SAGE-GROUSE NESTING AND BROOD HABITAT USE IN SOUTHERN CANADA

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Abstract: Greater sage-grouse (*Centrocercus urophasianus)* populations have declined from 66 to 92% during the last 30 years in Canada, where they are listed as endangered. We used radiotelemetry to examine greater sage-grouse nest and brood habitat use in Alberta and assess the relationship between habitat and the population decline. We also identified the patch size at which sage-grouse were selecting nest and brood-rearing sites. Nest areas were in silver sagebrush (*Artemisia cana*) stands that had greater amounts of tall cover ($P \leq 0.001$) at a patch size of 7.5 to 15 m in radius. Within those sagebrush stands, nests were located beneath the densest sagebrush present. Areas used for brood rearing had greater amounts of taller sagebrush cover in an area ≥15 m in radius than at random locations. Brood locations were not selected based on forb content; mesic areas containing forbs (20–40% cover) as a food resource for chicks were limiting (only 12% cover available). Overall cover of sagebrush is considerably lower in Canada (5–11%) compared with sagebrush (*Artemisia* spp.) cover in other areas throughout the range of greater sage-grouse (15–25%). If management goals are to provide suitable nesting and brood-rearing habitat, efforts should be directed toward protecting and enhancing sagebrush stands ≥30 m^2 and increasing overall sagebrush cover. Management strategies also should focus on increasing the availability of mesic sites and increasing the abundance of sites with >10% forb cover, to enhance brood rearing habitat.

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The distribution of sage-grouse (*Centrocercus* spp.) throughout North America has been reduced by at least 50% since the early 1900s. Populations have been extirpated from 5 of 16 U.S. states and 1 of 3 Canadian provinces (Braun 1998). Breeding populations have declined by 45 to 80% from numbers estimated during the 1950s (Braun 1998), and more recent data suggest that declines from 1985 to 1995 averaged 33% (Connelly and Braun 1997). The most severe declines have occurred at the northern fringe of the range, where the Alberta greater sage-grouse population has decreased from 66 to 92% since 1968 (Aldridge 2000). The historical range within Alberta and Saskatchewan has been reduced by approximately 90% (Aldridge 2000).

Long-term data on sage-grouse suggest that declines in population numbers are related to changes in productivity (Connelly and Braun 1997, Schroeder et al. 1999). Changes in productivity can be attributed to changes in reproductive effort (nesting effort and clutch size), reproductive success (nest success, breeding success, fledging success, chick survival), and/or postfledging mortality (Aldridge 2000). Many studies of declining sage-grouse populations have investigated reproductive effort and measures of reproductive success (Crawford and Lutz 1985, Schroeder 1997, Braun 1998). Population declines appear to be linked to nest success and/or measures of brood survival (Crawford and Lutz 1985, Schroeder et al. 1999). Unsuitable nesting and brood rearing habitat may contribute to decreases in productivity by reducing nest success and/or chick survival (Crawford and Lutz 1985, Sveum et al. 1998*a*).

Sage-grouse are associated with big sagebrush (*A. tridentata*) throughout most of their range, and nest success is higher in areas containing big sagebrush (Wallestad and Pyrah 1974, Connelly et al. 1991, DeLong et al. 1995). In Canada (Alberta and Saskatchewan), sage-grouse exist in a sparse, silver sagebrush (*A. cana*) ecosystem where big sagebrush does not occur (Aldridge 2000). Thus, less overall sagebrush cover results in a grass-dominated system.

Nest success usually is correlated with shrub cover; unsuccessful nests have less overall shrub cover (Wallestad and Pyrah 1974, Connelly et al. 1991, Sveum et al. 1998*b*). Tall grass cover also is positively correlated with nest success and is selected in areas immediately surrounding nest sites (Gregg et al. 1994, Sveum et al. 1998*b*). Sage-grouse usually nest under sagebrush (>90% of 154 nests in Wyoming, Patterson 1952; 91% of 87 nests in Idaho, Klebenow 1969; 79% of 83 nests in

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Idaho, Connelly et al. 1991; 71% of 93 nests in Washington, Sveum et al. 1998*b*), but some nests are placed under other shrubs (Patterson 1952, Klebenow 1969, Connelly et al. 1991, Gregg et al. 1994). It may be that females select nest sites based on suitable shrub overstory as well as herbaceous understory (Klebenow 1969, Sveum et al. 1998*b*, Schroeder et al. 1999). Klebenow (1969) suggested that females might be reacting to the uneven distribution of preferred cover within the available habitat. However, most studies have only considered vegetation immediately surrounding the nest site and thus at relatively small scales.

Forb cover is greater at sage-grouse brood use sites than at random sites, particularly the cover of forbs used as food (Klebenow and Gray 1968, Peterson 1970, Schoenberg 1982, Drut et al. 1994*a*, Sveum et al. 1998*a*). Broods tend to shift from nest sites in sagebrush uplands early in the brood-rearing period to more mesic sites later during the summer (Patterson 1952, Peterson 1970, Autenrieth 1981, Dunn and Braun 1986). This shift may be a result of the desiccation of forbs in sagebrush uplands and an increase in forb growth at more mesic sites later during the summer (Dunn and Braun 1986). These movements may include migrations if wetlands are limiting (Fischer et al. 1996). The initial selection for sagebrush at brood-rearing sites may be linked to selection for sagebrush at nest sites, since sagebrush is a relatively minor component of the diet of sage-grouse at this time. However, these sites usually have abundant insects and forbs at hatching, providing important food resources (Patterson 1952, Klebenow and Gray 1968, Peterson 1970).

Few studies have assessed whether habitat use by sage-grouse is based on a minimum patch size of certain vegetation characteristics. Dunn and Braun (1986) measured horizontal cover 5 and 10 m from the center of summer use sites. They found the extent of horizontal cover at 5 m, but not 10 m, contributed to statistically differentiating between summer use versus random sites. Data from telemetry studies indicate that sage-grouse select for certain vegetation characteristics at nest sites and brood use sites (Wallestad and Pyrah 1974; Schoenberg 1982; Dunn and Braun 1986; Drut et al. 1994*a*; Gregg et al. 1994; Sveum et al. 1998*a,b*). However, few attempts have been made to determine whether selection is taking place at a scale that extends beyond the immediate use site. Nest success and brood survival should be related to the scale at which a female selects habitat patches, which implies that females select nest and brood rearing locations based on vegetation characteristics of a certain patch size.

We examined greater sage-grouse habitat requirements at the northern fringe of the species range to ascertain whether sage-grouse select nest locations and brood locations based on vegetation characteristics, and whether there are certain scales at which they are selecting habitat. We tested the null hypotheses that (1) no differences occurred in vegetation characteristics between successful and unsuccessful nests; (2) no differences occurred between nest locations and random sites, or brood locations and random sites; and (3) sage-grouse were not selecting nesting or brood-rearing locations based on arbitrarily chosen patch sizes of 1 m^2, 15 m^2, or 30 m^2 surrounding nests and brood sites.

STUDY AREA

We monitored habitat use of greater sage-grouse within an area in southeastern Alberta, Canada, of approximately 4,000 km^2 in size (49°24′N, 110°42′W). Silver sagebrush was the dominant shrub and pasture sage (*A. frigida*) the dominant forb (Aldridge 1998). Common grasses included needle-and-thread (*Heterostipa comata*), june grass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Pascopyrum smithii*; Aldridge 2000). The primary land use in this area is cattle ranching, and some areas are active with oil and gas drilling. This area is semiarid, receiving about 332 mm of precipitation annually, and mean temperatures for July and January average 19.5 and –11.7 °C, respectively (Onefour AAFC Weather Station, Lethbridge Research Centre, Agriculture and Agri-food Canada).

METHODS

We captured females at 6 of 8 known active leks (traditional display arenas) from March through May 1998 and 1999 using walk-in traps (Schroeder and Braun 1991) or with a long-handled hoop net and hand-held spotlight (Giesen et al. 1982). Sex and age (yearlings [<2 years old] and adults [≥2 years old]) of all captured individuals were assigned based on the shape and length of the outermost primaries (Eng 1955; Crunden 1963; C. E. Braun, Grouse, Inc., Tucson, Arizona, USA, unpublished data). Captured females were fitted with a 14-g necklace-style radiotransmitter (RI-2B transmitters; Holohil Systems, Carp, Ontario, Canada).

We used a 3-element Yagi antenna and portable receiver (TR2 scanning receiver, Telonics, Mesa, Arizona, USA; Merlin 12 receiver, Custom Electronics of Urbana, Urbana, Illinois, USA) to locate females every other day during the nesting period (Musil et al. 1994, Schroeder 1997). We recorded locations in Universal Transverse Mercator (UTM) coordinates using a hand-held 12 Channel Global Positioning System (Garmin 12 XL and GPS II Plus units; Garmin International, Olathe, Kansas, USA). When signals could not be located, we searched the study area from a fixed-wing aircraft.

When approaching a nest, signals were triangulated until the marked bird could be observed from approximately 30 m with a pair of binoculars to minimize disturbance (Schroeder 1997). Nest site characteristics were measured similar to Klebenow (1969), Wallestad and Pyrah (1974), Musil et al. (1994), and Commons (1997). At each nest site, we estimated the percent sagebrush canopy cover, percent cover of grasses, nonpalatable forbs (prickly pear cactus [*Opuntia* spp.], ball cactus [*Coryphantha coccineus*], and moss phlox [*Phlox hoodii*]), palatable forbs, shrubs (other than sagebrush), and bare ground–dead materials within a 1-m^2 quadrat using a protocol similar to Daubenmire (1959). Shrub and understory vegetation were not stratified into separate layers when estimating cover. Therefore, cover estimates could not exceed 100%. The mean maximum height of vegetation in each of the above groups also was calculated for each plot using measurements of 3 of the tallest plants. To identify the scale at which habitat characteristics might be selected by grouse, we took measurements at the nest itself (hereafter referred to as the nest site) as well as at 8 additional dependent nonrandom 1-m^2 plots (hereafter referred to as the nest area). The additional plots were placed 7.5 and 15 m (4 each) from the nest site in each of the 4 cardinal directions, representing patch sizes of 15 m^2 and 30 m^2, respectively. To understand sage-grouse selection of sagebrush at nest and brood rearing locations, we also performed additional vegetation measurements on sagebrush. We used a similar method to Canfield's (1941) line intercept method (which may result in a more accurate measure of shrub [sagebrush] cover; Daubenmire 1959) to estimate canopy cover of live sagebrush in the nesting area along 4 15-m transects radiating from the nest site in each cardinal direction. We estimated the density of sagebrush by counting the number of plants within 0.5 m of the transect (Commons 1997). The mean height of sagebrush along these transects also was estimated by averaging the height (nearest 5 cm) of each plant. Measurements were recorded separately for the first (0–7.5 m) and second half (7.5–15 m) of the transect.

Measurements of habitat characteristics also were taken at a dependent random location using the same protocol for plots and line transects, focusing on the random site and area. We chose the random location by walking between 100 and 500 m (distance randomly chosen) in a random direction from the nest site. The closest sagebrush plant to the random location was used as the random nest site, since most nests are placed under sagebrush (Patterson 1952, Klebenow 1969, Connelly et al. 1991, Sveum et al. 1998*b*). The dependent nonrandom plots represented non-nest site characteristics within 15 m (30 m^2) of the use site, and the dependent random plots represented non-nest site characteristics 100 to 500 m away.

We considered a nest successful if the shell membranes of 1 or more eggs in the nest were detached (Klebenow 1969). A nest was considered unsuccessful if eggs were broken, or if the membranes of egg shells remained intact. Vegetation characteristics were measured at nest and random locations immediately following a successful hatch, or after a predation event.

Broods were located using radiotelemetry and, typically, we attempted to get within 100 m of females and their broods once per week. These locations were used for habitat measurements. We tried not to flush females and their broods at an early age (≤3 weeks old). Older broods (≥3 weeks old) were intentionally flushed once per week to estimate chick survival. Brood use locations were recorded in UTM coordinates, and we returned the following day to measure vegetation characteristics. We performed the same vegetation measurements at brood-use locations and corresponding dependent random locations that we performed at nest sites.

Most vegetation variables had non-normal distributions, and means of some variables were correlated with the variances; therefore, we log transformed all variables for statistical analyses. However, for reporting purposes, we present means and standard errors of the untransformed data.

We used forward stepwise Discriminant Function Analysis (DFA) to determine whether a linear function of 1 or more variables discriminated between successful and unsuccessful nest locations. We also used DFA to determine whether early and late brood-rearing periods could be discriminated using vegetation characteristics. We used a multivariate paired *T*-test (T^2; Morrison 1990) to test for differences between vegetation characteristics at use (nests and broods) versus random locations. We chose a paired design to account for individual microsite differences, and because our random locations were dependent on use site locations. We chose a multivariate test, which allowed us to investigate potential interactions between variables and identify overall differences between habitat at use and random locations. When the overall model was significant, we used a post hoc limits test of confidence intervals to test for differences between nests or brood locations and random locations. If the 95% confidence interval difference for the tested variable did not include zero, the variable was considered to make a significant contribution to the model (Morrison 1990).

We conducted all analyses at 4 different scales. First, a test was completed using only the 1-m^2 plot at the use site (nest or brood) to differentiate between vegetation characteristics at use sites alone (successful vs. unsuccessful nests) and nest or brood-use sites versus random sites. We analyzed vegetation characteristics for nesting and brood rearing areas by averaging measurements from all 9 plots for each use and random location. We analyzed vegetation characteristics at 2 intermediate scales by averaging measurements from the 4 plots at the 7.5-m radius (area of 15 m^2) and the 4 plots at the 15-m radius (30 m^2; successful vs. unsuccessful nests and nest–brood vs. random sites). For all analyses, results were considered significant when $\alpha < 0.05$. In cases where we were testing the same hypotheses and/or using the same data to test hypotheses, we applied a Bonferroni correction (Rice 1989, Sokal and Rolf 1995).

RESULTS

We captured and fitted 7 females (4 adults and 3 yearlings) with transmitters during 1998 and 34 females (23 adults and 11 yearlings) during 1999. We gathered data for the individual breeding seasons of 22 of these females.

Eleven habitat variables from plot measurements were available to enter into our models. We only entered data for sagebrush cover, shrub cover, palatable forb cover, and grass cover because the other variables were highly correlated with heights or bare ground ($r_s > 0.70$, using a correlation matrix for all use and random habitat measurements combined), indicating these variables measured similar habitat characteristics. We did not incorporate line transect data into models, since they were measured at different scales. Measurements of both sagebrush density and line intercept of sagebrush along transects were both highly correlated with sagebrush cover estimates from plots ($r_s = 0.811$) and thus reflected biologically similar characteristics. We analyzed transect data individually using univariate statistics to compare sagebrush characteristics.

Nests

During 1998, we located 3 nests of radiomarked birds and 2 additional nests of unmarked females. During 1999, we located 24 nests used by radiomarked birds, for a total of 29 nests (24 first nest and 5 renesting attempts). Yearlings constructed 4 of the nests, adults made 23 nests, and 2 nests were of unmarked females of unknown age. Due to small numbers of yearlings captured, renesting attempts, and nests located during 1998, we could not statistically test for differences in vegetation characteristics between years, age of females, or nest order.

We measured vegetation at all 29 nests (14 successful and 15 unsuccessful nests) and 29 dependent random locations. Nest success in our study (percent of all nests that hatched ≥1 egg including renesting attempts) was 46.2% for 26 nests; 1 of 3 nests during 1998, 11 of 23 nests during 1999. The 2 nests from unmarked birds were not included in this estimate, nor was a third nest, because of transmitter difficulties.

We located 26 of 29 (89.6%) nests under silver sagebrush. One nest was under common snowberry (*Symphoricarpos albus*) and 1 was in tall grass along an irrigation dike (although there were some dead shrubs present of an unidentified invasive *Artemisia* species). The other nest was under an uprooted Russian thistle (*Salsola kali*) plant in a wheat stubble field. Two of 26 nests under sagebrush had ≤15% cover of sagebrush, but >50% canopy cover of other shrubs (snowberry and rose [*Rosa* spp.]).

Nest Habitat Selection

Vegetation at nest sites differed from that at random sites (T^2 = 18.35, $P \le 0.001$; Table 1); however, a limits test on the 95% confidence intervals indicated that sagebrush cover was the only variable that discriminated between nests and random sites (1-m plot). Sagebrush cover

Table 1. Vegetation characteristics at sage-grouse nests and random locations. Values are means (± 1 SE). Variables marked with a (*) were entered into the model. Means marked with a (*) contributed significantly to differentiating between nest locations and random locations for that scale. (n = 29 for nests and random locations at all scales.)

	Site		7.5-m plots		15-m plots		All 9 plots	
Variable	Nest	Random	Nest	Random	Nest	Random	Nest	Random
Cover (%)								
Sagebrush*	31.9* (4.07)	15.7* (2.44)	7.6* (1.14)	3.6* (0.86)	7.3 (1.41)	4.9 (1.04)	10.2 (1.26)	5.5 (0.77)
Shrub*	7.4 (3.70)	1.7 (1.39)	3.3 (1.91)	1.1 (0.41)	1.67 (0.62)	1.4 (0.41)	3.1 (1.43)	1.3 (0.36)
Unpalatable forb	0.3 (0.24)	0.2 (0.2)	0.9 (0.28)	1.1 (0.25)	0.6 (0.19)	1.2 (0.35)	0.7 (0.20)	1.1 (0.26)
Palatable forb*	8.1 (1.12)	8.4 (1.03)	10.3 (1.55)	10.6 (1.53)	9.4 (1.18)	11.9 (1.58)	9.7 (1.15)	10.9 (1.39)
Grass*	31.9 (3.96)	41.7 (4.83)	41.7 (3.70)	41.7 (4.04)	44.0 (3.70)	42.9 (3.38)	41.6 (3.44)	42.2 (3.6)
Dead–bare ground	20.34 (4.20)	32.2 (4.01)	36.1 (4.00)	41.9 (4.17)	37.0 (4.14)	37.7 (3.21)	34.8 (3.80)	39.0 (3.64)
Height (cm)								
Sagebrush	41.3 (3.78)	27.5 (3.38)	20.8 (2.46)	14.4 (2.10)	23.4 (3.11)	16.3 (2.19)	26.5 (2.56)	22.2 (1.77)
Shrub	8.6 (3.42)	2.2 (1.35)	8.3 (2.50)	5.7 (2.89)	9.3 (3.27)	10.0 (3.75)	15.7 (3.67)	10.9 (3.53)
Unpalatable forb	0.4 (0.31)	0.1 (0.07)	2.5 (0.70)	2.3 (0.56)	2.2 (0.67)	1.7 (0.43)	3.0 (0.71)	2.4 (0.47)
Palatable forb	15.5 (2.22)	11.2 (1.24)	13.6 (1.78)	12.5 (1.11)	13.8 (1.56)	13.6 (1.15)	14.5 (1.51)	12.9 (10.7)
Grass	30.9 (3.58)	28.5 (1.97)	27.2 (2.21)	25.7 (1.92)	27.7 (2.39)	27.0 (1.84)	27.9 (2.34)	26.6 (1.80)

also was dominant at nest sites (31.9 ± 4.07%), and more than double that of random sites (15.7 ± 2.44%; Table 1). Shrub cover was also greater at nest sites, although not significantly. No vegetation height measurements were entered into the model due to correlations with cover. Sagebrush height and grass height both were greater at nests than random sites, however, not significantly ($P \geq 0.01$; univariate paired *t*-test using a Bonferroni correction factor). Within nesting areas, we placed nests under sagebrush plants that averaged 41.3 ± 3.78 cm in height (Table 1).

Nesting areas could be differentiated from random locations at the 7.5-m scale ($T^2 = 32.2$, $P \leq 0.001$). Sagebrush cover was the only variable that significantly discriminated at this scale and was greater at nest locations (7.6 ± 1.14% vs. 3.6 ± 0.86%). A univariate paired *t*-test indicated that none of the height measurements at the 7.5-m scale differed between nest and random locations ($P \geq 0.01$, using a Bonferroni correction factor), even though sagebrush and other shrubs were taller in nesting areas.

Nest locations could not be differentiated from random locations at the 15-m scale ($T^2 = 5.64$, = 1.26, $P \geq 0.05$), or over the entire nesting area (all 9 plots: $T^2 = 17.52$, = 3.91, $P \geq 0.05$). None of the 5 height variables at nest locations at the 15-m scale alone or over all 9 plots combined differed from random locations ($P \geq 0.01$, using a Bonferroni correction factor).

We combined sagebrush and other shrub cover to test whether nest locations could be differentiated from random locations on this basis. Overall shrub cover did allow for differentiation of nests from random locations at the nest site ($T^2_{4, 25} = 20.12$, $P \leq 0.01$), at the 7.5-m scale ($T^2_{4, 25} = 17.62$, $P \leq 0.01$), and for all 9 plots combined ($T^2_{4, 25} = 18.81$, $P \leq 0.01$), but not at the 15-m scale alone ($T^2_{4, 25} = 4.94$, $P \geq 0.05$).

Nesting Habitat Characteristics by Nest Fate

We incorporated grass height into the DFA model to test for differences between successful and unsuccessful nests only. Grass cover was only weakly correlated with grass height ($r_s \leq 0.209$). Successful nest sites (1-m^2 plot over nest) could not be significantly differentiated from unsuccessful nests ($F_{4, 24} = 2.69$, $P > 0.068$; Tables 2–3), but there was a trend for more sagebrush, shrub, and forb cover, but less grass cover, and taller vegetation in all 5-cover classes at successful nests (Table 4). Overall (all 9 plots combined: $F_{2, 26} = 6.17$, $P < 0.006$; Table 4), and at both scales (7.5-m plots: $F_{2, 26} = 3.77$, $P < 0.023$; 15-m plots: $F_{2, 26} =$

Table 2. Discriminant Function Analysis of vegetation characteristics at successful and unsuccessful sage-grouse nests. Sagebrush cover, shrub cover, palatable forb cover, grass cover, and grass height were the only variables entered into the model. The models for the 7.5-m, 15-m, and all 9 plot scales were all significant ($P < 0.05$).

Overall model	All 9 plots	15-m plots	7.5-m plots
Wilks' λ	0.678	0.617	0.688
F	6.17	8.056	3.772
P	0.0064	0.0016	0.023
Correct classification (%)	75.9	82.8	72.4

Table 3. Variables that contributed significantly to discriminating between successful (n = 14) and unsuccessful (n = 15) nests for that scale are shown below (P < 0.05). The larger the Wilks' λ, the greater the variable contributed to the discriminant function. SCC = Standardized Canonical Coefficient.

	All 9 plots				15-m plots				7.5-m plots			
Variable	Wilks' λ	P	R^2	SCC	Wilks' λ	P	R^2	SCC	Wilks' λ	P	R^2	SCC
Grass cover	0.937	0.004	0.204	–1.039	0.861	0.003	0.223	–0.979	0.908	0.009	0.094	–0.926
Palatable forb cover									0.740	0.182	0.077	0.494
Grass height	0.830	0.023	0.204	0.845	0.862	0.003	0.230	0.980	0.725	0.260	0.123	0.430

8.056, P < 0.005; Table 4), successful nests could be successfully differentiated from unsuccessful nests by the vegetation structure of the nesting area, allowing for correct classification of 72.4 to 82.8% of the time (Table 2). Grass cover contributed the most to each of the 3 discriminant function models, and in all cases, the height of grass also was a significant contributor (Table 3). Palatable forb cover made a significant contribution to the discriminant function at the 7.5-m scale and was greater at successful nests. Successful females chose nesting areas with less grass cover compared with unsuccessful females, but the grass was taller in nesting areas surrounding successful nests (Table 4).

Brood Habitat

We obtained data on habitat use for 15 different radiomarked females and their broods. Vegetation characteristics were measured at 91 brood locations (63 for broods <7 wk old and 28 for broods 7–12 wk old) and 91 corresponding dependent random locations. We entered sagebrush cover, shrub cover, forb cover, and grass cover into a forward stepwise DFA, but could not discriminate between early (<7 wk old) and late brood (7–12 wk old) locations ($P \geq 0.05$), indicating that no shift occurred in brood habitat. Thus, we combined early and late brood-rearing locations to test for overall habitat selection (use vs. random locations).

Brood-use sites (1-m^2 plot centered where the marked female and her brood were located) could be differentiated from random sites ($T^2_{4, 87}$ = 155.07, $P \leq 0.001$; Table 5). Brood-rearing areas also could be differentiated from random areas overall (all 9 plots: $T^2_{4, 87}$ = 72.06, $P \leq 0.001$), and at both the 7.5-m ($T^2_{4, 87}$ = 21.48, $P \leq 0.001$) and 15-m scales ($T^2_{4, 87}$ = 28.79, $P \leq 0.001$; Table 5). A limits test indicated that the only variable entered into each model that allowed for differentiation was sagebrush cover. Palatable forb cover was low at brood-use locations, ranging from 10.9 to 12.9% at the different scales (Table

Table 4. Vegetation characteristics at successful and unsuccessful sage-grouse nests. Values are means (± 1 SE). Variables marked with a (*) were entered into the Discriminant Function Analysis. Means marked with a (*) contributed significantly to discriminating between successful (n = 14) and unsuccessful (n = 15) nests for that scale (P < 0.05, Table 2).

	Nest site		7.5-m plots		15-m plots		All 9 plots	
Variable	Successful	Unsuccessful	Successful	Unsuccessful	Successful	Unsuccessful	Successful	Unsuccessful
Cover (%)								
Sagebrush*	32.9 (7.05)	31.0 (4.58)	7.9 (1.57)	7.3 (1.7)	8.5 (2.50)	6.3 (1.43)	10.9 (2.03)	9.5 (1.57)
Shrub*	8.9 (4.89)	6.0 (5.65)	2.2 (1.5)	4.3 (3.46)	1.4 (0.69)	1.9 (1.04)	2.6 (1.16)	3.4 (2.6)
Unpalatable forb	0.7 (0.49)	0.0	0.4 (0.20)	1.4 (0.49)	0.4 (0.28)	0.8 (0.26)	0.4 (0.24)	1.0 (0.30)
Palatable forb*	10.4 (2.06)	6.0 (0.72)	13.9 (2.75)	7.0 (1.03)	10.3 (2.11)	8.7 (1.20)	11.9 (2.09)	7.6 (0.84)
Grass*	26.8 (5.61)	36.7 (5.47)	33.2* (5.80)	49.7* (3.78)	36.2* (5.32)	51.3* (4.51)	33.8* (5.36)	48.9* (3.60)
Dead–bare ground	20.4 (6.08)	20.3 (6.01)	42.4 (6.51)	30.3 (4.46)	43.3 (6.89)	31.1 (4.47)	40.4 (6.47)	29.5 (3.93)
Height (cm)								
Sagebrush	42.0 (6.69)	40.7 (4.04)	18.6 (2.98)	22.9 (3.88)	20.2 (4.31)	26.4 (4.48)	24.4 (4.31)	28.5 (3.43)
Shrub	12.1 (5.73)	5.4 (3.89)	5.9 (2.41)	10.5 (4.28)	6.1 (2.91)	12.2 (5.72)	15.2 (4.46)	16.1 (5.90)
Unpalatable forb	0.9 (0.63)	0.0	0.6 (0.33)	4.3 (1.16)	0.4 (0.27)	3.8 (1.13)	1.1 (0.52)	4.9 (1.1)
Palatable forb	20.1 (3.85)	11.2 (1.88)	17.4* (2.91)	10.1* (1.73)	17.0 (2.75)	10.7 (1.22)	18.5 (2.45)	10.8 (1.24)
Grass*	37.0 (6.53)	25.3 (2.83)	29.9* (3.61)	24.8* (2.60)	32.8* (3.98)	23.0* (2.26)	31.6* (4.06)	24.4* (2.25)

Table 5. Vegetation characteristics at brood use and random locations. Values are shown as means (± 1 SE). Variables marked with a (*) were entered into the model. Means marked with a (*) contributed significantly to differentiating between brood locations and random locations for that scale.

Variable	Site		7.5-m plot		15-m plot		All 9 plots	
	Brood	Random	Brood	Random	Brood	Random	Brood	Random
Cover (%)								
Sagebrush*	20.9* (1.63)	2.9* (0.54)	7.1* (0.68)	4.7* (0.50)	7.3* (0.69)	4.6* (5.52)	8.7* (0.65)	4.5* (0.47)
Shrub*	1.2 (0.39)	1.7 (0.92)	1.6 (0.34)	1.9 (0.53)	2.0 (0.53)	2.1 (0.62)	1.7 (0.36)	2.0 (0.57)
Unpalatable forb	0.9 (0.23)	1.4 (0.36)	1.1 (0.20)	1.4 (0.25)	1.1 (0.19)	1.3 (0.21)	1.1 (0.15)	1.3 (0.21)
Palatable forb*	10.9 (1.20)	11.5 (1.52)	12.8 (1.21)	11.5 (1.23)	12.9 (1.07)	10.7 (1.06)	12.6 (1.10)	11.2 (1.14)
Grass*	34.2 (2.05)	36.9 (2.52)	36.0 (1.71)	33.8 (1.84)	35.2 (1.75)	36.6 (1.98)	35.4 (1.61)	35.4 (1.89)
Dead–bare ground	32.0 (2.07)	45.5 (2.72)	41.5 (1.73)	46.7 (2.14)	41.6 (1.76)	44.7 (2.07)	40.5 (1.65)	45.7 (2.06)
Height (cm)								
Sagebrush height	32.0 (2.36)	7.6 (1.2)	22.9 (1.61)	16.0 (1.52)	21.9 (1.48)	15.5 (1.34)	27.6 (1.61)	17.8 (1.30)
Shrub height	2.5 (0.83	2.2 (0.89)	6.7 (1.22)	5.3 (11.78)	7.0 (1.29)	6.4 (1.34)	8.8 (1.35)	6.9 (1.29)
Unpalatable forb	1.4 (0.50)	1.2 (0.51)	2.9 (0.42)	2.2 (0.35)	2.3 (0.39)	2.0 (0.32)	4.1 (0.57)	2.8 (0.40)
Palatable forb	21.7 (1.46)	15.3 (1.37)	20.7 (1.16)	17.5 (1.13)	20.4 (1.07)	17.5 (1.18)	20.8 (1.05)	17.8 (1.11)
Grass	45.3 (1.86)	36.6 (2.01)	41.5 (1.36)	39.1 (1.72)	43.1 (1.33)	39.7 (1.50)	42.5 (1.30)	39.5 (1.53)

5). None of the vegetation height measurements were entered into the model because of correlations with cover measurements. However, the heights of all vegetation types at brood sites and brood-rearing areas (7.5-m scale, 15-m scale, and overall) were greater than at random sites (Table 5). Only the height of sagebrush and palatable forbs was significantly greater at brood-use locations for all scales ($P \le 0.01$, using a Bonferroni correction factor). Grass was significantly taller at the brood locations compared with random locations, but only at the site level ($P \le 0.01$).

Line Transects

Since sagebrush was the only variable that differentiated between use and random locations, we compared line intercept and transect data to assess which characteristics of sagebrush were selected by sage-grouse (Table 6). At nesting locations, sagebrush cover was greater over the entire 15-m radius surrounding nest sites, when compared with random locations. Cover also was greater at nesting areas than random locations at 0 to 7.5 m from the nest and between 7.5 and 15 m from the nest. However, our estimate of sagebrush cover at nest locations using the line intercept method (all 15 m; 4.5 ± 0.65%; Table 6) was significantly less than that using all 9 plots (10.2 ± 1.26%; t_{28} = 8.93, $P \le 0.001$; Table 1).

Sagebrush density within the 15-m radius was greater surrounding nest sites than random sites ($P \le 0.017$, using a Bonferroni correction factor). However, when separated into the 2 scales, density was only greater ≤7.5 m from nest sites ($P \le 0.017$) and not from 7.5 to 15 m ($P \ge 0.017$). Sagebrush height along line transects was not signifi-

Table 6. Sagebrush characteristics at use locations (nests and broods) and random locations along line transects. Values are means (± 1 SE). Means marked with a (*) were significantly different between use locations and random locations for that scale using a univariate paired *t*-test. A Bonferroni correction was used (α = 0.017).

Variable	≤7.5 m		7.5 m to 15 m		All 15 m of transect	
	Use	Random	Use	Random	Use	Random
Nests (*n* = 29)						
Percent cover (line intercept)	5.6* (0.75)	2.9* (0.52)	3.5* (0.64)	1.8* (0.51)	4.5* (0.65)	2.4* (0.48)
Height (cm)	26.4 (2.50)	19.9 (1.59)	22.1 (2.54)	17.1 (1.31)	24.4 (2.45)	18.5 (1.29)
Density (number plants/m^2)	2.1* (0.28)	1.5* (0.36)	1.7 (0.24)	1.4 (0.30)	1.9* (0.25)	1.4* (0.32)
Broods (*n* = 91)						
Percent cover (line intercept)	5.8* (0.47)	2.4* (0.30)	4.3* (0.42)	2.7* (0.36)	5.0* (0.42)	2.5* (0.31)
Height (cm)	26.0* (1.60)	19.0* (1.57)	24.2* (1.42)	17.6* (1.30)	25.6* (1.45)	19.6* (12.7)
Density (number plants/m^2)	1.9* (0.19)	1.2* (0.16)	1.8* (0.17)	1.2* (0.14)	1.8* (0.17)	1.2* (0.14)

cantly different between nest and random locations at all scales ($P \geq 0.017$; Table 6). Sagebrush height (24.4 ± 2.45 cm) for the entire nesting area along transects was not different from estimates using all 9 plots (26.5 ± 2.56 cm; $t_{28} = 2.03$, $P \geq 0.05$).

Using line transect data, brood use areas had taller sagebrush with more canopy cover and greater density of sagebrush than random locations at all 3 scales (≤7.5 m from brood sites, 7.5 to 15 m from sites, and over all 15 m; $P \leq 0.017$; Table 6). However, as was the case for nest locations, values for sagebrush cover at brood locations (all 15-m intercept; 5.0 ± 0.42%; Table 6) were significantly less than values estimated using plots (8.7 ± 0.65%; $t_{90} = 12.94$, $P \leq 0.001$; Table 1). Sagebrush height estimated at brood locations from line transects (25.6 ± 1.45 cm; Table 6) was similar to height estimated from plots (27.6 ± 1.61 cm; $t_{90} = 1.81$, $P \geq 0.05$; Table 5).

DISCUSSION

Nest success in our study (46.2%) was comparable to other areas (typically 30 to 60%; Schroeder et al. 1999), despite the fact that less available sagebrush habitat exists in Alberta than in other areas. The lack of cover likely is related to the species of sagebrush present. As mentioned, silver sagebrush (the only shrubby species of sagebrush that occurs in Alberta) is smaller than most sagebrush species and does not provide as much cover (Aldridge 1998) as big sagebrush (*A. tridentata*), which is found throughout the core range of sage-grouse.

Successful nests could not be differentiated from unsuccessful nests in our study by the vegetation characteristics at the nest site itself. However, vegetation surrounding successful nests (within 15 m) had taller grass than unsuccessful nests, but less cover. In Alberta, Seida (1998) found that artificial sage-grouse nests were more likely to be successful if they had taller grass and more forb cover at the nest site. In a similar experiment, Watters (2000) found that successful nests had taller forbs and grass, but less grass cover and shorter sagebrush surrounding the nest. These results are similar to those of both natural (Gregg et al. 1994, Sveum at al. 1998*a*) and artificial nests (Delong et al. 1995) in other locations. This highlights the importance of greater cover of medium-height sagebrush, tall grasses, and herbaceous understory to obscure nests.

Most sage-grouse nests are found under sagebrush (Patterson 1952, Klebenow 1969, Connelly et al. 1991, Gregg at al. 1994, Sveum et al. 1998*b*), with apparent selection for taller plants that generally provide more cover (Wallestad and Pyrah 1974, Musil et al. 1994). We found similar results, with 89.6% (26/29) of nests located under sagebrush plants that were taller ($\bar{x} = 41.3 \pm 3.78$ cm) and provided greater canopy cover ($\bar{x} = 31.9 \pm 4.07\%$) than was available. Selection for sagebrush occurred at the nest area scale as well. Habitat within 7.5 m of nest sites had greater density of sagebrush with more sagebrush cover, compared with available cover. However, it is possible that sage-grouse were selecting nesting areas based on patches of sagebrush that provide more cover at a scale that we did not test: between 7.5 m and 15 m in radius.

When sagebrush and other shrub cover were combined in our analysis, total shrub cover at nest sites, as well as shrub cover within 7.5 m of nest sites, was greater than at random locations. Although Sveum et al. (1998*b*) found no difference in probability of success for nests under sagebrush compared with nests under other plants, Connelly et al. (1991) found that nests under non-sagebrush plants were less successful ($P \leq 0.025$). In the Connelly et al. (1991) study, 21% of nests (18/84) were under species other than live sagebrush, although ≥16% of the available canopy cover in the area comprised sagebrush. This suggests that sage-grouse may select nest sites based on suitable amounts of shrub and herbaceous cover (Connelly et al. 1991, Sveum et al. 1998*b*). As long as suitable cover is available, the species that provides it may be less important.

Sage-grouse selection of nest habitat appears to be based on structure; shrubs (primarily sagebrush) that provided more cover and generally were taller in an area at least 7.5 m in radius but less than 15 m in radius were selected as nesting areas. Within 15 m of the nest site, successful nests had taller grass than unsuccessful nests. The tallest shrubs providing the greatest cover within those stands typically were used for nest sites. Other studies have shown that sage-grouse tend not to place nests under the tallest available sagebrush (Klebenow 1969, Gregg et al. 1994, Sveum at al. 1998*b*). This is because tall shrubs often are associated with reduced lateral cover, due to a depleted understory (Klebenow 1969). In our study, grass cover within nesting areas ($\bar{x} = 41.6 \pm 3.6\%$ for all 9 plots; Table 1) was greater than that found around nests in other studies (range 4–32% cover; Klebenow 1969, Connelly et al. 1991, Sveum et al. 1998*b*). Since the canopy of silver sagebrush is not as dense as big sagebrush, the understory may not be as sheltered and thus not as depleted. If sage-grouse in Canada select the tallest sagebrush available, the understory may still be suitable to provide lateral cover for nests.

Sveum et al. (1998*b*) found that sage-grouse chose nest locations based on vegetative characteristics at both the nest-site and nest-area levels, similar to our study. However, they did not test for vegetation differences at different distances from nest sites and were unable to compare vegetation characteristics between nest sites and nest areas because of differences in measurement scales. Our study is the first to show that sage-grouse select nesting areas based on habitat characteristics of a certain patch size (≥15 m^2 but ≤30 m^2) and that nest sites are selected within those patches.

Broods remained in areas with dense, tall sagebrush, which was comparable to sagebrush characteristics at nest locations. Greater sagebrush cover differentiated brood rearing sites and areas from random locations at all measured scales using both plots and transects (all 9 plots: 8.7 vs. 4.5%; Table 5; all 15 m of transects: 5.0 vs. 2.5%; Table 6). In contrast, several studies have shown that females with broods selected areas with less sagebrush (range 8.5–14% cover) compared with what was available (range 14.3–20% cover; Klebenow 1969, Dunn and Braun 1986, Sveum et al. 1998*a*). Our data are the first to suggest that female sage-grouse select locations with greater sagebrush cover to raise their broods than available at random locations, even though a lower availability of sagebrush exists in our study area.

Grass height at brood-rearing locations was (42.5 ± 1.30 cm) similar to that at random locations, but considerably taller than the >18-cm tall grass cover that broods selected for in Washington (Sveum et al. 1998*a*). However, Sveum et al. (1998*a*) separated grass into tall (>18 cm) and short (<18 cm) grass cover. We measured only the mean maximum height of grass, which likely overestimated mean grass height. Sage-grouse may be selecting for tall versus short grass cover, extending beyond the immediate brood (or nest) site, which we did not test.

Forb cover in brood-use areas averaged 12.6% for the entire brood-rearing period. Schoenberg (1982) found that young broods in Colorado used areas with relatively low forb cover (6.9%) and quickly moved to wet meadows where forbs constituted 41.3% of the cover. Peterson (1970) also found that forb cover was important, accounting for 33% of the available cover at brood-use sites. Forb cover in Oregon was estimated to be 10–14% for early brood-rearing locations and 19–27% for late brood-rearing locations (Drut et al. 1994*a*). These authors suggested that 12–14% forb cover might represent the minimum cover needed for brood habitat.

We did not observe a shift in habitat used by broods, which typically occurs due to dietary requirements of chicks (Martin 1970; Peterson 1970; Johnson and Boyce 1990; Drut et al. 1994*a,b*). Early brood-rearing locations tend to be in sagebrush uplands, but as temperature increases and moisture decreases, forbs become desiccated and broods move to more mesic sites that have increased availability of forbs (Peterson 1970, Dunn and Braun 1986, Sveum et al. 1998*a*). However, the lack of a shift in brood habitat between early and late brood rearing in our study suggests that differences in the availability of forbs probably did not exist. Forbs were available throughout the study area (11.2%) in similar proportions to what females selected at brood-rearing locations (12.6%), suggesting that key brood habitat in moist areas and drainages may be limiting in southeastern Alberta. Despite the low forb cover compared with other studies, it may have been high for the study area, since spring precipitation was above average in both years of our study (Aldridge 2000).

For both nest and brood locations, the line intercept method resulted in significantly lower estimates of sagebrush canopy cover than estimates generated from plots. However, the measures were highly correlated (r_s = 0.906), indicating that both techniques accurately reflect relative sagebrush cover. Estimating cover with few quadrats (<20) may result in overestimates of shrub canopy cover and result in large standard errors (Daubenmire 1959), as may have been the case in our study. However, sagebrush cover estimates for the 9 plots in our study (10.2 ± 1.26%) had similar standard errors compared with cover estimates from the line intercept method (4.5 ± 0.65%). The recent sage-grouse habitat management guidelines suggest that 15–25% sagebrush canopy cover is required for sage-grouse breeding habitat (Connelly et al. 2000). With such low availability of sagebrush in our study area (nest plots 10.2% [Table 1], nest line intercept 4.5% [Table 6]), suitable sagebrush habitat appears to be limiting within southeastern Alberta, regardless of the measurement method. However, none of the information from which these guidelines are based was from studies performed on sage-grouse populations located in a silver sagebrushdominated community, and the historical density of sagebrush in southern Alberta is unknown.

Nest success (46.2%) in our study was within the range reported for sage-grouse in other areas. However, chick survival (percentage of chicks that survived from hatch to 50 days of age) over the course of our study was only 14–23% (Aldridge and Brigham 2001). This is extremely low, given that estimates of 33–38% have been found in slightly declining populations (June 1963, Schroeder 1997). Despite low chick survival estimates, grass cover and height likely contributed to suitable escape cover throughout the study area. However, the lack of cover from sagebrush ultimately may make the available escape cover unacceptably low, and the lack of forb availability may result in low-quality brood rearing habitat.

MANAGEMENT IMPLICATIONS

Management strategies for sage-grouse should consider identifying all sagebrush stands that are at least 15 m^2 (preferably 30 m^2) and protecting and enhancing these stands. These stands also should have a suitable understory of tall grasses and forbs to enhance nest concealment. Our results suggest that managing for suitable nesting areas also will provide suitable brood-rearing sites for sage-grouse, at least during some years. However, the guidelines for sage-grouse habitat management (Connelly et al. 2000) based on current habitat-related research (Schroeder et al. 1999), suggest that 15–25% sagebrush cover is necessary to meet various life history requirements. The history of the sagebrush ecosystem in Canada over the last 100 years is poorly understood, but changes in sagebrush density or abundance may be critical to sage-grouse populations at the northern fringe of their range. Silver sagebrush is 1 of the few *Artemisia* species that is fairly fire resistant. It resprouts vigorously after fires through root sprouts and rhizomes (Beetle 1960). Fire suppression on the prairies since European settlement could have reduced the regeneration of sagebrush and thus its abundance.

Greater sage-grouse in southern Alberta used areas with only 5–11% sagebrush cover. Management strategies should first be directed at protecting and maintaining current available sagebrush cover. Second, managing the landscape to increase both the abundance and availability of sagebrush should result in increased abundance and distribution of sage-grouse. An increase in live sagebrush cover by as little as 5% from current levels of available sagebrush cover (5–11%) might be enough to elevate productivity and stabilize, or even increase, sage-grouse population numbers in Canada.

Important mesic areas, such as wet meadows that provide high-quality succulent forbs (20–40% cover), may be lacking within the Canadian range of sage-grouse, since only 12% cover of forbs was available. This decreased availability of food resources for chicks may be related to reduced chick survival and overall low recruitment (Aldridge and Brigham 2001). Precipitation was above average during this study, and the availability of forbs may be even lower in years with below-average spring precipitation. Mesic areas with higher forb availability should be identified and protected to increase the availability of valuable food resources for females and their broods, potentially resulting in increased chick survival. Management strategies should focus on enhancing the number and quality of mesic sites where increased forb growth can occur, managing for brood-rearing habitat as well as suitable sagebrush cover. Land managers implementing water developments for livestock need to consider the potential negative effects those developments might have on key wetlands and mesic sites. Future research needs to address the potential negative effects that cattle might have on reducing the amount of succulent forbs in mesic habitats that are necessary for sage-grouse chick survival.

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LITERATURE CITED

ALDRIDGE, C. L. 1998. Status of the sage grouse (*Centrocercus urophasianus urophasianus*) in Alberta. Wildlife Status Report 13, Alberta Environmental Protection, Wildlife Management Division, and Alberta Conservation Association, Edmonton, Canada.

———. 2000. Reproduction and habitat use by sage grouse (*Centrocercus urophasianus*) in a northern fringe population. Thesis, University of Regina, Saskatchewan, Canada.

———, AND R. M. BRIGHAM. 2001. Nesting and reproductive activities of greater sage-grouse in a declining northern fringe population. Condor 104:537–543.

AUTENRIETH, R. E. 1981. Sage grouse management in Idaho. Wildlife Bulletin 9, Idaho Department of Fish and Game, Boise, USA.

BEETLE, A. A. 1960. A study of sagebrush: the section Tridentatae of *Artemisia*. Bulletin 368, University of Wyoming Agricultural Experiment Station, Laramie, USA.

BRAUN, C. E. 1998. Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78:139–156.

CANFIELD, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388–394.

COMMONS, M. L. 1997. Movement and habitat use by Gunnison sage grouse (*Centrocercus minimus*) in southwestern Colorado. Thesis, University of Manitoba, Winnipeg, Canada.

CONNELLY, J. W., AND C. E. BRAUN. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology 3:229–234.

———, M. A. SCHROEDER, A. R. SANDS, AND C. E. BRAUN. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967–985.

———, W. L. WAKKINEN, A. D. APA, AND K. P. REESE. 1991. Sage grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55:521–524.

CRAWFORD, J. A., AND R. S. LUTZ. 1985. Sage grouse population trends in Oregon, 1941–1983. Murrelet 66:69–74.

CRUNDEN, C. W. 1963. Age and sex of sage grouse from wings. Journal of Wildlife Management 27:846–850.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33:43–64.

DELONG, A. K., J. A. CRAWFORD, AND D. C. DELONG, JR. 1995. Relationship between vegetational structure and predation of artificial sage grouse nests. Journal of Wildlife Management 59:88–92.

DRUT, M. S., J. A. CRAWFORD, AND M. A. GREGG. 1994*a*. Brood habitat use by sage grouse in Oregon. Great Basin Naturalist 54:170–176.

———, W. H. PYLE, AND J. A. CRAWFORD. 1994*b*. Diets and food selection of sage grouse chicks in Oregon. Journal of Range Management 47:90–93.

DUNN, P. O., AND C. E. BRAUN. 1986. Summer habitat use by adult female and juvenile sage grouse. Journal of Wildlife Management 50:228–235.

ENG, R. L. 1955. A method for obtaining sage grouse age and sex ratios from wings. Journal of Wildlife Management 19:267–272.

FISCHER, R. A., K. P. REESE, AND J. W. CONNELLY. 1996. Influence of vegetal moisture content and nest fate on timing of female sage grouse migration. Condor 98:868–872.

GIESEN, K. M., T. J. SCHOENBERG, AND C. E. BRAUN. 1982. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:223–231.

GREGG, M. A., J. A. CRAWFORD, M. S. DRUT, AND A. K. DELONG. 1994. Vegetational cover and predation of sage grouse nests in Oregon. Journal of Wildlife Management 58:162–166.

JOHNSON, G. D., AND M. S. BOYCE. 1990. Feeding trials with insects in the diet of sage grouse chicks. Journal of Wildlife Management 54:89–91.

JUNE, J. W. 1963. Wyoming sage grouse population measurement. Proceedings of the Annual Conference of the Western Association of State Game and Fish Commissioners 43:206–211.

KLEBENOW, D. A. 1969. Sage grouse nesting and brood habitat in Idaho. Journal of Wildlife Management 33:649–661.

———, AND G. M. GRAY. 1968. Food habits of juvenile sage grouse. Journal of Range Management 21:80–83.

MARTIN, N. S. 1970. Sagebrush control relates to habitat and sage grouse occurrence. Journal of Wildlife Management 34:313–320.

MORRISON, D. F. 1990. Multivariate statistical methods. Third edition. McGraw-Hill, New York, USA.

MUSIL, D. D., K. P. REESE, AND J. W. CONNELLY. 1994. Nesting and summer habitat use by translocated sage grouse (*Centrocercus urophasianus*) in central Idaho. Great Basin Naturalist 54:228–233.

PATTERSON, R. L. 1952. The sage grouse in Wyoming. Sage Books, Denver, Colorado, USA.

PETERSON, J. G. 1970. The food habits and summer distribution of juvenile sage grouse in central Montana. Journal of Wildlife Management 34:147–155.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

SCHOENBERG, T. J. 1982. Sage grouse movements and habitat selection in North Park, Colorado. Thesis, Colorado State University, Fort Collins, USA.

SCHROEDER, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99:933–941.

———, AND C. E. BRAUN. 1991. Walk-in traps for capturing greater prairie-chickens on leks. Journal of Field Ornithology 62:378–385.

———, J. R. YOUNG, AND C. E. BRAUN. 1999. Sage grouse (*Centrocercus urophasianus*). The birds of North America, number 425. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

SEIDA, T. L. 1998. The influence of vegetative characteristics on predation at artificial sage grouse nests. Thesis, University of Regina, Saskatchewan, Canada.

SOKAL R. R., AND F. J. ROLF. 1995. Biometry: the principles and practice of statistics in biological research. Third edition. W. H. Freeman, New York, USA.

SVEUM, C. M., J. A. CRAWFORD, AND W. D. EDGE. 1998*a*. Use and selection of brood-rearing habitat by sage grouse in south-central Washington. Great Basin Naturalist 58:344–351.

———, M. D. EDGE, AND J. A. CRAWFORD. 1998*b*. Nesting habitat selection by sage grouse in south-central Washington. Journal of Range Management 51:265–269.

WALLESTAD, R. O., AND D. B. PYRAH. 1974. Movements and nesting of sage grouse hens in central Montana. Journal of Wildlife Management 38:630–633.

WATTERS, M. E. 2000. The effect of vegetative characteristics on predation of artificial sage grouse (*Centrocercus urophasianus*) nests. Thesis, University of Regina, Saskatchewan, Canada.

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