (Hamerstrom and others, 1957) as a tool for maintaining populations of Greater

Prairie-Chickens (Ryan and others, 1998). In North Dakota, Kirsch and others (1973) noted that haylands did not support Greater Prairie-Chickens or Sharp-tailed Grouse. In Oklahoma, Bidwell and others (2003) indicated that haying before July 1 destroyed nests or killed young chicks, but haying after July 10 missed the optimal combination of forage protein and production for livestock. Late haying also does not allow enough time for vegetation regrowth to maintain adequate nesting cover and plant vigor for the next growing season (Bidwell and others, 2003). In Wisconsin, Greater Prairie-Chicken hens showed strong selection of hayfields during selection of nest sites within their home ranges but showed no affinity for hayfields at the landscape level (Hardy and others, 2020). In Illinois, Westemeier and Buhnerkempe (1983) reported that hatching densities of successful prairie-chicken nests in seeded native grass stands were higher in high-mowed (>30 cm; 0.18 hatch per ha) stands than densities in seeded native grass stands that were hayed (0.05 hatch per ha) or undisturbed (0.08 hatch per ha). In Illinois and Missouri, harvest of forage caused loss of Greater Prairie-Chicken nests and young (Yeatter, 1963; Ryan and others, 1998).

Prairie-chicken broods may forage in areas that have been disturbed by haying, burning, or grazing. In the SNG in North Dakota, Greater Prairie-Chicken broods foraged in areas that had been mowed or grazed and used adjacent dense vegetation for loafing or escape cover (Manske and Barker, 1988). In Minnesota, Svedarsky (1988) reported that, after hatching, broods generally moved directly from undisturbed cover surrounding nests to bluestem grasslands that had been hayed, burned, or grazed the previous year. In a large tallgrass prairie in Missouri, prairie-chicken broods foraged in prairie hayfields and pastures (Burger and others, 1989).

Management Frequency

The timing of optimal nesting conditions after a recent disturbance (burning, grazing, haying) or after a recent seeding is difficult to quantify because of large site-to-site and regional variability. Kirsch (1974) suggested that prairie-chickens in North Dakota probably do not begin nesting in newly seeded grasslands until 2–3 years after appropriate residual cover has been established. Stands tend to lose their value as nesting habitat between 5 and 7 years after seeding, indicating that decreasing vigor of the plants and succession had made those areas less suitable to Greater Prairie-Chickens (Kirsch and others, 1973). In Minnesota, Kimmel and others (1994) noted that cool-season grass CRP plantings lose value as nesting cover sooner than warm-season grass plantings, and that cool-season plantings should be rejuvenated more often (every 3–5 years) than warm-season plantings. In Missouri, 72 percent of 37 nests in prairie occurred 2 years after haying, and the remainder were in prairies with various postdisturbance ages (Jones, 1988). In Illinois, Sanderson and others (1973) documented low nest densities in (1) newly seeded meadows in their first full growing season, (2) meadows burned the previous August

or March, and (3) fields hayed the previous year. Sanderson and others (1973) and Westemeier (1973) determined that more optimal prairie-chicken nesting habitat in Illinois was in redtop and timothy seedings during the second to fourth growing seasons after implementation of management treatments than in the fifth or later growing seasons. The management treatments included idle (that is, no disturbance); seeding; burning; haying; or high mowing for seed, weed control, or structure enhancement.

Early spring availability of good residual cover is important for Greater Prairie-Chickens because it permits early nesting by experienced hens, which lay the largest clutches, and increases the total period available for nesting, which may accommodate one or two renesting attempts if needed (Kirsch, 1969). In Minnesota, early nests have the potential to produce more offspring because early nests have larger clutches than later nests and because broods tend to hatch before heavy spring rains; furthermore, chicks that hatch earlier in the season will be older going into the fall and may have higher survival (Svedarsky, 1979).

Planted Cover

Planted cover, such as grasslands enrolled in the CRP, may provide suitable habitat in some parts of the Greater Prairie-Chicken's range or during some periods in the species' annual cycle (Boyd and others, 2011). CRP grasslands are important habitats for Greater Prairie-Chickens as they provide habitat diversity and connectivity, contribute to increased grassland patch size, promote range expansion, and mitigate for grassland loss. Rodgers and Hoffman (2005) reviewed the effects of the first decade (1985–95) of CRP grassland management on Greater Prairie-Chicken populations and noted that range expansions or population increases were dependent on maintaining height and density of grass stands specific to the species' needs. Range expansions or population increases occurred in native, warm-season grasslands in southwestern Nebraska and western Kansas and in tame, cool-season grasslands in North Dakota, South Dakota, southeastern Nebraska, and Minnesota (Rodgers and Hoffman, 2005). No range expansions or population increases were reported for Colorado, central Kansas, or Missouri. In Colorado, CRP stands reached a height of only 10–15 cm and provided insufficient cover for Greater Prairie-Chickens; in Missouri and central Kansas, stands became too tall and dense for Greater Prairie-Chickens (Rodgers and Hoffman, 2005).

In west-central Kansas, Fields (2004) reported that nesting hens (Greater and Lesser prairie-chickens combined) used grass CRP fields (that is, CRP fields seeded with just grass species) and interseeded CRP fields (that is, grass CRP fields interseeded with forbs) more than expected based on availability. Nesting hens used cropland, rangeland, and forb CRP fields (that is, CRP fields seeded with both grass and forbs) less than expected. Greater use of interseeded CRP fields and grass CRP fields was attributed to greater abundance

of invertebrates and cover provided by these two habitats, respectively. Hens with broods used cropland less than expected but showed no selection for any of the other habitat types (Fields, 2004). In a sample of 289 nests in western Minnesota, Toepfer (unpub. data in Svedarsky and others, 1999) reported that 66.1 percent of the nests were in CRP grasslands and 33.9 percent were in grasslands dominated by native species, but nesting success was higher in the native grasslands than in the CRP grasslands. Toepfer did not test whether the habitats selected for nesting reflected the overall composition of CRP and native prairie in the landscape or whether the results reflected greater attraction to CRP grasslands by prairie-chickens. The CRP grasslands generally lacked the plant species diversity of native grasslands and often consisted of only one or two plant species. In a second Minnesota study, Kimmel and others (1994) evaluated cover characteristics of warm-season and cool-season grasses in established CRP plantings. Kimmel and others (1994) determined that percentage of litter cover increased with stand age for cool-season plantings but not for warm-season plantings. Litter depth was not related to stand age in either type of planting. Values for VOR declined with age of cool-season grass stands but increased with age of warm-season grass stands (Kimmel and others, 1994).

Woody Vegetation

Current populations of Greater Prairie-Chickens are largely confined to grassland landscapes, although the species may use shrubs or trees during some portions of their annual cycle (for example, for winter or nighttime roosting habitat; Svedarsky, 1979; Manske and Barker, 1988; Toepfer and Eng, 1988; Rosenquist, 1996; Johnson and others, 2020) or in some landscapes (Emery, 2013). Historically, the species may have used woody vegetation more frequently (for example, to access acorns; Gross, 1928, 1930; Schmidt, 1936; Johnson and others, 2020). Populations persist in savanna areas (for example, SNG in North Dakota), but the species avoids large expanses of wooded areas (Bidwell and others, 2003; Roberts and others, 2021). The species is considered highly sensitive to encroachment of woody plants into grasslands (Roberts and others, 2021). Trees also may produce an edge effect that encourages mammalian predators to hunt in an area and may provide perch sites for potential avian nest predators, such as American Crow (*Corvus brachyrhynchos*) and Black-billed Magpie (*Pica hudsonia*) (Bakker, 2003). Ammann (1957) and Hamerstrom and others (1957) suggested that optimal landscapes for Greater Prairie-Chickens should include <25 percent woody cover. In Nebraska, female Greater Prairie-Chickens avoided wooded areas and row crop fields (Raynor and others, 2019). In the Flint Hills of north-eastern Kansas, Greater Prairie-Chicken usage (measured by lek occurrence) declined as woody plant-dominated regimes displaced grassland-dominated regimes over a 23-year period (Roberts and others, 2021). In another Kansas study, Greater

Prairie-Chicken hens selected nesting locations with minimal tree cover (Hovick and others, 2015c). In the Flint Hills in Oklahoma, Greater Prairie-Chickens consistently avoided woodlands during all seasons (lekking, nesting, postnesting, and nonbreeding) (Londe and others, 2019). In Oklahoma, the expansion of eastern redcedar (*Juniperus virginiana*) and other woody vegetation into native prairies and other grasslands has resulted in habitat loss and commensurate declines in populations of Greater Prairie-Chicken and other grassland birds (Bidwell and others, 2016).

In northwestern Minnesota, Emery (2013) reported that hens with broods selected small clumps of tall, deciduous trees with an understory of grassland cover in a landscape dominated by soybeans. Studies in Minnesota (Svedarsky, 1979) and Missouri (McKee and others, 1998) reported that the presence of woody vegetation lowered Greater Prairie-Chicken nest success. In Wisconsin, Greater Prairie-Chicken hens selected areas where trees and shrubs had been mechanically removed and sprayed by herbicides during the current and previous year (Hardy and others, 2020). Hens were 2.7 times more likely to occupy areas where trees and shrubs had been removed during the previous year. Shrub and tree removal had a positive influence on hen survival, did not appear to affect brood survival, and had a weak or ambiguous relationship with nest survival (Hardy and others, 2020). In southwestern Missouri, McKee (1995) reported that 57.7 percent of 26 clutches hatched when woody cover at the nests was ≤ 5 percent, but only 17.6 percent of 17 clutches hatched when woody cover at the nests was > 5 percent. In another Missouri study, translocated and resident Greater Prairie-Chickens showed a strong avoidance of wooded areas (Carrollson and others, 2014).

Habitat and Predator Relationships

Greater Prairie-Chickens evolved with a variety of opportunistic predators (Schroeder and Baydack, 2001). Primary predators of Greater Prairie-Chicken nests include bullsnake (*Pituophis catenifer*), ground squirrels (Sciuridae), striped skunk (*Mephitis mephitis*), American badger (*Taxidea taxus*), Virginia opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), coyote, Black-billed Magpie, and American Crow (Gross, 1930; Lehmann, 1941; Yeatter, 1963; Svedarsky, 1988; Schroeder and Baydack, 2001; Bakker, 2003; Winder and others, 2016). Primary predators of adult and juvenile Greater Prairie-Chickens include coyote, red fox, Red-tailed Hawk (*Buteo jamaicensis*), Rough-legged Hawk (*Buteo lagopus*), Broad-winged Hawk (*Buteo platypterus*), Northern Harrier (*Circus hudsonius*), Great Horned Owl, and Northern Goshawk (*Accipiter gentilis*) (Berger and others, 1963; Hamerstrom and others, 1965; Sparling, 1975; Sparling and Svedarsky, 1978; Svedarsky, 1979, 1981; Rosenquist, 1996; Schroeder and Baydack, 2001).

In the northern portions of the species' range, the Greater Prairie-Chicken is exposed to predation by migrating, overwintering, or breeding Northern Goshawks. F.N. Hamerstrom

(deceased; Wisconsin Department of Natural Resources, Plainfield, Wisconsin, written commun., [n.d.]) suggested that the Greater Prairie-Chicken may have had limited evolutionary experience with the Northern Goshawk (but see Ross and others, 2006, who argued that the Greater Prairie-Chicken was native to northern prairies before European settlement). Where Northern Goshawk and prairie-chicken ranges overlap (mostly in Minnesota and Wisconsin), goshawks can be effective predators of adult prairie-chickens, especially those that display in late winter or early spring. Thus, spring may be a period of high mortality for male prairie-chickens because of their greater exposure (and perhaps reduced alertness) on booming grounds and the possible presence of increased numbers of migratory raptors. Toepfer (1988) reported the following number of published accounts of predation per raptor species of prairie-chickens on booming grounds: 10 Northern Goshawks, 2 Cooper's Hawks (*Accipiter cooperii*), 1 Red-tailed Hawk, 1 Great Horned Owl, and 1 Snowy Owl (*Bubo scandiacus*). Sparling (1975) and Svedarsky (1981) observed Northern Goshawks killing adult male prairie-chickens on booming grounds in Minnesota, and Burger (1988) had evidence of three Red-tailed Hawks killing prairie-chickens on booming grounds in Missouri. In South Dakota, Norton (2005) observed nestling Great Horned Owls feeding on an adult Greater Prairie-Chicken. In south-central Nebraska, Caven and others (2017) reported two observations of Prairie Falcons (*Falco mexicanus*) attempting to depredate Greater Prairie-Chickens at leks; one of the two attempts appeared to be successful.

Depredation of nests and broods is a potential limiting factor for Greater Prairie-Chicken populations. Nest predation is the primary cause of reproductive loss (Johnson and others, 2020). In South Dakota, the overall nest success of 50 Greater Prairie-Chicken nests was 80.2 percent; predation was the main cause of nest failure (Norton, 2005). In that same study, the survival rate of 85 Greater Prairie-Chicken chicks from hatching to fledging was 0.34; raptors were the main cause of chick mortality (Norton, 2005). In Nebraska, only 19 percent of 221 chicks from 20 broods survived to day 21, and chick mortality events were highest within 14 days of hatch (Schole and others, 2011). The cause of mortality for 87 percent of 24 radio-marked chicks was depredation. In Kansas, 67.6 percent of 34 Greater Prairie-Chicken nests failed because of depredation (Augustine and Sandercock, 2011). In north-central Kansas, Winder and others (2016) identified seven nest predators at Greater Prairie-Chicken nests; most nest depredation occurred during crepuscular or nighttime periods. Variation in nest attendance by female Greater Prairie-Chickens did not indicate avoidance of predator activity and was likely driven by physiological requirements of the female. Raptor depredation was the main cause of death for radio-marked chicks, followed by mammalian depredation. In a third Kansas study, 30 of 59 prairie-chicken (Greater and Lesser prairie-chickens combined) nests failed to hatch at least one chick; depredation accounted for 94 percent of nest failures (Fields, 2004). In

Missouri, Burger (1988) reported that 60 percent of 63 radio-marked prairie-chicken mortalities were the result of depredation by raptors, particularly Great Horned Owls and Red-tailed Hawks.

Predation is a commonly cited cause of mortality during translocations (Carrlson and others, 2014). In Missouri, 87.5 percent of 32 mortalities of translocated and resident Greater Prairie-Chickens were due to predation (Carrlson and others, 2014).

Human-modified landscapes and concomitant habitat changes have affected the density and search efficiency of some predators, making grassland-nesting birds and their nests and young more vulnerable to predation (Manzer and Hannon, 2005; McNew and others, 2011a); for example, trees along roads and drainage ditches, tree encroachment into grasslands, and electrical power poles provide perch sites from which raptors can hunt (Walk, 2004; Manzer and Hannon, 2005; Hovick and others, 2014b). In Kansas, McNew and others (2011a, 2012a) studied the life-history traits of Greater Prairie-Chicken populations on three independent sites with various degrees of landscape alteration. The first site was in contiguous grasslands (185-ha average grassland patch size, road density of 0.32 km of roads per km², 3 percent cropland) within the Flint Hills and was annually burned and intensively grazed (one head of livestock per 0.8 ha for 90 days). The second site, also in the Flint Hills, was in less-contiguous grasslands (average grassland patch size of 51 ha, road density of 0.57 km of road per km², 10 percent cropland) and was annually burned and moderately grazed (one head of livestock per 1.6 ha for 180 days). The two study sites in the Flint Hills both had low nest (7 percent and 12 percent, respectively) and brood (29 percent and 38 percent, respectively) survival but higher survival of adult females (47 percent and 68 percent, respectively) (McNew and others, 2011a, 2012a). The third site was in the Smoky Hills and was highly fragmented by agricultural development (average grassland patch size of 15 ha, a road density of 1.4 km per km², and 38 percent cropland); was infrequently burned, with fire return intervals >1 year; and had the lowest grazing intensity of the three study sites (one head of livestock per ≥2 ha for 90 days). On this site, there was higher nest (16 percent) and brood (48 percent) survival and lower adult female survival (32 percent) (McNew and others, 2011a). Predation was the primary cause of failed nests (94 percent) and adult female mortality (90 percent) (McNew and others, 2011a, 2012a). McNew and others (2011a) concluded that increased depredation of adult females was induced by a heavily fragmented landscape.

Trails may foster nest predation, and dense vegetation may be a barrier to predators (Capel, 1965; Schranck, 1972; DeLong and others, 1995). Capel (1965) reported that artificial waterfowl nests placed close to livestock trails experienced higher losses to predators than those placed farther from livestock trails. In North Dakota, Kirsch (1969) determined that red foxes readily used vehicle trails as access routes into idle cover.

Red fox and striped skunk are considered two of the most common mammalian predators of prairie-chicken nests throughout most of the eastern portion of the species' current range (Svedarsky, 1988). In a Minnesota study, 25 percent of 16 failed nests were depredated by striped skunks and 18.8 percent were depredated by red foxes (Svedarsky, 1988). However, red foxes generally have more impact on nesting prairie-chickens than striped skunks because they also commonly prey on nesting hens. Of 21 radio-marked hens in this study, 10 hens were lost to red fox or raptor predation (Svedarsky, 1988). Svedarsky (1988) reported that December prices for fox furs (an indicator of trapping pressure) over an 11-year period in Polk County, Minnesota, were positively correlated with booming-ground counts of Greater Prairie-Chickens that were completed two springs later. Svedarsky (1988) concluded that heavy trapping pressure during fall and winter on red fox and other potential predators, such as striped skunks and feral domestic cats (*Felis catus*), resulted in lower mammalian predator populations and more successful nesting and brood rearing in the following summer, as reflected in higher booming ground counts in the subsequent spring. Further evidence for the high impact of foxes on large ground-nesting birds can be found in the literature on ground-nesting waterfowl in grasslands. Waterfowl nest success typically increases in areas where coyotes tend to displace foxes (Ball and others, 1995; Sovada and others, 1995). In Montana, Ball and others (1995) studied waterfowl nesting in a heavily grazed grassland and recorded at least 48 broods per 100 breeding pairs, with variation in productivity attributed to grassland block size and red fox domination compared with coyote domination. In North Dakota and South Dakota, Sovada and others (1995) studied comparable study areas, except that some areas were dominated by red foxes and others by coyotes. Waterfowl nests in coyote-dominated areas experienced nearly twice (32 percent) the nesting success as those in fox-dominated areas (17 percent). During a 2-year study in Minnesota, Svedarsky (1992) reported an increase in apparent nest success from 8.3 percent of 12 nests to 61.3 percent of 31 nests for ground-nesting waterfowl and prairie grouse; Svedarsky (1992) suggested that an increase in coyote activity between the 2 years may have displaced red foxes, resulting in increased nest success in the second year.

Predator communities and densities vary spatially and temporally over the range of prairie-chickens. The distribution and abundance of coyotes in North America has expanded dramatically since the beginning of the 20th century (Newsome and Ripple, 2015; Cherry and others, 2016; Hody and Kays, 2018). For example, scent-post visitation indices suggested a doubling of coyote abundance in the agriculture and transition zones in Minnesota (which would include the prairie-chicken range) between 1978 and 2015; red fox populations have been relatively stable in Minnesota in recent years but populations have remained below the long-term average since 2006 (Dexter, 2016).

Since 1988, mammalian predators have been controlled at Prairie Ridge State Natural Area in Jasper and Marion counties in Illinois to improve nesting success of the Greater Prairie-Chicken and other ground-nesting birds (Walk, 2004). About 85 mammalian predators are removed from each county annually; apparent nesting success of 20 prairie-chicken nests from 1997 to 2000 was 55 percent (Walk, 2004).

Effects of Management on Invertebrate Resources

Habitat management can affect invertebrate populations, which are important food sources for prairie-chickens. In western North Dakota, Manske and Onsager (1996) reported that the migratory grasshopper (*Melanoplus sanguinipes*) abundance was 66–75 percent lower on twice-over grazed pastures than on season-long grazed pastures; apparently, the greater vegetation cover in the twice-over pasture reduced access for egg laying by grasshoppers. Grasshoppers favored bare, firm soil. Noetzel (1990, p. 7), however, noted that “Grasshoppers usually prefer to oviposit in undisturbed (not tilled) sites such as roadsides, pasture, CRP, and weedy fallow. Weedy fallow is attractive to grasshopper egg laying, both because the weeds attract [grass]hoppers and the soil is firm.” Clubine (2002, p. 3) reported that “The Osage (Oklahoma) and Flint Hills (Kansas) have been assaulted with broadleaf herbicides over the last 50 years, often by aircraft. The effect has been near total elimination of forbs, most of which are...used by prairie insects which are critical food for newly hatched grassland birds...” In Minnesota, Tester and Marshall (1961) reported that burning resulted in an increase in abundance of Orthoptera, Coleoptera, and Homoptera. However, Halvorsen and Anderson (1979) measured greater insect densities (770,395 per ha) in unburned control plots than in burned plots (44,460 per ha) in a Greater Prairie-Chicken management area in central Wisconsin. Hemiptera, Coleoptera, and Homoptera represented 70 percent of insects in the samples. Burning resulted in a significant increase in numbers of Hemiptera and Homoptera on a central Missouri prairie (Cancelado and Yonke, 1970) and certain families of Coleoptera, Diptera, and Homoptera on a Minnesota prairie (Van Amburg and others, 1981). In Missouri, Jones (1988) observed that haying may cause insects to concentrate near ground level, thus making them more readily available for foraging by prairie-chickens. The trade-off of foraging for insects in the open, however, is greater exposure of prairie-chickens to predators. For example, in Minnesota, Svedarsky (1979) observed a female Northern Harrier depredate a 30-day-old, juvenile Greater Prairie-Chicken in a recently hayed alfalfa field that was 2.5 cm tall.

Energy Development and Infrastructure

Optimal sites for wind-energy development typically overlap with Greater Prairie-Chicken habitats, particularly in the Flint Hills (McNew and others, 2014; Winder and others,

2014a; Ciarlante, 2018; Londe and others, 2019). Beston and others (2016) developed a prioritization system for 428 avian species to identify species most likely to experience population declines in the United States from wind facilities based on the species' current conservation status and the species' expected risk from wind turbines. At a score of 4.27 out of nine, the Greater Prairie-Chicken was among 40 species evaluated with an average priority score of at least a four or above out of nine. Beston and others (2016) estimated that 4.91 percent of the Greater Prairie-Chicken breeding population in the United States is exposed to wind facilities.

Research on the effects of wind-energy development on grouse has investigated direct effects, including collision mortalities (Winder and others, 2014a); indirect effects, including avoidance behaviors associated with wind turbines and other anthropogenic structures (Pruett and others, 2009; Winder and others, 2014b); and changes in trophic interactions or predation risk (Winder and others, 2014a, 2014b; Smith and others, 2017). At a small, 36-turbine wind facility in the Nebraska Sandhills, Smith and others (2016) observed lekking behaviors and male and female attendance at 15 leks in a distance gradient from 0.7 to 23.3 km from a wind facility. Female lek attendance at leks closer to wind turbines did not differ from attendance farther from turbines. Males closer to turbines spent less time in nonbreeding behaviors than males farther from turbines (Smith and others, 2016). Distance from wind turbines did not affect time spent performing booming displays, flutter, jumps, or agonistic behaviors. Smith and others (2017) reported that distance to wind turbines had no effect on daily survival of female prairie-chickens, that site occupancy of avian predators was lower within 2 km of turbines than beyond 2 km, and that site occupancy of coyotes did not vary significantly throughout their study site. Occupancy of other potential mammalian predators increased as distance from turbines increased (Smith and others, 2016). In another study at the same wind facility, Whalen and others (2017, 2018, 2019a, 2019b) reported that male Greater Prairie-Chickens adjusted the acoustic properties of their low-frequency vocalizations (that is, boom, cackle, whine, and whoop) in response to the noise generated by wind turbines. In particular, boom and whoop sound pressure levels and whine fundamental frequency were higher, boom duration was shorter, and biphonations in cackle vocalizations occurred less often at leks within 1 km of wind turbines compared to vocalizations at leks >1 km from wind turbines (Whalen and others, 2018). Noise associated with wind facilities has the potential to impact reproductive behavior and success by altering the effectiveness of vocal communications (Raynor and others, 2017, 2018; Whalen and others, 2017, 2018, 2019a). In particular, Whalen and others (2019b) reported that prairie-chicken vocalizations at small leks have the greatest potential to be masked by wind turbine noise, which may affect the breeding success of male and female prairie-chickens. In a third study at this wind-energy facility, Harrison (2015) and Harrison and others (2017) indicated that there was little evidence of an effect from the wind-energy facility on Greater Prairie-Chicken nest

survival; the significant factors determining nest-site selection were habitat factors (VOR, percent litter cover, percent standing dead vegetation cover, and litter depth) and landscape factors (distance to nearest highway or county roads, distance to transmission line). Similarly, Raynor and others (2019) reported that female Greater Prairie-Chickens showed no selection for or avoidance of wind turbines at this wind-energy facility, based on the availability of these features across their home range.

At a 67-turbine wind facility in northcentral Kansas, McNew and others (2014) did not detect an effect of wind-energy development on nest-site selection or nest survival of Greater Prairie-Chickens. At the same facility, Winder and others (2014a) reported that survival rate of female Greater Prairie-Chickens was significantly higher during the 3-year postconstruction period (0.57) than during the preconstruction period (0.32). Collision mortality events were rare and mostly associated with fences or transmission lines, and there was no increase in mortality because of predation. The proportion of mortalities attributed to avian predators, mammalian predators, and collisions also did not differ between the wind turbine preconstruction and postconstruction periods. Winder and others (2014a) suggested that wind-energy development may have affected predator activity through increased raptor mortality and avoidance behavior by mammalian predators, which may have resulted in decreased Greater Prairie-Chicken predation. Winder and others (2014b) did, however, find evidence of behavioral avoidance of wind turbines by female Greater Prairie-Chickens; females occurred at greater distances from wind turbines during the breeding season, and there was almost a two-fold increase in average home-range size from 54 km² during the preconstruction phase to 97 km² during the postconstruction phase (Winder and others, 2014b). Winder and others (2015b) reported that distance to wind turbine had a negative effect on lek persistence for leks that were <8 km from turbines during a 2–3 year postconstruction period; abandonment rate was about three times higher for leks <8 km from a turbine compared to leks that were 8 km or more from a turbine. Winder and others (2015b) also reported that the body mass of male prairie-chickens was about 2 percent lower during the postconstruction period, but the distance to wind turbines did not affect male body mass. In another Kansas study, oil and gas infrastructure had little impact on prairie-chicken nest placement or nest survival (Hovick and others, 2015c).

In northwestern Oklahoma, Pruett and others (2009) evaluated avoidance behavior of radio-tagged Greater Prairie-Chickens in response to power-transmission lines. The presence of tall structures in prairies led to avoidance of suitable habitat by prairie-chickens and served as a barrier to their movement. Female Greater Prairie-Chickens appeared to place nests and leks away from transmission lines; seven of 74 leks and one of 74 nests were within 2 km of a powerline. Most tracking locations of prairie-chickens were >1 km from a powerline (Pruett and others, 2009). In the Flint Hills in Oklahoma, female Greater Prairie-Chickens were more sensitive

to energy development during the postnesting and nonbreeding seasons than during the lekking and nesting seasons; avoidance distances differed across seasons, with avoidance thresholds up to 300–600 m for powerlines, 300–1,000 m for oil wells, and 80–100 m for roads (Londe and others, 2019). During the lekking period, females avoided powerlines, but use increased in areas of home ranges that were close to oil wells. During nest-site selection, female Greater Prairie-Chickens showed minimal avoidance of energy development (Londe and others, 2019). During the postnesting (brooding) period, female Greater Prairie-Chickens avoided powerlines, roads, and oil wells; the estimated avoidance distance during the postnesting period for powerlines, roads, and oil wells was 288, 74, and 325 m, respectively (Londe and others, 2019). In a third Oklahoma study, Ciarlante (2018) reported that prairie-chickens (Greater and Lesser prairie-chickens combined) occupied 7.95 percent of the State and estimated that the total area occupied by prairie-chickens in Oklahoma would be reduced to 1.5 percent if wind turbines were allowed to utilize this space.

The presence of other infrastructure (for example, center-pivot irrigation) also may affect prairie-chicken occurrence. In the Nebraska Sandhills, the distance to the nearest center-pivot irrigation location had the greatest effect on habitat use by female Greater Prairie-Chickens, followed by distance to the nearest wet meadow and distance to the nearest agriculture field (Hiller and others, 2019). The probability of Greater Prairie-Chicken presence increased with increasing distance to the nearest center-pivot location from 0 to 20 km; the probability of Greater Prairie-Chicken presence was >0.5 with distances >7 km from a center-pivot location (Hiller and others, 2019).

Translocation

Wild-trapped birds have been translocated to reintroduce or supplement Greater Prairie-Chicken populations in areas where they had been extirpated, areas where populations were low, or areas outside of their known historical range (Kruse, 1973; Toepfer, 1988; Toepfer and others, 1990; Westemeier and others, 1998a; Snyder and others, 1999; Niemuth, 2003; Walk, 2004; Bateson and others, 2014; Carrlson and others, 2014; Mussman and others, 2017). Historically, early efforts to translocate Greater Prairie-Chickens and other prairie grouse were unsuccessful, primarily because habitat was limited at the release sites or because managers and researchers failed to recognize the dispersal capabilities of the species, but new techniques and recognition of the dispersal capabilities and habitat needs of these species have increased the probability of success for translocations (Walk, 2004). Bateson and others (2014) evaluated the genetic diversity of 110 female Greater Prairie-Chickens that were translocated between 2006 and 2009 from Minnesota to Wisconsin, where genetic diversity was lower. Two years after the final translocation, the researchers detected introgression of unique Minnesota

alleles, and the translocation temporarily stemmed the ongoing erosion of genetic variation through genetic drift. In another Wisconsin study, Hardy and others (2018) evaluated factors that had the greatest relative influence on population viability of four populations of Greater Prairie-Chickens that were reinforced by translocations from within and outside of the study area. The largest decreases in site-specific extinction and largest increases in the number of sites persisting for 50 years were observed when more vulnerable populations were targeted for reinforcement (that is, the release of prairie-chickens into an existing population of conspecifics). Reinforcing the most stable populations resulted in the largest reduction in extinction probability (Hardy and others, 2018). Greater Prairie-Chickens that were translocated from Minnesota and Kansas to Illinois showed similar nesting cover preferences (smooth brome, redtop, timothy) as prairie-chickens native to Illinois (Westemeier and others, 1995). Fields in which 11 birds successfully nested had 100 percent VORs of 20 cm in late March. By the time of hatching (about June 1), VORs averaged 40 cm in Illinois, and in contrast to the slow green-up of native grasses, introduced cool-season grasses such as smooth brome and timothy provided early concealment for nesting prairie-chickens. Plant species composition was not as important because structural requirements were met (Westemeier and others, 1995). Translocations of Greater Prairie-Chickens into southeastern Illinois from larger, genetically diverse populations effectively removed detrimental variation associated with inbreeding depression, restored genetic variation to historical levels, and resulted in immediate increases in fitness (Bouzat and others, 2009). The researchers concluded that translocation can be an effective management tool for genetic restoration of wild populations nearing extinction, but the long-term viability of the population may not be certain unless the conditions that led to a species decline, such as habitat loss, are reversed. In Missouri, Carrlson and others (2014) compared survival between 58 resident and 54 newly translocated Greater Prairie-Chickens that were sourced from 325 km away in Kansas. Although survival increased throughout the breeding season for both resident and translocated prairie-chickens, translocated birds had lower average survival than resident birds through the breeding season. Resident and translocated prairie-chickens selected core protected prairie habitat over agriculture and avoided grasslands on private land (Carrlson and others, 2014). Using those same 58 resident and 54 translocated Greater Prairie-Chickens, Kemink and Kesler (2013) compared movement behavior using radio telemetry, and the authors reported that 54 percent of the translocated females and 19 percent of the translocated males permanently emigrated from the release site. Translocated prairie-chickens covered larger areas and had more elevated movements immediately following release compared to resident prairie-chickens. Kemink and Kesler (2013) concluded that post-translocations of prairie-chickens were likely associated with exploration rather than directional orientation toward their original capture locations.

Management Recommendations from the Literature

The Greater Prairie-Chicken is considered an area-sensitive species that requires large expanses of grassland habitat and open space (Hamerstrom and others, 1957; Samson, 1980; Horak, 1985; Sample and Mossman, 1997; Niemuth, 2000, 2011; Ribic and others, 2009; Herse and others, 2020). The species will benefit from large, unfragmented grasslands that are close to other populations of Greater Prairie-Chickens (Hamerstrom and others, 1957; Ryan and others, 1998; Johnson and others, 2003; Niemuth, 2003, 2011). Where necessary, Hamerstrom and Hamerstrom (1973) noted that protection of smaller habitat patches is warranted to ensure connectivity between populations.

Greater Prairie-Chickens require a variety of grassland habitats during their annual life cycle (Patten and others, 2007; Johnson and others, 2020). Hamerstrom and Hamerstrom (1973) suggested that management should provide all annual life-cycle requirements within the home range of the Greater Prairie-Chicken. Hardy and others (2020) suggested that such a goal could be reached by ensuring landscape heterogeneity during grassland management and concluded that it may be necessary to manage areas using several different management practices to provide habitat during multiple life-history stages of the Greater Prairie-Chicken. Boyd and others (2011), however, cautioned that too much heterogeneity (that is, heterogeneity made up of undesirable seral stages) may lead to fragmentation of useable habitat and negatively affect Greater Prairie-Chickens and other prairie grouse. Carrlson and others (2014) observed strong prairie-chicken selection for large and protected prairies of tallgrass prairies and recommended that habitat management should focus on expansion of core protected patches of prairie to promote higher survival and better chances of conservation success; core protected areas are high-quality habitats surrounded by a buffer-zone matrix of neutral (for example, agriculture) and non-hostile (for example, grasslands with few trees in the vicinity) habitats. Westemeier and others (1998a) stated that small, isolated Greater Prairie-Chicken populations, such as those in Illinois, cannot be conserved indefinitely with inadequate habitat. Ryan and others (1998) recommended managing contiguous prairie tracts over smaller, scattered prairie tracts within a landscape of privately owned agricultural land, because contiguous landscapes were more productive for Greater Prairie-Chickens.

Acknowledging that connectivity among prairie-chicken populations is an important component of prairie-chicken conservation, Niemuth (2000, 2011) recommended that future prairie-chicken conservation and management actions include a broad-scale landscape approach that focuses on maintaining appropriate landscape conditions so that the species can persist through time and flourish when local conditions (vegetation height, density, and composition) are favorable. Conversely, the intended benefits of modifying a patch with

suitable local characteristics may not be reached in an unsuitable landscape matrix. A landscape perspective is preferred over an approach that focuses on minimum area requirements because spatial landscape characteristics can influence metapopulation dynamics (for example, migration, isolation, and extinction processes among local populations) and patterns of area sensitivity (Ribic and others, 2009; Niemuth, 2011). Spatially explicit habitat models developed by Runia and others (2021) for North Dakota and South Dakota identified areas with high Greater Prairie-Chicken abundance where existing grasslands should be protected but also provided a conservation tool to identify and prioritize grasslands that could be restored to expand or connect existing populations of Greater Prairie-Chickens. Niemuth (2011) described characteristics of spatially explicit landscape models that would improve their applicability for conserving populations of grouse: models should incorporate prairie grouse biology, be developed at appropriate scales, and use accurate data with spatial and thematic resolution that are sufficiently fine to target sites for specific conservation actions.

Landscapes most suitable for Greater Prairie-Chicken lek sites consist of relatively higher elevation, grassland cover, low densities of anthropogenic structures (for example, energy development), and no trees (Gregory and others, 2011; Hovick and others, 2015b, 2015c). At a local scale, maintenance of lekking habitat has been a primary focus of management efforts because leks are easier to locate than nests and because female prairie-chickens usually select nest sites close to a lek (Anderson and Toepfer, 1999; Westemeier and Gough, 1999; Toepfer, 2007; Niemuth, 2011; Hovick and others, 2015b). Hovick and others (2015b) indicated that management practices that are focused on maintaining grassland cover while reducing the threat from woody encroachment and anthropogenic development are likely to benefit Greater Prairie-Chicken lek-site suitability. Merrill and others (1999) suggested that grasslands around traditional leks should be enlarged by restoring prairies and planting grasslands (for example, CRP). Svedarsky and Van Amburg (1996, p. 94) emphasized the importance of lek surveys in measuring the effectiveness of management actions: “booming grounds are an important reference point for management and an essential orientation and breeding center for prairie chickens.” Westemeier (1971, p. ii) suggested that “the number of cocks using a booming ground is a useful index of the quality of the neighboring habitat,” and thus is a general measure of the success of management actions as well as an indicator of population levels. Hamerstrom and Hamerstrom (1973) also indicated that the number of males on a lek can be used as an index of habitat quality, but Niemuth (2011) cautioned that lek-based landscape models and nonspatial population models make a variety of assumptions about what lek counts represent for populations of prairie-chickens and other prairie grouse. For example, lek attendance by males is not constant and may vary with weather, time of day and season, changes in land use, lek age, and presence of predators. Gregory and others (2011) further cautioned that male Greater Prairie-Chickens

may continue to display at leks after habitat degradation owing to site fidelity. In eastern Kansas, 15–20 percent of active leks were in areas of low suitability; low-suitability areas were generally in low-lying areas and were comprised of 51 percent grassland, 33 percent agriculture, 9 percent forests, 4 percent urban, and 3 percent water (Gregory and others, 2011). Niemuth (2011) and Runia and others (2021) suggested that the value of lek counts and survey data will increase if multiple State and Federal agencies adopt common standards and methodologies and if precise locations and lek attendance data are recorded.

Based on the hotspot theory of lek-site selection, nesting habitat may be a key factor driving lek-site selection, and thus lek sites often are near good nesting cover (Hovick and others, 2015a, 2015b). Several researchers recommended rejuvenating nesting cover by disturbing the vegetation every 3–5 years, especially by prescribed fires, to improve cattle forage, suppress woody vegetation encroachment, remove excess residual vegetation, and maintain plant vigor (Kirsch and others, 1973; Westemeier and Buhnerkempe, 1983; Horak, 1985; Toepfer, 1988; Applegate and Horak, 1999; Westemeier and Gough, 1999). In the eastern portion of the species’ current range, Svedarsky (1979) recommended that residual nesting cover should be managed to have 100 percent VOR at 25 cm and structure similar to managed smooth brome. Cover of this general structure should consist of at least 25–30 percent of management areas (Westemeier, 1971; Svedarsky and Van Amburg, 1996; Westemeier and Gough, 1999), should be near a similar percentage of brood habitats, and should be available early in the growing season (that is, March) to facilitate greater productivity of early nests (Yeatter, 1943; Baker, 1953). Some litter should be present, perhaps 5 cm, but litter depths >10 cm, litter coverage >25 percent, and maximum vegetation heights >50 cm are discouraged (McKee and others, 1998). Residual nesting cover is considered one of the key limiting factors throughout the range of the Greater Prairie-Chicken (Hamerstrom and others, 1957; Eng and others, 1988; Vodehnal, 1999) but may be more limiting in the western part of the range, where grazing is a more predominant land use. This limitation may result from lower primary productivity in drier western areas, season-long grazing, or the practices of mowing lowlands and excessive spring burning to increase livestock utilization (Eng and others, 1988; Applegate and Horak, 1999; Horton and Wolfe, 1999; Vodehnal, 1999). Modifying these practices by reducing burn frequency, adjusting the seasonality of burning, and reducing grazing intensity may provide the optimal residual cover needed by Greater Prairie-Chickens (Robbins and others, 2002). Buhnerkempe and others (1984, p. 385) concluded that “habitat should be managed so that 90% of the standing vegetation is distributed below 40 cm and the vertical aspect of vegetation should be dense up to that level.” The highest vegetation in the field should not exceed 80 cm.” McNew and others (2013) recommended that management focused on improving nesting habitat occur at the regional level by increasing the availability of nesting sites with standing litter or new growth to ≥ 25 cm during the nesting

period (April–July). Londe and others (2021b) suggested that maintaining nesting areas with adequate cover, such as taller vegetation, helps ensure cooler nest-site temperatures, helps maintain population viability, and helps buffer prairie-chicken populations against extreme temperatures and precipitation events. Kimmel and others (1994) suggested that cool-season grass plantings should be managed more frequently than warm-season grass plantings because cool-season grass plantings lose nesting cover value sooner as litter builds up. Westemeier (1973) recommended that no more than one-half of the nesting cover within 1,600 m of a traditional booming ground should be burned within a year.

Svedarsky (1988) recommended that brood-rearing habitats should be near nesting cover and provide physical protection from weather and predators; facilitate chick movement at ground level; support abundant insects; provide forbs, especially legumes, for insect diversity and as a direct food source; and provide openings for loafing and dusting. Brood habitats are generally different from nesting cover (Jones, 1963a, 1963b; Burger, 1988; Jones, 1988; Toepfer, 1988); the former requires more recent disturbances, and the latter generally needs to be disturbed less often between growing seasons to be used by nesting hens (Svedarsky, 1988). Norton and others (2010) cautioned against planting Japanese brome to improve Greater Prairie-Chicken brood habitat in the northern Great Plains. Planting shorter vegetation (for example, western wheatgrass) in valleys and flat areas would be beneficial to broods. Norton and others (2010) indicated that a diverse herbaceous component in both upland and lowland areas would facilitate chick movement and provide overhead cover from predators and cover from prolonged exposure to solar radiation.

Maintaining heavy cover (VOR >30 cm) for roosting, especially in lowlands, which are preferred roosting areas, will benefit Greater Prairie-Chickens (Ammann, 1957; Svedarsky, 1979; Toepfer, 1988; Toepfer and Eng, 1988). Use of lowlands for roosting may be related to predator avoidance (Gratson, 1988). In northern regions, herbaceous forbs and some woody vegetation are important to promote an adequate accumulation of snow that is necessary for snow burrowing (Toepfer, 1988; Rosenquist, 1996). Cattails (*Typha* spp.) and bulrushes (*Scirpus* spp.) provide adequate roosting cover if snow becomes crusted and inaccessible for snow burrowing (Hamerstrom and others, 1957). If wintering habitat is a limiting factor, Niemuth (2011) cautioned that lek-based habitat models may not include wintering habitat, necessitating adjustments in research, modeling, and conservation efforts.

Minimizing woody vegetation in grasslands is beneficial to Greater Prairie-Chickens because its presence is associated with lower nest success (Svedarsky, 1979; McKee and others, 1998), increased raptor predation (Peterson, 1979), and reduced open space and broad horizons preferred by Greater Prairie-Chickens and other prairie grouse (Fuhlendorf and others, 2017). Woody vegetation also contributes to habitat fragmentation, which is generally detrimental to area-sensitive species, such as the Greater Prairie-Chicken (Sample and

Mossman, 1997; Mechlin and others, 1999). Berger (2020) indicated that controlling eastern redcedar can be mutually beneficial to both prairie-chickens and livestock because prairie-chickens are intolerant of woody cover and because redcedars compete with grasses for water, nutrients, and sunlight, which can reduce forage availability for livestock. Raynor and others (2019) recommended reducing the presence of trees in the Nebraska Sandhills because female Greater Prairie-Chickens avoided wooded areas during the breeding season. To increase or maintain the number of males at individual leks, Adkins and others (2019) recommended protecting the areas surrounding known leks from encroachment by forests and developed areas. In northwestern Minnesota, Svedarsky (1979) recommended rotational spring burning of preferred Greater Prairie-Chicken nesting habitats and fall burning of willow lowlands to create better brood habitat. To increase core grassland areas for Greater Prairie-Chicken use, Roberts and others (2021) recommended strategic restoration of grassland boundaries by prioritizing and protecting core grassland areas from woody plant encroachment via frequent fires and local eradication of invasive woody vegetation.

Broadway (2015) recommended that periodic disturbances and management practices (for example, prescribed burning) that increase forb production and bare ground while reducing woody encroachment should emulate the spatial and temporal variation of historical disturbances in mixed and tallgrass prairie ecosystems, given that Greater Prairie-Chickens evolved under mechanistic abiotic factors that created heterogeneous plant communities. Bailey (1976) called for more prescribed fires to maintain grasslands and shrublands. Obermeyer and others (2011) suggested that the ideal fire-return intervals for Greater Prairie-Chickens is once every 3 years in tallgrass prairies, once every 5 years in mixed-grass prairies, and once every 7 years in shortgrass prairies. Frequent burning adversely affected habitat structure and reduced nesting success, and infrequent burning allowed woody plants to degrade habitat (Obermeyer and others, 2011). McNew and others (2012b) recommended rotational prescribed fires in tallgrass prairies at intervals no longer than 4 years.

Rice and Carter (1982) recommended that grazing management within the Fort Pierre National Grassland in South Dakota should consist of rest-rotation (that is, idling some pastures each year) and winter-pasture (that is, not grazing during the growing season) grazing systems. The rest-rotation system allows rancher permittees to maintain livestock allocations, while supporting the production of over four times as many prairie-chickens as in the deferred-rotation system. Rice and Carter (1982) also recommended that deferred-rotation grazing systems be discontinued on the Fort Pierre National Grassland because the minimum cover requirements for prairie-chickens of about 1,121 kg per ha of ungrazed forage could not be attained using this system. In southeastern Nebraska, Matthews and others (2013) recommended controlled burns, interseeding of forbs, tree removal, and prescribed grazing, which are techniques that would maintain the heterogeneity of established grasslands as well as benefit newly established grasslands.

Several studies have reported that Greater Prairie-Chickens and other grassland birds may benefit from the interaction between fire and grazing (Gregory and others, 2011; Hovick and others, 2014a, 2015c; McNew and others, 2015; Winder and others, 2017, 2018; Starns and others, 2020). Several authors have recommended changes in land management in the Flint Hills from annual spring burns to a patch-burn rotational system to promote grassland heterogeneity that provides sufficient vegetation cover (structure and composition) for lekking, nesting, brooding, and roosting (Gregory and others, 2011; Londe and others, 2019; Starns and others, 2020). In the Kansas Flint Hills, Winder and others (2018) concluded that habitat conditions generated by the patch-burn grazing system provided improved concealment and reduced mortality risk for female Greater Prairie-Chickens compared to habitat conditions generated by the IESB grazing system; the authors recommended providing incentives to private landowners to encourage implementation of the patch-burn grazing system to increase habitat heterogeneity in the Flint Hills. Hovick and others (2015c) suggested that Greater Prairie-Chickens benefit from patch-burn grazing in the Flint Hills because this practice creates areas with residual biomass to increase vegetation height for nesting, decreases the expansion of woody vegetation that is avoided by female prairie-chickens, and may buffer against reproductive losses associated with a variable climate. Hovick and others (2015a) emphasized the importance of managing for heterogeneous landscapes to create a broad range of thermal environments, which allows prairie-chickens to select nesting areas that improve thermal regulation and provide energy for other metabolic processes, especially in the context of projected increases in temperature from climate change.

Targeted outreach with land managers and adoption of bird-friendly haying schedules may improve the conservation status of Greater Prairie-Chickens and other imperiled grassland-nesting birds (Gruntorad and others, 2021). Gruntorad and others (2021) reported that 60 percent of landowners surveyed in the Nebraska Sandhills were willing to delay hay harvest for the conservation of both songbirds and gamebirds (including the Greater Prairie-Chicken) to allow birds to successfully nest and raise young. Several researchers recommended harvesting hayfields after nesting and brood rearing are completed (Hamerstrom and others, 1957; Westemeier, 1971, Niemuth, 2000). In Minnesota, Svedarsky (1979) recommended haying before May 25 or after July 15 to safeguard young prairie-chicken broods.

Loss of grasslands to crop production has been the greatest factor contributing to the decline of prairie-chicken populations, but small amounts of cropland in a grass-dominated landscape can have a positive effect on Greater Prairie-Chicken abundance and its long-term persistence by providing additional food resources during certain portions of the year (Hamerstrom and others, 1957; Niemuth, 2011). In the northern portion of the species' range, agricultural crops may promote optimal winter survival of Greater Prairie-Chickens (Hamerstrom and others, 1957; Toepfer, 1988; Vodehnal, 1999; Westemeier and Gough, 1999). In addition to their

winter values, food plots are readily used as spring feeding areas for adults and summer brood areas for hens and chicks (Hamerstrom, 1963; Svedarsky, 1979). Food plots or waste grain within management areas can minimize prairie-chicken movements (and perhaps mortality) if they are accessible to prairie-chickens that are using optimal roosting habitat (Burger, 1988; Rosenquist, 1996). Sunflowers are considered a premium winter food in terms of preference and palatability, but corn, because of its resistance to being knocked down by snow throughout the winter, and cereal grains are recommended as well (Church and others, 1989). Applegate and Horak (1999) and Westemeier and Gough (1999) suggested that, in most areas, the landscape should have a ratio of 25:75 cropland to grassland that provides nesting, brood-rearing, and roosting cover. Bidwell and others (2003) suggested that food plots <4 ha have little effect on Greater Prairie-Chicken survival in winter and may concentrate predators, but food plots may be important in regions where prairies and shrublands have been degraded or converted to introduced grasses. Bidwell and others (2003) further indicated that cultivated food plots may not be necessary for Greater Prairie-Chickens in large ($\geq 4,047$ ha), heterogeneous grasslands that are in various stages of plant succession.

CRP grasslands and other planted grasslands on private lands provide suitable habitat for Greater Prairie-Chickens throughout the year (Giesen and Schroeder, 1999; Merrill and others, 1999; Svedarsky and others, 2000; Rodgers and Hoffman, 2005; Adkins and others, 2019, 2021). Matthews and others (2013) recommended maintaining Federal farm programs, such as CRP, because these programs provide critical nesting habitat for Greater Prairie-Chickens. CRP enrollments that are large and contiguous with existing grasslands and wetlands are likely to have the highest conservation value for Greater Prairie-Chickens (Adkins and others, 2021). Maintaining existing CRP grasslands and wetlands in landscapes that have high levels of CRP grassland and wetland cover will have a positive influence on Greater Prairie-Chicken conservation (Adkins and others, 2019, 2021). Focusing management efforts on CRP enrollments contiguous to grasslands with known leks is likely to increase Greater Prairie-Chicken lek density and the number of males at leks (Adkins and others, 2019). Rodgers and Hoffman (2005) indicated that periodic haying or grazing could provide an opportunity to enhance CRP stand quality. In Missouri, however, Christisen and Krohn (1980) observed prairie-chickens in plantings of meadow fescue (*Schedonorus arundinaceus*), a cool-season tame grass, but suggested that meadow fescue was marginal grassland habitat because it formed dense sod and had a sparse overstory.

Direct efforts to control predator populations to increase numbers or productivity of Greater Prairie-Chickens and other prairie grouse are uncommon (Simpson and Esker, 1997; Schroeder and Baydack, 2001; Walk, 2004). Predator control typically is not practical because of the cost and intensity required at large scales and the negative sociopolitical ramifications (Williams and others, 1999; Schroeder and Baydack,

2001). Predator management for prairie grouse generally has been addressed through habitat manipulations and other habitat management alternatives. These include (1) improving characteristics of nesting and brood cover, (2) reducing predator access trails in nesting and brood cover, (3) reducing potential mammalian predator den sites (for example, rock piles, bulldozed piles of brush, and abandoned buildings), and (4) reducing potential raptor nesting sites and hunting perches (Anderson, 1969; Peterson, 1979; Westemeier, 1984; Walk, 2004). Because Great Horned Owls, Red-tailed Hawks, and many other raptors hunt from perches (Peterson, 1979) and because Greater Prairie-Chickens require high amounts of open space (Johnson and others, 2020), tree removal to reduce raptor hunting perches in prairie-chicken habitat has become a recommended practice in Illinois (Walk, 2004), Minnesota (Svedarsky, 1979; D.R. Trauba, Minnesota Department of Natural Resources, Watson, Minnesota, written commun., [n.d.]), Missouri (Burger, 1988), and Wisconsin (Keir, 1999). Tree removal reduces nesting sites for Great Horned Owls and Red-tailed Hawks, species that are uncommon in open prairie (R.K. Murphy, Eagle Environmental, Inc., Albuquerque, New Mexico, written commun., [n.d.]). Nesting sites for American Crows and Black-billed Magpies (nest predators in some areas) also would be reduced by tree removal. For the critically endangered Attwater's Prairie-Chickens, predator-deterrent fences to mitigate unusually high nest predation substantially increased nesting success; 82 percent of fenced nests successfully hatched at least one egg compared to 12 percent of unfenced nests (Morrow and Toepfer, 2020).

High predation rates negate the value of providing adequate nesting and brood-rearing cover, which emphasizes the importance of placing a high priority on managing habitats to reduce predation impacts during the nesting and brood-rearing periods (Svedarsky, 1979; Augustine and Sandercock, 2011). As with waterfowl, Greater Prairie-Chickens will benefit from management actions that maintain optimal residual cover for nesting (Duebbert, 1969), brood-rearing, and roosting; reduce or prevent predator access trails in all cover types (Capel, 1965; Kirsch, 1969); reduce nesting or denning sites for predators; reduce raptor hunting perches; and increase the block size of nesting cover (Johnson, 1985; Burger, 1988). In Missouri, Burger (1988, p. 100) recommended that "Management of greater acreages of nesting cover in larger tracts may reduce prairie-chicken nesting density and predator efficiency, thereby increasing nest success and female survival."

In Kansas, Hovick and others (2015b) recommended that future human development should avoid areas identified as highly suitable for Greater Prairie-Chicken leks (that is, areas of somewhat higher elevations, consisting of grassland vegetation and low densities of anthropogenic structures) and focus development on land-cover types of lower conservation concern. Raynor and others (2017) similarly recommended siting human-made infrastructure within row crops, urban peripheries, and other habitats that are already experiencing fragmentation and increased anthropogenic noise rather than in intact open grasslands.

In response to concerns regarding possible impacts (for example, noise, habitat disruption, disturbance, fragmentation, increased predator access) of wind facilities on prairie grouse, the U.S. Fish and Wildlife Service (Manville, 2004) recommended avoiding placement of wind turbines within 8 km of known leks for prairie grouse. Studies by Winder and others (2014b, 2015b) supported the 8-km buffer zone as an appropriate distance for the siting of turbines during energy development. Winder and others (2014b, 2015b) showed that male and female Greater Prairie-Chickens have negative behavioral responses to wind-energy development within 8 km of wind turbines. Because large, intact native prairies are irreplaceable and critical to sustaining populations of Greater Prairie-Chickens, Obermeyer and others (2011) recommended that areas with remaining grassland cover of >95 percent intactness should be avoided for wind-energy development and that no turbines be placed within a 1.6 km surrounding buffer. Obermeyer and others (2011) further recommended that impacts to optimal prairie-chicken habitat from wind-energy development should be offset through habitat restoration on existing intact grasslands.

Ring-necked Pheasants adversely impact Greater Prairie-Chicken abundance through nest parasitism, competition for habitat, disease transmission, and aggressive behavior at leks (Kimmel, 1988). Several researchers have recommended against introducing or managing to increase Ring-necked Pheasants in areas supporting remnant populations of Greater Prairie-Chickens (Gross, 1930; Leopold, 1931; Cottam and others, 1942; Grange, 1948; Hamerstrom and others, 1957; Sharp, 1957; Vance and Westemeier, 1979; Westemeier and others, 1998b). Leopold (1931) cautioned against introducing pheasants into areas supporting Greater Prairie-Chickens and suggested controlling pheasant numbers through hunting. Westemeier (1983) listed several management strategies to control pheasants in areas that support prairie-chickens, including mowing grass to 30 cm to reduce its attractiveness as escape cover for pheasants, burning in the fall rather than in the winter or spring to reduce roosting habitat for pheasants, live trapping and moving pheasants, establishing controlled pheasant hunting or shooting on sanctuaries that support prairie-chickens, and managing for pheasant habitat to draw pheasants away from critical prairie-chicken areas. In Illinois, control of pheasants by habitat manipulations and opportunistic shooting on prairie-chicken sanctuaries successfully eliminated parasitism of prairie-chicken nests by pheasants (Westemeier, 1988a). Niemuth (2011) recommended further investigation on habitat selection of prairie-chickens and other prairie grouse in relation to pheasant parasitism; landscape models that focus on interactions between prairie grouse and pheasants will help guide management to benefit prairie-chickens while minimizing or avoiding the negative effects associated with pheasants.

Berger (2020) indicated that Greater Prairie-Chickens and Sharp-tailed Grouse have competing resource needs and population drivers. In areas where the two species' ranges overlap, comanaging for the two species may force resource managers to prioritize conservation of one species over the other. Berger

(2020) suggested that prairie grouse conservation actions may be more effective if they are tailored to the individual species. Hiller and others (2019) indicated that successful management of these sympatric grouse species relies on knowledge of the differences in their life histories, habitat partitioning, and other considerations. Given that the Greater Prairie-Chicken's range has contracted more than the Sharp-tailed Grouse's range in the Great Plains and that the Greater Prairie-Chicken may be less adaptable than the Sharp-tailed Grouse, Hiller and others (2019) recommended that managers may want to first consider the potential outcomes of management on the Greater Prairie-Chicken before considering the outcomes on the Sharp-tailed Grouse. However, Obermeyer and others (2011) recommended that, where Greater and Lesser prairie-chickens' ranges overlap, preference should be given to restoration of Lesser Prairie-Chicken habitat because Lesser Prairie-Chickens are of higher conservation concern.

References

- Adkins, K., Roy, C.L., Andersen, D.E., and Wright, R.G., 2019, Landscape-scale Greater Prairie-Chicken-habitat relations and the Conservation Reserve Program: The Journal of Wildlife Management, v. 83, no. 6, p. 1415–1426. [Also available at <https://doi.org/10.1002/jwmg.21724>.]
- Adkins, K., Roy, C.L., Wright, R.G., and Andersen, D.E., 2021, Simulating strategic implementation of the CRP to increase Greater Prairie-Chicken abundance: The Journal of Wildlife Management, v. 85, no. 1, p. 27–40. [Also available at <https://doi.org/10.1002/jwmg.21960>.]
- Allen, M.S., and Palmer, M.W., 2011, Fire history of a prairie/forest boundary—More than 250 years of frequent fire in a North American tallgrass prairie: Journal of Vegetation Science, v. 22, no. 3, p. 436–444. [Also available at <https://doi.org/10.1111/j.1654-1103.2011.01278.x>.]
- Ammann, G.A., 1957, The prairie grouse of Michigan—Including results of investigations under Federal Aid in Wildlife research projects Michigan 5-R, 37R, and 70-R: Lansing, Mich., Michigan Department of Conservation, Game Division, 200 p.
- Anderson, L.C., 2012, Nest and brood site selection and survival of Greater Prairie-Chickens in the eastern Sandhills of Nebraska: Lincoln, Nebr., University of Nebraska, Master's Thesis, 141 p.
- Anderson, L.C., Powell, L.A., Schacht, W.H., Lusk, J.J., and Vodehnal, W.L., 2015, Greater Prairie-Chicken brood-site selection and survival in the Nebraska Sandhills: The Journal of Wildlife Management, v. 79, no. 4, p. 559–569. [Also available at <https://doi.org/10.1002/jwmg.876>.]
- Anderson, R.K., 1969, Mating and interspecific behavior of Greater Prairie Chickens: Madison, Wisc., University of Wisconsin, Ph.D. Dissertation, 131 p.
- Anderson, R.K., and Toepfer, J.E., 1999, History, status and management of the Greater Prairie-Chicken in Wisconsin, in Svedarsky, W.D., Hier, R.H., and Silvy, N.J., eds., The Greater Prairie-Chicken—A national look: St. Paul, Minn., University of Minnesota, Agricultural Experiment Station, Miscellaneous Publication 99-1999, p. 39–58.
- Applegate, R.D., and Horak, G.J., 1999, History and status of the Greater Prairie-Chicken in Kansas, in Svedarsky, W.D., Hier, R.H., and Silvy, N.J., eds., The Greater Prairie-Chicken—A national look: St. Paul, Minn., University of Minnesota, Agricultural Experiment Station, Miscellaneous Publication 99-1999, p. 113–121.
- Augustine, J.K., and Sandercock, B.K., 2011, Demography of female Greater Prairie-Chickens in unfragmented grasslands in Kansas: Avian Conservation & Ecology, v. 6, no. 1, 2. [Also available at <https://doi.org/10.5751/ACE-00429-060102>.]
- Augustine, J.K., and Trauba, D.R., 2014, Potential for behavioral reproductive isolation between Greater Prairie-Chickens and Sharp-tailed Grouse in west-central Minnesota: Journal of Ethology, v. 33, p. 15–24. [Also available at <http://doi.org/10.1007/s10164-014-0410-8>.]
- Bailey, A.W., 1976, Alberta's rangeland resources: Range-man's Journal, v. 3, no. 2, p. 44–46.
- Bain, M.R., and Farley, G.H., 2002, Display by apparent hybrid prairie-chickens in a zone of geographic overlap: The Condor, v. 104, no. 3, p. 683–687. [Also available at <https://doi.org/10.1093/condor/104.3.683>.]
- Baker, M.F., 1953, Prairie chickens of Kansas: Lawrence, Kans., University of Kansas, Museum of Natural History, State Biological Survey of Kansas, Miscellaneous Publication, no. 5, 68 p.
- Bakker, K.K., 2003, A synthesis of the effect of woody vegetation on grassland nesting birds: Proceedings of the South Dakota Academy of Science, v. 82, p. 119–141.
- Ball, I.J., Eng, R.L., and Ball, S.K., 1995, Population density and productivity of ducks on large grassland tracts in north central Montana: Wildlife Society Bulletin, v. 23, no. 4, p. 767–773.
- Ballard, W.B., and Robel, R.J., 1974, Reproductive importance of dominant male Greater Prairie-Chickens: The Auk, v. 91, no. 1, p. 75–85. [Also available at <http://doi.org/10.2307/4084663>.]

- Bateson, Z.W., Dunn, P.O., Hull, S.D., Henschen, A.E., Johnson, J.A., and Whittingham, L.A., 2014, Genetic restoration of a threatened population of Greater Prairie-Chickens: *Biological Conservation*, v. 174, p. 12–19. [Also available at <https://doi.org/10.1016/j.biocon.2014.03.008>.]
- Beehler, B.M., and Foster, M.S., 1988, Hotshots, hotspots, and female preference in the organization of lek mating systems: *American Naturalist*, v. 131, no. 2, p. 203–219. [Also available at <http://doi.org/10.1086/284786>.]
- Bélisle, M., 2005, Measuring landscape connectivity—The challenge of behavioral landscape ecology: *Ecology*, v. 86, no. 8, p. 1988–1995. [Also available at <https://doi.org/10.1890/04-0923>.]
- Bellinger, M.R., 2001, Loss of genetic variation in Greater Prairie-Chickens following a population bottleneck in Wisconsin: Milwaukee, Wisc., University of Wisconsin, Master's Thesis, 30 p.
- Bellinger, M.R., Johnson, J.A., Toepfer, J., and Dunn, P., 2003, Loss of genetic variation in Greater Prairie-Chickens following a population bottleneck in Wisconsin, U.S.A: *Conservation Biology*, v. 17, no. 3, p. 717–724. [Also available at <https://doi.org/10.1046/j.1523-1739.2003.01581.x>.]
- Berger, D.D., Hamerstrom, F., and Hamerstrom, F.N., Jr., 1963, The effect of raptors on Prairie Chickens on the booming grounds: *The Journal of Wildlife Management*, v. 27, no. 4, p. 778–791. [Also available at <https://doi.org/10.2307/3798493>.]
- Berger, D.J., 2020, Prairie grouse population trends and their historical drivers in the Nebraska Sandhills: Lincoln, Nebr., University of Nebraska, Master's Thesis, 242 p.
- Beston, J.A., Diffendorfer, J.E., Loss, S.R., and Johnson, D.H., 2016, Prioritizing avian species for their risk of population-level consequences from wind energy development: *PLoS One*, v. 11, no. 3, p. e0150813. [Also available at <https://doi.org/10.1371/journal.pone.0150813>.]
- Bidwell, T.G., Engle, D.M., Mosely, M.E., and Masters, R.E., 2016, Invasion of Oklahoma rangelands and forests by eastern redcedar and ashe juniper: Stillwater, Okla., Oklahoma State University, 12 p.
- Bidwell, T.G., Fuhlendorf, S., Harmon, S., Horton, R., Manes, R., Rodgers, R., Sherrod, S., and Wolfe, D., 2003, Ecology and management of the Greater Prairie-Chicken. Stillwater, Okla., Oklahoma State University, Extension Circular E-969, 13 p.
- Blanco-Fontao, B., Sandercock, B.K., Obeso, J.R., McNew, L.B., and Quevedo, M., 2013, Effects of sexual dimorphism and landscape composition on the trophic behavior of Greater Prairie-Chicken: *PLoS One*, v. 8, no. 11, p. e79986. [Also available at <https://doi.org/10.1371/journal.pone.0079986>.]
- Blus, L.J., and Walker, J.A., 1966, Progress report on the prairie grouse nesting study in the Nebraska Sandhills: *Nebraska Bird Review*, v. 34, no. 2, p. 23–30.
- Bouzat, J.L., Johnson, J.A., Toepfer, J.E., Simpson, S.A., Esker, T.L., and Westemeier, R.L., 2009, Beyond the beneficial effects of translocations as an effective tool for the genetic restoration of isolated populations: *Conservation Genetics*, v. 10, p. 191–201. [Also available at <https://doi.org/10.1007/s10592-008-9547-8>.]
- Bowman, T.J., and Robel, R.J., 1977, Brood break-up, dispersal, mobility, and mortality of juvenile prairie chickens: *The Journal of Wildlife Management*, v. 41, no. 1, p. 27–34. [Also available at <https://doi.org/10.2307/3800087>.]
- Boyd, C., Peterson, S., Gilgert, W., Rodgers, R., Fuhlendorf, S., Larsen, R., Wolfe, D., Jensen, K.C., Gonzales, P., Nenneman, M., Danvir, R., Dahlgren, D., and Messmer, T., 2011, Looking toward a brighter future for lekking grouse: *Rangelands*, v. 33, no. 6, p. 2–11. [Also available at <https://doi.org/10.2111/1551-501X-33.6.2>.]
- Bradbury, J.W., and Gibson, R.M., 1983, Leks and mate choice, in Bateson, P.P.G., ed., *Mate choice*: Cambridge, United Kingdom, Cambridge University Press, p. 109–138.
- Breisjøberget, J.I., Odden, M., Wegge, P., Zimmermann, B., and Andreassen, H., 2018, The alternative prey hypothesis revisited—Still valid for Willow Ptarmigan population dynamics: *PLoS One*, v. 13, no. 6, p. e0197289. [Also available at <https://doi.org/10.1371/journal.pone.0197289>.]
- Broadway, M.S., 2015, Greater Prairie-Chicken (*Tympanuchus cupido*) demographics in fragmented Wisconsin landscapes—Examining limiting vital rates: Stevens Point, Wisc., University of Wisconsin, Master's Thesis, 77 p.
- Brown, D.L., 1968, Prairie-chicken range appraisal: Texas Parks and Wildlife Department, Job Progress Report Project No. W-92-R-4, 12 p.
- Buhnerkempe, J.E., Edwards, W.R., Vance, D.R., and Westemeier, R.L., 1984, Effects of residual vegetation on prairie-chicken nest placement and success: *Wildlife Society Bulletin*, v. 12, no. 4, p. 382–386.

- Burger, L.W., Jr., 1988, Movements, home range, and survival of female prairie chickens in relation to habitat pattern: Columbia, Mo., University of Missouri, Master's Thesis, 108 p.
- Burger, L.W., Ryan, M., and Jones, D.P., 1989, Prairie-chicken ecology in relation to landscape patterns: *Missouri Prairie Journal*, v. 11, p. 13–15.
- Cancelado, R., and Yonke, T.R., 1970, Effect of prairie burning on insect populations: *Journal of the Kansas Entomological Society*, v. 43, no. 3, p. 274–281.
- Cannon, R.W., and Knopf, F.L., 1981, Lek numbers as a trend index to prairie grouse populations: *The Journal of Wildlife Management*, v. 45, no. 3, p. 776–778. [Also available at <https://doi.org/10.2307/3808720>.]
- Capel, S.W., 1965, The relationship between grazing and predator activity in four types of waterfowl nesting cover: Columbia, Mo., University of Missouri, Master's Thesis, 78 p.
- Carlson, C.E., 1942, The prairie chicken in Minnesota: *Conservation Volunteer*, v. 4, no. 20, p. 45–49.
- Carrlson, K.M., Kesler, D.C., and Thompson, T.R., 2014, Survival and habitat use in translocated and resident Greater Prairie-Chickens: *Journal of Nature Conservation*, v. 22, no. 5, p. 405–412. [Also available at <https://doi.org/10.1016/j.jnc.2014.03.008>.]
- Caven, A.J., Wiese, J.D., and Wallauer, W.R., 2017, Prairie Falcon depredation attempts on a Greater Prairie-Chicken lek in south-central Nebraska: *Prairie Naturalist*, v. 49, no. 2, p. 76–78.
- Cherry, M.J., Howell, P.E., Seagraves, C.D., Warren, R.J., and Conner, L.M., 2016, Effects of land cover on coyote abundance: *Wildlife Research*, v. 43, p. 662–670. [Also available at <https://doi.org/10.1071/WR16052>.]
- Christisen, D.M., and Krohn, R.B., 1980, Land use—A key to Greater Prairie-Chicken habitat in Missouri, in Vohs, P.A., ed., *Proceedings of the Prairie Grouse Symposium*: Stillwater, Okla., Oklahoma State University, p. 55–58.
- Church, K.E., Heffron, M., and Parrish, J.W., 1989, Assimilated energy of winter foods by Greater Prairie-Chickens, in Svedarsky, W.D., ed., *Abstracts of the Proceedings of the eighteenth Prairie Grouse Technical Council Conference*: Crookston, Minn., University of Minnesota, p. 10–11.
- Ciarlante, C.A., 2018, The intersection of wind energy and wildlife management—A case study of prairie-chickens and wind turbine site selection in Oklahoma: Norman, Okla., University of Oklahoma, Master's Thesis, 59 p.
- Clifton, A.M., and Kremetz, D.G., 2006, Estimating numbers of Greater Prairie-Chickens using mark-resight techniques: *The Journal of Wildlife Management*, v. 70, no. 2, p. 479–484. [Also available at [https://doi.org/10.2193/0022-541X\(2006\)70\[479:ENOGPU\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[479:ENOGPU]2.0.CO;2).]
- Clubine, S., 2002, Editorial: Clinton, Mo., Missouri Department of Conservation, *Native Warm-Season Grass Newsletter*, v. 21, no. 3, p. 1–3.
- Coates, M.E., Hewitt, D., and Golob, P., 1970, A comparison of the effects of raw and heated soya-bean meal in diets for germ-free and conventional chicks: *British Journal of Nutrition*, v. 24, no. 1, p. 213–225. [Also available at <https://doi.org/10.1079/BJN19700022>.]
- Cooke, W.W., 1888, Report on bird migration in the Mississippi Valley in the years 1884 and 1885: Washington, D.C., U.S., Department of Agriculture, Division of Economic Ornithology, *Bulletin No. 2.*, 313 p. [Also available at <https://doi.org/10.5962/bhl.title.54982>.]
- Coppedge, B.R., Fuhlendorf, S.D., Harrell, W.C., and Engle, D.M., 2008, Avian community response to vegetation and structural features in grasslands managed with fire and grazing: *Biological Conservation*, v. 141, no. 5, p. 1196–1203. [Also available at <https://dx.doi.org/10.1016/j.biocon.2008.02.015>.]
- Cottam, C., Leopold, A., Finley, W.L., and Cahalane, V.H., 1942, Report of the Committee on Bird Protection, 1941: *The Auk*, v. 59, no. 2, p. 286–300. [Also available at <https://doi.org/10.2307/4079558>.]
- Coues, E., 1874, *Birds of the Northwest—A hand-book of the ornithology of the region drained by the Missouri River and its tributaries*: Washington, D.C., U.S. Department of the Interior, Geological Survey of the Territories, *Miscellaneous Publications No. 3*, 791 p. [Also available at <https://doi.org/10.5962/bhl.title.54063>.]
- Dastagir, S., DiMinni, K., Pritsky, J., and Saadati, H., 1997, *Evolution of leks*: New York, N.Y., Department of Biology, College of Arts and Science, New York University, 13 p.
- DeLong, A.K., Crawford, J.A., and DeLong, D.C., Jr., 1995, Relationships between vegetational structure and predation of artificial Sage Grouse nests: *The Journal of Wildlife Management*, v. 49, no. 1, p. 88–92. [Also available at <https://doi.org/10.2307/3809119>.]
- Dexter, M.H., ed., 2016, *Status of wildlife populations, Fall 2016*: St. Paul, Minn., Minnesota Department of Natural Resources, Division of Fish and Wildlife, 326 p.
- Drobney, R.D., and Sparrowe, R.D., 1977, Land use relationships and movements of Greater Prairie-Chickens in Missouri: *Transactions of the Missouri Academy of Science*, v. 10–11, p. 146–160.

- Duebbert, H.F., 1969, High nest density and hatching success of ducks on South Dakota CAP land: Transactions of the North American Wildlife and Natural Resources Conference, v. 34, p. 218–228.
- Emery, N., 2013, Seasonal resource selection, site-specific brood predictors, and nest characteristics of Greater Prairie-Chicken hens in northwestern Minnesota: Grand Forks, N. Dak., University of North Dakota, Master's Thesis, 74 p.
- Eng, R.L., Toepfer, J.E., and Newell, J.A., 1988, Management of livestock to improve and maintain prairie habitat on the Sheyenne National Grasslands, in Bjugstad, A.J., technical coordinator, Prairie chickens on the Sheyenne National Grasslands: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-159, p. 55–57.
- Fields, T.L., 2004, Breeding season habitat use of Conservation Reserve Program (CRP) land by Lesser Prairie-Chickens in west central Kansas: Fort Collins, Colo., Colorado State University, Master's Thesis, 136 p.
- Fuhlendorf, S.D., and Engle, D.M., 2001, Restoring heterogeneity on rangelands—Ecosystem management based on evolutionary grazing patterns: *BioScience*, v. 51, no. 8, p. 625–632. [Also available at [https://doi.org/10.1641/0006-3568\(2001\)051\[0625:RHOREM\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0625:RHOREM]2.0.CO;2).]
- Fuhlendorf, S.D., and Engle, D.M., 2004, Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie: *Journal of Applied Ecology*, v. 41, no. 4, p. 604–614. [Also available at <https://doi.org/10.1111/j.0021-8901.2004.00937.x>.]
- Fuhlendorf, S.D., Hovick, T.J., Elmore, R.D., Tanner, A.M., Engle, D.M., and Davis, C.A., 2017, A hierarchical perspective to woody plant encroachment for conservation of prairie-chickens: *Rangeland Ecology and Management*, v. 70, no. 1, p. 9–14. [Also available at <https://doi.org/10.1016/j.rama.2016.08.010>.]
- Fuhlendorf, S.D., Woodward, A.J.W., Leslie, D.M., Jr., and Shackford, J.S., 2002, Multi-scale effects of habitat loss and fragmentation on Lesser Prairie-Chicken populations of the U.S. southern Great Plains: *Landscape Ecology*, v. 17, no. 7, p. 617–628. [Also available at <https://doi.org/10.1023/A:1021592817039>.]
- Gibson, R.M., Aspbury, A.S., and McDaniel, L.L., 2002, Active formation of mixed-species grouse leks—A role for predation in lek evolution?: *Proceedings of the Royal Society of London B*, v. 269, no. 1509, p. 2503–2507. [Also available at <https://doi.org/10.1098/rspb.2002.2187>.]
- Giesen, K.N., and Schroeder, M.A., 1999, Population status and distribution of Greater Prairie-Chickens in Colorado, in Svedarsky, W.D., Hier, R.H., and Silvy, N.J., eds., *The Greater Prairie-Chicken—A national look*: St. Paul, Minn., University of Minnesota, Agricultural Experiment Station, Miscellaneous Publication 99-1999, p. 99–104.
- Golner, D.P., 1997, Analysis of habitat selection by female Greater Prairie Chickens in central Wisconsin: Stevens Point, Wisc., University of Wisconsin, Master's Thesis, 145 p.
- Grange, W.B., 1948, Wisconsin grouse problems: Madison, Wisc., Wisconsin Conservation Department, Publication No. 328-A, 318 p.
- Gratson, M.W., 1988, Spatial patterns, movements, and cover selection by Sharp-tailed Grouse, in Bergerud, A.T., and Gratson, M.W., eds., *Adaptive strategies and population ecology of northern grouse*: Minneapolis, Minn., University of Minnesota Press, p. 158–192.
- Gregory, A.J., McNew, L.B., Prebyl, T.J., Sandercock, B.K., and Wisely, S.M., 2011, Hierarchical modeling of lek habitats of Greater Prairie-Chickens, in Sandercock, B.K., Martin, K., and Segelbacher, G., eds., *Ecology, conservation, and management of grouse*: Berkeley, Calif., University of California Press, *Studies in Avian Biology*, p. 21–32. [Also available at <https://doi.org/10.1525/9780520950573-004>.]
- Gregory, A.J., Wisely, S.M., McNew, L.B., and Sandercock, B.K., 2018, A landscape perspective on rates of multiple paternity and brood parasitism among Greater Prairie-Chickens across Kansas, USA: *The Wilson Journal of Ornithology*, v. 130, no. 3, p. 626–638. [Also available at <https://doi.org/10.1676/17-043.1>.]
- Gross, A.O., 1928, The Heath Hen: *Memoirs of the Boston Society of Natural History*, v. 6, p. 491–588.
- Gross, A.O., 1930, Progress report of the Wisconsin prairie chicken investigation: Madison, Wisc., Wisconsin Conservation Commission, 112 p.
- Grosz, K.L., 1982, Sharp-tailed Grouse nesting and brood-rearing habitat in grazed and nongrazed treatments in south central North Dakota: Fargo, N. Dak., North Dakota State University, Master's Thesis, 72 p.
- Gruntorad, M.P., Graham, K.A., Arcilla, N., and Chizinski, C.J., 2021, Is hay for the birds? Investigating landowner willingness to time hay harvests for grassland bird conservation: *Animals (Basel)*, v. 11, no. 1030, p. 1–16. [Also available at <https://doi.org/10.3390/ani11041030>.]

- Hagen, C.A., Jamison, B.E., Robel, R.J., and Applegate, R.D., 2002, Ring-necked Pheasant parasitism of Lesser Prairie-Chicken nests in Kansas: *The Wilson Bulletin*, v. 114, no. 4, p. 522–524. [Also available at [https://doi.org/10.1676/0043-5643\(2002\)114\[0522:RNPPOL\]2.0.CO;2](https://doi.org/10.1676/0043-5643(2002)114[0522:RNPPOL]2.0.CO;2).]
- Halfmann, D.H., Toepfer, J.E., and Blondin, M.W., 2001, Natal dispersal of Greater Prairie-Chickens in Wisconsin, in Horton, R.E., compiler, *Proceedings of the twenty-fourth Prairie Grouse Technical Conference*: Woodward, Okla., p. 32–33.
- Halvorsen, H.H., and Anderson, R.K., 1979, An evaluation of grassland management techniques in central Wisconsin, in Anderson, R.K., ed., *Proceedings of the thirteenth Prairie Grouse Technical Council Conference*: Stevens Point, Wisc., University of Wisconsin, p. 10–12.
- Hamerstrom, F., Berger, D.D., and Hamerstrom, F.N., Jr., 1965, The effect of mammals on prairie chickens on booming grounds: *The Journal of Wildlife Management*, v. 29, no. 3, p. 536–542 [Also available at <https://doi.org/10.2307/3798054>.]
- Hamerstrom, F., and Hamerstrom, F., 1961, Status and problems of North American grouse—A contribution from the Wilson Ornithological Society Conservation Committee: *The Wilson Bulletin*, v. 73, no. 3, p. 284–294.
- Hamerstrom, F., and Hamerstrom, F., 1963, The symposium in review: *The Journal of Wildlife Management*, v. 27, no. 4, p. 868–887. [Also available at <https://doi.org/10.2307/3798501>.]
- Hamerstrom, F.N., Jr., 1939, A study of Wisconsin prairie chickens and Sharp-tailed Grouse: *The Wilson Bulletin*, v. 51, no. 2, p. 105–120.
- Hamerstrom, F.N., Jr., 1963, Sharptail brood habitat in Wisconsin's northern Pine Barrens: *The Journal of Wildlife Management*, v. 27, no. 4, p. 793–802. [Also available at <https://doi.org/10.2307/3798494>.]
- Hamerstrom, F.N., Jr., and Hamerstrom, F., 1949, Daily and seasonal movements of Wisconsin prairie chickens: *The Auk*, v. 16, no. 4, p. 312–337. [Also available at <https://doi.org/10.2307/4080275>.]
- Hamerstrom, F.N., Jr., and Hamerstrom, F., 1968, Water and the prairie chickens: *Wisconsin Academy of Science*, v. 15, p. 10–11.
- Hamerstrom, F.N., Jr., and Hamerstrom, F., 1973, The prairie chicken in Wisconsin—Highlights of a 22-year study of counts, behavior, movements, turnover, and habitat: Madison, Wisc., Wisconsin Department of Natural Resources, Technical Bulletin 64, 52 p.
- Hamerstrom, F.N., Jr., Hopkins, F., and Rinzel, A.J., 1941, An experimental study of browse as a winter diet for prairie chicken: *The Wilson Bulletin*, v. 53, no. 3, p. 185–195.
- Hamerstrom, F.N., Jr., Mattson, O.E., and Hamerstrom, F., 1957, A guide to prairie chicken management: Madison, Wisc., Wisconsin Conservation Department, Technical Wildlife Bulletin, no. 15, 128 p.
- Hanski, I.A., and Gaggiotti, O.E., eds., 2004, *Ecology, genetics and evolution of metapopulations*: San Diego, Calif., Elsevier Academic Press, 696 p.
- Hanski, I.A., and Gilpin, M.E., eds., 1997, *Metapopulation biology—Ecology, genetics, and evolution*: San Diego, Calif., Academic Press, 335 p.
- Hardy, M.A., Broadway, M.S., Pollentier, C.D., Radeloff, V.C., Riddle, J.D., Hull, S.D., and Zuckerberg, B., 2020, Responses to land cover and grassland management vary across life-history stages for a grassland specialist: *Ecology and Evolution*, v. 10, no. 23, p. 12777–12791. [Also available at <https://doi.org/10.1002/ece3.6805>.]
- Hardy, M.A., Hull, S.D., and Zuckerberg, B., 2018, Swift action increases the success of population reinforcement for a declining prairie grouse: *Ecology and Evolution*, v. 8, no. 3, p. 1906–1917. [Also available at <https://doi.org/10.1002/ece3.3776>.]
- Harrison, J.O., 2015, Assessment of disturbance effects of an existing wind energy facility on Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) breeding season ecology in the Sandhills of Nebraska: Lincoln, Nebr., University of Nebraska, Master's Thesis, 163 p.
- Harrison, J.O., Bomberger Brown, M., and Powell, L.A., 2018, Wild Turkey (*Meleagris gallopavo*) parasitism of a Greater Prairie-Chicken (*Tympanuchus cupido*) nest in Nebraska: *Grouse News*, v. 55, p. 8–11.
- Harrison, J.O., Bomberger Brown, M.B., Powell, L.A., Schacht, W.H., and Smith, J.A., 2017, Nest site selection and nest survival of Greater Prairie-Chickens near a wind energy facility: *The Condor*, v. 119, no. 4, p. 659–672. [Also available at <https://doi.org/10.1650/CONDOR-17-51.1>.]
- Heady, H.F., 1974, Theory of seasonal grazing: *Rangeman's Journal*, v. 1, no. 2, p. 37–38.
- Hensel, R.L., 1923, Effect of burning on vegetation in Kansas pastures: *Journal of Agricultural Research*, v. 23, no. 8, p. 631–644.
- Herse, M.R., With, K.A., and Boyle, W.A., 2020, Grassland fragmentation affects declining tallgrass prairie birds most where large amounts of grassland remain: *Landscape Ecology*, v. 35, no. 12, p. 2791–2804. [Also available at <https://doi.org/10.1007/s10980-020-01064-y>.]

- Hess, B.D., Dunn, P.O., and Whittingham, L.A., 2012, Females choose multiple mates in the lekking Greater Prairie-Chicken (*Tympanuchus cupido*): *The Auk*, v. 129, no. 1, p. 133–139. [Also available at <https://doi.org/10.1525/auk.2011.11095>.]
- Higgins, K.F., 1984, Lightning fires in North Dakota grasslands and in pine-savanna lands of South Dakota and Montana: *Journal of Range Management*, v. 37, no. 2, p. 100–103. [Also available at <https://doi.org/10.2307/3898892>.]
- Higgins, K.F., Kruse, A.D., and Piehl, J.L., 1989, Effects of fire in the northern Great Plains: Brookings, S. Dak., South Dakota State University, Publication EC 761, 47 p.
- Higgins, K.F., Naugle, D.E., and Forman, K.J., 2002, A case study of changing land use practices in the northern Great Plains, U.S.A.—An uncertain future for waterbird conservation: *Waterbirds*, v. 24, Special Publication no. 2, p. 42–50.
- Hiller, T.L., McFadden, J.E., Powell, L.A., and Schacht, W.H., 2019, Seasonal and interspecific landscape use of sympatric Greater Prairie-Chickens and Plains Sharp-tailed Grouse: *Wildlife Society Bulletin*, v. 43, no. 2, p. 244–255. [Also available at <https://doi.org/10.1002/wsb.966>.]
- Hody, J.W., and Kays, R., 2018, Mapping the expansion of coyotes (*Canis latrans*) across North and Central America: *ZooKeys*, v. 759, p. 81–97. [Also available at <https://doi.org/10.3897/zookeys.759.15149>.]
- Höglund, J., and Alatalo, R.V., 1995, *Leks*: Princeton, N.J., Princeton University Press, 198 p. [Also available at <https://doi.org/10.1515/9781400864157>.]
- Hoppe, I.R., Harrison, J.O., Raynor, E.J., IV, Bomberger Brown, M., Powell, L.A., and Tyre, A.J., 2019, Temperature, wind, vegetation, and roads influence incubation patterns of Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) in the Nebraska Sandhills, USA: *Canadian Journal of Zoology*, v. 97, no. 1, p. 91–99. [Also available at <https://doi.org/10.1139/cjz-2018-0130>.]
- Horak, G.J., 1985, Kansas prairie chickens: Pratt, Kans., Kansas Fish and Game Commission, Wildlife Bulletin, no. 3, 65 p.
- Horak, G.J., and Applegate, R.D., 1998, Greater Prairie-Chicken management: *Kansas School Naturalist*, v. 45, no. 1, p. 1–15.
- Horton, R.E., and Wolfe, D.H., 1999, Status and management of the Greater Prairie-Chicken in Oklahoma, in Svedarsky, W.D., Hier, R.H., and Silvy, N.J., eds., *The Greater Prairie-Chicken—A national look*: St. Paul, Minn., University of Minnesota, Agricultural Experiment Station, Miscellaneous Publication 99-1999, p. 105–111.
- Houston, C.S., 2002, Spread and disappearance of the Greater Prairie-Chicken, *Tympanuchus cupido*, on the Canadian prairie and adjacent areas: *Canadian Field-Naturalist*, v. 116, no. 1, p. 1–21.
- Hovick, T.J., Allred, B.W., Elmore, R.D., Fuhlendorf, S.D., Hamilton, R.G., and Breland, A., 2015a, Dynamic disturbance processes create dynamic lek site selection in a prairie grouse: *PLoS One*, v. 10, no. 9, p. e0137882. [Also available at <https://doi.org/10.1371/journal.pone.0137882>.]
- Hovick, T.J., Dahlgren, D.K., Papes, M., Elmore, R.D., and Pitman, J.C., 2015b, Predicting Greater Prairie-Chicken lek site suitability to inform conservation actions: *PLoS One*, v. 10, no. 8, p. e0137021. [Also available at <https://doi.org/10.1371/journal.pone.0137021>.]
- Hovick, T.J., Elmore, R.D., Allred, B.W., Fuhlendorf, S.D., and Dahlgren, D.K., 2014a, Landscapes as a moderator of thermal extremes—A case study from an imperiled grouse: *Ecosphere*, v. 5, no. 3, p. 1–12. [Also available at <https://doi.org/10.1890/ES13-00340.1>.]
- Hovick, T.J., Elmore, R.D., Dahlgren, D.K., Fuhlendorf, S.D., and Engle, D.M., 2014b, Evidence of negative effects of anthropogenic structures on wildlife—A review of grouse survival and behaviour: *Journal of Applied Ecology*, v. 51, p. 1680–1689. [Also available at <https://doi.org/10.1111/1365-2664.12331>.]
- Hovick, T.J., Elmore, R.D., Fuhlendorf, S.D., and Dahlgren, D.K., 2015c, Weather constrains the influence of fire and grazing on nesting Greater Prairie-Chickens: *Rangeland Ecology and Management*, v. 68, no. 2, p. 186–193. [Also available at <https://doi.org/10.1016/j.rama.2015.01.009>.]
- Howe, H.F., 1994, Managing species diversity in tallgrass prairie—Assumptions and implications: *Conservation Biology*, v. 8, no. 3, p. 691–704. [Also available at <https://doi.org/10.1046/j.1523-1739.1994.08030691.x>.]
- Huschle, G., and Toepfer, J.E., 2020, Trends in a Greater Prairie Chicken population established by translocation in North Dakota: *Prairie Naturalist*, v. 52, no. 1, p. 76–79.
- Huss, D.L., 1996, The role of domestic livestock in desertification control: Santiago, Chile, Food and Agriculture Organization of the United Nations, 91 p., accessed February 2020 at <http://www.fao.org/3/x5321e/x5321e00.htm#Contents>.
- Jamison, B.E., and Alleger, M.R., 2009, Status of Missouri Greater Prairie-Chicken populations and preliminary observations from ongoing translocations and telemetry: *Grouse News*, no. 38, p. 15–24.
- Jensen, W.F., 1992, Historical review of prairie chicken management on the Sheyenne National Grasslands: Bismarck, N. Dak., North Dakota Game and Fish Department, 155 p.

- Johnsgard, P.A., and Wood, R.E., 1968, Distributional changes and interaction between prairie chickens and Sharp-tailed Grouse in the Midwest: *The Wilson Bulletin*, v. 80, no. 2, p. 173–188.
- Johnson, C.E., 1934, Recollections of the prairie chicken and the Sharp-Tailed Grouse in northwestern Minnesota: *The Wilson Bulletin*, v. 46, no. 1, p. 3–17.
- Johnson, J.A., Schroeder, M.A., and Robb, L.A., 2020, Greater Prairie-Chicken (*Tympanuchus cupido*) (ver. 1.0), in Poole, A.F., ed., *Birds of the world*: Ithaca, N.Y., Cornell Lab of Ornithology, accessed September 2021 at <https://birdsoftheworld.org/bow/species/grpchi/cur/introduction>. [Also available at <https://doi.org/10.2173/bow.grpchi.01>.]
- Johnson, J.A., Toepfer, J.E., and Dunn, P.O., 2003, Contrasting patterns of mitochondrial and microsatellite population structure in fragmented populations of Greater Prairie-Chickens: *Molecular Ecology*, v. 12, no. 12, p. 3335–3347. [Also available at <https://doi.org/10.1046/j.1365-294X.2003.02013.x>.]
- Johnson, M.D., and Knue, J., 1989, *Feathers from the prairie, a short history of upland game birds*: Bismarck, N. Dak., North Dakota Game and Fish Department, 292 p.
- Johnson, R.G., 1985, *Effects of prairie management practices on prairie birds*: Madison, Wisc., University of Wisconsin, Master's Thesis, 53 p.
- Jones, D.P., 1988, *Breeding ecology and habitat use of Greater Prairie-Chickens in relation to habitat pattern*: Columbia, Mo., University of Missouri, Master's Thesis, 90 p.
- Jones, R.E., 1963a, *A comparative study of the habitats of the Lesser and Greater prairie-chickens in Oklahoma*: Stillwater, Okla., Oklahoma State University, Ph.D. Dissertation, 160 p.
- Jones, R.E., 1963b, *Identification and analysis of Lesser and Greater prairie chicken habitat*: *The Journal of Wildlife Management*, v. 27, no. 4, p. 757–778. [Also available at <https://doi.org/10.2307/3798492>.]
- Keir, J.R., 1999, *Wisconsin prairie chicken management—An agency perspective*, in Svedarsky, W.D. Hier, R.H. and Silvy, N.J., eds., *The Greater Prairie Chicken—A national look*: Saint Paul, Minn., University of Minnesota Agricultural Experiment Station, Miscellaneous Publication 99-1999, p. 59–62.
- Kellogg, F.E., and Doster, G.L., 1982, *Efficiency of dogs in locating bobwhites*: *National Quail Symposium Proceedings*, v. 2., article 5, p. 31–34.
- Kemink, K.M., and Kesler, D.C., 2013, *Using movement ecology to inform translocation efforts—A case study with and endangered lekking bird species*: *Animal Conservation*, v. 16, no. 4, p. 449–457. [Also available at <https://doi.org/10.1111/acv.12015>.]
- Kendeigh, C.S., 1944, *Measurement of bird populations: Ecological Applications*, v. 14, no. 1, p. 67–106. [Also available at <https://doi.org/10.2307/1961632>.]
- Kimmel, R.O., 1988, *Potential impacts of Ring-Necked Pheasants on other game birds*, in Hallett, D.L., Edwards, W.R., and Burger, G.V., eds., *Pheasants—Symptoms of wildlife problems on agricultural lands*: Bloomington, Ind., North Central Section of The Wildlife Society, p. 253–265.
- Kimmel, R.O., Berner, A.H., Haroldson, K.J., and Welsh, R.J., 1994, *Cover quality of CRP grasslands*: St. Paul, Minn., Minnesota Department of Natural Resources, Wildlife Populations and Research Unit Report, 5 p.
- Kirsch, L.M., 1969, *Waterfowl production in relation to grazing*: *The Journal of Wildlife Management*, v. 33, no. 4, p. 821–828. [Also available at <https://doi.org/10.2307/3799313>.]
- Kirsch, L.M., 1974, *Habitat management considerations for prairie chickens*: *Wildlife Society Bulletin*, v. 2, no. 3, p. 124–129.
- Kirsch, L.M., Klett, A.T., and Miller, H.W., 1973, *Land use and prairie grouse population relationships in North Dakota*: *The Journal of Wildlife Management*, v. 37, no. 4, p. 449–453. [Also available at <https://doi.org/10.2307/3800307>.]
- Kobriger, G.D., 1965, *Status, movements, habitats, and foods of prairie grouse on a sandhills refuge*: *The Journal of Wildlife Management*, v. 29, no. 4, p. 788–800. [Also available at <https://doi.org/10.2307/3798555>.]
- Kobriger, G.D., Vollink, D.P., McNeill, M.E., and Higgins, K.F., 1988, *Prairie chicken populations of the Sheyenne Delta in North Dakota*, in Bjugstad, A.J., technical coordinator, *Prairie Chickens on the Sheyenne National Grasslands*: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-159, p. 1–7.
- Kohn, S.C., 1976, *Sharp-tailed Grouse nesting and brooding habitat in southwestern North Dakota*: Brookings, S. Dak., South Dakota State University, Master's Thesis, 123 p.
- Korschgen, L.J., 1962, *Food habits of Greater Prairie Chickens in Missouri*: *American Midland Naturalist*, v. 68, no. 2, p. 307–318. [Also available at <https://doi.org/10.2307/2422736>.]

- Krapu, G.L., 1974, Feeding ecology of Pintail hens during reproduction: *The Auk*, v. 91, no. 2, p. 278–290.
- Kruse, A.D., 1973, Prairie chicken restoration projects, in Svedarsky, W.D., and Wolfe, T., eds., *The prairie chicken in Minnesota*: Crookston, Minn., University of Minnesota, p. 40–46.
- Lehmann, V.W., 1941, Attwater's Prairie-Chicken—Its life history and management: Washington, D.C., U.S. Fish and Wildlife Service, *North American Fauna*, no. 57, 63 p. [Also available at <https://doi.org/10.3996/nafa.57.0001>.]
- Leopold, A., 1931, Report on a game survey of the north central States: Washington, D.C., American Game Association, 299 p.
- Leopold, A., 1933, *Game management*: New York, N.Y., Charles Scribner's Sons, 481 p.
- Londe, D.W., 2020, Spatial and temporal variability in environmental conditions and its influence on the habitat selection and reproduction of the Greater Prairie-Chicken: Stillwater, Okla., Oklahoma State University, Ph.D. Dissertation, 129 p.
- Londe, D.W., Elmore, R.D., Davis, C.A., Fuhlendorf, S.D., Hovick, T.J., Luttbeg, B., and Rutledge, J., 2021a, Fine-scale habitat selection limits trade-offs between foraging and temperature in a grassland bird: *Behavioral Ecology*, v. 32, no. 4, p. 625–637. [Also available at <https://doi.org/10.1093/beheco/ab012>.]
- Londe, D.W., Elmore, R.D., Davis, C.A., Fuhlendorf, S.D., Hovick, T.J., Luttbeg, B., and Rutledge, J., 2021b, Weather influences multiple components of Greater Prairie-Chicken reproduction: *The Journal of Wildlife Management*, v. 85, no. 1, p. 121–134. [Also available at <https://doi.org/10.1002/jwmg.21957>.]
- Londe, D.W., Fuhlendorf, S.D., Elmore, R.D., Davis, C.A., and Rutledge, J., 2019, Female Greater Prairie-Chicken response to energy development and rangeland management: *Ecosphere*, v. 10, no. 12, p. e02982. [Also available at <https://doi.org/10.1002/ecs2.2982>.]
- Manske, L.L., 1980, Habitat, phenology and growth of selected sandhills range plants: Fargo, N. Dak., North Dakota State University, Ph.D. Dissertation, 154 p.
- Manske, L.L., 1987, activity of prairie grouse on the Sheyenne National Grasslands, North Dakota: *Newsletter of the Minnesota Prairie Chicken Society*, v. 13, p. 1–3.
- Manske, L.L., and Barker, W.T., 1981, The prairie grouse on the Sheyenne National Grasslands, North Dakota: Fargo, N. Dak., North Dakota State University, Research Report, 238 p.
- Manske, L.L., and Barker, W.T., 1988, Habitat usage by prairie grouse on the Sheyenne National Grasslands, in Bjugstad, A.J., technical coordinator, *Prairie chickens on the Sheyenne National Grasslands*: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-159, p. 8–20.
- Manske, L.L., Barker, W.T., and Biondini, M.E., 1988, Effects of grazing management treatment on grassland plant communities and prairie grouse habitat, in Bjugstad, A.J., technical coordinator, *Prairie chickens on the Sheyenne National Grasslands*: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-159, p. 58–72.
- Manske, L.L., and Onsager, J.A., 1996, Grasshopper populations can be reduced by grazing management: Dickinson, N. Dak., North Dakota State University, Dickinson Research Extension Center, DREC 96-1014, 3 p.
- Manville, A.M., II, 2004, Prairie grouse leks and wind turbines—U.S. Fish and Wildlife Service justification for a 5-mile buffer from leks; additional grassland songbird recommendations: Arlington, Va., U.S. Fish and Wildlife Service, Division of Migratory Bird Management, peer-reviewed briefing paper, 17 p.
- Manzer, D.L., and Hannon, S.J., 2005, Relating grouse nest success and corvid density to habitat—A multi-scale approach: *The Journal of Wildlife Management*, v. 69, no. 1, p. 110–123. [Also available at [https://doi.org/10.2193/0022-541X\(2005\)069%3C0110:RGNSAC%3E2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)069%3C0110:RGNSAC%3E2.0.CO;2).]
- Marshall, W.H., 1963, Radio tracking of porcupines and Ruffed Grouse, in Slater, L.E., ed., *Bio-telemetry—The use of telemetry in animal behavior and physiology in relation to ecological problems*: New York, N.Y., Pergamon Press, p. 173–178.
- Matthews, T., 2009, Nest and brood survival and habitat selection of Ring-necked Pheasants and Greater Prairie-Chickens in Nebraska: Lincoln, Nebr., University of Nebraska, Ph.D. Dissertation, 136 p.
- Matthews, T.W., Tyre, A.J., Taylor, J.S., Lusk, J.J., and Powell, L.A., 2011, Habitat selection and brood survival of Greater Prairie-Chickens, in Sandercock, B.K., Martin, K., and Segelbacher, G., eds., *Ecology, conservation, and management of grouse*: Berkeley, Calif., University of California Press, *Studies in Avian Biology*, p. 179–197. [Also available at <https://doi.org/10.1525/9780520950573-015>.]
- Matthews, T.W., Tyre, A.J., Taylor, J.S., Lusk, J.J., and Powell, L.A., 2013, Greater Prairie-Chicken nest success and habitat selection in southeastern Nebraska: *The Journal of Wildlife Management*, v. 77, no. 6, p. 1202–1212. [Also available at <https://doi.org/10.1002/jwmg.564>.]

- Mattise, S.N., 1978, Effects of grazing systems on Sharp-tailed Grouse habitat: Brookings, S. Dak., South Dakota State University, Master's Thesis, 46 p.
- McDonald, L., Griswold, J., Rintz, T., and Gardner, G., 2012, Results of the 2012 range-wide survey of Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*): Phoenix, Ariz., Western Association of Fish and Wildlife Agencies, 43 p.
- McKee, G., 1995, Ecology of Greater Prairie-Chickens in relation to habitat characteristics in southwestern Missouri: Columbia, Mo., University of Missouri, Master's Thesis, 112 p.
- McKee, G., Ryan, M.R., and Mechlin, L.M., 1998, Predicting Greater Prairie-Chicken nest success from vegetation and landscape characteristics: *The Journal of Wildlife Management*, v. 62, no. 1, p. 314–321. [Also available at <https://doi.org/10.2307/3802294>.]
- McNew, L.B., 2010, An analysis of Greater Prairie-Chicken demography in Kansas—The effects of human land use on the population ecology of an obligate grassland species: Manhattan, Kans., Kansas State University, Ph.D. Dissertation, 132 p.
- McNew, L.B., Gregory, A.J., and Sandercock, B.K., 2013, Spatial heterogeneity in habitat selection—Nest site selection by Greater Prairie-Chickens: *The Journal of Wildlife Management*, v. 77, no. 4, p. 791–801. [Also available at <https://doi.org/10.1002/jwmg.493>.]
- McNew, L.B., Gregory, A.J., Wisely, S.M., and Sandercock, B.K., 2011a, Human-mediated selection on life-history traits of Greater Prairie-Chickens, in Sandercock, B.K., Martin, K., and Segelbacher, G., eds., *Ecology, conservation, and management of grouse*: Berkeley, Calif., University of California Press, *Studies in Avian Biology*, p. 255–266. [Also available at <https://doi.org/10.1525/9780520950573-021>.]
- McNew, L.B., Gregory, A.J., Wisely, S.M., and Sandercock, B.K., 2011b, Reproductive biology of a southern population of Greater Prairie-Chickens, in Sandercock, B.K., Martin, K., and Segelbacher, G., eds., *Ecology, conservation, and management of grouse*: Berkeley, Calif., University of California Press, *Studies in Avian Biology*, p. 209–221. [Also available at <https://doi.org/10.1525/9780520950573-017>.]
- McNew, L.B., Gregory, A.J., Wisely, S.M., and Sandercock, B.K., 2012a, Demography of Greater Prairie-Chickens—Regional variation in vital rates, sensitivity values, and population dynamics: *The Journal of Wildlife Management*, v. 76, no. 5, p. 987–1000. [Also available at <https://doi.org/10.1002/jwmg.369>.]
- McNew, L.B., Hunt, L.M., Gregory, A.J., Wisely, S.M., and Sandercock, B.K., 2014, Effects of wind energy development on nesting ecology of Greater Prairie-Chickens in fragmented grasslands: *Conservation Biology*, v. 28, no. 4, p. 1089–1099. [Also available at <https://doi.org/10.1111/cobi.12258>.]
- McNew, L.B., Prebyl, T.J., and Sandercock, B.K., 2012b, Effects of rangeland management on the site occupancy dynamics of prairie-chickens in a protected prairie preserve: *The Journal of Wildlife Management*, v. 76, no. 1, p. 38–47. [Also available at <https://doi.org/10.1002/jwmg.237>.]
- McNew, L.B., and White, W.J., 2012, First case of renesting after brood loss by a Greater Prairie-Chicken: *The Wilson Journal of Ornithology*, v. 124, no. 1, p. 185–187. [Also available at <https://doi.org/10.1676/11-135.1>.]
- McNew, L.B., Winder, V.L., Pitman, J.C., and Sandercock, B.K., 2015, Alternative rangeland management strategies and the nesting ecology of Greater Prairie-Chickens: *Rangeland Ecology and Management*, v. 68, no. 3, p. 298–304. [Also available at <https://doi.org/10.1016/j.rama.2015.03.009>.]
- Mechlin, L.M., Cannon, R.W., and Christisen, D.M., 1999, Status and management of the Greater Prairie-Chicken in Missouri, in Svedarsky, W.D., Hier, R.H., and Silvy, N.J., eds., *The Greater Prairie-Chicken—A national look*: St. Paul, Minn., University of Minnesota, Agricultural Experiment Station, Miscellaneous Publication 99-1999, p. 129–142.
- Merrill, M.D., Chapman, K.A., Poiani, K.A., and Winter, B., 1999, Land-use patterns surrounding Greater Prairie-Chicken leks in northwestern Minnesota: *The Journal of Wildlife Management*, v. 63, no. 1, p. 189–198. [Also available at <https://doi.org/10.2307/3802500>.]
- Minnesota Prairie Plan Working Group, 2011, *Minnesota Prairie Conservation Plan*: Minneapolis, Minn., Minnesota Prairie Plan Working Group, 55 p.
- Mohler, L.L., 1952, Fall and winter habits of Prairie Chickens in southwest Nebraska: *The Journal of Wildlife Management*, v. 16, no. 1, p. 9–23. [Also available at <https://doi.org/10.2307/3797174>.]
- Monson, G.W., 1934, The birds of Berlin and Harwood townships, Cass County, North Dakota: *The Wilson Bulletin*, v. 41, no. 1, p. 37–58.
- Morrow, M.E., Koutsos, E.A., and Toepfer, J.E., 2019, Nutrient profiles of wild and captive Attwater's and Greater prairie-chicken eggs: *Journal of Fish and Wildlife Management*, v. 10, no. 1, p. 38–50. [Also available at <https://doi.org/10.3996/062018-JFWM-052>.]

- Morrow, M.E., and Toepfer, J.E., 2020, Use of predator-deterrent fences to increase Attwater's Prairie-Chicken nest success: *Journal of Fish and Wildlife Management*, v. 11, no. 2, p. 455–462. [Also available at <https://doi.org/10.3996/112019-JFWM-099>.]
- Mussman, S.M., Douglas, M.R., Anthonysamy, W.J.B., Davis, M.A., Simpson, S.A., Louis, W., and Douglas, M.E., 2017, Genetic rescue, the Greater Prairie Chicken and the problem of conservation reliance in the Anthropocene: *Royal Society Open Science*, v. 4, no. 2, p. 160736. [Also available at <https://doi.org/10.1098/rsos.160736>.]
- National Geographic Society, 2011, *Field guide to the birds of North America* (6th ed.): Washington, D.C., National Geographic Society, 576 p.
- Newell, J.A., 1987, Nesting and brood-rearing ecology of the Greater Prairie-Chicken in the Sheyenne National Grasslands, North Dakota: Bozeman, Mont., Montana State University, Master's Thesis, 111 p.
- Newell, J.A., Toepfer, J.E., and Eng, R.L., 1986, Nesting and brood-rearing ecology of the Greater Prairie-Chicken in the Sheyenne National Grasslands, North Dakota: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; Bozeman, Mont., Montana State University, Fish and Wildlife Program, Progress Report, Agreement Number 28-C2-204, 75 p.
- Newell, J.A., Toepfer, J.E., and Rumble, M.A., 1988, Summer brood-rearing ecology of the Greater Prairie-Chicken on the Sheyenne National Grasslands, in Bjugstad, A.J., technical coordinator, *Prairie chickens on the Sheyenne National Grasslands*: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-159, p. 24–31.
- Newsome, T.M., and Ripple, W.J., 2015, A continental scale trophic cascade from wolves through coyotes to foxes: *Journal of Animal Ecology*, v. 84, no. 1, p. 49–59. [Also available at <https://doi.org/10.1111/1365-2656.12258>.]
- Nicholls, C., and Altieri, M., 2013, Plant biodiversity enhances bees and other insect pollinators in agroecosystems—A review: *Agronomy for Sustainable Development*, v. 33, no. 2, p. 257–274. [Also available at <https://doi.org/10.1007/s13593-012-0092-y>.]
- Niemuth, N.D., 2000, Land use and vegetation associated with Greater Prairie-Chicken leks in an agricultural landscape: *The Journal of Wildlife Management*, v. 64, no. 1, p. 278–286. [Also available at <https://doi.org/10.2307/3803000>.]
- Niemuth, N.D., 2003, Identifying landscapes for Greater Prairie-Chicken translocation using habitat models and GIS—A case study: *Wildlife Society Bulletin*, v. 31, no. 1, p. 145–155.
- Niemuth, N.D., 2005, Landscape composition and Greater Prairie-Chicken lek attendance—Implications for management: *Prairie Naturalist*, v. 37, no. 3, p. 127–142.
- Niemuth, N.D., 2011, Spatially explicit habitat models for prairie grouse, in Sandercock, B.K., Martin, K., and Segelbacher, G., eds., *Ecology, conservation, and management of grouse*: Berkeley, Calif., University of California Press, *Studies in Avian Biology* no. 39, p. 3–20. [Also available at <https://doi.org/10.1525/9780520950573-003>.]
- Noetzel, D.M., 1990, *Grasshopper management*: St. Paul, Minn., University of Minnesota, Extension Bulletin Number AG-FO-3936, 10 p.
- Nooker, J.K., and Sandercock, B.K., 2008, Phenotypic correlates and survival consequences of male mating success in lek-mating Greater Prairie-Chickens (*Tympanuchus cupido*): *Behavioral Ecology and Sociobiology*, v. 62, no. 9, p. 1377–1388. [Also available at <https://doi.org/10.1007/s00265-008-0566-8>.]
- Norton, M.A., 2005, Reproductive success and brood habitat use of Greater Prairie-Chickens and Sharp-tailed Grouse on the Fort Pierre National Grassland of central South Dakota: Brookings, S. Dak., South Dakota State University, Master's Thesis, 64 p.
- Norton, M.A., Jensen, K.C., Leif, A.P., Kirschenmann, T.R., and Wolbrink, G.A., 2010, Resource selection of Greater Prairie-Chicken and Sharp-tailed Grouse broods in central South Dakota: *Prairie Naturalist*, v. 42, no. 3–4, p. 100–108.
- Obermeyer, B., Manes, R., Kiesecker, J., Fargione, J., and Sochi, K., 2011, Development by design—Mitigating wind development's impacts on wildlife in Kansas: *PLoS One*, v. 6, no. 10, p. e26698. [Also available at <https://doi.org/10.1371/journal.pone.0026698>.]
- Over, W.H., and Thoms, C.S., 1920, *Birds of South Dakota*: South Dakota Geological and Natural History Bulletin, v. 9, p. 73–76.
- Oyler-McCance, S.J., DeYoung, R.W., Fike, J.A., Hagen, C.A., Johnson, J.A., Larsson, L.C., and Patten, M.A., 2016, Rangewide genetic analysis of Lesser Prairie-Chicken reveals population structure, range expansion, and possible introgression: *Conservation Genetics*, v. 17, p. 643–660. [Also available at <https://doi.org/10.1007/s10592-016-0812-y>.]

- Patten, M.A., Pruett, C.L., and Wolfe, D.H., 2011, Home range size and movements of Greater Prairie-Chickens, in Sandercock, B.K., Martin, K., and Segelbacher, G., eds., Ecology, conservation, and management of grouse: Berkeley, Calif., University of California Press, Studies in Avian Biology, p. 51–62. [Also available at <https://doi.org/10.1525/9780520950573-006>.]
- Patten, M.A., Shochat, E., Wolfe, D.H., and Sherrod, S.K., 2007, Lekking and nesting response of the Greater Prairie-Chicken to burning of tallgrass prairie, in Masters, R.E., and Galley, K.E.M., eds., Proceedings of the twenty-third Tall Timbers Fire Ecology Conference: Tallahassee, Fla., Tall Timbers Research Station, p. 149–155.
- Peterson, L., 1979, Ecology of Great Horned Owls and Red-tailed Hawks in southeastern Wisconsin: Madison, Wis., Wisconsin Department of Natural Resources, Technical Bulletin 111, 63 p.
- Peterson, M.J., and Silvy, N.J., 1994, Spring precipitation and fluctuations in Attwater's Prairie-Chicken numbers—Hypotheses revisited: The Journal of Wildlife Management, v. 58, no. 2, p. 222–229. [Also available at <https://doi.org/10.2307/3809384>.]
- Peterson, M.J., and Silvy, N.J., 1996, Reproductive stages limiting productivity of the endangered Attwater's Prairie Chicken: Conservation Biology, v. 10, no. 4, p. 1264–1276. [Also available at <https://doi.org/10.1046/j.1523-1739.1996.10041264.x>.]
- Powell, L.A., Schacht, W.H., Ewald, J.P., and McCollum, K.R., 2020, Greater Prairie-Chickens and Sharp-tailed Grouse have similarly high nest survival in the Nebraska Sandhills: Prairie Naturalist, v. 52, no. 2, p. 58–75.
- Pruett, C.L., Patten, M.A., and Wolfe, D.H., 2009, Avoidance behavior by prairie grouse—Implications for development of wind energy: Conservation Biology, v. 23, no. 5, p. 1253–1259. [Also available at <https://doi.org/10.1111/j.1523-1739.2009.01254.x>.]
- Pyne, S.J., 1986, These conflagrated prairies—A cultural fire history of the grasslands, in Clambey, G.C., and Pemble, R.H., eds., The prairie—Past, present, and future: Proceedings of the ninth North American Prairie Conference, Fargo, N. Dak., North Dakota State University, Tri-College Center for Environmental Studies, p. 131–137.
- Raynor, E.J., Harrison, J.O., Whalen, C.E., Smith, J.A., Schacht, W.H., Tyre, A.J., Benson, J.F., Bomberger Brown, M., and Powell, L.A., 2019, Anthropogenic noise does not surpass land cover in explaining habitat selection of Greater Prairie-Chicken (*Tympanuchus cupido*): The Condor, v. 121, no. 4, p. 1–15. [Also available at <https://doi.org/10.1093/condor/duz044>.]
- Raynor, E.J., Powell, L.A., and Bomberger Brown, M., 2018, Evaluating Greater Prairie-Chicken vocalizations—Assessing variation in lek vocalizations at an existing wind energy facility in Nebraska: Grouse News, v. 55, p. 12–14.
- Raynor, E.J., Whalen, C.E., Bomberger Brown, M., and Powell, L.A., 2017, Location matters—Evaluating Greater Prairie-Chicken (*Tympanuchus cupido*) boom chorus propagation: Avian Conservation & Ecology, v. 12, no. 2, 17. [Also available at <https://doi.org/10.5751/ACE-01126-120217>.]
- Reinking, D.L., 2005, Fire regimes and avian responses in the central tallgrass prairie: Studies in Avian Biology, v. 30, p. 116–126.
- Ribic, C.A., Koford, R.R., Herkert, J.R., Johnson, D.H., Niemuth, N.D., Naugle, D.E., Bakker, K.K., Sample, D.W., and Renfrew, R.B., 2009, Area sensitivity in North American grassland birds—Patterns and processes: The Auk, v. 126, no. 2, p. 233–244. [Also available at <https://doi.org/10.1525/auk.2009.1409>.]
- Rice, L.A., and Carter, A.V., 1982, Evaluation of South Dakota grassland management practices as they affect prairie chicken populations, 1974–1978: Pierre, S. Dak., South Dakota Department of Game, Fish and Parks, Completion Report No. 84-11, 25 p.
- Robbins, M.B., Peterson, A.T., and Ortega-Huerta, M.A., 2002, Major negative impacts of early intensive cattle stocking on tallgrass prairies—The case of the Greater Prairie-Chicken (*Tympanuchus cupido*): North American Birds, v. 56, no. 2, p. 239–244.
- Robel, R.J., 1966, Booming territory size and mating success of the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*): Animal Behaviour, v. 14, nos. 2–3, p. 328–331, [Also available at [https://doi.org/10.1016/S0003-3472\(66\)80092-1](https://doi.org/10.1016/S0003-3472(66)80092-1).]
- Robel, R.J., 1970, Possible role of behavior in regulating Greater Prairie Chicken populations: The Journal of Wildlife Management, v. 34, no. 2, p. 306–312. [Also available at <https://doi.org/10.2307/3799014>.]
- Robel, R.J., and Ballard, W.B., Jr., 1974, Lek social organization and reproductive success in the Greater Prairie-Chicken: American Zoologist, v. 14, no. 1, p. 121–128. [Also available at <https://doi.org/10.1093/icb/14.1.121>.]
- Robel, R.J., Briggs, J.N., Cebula, J.J., Silvy, N.J., Viers, C.E., and Watt, P.G., 1970a, Greater Prairie-Chicken ranges, movements, and habitat usage in Kansas: The Journal of Wildlife Management, v. 34, no. 2, p. 286–306. [Also available at <https://doi.org/10.2307/3799013>.]

- Robel, R.J., Briggs, J.N., Dayton, A.D., and Hulbert, L.C., 1970b, Relationships between visual obstruction measurements and weight of grassland vegetation: *Journal of Range Management*, v. 23, no. 4, p. 295–297. [Also available at <https://doi.org/10.2307/3896225>.]
- Roberts, C.P., Uden, D.R., Cady, S.M., Allred, B., Fuhlendorf, S., Jones, M.O., Maestas, J.D., Naugle, D., Olsen, A.C., Smith, J., Tack, J., and Twidwell, D., 2021, Tracking spatial regimes as an early warning for a species of conservation concern: *Ecological Applications*, v. 31, p. e02480. [Also available at <https://doi.org/10.1002/eap.2480>.]
- Roberts, T.S., 1936, *The birds of Minnesota revised edition*, volume 1: Minneapolis, Minn., University of Minnesota Press, 718 p.
- Rocha, C., Durau, J.F., Barrilli, L.N.E., Dahlke, F., Maiorka, P., and Maiorka, A., 2014, The effect of raw and roasted soybeans on intestinal health, diet digestibility, and pancreas weight of broilers: *Journal of Applied Poultry Research*, v. 23, no. 1, p. 71–79. [Also available at <https://doi.org/10.3382/japr.2013-00829>.]
- Rodgers, R.D., and Hoffman, R.W., 2005, Prairie grouse response to Conservation Reserve Program grasslands—An overview, in Allen, A.W., and Vandever, M.W., eds., *The Conservation Reserve Program—Planting for the future. Proceedings of a national conference*, Fort Collins, Colo., June 6–9, 2004: U.S. Geological Survey Scientific Investigation Report 2005–5145, p. 120–128.
- Rosenquist, E.L., 1996, Winter aspects of prairie chicken ecology in northwest Minnesota: St. Cloud, Minn., St. Cloud State University, Master's Thesis, 72 p.
- Rosenquist, E.L., and Toepfer, J.E., 1995, A preliminary report on the winter ecology of the Greater Prairie-Chicken in northwest Minnesota, in Kobriger, G.D., ed., *Proceedings of the twenty-first Prairie Grouse Technical Council Conference*: Dickinson, N. Dak., North Dakota Game and Fish Department, p. 15–16.
- Ross, J.D., Arndt, A.D., Smith, R.F.C., Johnson, J.A., and Bouzat, J.L., 2006, Re-examination of the historical range of the Greater Prairie Chicken using provenance data and DNA analysis of museum collections: *Conservation Genetics*, v. 7, no. 5, p. 735–751. [Also available at <https://doi.org/10.1007/s10592-005-9110-9>.]
- Roy, C.L., and Gregory, A.J., 2019, Landscape genetic evaluation of a tallgrass prairie corridor using the Greater Prairie-Chicken (*Tympanuchus cupido*): *Landscape Ecology*, v. 34, p. 1425–1443. [Also available at <https://doi.org/10.1007/s10980-019-00862-3>.]
- Rumble, M.A., Newell, J.A., and Toepfer, J.E., 1988, Diets of Greater Prairie-Chickens on the Sheyenne National Grasslands, in Bjugstad, A.J., technical coordinator, *Prairie chickens on the Sheyenne National Grasslands: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-159*, p. 49–54.
- Runia, T.J., 2009, Influence of the Conservation Reserve Program and landscape composition on the spatial demographics of prairie grouse in northeastern South Dakota: Brookings, S. Dak., South Dakota State University, Master's Thesis, p. 96.
- Runia, T.J., Solem, A.J., Niemuth, N.D., and Barnes, K.W., 2021, Spatially explicit habitat models for prairie grouse—Implications for improved population monitoring and targeted conservation: *Wildlife Society Bulletin*, v. 45, no. 1, p. 36–54. [Also available at <https://doi.org/10.1002/wsb.1164>.]
- Ryan, M.R., Burger, L.W., Jr., Jones, D.P., and Wywiałowski, A.P., 1998, Breeding ecology of Greater Prairie-Chickens (*Tympanuchus cupido*) in relation to prairie landscape configuration: *American Midland Naturalist*, v. 140, no. 1, p. 111–121. [Also available at [https://doi.org/10.1674/0003-0031\(1998\)140\[0111:BEOGPC\]2.0.CO;2](https://doi.org/10.1674/0003-0031(1998)140[0111:BEOGPC]2.0.CO;2).]
- Sample, D.W., and Mossman, M.J., 1997, *Managing habitat for grassland birds—A guide for Wisconsin*: Madison, Wisc., Wisconsin Department of Natural Resources, 154 p.
- Samson, F.B., 1980, Island biogeography and the conservation of prairie birds, in Kucera, C.L., ed., *Proceedings of the North American Prairie Conference*: Springfield, Mo., Southwest Missouri State University, p. 293–305.
- Sanderson, G.C., Westemeier, R.L., and Edwards, W.R., 1973, Acquisition and management of prairie chicken sanctuaries in Illinois, in Svedarsky, W.D., and Wolfe, T., eds., *The Prairie chicken in Minnesota*: Crookston, Minn., University of Minnesota, p. 59–79.
- Scarnecchia, D.L., 1985, The animal-unit and animal-unit-equivalent concepts in range science: *Journal of Range Management*, v. 38, no. 4, p. 346–349. [Also available at <https://doi.org/10.2307/3899419>.]
- Schindler, A.R., Haukos, D.A., Hagen, C.A., and Ross, B.E., 2020, A multispecies approach to manage effects of land cover and weather on upland game birds: *Ecology and Evolution*, v. 10, no. 24, p. 14330–14345. [Also available at <https://doi.org/10.1002/ece3.7034>.]
- Schmidt, F.J.W., 1936, Winter food of the Sharp-tailed Grouse and Pinnated Grouse in Wisconsin: *The Wilson Bulletin*, v. 48, no. 3, p. 186–203.

- Schole, A.C., Matthews, T.W., Powell, L.A., Lusk, J.J., and Taylor, J.S., 2011, Chick survival of Greater Prairie-Chickens, in Sandercock, B.K., Martin, K., and Segelbacher, G., eds., Ecology, conservation, and management of grouse: Berkeley, Calif., University of California Press, Studies in Avian Biology, p. 247–254. [Also available at <https://doi.org/10.1525/9780520950573-020>.]
- Schranck, B.W., 1972, Waterfowl nest cover and some predation relationships: *The Journal of Wildlife Management*, v. 36, no. 1, p. 182–186. [Also available at <https://doi.org/10.2307/3799210>.]
- Schroeder, M.A., 1991, Movement and lek visitation by female Greater Prairie-Chickens in relation to predictions of Bradbury's female preference hypothesis of lek evolution: *The Auk*, v. 108, no. 4, p. 896–903.
- Schroeder, M.A., and Baydack, R.K., 2001, Predation and the management of prairie grouse: *Wildlife Society Bulletin*, v. 29, no. 1, p. 24–32.
- Schroeder, M.A., and Braun, C.E., 1992, Seasonal movement and habitat use by Greater Prairie-Chickens in northeastern Colorado: Fort Collins, Colo., Colorado Division of Wildlife, Special Report, no. 68, 44 p.
- Schroeder, M.A., and Braun, C.E., 1993, Partial migration in a population of Greater Prairie-Chickens in northeastern Colorado: *The Auk*, v. 110, no. 1, p. 21–28.
- Schroeder, M.A., and Robb, L.A., 2003, Fidelity of Greater Sage-Grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape: *Wildlife Biology*, v. p., 291–299. [Also available at <https://doi.org/10.2981/wlb.2003.017>.]
- Schroeder, M.A., and White, G.C., 1993, Dispersion of Greater Prairie-Chicken nests in relation to lek location—Evaluation of the hot-spot hypothesis of lek evolution: *Behavioral Ecology*, v. 4, no. 3, p. 266–270. [Also available at <https://doi.org/10.1093/beheco/4.3.266>.]
- Schwartz, C.W., 1945, The ecology of the prairie chicken in Missouri: *University of Missouri Studies*, v. 20, p. 1–99.
- Sedivec, K.K., and Barker, W.T., 1989, Effects of grazing systems on upland nesting birds in south central North Dakota. Phase III: Fargo, N. Dak., North Dakota State University, 125 p.
- Shaffer, J.A., and DeLong, J.P., 2019, The effects of management practices on grassland birds—An introduction to North American grasslands and the practices used to manage grasslands and grassland birds, chap. A of Johnson, D.H., Igl, L.D., Shaffer, J.A., and DeLong, J.P., eds., The effects of management practices on grassland birds: U.S. Geological Survey Professional Paper 1842, 63 p., <https://doi.org/10.3133/pp1842A>.
- Shaffer, J.A., Igl, L.D., and Johnson, D.H., 2019, The effects of management practices on grassland birds—Rates of Brown-headed Cowbird (*Molothrus ater*) parasitism in nests of North American grassland birds, chap. PP of Johnson, D.H., Igl, L.D., Shaffer, J.A., and DeLong, J.P., eds., The effects of management practices on grassland birds: U.S. Geological Survey Professional Paper 1842, 24 p., accessed September 2020 at <https://doi.org/10.3133/pp1842PP>.
- Sharp, W.M., 1957, Social and range dominance in gallinaceous birds—Pheasants and prairie grouse: *The Journal of Wildlife Management*, v. 21, no. 2, p. 242–244. [Also available at <https://doi.org/10.2307/3797597>.]
- Shiflet, T.N., and Heady, H.F., 1971, Specialized grazing systems—Their place in range management: U.S. Department of Agriculture, Soil Conservation Service TP-152, 13 p.
- Sidle, J.G., 2005, In my opinion—Grouching and grazing on National Grasslands: *Wildlife Society Bulletin*, v. 33, no. 3, p. 1139–1144. [Also available at [https://doi.org/10.2193/0091-7648\(2005\)33\[1139:IMOGAG\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2005)33[1139:IMOGAG]2.0.CO;2).]
- Silvy, N.J., 1968, Movements, monthly ranges, reproductive behavior, and mortality of radio-tagged Greater Prairie Chickens: Manhattan, Kans., Kansas State University, Master's Thesis, 135 p.
- Silvy, N.J., Griffin, C.P., Lockwood, M.A., Morrow, M.E., and Peterson, M.J., 1999, The Attwater's Prairie-Chicken—A lesson in conservation biology research, in Svedarsky, W.D., Hier, R.H., and Silvy, N.J., eds., The Greater Prairie-Chicken—A national look: St. Paul, Minn., University of Minnesota, Agricultural Experiment Station, Miscellaneous Publication 99-1999, p. 153–162.
- Simpson, S.A., and Esker, T.E., 1997, Prairie Ridge State Natural Area habitat plan: Springfield, Ill., Illinois Department of Natural Resources, Division of Natural Heritage, 80 p.

- Skinner, R.M., 1977, A comparison of grassland structure and prairie chicken use in Missouri, *in* Rice, L.A., ed., Proceedings of the 12th Prairie Grouse Technical Council Conference: Pierre, S. Dak., South Dakota Department Game, Fish, and Parks, p. 12.
- Smith, J.A., Brown, M.B., Harrison, J.O., and Powell, L.A., 2017, Predation risk—A potential mechanism for effects of a wind energy facility on Greater Prairie-Chicken survival: *Ecosphere*, v. 8, no. 6, p. e01835. [Also available at <https://doi.org/10.1002/ecs2.1835>.]
- Smith, J.A., Whalen, C.E., Bomberger Brown, M., and Powell, L.A., 2016, Indirect effects of an existing wind energy facility on lekking behavior of Greater Prairie-Chickens: *Ethology*, v. 122, no. 5, p. 419–429. [Also available at <https://doi.org/10.1111/eth.12489>.]
- Snyder, J.W., Pelrin, E.C., and Crawford, J.A., 1999, Translocation histories of prairie grouse in the United States: *Wildlife Society Bulletin*, v. 27, no. 2, p. 428–432.
- Sovada, M.A., Sargeant, A.B., and Grier, J.W., 1995, Differential effects of coyotes and red foxes on duck nest success: *The Journal of Wildlife Management*, v. 59, no. 1, p. 1–9. [Also available at <https://doi.org/10.2307/3809108>.]
- Sparling, D.W., Jr., 1975, Prairie chicken killed by Goshawk: *Loon*, v. 47, no. 4, p. 191–192.
- Sparling, D.W., Jr., and Svedarsky, W.D., 1978, Responses to prairie grouse to avian and mammalian visitors on display grounds in northwestern Minnesota: *Prairie Naturalist*, v. 10, no. 1, p. 17–22.
- Starns, H.D., Fuhlendorf, S.D., Elmore, R.D., Twidwell, D., Thacker, E.T., Hovick, T.J., and Lutbeg, B., 2020, Effects of pyric herbivory on prairie-chicken (*Tympanuchus* spp) habitat: *PLoS One*, p. e0234983. [Also available at <https://doi.org/10.1371/journal.pone.0234983>.]
- Svedarsky, W.D., 1979, Spring and summer ecology of female Greater Prairie-Chickens in northwestern Minnesota: Grand Forks, N. Dak., University of North Dakota, Ph.D. Dissertation, 166 p.
- Svedarsky, W.D., 1981, Goshawk kills prairie chicken on booming ground in northwest Minnesota: *Loon*, v. 53, no. 2, p. 112–113.
- Svedarsky, W.D., 1983, Reproductive chronology of Greater Prairie-Chickens in Minnesota and recommendations for censusing and nest searching: *Prairie Naturalist*, v. 15, no. 3, p. 120–124.
- Svedarsky, W.D., 1988, Reproductive ecology of female Greater Prairie-Chickens in Minnesota, *in* Bergerud, A.T., and Gratson, M.W., eds., Adaptive strategies and population ecology of northern grouse: Minneapolis, Minn., University of Minnesota Press, p. 193–267.
- Svedarsky, W.D., 1992, Biological inventory of a multi-purpose flood control impoundment in northwest Minnesota and potentials for nongame and game bird management: Crookston, Minn., University of Minnesota, Northwest Research and Outreach Center, Miscellaneous Publication, 114 p.
- Svedarsky, W.D., Buckley, P.E., and Feiro, T.A., 1986, Effects of 13 years of annual burning on an aspen-prairie ecotone in northwestern Minnesota, *in* Clambey, G.C., and Pemble, R.H., eds., Proceedings of the ninth North American Prairie Conference: Fargo, N. Dak., North Dakota State University, Tri-College Center for Environmental Studies, p. 118–122.
- Svedarsky, W.D., and Van Amburg, G.L., 1996, Integrated management of the Greater Prairie-Chicken and livestock on the Sheyenne National Grasslands: Crookston, Minn., University of Minnesota, Northwest Research and Outreach Center, 243 p.
- Svedarsky, W.D., Westemeier, R.L., Robel, R.J., Gough, S., and Toepfer, J.E., 2000, Status and management of the Greater Prairie-Chicken *Tympanuchus cupido pinnatus* in North America: *Wildlife Biology*, v. 6, no. 4, p. 277–284. [Also available at <https://doi.org/10.2981/wlb.2000.027>.]
- Svedarsky, W.D., Wolfe, T.J., and Toepfer, J.E., 1999, Status and management of the Greater Prairie Chicken in Minnesota, *in* Svedarsky, W.D., Hier, R.H., and Silvy, N.J., eds., The Greater Prairie Chicken—A national look: St. Paul, Minn., University of Minnesota, Agricultural Experiment Station, Miscellaneous Publication 99-1999, p. 25–38.
- Swanson, G.A., Meyer, M.I., and Serie, J.R., 1974, Feeding ecology of breeding Blue-winged Teals: *The Journal of Wildlife Management*, v. 38, no. 3, p. 396–407. [Also available at <https://doi.org/10.2307/3800869>.]
- Syrowitz, J., 2013, Brood habitat and invertebrate biomass of the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*) in northwestern Minnesota: Winnipeg, Manitoba, University of Manitoba, Master's Thesis, 172 p.
- Taylor, P.D., Fahrig, L., Henein, K., and Merriam, G., 1993, Connectivity is a vital element of landscape structure: *Oikos*, v. 68, no. 3, p. 571–572. [Also available at <https://doi.org/10.2307/3544927>.]
- Tester, J.R., and Marshall, W.M., 1961, A study of certain plant and animal interrelations on a native prairie in northwestern Minnesota: Minnesota Museum of Natural History, Occasional Papers, no. 8, p. 1–51.
- Toepfer, J.E., 1988, The ecology of the Greater Prairie-Chicken as related to reintroductions: Bozeman, Mont., Montana State University, Ph.D. Dissertation, 533 p.

- Toepfer, J.E., 2003, Prairie chickens and grasslands—2000 and beyond. A report to the Council of Chiefs: Elm Grove, Wis., Society of *Tympanuchus cupido pinnatus*, Ltd., 58 p.
- Toepfer, J.E., 2007, Status and management of the Greater Prairie-Chicken in Wisconsin—2006: Passenger Pigeon, v. 69, no. 3, p. 258–289.
- Toepfer, J.E., and Eng, R.L., 1988, Winter ecology of the Greater Prairie-Chicken on the Sheyenne National Grasslands, North Dakota, in Bjugstad, A.J., technical coordinator, Prairie Chickens on the Sheyenne National Grasslands: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-159, p. 32–48.
- Toepfer, J.E., Eng, R.L., and Anderson, R.K., 1990, Translocating prairie grouse—What have we learned?: Transactions of the North American Wildlife and Natural Resources Conference, v. 55, p. 569–579.
- Toepfer, J.E., Pratt, A., Trauba, D.A., and Vacek, S.C., 2005, Parasitism of prairie chicken nests by pheasants in Minnesota, in Proceedings of the twenty-sixth Prairie Grouse Technical Council, Valentine, Nebr., p. 19.
- Toney, T.E., 1980, Foods of prairie chickens on managed prairie, in Vohs, P.A., ed., Proceedings of the Prairie Grouse Symposium: Stillwater, Okla., Oklahoma State University, p. 81–84.
- Towne, E.G., and Craine, J.M., 2016, A critical examination of timing of burning in the Kansas Flint Hills: Rangeland Ecology and Management, v. 69, no. 1, p. 28–34. [Also available at <https://doi.org/10.1016/j.rama.2015.10.008>.]
- Uresk, D.W., 2010, Cattle weights on USDA Forest Service lands by State with cow and calf forage consumption: Rangelands, v. 32, no. 4, p. 26–29. [Also available at <https://doi.org/10.2111/Rangelands-D-10-00023.1>.]
- Van Amburg, G.L., Swaby, J.A., and Pemble, R.H., 1981, Response of arthropods to a spring burn of tall grass prairie in northwestern Minnesota, in Stuckey, R.L., and Reese, K.J., eds., The prairie peninsula—In the “shadow” of Transeau: Proceedings of the sixth North American Prairie Conference, Columbus, Ohio, Ohio State University, p. 240–244.
- Van Poollen, H.W., and Lacey, J.R., 1979, Herbage response to grazing systems and stocking intensities: Journal of Range Management, v. 32, no. 4, p. 250–253. [Also available at <https://doi.org/10.2307/3897824>.]
- Vance, D.R., and Westemeier, R.L., 1979, Interactions of pheasants and prairie chickens in Illinois: Wildlife Society Bulletin, v. 7, no. 4, p. 221–225.
- Viers, C.E., 1967, Home range and movements of the Greater Prairie-Chicken with notes on activities: Manhattan, Kans., Kansas State University, Master’s Thesis, 78 p.
- Vodehnal, W.L., 1999, Status and management of the Greater Prairie-Chicken in Nebraska, in Svedarsky, W.D., Hier, R.H., and Silvy, N.J., eds., The Greater Prairie-Chicken—A national look: St. Paul, Minn., University of Minnesota, Agricultural Experiment Station, Miscellaneous Publication 99-1999, p. 81–98.
- Vogel, J.A., 2015, An unexpected journey—Greater Prairie-Chicken travels nearly 4000 km after translocation to Iowa: American Midland Naturalist, v. 174, no. 2, p. 343–349. [Also available at <https://doi.org/10.1674/0003-0031-174.2.343>.]
- Walk, J.W., 2004, A plan for the recovery of the Greater Prairie-Chicken in Illinois: Springfield, Ill., Office of Resource Conservation, Illinois Department of Natural Resources, 72 p.
- Walk, J.W., Kershner, E.L., and Warner, R.E., 1999, Oological notes from Jasper County, Illinois: Transactions of the Illinois State Academy of Science, v. 92, nos. 3 and 4, p. 285–288.
- Westemeier, R.L., 1971, The history and ecology of prairie chickens in central Wisconsin: Madison, Wis., University of Wisconsin, College of Agriculture and Life Sciences, Research Bulletin, no. 281, 63 p.
- Westemeier, R.L., 1973, Prescribed burning in grassland management for prairie chickens in Illinois, in Komarek, R., ed., Proceedings of the Tall Timbers Fire Ecology Conference: Tallahassee, Fla., Tall Timbers Research Station, p. 317–338.
- Westemeier, R.L., 1980, Greater Prairie-Chicken status and management—1968–1979, in Vohs, P.A., ed., Proceedings of the Prairie Grouse Symposium: Stillwater, Okla., Oklahoma State University, p. 8–17.
- Westemeier, R.L., 1983, Responses and impact by pheasants on prairie-chicken sanctuaries in Illinois—A synopsis, in Dumke, R. Stiehl, R.B., and Kahl, R.B., eds., Perdix III—Gray Partridge/Ring-necked Pheasant Workshop: Madison, Wis., Wisconsin Department of Natural Resources, p. 117–122.
- Westemeier, R.L., 1984, Annual Prairie Chicken management report to cooperators: Effingham, Ill., Illinois Natural History Survey, 31 p.
- Westemeier, R.L., 1985, Management plan for native prairie-chickens in Illinois: Effingham, Ill., Illinois Natural History Survey, W-66-R.

- Westemeier, R.L., 1988a, An evaluation of methods for controlling pheasants on Illinois prairie-chicken sanctuaries, *in* Hallett, D.L., Edwards, W.R., and Burger, G.V. eds.: Pheasants—Symptoms of wildlife problems on agricultural lands: Bloomington, Ind., North Central Section, The Wildlife Society, p. 267–288.
- Westemeier, R.L., 1988b, Development of prairie pasture demonstration areas, Phase II: Effingham, Ill., Illinois Natural History Survey, Final Report, 22 p.
- Westemeier, R.L., Brawn, J.D., Simpson, S.A., Esker, T.L., Jansen, R.W., Walk, J.W., Kershner, E.L., Bouzat, J.L., and Paige, K.N., 1998a, Tracking the long-term decline and recovery of an isolated population: *Science*, v. 282, no. 5394, p. 1695–1698. [Also available at <https://doi.org/10.1126/science.282.5394.1695>.]
- Westemeier, R.L., and Buhnerkempe, J.E., 1983, Responses of nesting wildlife to prairie grass management in prairie chicken sanctuaries in Illinois, *in* Brewer, R., ed., Proceedings of the eighth North American Prairie Conference: Kalamazoo, Mich., Western Michigan University, p. 36–46.
- Westemeier, R.L., Buhnerkempe, J.E., Edwards, W.R., Brawn, J.D., and Simpson, S.A., 1998b, Parasitism of Greater Prairie-Chicken nests by Ring-necked Pheasants: *The Journal of Wildlife Management*, v. 62, no. 3, p. 854–863. [Also available at <https://doi.org/10.2307/3802536>.]
- Westemeier, R.L., and Gough, S., 1999, National outlook and conservation needs for Greater Prairie-Chickens, *in* Svedarsky, W.D., Hier, R.H., and Silvy, N.J., eds., The Greater Prairie-Chicken—A national look: St. Paul, Minn., University of Minnesota, Agricultural Experiment Station, Miscellaneous Publication 99-1999, p. 169–187.
- Westemeier, R.L., Jansen, R.W., and Simpson, S.A., 1995, Nest and brood habitat used by translocated Greater Prairie-Chickens in Illinois, *in* Kobriger, G.D., ed., Proceedings of the twenty-first Prairie Grouse Technical Council Conference: Dickinson, N. Dak., North Dakota Game and Fish Department, p. 17.
- Westemeier, R.L., and Vance, D.R., 1972, Responses of prairie chickens to habitat manipulations: Illinois Department of Conservation and Natural History Survey Research Letter, v. 15, no. 10, p. 1–3.
- Whalen, C.E., Bomberger Brown, M., McGee, J., Powell, L.A., and Walsh, E.J., 2017, Acoustic characteristics of lekking male Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) vocalizations: *Great Plains Research*, v. 27, no. 2, p. 93–108. [Also available at <https://doi.org/10.1353/gpr.2017.0018>.]
- Whalen, C.E., Bomberger Brown, M., McGee, J., Powell, L.A., and Walsh, E.J., 2018, Male Greater Prairie-Chickens adjust their vocalizations in the presence of wind turbine noise: *The Condor*, v. 120, no. 1, p. 137–148. [Also available at <https://doi.org/10.1650/CONDOR-17-56.1>.]
- Whalen, C.E., Bomberger Brown, M., McGee, J., Powell, L.A., and Walsh, E.J., 2019a, Effects of wind turbine noise on the surrounding soundscape in the context of Greater Prairie-Chicken courtship vocalizations: *Applied Acoustics*, v. 153, p. 132–139. [Also available at <https://doi.org/10.1016/j.apacoust.2019.04.022>.]
- Whalen, C.E., Bomberger Brown, M., McGee, J., Powell, L.A., and Walsh, E.J., 2019b, Wind turbine noise limits propagation of Greater Prairie-Chicken boom chorus, but does it matter?: *Ethology*, v. 125, no. 12, p. 863–875. [Also available at <https://doi.org/10.1111/eth.12940>.]
- Wight, H.M., 1931, Quantitative methods in upland game bird investigation: *The Auk*, v. 48, no. 4, p. 553–558. [Also available at <https://doi.org/10.2307/4076260>.]
- Williams, B.K., Koneff, M.D., and Smith, D.A., 1999, Evaluation of waterfowl conservation under the North American Waterfowl Management Plan: *The Journal of Wildlife Management*, v. 63, no. 2, p. 417–440. [Also available at <https://doi.org/10.2307/3802628>.]
- Wilsey, C., Taylor, L., Bateman, B., Jensen, C., Michel, N., Panjabi, A., and Langham, G., 2019, Climate policy action needed to reduce vulnerability of conservation-reliant grassland birds in North America: *Conservation Science and Practice*, v. 1, no. 4, p. e21. [Also available at <https://doi.org/10.1111/csp2.21>.]
- Wilson, A.D., 1986, Principles of grazing management systems: *Proceedings of the International Rangeland Congress*, v. 2, p. 221–225.
- Winder, V.L., Carrlson, K.M., Gregory, A.J., Hagen, C.A., Haukos, D.A., Kesler, D.C., Larsson, L.C., Matthews, T.W., McNew, L.B., Patten, M.A., Powell, L.A., Smith, J.A., Thompson, T., Wolfe, D.H., and Sandercock, B.K., 2015a, Factors affecting female space use in ten populations of prairie chickens: *Ecosphere*, v. 6, no. 9, p. 1–17. [Also available at <https://doi.org/10.1890/ES14-00536.1>.]
- Winder, V.L., Gregory, A.J., McNew, L.B., and Sandercock, B.K., 2015b, Responses of male Greater Prairie-Chickens to wind energy development: *The Condor*, v. 117, no. 2, p. 284–296. [Also available at <https://doi.org/10.1650/CONDOR-14-98.1>.]

- Winder, V.L., Herse, M.R., Hunt, L.M., Gregory, A.J., McNew, L.B., and Sandercock, B.K., 2016, Patterns of nest attendance by female Greater Prairie-Chickens (*Tympanuchus cupido*) in northcentral Kansas: *Journal of Ornithology*, v. 157, p. 733–745. [Also available at <https://doi.org/10.1007/s10336-016-1330-x>.]
- Winder, V.L., McNew, L.B., Gregory, A.J., Hunt, L.M., Wisely, S.M., and Sandercock, B.K., 2014a, Effects of wind energy development on survival of female Greater Prairie-Chickens: *Journal of Applied Ecology*, v. 51, no. 2, p. 395–405. [Also available at <https://doi.org/10.1111/1365-2664.12184>.]
- Winder, V.L., McNew, L.B., Gregory, A.J., Hunt, L.M., Wisely, S.M., and Sandercock, B.K., 2014b, Space use by female Greater Prairie-Chickens in response to wind energy development: *Ecosphere*, v. 5, no. 1, article 3. [Also available at <https://doi.org/10.1890/ES13-00206.1>.]
- Winder, V.L., McNew, L.B., Pitman, J.C., and Sandercock, B.K., 2017, Space use of female Greater Prairie-Chickens in response to fire and grazing interactions: *Rangeland Ecology and Management*, v. 70, no. 2, p. 165–174. [Also available at <https://doi.org/10.1016/j.rama.2016.08.004>.]
- Winder, V.L., McNew, L.B., Pitman, J.C., and Sandercock, B.K., 2018, Effects of rangeland management on survival of female Greater Prairie-Chickens: *The Journal of Wildlife Management*, v. 82, no. 1, p. 113–122. [Also available at <https://doi.org/10.1002/jwmg.21331>.]
- Winter, M., Johnson, D.H., Dechant, J.A., Donovan, T.M., and Svedarsky, W.D., 1999, Evaluation of the Bird Conservation Area concept in the northern tallgrass prairie. Annual report—1999: Jamestown, N. Dak., U.S. Geological Survey, Northern Prairie Wildlife Research Center, 19 p.
- Winter, M., Johnson, D.H., Dechant, J.A., Donovan, T.M., and Svedarsky, W.D., 2001, Evaluation of the Bird Conservation Area concept in the northern tallgrass prairie. Annual report—2001: Jamestown, N. Dak., U.S. Geological Survey, Northern Prairie Wildlife Research Center, 24 p.
- Winter, M., Johnson, D.H., Donovan, T.M., and Svedarsky, W.D., 1998, Evaluation of the Bird Conservation Area concept in the northern tallgrass prairie. Annual report—1998: Jamestown, N. Dak., U.S. Geological Survey, Northern Prairie Wildlife Research Center, 41 p.
- Winter, M., Johnson, D.H., and Faaborg, J., 2000, Evidence for edge effects on multiple levels in tallgrass prairie: *The Condor*, v. 102, no. 2, p. 256–266. [Also available at [https://doi.org/10.1650/0010-5422\(2000\)102\[0256:EFEEOM\]2.0.CO;2](https://doi.org/10.1650/0010-5422(2000)102[0256:EFEEOM]2.0.CO;2).]
- Woodward, A.J.W., Fuhlendorf, S.D., Leslie, D.M., Jr., and Shackford, J., 2001, Influence of landscape composition and change on Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) populations: *American Midland Naturalist*, v. 145, no. 2, p. 261–274. [Also available at [https://doi.org/10.1674/0003-0031\(2001\)145\[0261:IOLCAC\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2001)145[0261:IOLCAC]2.0.CO;2).]
- Yeatter, R.E., 1943, The prairie chicken in Illinois: *Illinois Natural History Survey Bulletin*, v. 22, no. 4, p. 377–416.
- Yeatter, R.E., 1963, Population responses of prairie chickens to land use changes in Illinois: *The Journal of Wildlife Management*, v. 27, no. 4, p. 739–757. [Also available at <https://doi.org/10.2307/3798491>.]
- Zimmerman, J.L., 1997, Avian community responses to fire, grazing, and drought in the tallgrass prairie, in Knopf, F.L., and Samson, F.B., eds., *Ecology and conservation of Great Plains vertebrates*: New York, N.Y., Springer, p. 167–180. [Also available at https://doi.org/10.1007/978-1-4757-2703-6_7.]

Table C1. Measured values of vegetation structure and composition in Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) 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; <, less than; --, no data; CRP, Conservation Reserve Program; >, greater than]

| Study | State or province | Habitat | Management practice or treatment | Vegetation height (cm) | Vegetation height-density (cm) | Grass cover (%) | Forb cover (%) | Shrub cover (%) | Bare ground cover (%) | Litter cover (%) | Litter depth (cm) |
|---|-------------------|---|--|------------------------|--------------------------------|-----------------|-------------------|-----------------|-----------------------|------------------|-------------------|
| Anderson, 2012 (nests) | Nebraska | Sandhill prairie | Grazed | 24.6 | 10.8 ^a | 29.2 | 3.0 | 4.9 | 3.6 | 44.6 | <0.1 |
| Anderson, 2012 (brood sites) | Nebraska | Sandhill prairie | Grazed | 27.0 | 6.9 ^a | 33.3 | 4.3 | 4.2 | 11.4 | 34.5 | <0.1 |
| Blus and Walker, 1966 (nests) | Nebraska | Sandhill prairie | Grazed, hayed | 12.7 | -- | -- | -- | -- | -- | -- | -- |
| Buhnerkempe and others, 1984 (fields with successful nests only) | Illinois | Tame grassland | Burned, hayed, seed harvest | 65.5 | 33.6 ^a | -- | -- | -- | -- | -- | 4.2 |
| Buhnerkempe and others, 1984 (fields with unsuccessful nests only) | Illinois | Tame grassland | Burned, hayed, seed harvest | 61 | 24.9 ^a | -- | -- | -- | -- | -- | 5.6 |
| Buhnerkempe and others, 1984 (fields with both successful and unsuccessful nests) | Illinois | Tame grassland | Burned, hayed, seed harvest | 78.7 | 25.4 ^a | -- | -- | -- | -- | -- | 5.5 |
| Drobney and Sparrowe, 1977 (nests) | Missouri | -- | -- | 45 | -- | -- | -- | -- | -- | -- | -- |
| Emery, 2013 (nests) | Minnesota | Tame grassland (CRP) | Smooth brome (<i>Bromus inermis</i>) monoculture | -- | 23 | -- | -- | -- | -- | -- | 3.6 |
| Emery, 2013 (nests) | Minnesota | Tame grassland (CRP) | Other introduced grasses | -- | 23.9 ^a | -- | -- | -- | -- | -- | 3.0 |
| Emery, 2013 (nests) | Minnesota | Tallgrass prairie | Restored native prairie | -- | 18.4 ^a | -- | -- | -- | -- | -- | 3.5 |
| Harrison, 2015 ^b | Nebraska | Sandhill prairie | Grazed | 21.1 | 13.1 ^a | 27.7 | 5.1 | 2.2 | -- | 74.7 | 9.1 |
| Jones, 1963a (leks) | Oklahoma | Sand sagebrush grassland (<i>Artemisia filifolia</i>) | Grazed | 15.3 | -- | 34.7 | 11.8 ^c | -- | -- | -- | -- |
| Jones, 1963a (nests) | Oklahoma | Sand sagebrush grassland | Grazed | 45 | -- | 64.5 | 19.9 ^c | -- | -- | -- | -- |
| Jones, 1963a (broods) | Oklahoma | Sand sagebrush grassland | Grazed | -- | -- | 26.3 | 13.1 ^c | -- | -- | -- | -- |
| Londe, 2020 | Oklahoma | Introduced grasses | >24 months postfire, grazed (low heterogeneity) | 43.1 | -- | 94.7 | 1 | 0.1 | 3.4 | 2.9 | -- |
| Londe, 2020 | Oklahoma | Native tallgrass prairie and grass/shrub communities | >24 months postfire, grazed (moderate heterogeneity) | 58.4 | -- | 45.8 | 17 | 0.8 | 12.1 | 18.1 | -- |

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[cm, centimeter; %, percent; <, less than; --, no data; CRP, Conservation Reserve Program; >, greater than]

| Study | State or province | Habitat | Management practice or treatment | Vegetation height (cm) | Vegetation height-density (cm) | Grass cover (%) | Forb cover (%) | Shrub cover (%) | Bare ground cover (%) | Litter cover (%) | Litter depth (cm) |
|---|-------------------|--|--|---------------------------------------|--------------------------------|-----------------|----------------|-----------------|-----------------------|------------------|-------------------|
| Londe, 2020 ^b | Oklahoma | Native tallgrass prairie and grass/shrub communities | >24 months postfire, grazed (high heterogeneity) | 81.5 | -- | 47.5 | 14.3 | 22.9 | 12.1 | 15.2 | -- |
| Londe and others, 2021a | Oklahoma | Tallgrass prairie | 0–12 months postfire, grazed | 50.4 | 33 | 34.4 | 15.5 | 0.7 | 38.7 | 6.7 | 0.5 |
| Londe and others, 2021a | Oklahoma | Tallgrass prairie | 13–24 months postfire, grazed | 77.2 | 52.5 | 53.3 | 11.6 | 0.5 | 3.9 | 24.1 | 7.4 |
| Londe and others, 2021a | Oklahoma | Tallgrass prairie | >24 months postfire, grazed | 76.7 | 52.6 | 42.3 | 11.6 | 1.1 | 2.7 | 37.4 | 10.4 |
| Manske and Barker, 1988 (nests) | North Dakota | Tallgrass prairie | Multiple | -- | 29 ^a | -- | -- | -- | -- | -- | -- |
| Manske and Barker, 1988 (nest sites) | North Dakota | Tallgrass prairie | Multiple | -- | 25 ^a | -- | -- | -- | -- | -- | -- |
| Manske and others, 1988 | North Dakota | Tallgrass prairie | Grazed | -- | >15 ^a | -- | -- | -- | -- | -- | -- |
| Matthews and others, 2011 (broods) | Nebraska | Multiple | Multiple | -- | 24 ^a | -- | 33.6 | -- | 24.8 | -- | -- |
| Matthews and others, 2013 (nests) | Nebraska | Multiple | Multiple | -- | -- | -- | >25 | -- | -- | <25 | -- |
| McNew and others, 2013 (nests) | Kansas | Tallgrass prairie (contiguous) | Burned, intensively grazed | 54 ^d | 30 ^a | 57 | 19 | -- | 12 | -- | -- |
| McNew and others, 2013 (nests) | Kansas | Tallgrass prairie (fragmented) | Burned, grazed | 40 ^d | 24 ^a | 49 | 11 | -- | 13 | -- | -- |
| McNew and others, 2013 (nests) | Kansas | Tallgrass prairie (contiguous) | Burned, grazed | 42 ^d | 28 ^a | 52 | 35 | -- | 9 | -- | -- |
| McNew and others, 2014 (nests) | Kansas | Tallgrass prairie | Burned, grazed | -- | 26 ^a | 50.8 | 11.2 | 0.7 | -- | -- | -- |
| Norton and others, 2010 (broods) | South Dakota | Restored mixed-grass prairie | Grazed | -- | 35 ^a | 17.9 | 7.3 | -- | -- | -- | -- |
| Powell and others, 2020 | Nebraska | Sandhill prairie | Grazed | 43.8 ^c , 47.7 ^f | 17 ^a | -- | -- | -- | -- | -- | 7.8 |
| Schroeder and Braun, 1992 ^b (successful nests) | Colorado | Sand sagebrush grassland | -- | 4.8–113 | 5.4 ^a | 72.5 | 15.7 | 12.5 | 13.2 | -- | -- |
| Schroeder and Braun, 1992 ^b (unsuccessful nests) | Colorado | Sand sagebrush grassland | -- | 4.8–108.9 | 6 ^a | 74.2 | 13.7 | 15.4 | 10.6 | -- | -- |

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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 (%) | Bare ground cover (%) | Litter cover (%) | Litter depth (cm) |
|--|-------------------|------------------|-------------------------------------|------------------------|--------------------------------|-----------------|----------------|-----------------|-----------------------|------------------|-------------------|
| Svedarsky, 1979 (nests) | North Dakota | Tame grassland | -- | -- | 22 ^a | -- | -- | -- | -- | -- | 8.6 |
| Svedarsky, 1979 (nests) | North Dakota | Native grassland | -- | -- | 20 ^a | -- | -- | -- | -- | -- | 9.5 |
| Svedarsky, 1979 (successful nests) | North Dakota | Multiple | Multiple | -- | 22 ^a | -- | -- | -- | -- | -- | 7.8 |
| Svedarsky, 1979 (unsuccessful nests) | North Dakota | Multiple | Multiple | -- | 20 ^a | -- | -- | -- | -- | -- | 11.9 |
| Svedarsky, 1979 (nests) | North Dakota | Tame grassland | Smooth brome | -- | 27 ^a | -- | -- | -- | -- | -- | 9.6 |
| Svedarsky, 1979 (nests) | North Dakota | Tame grassland | Redtop (<i>Agrostis gigantea</i>) | -- | 18 ^a | -- | -- | -- | -- | -- | 5.3 |
| Svedarsky, 1979 (nests in all other habitats) | North Dakota | Multiple | Multiple | -- | 18 ^a | -- | -- | -- | -- | -- | 9.4 |
| Toepfer, 1988 | Wisconsin | Multiple | Multiple | 25–100 ^d | -- | -- | -- | -- | -- | -- | -- |
| Westemeier and others, 1995 (early-season nests) | Illinois | Tame grassland | -- | -- | 20 ^a | -- | -- | -- | -- | -- | -- |
| Westemeier and others, 1995 (late-season nests) | Illinois | Tame grassland | -- | -- | 40 ^a | -- | -- | -- | -- | -- | -- |

^aVisual obstruction reading (Robel and others, 1970b).

^bThe sum of the percentages is greater than 100%, based on methods described by the author.

^cWestern ragweed (*Ambrosia psilostachya*) cover.

^dGrass height.

^eEffective height of residual cover and all vegetation, respectively.

^fStanding dead vegetation height.

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