Gunnison Sage-Grouse

Centrocercus minimus

Order GALLIFORMES – Family PHASIANIDAE

Introduction

Sage-Grouse (*Centrocercus* spp.) are closely associated with sagebrush (*Artemisia*) ecosystems in western North America. Those Sage-Grouse occurring in southwestern Colorado and southeastern Utah exhibit unique characteristics that have been considered sufficient to treat these birds as a distinct species – the Gunnison Sage-Grouse (*C. minimus*) (Young et al. 2000). Gunnison Sage-Grouse are geographically isolated from populations of Greater Sage-Grouse (*C. urophasianus*) and number fewer than 5,000 individuals (USDI 2013). The small numbers of Gunnison Sage-Grouse distributed within fragmented landscapes provide a challenge for conservation and management efforts (Oyler-McCance et al. 2001, Braun et al. 2014). Considered a globally endangered species by key conservation groups, Gunnison Sage-Grouse have also been designated as Threatened by the U.S. Fish and Wildlife Service.

Male Gunnison Sage-Grouse displaying for females at lek, Gunnison Basin, CO, April. As males strut, multiple females will often visit his territory on the lek.

Gunnison Sage-Grouse, in comparison with Greater Sage-Grouse, are substantially smaller and lighter with shorter rectrices, more distinct white barring on the rectrices, and are genetically distinct (Oyler-McCance et al. 1999, Oyler-McCance et al. 2015). In addition, male Gunnison Sage-Grouse have longer and thicker filoplumes, and have distinct courtship displays (Young et al. 1994). Although the species has been distinctively different from Greater Sage-Grouse for millennia, limited research has focused on the Gunnison Sage-Grouse. Naturally, initial research on the Gunnison Sage-Grouse focused on factors describing the species, such as morphology (Hupp and Braun 1991), breeding behavior (Young et al. 1994), and genetics (Oyler-McCance et al. 1999), which led to its formal recognition as a distinct species (Young et al. 2000). More recently, other studies have described various aspects of habitat (Oyler-McCance et al. 2001, Aldridge et al. 2012), movement behavior (Commons 1997), effective population size (Stiver et al. 2008), population genetics (Oyler-McCance et al. 2005, Oyler-McCance et al. 2015), population dynamics (Davis et al. 2014, 2015; Stanley et al. 2015), and historical distribution (Braun et al. 2014, Braun and Williams 2015). This account emphasizes studies specific to Gunnison Sage-Grouse, but incorporates information on Greater Sage-Grouse as appropriate.

Distinguishing Characteristics

Description

The Gunnison Sage-Grouse is the second largest grouse in North America, with males weighing from 1.7–2.4 kg and females 0.9–1.3 kg (Young et al. 2000). The adult male has fuscous upperparts, profusely marked with drab gray and white; long and pointed rectrices with white bars; plain brown primaries; chin and throat sepia (blackish); sides of neck, breast, and upper belly whitish and slightly distended, forming a ruff; belly and undertail coverts sepia with large white spots on tips of undertail coverts; and buff thighs. The head has a yellow-green fleshy comb above each eye, and long filoplumes that arise from the back of the neck (Young et al. 2000).

During courtship displays, the tail is fanned and upper breast distended, exposing 2 greenish-yellow patches of bare skin on the frontal area of the lower throat and breast. These apteria are briefly exposed during the display, appearing as round or oblong 'balloons.' The adult female is similar to the male but smaller and has fuscous feathers, marked with drab gray and white on the head and breast, creating a more cryptic appearance overall than in the male. Relative to the male, females lack the distensible bare skin patches on the breast and have a smaller and duller yellow-green comb over each eye (Young et al. 2000). Juveniles resemble adults of their sex but may be distinguished for up to 17 months by the retained outermost two juvenal primaries, which are more pointed than adult primaries (Braun and Schroeder 2015).

Identification

Although geographically isolated, Gunnison Sage-Grouse are generally similar to the Greater Sage-Grouse. They are distinguished from that species by smaller size, differences in movement patterns and acoustical components of male courtship displays, longer and thicker filoplumes on the neck of the male, and a more distinctly barred tail pattern. Their large size, long pointed tail, and distinctive plumage pattern distinguish males from all other North American grouse. The smaller and less boldly marked females could be more easily confused with female Greater Sage-Grouse, were it not for non-overlapping distributions. The Dusky Grouse (*Dendragapus obscurus*) is distinguished from female sage-grouse by slightly smaller size, rounded (not pointed) tail, and plainer underparts that lack a blackish belly patch. Sharp-tailed Grouse (*Tympanuchus*

phasianellus) are distinguished from female sage-grouse by smaller size, short tail, white undertail coverts, and white-chevron markings on the breast and flanks.

Distribution

eBird data (http://ebird.org/content/ebird/) provide detailed looks at the range of this species throughout the years: eBird Year-round Range and Point Map for Gunnison Sage-Grouse.

The Americas

Gunnison Sage-Grouse were formerly native to sw. Colorado, n. New Mexico, se. Utah, and ne. Arizona (Young et al. 2000, Schroeder et al. 2004, Braun et al. 2014, Braun and Williams 2015), south and east of the Colorado River (Fig. 1; Fig. 2). Their range is now greatly reduced and the species has been extirpated from New Mexico and Arizona as well as large portions of its former range in Colorado and Utah. Seven small localized populations exist in 8 counties in Colorado and 1 county in Utah (Braun et al. 2014) (Fig. 3). Hinsdale Co. has been considered either as occupied (Braun et al. 2014) or as potential habitat (Gunnison Sage-Grouse Rangewide Steering Committee 2005). Gunnison Sage-Grouse in Montezuma Co., Colorado and Grand Co., Utah (shown in Fig. 2) have not been observed since the mid-1990s and early 2000s, respectively (CEB).

Figure 1. Distribution of Gunnison Sage-Grouse.

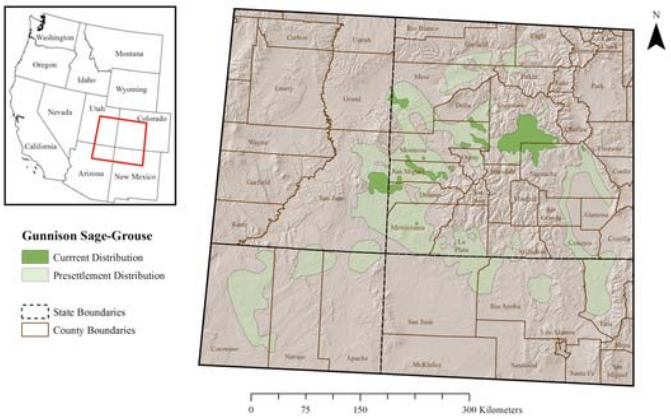

Figure 2. Current and pre-settlement distribution of Gunnison Sage-Grouse. Current (Gunnison Sage-Grouse Rangewide Steering Committee 2005) and pre-settlement (Schroeder et al. 2004) distribution of Gunnison Sage-Grouse. Depiction of the current range of Gunnison Sage-Grouse may be imprecise because of recent and continuing declines in population sizes and occupied range.

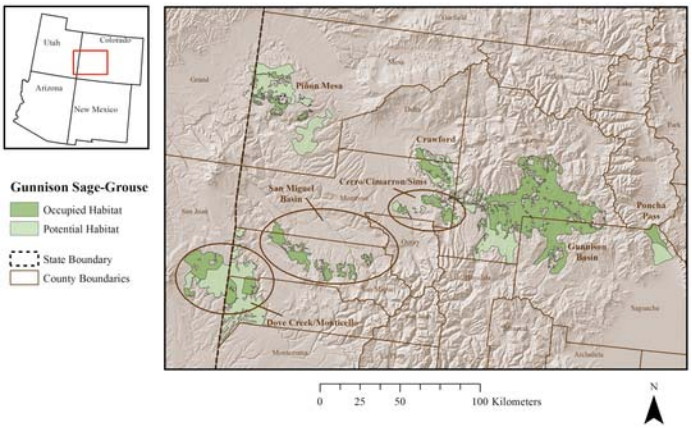

Figure 3. Distribution of seven recognized populations of Gunnison Sage-Grouse. Distribution of seven recognized populations of Gunnison Sage-Grouse considering Monticello, Utah and Dove Creek, Colorado as one population (Gunnison Sage-Grouse Rangewide Steering Committee 2005). Occupied habitat refers to "areas of suitable habitat known to be used by Gunnison Sage-Grouse within the last 10 years from the date of mapping" and potentially suitable habitat refers to "unoccupied habitats that could be suitable for occupation of sage-grouse if practical restoration were applied" (Gunnison Sage-Grouse Rangewide Steering Committee 2005).

Outside The Americas

Not known to exist outside of the United States but fossil evidence from New Mexico (Harris 1989) indicates that *Centrocercus* occurred in Hidalgo Co. immediately north of the states of Chihuahua and Sonora, Mexico. The present habitat on both sides of the international boundary in this location, while not now suitable, is extensive and extends well south into Mexico. Based on the current distribution of Gunnison Sage-Grouse, it is most likely that the fossil sage-grouse in New Mexico were the Gunnison species.

Historical Changes

Gunnison Sage-Grouse breed where suitable habitat remains within 8 counties of sw. Colorado (south of the Colorado-Eagle river system) and 1 county in se. Utah. Seven populations

persist (Fig. 3) identified as Gunnison Basin (centered about Gunnison, Gunnison Co., Colorado); Poncha Pass (Saguache Co., Colorado); Crawford (e. Delta Co. and ne. Montrose Co., Colorado); Cerro Summit-Cimarron-Sims Mesa (e. Montrose Co., Colorado); Pinon Mesa (north of Gateway, Mesa Co., Colorado); San Miguel Basin (south and west of Norwood, San Miguel Co., Colorado); and Monticello-Dove Creek (Monticello, San Juan Co., Utah and Dolores Co., Colorado; Braun et al. 2014; see also Beck et al. 2003). Local populations undertake seasonal shifts in location and use of habitat types (Hupp and Braun 1989b, Commons et al. 1999).

Gunnison Sage-Grouse are currently limited to 4,787 km^2 of sw. Colorado and nearby neighboring Utah which represent only 10% of the potential habitat of its estimated pre-settlement distribution (46,521 km^2; Schroeder et al. 2004). This species formerly occurred in 22 counties of Colorado (Braun 1995, Braun et al. 2014). Gunnison Sage-Grouse formerly occurred in New Mexico (Bailey 1928, Ligon 1961, Merrill 1967, Hubbard 1970, Braun and Williams 2015); those formerly in extreme ne. Arizona, extreme sw. Kansas, and adjacent nw. Oklahoma are presumed to also represent this species (Young et al. 2000, Braun and Williams 2015).

Fossil History

There are Pleistocene fossils of sage-grouse from Arizona (Rea and Hargrave 1984), Colorado (Emslie 2004), New Mexico (Howard and Miller 1933, Howard 1962, Gillespie 1985, Harris 1989, Brasso and Emslie 2006), and Utah (Emslie and Heaton 1987) and may represent this species.

Systematics

Geographic Variation

None.

Subspecies

None.

Related Species

The grouse either are treated as a subfamily (Tetraoninae) in a broad Phasianidae (e.g., Sibley and Monroe 1990, Ellsworth et al. 1995, 1996) or as a separate family (Tetraonidae) sister to the Phasianidae (e.g., del Hoyo et al. 1994, Dudley et al. 2006, Wang et al. 2013). The American Ornithologists' Union (1998) follows the former treatment, and if Tetraonidae is treated as a family then Phasianidae as currently defined is paraphyletic (Gutiérrez et al. 2000, Dimcheff et al. 2002). Within the Tetraoninae, the prairie grouse (*Tympanuchus* and *Centrocercus*), with the Blue Grouse complex (*Dendragapus*), constitute a distinct evolutionary radiation (Gutiérrez et al. 2000, Dimcheff et al. 2002, Drovetski 2002). The sister group to this radiation is less clear, although it may be either *Lagopus* (the ptarmigan) or Tetrao (the Old World black grouse and capercailles). The genus *Centrocercus* is morphologically, genetically, and behaviorally distinct from other grouse (Short 1967, Johnsgard 1983, Ellsworth et al. 1995, 1996).

Sister relationships within *Centrocercus* are straightforward, as there are but two species in the genus, of which *C. minimus* was named only recently (Young et al. 2000). In addition to being markedly smaller and having the rectrices more distinctly barred, filoplumes on the neck more extensive, and different mating displays (Young 1994, Young et al. 1994, Welch et al. 1995), the two species differ in several neutral genetic markers (Oyler-McCance and Quinn 2011). Mitochondrial DNA haplotypes are not reciprocally monophyletic, implying that speciation was recent (Oyler-McCance et al. 1999). A genomic analysis of the two species affirmed species limits (Oyler-McCance et al. 2015). Rapid changes in morphology, plumage, and behavior have been noted in species with strong sexual selection, species that include lekking grouse (Ellsworth et al. 1995, Spaulding 2007, Oyler-McCance et al. 2010, Oyler-McCance et al. in press). Hybrids involving *C. minimus* are not known.

Migration

Nature Of Migration In The Species

Gunnison Sage-Grouse are resident in some areas and/or make seasonal migrations up to at least 40 km between winter-use areas and those used for breeding and nesting (Hupp and Braun 1989b, M.L. Commons unpublished). Variation in movements associated with gender, seasonal habitat quality and distribution, and weather, remain unstudied, as do effects of habitat fragmentation. Radio-tracking studies suggest that Gunnison Sage-Grouse in the Dove Creek and Crawford populations remain within 5 km of lek sites throughout the year while those in the San Miguel Basin and Pinon Mesa populations move to lower elevations during winter (Commons 1997, M.L. Commons unpublished data). Birds in the western portion of the Gunnison Basin overwintered within 4.7 km (SD = 4.0) of their lek of capture (n = 25 males and 46 females; C.L. Aldridge unpublished data) and females nested an average of 2.1 km (SD = 2.1) from their lek of capture/attendance (Range = 0.02 to 10.1 km, n = 92; Aldridge et al. 2012). Analysis of microsatellite and mtDNA sequence data has found some evidence of movements among populations, yet substantial genetic structure exists among populations indicating that gene flow is reduced and movements among populations are rare (Oyler-McCance et al. 2005).

Timing And Routes Of Migration

Migration in fall and early winter appears related to snow depth, with birds moving from higher elevations to lower or more protected areas (west- and south-facing slopes). Movements during winter are related to availability of sagebrush above the snowline, with birds moving to ridge tops or to areas where snow does not accumulate to over 50–60 cm (Hupp and Braun 1989b). Movements in spring to breeding areas are the reverse of those in fall and winter. Desiccation of succulent forbs within nesting locations may result in movements away from nesting locations to summering areas (M. L. Commons, unpublished data).

Migratory Behavior

Movements of Gunnison Sage-Grouse from winter-use areas to those used for breeding may be abrupt in some areas (e.g., Dry Creek Basin to Miramonte Reservoir). Movements of females, especially those with broods, are gradual in summer (although more abrupt after nest failure and departure of males from leks), and again abrupt in late fall (M. L. Commons, unpublished data).

Control And Physiology

Distance and timing of migratory movements in Gunnison Sage-Grouse are influenced by rain during summer, snow accumulation in late fall (affecting access to resources), and distribution of habitat (M.L. Commons, unpublished data).

Habitat

Breeding Range

The Gunnison Sage-Grouse is closely associated with sagebrush (*Artemisia*) ecosystems. Sagebrush habitats have significant natural variation in vegetative composition, habitat fragmentation, topography, substrate, weather, and frequency of fire. Consequently, Gunnison Sage-Grouse are adapted to use a mosaic of sagebrush habitats throughout their range. They are found in sagebrush along riparian areas, adjacent to piñon–juniper stands, and in intermountain basins in areas dominated by several species of *Artemisia* (*A. cana*, *A. nova*, *A. tridentata*) and Gambel's oak (*Quercus gambelii*), serviceberry (*Amelanchier* spp.), and snowberry (*Symphoricarpos* spp.) (Braun et al. 2014). Gunnison Sage-Grouse are less likely to show avoidance behavior of large shrubs and may be found near and within stands of aspen, piñon–juniper and fir (Young pers. obs., Commons et al. 1999, Braun et al. 2014). Reconstruction of historical descriptions of habitat within the current range of Gunnison Sage-Grouse indicates large contiguous expanses of mature sagebrush (*A. tridentata*), approximately 20% of area covered with dense sagebrush, 15% with scattered sagebrush, and 19% with scattered trees among sagebrush (Bukowski and Baker 2013).

Sagebrush habitat, Gunnison Basin, CO, April. Gunnison Sage-Grouse are a sagebrush obligate, relying on the shrub species and its ecosystem for every part of their life cycle.

Leks. Leks occur in valley bottoms, basins, ridges, and broad sloping expanses including agricultural fields with alfalfa, wheat, and pinto beans as well as former crop fields now in the Conservation Reserve Program (CRP) (Young 1994, Commons 1997). Several active leks occur in irrigated pastures and where ranchers feed livestock during winter; these sites were historically sagebrush dominated. There is no evidence that lek habitat is limiting.

Nests. Placed in relatively thick vegetative cover, usually dominated by big sagebrush (Young 1994, Aldridge et al. 2012). Vegetatively diverse habitats within 8 km of leks may provide the best nesting environments by ensuring both horizontal and vertical concealment (Young 1994). Females in the western portion of the Gunnison Basin selected nest sites in areas with a higher proportion of sagebrush cover >5% (within a 1.5-km radius; Homer at al. 2013), that were more productive (within 1 km), had lower density of maintained roads (class 1-4; within 6.4 km), a moderate distance from water, and farther from conifer–juniper forests (Aldridge et al. 2012). At a more local patch scale (0.564-km radius from nest), females selected sagebrush patches with greater proportions of taller big sagebrush cover (>10%), that were farther from residential development, water sources, major roads (class 1 or 2), and had higher productivity (Aldridge et al. 2012).

Broods. Hens with broods occur in rich mosaics of habitat, including sagebrush, oakbrush, riparian meadows, greasewood (*Sarcobatus* spp.) bottoms, alfalfa, grain and bean fields, irrigated pastures, and trails; the common feature of brood areas is that they are rich in forbs and insects (Young 1994, Commons 1997). Hens with broods respond to dry conditions during mid- and late summer by foraging along stream courses, in agricultural fields, and moving uphill on north-facing slopes.

Summer. Radio-tracked Gunnison Sage-Grouse in Utah used Conservation Reserve Program areas in proportion to their availability, but seemed to avoid these fields when livestock were present (Lupis et al. 2006).

Male Gunnison Sage-Grouse being fitted with radio transmitter, Gunnison Basin, CO, April. Researchers place radio transmitters on grouse to learn more about their habitat use.

Spring And Fall Migration

No information, but migrates only short distances.

Winter Range

Gunnison Sage-Grouse move to areas on north-facing slopes with dense stands of sagebrush in late fall and then to sagebrush-dominated flats and broad west- and south-facing slopes with taller sagebrush at the periphery, and with shorter sagebrush along ridge tops in winter. Variation in topography and height of sagebrush ensures the availability of sagebrush in different snow conditions (Hupp and Braun 1989b) with grouse tending to use denser and taller sagebrush when snow cover is deep and extensive (Hupp and Braun 1989b). During winter, males use sagebrush greater than expected relative to availability and used all other habitat types less than expected (C.L. Aldridge unpublished data), particularly within landscapes fragmented by agricultural fields (Commons 1997). In San Juan Co., Utah, mixed-gender flocks often exceeding 20 birds used black sagebrush and big sagebrush in higher proportion than the availability of these habitat types (Ward 2007).

Food Habits

Feeding

Main Foods Taken

Sagebrush is eaten in all seasons, and succulent forbs and invertebrates are consumed when available.

Microhabitat For Foraging

Gunnison Sage-Grouse generally forage in open habitats at ground level or up to 50 cm above the ground on top of snow. They tend to forage at sites with higher canopy cover and taller sagebrush than in random locations (Hupp and Braun 1989b). Gunnison Sage-Grouse select moist sites for foraging when available (Young 1994).

Feeding sites are not distributed proportionately among topographic categories on the landscape (Hupp and Braun 1989b). Gunnison Sage-Grouse choose winter foraging sites based on relationship between sagebrush height and snow depth (where sagebrush exposure above snowline is maximized); feeding distribution changes as snow pack increases through winter, and varies among years in accordance with snow accumulation (Hupp and Braun 1989b). Accumulation of 30 cm of snow may trigger a threshold response in winter foraging location and movement to steeper slopes (Hupp 1987). There is an apparent preference (possibly to avoid predation) for mesic drainages (where sagebrush is tallest and canopy cover highest) and avoidance of northeastern aspects with greater than 5% slope (Hupp and Braun 1989b). Drainages comprise less than 3% of available habitat and represent a component of critical winter habitat for Gunnison Sage-Grouse. Highest use (but in proportion to availability) was on southwest-facing aspects with slope greater than 5%, in addition to flatter terrain during low snow pack periods, and xeric sites dominated by black sagebrush (Hupp 1987, Hupp and Braun 1989b). Gunnison Sage-Grouse appear to select foraging locations based on topography and vegetative characteristics, favoring drainages and tall sagebrush with high canopy cover that offer protection from harsh (cold and or windy) conditions (Hupp and Braun 1989b); moist sites in drainages and swales are selected for foraging during spring, summer, and fall (Young 1994, Commons 1997).

Food Capture And Consumption

Gunnison Sage-Grouse forage mostly on low-growing plants at ground or snow levels and will reach higher to take desired items such as leaves and flowers. Foods are swallowed as parts or whole leaves and or flowers (CEB).

Diet

Winter. In winter, sage-grouse are highly dependent on sagebrush for forage (Eng and Schladweiler 1972, Wallestad 1975, Remington and Braun 1985). Overwintering Gunnison Sage-Grouse consume leaves of several subspecies of big sagebrush, black sagebrush, little (low) sagebrush (*A. arbuscula*), and winterfat (*Eurotia lanata*) (Barber 1968, CEB). In the Gunnison Basin, mountain big sagebrush (*A. t. vaseyana*) was the most prevalent subspecies of sagebrush at foraging sites and was likely the most palatable (Vasquez 2003, Stanek 2004).

Breeding. Gunnison Sage-Grouse eat leaves of several subspecies of big sagebrush, black sagebrush, little (low) sagebrush, winterfat, and forbs including sprouting alfalfa and flowers of pinto beans (CEB).

Summer. Leaves of winterfat, forbs including alfalfa, clovers (*Trifolium* spp.), pinto bean sprouts and flowers, soft wheat kernels, and any low growing succulent native and exotic forbs are eaten by Gunnison Sage-Grouse in summer (CEB). In an agriculturally fragmented landscape, males north of Dove Creek, Colorado foraged in sites dominated by alfalfa, forbs, and grasses and where sagebrush was shorter than in random sites (Commons 1997). In San Juan County, Utah, 75% of summer locations were in CRP fields where forbs and grasses were more abundant and arthropod abundance and diversity were higher than in agricultural fields (Ward 2007). In summer and early fall (through September), Gunnison Sage-Grouse in the Gunnison Basin were observed feeding on mountain big sagebrush, fringed sage (*A. frigida*), dandelion (*Taraxacum* spp.), and a mustard species (Maddox and Young 2001). During this time period, 62% of fecal pellets contained mountain big sagebrush and 27% contained Wyoming big sagebrush (*A. t. wyomingensis*) (Maddox and Young 2001). In addition to sagebrush leaves, feces also contained seeds, forbs (holly-leaf clover, dandelion), ants, beetles, and other invertebrates (Maddox and Young 2001). By October, all pellets contained only sagebrush leaves (Maddox and Young 2001).

Food Selection And Storage

Some indirect evidence indicates selectivity of sagebrush species by Gunnison Sage-Grouse (Maddox and Young 2001, Vasquez 2003), which appears to be related to nutritive quality of leaves (see Nutrition and Energetics, below).

The crop is the main temporary food storage organ followed by a non-muscular gizzard, which does not retain hard seeds or stones for grinding (CEB). Gunnison Sage-Grouse may be similar to Greater Sage-Grouse, which have been observed pecking at soil in Wyoming and Colorado, especially around salt blocks and exposed mineral soil (CEB, CLA). No evidence of food storage in the environment.

Nutrition And Energetics

The digestive system of sage-grouse is uniquely adapted for consumption of sagebrush leaves (Barber 1968). Specific species or subspecies of sagebrush are preferred because of higher nutritive value and/or lower toxins (Remington and Braun 1985). Indirect evidence from the Gunnison Basin suggests some taxonomic selectivity of sagebrush by Gunnison Sage-Grouse (Maddox and Young 2001, Vasquez 2003). Plant secondary metabolites (PSM; monoterpenes, phenolics) have a significant role in Greater Sage-Grouse habitat selection at multiple spatial scales; sage-grouse selectively feed on sagebrush plants with relatively high protein and relatively low PSM, avoid sagebrush plants with higher toxin concentration, and within stands of sagebrush, sage-grouse select patches and individual plants with lower toxins (Frye et al. 2013). Crude protein and concentration of 6 distinct monoterpenes did not differ in mountain big sagebrush at varying topographical sites in the Gunnison Basin, and did not differ between browsed and unbrowsed sagebrush plants, suggesting that during winter Gunnison Sage-Grouse may not feed on patches or individual sagebrush plants based on phytochemistry (Hupp 1987). Lack of foraging selectivity may be related to relatively high crude protein (20%) levels in mountain big sagebrush in the Gunnison Basin (Hupp 1987).

Whether foraging is selective or non-selective, male Gunnison Sage-Grouse gain weight over winter and accumulate energy reserves prior to the breeding season (Hupp 1987). Lipid reserves of male sage-grouse of both species are highest following winters of low snowfall and also larger during early courtship than during late courtship (Hupp and Braun 1989a). Males catabolized 66 g of endogenous fat reserves during courtship, which accounts for less than 10% of their energetic needs during this annual cycle event (Hupp 1987). Lipid reserves are not adequate to meet full energetic cost of courtship but may provide a caloric advantage during the short period of peak female attendance on leks (Hupp 1987).

Metabolism And Temperature Regulation

Lipid reserves of male sage-grouse (both species) decline during the breeding period when they rely heavily on exogenous food resources (Hupp and Braun 1989a) to maintain body mass. Whereas endogenous lipids are stored over winter and mobilized during the lek courtship period to partially meet energetic demands, endogenous protein is not catabolized by Gunnison Sage-Grouse during courtship (Hupp 1987).

During winter, Gunnison Sage-Grouse forage and roost in topographic areas where sagebrush is taller (drainages) or aspect (south or west facing slopes) is more favorable for maintaining body temperature (Hupp and Braun 1989b). Gunnison Sage-Grouse routinely use snow burrows in winter for subnivean roosting (Stanek 2004, JRY, PAM). Winter snow accumulations of 25 cm trigger snow burrowing; Gunnison Sage-Grouse dig shallow burrows in soft snow or depth hoar (Stanek 2004). Shallow burrows suggest that subnivean roosting is an anti-predator strategy, whereas deeper snow burrows suggest thermoregulation (Stanek 2004).

Drinking, Pellet Casting, And Defecation

Sage-grouse commonly seek water in seeps, ponds, and small streams, and ingest snow in winter. Sage-grouse defecate two types of droppings; firm fibrous pellets (mostly pieces of sagebrush leaves) and soft caecal masses (mostly bacteria from their caecum) that are initially fluid but become tar-like in texture. Birds can deposit ‘piles’ of 30 (females) to 50 (males) pellets overnight in areas where birds commonly roost near leks and in winter-use areas along ridge tops and in denser and taller sagebrush when snow cover occurs. Pellet piles often have a caecal dropping that is emitted after most pellets have been deposited (CEB). Caecal droppings are common in early morning after night roosting and are especially noticeable on leks in spring. They also are emitted after prolonged bouts of resting. Females deposit large “clocker” droppings away from the nest, possibly to reduce detection of the nest site by potential predators.

Sounds

Sound selections for Gunnison Sage-Grouse can be found in the Audio Gallery, or in the full catalog of Gunnison Sage-Grouse sound at Macaulay Library (http://macaulaylibrary.org/).

Vocalizations

The array of sounds and vocalizations made by Gunnison Sage-Grouse has similarities with those of the Greater Sage-Grouse, but with key differences that are implicit in the species distinctiveness.

Development

Esophageal skin patches that are inflated during breeding displays produce sounds that seem to be louder in adult male Gunnison Sage-Grouse than in younger males, a pattern similar to Greater Sage-Grouse (Clarke et al. 1942). While yearling males are frequently seen on display sites and occasionally perform displays, the extent to which learning is a component of male or female sound production in Gunnison Sage-Grouse is unknown.

Array Of Sounds

Males. Male sage-grouse produce numerous vocal and nonvocal sounds when performing their Strutting Display. Mating vocalizations of male Gunnison Sage-Grouse differ in many ways from the vocalizations of male Greater Sage-Grouse (Young et al. 1994). Males usually perform their displays from breeding territories on leks during predawn and at dawn. Sounds associated with breeding are also uttered during crepuscular periods and nights with bright moonlight and in the predawn darkness (Young 1994, Stiver 2007). Mating display sounds

within the Gunnison Sage-Grouse are highly stereotypic, and differences between males are relatively small (Young et al. 1994). The Strutting Display of male Gunnison Sage-Grouse is performed at a slower rate than that of the Greater Sage-Grouse (Barber 1991, Young et al. 1994).

Plop. The Plop (Hjorth 1970), also described as "air sac pops" (Gibson and Bradbury 1985) or "snaps" (Wiley 1973a), is a distinctive broadband sound, amplified by the air-filled esophageal pouches that can be heard up to 2-km away. They sound much like boiling water when several males are producing them at once. During Plops, compressed air in the esophageal pouches causes the cervical apteria to become fully distended. Typically 9 Plops are produced during the Strutting Display (Young et al. 1994) rather than the two produced by Greater Sage-Grouse.

Whistle. A frequency-modulated Whistle is uttered between the 7th and 8th Plops (Greater Sage-Grouse produce the Whistle between 1st and 2nd Plops).

Snorting. Snorting (JRY), also known as hooting (Hjorth 1970), is a sudden release of air at end of the Strutting Display. No air is visibly released during the actual sounds produced during the Strutting Display.

Wing Swish. Produced by the wing brushing against the stiff, white feathers of the upper chest (Hjorth 1970, Wiley 1973a, Gibson and Bradbury 1985, Young et al. 1994). The sound amplitude and the number of wing swishes in Gunnison Sage-Grouse are different from those in Greater Sage-Grouse, being quieter, reduced in movement, and broader in frequency range within each strut (Young et al. 1994).

Tail Rattle. Tail retrices produce a sound when they rub against each other as they vibrate; this tail-rattling occurs at end of the Strutting Display and during aggressive interactions with other males often following a Strutting Display and occurring at territorial boundaries during disputes (Hjorth 1970, Young 1994).

Chatter Call. A rapid, low-volume, low-frequency vocalization uttered during aggressive interactions between and among males. (Hjorth 1970, JRY, J. A. Hill).

Females. Because of the difficulty in observing sage-grouse when they are not on leks, sounds of females are poorly understood. No studies of vocalizations away from leks have been done although female Greater Sage-Grouse have been observed vocalizing during aggressive interactions with other females (MAS). J. A. Hill studied female vocalizations on a lek in the Gunnison Basin for one season and found several female vocalizations associated with specific behaviors (arrival, departure-intention calls, solicitation, and following copulations). Females also made aggressive vocalizations toward each other occasionally vocalizing while charging another female.

Quacking Call. A 2- to 4-note, kak-kak-kak-kak, uttered by females as they arrive or depart from a lek. Quacking is also uttered when females are flushed (Young 1994).

Contact Call. A single soft note, cu-uk, cu-uk that may be repeated frequently. The call is uttered primarily by brood hens to maintain the integrity of broods, but may also be uttered by females traveling in groups on a lek.

Chatter Call. Rapid, low-volume chatter calls are given by females on the lek when involved in female-female aggressive interactions. (Hjorth 1970, JRY, J. A. Hill).

Juveniles. Communication between hens and chicks is continuous; Contact Calls of slightly different pitches, cu-uk, cu-uk, are uttered by hen and See-ah Calls by chicks.

See-ah Call. When chicks become separated from the brood, they utter a louder and longer see-ah, a long whistle-like call that starts low and rises in pitch with a lingering phase as the end.

Nonvocal Sounds

See Array of Sounds, above.

Behavior

Behaviors of Gunnison Sage-Grouse are not well studied other than their breeding behaviors and incidental observations during radio-tracking studies.

Locomotion

The Gunnison Sage-Grouse is a strong flier, but is mostly a ground-dwelling bird that usually only resorts to hiding or flying when threatened. This species typically can outfly a Golden Eagle (Aquila chrysaetos) if the eagle misses on the stoop (JRY).

Adult male Gunnison Sage-Grouse in flight, Gunnison Basin, CO, April. Adult male Gunnison Sage-Grouse departing a lek.

Self-Maintenance

Preening, Head-Scratching, Stretching, Bathing, Etc.

Sage-grouse dust-bathe, rolling in shallow depressions in small, bare areas. They may even roost during the day in small shallow

depressions in sandy or loose soils (CLA). Both males and females spend significant time preening on leks and during the day. Information on actual proportion of time spent in self-maintenance is not available.

Sleeping, Roosting, Sunbathing

Gunnison Sage-Grouse typically roost on the ground surface, and in winter frequently burrow into the snow (Hupp 1987, J. Stanek and M. Vasquez, pers. comm.). Small groups (3–5 individuals) of sage-grouse often roost in close proximity (within 1 m, CEB). An investigation of 20 snow roosts and 56 subnivean tunnels within the Gunnison Basin during winter 2003–2004 found no evidence that Gunnison Sage-Grouse roost near sagebrush; instead, they occupy interspaces between individual plants or sagebrush patches (J. Stanek and M. Vasquez, pers. comm.). Grouse did not burrow through hard wind slabs, but rather remained in the softer snow layers. The average length of caves was 49 cm (range = 27–110 cm); average length of tunnels was 97 cm (range = 53–174 cm). Mean tunnel depth, from snow surface to burrow bottom was 26 cm (range = 17–35 cm); mean cave depth was 30 cm (range = 22–40 cm). Roosting locations at the end of the tunnels contained fecal pellets 85% of the time. During mating season, males are often solitary or separated by several meters at roost sites; they often sleep on ridges near leks (JRY). Juveniles roost with hens during late spring, summer, and early autumn and may be underneath (small chicks) or touching hens (CEB). Throughout the year, birds loaf during the day in sheltered locations, depending on the weather.

Daily Time Budget

No studies of time budgets have been conducted for Gunnison Sage-Grouse.

Agonistic Behavior

Physical Interactions

Male. Many physical interactions occur on leks. Males may move back and forth in front of each other and settle down about 0.5 m apart, head to tail, in Face-Past, or Parallel Reversed display (Hjorth 1970, Wiley 1973a, Young 1994). If either male moves, the other typically moves with him, maintaining spacing and position. Males may remain in this position for over 1 h, particularly at the end of the morning display period (JRY). Face-Past display and other activities may lead to Wing Fights: males crouch forward with their bodies parallel to the ground, lower their tails, and lash out at each other with their wings, occasionally jumping a few centimeters in the air and smashing their wings down on the other male. Males rarely peck at each other, but may briefly grab other males with their bills (Hjorth 1970, JRY). Wing Fights occur more frequently at the beginning of the display season prior to females' arrival, when several females are present on male territories, and when adjacent males cross territorial boundaries. In addition, Wing Fights and chases at end of season are frequent and typically directed at yearling or unestablished males (Wiley 1973b, JRY). Yearling males rarely attend leks until the peak of the breeding season (Eng 1963, Gibson and Bradbury 1987) and are often chased by a series of males across leks and driven from breeding sites completely (JRY). There are few observations of agonistic behaviors during other seasons.

Two male Gunnison Sage-Grouse fighting, Gunnison Basin, CO, April. A wing fight between two males at a territory boundary on a lek in the Gunnison Basin, Colorado.

Two male Gunnison Sage-Grouse fighting, Gunnison Basin, CO, April. Wingfights at territory boundaries are not uncommon during the lekking season for males.

Two male Gunnison Sage-Grouse fighting, Gunnison Basin, CO, April. A wing fight between two males at a territory boundary on a lek in the Gunnison Basin, Colorado.

Female. Hens occasionally chase other hens from males on a lek by forward rushes and pecks, often uttering the Chatter Call during the attack (Scott 1942, Hjorth 1970, Wiley 1973b, JRY, J. A. Hill, pers. comm.). No documentation of aggressive behavior between females during brood-rearing and winter seasons.

Females on a lek, Gunnison Basin, CO, April. Females on a lek in the Gunnison Basin.

Spacing

Territoriality

Adult male Gunnison Sage-Grouse are territorial on leks during the breeding season, actively defending areas of 5–100 m2 (JRY). Yearling males rarely defend territories or breed. Leks vary in size (1–20 ha) and males may move around a given lek "area" to adjacent openings and ridges both within mornings and across seasons (JRY). Males will follow females off lek, especially near the end of the morning display. Thus, leks can be less 'fixed' in physical space and dominance relationships among males may be more hierarchical rather than territorial (JRY, CEB). Neither males nor females are known to show any territorial behavior off leks; however, such behaviors have not been studied with these cryptic birds.

Individual Distance

Individual Gunnison Sage-Grouse within a group, during most of the year, are often within a few meters of each other. Males may be spaced on leks, from a few meters to over 100 m apart. Females on leks may be 1–3 m apart and obtain densities as high as 20 individuals/5m2 (JRY, L. A. Higgins, J. A. Hill pers. comm.).

Sexual Behavior

Mating System And Sex Ratio

The species uses a lek mating system in which males provide neither paternal care nor resources such as nesting or foraging sites. Female Gunnison Sage-Grouse are thought to be similar to Greater Sage-Grouse for which females exhibit relative unanimity in mate choice (Gibson et al. 1991), resulting in only a small percentage of males mating. In general, 10–15% of male Gunnison Sage-Grouse on a given lek breed and 1–2 may account for up to 90% of all of the copulations on that lek area (Young 1994). The sex ratio among the San Miguel Basin population was 1 male to 2.13 females at leks (Stiver et al. 2008). Mating is brief, lasting only a few seconds, and males may mate with other females within a minute or two and may mate more than 10 times in a morning (JRY). Genetic studies of Greater Sage-Grouse suggest that multiple paternities and off-lek mating may be more common than previously thought, and may increase male contributions to genetic diversity (Semple et al. 2001, Bush et al. 2010, Bird et al. 2013). Numerous possible explanations exist for the high variability in rates of mating success among Greater Sage-Grouse males. Successful males may be dominant (Bradbury and Gibson 1983), centrally located on the lek (Scott 1942, Wiley 1973b), more active (Gibson and Bradbury 1985, Hartzler and Jenni 1988, Gibson 1990, Gibson et al. 1991, Young et al. 1994, Gibson 1996), more visually and/or vocally attractive (Gibson and Bradbury 1985; Gibson 1989, 1990, 1996), and/or have fewer parasites (Boyce 1990, Spurrier et al. 1990). In addition, females may add to the complicated system by selecting leks that are far from nesting areas (e.g., >16 km for one Gunnison female) and/or copying the mating choices of other females (Wiley 1973b, Hartzler and Jenni 1988, Gibson et al. 1991). Male Gunnison Sage-Grouse with higher mating success were those that were slow, but persistent, in their display (Young 1994).

Courtship

Male Gunnison Sage-Grouse have a highly developed and spectacular mating display that is referred to, in total, as the Strutting Display. This display begins with male's taking a step or two forward, raising his wings, producing a distinctive set of loud "Plops" produced in conjunction with the expansion of the male's large esophageal pouches, and tossing their filoplumes over their head. Throughout their displays, males hold their rectrices fanned in an upright position, filoplumes and yellow eye-combs erect, and air sacs partially distended. Males culminate their display with a distinct Tail Rattle at the end of this display (Young et al. 1994). Successful males perform Strutting Display 6–10 times/min (Young et al. 1994) for 3–4 h/d with highest activity centered around, and shortly after, sunrise for up to 3 mo during spring. Females begin visiting leks 1–2 wk after males set up territories (JRY); they wander through male territories throughout early morning and may revisit one lek and/or visit several leks during a season. Mating is relatively synchronous: over 50% of all matings on a given lek occur within 5–10 d, typically in April (JRY). Females move individually or in groups of up to 20 among displaying males. An individual female eventually solicits copulation from a male by squatting on her belly, lifting her wings slightly, and spreading her primaries along the ground. The male steps on the female's back for cloacal contact and spreads his wings with his primaries touching the ground; copulation lasts only a few seconds. After successful copulation, the female makes a short dash away from the male and vigorously shakes her wings and tail. If the female does not shake, she returns to the same male to

copulate again. Typically, the female departs the lek within 20 min of copulation (JRY).

A female Gunnison Sage-Grouse solicits a male for copulation, Gunnison Basin, CO, April.

Male Gunnison Sage-Grouse displaying for females at lek, Gunnison Basin, CO, April. Several males gathering and displaying in their lek territories on a lek in the Gunnison Basin, Colorado.

Adult male Gunnison Sage-Grouse performing 'Strut' display, Gunnison Basin, CO, April. A male Gunnison Sage-grouse performing a strut display on a lek in the Gunnison Basin, Colorado. Gunnison Sage-grouse pop their air sacs 9 times instead of the 2 typical of the Greater Sage-grouse during their mating displays.

Adult male Gunnison Sage-Grouse, Gunnison Basin, CO, April. The filoplumes thrown above this male Gunnison Sage-grouse's head is one of the many distinctive display features of the species.

Social And Interspecific Behavior

Degree Of Sociality

Both species of sage-grouse are highly social during the winter, forming flocks of several dozen up to 100 birds; these flocks may contain only one sex. However, individuals do not appear to share snow roosts. During breeding, nesting and brood-rearing, and winter, segregation by sex of Gunnison Sage-Grouse is common. Generally, a few weeks after eggs hatch, hens may join with other hens and their chicks in areas containing abundant green forbs and insects. As the brood season progresses toward autumn, other individuals join these flocks and grouse move to areas with greater cover (sagebrush).

Nonpredatory Interspecific Interactions

Both species of sage-grouse may be seen with ungulates such as pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), horses, and cattle on leks and near feeding sites. Females with chicks may also be seen near Dusky Grouse in brood habitat. Sage-grouse frequently crouch when raptors or corvids fly overhead.

Predation

Predation is potentially a major cause of mortality of young age classes and adults on leks, on nests, and during winter, but few specific data exist. Evidence of mortalities of males not uncommon on or near leks for both species (CEB).

Kinds Of Predators

In 7 of 11 d at the peak of mating on a lek in Gunnison, Colorado, Golden Eagles flew over or attacked sage-grouse, terminating the breeding display for the morning (JRY). Although most attacks are unsuccessful, Golden Eagles have been observed killing and/or consuming Gunnison Sage-Grouse (JRY). Other observations of predation specific to Gunnison Sage-Grouse are limited. Field observers have reported rare cases of coyotes (*Canis latrans*) and bobcats (*Felis rufus*) successfully attacking and killing Gunnison Sage-Grouse. Juvenile sage-grouse (particularly young chicks) are likely taken by additional predators, including Common Ravens (*Corvus corax*), red fox (*Vulpes vulpes*), and weasels (*Mustela* spp.; Rogers 1964). Egg predators may include all of the above and ground squirrels (Spermophilus spp.), badgers (*Taxidea taxus*), American Crows (*Corvus brachyrhynchos*), and Black-billed Magpies (*Pica hudsonia*). Some of the above may be secondary egg predators such as ground squirrels (Michener 2005).

Adult male Gunnison Sage-Grouse displaying in snowy habitat, Gunnison Basin, CO, April. A male Gunnison Sage-Grouse displaying on a snowy ridge after being displaced from its lek by a hunting Golden Eagle.

Common Raven harassing male Gunnison Sage-Grouse, Gunnison Basin, CO, April. An increasingly frequent sight in the Gunnison Basin is seeing Raven's harass the Gunnison Sage-grouse on their leks.

Manner Of Predation

Golden Eagles generally attacked Gunnison Sage-Grouse on leks at or after dawn (JRY); they dive at and seek to hit the grouse on the ground or in the air as a grouse flushes. Males with the greatest numbers of matings often seem to be more at risk, because they display long after other males have crouched and/or flushed to avoid attacks (Wiley 1973b, Hartzler 1974, JRY). Predators occasionally kill sage-grouse on or adjacent to their nests and likely capture some at roost sites or while feeding and loafing (CEB, JRY).

Response To Predators

Sage-grouse avoid predation by crouching in the open or under herbaceous or shrub cover, or by flying in the opposite direction of the attack (JRY). Predation may be a major cause of mortality for young age classes and adults on leks, on nests, and during winter, but few data are available.

Breeding

Phenology

Pair Formation

Gunnison Sage-Grouse do not form pair bonds. Leks are occupied from mid-Mar through late May, depending on elevation (Rogers 1964). Average copulation date is mid-Apr in Colorado (Young 1994). Annual variation in weather causes fluctuations of about 1–2 wk in the date of nest initiation (Young 1994).

Nest-Building

The nest bowl is a simple depression at the base of a shrub, generally sagebrush, and is formed prior to the initiation of clutch laying. The nest bowl may be unlined or lined with sagebrush leaves and bark strips of a 1–6 cm thickness. Less common is grass or pine needles (Young 1994).

First/Only Brood Per Season

Renesting, while physiologically possible, appears to be uncommon in the Gunnison Basin population (JRY).

Nest Site

Selection Process

Female Greater Sage-Grouse typically select nest areas 1–2 wks before copulation (Bradbury et al. 1989a) and female Gunnison Sage-Grouse are likely similar. Comparison of movements of adult and yearling females after their visits to leks indicates that some yearlings select nest sites after copulation (MAS).

Microhabitat

Almost all nests are placed in the shade of vertical cover, such as overhanging sagebrush. Females in the Gunnison Basin generally nest under live sagebrush (86.5%, n = 37), but some nests were under dead sagebrush, snowberry, and, in one case, a

small Douglas Fir (*Pseudotsuga menziesii*) (Young 1994). Sagebrush canopy cover along transects through the patch where nests were placed in the western portion of the Gunnison Basin averaged 38.5% (SD = 12.3) with most of the cover (27.6%) coming from live sagebrush (*n* = 92; Stanley et al. 2015). Within the patch surrounding nests, total shrub cover averaged 43.1% (SD = 14.3), and grass cover averaged 46.3% (SD = 17.3; Stanley et al. 2015).

Site Characteristics

Females in the Gunnison Basin nest under sagebrush of greater than average height and width; however, nest shrubs were not the tallest shrub in the immediate vicinity (*n* = 37, Young 1994). Nests were in areas with an average sagebrush height of 40.8 cm (SD = 8.6) and an average width of 75.4 cm (SD = 14.8). Nest shrubs averaged 55.6 cm (SD = 9.7) in height and 114.4 cm (SD = 24.8) in width. The density of sagebrush at nest sites averaged 1.9 plants/m2 (SD = 0.7, range = 0.5–3.3) and density of other shrubs was 1.9 plants/m2 (SD = 1.2, range = 0–4.7). Total shrub density at nest sites averaged 3.7 plants/m2 (SD = 1.6, range = 0.5–7.0) (Young 1994). Shrub height over nest averaged 60.5 cm (SD = 15.6, *n* = 92; Stanley et al. 2015).

Nest cover was dominated by sagebrush, and sagebrush cover ranged from 11.6 to 42.7% and averaged 26% (SD = 24.8). Other shrub cover averaged 7.9% (SD = 6.7, range = 0–28). Forbs comprised 3.7% (SD = 3.3, range = 1.0–13.4) and grasses 9.5% (SD = 6.3, range = 1.0–37.1) of the cover at nest sites (Young 1994).

Nest-to-lek distance. Average distance between a female's nest and the lek nearest her capture site was 4.2 km (SD = 3.5, *n* = 37; Young 1994). Average distance from 92 nest sites to the lek of attendance in the western portion of the Gunnison Basin was 2.1 km (SD = 2.1, range = 0.015–10.1; Aldridge et al. 2012).

Nest

Construction Process

No Data

Structure And Composition Matter

Nesting material primarily consists of grasses or sagebrush leaves, although sagebrush bark strips are common (*n* = 37, Young 1994)

Dimensions

Nests were, on average, 22 cm diameter and 5 cm deep (*n* = 37, Young 1994)

Microclimate

No Data

Maintenance Or Reuse Of Nests

No evidence that females reuse nests; however, within a given year, some appear to nest within 200 to 300 m of a nest used in the previous year (Young 1994).

Use Of Non-Breeding Nests

No non-breeding nests documented.

Gunnison Sage-Grouse nest with eggs, Gunnison Basin, CO.

Eggs

Shape

Ovate.

Size

Eggs average 54.5 mm (SD = 1.4 mm) in length and 38.0 mm (SD = 0.7 mm) in diameter (Young 1994).

Mass

Average preincubation mass was 46.1 g for 217 eggs of Greater Sage-Grouse in northern Colorado (Petersen 1980).

Color

Primary colors range from deep olive-buff and light olive-buff to greenish drab and greenish white with lighter shades of brown or olive green; eggs marked with small spots and fine dots of chocolate brown and brownish olive (Girard 1937, Patterson 1952, Short 1967).

Egg-Laying

The first egg is likely laid 3–14 d after copulation as in Greater Sage-Grouse (Scott 1942, Petersen 1980). Eggs are laid approximately daily until 5–10 are laid (JRY).

Incubation

Onset Of Broodiness And Incubation In Relation To Laying

Incubation likely commences 0–2 d after the last egg is laid (JRY).

Incubation Patch

Female only.

Incubation Period

Lasts approximately 25–29 d.

Female Gunnison Sage-Grouse on nest, Gunnison Basin, CO.

Parental Behavior

Only the female incubates. Hens take short incubation recess for feeding at a distance from their nests up to twice per day. Eggs are not known to be covered when the female leaves the nest during incubation. Hens are extremely secretive and cryptic on nests (JRY, CEB).

Hatching

Shell-Breaking And Emergence

Hatching of the entire clutch in Greater Sage-Grouse may take as little as 1 h (Wallestad 1971).

Parental Assistance And Disposal Of Eggshells

Eggshells and unhatched eggs are left in nest.

Young Birds

Condition At Hatching

Chicks are wet but dry quickly and leave the nest with the hen shortly after hatching.

Gunnison Sage-Grouse chick, Gunnison Basin, CO. Three week-old chick.

Growth And Development

Growth in mass is rapid. Growth of feathers is also rapid; chicks can fly weakly by 2-3 wks age and relatively strongly at 3-5 wks (JRY).

Gunnison Sage-Grouse at five months-old, Gunnison Basin, CO. Five month-old Gunnison Sage-Grouse.

Parental Care

Brooding

Brooding hens squat low with wings drooped and lower feathers ruffled to shelter chicks. When walking/feeding, communication is continuous; Contact Calls of slightly different pitches are uttered by hen and See-ah Calls by chicks. Brooding females walk in relatively lightly vegetated areas while chicks feed 1–10 m away.

Wild surrogate brood female, Gunnison Basin, CO.

Feeding

Chicks are able to feed immediately after hatching and invertebrates dominate their diet; within a few days of hatch, they may imitate hens by picking at same buds and blossoms, which may have small insects that the hen eats.

Cooperative Breeding

None reported.

Brood Parasitism

None reported.

Fledgling Stage

Chicks sit underneath hen's wings or breast feathers during brooding. Communication (See-ah Calls of chicks and Contact Calls from hen) is continuous. Chicks feed within 1–10 m of hen. When chicks become separated from the brood, they utter louder and longer See-ah Calls. Movements of Greater Sage-Grouse are not dramatically different for chicks of different ages; a movement of 150 m was observed in a 2-h period immediately after hatching (Barber 1991). Movements may be in response to habitat quality, food availability, and/or the risk of predation.

Immature Stage

Juveniles may flock together, disperse, and/or move toward winter habitats with increasingly larger flocks of Gunnison Sage-Grouse.

Demography and Populations

Measures Of Breeding Activity

Age At First Breeding

Male. Although yearling-male Gunnison Sage-Grouse can breed, older males do most breeding (JRY; see also Greater Sage-Grouse, Eng 1963, Wiley 1973b, 1974, Hartzler and Jenni 1988). Numbers of male Greater and Gunnison Sage-Grouse attending leks increase during the breeding season as yearlings visit leks (Eng 1963, Wiley 1974, Hartzler and Jenni 1988, JRY).

Female. Observations of nesting likelihood for all age groups of female Gunnison Sage-Grouse indicate that some females do not nest (Young 1994, CEB). This estimate may be partly the result of nests being destroyed by predators before being located by observers but also based on examination of post-ovulatory follicles. Research on follicular development in Greater Sage-Grouse indicated that at least 93–97% of 395 females in northern Colorado had laid eggs during their previous breeding season (Braun 1979); this research supports the possibility that nesting attempts are under-represented in the literature due to less frequent locations of radio-marked females (Aldridge and Brigham 2001). Despite the problems with examining nesting likelihood of yearlings (e.g., relatively large and irregular spring movements, later date of nest initiation, and lower likelihood of renesting), research indicates that fewer yearlings are likely to nest than adults (Braun 1979, Young 1994).

Clutch

Mean clutch size in Gunnison Basin, Colorado reported as 6.8 eggs (SD = 0.7, *n* = 24) by Young (1994); another study there reported 6.0 eggs (range = 3 to 9, *n* = 77; Stanley et al. 2015); 6.7 eggs (*n* = 7) in the San Miguel Basin, Colorado (Stiver 2007); and in Utah clutch size ranged from 6 to 10 (*n* = 3; Swenson 2003, Lupis 2005).

Annual And Lifetime Reproductive Success

Females rear only 1 brood/season. If the first clutch is depredated or abandoned during laying or early in incubation, a few females may renest (Young 1994).

Hatchability

Proportion of eggs hatching in successful Colorado nests varies from 72% (*n* = 7 nests, San Miguel Basin, Stiver 2007) to 93% (*n* = 57, Gunnison Basin, Stanley et al. 2015).

Nest Success

Proportion of all nests that hatch one or more eggs (apparent nest success) was 43.2% (*n* = 37; Gunnison Basin, Young 1994); 58.2% (*n* = 98; Gunnison Basin, Stanley et al. 2015), and 26.9% (*n* = 26, San Miguel Basin, Stiver 2007). Average estimates of apparent nest success from primary flight feather molt of harvested hens in the Gunnison Basin were 51% for yearling females (*n* = 422 of 824) and 67% for adult females (*n* = 703 of 1,051) between 1977 and 1998 (Braun et al. 2015). The unbiased daily nest survival rate in the Gunnison Basin was 0.982; 50% when extrapolated over 38 days of laying and incubating combined (Stanley et al. 2015).

Factors Associated With Nest Success

Nest success of both species of sage-grouse is higher in areas of big sagebrush and/or antelope bitterbrush (*Purshia tridentata*), and/or relatively tall and thick grass, forb, and shrub cover (Young 1994, DeLong et al. 1995). Limited local vegetation or landscape variables affected nest survival in the Gunnison Basin; taller grasses appeared to increase nest survival (Stanley et al. 2015). Residual grasses available during nesting are important to nest success (Crawford et al. 2004). Selection is strong for sagebrush at and surrounding nest sites (Aldridge et al. 2012) that may mask effects on nest survival (Stanley et al. 2015). Greater Sage-Grouse nest success is lower in areas where shrub cover is reduced by plowing (Trueblood 1954) and appears to be positively correlated with April to June precipitation (Gill 1966). Nest success may be positively correlated with age of the hen (Braun 1984, Young 1994, Braun et al. 2015).

Annual Reproductive Success

The proportion of all females that hatch at least 1 egg during a breeding season varies from 18.9% (Stiver 2007) and 35% (Young 1994) to as high as 60% (average over 1977–1998) (Braun et al. 2015). Annual productivity of sage-grouse is a function of annual reproductive success and survival of chicks in broods. Many factors that are related to nest success in Greater Sage-Grouse are also related to annual productivity, including food availability (Pyle and Crawford 1996), habitat quality (Sveum et al. 1998), and/or variation in weather (Blake 1970, Rich 1985).

Life Span And Survivorship

Survival rates for Gunnison Sage-Grouse vary by year, sex, and age (Davis et al. 2015) as do those for Greater Sage-Grouse (Zablan et al. 2003). Most results indicate that females survive at a higher rate than males, possibly because of sexual dimorphism and display behavior of males (Swenson 1986): survival was 55% for 1,800 banded females, 52% for 1,892 banded yearling males, and 38% for 1,935 banded adult male Greater Sage-Grouse in Colorado (Zablan et al. 2003). Survival was 61% for female and 39% for male Gunnison Sage-Grouse (n = 132 birds) with no differences between age classes (Davis et al. 2015). The lower survival rate of males is the reason why the male:female sex ratio declines as birds age (Braun 1984, Braun et al. 2015). The low survival rate of males also appears to be reflected in the 15–47% return rate of territorial males on leks between years (Dunn and Braun 1985, Gibson 1992). Estimated average annual survival of Gunnison Sage-Grouse in the Gunnison Basin based on wing examination (n = 3,057 wings) from 1977 through 1998 was 46% for adult males and 56% for adult females (Braun et al. 2015), and this varied among years.

Low survival of juveniles has been inferred by declines in average brood size (18.4–68.4%) during summer (Keller et al. 1941). Lack of residual cover, drought, fire, and poor land management practices may increase rate of predation (Braun et al. 1977, Young 1994).

Disease And Body Parasites

Within the Gunnison Basin, feather lice (Mallophaga) and tapeworms (Platyhelminthes) have been recorded for Gunnison Sage-Grouse, but there is no specific study of parasites or diseases (CEB).

Causes Of Mortality

Predation of eggs and all age classes of sage-grouse is likely the primary cause of mortality. Other causes of mortality include human disturbance, livestock, farm machinery, moving vehicles, electric or telephone wires, fences, pesticides, fire, flood, drought, sun exposure, heavy rain and cold weather (Rogers 1964, Barber 1991, CEB), and disease, including presumably West Nile virus, which has been reported for Greater Sage-Grouse (Naugle et al. 2004).

Range

Initial Dispersal From Natal Site

Median natal dispersal from place of hatching to place of breeding or attempted breeding for Gunnison Sage-Grouse is unknown. Dispersal is distinct from brood breakup (Browers and Flake 1985) and in Greater Sage-Grouse is relatively gradual and sporadic (Dunn and Braun 1986a, b).

Fidelity To Breeding And Wintering Sites

Breeding. Males marked on specific leks in the Gunnison Basin, if known to be alive, tended to return to those leks in subsequent years (JRY, CEB). Movements among leks within and between years are suspected but not documented. Male adult Greater Sage-Grouse in northern Colorado occasionally visit more than 1 lek within a breeding season: 63.6% of 22 males (Emmons and Braun 1984), 18.5% of 54 males (Dunn and Braun 1985). Yearling males make most visits to more than 1 lek: 100% of 11 yearlings versus 27.3% of 11 adults (Emmons and Braun 1984). Most males return to the same lek year to year, but occasionally shift territories (Gibson and Bradbury 1986, Hartzler and Jenni 1988). Females also occasionally visit more than 1 lek: 10.8% of 37 females (Dunn and Braun 1985).

Female Gunnison Sage-Grouse generally display fidelity to their nesting areas between years; nests between consecutive years were separated by an average of 0.5 km (n = 5 females; Young 1994). Fidelity may be related to age and/or nest success (Dunn and Braun 1985, JRY).

Wintering. It is expected that most sage-grouse display some fidelity to overwintering areas but specific details for Gunnison Sage-Grouse remain unknown. Distances moved by birds to overwintering areas from lek of capture/attendance was 4.7 km (SD = 4.0, n = 25 males and 46 females; C.L Aldridge unpubl. data)

Home Range

Variability in techniques used to estimate home range size makes comparisons of seasonal ranges difficult: seasonal changes in home range likely mimic those of Greater Sage-Grouse: breeding range = 0.1–28.6 km^2 (Bradbury et al. 1989); summer range = 0.1–25.9 km^2 (Bradbury et al. 1989, Hofmann 1991); autumn range = 22.5–44.2 km^2 (Hofmann 1991); and winter range = 0.6–18.2 km^2 (MAS personal communication). There have been few estimates of Gunnison Sage-Grouse home ranges reported. In one small population of Gunnison Sage-Grouse in limited habitat in Utah, winter home ranges varied from 2.3–3.5 km^2 (n = 4, Ward 1997).

Population Status

Numbers

Seven populations are known (Fig. 3); total population is less than 5,000 individuals of which about 3,500 to 4,000 occur in the Gunnison Basin, Colorado (Young et al. 2000, USDI 2010, 2013). The two most common models used to estimate Gunnison Sage-Grouse population size to determine trends yielded estimates ranging from 17 to 146 individuals in 2014 for the 6 populations outside of the Gunnison Basin (Colorado Parks and Wildlife 2014 lek count data) and the Gunnison population continues to represent 85-90% of the global population of the species. The actual effective population sizes may be considerably smaller (Stiver et al. 2008).

Trends

The average number of male Gunnison Sage-Grouse counted on leks in the Gunnison Basin declined by 60% from 1953 to 1993 (Young et al. 2000). Currently, population trends show that 6 of the 7 populations have declined during the past decade while the Gunnison population has remained relatively stable (USDI 2010, and Colorado Parks and Wildlife lek count data). While

the Gunnison population has recently realized some stabilization, estimated fall population sizes in 1979 and 1983 based on hunter harvest were each approximately 7,000 birds (CEB).

Population Regulation

The presence of cyclic changes in Gunnison Sage-Grouse populations is unknown, but cycles have been suggested for Greater Sage-Grouse (Rich 1985). Most evidence indicates that populations only weakly fluctuate (or not at all) in periodic cycles (Braun 1998). However, Greater Sage-Grouse populations in Wyoming cycled with a regular periodicity of 6–9 years from 1965 to 2008 (Fedy and Aldridge 2011). Nest success is usually cited as the most significant parameter influencing the population dynamics of Gunnison Sage-Grouse (Stanley et al. 2015). Nest success in Greater Sage-Grouse appears to be influenced by extrinsic factors such as weather (Gill 1966, Blake 1970, Hanf et al. 1994), habitat alteration (Trueblood 1954, Klebenow 1969, Fischer et al. 1996), and predators (Autenrieth 1981). Similar extrinsic factors may also influence survival of juveniles. If intrinsic factors influence populations, they do so to a much lesser extent than extrinsic factors; intrinsic factors are also poorly understood (Aldridge and Boyce 2008).

Genetics

Compared to Greater Sage-Grouse, Gunnison Sage-Grouse have significantly lower levels of genetic diversity measured initially using microsatellites and mtDNA (Oyler-McCance et al. 1999, Oyler-McCance et al. 2005), and later confirmed at the genomic level using single nucleotide polymorphisms (Oyler-McCance et al. 2015, Oyler-McCance et al. In Press). This low level of genetic diversity may be due to a founder event associated with speciation (Oyler-McCance et al. 1999). There is a high degree of genetic structure and low gene flow among the 7 recognized Gunnison Sage-Grouse populations (Oyler-McCance et al. 2005). The Dove Creek/Monticello population and the Piñon Mesa population (Fig. 3) are the most differentiated and also have the lowest levels of genetic diversity. The patterns of genetic structure may have changed since 2005 as the smaller populations have been augmented with grouse moved from the larger Gunnison Basin population.

Conservation and Management

Effects Of Human Activity

Hunting

Market hunting, overharvesting, and poaching once reduced or limited populations of sage-grouse (Hornaday 1916, Girard 1937). A report in the Lake City Times (Colorado) on 13 September 1894, read, “Billy Green, a genial fireman on the 64, bagged 863 grouse [now known to be Gunnison Sage-Grouse] while out hunting on Sapinero last Sunday.” In 2014, the high count for the global range of Gunnison Sage-Grouse was 963 males, just 100 more than the fireman was reported to have harvested in one day. Gunnison Sage-Grouse have not been hunted in the Gunnison Basin since 2000 and not legally in other areas of Colorado since 1995; hunting in Utah has not been allowed since 1989 (Gunnison Sage-Grouse Rangewide Steering Committee 2005).

Crop Damage

Gunnison Sage-Grouse will forage in alfalfa, pinto bean, and wheat fields in some areas, but any possible crop damage has not been measured.

Pesticides And Other Contaminants/Toxics

There are no data from within the range of Gunnison Sage-Grouse that pesticides have reduced insect availability, or that herbicides have reduced forb availability. However, reduced forbs and insects can have significant impacts on nesting females and chicks of Greater Sage-Grouse during the breeding season (Eng 1952, Carr and Glover 1970, Klebenow 1970, Johnson and Boyce 1990, Willis et al. 1993). Immediate mortality of birds that are exposed to spray, particularly insecticides such as dimethoate and methamidophos (Blus et al. 1989), has been a factor for Greater Sage-Grouse in Idaho. Normal use of herbicides is rarely problematic, but 200 mg of toxaphene/kg of body weight (Post 1951a) and 500 mg of chlordane/kg of body weight (Post 1951b) are toxic to sage-grouse. Strychnine may also kill these birds (Ward et al. 1942).

Alteration Of Habitat

Historically, the Gunnison Sage-Grouse is thought to have occupied 22 counties in sw. Colorado (Fig. 2), and was extirpated from all but 8 of those counties (Braun et al. 2014). In Rogers’ (1964) description of the distribution of sagebrush in Colorado, he noted that sagebrush distributions described previously (Cary 1911) still contained sagebrush in the early 1960s, yet due to human activities, many were no longer dominated by sagebrush. Rogers (1964) emphasized that human activities that impacted sagebrush were overgrazing, irrigation projects, and dry farming. Braun (1995) compared Rogers’ (1964) distribution of sagebrush with that of 1993–1994 and linked population declines of Gunnison Sage-Grouse to habitat loss (conversion of big sagebrush into farmland or housing developments), habitat degradation (heavy livestock grazing, sagebrush removal, road and powerline development through sagebrush, and human disturbance), and habitat fragmentation.

Oyler-McCance et al. (2001) quantified changes in sagebrush-dominated areas between the 1950s and the 1990s using low-level aerial photographs. They documented a 20% loss of sagebrush habitat (155,673 ha), and found substantial fragmentation in 37% of plots sampled during that time period. Oyler-McCance et al. (2001) additionally noted that what was once sagebrush (as reported by Rogers in 1964) had already been lost to other land uses before the oldest photographs were taken. Braun et al. (2014) estimated the timing of Gunnison Sage-Grouse extirpation from their historical distribution and showed that the species was likely extirpated in seven counties by the early 1960s, before earliest photos used by Oyler-McCance et al. (2001). In discussing the possibility of restoration of altered habitats, Braun et al. (2014) noted that restoring extirpated populations or augmenting small

populations is problematic due to degradation, fragmentation, and permanent loss of suitable habitat from agricultural activities, gas and oil development, and expansion of homes and ranchettes. Nesting females avoided habitats within about 2.5 km of residential developments (Aldridge et al. 2012).

Disturbance At Nest And Lek Sites

The rate of abandonment of both species of sage-grouse nests ranges from 0.0 to 21.3% (Petersen 1980, Young 1994). Likelihood of abandonment is higher when nests are disturbed early in the incubation period. In general, Gunnison Sage-Grouse are quicker to flush or depart areas when disturbed than Greater Sage-Grouse (JRY). Mining activity (Eng et al. 1979, Tate et al. 1979, Braun 1986, Remington and Braun 1991), oil wells (Rogers 1964, Call and Maser 1985), livestock (J. W. Connelly pers. comm.), or military activity (Hofmann 1991, Cadwell et al. 1994) may adversely influence display activity of Greater Sage-Grouse when disturbances are near breeding areas; increased noise level may be a primary factor (Rogers 1964, Braun 1986, Patricelli et al. 2013). Despite impacts of mining on localized areas, the influence on overall populations is not readily apparent (Remington and Braun 1991).

Acoustic Studies

Low frequency (<2,000 Hz), high amplitude, and low duration anthropogenic noises impacted male Gunnison Sage-Grouse behaviors 50% of the time at a Watchable Wildlife lek site in the Gunnison Basin (Hicks et al. 2012). Noises generated by sage-grouse viewers and from fast moving trucks on a county road were most highly associated with male disturbance behaviors (Hicks et al. 2012). Anthropogenic noise impacts male lek behavior more when fewer females attend the lek (Profera and Braun 1985, Hicks et al. 2012), and flushing occurs at greater distances when humans approach the lek on foot compared to in a vehicle (Profera and Braun 1985). Male vocalizations in another Gunnison Basin study conducted on 12 leks, declined significantly during and after short-term, intermittent noise events (Piquette et al. 2014). Collectively, noise from automobiles, jet airplanes and low-flying propeller planes produced noise at leks that averaged 15 dBA above ambient levels; peak amplitudes of 80 dBA were produced by low-flying propeller planes (Piquette et al. 2014). The Gunnison Basin Rangewide Conservation Plan includes a 10 dBA above ambient noise limit on continuous noise around Gunnison Sage-Grouse leks, however, it does not address intermittent noise, nor does it quantify ambient noise levels. Ambient noise levels measured in the Gunnison Basin are 17 dBA (Piquette et al. 2014).

Management

The International Union for the Conservation of Nature recognizes the Gunnison Sage-Grouse as a red-listed, or globally endangered, species (Storch 2000). The National Audubon Society listed the Gunnison Sage-Grouse in 2006 as one of the 10 most endangered birds in North America. Also in 2006, the U.S. Fish and Wildlife Service (USFWS) removed the species from any protection under the Endangered Species Act (ESA). Central to the listing determination was the conclusion that the population had experienced no significant decline during the past decades, a finding that is in direct contrast to the Gunnison Sage-Grouse Rangewide Conservation Plan published in 2005. The USFWS reconsidered the listing status of the species in 2010 and once again recognized it as a Candidate species, meaning protection was warranted, but precluded by higher priority listed species. In November 2014 the Gunnison Sage-Grouse was listed as Threatened under the U.S. Endangered Species Act (USDI 2014). This designation is being challenged as unnecessary by the State of Colorado, and by two different environmental groups as insufficient, with both environmental groups seeking listing as Endangered.

Hunting Legislation

The first legislation to protect sage-grouse from overharvest in Colorado was passed in 1877 (Rogers 1964). Hunting of Gunnison Sage-Grouse under a variety of different regulations, including some closures, continued through 2000 (Braun et al. 2015) when the season was closed even though it continued to be listed as a game species.

Predator Control

Predator removals have not been shown to improve long-term size and stability of Greater Sage-Grouse populations in Oregon (Willis et al. 1993) or Wyoming, where reducing Common Raven population density by 61% did not improve Greater Sage-Grouse nesting success (Dinkins 2013); the need for this management activity for Gunnison Sage-Grouse has been considered and implemented in limited areas (Miramonte Basin). A predator control program in the Miramonte Basin was conducted in 2011–2012 at a cost of $77,000 to remove 151 coyotes and 101 Common Ravens, as well as 2 bobcats, 8 badgers, 3 red fox, and 2 raccoons (Procyon lotor) (M. L. Phillips, unpubl. report). This activity failed to result in an increase in apparent population size.

Food And Water Provision

Water development has not been shown to increase sage-grouse populations (Cadwell et al. 1994).

Habitat Maintenance And Improvement

Most recent management designed to benefit Gunnison Sage-Grouse has been directed toward maintenance and improvement of habitat. Strategies to improve habitats for sage-grouse include manipulation of grazing pressure, control of burning, restoration of native habitat, support of agricultural set-aside programs, protection of natural water sources, and establishment of preserves (Braun et al. 1977, Call 1979, Klebenow 1985, Welch et al. 1990). Target of management efforts has often been habitat within 3 km of leks; this effort is based on research showing that most females nest within 3 km of the nearest lek (Gill 1965, Swope 1969, Braun et al. 1977, Ellis et al. 1989, Aldridge et al. 2012). Consequently, recent efforts to assess habitat have concentrated on use of both Habitat Suitability Index (HSI) and remote-sensing approaches (Homer et al. 1993, Cadwell et al. 1994, Edelmann et al. 1998, Homer et al. 2013).

Habitat management is also used to maintain the integrity of specific populations by focusing attention on fragmentation and corridors within landscapes, seasonal distribution of habitat (Aldridge et al. 2012, Fedy et al. 2014), and quality and quantity of habitat necessary to support minimum viable populations (Braun et al. 1994). The Western States Sage and Columbian Sharp-tailed Grouse Workshop has promoted advancement of these goals by encouraging uniform collection and sharing of data among states and development of management plans for specific populations of sage-grouse within states.

Population Transplantation

Movement of individuals to small isolated populations may be necessary to maintain long-term genetic health (Bouzat et al. 1998, Kahn et al. 1999, Oyler-McCance et al. 1999). This practice has been implemented for all of the small populations of Gunnison Sage-Grouse outside of the Gunnison Basin in Colorado (Braun et al. 2014). Transplantation, as has been currently done, has not been shown to improve the possibility of increasing population viability of any of the small populations over time (Davis 2012). However, moving individuals does improve the estimated population size (Davis 2015), and may have prevented imminent extirpation of some of the smaller populations (Wiechman et al. 2011). In addition to population transplantation, there have been some initial captive breeding studies of Gunnison Sage-Grouse with mixed results (Wiechman et al. 2011, Lloyd et al. 2014).

Gunnison Sage-Grouse chicks, Gunnison Basin, CO. Chicks are one week old.

Appearance

Gunnison Sage-Grouse have 10 primaries, 15 secondaries (including 4–5 tertials), and 18–20 rectrices. The wings are moderately rounded (the longest primary is among p6–p7 and the outermost primary, p10, is 25% shorter than the longest primary) and the tail consists of attenuated ornamental rectrices, relatively long and pointed when the tail is closed but rounded when spread for display in males (outermost rectrix more than 60 mm shorter than innermost rectrix). No geographic variation in appearance or molt strategies reported.

Molts

General

Molt and plumage terminology follow Humphrey and Parkes (1959) as modified by Howell et al. (2003, 2004). The following account is based on information from both Greater and Gunnison Sage-Grouse, which are assumed to exhibit similar molting strategies. The two species of sage-grouse likely exhibit a Complex Alternate Strategy (cf. Howell et al. 2003, Howell 2010), including incomplete to complete prebasic molts, an incomplete preformative molt, and limited prealternate molts in both first and definitive cycles (Fig. 4; Dwight 1900; Pyle 2007, 2008). A limited Definitive Prealternate Molt has been documented only in adult males thus far (Pyle 2007); study needed toward its occurrence in females and first-cycle males. If this molt were absent in first-cycle birds the species would exhibit a Simple Alternate Strategy (Howell et al. 2003, Howell 2010).

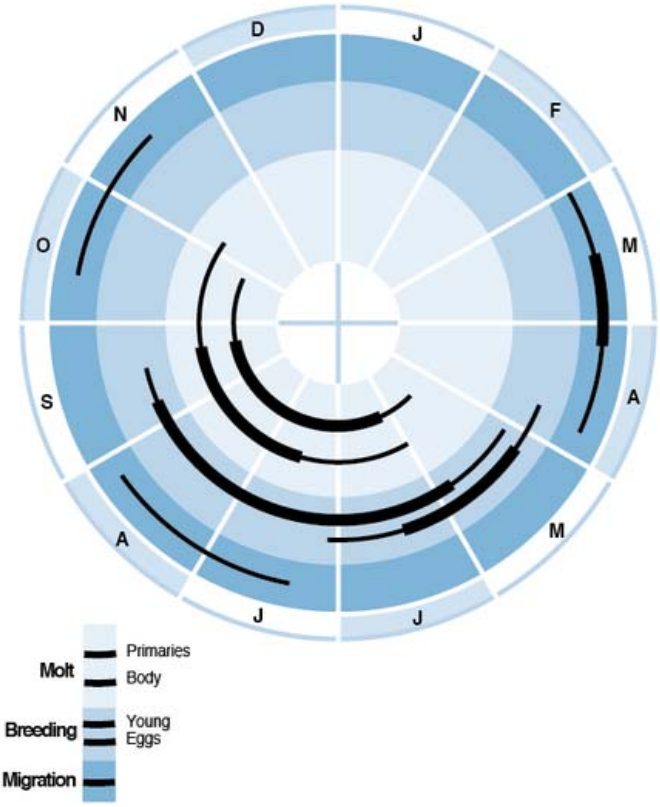

Figure 4. Annual cycle of molt of Gunnison Sage-Grouse. Thick lines show peak activity; thin lines, range of activity.

PreJuvenile (First Prebasic) Molt

Complete, primarily Jun–Jul, occurring on or near the natal territory. Little information is available on timing or sequence of pennaceous feather irruption and development. Tips of juvenile inner primaries (p1–p8) present at hatching; the two outer primaries (p9 and p10) emerge about day 24, and continue to grow while inner primaries begin replacement during the

Preformative Molt (see below). Primaries have developed sufficiently such that chicks can fly weakly by 10 d of age and relatively strongly at 5 wk (Girard 1937, J. W. Connelly pers. comm.). No detailed information on when other feather groups emerge. Prejuvenile Molt completed in approximately 1 mo.

Preformative Molt

"First Prebasic" or "Prebasic I" Molt of Humphrey and Parkes (1959) and later authors; see revision by Howell et al. (2003). Incomplete, primarily Jun–Oct. Commences with replacement of innermost primary (p1) at about 24 d of age, overlapping completion of Prejuvenile Molt of outer primaries and body feathers. Preformative Molt includes all feathers except the outer two primaries (p9–p10) and corresponding primary coverts. Sequence of flight-feather replacement follows that of the Prebasic Molt (below). Molt of body feathers begins about the same time p1 is being replaced and continues until rectrices, middle secondaries, and p8 are fully grown.

First And Definitive Prealternate Molts

Limited, May–Jul (Fig. 4). Specimen evidence indicates a molt of head, neck, throat, and breast feathers occurs in definitive-cycle males of Greater Sage-Grouse, from approximately 16 May to 1 July (Pyle 2007). No evidence currently available documenting occurrence of this molt in first-cycle birds and females but likely does occur as in ptarmigan and ducks; study needed. Nomenclature considering this the Prealternate Molt as opposed to part of the Prebasic Molt follows Pyle (2007).

Definitive Prebasic Molt

Incomplete to complete, primarily Jun–Oct. An examination of Greater Sage-Grouse specimens (both sexes) found primaries molting from 3 Jun to 3 Oct (n = 33) and body feathers molting from 6 Jul to 16 Oct (n = 22; Pyle 2007). Primaries replaced distally (p1 to p10); secondaries may be replaced proximally from s1 and distally from the tertials; rectrices generally replaced proximally (from r9 or r10 to r1) on each side of tail, with some variation possible. Both the Second and Definitive Prebasic molts can be incomplete in some birds, with the outer primary (p10) and up to seven secondaries retained (Pyle 2008). Timing of Definitive Prebasic Molt similar in males and females as far as known.

Plumages

Following based on descriptions, largely of Greater Sage-Grouse, in Dwight (1900), Brooks (1930), Aldrich (1946), Ridgway and Friedmann (1946), Patterson (1952), Short (1967), Johnsgard (1983),Young et al. (1994, 2000), and Madge and McGowan (2002); see Petrides (1942), Crunden (1963), Gill (1967), Beck et al. (1975), Pyle (2008), and Braun and Schroeder (2015) for criteria related to age and sex determinations. Plumages of Greater Sage-Grouse and Gunnison Sage-Grouse similar, except as noted below. Definitive plumage essentially assumed at Formative Plumage in females and at Second Prebasic Plumage in males; sexes similar in Juvenile Plumage and differ moderately in Formative Plumage and more distinctly in Definitive Basic Plumage. Numbered color names from Smithe (1975), unless noted otherwise.

Natal Down

Present May–Jul, on or near natal territory. Chicks completely downy, the down generally mottled in pattern, spotted with black, brown, buff, and white. Head paler, with bolder spots and short black and brown spots; 2 brownish, black-edged spots on foreneck; upper breast buff, mottled black (Short 1967, Johnsgard 1983). Dark markings less distinct than in most other species of grouse, resulting in more mottled appearance.

Juvenile (First Basic) Plumage

Present primarily Jun–Aug. Similar to Definitive Basic female except feathers more mottled, drabber gray and more glaucous (79) and fuscous (less white and sepia, 119); secondaries broadly fringed buff. Juvenile feathers more pointed and narrow with a white center streak than definitive basic feathers, and rectrices also shorter (<100 mm) and more filamentous (Pyle 2008).

Formative Plumage

Present primarily Aug–Jun. Males and females similar to each sex in Definitive Basic Plumage, but outer two primaries (p9–p10) and corresponding primary coverts retained juvenile, narrower and contrastingly worn compared with inner primaries (p1–p8); p9 may have more buff mottling to the outer web and the corresponding primary covert usually with a pale shaft streak, especially in females (Figures 128 and 129 in Pyle 2008); s3 sometimes with buff markings mimicking the juvenile pattern of this feather; black throat of male heavily mottled whitish in Oct–Jun.

First And Definitive Alternate Plumages

Present primarily Jun–Aug in definitive-cycle males, and probably also in females and first-cycle birds (see Prealternate Molts, above). Similar to Formative Plumage and Definitive Basic Plumage, respectively, but head, neck, throat and breast of males with brownish feathers, resulting in protective coloration for wing-feather molt (Pyle 2007). Females may have replaced feathers of similar color to surrounding Formative or Basic feathers.

Definitive Basic Plumage

Present primarily Sep–Jun.

Male. Crown dark grayish brown and fuscous, mixed with drab gray and white, becoming slightly darker dorsally with wear; auricular region densely feathered with short, dark-grayish-brown feathers tipped with drab gray; thin white supercilium extends from above supraocular comb in front of eye to ear opening. Feathers on nape and neck fuscous mixed with horizontal bars of drab gray and white; back of neck with several ornamental nuchal filoplumes, 120–175 mm in length and extending 80–160 mm beyond surrounding neck-feathers, broad and with white extending less than 20 mm at base, with long thin narrow tips of dark sepia (119) to blackish (these feathers are shorter and paler brown with whitish markings in Greater Sage-Grouse). Back feathers and scapulars fuscous with white or pale horn-colored shafts, the feathers with broken, jagged white or drab-gray bars and blotches; lower back

becomes grayish brown or dusky brown; uppertail coverts pointed and dark grayish brown, with broken, jagged bars of white and some drab gray. Rectrices long, gradually tapering to point, dusky brown to sepia with moderately distinct white bars (rectrices less distinctly barred and more mottled in Greater Sage-Grouse). Primaries and alula solid hair brown with occasional drab-gray blotches on leading edges; upperwing primary coverts similar except often tipped whitish; secondaries and upperwing greater coverts similar to primaries except blotches whiter and increase in density and size proximally; upperwing median and lesser coverts sepia with a buff U-shaped band, buff subterminal mottling, and narrow pale tips (Figure 130 in Pyle 2008). Chin, throat, and central upper breast black to sepia, blotched with occasional white and tinged with glaucous (79), bordered on sides of neck with indistinct whitish stripes extending in V-shaped pattern from behind auriculars to center of breast; lower sides of neck and sides of breast covered with loose skin covered with short, white, scalelike feathers surrounding two bare cervical apteria, one on each side of breast, separated by narrow (10-20 mm wide) vertical band of white feathers. When breast pouches are inflated for display, white feathers extend anteriorly to cover sides of neck and up to most of the head. Sides of breast and flanks fuscous with broken, jagged, white or drab-gray bars and blotches; feathers from center breast to abdomen become larger with increasing amounts of sepia to tips, forming black belly patch, the feathers of abdomen with basal portions mixed with glaucous and white; tibia covered with soft down-like glaucous feathers; tarsi with short feathers increasingly mottled drab gray and dark drab as they approach toes; undertail coverts sepia with white shafts and large, white, round spot on tips; underwing coverts white; undersides of primaries and secondaries whitish gray to grayish.

Female. Generally similar to male but ornamental nuchal filoplumes lacking; drab-gray blotches of upperparts and flanks whiter; neck averages paler in appearance; upperwing median and lesser coverts with more buff mottling and indistinct whitish bars (Figure 130 in Pyle 2008); white, scale-like feathers on neck and breast of male replaced by feathers similar in color and structure to those of back; cervical apteria absent; black abdominal patch surrounded by border of mostly white feathers, mottled with sepia on flanks. Female rectrices are shorter than male rectrices, and are mottled throughout.

In both sexes, Definitive Basic Plumage separated from Formative Plumage by two primaries (p9–p10) and corresponding primary coverts more uniform in shape, coloration, and wear with inner primaries (Figures 128 and 129 in Pyle 2008); s3 without buff markings; throat of male uniformly black Oct–Jun. Occasional birds in Basic Plumage may retain the outer primary, and possibly can be identified as Second Cycle if retained primary is juvenile or at least Third Cycle if retained primary is basic (Pyle 2008).

Adult female Gunnison Sage-Grouse, Gunnison Basin, CO, April. Adult female Gunnison Sage-Grouse are smaller and more cryptic than males. Relative to the male, females lack the distensible bare skin patches on the breast and have a smaller and duller yellow-green comb over each eye.

Bare Parts

Bill And Gape

Bill is short and sepia (119).

Iris

Raw umber (123).

Bare Skin

Small yellow-green supraocular comb extends from slightly in front of to slightly behind each eye of male. Female has similar but smaller comb. Cervical apteria in male are yellow ocher and prominent during breeding season; color fades when apteria expand during Strutting Display (see Behavior: sexual behavior, above). Female lacks cervical apteria.

Legs And Feet

Legs and feet (excluding toes) fully feathered. Toenails sepia (119) or dark grayish brown. The pectinate toes are extremely variable in color, generally ranging between clay color and olive brown.

Measurements

Linear

Tarsus

Adult male, 69.2 mm ± 1.7 SD (47); adult female, 58.6 ± 2.2 SD (13); yearling male, 67.8 ± 2.0 SD (35); yearling female, 58.1 ± 1.2 SD (5) (Hupp and Braun 1991).

Culmen

Adult male, 32.5 mm ± 1.4 SD (47); adult female, 27.5 ± 1.2 SD (13); yearling male, 31.1 ± 1.6 SD (35); yearling female, 27.8 ± 0.8 SD (5) (Hupp and Braun 1991).

Wing Length

Wing to longest primary with wing slightly flattened: Adult male, 303 mm ± 5 SD (47); adult female, 260 ± 9 SD (13); yearling male, 293 ± 11 SD (35); yearling female, 251 ± 5 SD (5) (Hupp and Braun 1991).

Mass

Gunnison Sage-Grouse males are heavier than females (2.1 kg vs. 1.2 kg); adults are heavier than yearlings; yearling males, 1.7 kg; yearling females, 1.1 kg (Hupp and Braun 1991, Young 1994, JRY). Both sexes are lightest in early autumn; males are heaviest in early spring, females heaviest in late spring. Sage-grouse males lose mass during the breeding season; females gain mass as they approach the nesting season (Beck and Braun 1978). Sexual dimorphism in mass is manifested as early as 20 d after hatching in Greater Sage-Grouse (Johnson and Boyce 1991); similar growth rate differences expected for Gunnison Sage-Grouse.

Priorities for Future Research

Gunnison Sage-Grouse have been a focus of research on habitat and mating systems only since the mid-1980s. Despite the attention, basic behavioral questions remain: how, why and when do females, males, and chicks select forage? To what degree is learning a component of mate choice and habitat selection? Do individuals within winter flocks share high levels of relatedness? How can human-wildlife conflicts be better mediated? Although recent efforts have emphasized habitat selection, genetic population structure, and the survival and habitat selection of birds introduced into smaller populations, the species conservation status (Storch 2000, USDI 2013) warrants an intensification of research efforts.

Future research should concentrate on providing the information necessary to optimize rangewide and regional management plans for Gunnison Sage-Grouse and to mitigate and reduce human-wildlife conflicts. This research should generate management implications regarding the size, quality, distribution, and fragmentation of Gunnison Sage-Grouse habitat; seasonal distribution and habitat use in each population; the effects of land use such as recreation, grazing, crop production, energy development and mining; genetic and demographic associations with minimum viable population size; connectivity across landscapes both within and between populations; and the importance of maintaining genetic variability. Fundamentally, answers to questions related to the quantity and configuration of habitat are required to sustain viable populations and are most likely to inform management efforts with a high likelihood of maintaining and enhancing the species.

The need for effective management of the Gunnison Sage-Grouse has reached a critical stage. Private, state, and federal land managers and wildlife biologists need information on maintaining presently used habitats, improving degraded habitats, and reducing or eliminating disturbances and fragmentation of existing habitats. Restoring or creating habitat will require more resources (dollars and time) than saving and maintain remaining habitats. This might only be effective if done through collaborative efforts with unbiased involvement and data sharing among all agencies and stakeholders involved in sage-grouse and sagebrush conservation. Of equal importance are fostering and garnering community and political support for the research and management actions needed to conserve the species and restore the landscapes it needs for continued survival.

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