Characteristics and Dynamics of Greater Sage-Grouse Populations

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Abstract. Early investigations supported the view that Greater Sage-Grouse (*Centrocercus urophasianus*) population dynamics were typical of other upland game birds. More recently, greater insights into the demographics of Greater Sage-Grouse revealed this species was relatively unique because populations tended to have low winter mortality, relatively high annual survival, and some populations were migratory. We describe the population characteristics of Greater Sage-Grouse and summarize traits that make this grouse one of North America's most unique bird species. Data on movements, lek attendance, and nests were obtained from available literature, and we summarized female demographic data during the breeding season for the eastern and western portions of the species' range. Lengthy migrations between distinct seasonal ranges are one of the more distinctive characteristics of Greater Sage-Grouse. These migratory movements (often >20 km) and large annual home ranges (>600 km^2) help integrate Greater Sage-Grouse populations across vast landscapes of sagebrush (*Artemisia* spp.)–dominated habitats. Clutch size of Greater Sage-Grouse averages seven to eight eggs and nest success rates average 51% in relatively nonaltered habitats while those in altered habitats average 37%. Adult female Greater Sage-Grouse survival is greater than adult male survival and adults have lower survival than yearlings, but not all estimates of survival rates are directly comparable. The sex ratio of adult Greater Sage-Grouse favors females but reported rates vary considerably. Long-term age ratios (productivity) in the fall have varied from 1.4 to 3.0 juveniles/adult female.

Key Words: Artemisia, *Centrocercus urophasianus*, demographics, Greater Sage-Grouse, movements, nesting, populations, reproduction, sagebrush, survival.

Características y Dinámicas de Poblaciones del Greater Sage-Grouse

Resumen. Las investigaciones tempranas del Greater Sage-Grouse (*Centrocercus urophasianus*) apoyaron la visión que la dinámica de población de esta especie era típica de otras aves de caza de la altiplanicie. Más recientemente, mayores discernimientos en los datos demográficos del Greater Sage-Grouse revelaron que esta especie es relativamente única porque las poblaciones tendieron a tener mortalidad baja en el invierno, supervivencia anual relativamente alta, y algunas poblaciones eran migratorias. Describimos las características de la población del Greater Sage-Grouse y resumimos los rasgos que hacen a este grouse una de las especies de aves más

únicas de Norteamérica. Datos sobre los movimientos, concurrencia a los leks (asambleas de cortejo), y nidos fueron obtenidos de la literatura disponible, y resumimos datos demográficos de las hembras durante la temporada de cría para las partes orientales y occidentales del territorio de esta especie. Las largas migraciones entre los distintos territorios estacionales son una las características más distintivas del Greater Sage-Grouse. Estos movimientos migratorios (a menudo >20 km) y gran extensión del territorio anual habitado (>600 km^2) ayudan a integrar poblaciones del Greater Sage-Grouse a través de vastos paisajes de habitats dominados por artemisa (*Artemisia* spp.). El tamaño de puesta promedio del Greater Sage-Grouse es de entre siete y ocho huevos, y el éxito de la anidada promedia en un 51% en habitats relativamente no alterados mientras que en habitats alterados el promedio de éxito es de un 37%. La supervivencia de hembras adultas de Greater Sage-Grouse es mayor que la supervivencia de machos adultos, y los adultos tienen menor tasa de supervivencia que los juveniles, pero no todas las estimaciones de las tasas de supervivencia son directamente comparables. La proporción de sexos en adultos del Greater Sage-Grouse favorece a las hembras, pero las tasas divulgadas varían considerablemente. Las tasas de productividad (relación entre grupos de distinta edad) a largo plazo en el otoño han variado de 1.4–3.0 juveniles/hembra adulta.

Palabras Clave: anidación, artemisa (sagebrush), *Artemisia, Centrocercus urophasianus,* datos demográficos, Greater Sage-Grouse, movimientos, poblaciones, reproducción, supervivencia.

A population has been defined as a group of individuals of the same species that occupy an area of sufficient size to permit normal dispersal and/or migration behavior and in which numerical changes are largely determined by birth and death processes (Berryman 2002). For many years it was assumed that the demographics of populations (e.g., reproductive rates, survival, and effects of exploitation) were the same for all species of upland game (Allen 1962, Strickland et al. 1994). Allen (1962) summarized this paradigm well when he reported that small animal populations operate under a 1-year plan of decimation and replacement, nature habitually maintains a wide margin of overproduction, and a huge surplus of animals dies whether or not they are harvested. Early management investigations reinforced the view that the Greater Sage-Grouse (hereafter sage-grouse) was a typical upland game bird, similar in demographics and movements to Ring-necked Pheasant (*Phasianus colchicus*), Northern Bobwhite (*Colinus virginianus*), and Ruffed Grouse (*Bonasa umbellus*). For example, Wallestad (1975a) reported that sage-grouse populations in Montana during the breeding season, and possibly for the entire year, were centered and localized around strutting grounds (leks). This view of localized sage-grouse populations was prevalent through the 1970s, despite earlier work demonstrating that sage-grouse had relatively large annual ranges (Dalke et al. 1963). Early research also suggested these localized sage-grouse populations had relatively high annual turnover with high overwinter mortality (Wallestad 1975a).

With the advent of improved telemetry techniques in the 1980s and more recently the use of genetics, biologists gained greater insight into characteristics of sage-grouse populations. It slowly became evident that sage-grouse did not fit the typical paradigm for upland game birds because populations tended to have low winter mortality and relatively high annual survival, and many populations were migratory (Schroeder et al. 1999; Connelly et al. 1988, 2000c). Little evidence suggests that populations of sage-grouse produce a large annual surplus (Connelly et al. 2000a,c; Hausleitner 2003; Holloran et al. 2005). Recognition of these characteristics has influenced conservation and management of sage-grouse populations. Our objectives were to describe population characteristics of sage-grouse and summarize the traits that make this grouse one of North America's most interesting and unique bird species.

DATA SYNTHESIS

We summarized data on movement, fidelity, home range, lek attendance and timing, and nest locations from available literature. We used descriptive statistics for comparisons to avoid quantitative

ritual (Guthery 2008) and because of differences in field and analytical techniques among studies. Stiver et al. *(2006)* established seven Sage-Grouse Management Zones (SMZs); they suggested that stressors to sage-grouse populations differ across the range of the species and identified different management goals for sage-grouse in the eastern and western portions of its range. Therefore, we summarized demographic data for female sage-grouse during the breeding season for the eastern (Great Plains, Wyoming Basin, and Colorado Plateau SMZs) and western (Southern Great Basin, Northern Great Basin, Snake River Plain, and Columbia Basin SMZs) portions of the species range (Fig. 3.1). We synthesized nest success for radio-marked sage-grouse by relative quality of the habitat within study areas, because of the documented importance of habitat quality to nest success. We assessed habitat qualitatively based on descriptions of habitat provided by authors of the reports and classified data as being from nonaltered or altered habitats. For example, if an author reported his or her study area was recently burned or highly fragmented, data would

be presented under altered habitat. Virtually all sagebrush habitats have sustained anthropogenic alterations (Connelly et al. 2004); thus, we refer to these terms exclusive of anthropogenic landscape features such as roads and power lines. We then compared nest success by age group among these habitats and compared nest success rates to those of other prairie and steppe-nesting grouse.

Several studies have urged caution to minimize observer-induced nest desertion or loss by sage-grouse (Patterson 1952, Wakkinen 1990, Sveum et al. 1998b, Wik 2002, Slater 2003). Holloran (2005) wore rubber boots to reduce human scent while confirming nest locations and subsequently monitored nests from ≥60 m to minimize human-induced nest abandonment or predation. Therefore, although these data were retained in tables presenting demographics (Tables 3.1, 3.2), we excluded data from our summary statistics of nest success (Table 3.3) if investigators indicated they used intrusive methods of monitoring—for example, flushing females from nests, candling or floating eggs, or using flagging or other highly visible markers to locate nests.
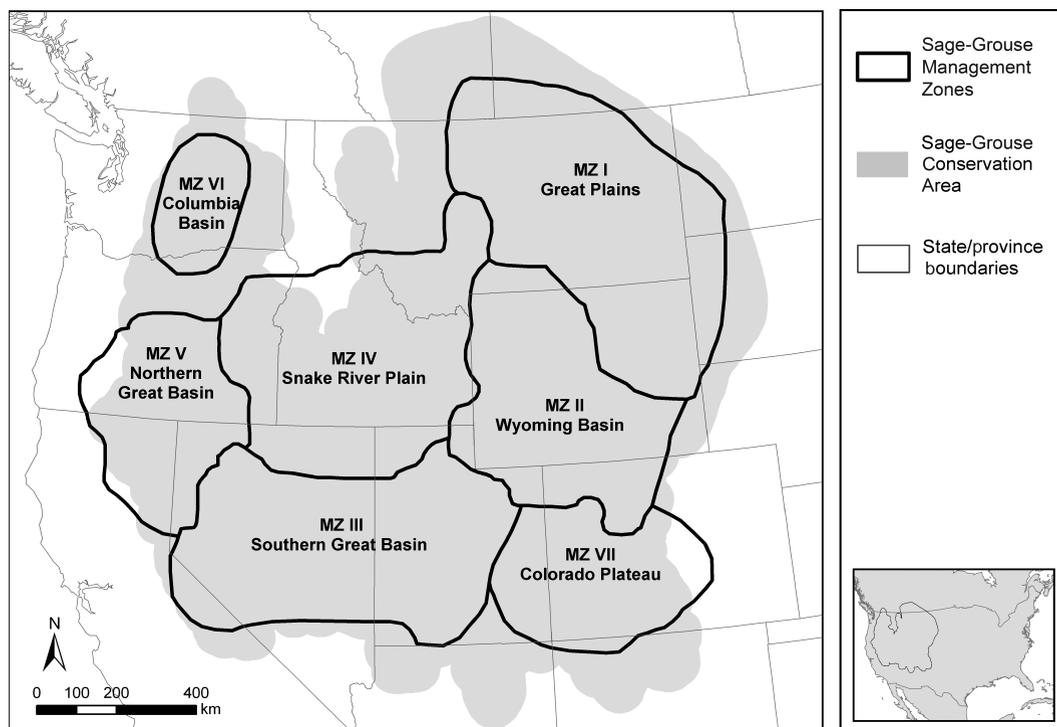

Figure 3.1. Sage-Grouse Conservation Area (adapted from Connelly et al., 2004; Knick and Connelly, this volume, Introduction) and Sage-Grouse Management Zones (Stiver et al. 2006).

TABLE 3.1

Demographic data for female Greater Sage-Grouse during the breeding season in the eastern portion of the species' range (after Schroeder et al. 1999).

All data represent average values for a given study.

State or province	Clutch size (N)	Percent likelihood of nesting (N)	Percent likelihood of renesting (N)	Percent nest success (N)	Percent population breeding success (N)	Source
Alberta	8 (28)	100 (28)	36 (14)	46 (26)	55 (22)	Aldridge and Brigham (2001)
				30 (93)		Aldridge (2005)
Colorado	7 (29)		38 (16)	45 (31)	47 (30)	Petersen (1980)
	7 (81)	85 (119)	12 (34)	55 (107)	57 (130)	Hausleitner (2003)
Montana	8 (22)	71 (31)		70 (20)	70 (20)	Wallestad and Pyrah (1974)
	8 (119)	78 (unknown) 93 (unknown)	19 (36) 43 (83)	46 (258)		Moynahan (2004)
North Dakota	8.3 (56)	96 (73)	28.6 (35)	47 (73)		Kaczor (2008)
South Dakota	8	92 (36)	10 (36)	31 (36)		Herman-Brunson (2007)
Wyoming	7 (154)			38 (216)[a]		Patterson (1952)
		77 (70)		50 (54)		Lyon and Anderson (2003)
		78 (111)	14 (73)	25 (97)		Slater (2003)
				60 (82)		Holloran (1999)
	7 (66)					Holloran (2005)
		81 (597)	9 (597)	49 (597)		Holloran et al. (2005)
		82 (73)		57 (14)	64 (42)	Kaiser (2006)
		67 (52)		66 (52)		Jensen (2006)
Range	7–8	67–100	9–38	25–70	47–70	
Average (SD)	7.5 (0.5)	82 (10.2)	19.7 (12.3)	48 (12.9)	58.6 (8.8)	

[a] Studies without radio telemetry.

MOVEMENTS, FIDELITY, AND HOME RANGE

Extensive movements between seasonal ranges and large annual home ranges are two of the more unique characteristics of sage-grouse life history (Dalke et al. 1960, Gill and Glover 1965, Berry and Eng 1985, Connelly et al. 1988, Bradbury et al. 1989). Movements of sage-grouse can be categorized into different types including:

(1) dispersal from place of hatching to place of breeding or attempted breeding, (2) movements of individuals within a season, (3) migration between distinct and spatially separated seasonal ranges, and (4) home ranges that sum all movement types seasonally or annually. These movement categories share considerable overlap, especially in the context of annual home or seasonal ranges that include daily movements to obtain food, visit loafing and roosting sites, and engage in breeding

TABLE 3.2

Demographic data for female Greater Sage-Grouse during the breeding season in the western portion of the species' range (after Schroeder et al. 1999).

All data represent average values for a given study.

State or province	Clutch size (N)	Percent likelihood of nesting (N)	Percent likelihood of renesting (N)	Percent nest success (N)	Percent population breeding success (N)	Source
California				40 (88)		Popham and Gutiérrez (2003)
				43 (95)		Kolada (2007)
Idaho	8 (47)			77 (47)[a]		Bean (1941)
	7 (30)	69 (242)	15 (79)	52 (166)	48 (52)	Connelly et al. (1993)
				51 (41)		Apa (1998)
	6 (25)	92 (38)	17 (18)	45 (38)		Wik (2002)
				45 (47)		Lowe (2006)
Oregon		78 (119)	9 (75)	15 (124)	15 (119)	Gregg (1991), Gregg et al. (1994)
			22 (19)	37 (76)		Coggins (1998)
			34 (143)			Gregg et al. (2006)
Nevada	7.3 (35)	90 (84)	38 (50)	40 (87)		Rebholz (2007)
Utah	7 (147)			60 (161)[a]		Rasmussen and Griner (1938)
				86 (36)[a]		Trueblood (1954)
		63 (19)		66 (19)		Bunnell (2000)
		63 (103)		71 (84)		Chi (2004)
	6 (unknown)	82 (28)		59 (22)		Dahlgren (2006)
Washington	9 (55)	100 (129)	87 (69)	37 (188)	61 (111)	Schroeder (1997)
	7 (38)	80 (95)	25 (44)	41 (93)	40 (95)	Sveum et al. (1998b)
Range	6–9	63–100	9–87	15–86	15–61	
Average (SD)	7.1 (1.1)	78.4 (13.3)	29.9 (26.4)	52.1 (18.2)	41.0 (19.4)	

[a] Studies without radio telemetry

TABLE 3.3
Nest success rates reported for radio-marked Greater Sage-Grouse throughout the species' range.

State or province	Percent nest success (N)			Source
	Yearlings	Adults	Both	
Nonaltered habitats				
California			40 (88)[b]	Popham and Gutiérrez (2003)
Colorado	46 (21)[a]	58 (81)	55 (107)	Hausleitner (2003)
Idaho	73 (15)	52 (23)	63 (40)	Wakkinen (1990)
			52 (75)	Connelly et al. (1991)
	56 (16)	55 (29)	54 (82)	Fischer (1994)
	42 (12)	52 (23)	45 (38)	Wik (2002)
Montana	44 (9)	77 (13)	64 (22)	Wallestad and Pyrah (1974)
Oregon			24 (49)	Gregg (1991)
			37 (63)	Coggins (1998)
Utah	66 (24)	70 (24)	69 (48)	Chi (2004)
			59 (22)	Dahlgren (2006)
Wyoming			35 (78)	Heath et al. (1997)
	67 (21)	76 (21)	71 (42)	Heath et al. (1998)
	57 (34)	64 (48)	61 (82)	Holloran (1999)
			50 (54)	Lyon (2000)
			29 (21)	Slater (2003)
	47 (unknown)	49 (unknown)	49 (484)[b]	Holloran et al. (2005)
	43 (21)	74 (31)	66 (52)	Jensen (2006)
Mean	54 (173+)	63 (293+)	51 (1447)	
Altered habitats				
Alberta	25 (4)	50 (22)	46 (26)	Aldridge and Brigham (2001)
			30 (93)	Aldridge (2005)
Idaho	33 (15)	50 (26)	44 (41)	Apa (1998)
	31 (16)	50 (30)	45 (47)	Lowe (2006)
Oregon			12 (51)	Gregg (1991)
			30 (20)	Hanf et al. (1994)
Washington			41 (93)	Sveum (1995)
			37 (188)	Schroeder (1997)
Wyoming			24 (76)[b]	Slater (2003)
	42 (53)	44 (211)	NA	Holloran (2005)
	57 (14)	64 (42)	62 (56)[b]	Kaiser (2006)
Mean	38 (102)	52 (331)	37 (691)	
Overall mean	49 (275+)	59 (624+)	46 (2,138)	

[a] Sample size in parentheses.
[b] Estimated from data provided in publication.

behavior, as well as migrations. Migration for sage-grouse has been defined as occurring when grouse move >10 km between seasonal ranges (Connelly et al. 2000c). Dispersal and migratory movements help quantify spatial attributes of a population and are fundamental components of the definition of a population (Berryman 2002).

Dispersal

Dispersal is paramount for integrating populations, recolonizing habitats, and maintaining genetic flow (Greenwood and Harvey 1982, Linberg et al. 1998, Barrowclough et al. 2004). Unfortunately, few data are available regarding dispersal by sage-grouse. In Colorado, median dispersal of females ($N = 12$) and males ($N = 12$) was 9 and 7 km, respectively, from their approximate places of hatching to their approximate places of breeding or attempted breeding (Dunn and Braun 1985). Dispersal appears to be discrete from brood breakup (Browers and Flake 1985), and the relatively few movements described seem to be rather gradual and sporadic (Dunn and Braun 1986a).

Seasonal Movements and Migration

Seasonal movement patterns are highly variable both within and among populations (Dalke et al. 1960, Connelly et al. 1988). Connelly et al. (2000c) reported that sage-grouse may have distinct winter, breeding, and/or summer use areas, or the seasonal-use areas may be integrated. For example, winter and breeding areas may be in the same general location or breeding and summer areas may be in the same location. Hence, it is possible for sage-grouse to migrate between two or three distinct seasonal home ranges, or not migrate. Regardless of their migratory status, sage-grouse tend to have large movements within a season when compared with other game birds, including Gray Partridge (*Perdix perdix*) (Weigand 1980, Church and Porter 1990), Ring-necked Pheasant (Hill and Robertson 1988), and Northern Bobwhite (Rosene 1969), which all exhibit relatively short (generally <10 km) movements. Grouse in nonmigratory populations tend to be relatively sedentary with seasonal movements <10 km, while birds in migratory populations may travel well over 100 km (Patterson 1952, Hulet 1983, Hagen 1999). Because of this variation, Connelly et al. (2000c) suggested that three sage-grouse movement patterns can

be defined: (1) nonmigratory—sage-grouse make one-way movements <10 km between or among seasonal ranges; (2) one-stage migration—grouse move ≥10 km between two distinct seasonal ranges; and (3) two-stage migration—grouse move ≥10 km among three distinct seasonal ranges.

The close configuration of winter and breeding habitat in some areas may result in comparatively short or nonexistent movements between winter and breeding areas, whereas long distances between breeding and summer habitat result in extensive movements (Connelly et al. 1988, Hagen 1999). Breeding habitat in some areas may be positioned between winter and summer range, such as Idaho (Dalke et al. 1960) and California (Bradbury et al. 1989). In contrast, a study in Wyoming indicated that breeding and summer ranges tended to be relatively close together and winter range was more distant (Berry and Eng 1985). In eastern Idaho, male ($N = 47$) and female sage-grouse ($N = 27$) moved an average of 32 km and 18 km, respectively, between seasonal areas (Connelly et al. 1988). Similarly, male ($N = 27$) and female sage-grouse ($N = 22$) moved an average of 24 km and 17 km, respectively, from breeding to summer range in southwestern Idaho (Wik 2002). In Colorado, female sage-grouse ($N = 76$) moved an average distance of 10 km between winter range and breeding areas (Hausleitner 2003). Numerous ideas have been proposed to explain sage-grouse movement patterns, including differences in seasonal habitat selection (Connelly et al. 1988), desiccation of succulent forbs during summer (Wallestad 1971, Fischer et al. 1996a), harsh winter weather (Dalke et al. 1960, Gill and Glover 1965, Connelly et al. 1988), seasonal site fidelity (Berry and Eng 1985, Connelly et al. 1988, Fischer et al. 1997), and sex class (Beck et al. 2006).

Peak autumn migration is mid-October through late November, spring migration is mid-February through mid-March, and summer migration occurs from late May through early August (Schroeder et al. 1999). Onset of migration may be associated with weather conditions (Berry and Eng 1985). Autumn movements by sage-grouse in Idaho are generally slow and meandering, with a travel rate of 0.3 km/day, and summer movements are more direct and rapid, with a rate of 0.9 km/day; males moved at a faster rate than females (Connelly et al. 1988). Robertson (1991) reported that migratory sage-grouse in southeastern Idaho moved an average of 0.8 km/day during winter.

Weather and habitat distribution influence migration patterns but are not always sufficient to explain relatively long migration distances in relation to short distances between seasonal habitat types. Sage-grouse often migrate farther than would be necessary to reach suitable habitat (Connelly et al. 1988, Jensen 2006). One possible explanation for this discrepancy is that in subsequent years birds may display fidelity to their first seasonal ranges (Berry and Eng 1985, Connelly et al. 1988, Schroeder and Robb 2003) and thus bypass other suitable habitat to reach these areas.

Site Fidelity

Understanding site fidelity is paramount to understanding seasonal movements. Fidelity to display sites (leks) has been well documented in sage-grouse populations (Dalke et al. 1963, Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985), a trait they share with other species of grouse that breed on leks (Schroeder and Robb 2003). In addition, visits to multiple leks tend to be less frequent for adult males than yearlings, suggesting an age-related period of establishment (Emmons and Braun 1984, Schroeder and Robb 2003).

Researchers have also examined fidelity of females to nesting areas. The distance between a female's nests in consecutive years was a median of 0.7 km (range = 0.0–2.6 km) in Idaho (Fischer et al. 1993) and averaged 3.0 km (SD = 6.8 km) in Washington (Schroeder and Robb 2003), 2.0 km (SD = 5.5 km) in Montana (Moynahan et al. 2007), 0.7 km in Wyoming (Holloran and Anderson 2005), 2.4 km (SD = 0.1) in North Dakota (Herman-Brunson 2007), and 1.1 km (SD = 0.4 km) in South Dakota (Kaczor 2008). Studies in Colorado, Washington, and Wyoming indicated that unsuccessful females moved farther between consecutive nests than successful females (Hausleitner 2003, Schroeder and Robb 2003, Holloran and Anderson 2005), but not in the Dakotas (Herman-Brunson 2007, Kaczor 2008).

Greater distance between nests did not increase the likelihood of nesting success. The average distance between first nests and renests was 2.3 km (SD = 5.2 km) in Montana (Moynahan et al. 2007), 2.6 km (SD = 4.5 km) in Washington (Schroeder and Robb 2003), and 1.9 km (SD = 0.4 km) in South Dakota (Kaczor 2008); within years, consecutive nests were closer together for adult than for year-

ling females in Washington. This behavior of yearling females suggests a period of establishment similar to that of yearling males. The relatively large distances in Washington may be explained by extensive habitat fragmentation; one exceptional female had consecutive nests 32 km apart (Schroeder and Robb 2003). In contrast, Hulet (1983) described a female sage-grouse in southeastern Idaho that moved 170 km among seasonal ranges and returned to nest within 25 m of her previous year's nest. Strong fidelity between seasonal ranges for radio-marked ($N = 5$) sage-grouse was also reported for sage-grouse in northwestern Colorado (Hagen 1999). Birds returned within 1.2 km (median = 0.7, range = 0.2–4.0 km) of the geometric center of seasonal use areas between years.

Home Range

Relatively large seasonal movements and highly clustered distributions of sage-grouse have made estimating home range size difficult (Hagen et al. 2001), and emphasize the wide range of natural variation in home ranges for the species. Some variation is associated with seasonal behavior, habitat requirements, and juxtaposition of habitats (Connelly and Markham 1983, Holloran 1999, Hausleitner 2003). On an annual basis, individuals may occupy areas 4–615 km^2 (Hagen 1999, Connelly et al. 2000c, Hausleitner 2003). Home ranges within a season can vary from <1 to 29 km^2 during the breeding season (Schroeder et al. 1999), <1 to 26 km^2 during summer (Wallestad 1975a, Connelly and Markham 1983, Hagen 1999), 23 to 44 km^2 during autumn (Schroeder et al. 1999), and <1 to 195 km^2 during winter (Wallestad 1975a, Robertson 1991, Hagen 1999). Migratory sage-grouse in southeastern Idaho occupied mean areas of 140 km^2 in winter (Robertson 1991), but a nonmigratory population in central Montana occupied winter home ranges of 11–31 km^2 (Wallestad 1975a). Relatively large seasonal and annual home ranges coupled with extensive movements make Greater Sage-Grouse a true landscape species (Connelly et al. 2004).

Relevance of Movement to Identification of Populations

Dispersal and migratory movements have been studied in relatively small portions of the range of sage-grouse and on rather small numbers of individuals (Connelly et al. 1988). In some cases,

sufficient individuals may have been marked to allow inferences to be drawn about the demographic importance of movements. Unfortunately, it is often impractical to use these movements to define populations of sage-grouse in North America using the approach recommended by Berryman (2002). Nevertheless, knowledge of movements in some portions of the range can be used to help spatially define some populations and extrapolated for assessments of the overall distribution of sage-grouse. Populations of sage-grouse have been considered distinct when they are separated from adjacent populations by at least 20 km of inhospitable and unoccupied habitat (Connelly et al. 2004). This distance is largely based on direct observations of grouse movements within occupied range and absence of movements through or over nonhabitat of sufficient size to apparently act as a barrier (Connelly et al. 1988, 2004).

BREEDING BIOLOGY

The Breeding Period

Male sage-grouse congregate on leks—arenas with relatively sparse cover—to display to and breed with females (Scott 1942, Patterson 1952, Giezentanner and Clark 1974, Connelly et al. 1981, Bergerud 1988a). An important factor affecting lek location appears to be proximity to, and configuration and abundance of, nesting habitat (Connelly et al. 1981, Connelly et al. 2000c). In fact, males may form and visit leks that are in areas of high female traffic (Bradbury and Gibson 1983, Gibson 1996).

Because up to 400 males may attend a lek, and because males form territories on leks, a lek can cover up to 20 ha (Scott 1942). Leks normally occur in the same location each year (Scott 1942, Patterson 1952). Some leks studied by early investigators (Scott 1942, Batterson and Morse 1948) have persisted for 28–67 years since first counted (Wiley 1973b, Hagen 2005). Dalke et al. (1963) reported the presence of broken bird-point arrowheads on one of the leks in their study area, suggesting that sage-grouse had used the site for at least 85 years. Leks and the number of attending males are regularly used to monitor the long-term status of populations because of their traditional locations (Connelly et al. 2003b, Connelly and Schroeder 2007).

Despite the traditional nature of leks, shifts in location may occur for numerous reasons. Gibson and Bradbury (1987) observed a shift in lek location following a severe winter, when traditional lek sites were covered in snow until May. Males may continue to use these new locations even when the snow is gone or in subsequent years. Sage-grouse may shift or abandon lek locations because of persistent disturbance and/or alteration of vegetative cover (Commons et al. 1999, Holloran 2005, Walker et al. 2007a). Intra- and intersexual behavioral interactions may also result in annual variation in lek location, but mechanisms are poorly understood. For example, female selection of specific males may encourage unselected males to alter location of lek territories. Over time female selection could result in the gradual shifting of a lek's location (Beehler and Foster 1988). This effect can be further exacerbated due to the formation of satellite leks during periods of relative abundance (Dalke et al. 1963). To consistently monitor leks spatially and temporally, researchers often consider multiple locations for a lek (including annual shifts and satellites) together as a lek complex (Connelly and Schroeder 2007).

Depending on snow depth, elevation, weather, and region, male sage-grouse begin the display season between the end of February and early April and end the display season in late May or early June (Eng 1963, Schroeder et al. 1999, Aldridge 2000, Hausleitner 2003). Adult males arrive at leks earliest in the season, followed by females and yearling males (Dalke et al. 1960, Eng 1963, Jenni and Hartzler 1978, Emmons and Braun 1984). Female attendance tends to be relatively synchronous, peaking in mid- to late March in Washington (Schroeder 1997), late March to early April in California (Bradbury et al. 1989) and Oregon (Hanf et al. 1994), and early to mid-April in Alberta (Aldridge and Brigham 2001), Colorado (Petersen 1980, Walsh 2002, Hausleitner 2003), Montana (Jenni and Hartzler 1978), and Wyoming (Patterson 1952). Females may also irregularly visit leks later in the breeding season due to renesting efforts (Eng 1963). Weather conditions may cause female attendance patterns to vary by up to 2 weeks (Jenni and Hartzler 1978, Schroeder 1997).

Male sage-grouse usually begin displaying on leks just prior to sunrise and depart shortly after sunrise as the display season begins (Jenni and Hartzler 1978). Males arrive on leks earlier and remain later as the season progresses, especially when females are present (Jenni and Hartzler 1978). During peak female attendance, males may

display for up to 3–4 hours each morning and often during late evening and night (Scott 1942, Patterson 1952, Hjorth 1970, Walsh 2002). Because of the delay in attendance by yearling males, peak male attendance typically occurs about 3 weeks after peak female attendance (Patterson 1952, Eng 1963, Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh et al. 2004). Emmons and Braun (1984) reported an average attendance rate over 5-day observation periods of 86% for radio-marked yearling males and 92% for adult males, and that 90% and 94% of yearling and adult male sage-grouse, respectively, attended leks during the period of high male counts (about 3 weeks after peak female attendance). These rates were pooled over 5-day periods and likely overestimated attendance. In contrast, Walsh et al. (2004) reported average daily male attendance rates of 42% and 19% for adult and yearlings, respectively. These authors indicated that on 58% of days in which seven radio-marked adult males were observed, they did not attend a lek. These rates were not adjusted for detection rate and are likely biased low. These studies are not directly comparable because investigators used different methodologies to measure attendance rates, but each study indicates that counts of males on leks represent minimum counts.

Nesting

Nest Location

An early synthesis of sage-grouse biology and management guidelines indicated that most females nest within 3.2 km of a lek (Braun et al. 1977), but recent literature suggests that many females nest farther from leks than previously suspected. The average distance between a female's nest and the nearest lek was 1.3–1.5 km in Idaho (Wakkinen et al. 1992, Fischer 1994), 2.7 km in North Dakota (Herman-Brunson 2007), 2.8 km in Colorado (Petersen 1980), 4.9 km in Alberta (Aldridge 2005), and 5.1 km in Washington (Schroeder et al. 1999). Similar nest-to-lek distances have also been recorded in Nevada (J. S. Sedinger, pers. comm.). Distances between a female's nest and her lek of capture were substantially larger than distances to the nearest lek (1.2–3.1 km larger) because females may not be captured or first observed at the lek nearest their nest (Petersen 1980, Wakkinen et al. 1992, Fischer 1994, Schroeder et al. 1999,

Herman-Brunson 2007). Other studies have illustrated similar variation in nest-to-lek distances (Berry and Eng 1985, Hanf et al. 1994, Holloran 1999, Lyon and Anderson 2003, Slater 2003, Moynahan et al. 2007). Juxtaposition of habitats, disturbance, and extent of habitat fragmentation may influence location of nests with respect to leks (Lyon and Anderson 2003, Connelly et al. 2004, Schroeder and Robb 2003). Females in highly fragmented habitats of Washington moved almost twice as far to nest (Schroeder et al. 1999) as females in relatively intact habitats of southeastern Idaho (Wakkinen et al. 1992, Fischer 1994). Similarly, females from undisturbed leks in southwestern Wyoming moved an average of 2.1 km to nests, while females from disturbed leks moved 4.1 km (Lyon and Anderson 2003).

Timing of Nesting

Peak egg laying and incubation periods vary from late March through mid-June, with renesting stretching into early July (Schroeder et al. 1999, Gregg 2006). The typical date for initiation of incubation appears to be about 3–4 weeks following peak female attendance on leks (Schroeder 1997, Aldridge and Brigham 2001, Hausleitner 2003). Adults initiated incubation on average nine days earlier than yearlings in north-central Washington (Schroeder 1997). Following an approximate incubation period of 27 days (Schroeder et al. 1999), the precocial chicks leave the nest soon after hatching, are capable of weak flight by ten days of age, and are capable of strong flight by five weeks of age (Schroeder et al. 1999).

Clutch Size

The clutch size of sage-grouse is variable but relatively low compared to other game birds (Edminster 1954, Schroeder 1997). The average clutch size is seven eggs for sage-grouse, but varies from six to nine eggs (Tables 3.1, 3.2). In contrast, clutch sizes for Ring-necked Pheasant and Sharp-tailed Grouse (*Tympanuchus phasianellus*) range from 10 to 12 and 11 to 12 eggs, respectively (Hill and Robertson 1988, Connelly et al. 1998). Variation in clutch size has been attributed to age (Wallestad and Pyrah 1974, Petersen 1980, Hausleitner 2003); nesting attempt, where first nest clutches were larger than those of renests (Kaczor 2008); and annual variation in conditions

(Schroeder 1997, Walker 2008). Nevertheless, Wik (2002) did not detect measurable variation in clutch size either annually or by nesting attempt. Sage-grouse clutch size estimates may be biased low if these estimates have been based on post-hatching nest examinations and partial clutch loss occurs prior to hatch.

Nest Likelihood

The average likelihood of a female nesting in a given year varies from 63% to 100% and averages 82% in the eastern part of the species' range (Table 3.1) and 78% in the western portion of the range (Table 3.2). Nest initiation rates tended to be higher for adults (78–100%) than yearlings (55–79%) in three separate studies in Idaho (Connelly et al. 1993; Wik 2002; N. A. Burke-pile, unpubl. data). Similarly, Holloran (2005) reported that nesting likelihood in Wyoming was greater for adult (85%) than yearling (67%) sage-grouse. Nest initiation rate was also higher for females captured on undisturbed leks in western Wyoming than for females captured on disturbed leks (Lyon and Anderson 2003).

Direct evidence from radiotelemetry studies has illustrated dramatic variation in renesting likelihood (Tables 3.1, 3.2). The average likelihood of renesting is 25% in the eastern portion of the range (Table 3.1) and 30% in the western portion (Table 3.2). Females were observed nesting two times after loss of first nest in Washington (Sveum 1995, Schroeder 1997), Nevada (Rebholz 2007), and Idaho (J. W. Connelly, pers. obs.). Adults were more likely to renest than yearlings in Washington (Schroeder 1997). The lower likelihood of renesting by yearlings may be due to later initiation of first nests and their shorter nesting season (Schroeder 1997), and drier conditions later in the nesting season (Hulet 1983). Higher renesting rates in southern Oregon were associated with improved habitat conditions; renesting rates increased from 14% to 30% as habitat improved (Coggins 1998). Gregg et al. (2006) reported that renesting was related to age of hen, nest initiation period, nest-loss period, and total plasma protein. Hens that renested had greater total plasma protein levels than nonrenesting hens (Gregg et al. 2006). Renesting rates in other game bird species, including Northern Bobwhite (Rosene 1969), Ring-necked Pheasant (Hill and Robertson 1988), Gray Partridge (Carroll 1993), and Greater Prairie-Chicken (*Tympanuchus cupido*; Norton 2005), tend to be higher, often exceeding 75%.

Nest Success

Reported nest success rates of sage-grouse vary between 15% and 86%, depending on habitat condition, methodology, and female age (Table 3.3). Nest success for sage-grouse appears comparable to that of other shrub and grassland grouse species, including 50–72% for Sharp-tailed Grouse (Connelly et al. 1998), 22–65% for Greater Prairie-Chicken (Schroeder and Robb 1993), 14–41% for Lesser Prairie-Chicken (*T. pallidicinctus*; Hagen and Giesen 2005), and 36–57% for White-tailed Ptarmigan (*Lagopus leucura*; Braun et al. 1993).

Baxter et al. (2008) stated that sage-grouse population declines are often related to poor nest success, but most reported nest success rates for sage-grouse are relatively high. The average nest success for 29 studies using radiotelemetry is 46%; 12 (37%) reported nest success rates are ≥50%, and 9 (30%) are <40% (Table 3.3). Moreover, when one compares relatively altered and unaltered habitats, success rates in unaltered habitats appear even higher. In relatively unaltered habitats, 11 of 18 (61%) studies report overall nest success rates ≥50%, and only four (22%) studies report nest success rates <40% (Table 3.3). Two of 12 (17%) studies in altered habitats report nest success rates ≥50%, and five (42%) studies report nest success <40% (Table 3.3).

Sage-grouse nest success rates were reported in central Montana using both apparent and maximum likelihood estimates (Moynahan et al. 2007). However, Moynahan et al. (2007) used repeated nest visits and flushed females on ≥2 visits to the nest site as part of their study methodology, with at least 24 (8%) nests abandoned due to observer influence. Similarly, Herman-Brunson (2007) reported low nest survival (31%, *N* = 29) but used multiple nest visits, flushed females from nests, and marked nests by placing flagging 20–40 m from the nest. Nest desertion by sage-grouse is relatively common during laying and early incubation, and there are a variety of causes of desertion, including field investigators (Patterson 1952). Most researchers avoid disturbing nesting sage-grouse because of concern that this species readily abandons nests following disturbance (Fischer et al. 1993, Sveum et al. 1998b, Wik 2002, Chi 2004, Holloran et al. 2005, Kaiser 2006,

Baxter et al. 2008). Thus, nest success rates reported by Moynahan et al. (2007) and Herman-Brunson (2007) may be related, in part, to field techniques rather than representative samples of nest survival. Recognizing this potential bias, Moynahan et al. (2007) attempted to identify nests abandoned due to observer influence and removed them from their analyses.

Apparent nest success rates derived from radio-telemetry studies may be biased high and unreliable (Kolada 2007, Moynahan et al. 2007). Apparent success likely overestimates nest success when nest visitation does not include the laying period (7–10 days) or sampling is inadequate for detecting a nesting attempt. However, Walker (2008) provided both apparent and maximum likelihood estimates for different areas and years in southeastern Montana and northeastern Wyoming. Most of these estimates were quite similar, and many of the maximum likelihood estimates were actually greater than apparent estimates. Clearly some caution should be used when interpreting levels of nest success from most studies until there is a better understanding of bias associated with different methods of estimating nest success.

Most investigators have not detected statistically different age-specific rates of nest success, except in central Montana, where adults had greater nest success than yearlings (Wallestad and Pyrah 1974). Nevertheless, 13 of 15 radiotelemetry studies indicated that nest success of adult hens was numerically greater than that of yearlings (Table 3.3).

Annual Reproductive Success

Annual reproductive success (probability of a female hatching ≥1 egg in a season) is more complex than nest success because it includes the likelihood of nesting and renesting. For example, if eastern range values are used (Table 3.1), approximately 39% of females successfully hatch one or more eggs in their first nest attempt (average nest likelihood = 82% $\times$ average nest success of 48%). When renest attempts are considered (average renesting likelihood = 20%), the average annual reproductive success is increased to approximately 43%, with about 9% of the average productivity due to renesting. Despite the averages, the high rate of renesting in north-central Washington was atypical for sage-grouse, resulting in 61% annual reproductive success, compared with the modest 37% nest success rate (Schroeder 1997; Table 3.2).

SURVIVAL AND POPULATION DYNAMICS

The definition of a population proposed by Berryman (2002) is somewhat unusual because it includes dispersal and migration behavior while ensuring that numerical changes within a population are largely driven by natality and mortality. In the accepted paradigm of upland game productivity, sage-grouse should regularly overproduce young or at least produce young in sufficient numbers to replace those lost through annual mortality (Allen 1962). Consequently, a strong relationship should exist among movement, productivity, and survival within a population, but little interaction should exist among populations. Information is now available on sage-grouse reproduction that allows us to explore this concept of overproduction and relationships among movement, productivity, and survival.

Survival

Survival in a sage-grouse population can be partitioned into three basic stages: (1) survival of chicks from hatching to brood breakup, usually early September; (2) survival of juveniles from early September to their recruitment to the breeding population, usually March; and (3) annual survival of breeding-age males and females. Recently, results from several studies were averaged to obtain an estimate of 10% survival for juveniles from hatch to breeding age, basically a combination of the first two stages (Crawford et al. 2004). This estimate was based in part on estimates of early juvenile survival, including 33% for Washington (Schroeder 1997), 60% for Wyoming (Holloran 1999), 7% for Utah (Bunnell 2000), and 19% for Alberta (Aldridge and Brigham 2001). At least two of these studies were from areas with fragmented or otherwise marginal sage-grouse habitats; thus, this estimate is likely biased low.

Direct information on survival of radio-marked chicks and juveniles has recently become available (Beck et al. 2006, Gregg 2006, Aldridge and Boyce 2007, Herman-Brunson 2007, Rebholz 2007, Kaczor 2008, Walker 2008). However, the time periods (18–51 days) and estimators (chick or brood survival) used make direct comparisons challenging. Gregg (2006) estimated that chick survival at 28 days posthatching was 39%; survival was higher for chicks from adult females

than for chicks from yearling females. Rebholz (2007) estimated chick survival to 18 days post-hatching at 44% in Nevada using methods similar to those of Gregg (2006). Apparent chick survival to 21 days posthatching was estimated between 34% and 42% in North Dakota and 32% and 50% in South Dakota, respectively (Herman-Brunson 2007, Kaczor 2008). In contrast, Aldridge and Boyce (2007) reported 12% survival of chicks to 51 days of age. Recruitment estimates from the Dakotas suggest that 6–17% of chicks were recruited into the spring breeding population (Herman-Brunson 2007, Kaczor 2008). Beck et al. (2006) reported relatively high survival of radio-marked juveniles (64–86%) from September until recruitment to the breeding population. Battazzo (2007) also found high winter survival of juveniles in Montana. Gender (Swenson 1986), food availability (Swenson 1986, Pyle and Crawford 1996, Holloran 1999, Huwer 2004), habitat quality (Pyle and Crawford 1996, Sveum et al. 1998a, Aldridge 2000, Huwer 2004, Gregg 2006), harvest rates (Wik 2002), age of brood female (Gregg 2006), and weather (Rich 1985) may impact juvenile survival, but lack of adequate survival estimates has made these potential relationships difficult to evaluate.

More information is available on adult survival than survival of other age groups, but a variety of field techniques (bands, radio transmitters, poncho-tags) reduce the comparability among studies. Survival for sage-grouse ($N = 6,021$) in Colorado was estimated using bands recovered from hunters (Zablan et al. 2003). These authors estimated survival to be 59% (95%CI, 57–61%) for adult females, 78% (95%CI, 72–75%) for yearling females, 37% (95%CI, 35–45%) for adult males, and 64% (95%CI, 57–65%) for yearling males. They recovered several sage-grouse ≥7 years of age. Yearling male prairie grouse may improve their survival to adulthood because they remain inconspicuous during their first year (Wittenberger 1978, Bergerud 1988b, Hagen et al. 2005). Annual survival of male sage-grouse was estimated to be 59% in Wyoming (June 1963), 58–60% in Idaho (Connelly et al. 1994, Wik 2002), and 30% in Utah (Bunnell 2000). Female survival was estimated to be 48–78% in Wyoming (June 1963, Holloran 1999, 2005), 48–75% in Idaho (Connelly et al. 1994, Wik 2002), 57% in Alberta (Aldridge and Brigham 2001), 61% in Colorado (Hausleitner 2003), and 37% in Utah

(Bunnell 2000). Adult sage-grouse were similar to juvenile grouse in having high winter survival. Winter survival rates ranged from 82% to 100% (Hausleitner 2003) in Colorado and from 85% to 100% in southwestern Idaho (Wik 2002). All estimates except June (1963) were based on known-fate analyses from telemetry data.

Mortality Patterns

Little range-wide effort has been expended to examine seasonal patterns of mortality for sage-grouse. The greatest seasonal mortality for adult male and female sage-grouse appears to occur in spring, summer, and fall (Connelly et al. 2000a, Wik 2002). In Idaho, 43% of all documented deaths of radio-marked sage-grouse occurred from March through June with no difference by gender (Connelly et al. 2000a). In contrast, only 2% of radio-marked sage-grouse deaths occurred from November through February. Similarly, Wik (2002) reported that in southwestern Idaho, overwinter survival of adult males ranged from 85–90%, and overwinter survival of adult females ranged from 88% to 100%. Generally, most research suggests that overwinter mortality of sage-grouse is low (Robertson 1991, Connelly et al. 2000a, Wik 2002, Hausleitner 2003, Beck et al. 2006), but Moynahan et al. (2006) reported relatively high mortality during one of three winters that spanned their study period in central Montana.

Causes of Mortality

Like all species of upland game birds, sage-grouse have a variety of predators. Nest predators include Common Raven (*Corvus corax*), gulls (*Larus* spp.), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), American badger (*Taxidea taxus*), and ground squirrels (*Spermophilus* spp.)(Patterson 1952; Hulet 1983; DeLong et al. 1995; Johnson and Braun 1999; Schroeder and Baydack 2001; Moynahan 2004; Coates 2007; Hagen, this volume, chapter 6). All of these predators except ground squirrels will also likely prey on young chicks. Investigators have recorded a western rattlesnake (*Crotalus viridus*) feeding on a sage-grouse chick and an adult female sage-grouse attacking a bull snake (*Pituophis catenifer*) adjacent to her nest (N. A. Burkepile, pers. comm.). Predators of older juvenile and adult sage-grouse include red fox, coyote, badger, bobcat (*Lynx rufus*), domestic cat,

weasels (*Mustela* spp.), and a variety of raptor species (Dunkle 1977; Schroeder et al. 1999; Schroeder and Baydack 2001; Hagen, this volume, chapter 6).

Other causes of mortality for sage-grouse include collisions with vehicle or agricultural machinery; disease; flying into fences, power lines, and other obstacles; and pesticide application (Blus et al. 1989, Connelly et al. 2000a, Connelly et al. 2004, Walker 2008). Five percent of radio-marked sage-grouse deaths in southeastern Idaho were attributed to causes other than predation or hunting (Connelly et al. 2000a). Additionally, 33% of mortalities of juvenile sage-grouse in a south-eastern Idaho study area were caused by collision with power lines (Beck et al. 2006).

Although most mortality of sage-grouse is due to predation (Connelly et al. 2000a), a substantial amount of mortality in some areas may be associated with hunting (Johnson and Braun 1999; Wik 2002; Connelly et al. 2003a; Zablan et al. 2003; Reese and Connelly, this volume, chapter 7). Reporting rates of 14.0–18.7% were estimated for a Colorado population of sage-grouse (Zablan et al. 2003). In contrast, average harvest rates were relatively low (3.3%, SE = 1.6%) in Oregon from 1993 to 2006 (Broms 2007). In southern Idaho, 15% of documented male sage-grouse deaths and 42% of female deaths were attributed to hunting (Connelly et al. 2000a), but <1% of female mortalities (*N* = 217) in northeast Wyoming and southeast Montana (2003–2006) were related to legal harvest (Walker 2008).

Sex and Age Ratios

Data on sex ratios are available from numerous states, but much of this information was obtained from hunter-harvested birds. The ratio of birds harvested in late summer in Wyoming ranged from 2.2 to 2.7 females per male (Patterson 1952), while the sex ratio for sage-grouse harvested in Colorado was 1.9 females per male (Rogers 1964). Autenrieth (1981) found highly variable sex ratio data among areas and years for adult sage-grouse shot throughout southern Idaho. From 1993 to 2006, sex ratios varied from 1.2 to 2.4 females per male in Oregon (Broms 2007). Sex ratio data obtained from harvested samples should be viewed with caution because there is likely a differential vulnerability by sex to hunting (Connelly et al. 2000a, Wik 2002).

Some information on sex ratios has been obtained by monitoring winter and spring populations. The sex ratio of sage-grouse spring breeding populations varied from 2.3 to 3 females per male in Colorado (Walsh et al. 2004) and Wyoming (Patterson 1952: 140), respectively. Primary sex ratios in northeast Nevada were approximately 1:1 over a 2-year period (Atamian 2007). During winter, the sex ratio for sage-grouse in northern Colorado was 1.6 females per male (Beck 1977).

Evidently the sex ratio of adult sage-grouse favors females, but reported rates vary considerably. Lower survival of males, possibly associated with breeding activities, is the primary reason the female-to-male ratio appears to increase for birds in older cohorts (Patterson 1952, Braun 1984, Swenson 1986, Zablan et al. 2003). However, Swenson (1986) suggested that lower male survival was due to greater physiological demands of male growth rates as chicks, thus indicating that disparate sex ratios begin to occur relatively soon after hatch. These survival rates are likely related to habitat quality (Swenson 1986, Barnett and Crawford 1994, Johnson and Braun 1999), which varies geographically and temporally; consequently, variation in sex ratios for sage-grouse should be expected.

Fish and wildlife agencies often use age ratios as an index to sage-grouse production (Beck et al. 1975, Hagen and Loughin 2008). The average age ratio in southern Idaho indicated by wing samples collected from 1961 to 1980 was 2.4 juveniles per adult female (Autenrieth 1981). These ratios appeared to vary substantially among areas and ranged from 2.0 to 2.8 juveniles per adult female. Overall, long-term age ratios in the fall have ranged from 1.4 to 3.0 juveniles per adult female. Since 1985, these ratios have been lower than long-term averages and generally ranged from 1.2 to 2.2 juveniles per adult female (Connelly and Braun 1997). Similarly, productivity (1993–2005) has varied from 0.8 to 2.3 juveniles per female in Oregon (Hagen and Loughin 2008).

CONSERVATION IMPLICATIONS

Sage-grouse do not fit the commonly accepted paradigm of upland game bird demographics (Allen 1962). Sage-grouse exhibit relatively high survival of breeding-age birds, especially in winter, and comparatively low productivity. Although average nest success is moderate (range-wide

average of 46%), the large number of nonnesting females (18–22%), low rate of renesting (20–30%), inability to produce more than one brood in one season, and possibly low chick survival combine to ensure that sage-grouse are unlikely to produce rapidly increasing populations, even under the best of circumstances. This is contrary to most other game bird species that yield a wide margin of overproduction (Allen 1962), and lends strong support to the contention that management decisions should not be based on dogmatic beliefs and findings from early wildlife studies (Williams et al. 2004a).

Sage-grouse populations occupy vast landscapes on an annual basis as a result of large home ranges and substantial dispersal/migratory movements of individual birds (Robertson 1991, Connelly et al. 2000c, Wik 2002, Hausleitner 2003, Zablan et al. 2003, Beck et al. 2006). High survival is an advantage, but low productivity and vast areas of occupation substantially increase the difficulty of managing sage-grouse populations. Our characterization of a population that incorporates movement has important ramifications (Berryman 2002). Juvenile sage-grouse that moved farther distances to seasonal ranges had lower overall survival than did juveniles that moved relatively short distances (Beck et al. 2006). Large movements of sage-grouse help to integrate vast areas of occupied landscape, but they may have a cost in terms of increased mortality and may also place populations at risk of disturbance from factors that would seem superficially to be insignificant. For example, large linear disturbances such as a highway and/or power line may effectively divide a population (Connelly et al. 2004, Jensen 2006, Doherty et al. 2008), and, even if the direct loss of habitat is small, effects of fragmentation may be dramatic. Clearly, assessment of population effects due to habitat loss or fragmentation must include an understanding of demographic attributes of sage-grouse populations. Even though much is known about demographic characteristics of sage-grouse, more information is needed. Moreover, our findings clearly underscore the need to standardize approaches to assessing demographics.

Estimates of breeding propensity could be biased high if most hens are captured on or near leks. Females that are relatively far from leks may have a lower likelihood of nesting. Monitoring females radio-marked during summer or fall or following females over multiple breeding seasons would provide some insight into this issue.

An assessment of density dependence in sage-grouse populations would provide a framework for improving our understanding of population dynamics. Sage-grouse populations may not typically be regulated by density-dependent mechanisms, but a better understanding of density dependence can help guide research directed at examining causal linkages between habitat and population dynamics (Garton et al., this volume, chapter 15). In addition, research that can relate variation in annual rates of change to changes in habitat and environmental conditions would allow development of powerful predictive models useful in guiding management decisions and evaluating proposed projects.

Substantial heterogeneity in fitness seems to occur among nesting females; females that successfully nested had higher annual survival than those that failed (Moynahan et al. 2006). This finding suggests that if there is a cost of breeding, it is masked by marked variation in quality among females and that populations may be maintained by a small core of highly fit individuals. Individual heterogeneity in fitness needs further investigation and will hopefully be addressed in the near future.

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