Variation in greater sage-grouse morphology by region and population

Michael A. Schroeder

Washington Department of Fish and Wildlife, P.O. Box 1077, Bridgeport, WA 98813, 509-686-2692, schromas@dfw.wa.gov

Draft report for the U.S. Fish and Wildlife Service, 8 September 2008

INTRODUCTION

The greater sage-grouse (*Centrocercus urophasianus*) is wildlife species with important conservation and management considerations in western North America. Research on sage-grouse has established their historical and current distribution (Schroeder et al. 2004) as well as providing an assessment of their populations and habitats (Connelly et al. 2004). This research helped define the presence of 41 distinct populations (Fig. 1) based on the Berryman's (2002) definition of a population; "as a group of individuals of the same species that live together in 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.

In addition to defining populations, research has provided an evaluation of the range-wide genetics of sage-grouse with an assessment of potential issues associated with population size, population connectivity, and sub-specific variation (Young 1994; Young et al. 1994; Oyler-McCance et al. 1999, 2005). Although research helped establish the Gunnison sage-grouse as a behaviorally and morphologically distinct species (Young et al. 1994), similar research within the remaining populations of greater sage-grouse has been somewhat limited (Oyler-McCance et al. 2005, Taylor and Young 2006). Oyler-McCance et al. (2005) showed that sage-grouse displayed relatively integrated genetics across their range with notable exceptions being the Moses Coulee, N Mono Basin, and S Mono Basin populations.

The initial objective of this research was to examine the availability of previously collected morphological and behavioral data from both published and unpublished sources. Although the collection of additional data would certainly aid in this process, this was not an objective for this initial phase of research. The overall goal of the research was to acquire and examine data with reference to variation associated with region, population, and/or previously established genetic characteristics. Because of the nature of this type of data (rarely published), it was believed that this initial report effort would be 'preliminary' and that analysis would continue as additional data was collected and/or acquired.

METHODS

Greater sage-grouse are sexually dimorphic with males typically 65-75 cm in length and females 50-60 cm in length; males are also substantially heavier. Yearlings (birds in their second year) are typically smaller than adults (birds in their third year or older). Many measurements of sage-grouse have been collected in various portions of the range,

though few measurements have received widespread use. There are several reasons for a lack of available and consistent morphometric data, but one of the principal reasons is that sage-grouse are often captured at night when it is difficult to make consistent and accurate measurements. The data in this report were compiled by population (Fig. 1), but populations varied dramatically in size, and thus the quantity of potential data (Table 1).

Fig. 1. Distribution of 41 established populations of greater sage-grouse in North America based on the distribution of suitable habitat and/or known lek sites (Connelly et al. 2004, Schroeder et al. 2004).

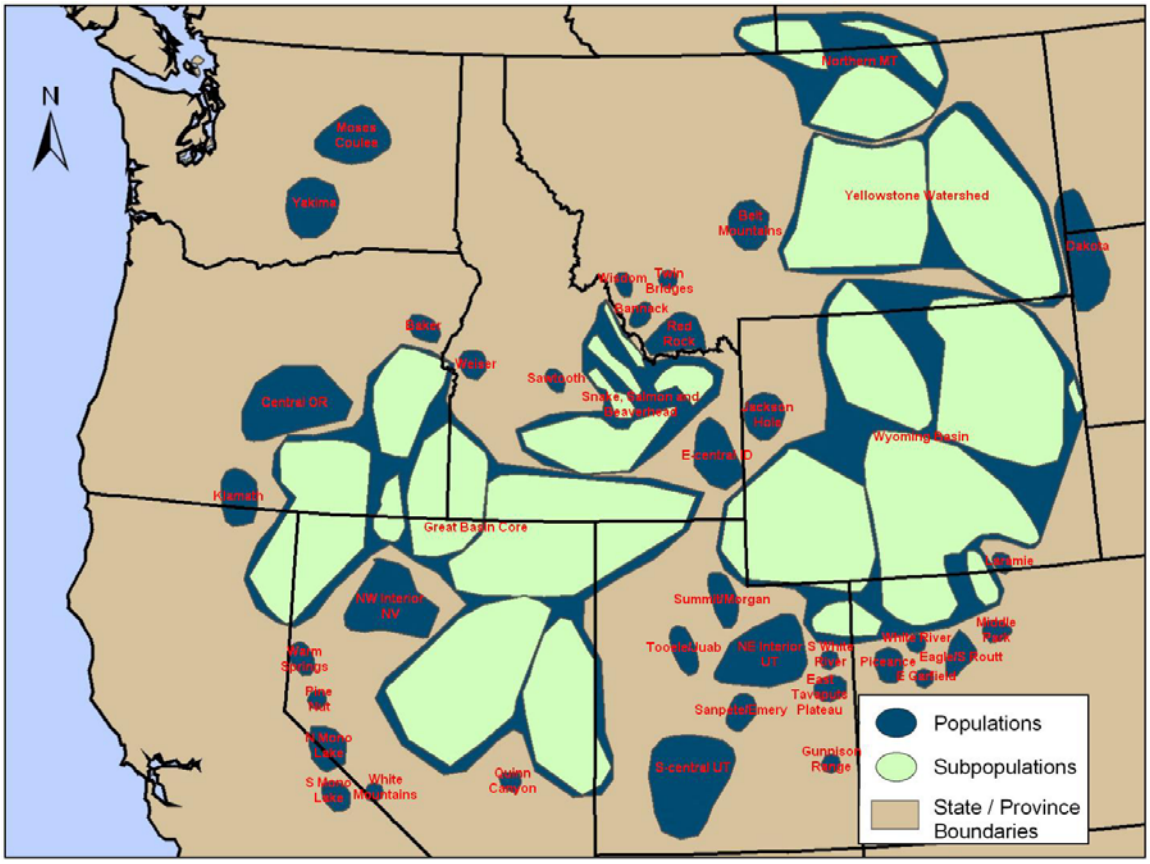

Table 1. Forty-one populations of greater sage-grouse in North America (Connelly et al. 2004) and their respective status with current presence and/or published research.

Population	**Selected research published within each population**[a]
Baker	
Bannack	
Belt Mountains	
Central OR	Hanf et al. 1994
E Garfield	
Eagle/S Routt	
East Tavaputs Plateau	
E-Central ID	
Great Basin Core	Nelson 1955, Crunden 1963, Pyrah 1963, Klebenow and Gray 1968, Savage 1968, Klebenow 1969, Oakleaf 1971, Call and Maser 1985, Klebenow 1985, Evans 1986, Zunino 1987, Martin 1990, Gregg 1991, Drut 1992, Gregg et al. 1993, Klott et al. 1993, Barnett and Crawford 1994, Drut et al. 1994a, Drut et al. 1994b, Gregg et al.

	1994, Pyle and Crawford 1996, Byrne 2002, Wik 2002, Popham and Gutiérrez 2003, Knerr and Messmer 2006, Taylor and Young 2006
Gunnison Range	Extinct (translocated from different population)
Jackson Hole	
Klamath	
Laramie	Extinct
Middle Park	
Moses Coulee	Schroeder 1997
Dakota	Smith 2003
N Mono Lake	Bradbury and Gibson 1983, Gibson and Bradbury 1985, Gibson and Bradbury 1987, Gibson 1989, Gibson 1990, Gibson et al. 1991, Gibson 1992, Gibson 1996a, Gibson 1996b, Taylor and Young 2006
NE Interior UT	Rasmussen and Griner 1938, Griner 1939, Batterson and Morse 1948, Lords 1951, Welch et al. 1990, Baxter 1991, Welch et al. 1991, Welch et al. 1995
Northern MT	Aldridge 1998, Aldridge and Brigham 2002, Aldridge 2005
NW Interior NV	
Piceance	
Pine Nut	
Quinn Canyon	Extinct
Red Rock	
S Mono Lake	Bradbury and Gibson 1983, Gibson and Bradbury 1985, Gibson and Bradbury 1987, Gibson 1989, Gibson 1990, Gibson et al. 1991, Taylor and Young 2006
S White River	Extinct
Sanpete/Emery	
Sawtooth ID	Translocation from different population; Musil et al. 1993, Musil et al. 1994
S-Central UT	Enyeart 1956, Baxter 1991
Snake, Salmon, and Beaverhead	Bean 1941, Stanton 1958, Crawford 1960, Dalke et al. 1960, Dalke et al. 1963, Connelly and Ball 1978, Autenrieth 1981, Connelly et al. 1981, Connelly 1982, Connelly and Markham 1983, Connelly et al. 1988, Wakkinen 1990, Connelly et al. 1991, Robertson 1991, Sime 1991, Wakkinen et al. 1992, Connelly et al. 1993, Fischer et al. 1993, Connelly et al. 1994, Fischer 1994, Fischer et al. 1996*a*, Fischer et al. 1996*b*, Fischer et al. 1997
Summit/Morgan	
Tooele/Juab	
Twin Bridges	
Warm Springs Valley	
Weiser	
White Mountains	
White River	Extinct
Wisdom	
Wyoming Basin	Girard 1937, Dargan et al. 1942, Allred 1946, Patterson 1952, June 1963, Rogers 1964, Gill 1965, Gill 1967, Beck et al. 1975, Beck and Braun 1978, Rothenmaier 1979, Goebek 1980, Petersen 1980, Schoenberg 1982, Braun 1984, Berry and Eng 1985, Braun and Beck 1985, Dunn and Braun 1985, Dunn and Braun 1986a, Dunn and Braun 1986b, Remington and Braun 1988, Klott and Lindzey 1990, Myers 1992, Zablan 1993, Apa 1998, Heath et al. 1998, Holloran 1999, Lyon 2000, Hausleitner 2003, Slater 2003
Yakima	Hofmann 1991, Caldwell et al. 1994, Sveum 1995, Sveum et al. 1998a, Sveum et al. 1998b
Yellowstone watershed	Eng 1952, Eng 1955, Eng 1963, Martin 1965, Gray 1967, Martin 1970, Eng 1971, Wallestad 1971, Eng and Schladweiler 1972, Wallestad and Pyrah 1974, Wallestad and Schladweiler 1974, Wallestad 1975, Martin 1976

[a]The literature is primarily referenced as an indication of some of the key research within the respective populations. Virtually none of the research has specific information on morphology of greater sage-grouse. In addition, a blank next to a population means that no specific research was identified for this report.

Mass is the most frequently obtained measurement and also one of the most problematic because it can vary by season and time of day, in addition to the variation associated with

sex, age, and individual. Researchers have recorded several measurements of length and width including total body (tip of tail to tip of extended beak), tarsus (base of middle toe to proximal end of the tarsus), middle toe (base of middle toe to tip of toe nail), culmen (straight line from tip of the upper mandible to the insertion of feathers above the mandible), wing or carpal (wrist to tip of the longest primary with the wing slightly flattened), tail (insertion point of tail feathers to tip of longest feather), comb (length of comb measured as a straight line), bill depth (widest point of the bill measured as a straight line top to bottom), and all the primaries (measure from proximal point of insertion to tip of straightened primary). Other measurements have also been obtained such as keel and head length, but these are somewhat difficult to accurately define, thus making measurements somewhat inconsistent. In addition to these measurements, the number of tail feathers is often recorded.

RESULTS

Greater sage-grouse demonstrate significant variation in body mass attributable to season (Fig. 2). Males peak in body mass in late winter or early spring, while females peak in late spring. This annual variation was consistent with other studies (Patterson 1952, Dalke et al. 1963). Variation in mass within a season (i.e., spring) also may be substantial (Fig. 2). Because of this seasonal variation, most comparisons of mass across the range focus on the breeding season (typically March, April, and May, or some combination of these months, Table 2). In addition, because most birds are captured during the breeding season, use of these data increases the potential sample sizes.

Fig. 2. Variation in body mass of greater sage-grouse by sex, age, and time of year in North Park, Colorado (Wyoming Basin, Beck and Braun 1978). Sample sizes are shown for each point.

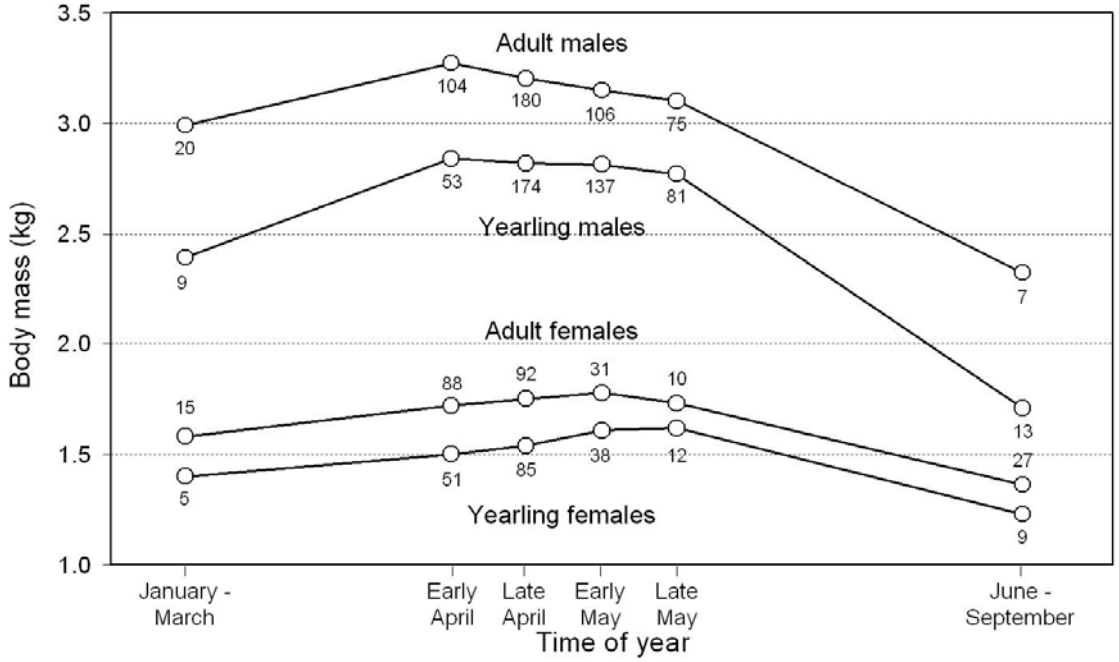

Table 2. Breeding-season mass (kg) of greater sage-grouse by sex, age, and population (SD = standard deviation, R = range).

Population	Adult male		Yearling male		Adult female		Yearling female		Source
	X	n	x	n	x	N	x	n	
Great Basin	2.54 (SD = 0.13, R = 2.29 – 2.80)	25	2.37 (SD = 0.25, R = 1.89 – 2.69)	10	1.41 (SD = 0.10, R = 1.28 – 1.65)	27	1.36 (SD = 0.08, R = 1.29 – 1.52)	10	MAS
Mono Lake (N and S)	2.6	199	2.2	29	1.3	29	1.2	25	R. M. Gibson, Pers. comm.
Moses Coulee	2.78 (SD = 0.18, R = 2.11 – 3.03)	24	2.44 (SD = 0.10, R = 2.32 – 2.64)	10	1.54 (SD = 0.08, R = 1.35 – 1.73)	62	1.39 (SD = 0.08, R = 1.24 – 1.62)	28	MAS
Northern MT	3.1	28	2.4	5	1.7	2	1.5	2	C. L. Aldridge, Pers. comm
Snake, Salmon, and Beaverhead	2.45 (R = 2.25 – 2.73)	?	2.18 (R = 1.98 – 2.28)	?	1.33 (R = 1.18 – 1.40)	?	1.25 (R = 1.20 – 1.23)	?	Pyrah 1954
Snake, Salmon, and Beaverhead	2.5	25	2.2	6	1.3	19	1.3	16	Dalke et al. 1963
Snake, Salmon, and Beaverhead	2.5	21	2.3	21	1.5	4	1.4	8	Autenrieth 1981
Wyoming Basin	2.71 (SD = 0.19, R = 2.33 – 3.18)	33	2.19	6	1.37	3	1.33	1	Patterson 1952
Wyoming Basin	3.19 (SD = 0.18)	465	2.81 (SD = 0.20)	445	1.74 (SD = 0.15)	221	1.55 (SD = 0.12)	186	Beck and Braun 1978
Wyoming Basin	2.92 (SD = 0.16)	50	2.53 (SD = 0.18)	260	1.63 (SD = 0.11)	143	1.48 (SD = 0.12)	168	Hupp and Braun 1991
Wyoming Basin	2.88 (SD = 0.22, R = 1.65 – 3.51)	315	2.54 (SD = 0.28, R = 1.50 – 3.42)	88	1.48 (SD = 0.22, R = 1.00 – 2.33)	109	1.35 (SD = 0.22, R = 0.9 – 1.97)	46	Diebert
Yakima	3.40	1		0	1.53	8	1.35	1	MAS
Yakima	2.8 (SD = 0.2)	25	1.3 (SD = 0.1)	4	1.6 (SD = 0.1)	8	1.3 (SD = 0.4)	9	Hofmann 1991
Yellowstone Watershed	2.9	28	2.53	18					Eng 1963
Yellowstone Watershed	2.86 (R = 2.45 – 3.90	80	2.50 (R = 2.23 – 2.95	52	1.59 (R = 1.27 – 1.95)	193	1.45 (R = 0.95 – 1.77	181	Wallestad 1975

An assessment of mass for greater sage-grouse during the breeding season illustrates that there is substantial variation in the quality of available data (Table 2). Sample sizes are occasionally missing and standard deviations are often not available. Nevertheless, the standard deviations that are available range between 0.08 and 0.28 kg, regardless of sex, age, area, or sample size. This consistency suggests that interpretations can be made across the range based on the available data. For example, adult males are significantly heavier than yearling males, yearling males are heavier than adult females, and adult females are heavier than yearling females.

When a regional comparison of averages is done within each sex and age category, the available mass data fall into two categories; relatively heavy and relatively light populations of birds. There is substantial overlap in standard error intervals among the 'heavy' birds and substantial overlap among the 'light' birds, but virtually no overlap in confidence intervals of the means between the respective populations. The 'heavy' populations of birds include northern Montana, Yellowstone Plateau, Wyoming Basin, Moses Coulee, and Yakima and the 'light' populations of birds include the Great Basin, Mono Lake (S and N combined for this analysis), Snake, Salmon, and Beaverhead populations. Although the light and heavy populations appear to encompass somewhat consistent regions (i.e., northern Colorado, Wyoming, Montana, Alberta, and Washington for 'heavy' populations and Oregon, California, Nevada, and Idaho for 'light' populations), there are many populations with no data available at this time.

Many length and width measurements have been recorded for greater sage-grouse, but few have been recorded in sufficient sample sizes for more than one population. One of the exceptions is length of primary feathers. Primary lengths have been recorded for several locations, but sufficient sample sizes are only available for the Great Basin (Hart Mountain) and Moses Coulee populations (MAS, Fig. 3). Primary lengths are longer for males than females for each age and area category. Primary lengths are also longer for adults than yearlings for most primaries (especially primaries 1-7 in males and 1-9 in females, Fig. 3). There are also significant differences in primary lengths for the Great Basin and Moses Coulee populations. Primaries tend to be longer for adult males (primaries 6-7), yearling males (primaries 4-8), adult females (primaries 1-2, 4-5, and 7-10), and yearling females (primaries 6-9) in the Moses Coulee population. There were no primaries that were longer in the Great Basin population. It is not clear if the longer primaries are related to the larger average mass of birds in the Moses Coulee populations.

Tail lengths were available for 4 different populations including Moses Lake, Yakima, Great Basin, and the Wyoming Basin (all data from MAS except for Wyoming Basin, P. Deibert, Pers. Comm.). Tail lengths were longer for males than females for each age and area category (Table 3); tail lengths were also longer for adults than yearlings for each sex and area category. A comparison of areas showed substantial differences. Yearling females in the Great Basin population had significantly shorter tails than yearling females in the Moses Coulee population. In contrast, adult males in the Moses Coulee population had significantly shorter tails than adult males in the Great Basin and in the Wyoming Basin. It is not clear if these differences in tail lengths had any significance beyond the statistics. It has been noted in observations and photos that the tails of sage-grouse may have slightly different profiles, but this has not been looked at in detail.

Fig. 3. Lengths of primaries 1 (proximal) through 10 (distal) for greater sage-grouse in the Moses Coulee (represented by red) and Great Basin (represented by green) populations. The 95% confidence intervals are shown for each sex and age category including adult males (dashes), yearling males (dots), adult females (solid line), and yearling females (dashes and dots).

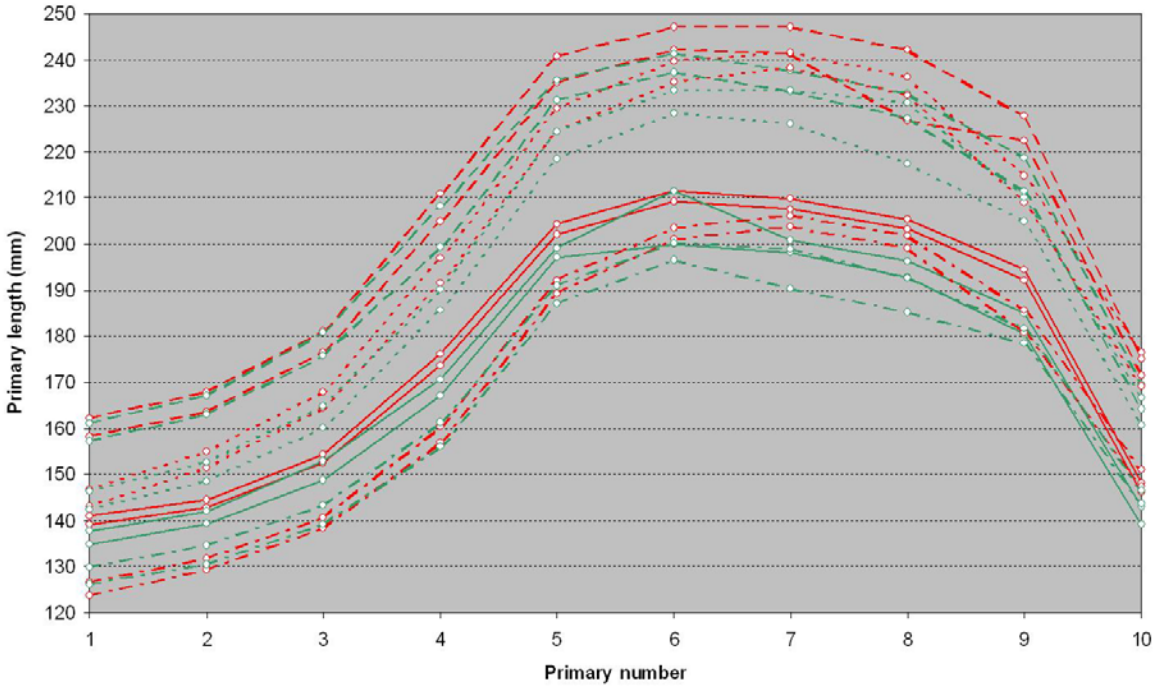

Table 3. Tail length measurements (nearest mm) by sex, age, and region for greater sage-grouse. All measurements were collected by MAS, except for the Wyoming Basin measurements which were collected by P. Deibert (Pers. Comm.).

Populations	Adult males		Yearling males		Adult females		Yearling females	
	x (N)	95% C.I.	x (N)	95% C.I.	x (N)	95% C.I.	x (N)	95% C.I.
Moses Coulee	284 (17)	275-292	250 (12)	245-254	195 (38)	193-197	185 (15)	183-187
Yakima	275 (1)	-	-	-	192 (7)	187-198	171 (1)	-
Great Basin	307 (24)	296-318	259 (11)	235-283	192 (26)	187-196	172 (16)	162-181
Wyoming Basin	314 (319)	311-318	256 (87)	248-263	199 (100)	194-203	184 (42)	178-190

Wing lengths were available for 3 different populations including Moses Lake, Great Basin, and the Wyoming Basin (two different study sites within the Wyoming Basin). There are other miscellaneous data available, but not enough for statistical comparison. Wing lengths were longer for males than females for each age and area category (Table 4). Wing lengths also tended to be longer for adults than yearlings for most sex and area category. A comparison of areas showed differences that were not easy to interpret. Birds in one portion of the Wyoming Basin (North Park, Colorado; Hupp and Braun 1991) tended to have the largest wing measurements when compared to other areas, including the other study area within the Wyoming Basin. Females in the Moses Coulee

Area had longer wing measurements than those in the Great Basin and in a portion of the Wyoming Basin (Deibert, Pers. Comm.). Males in the Moses Coulee also tended to be longer. Because the wing measurement is difficult to obtain consistently, care should be taken in these interpretations to make sure that the 'apparent' differences are not due to subtle differences in techniques.

Table 4. Wing length measurements by sex, age, and population for greater sage-grouse. Measurements were collected by MAS for Moses Coulee and the Great Basin and by Pat Deibert (Pers. Comm) and Hupp and Braun (1991) for the Wyoming Basin.

Populations	Adult males		Yearling males		Adult females		Yearling females	
	x (N)	95% C.I.	*x* (N)	95% C.I.	*x* (N)	95% C.I.	*x* (N)	95% C.I.
Moses Coulee	322 (24)	318-325	321 (12)	318-325	278 (57)	277-280	274 (21)	273-276
Great Basin	316 (20)	313-318	307 (19)	302-311	267 (36)	266-269	262 (33)	259-265
Wyoming Basin – Deibert	318 (319)	316-319	313 (87)	308-319	267 (109)	264-270	264 (46)	260-268
Wyoming Basin – Hupp and Braun	341 (50)	338-344	328 (151)	326-330	284 (35)	282-286	277 (29)	275-279

Other measurement of length and width were available, but they were not common enough for widespread comparison. There were also observations of the number of tail feathers. This characteristic has been noted for many other species of grouse, but has rarely been considered for greater sage-grouse. Because tail feathers frequently fall out when a bird is captured and because birds are often captured at night when it is difficult to find missing tail feathers, a certain amount of caution should be exercised when interpreting data on the number of tail feathers. For that reason, the analysis of tail feather number considered medians rather than averages (Table 4).

Table 5. Counts of tail feathers by sex and population for greater sage-grouse. Measurements were collected by P. Deibert (Pers. Comm) for the Wyoming Basin and MAS for the other populations.

Population	Sex	N	First most common		Second most common	
			Number of tail feathers	Frequency of occurrence	Number of tail feathers	Frequency of occurrence
Moses Coulee	Male	19	20	100.0		
Moses Coulee	Female	32	18	81.3	20	9.4
Yakima	Female	7	18	85.7		
Great Basin	Male	29	18	51.7	20	20.7
Great Basin	Female	32	18	75.0	17	15.6
E-central Idaho	Male	5	18	60.0		
Wyoming Basin	Male	187	18	26.2	20	21.4
Wyoming Basin	Female	4	16	50.0		

Male greater sage-grouse typically had either 18 or 20 tail feathers (Table 5). It was also common to find birds with 19 tail feathers and even as high as 23 (P. Deibert, Pers. Comm.). The most common number of tail feathers in each of the populations examined was 18, except for Moses Coulee, where it was 20. Moses Coulee was also the only population where the number of tail feathers appeared to be 'fixed'. The most common number of tail feathers for females was 18, with the only exception being the Wyoming Basin with 16 (Table 5). Because of the low sample size, particularly in Wyoming, care should be taken with interpretations.

The behavior of greater sage-grouse was also considered, but can be difficult because of the complexity (Taylor and Young 2006). In general, greater sage-grouse throughout the range display substantial similarity (Young et al. 1994). Consequently, only 'number of struts per minute' was considered here, since it is the only characteristic that has received a reasonable amount of attention in different locations (Table 6). Although there was regional variation in the strut rate of sage-grouse, it is not clear if this variation reflects population-level effects or other unexplained variation.

Table 6. Number of struts per minute observed in populations of greater sage-grouse.

Population	Struts/minute			Source
	N	*x*	SD	
Wyoming Basin	47	6.63	0.43	Wiley 1973
Mono Basin	18	7.22	0.68	Taylor and Young 2006
Great Basin – NE California	11	7.88	0.85	Taylor and Young 2006
Great Basin – N Nevada	7	6.88	0.41	Taylor and Young 2006

DISCUSSION

There is a substantial amount of data on sage-grouse morphology that has been collected and only a portion of that data is represented in this report. Although efforts were made to collect data for this analysis, these efforts were only partial successful. This was due to numerous reasons including: 1) the variable conditions of the data (often not available in a database); 2) different priorities of the researchers involved; 3) lack of motivation to share the data; and 4) inability to contact the appropriate researcher with relevant data. For this reason, it is believed that this effort is preliminary and that more data will be acquired for additional analyses in the future.

Analyses on the available morphometric data illustrated significant differences in numerous characteristics including body mass, wing length, tail length, and primary lengths. Many of these differences were associated with sex and age, but body mass also varied by season. There were also substantial morphometric differences associated with populations. Most of these differences were consistent with the observed regional variation in body mass. Birds from Washington and birds from northern Colorado to Alberta appeared to be larger than those in Idaho, Nevada, Oregon, and California. This regional variation was not consistent with previously established genetic characteristics (Oyler-McCance et al. 2005). It is possible that this regional variation is much more

subtle than observed here, but that the lack of morphometric data from many of the smaller populations has influenced the overall interpretation.

It is also apparent that this preliminary assessment of the available morphometric and behavioral data has not illustrated any unique characteristics of birds in the Moses Coulee, N Mono Lake, and S Mono Lake populations that would be consistent with the genetic assessment of possible isolation (Oyler-McCance et al. 2005). However, this morphometric data is incomplete and does not provide a clear assessment. For example, the only data available at this time for the N and S Mono Lake population was body mass and limited behavioral information. It is also possible that the apparent isolation of populations illustrated in the greater sage-grouse range map (Fig. 1) is a fairly recent phenomenon and that morphometric divergence relatively insignificant.

LITERATURE CITED

Aldridge, C. L. 1998. Status of the Sage Grouse (Centrocercus urophasianus urophasianus) in Alberta. Alberta Environ. Protection, Wildl. Manage. Div., and Alberta Conserv. Assoc., Edmonton. Wildl. Status Rep. 13.

Aldridge, C. L. 2005: Identifiying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. - PhD thesis, University of Alberta, Edmonton, Canada. 250 pp.

Aldridge, C. L. & R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada.- Journal of Wildlife Management 66:433-444.

Allred, W. 1946. Sage grouse trapping and transplanting. Proc. West. Assoc. State Game and Fish Comm. 26:143-146.

Apa, A. D. 1998. Habitat use and movements of sympatric sage and Columbian sharp-tailed grouse in southeastern Idaho. - PhD thesis, University of Idaho, Moscow, USA. 199 pp.

Autenrieth, R. E. 1981. Sage Grouse management in Idaho. Idaho Dep. Fish and Game, Boise. Wildl. Bull. 9.

Barnett, J. F., and J. A. Crawford. 1994. Pre-laying nutrition of Sage Grouse hens in Oregon. J. Range Manage. 47:114-118.

Batterson, W. M., and W. B. Morse. 1948. Oregon Sage Grouse. Oregon Game Comm., Portland. Oregon Fauna Serv. 1.

Baxter, R. J. 2007. The ecology of translocated greater sage-grouse in Strawberry Valley, Utah. M.Sc. thesis, Brigham Young University,

Bean, R. W. 1941. Life history studies of the Sage Grouse (Centrocercus urophasianus) in Clark County, Idaho. B.S. thesis, Utah State Agric. Coll., Logan.

Beck, T. D. I., and C. E. Braun. 1978. Weights of Colorado Sage Grouse. Condor. 80:241-243.

Beck, T. D. I., R. B. Gill, and C. E. Braun. 1975. Sex and age determination of Sage Grouse from wing characteristics. Colo. Div. Game, Fish and Parks, Denver. Game Info. Leafl. 49.

Berry, J. D., and R. L. Eng. 1985. Interseasonal movements and fidelity to seasonal use areas by female Sage Grouse. J. Wildl. Manage. 49:237-240.

Bradbury, J. W., and R. M. Gibson. 1983. Leks and mate choice. Pp. 109-138 in Mate choice (P. Bateson, ed.). Cambridge Univ. Press, Cambridge.

Braun, C. E. 1984. Attributes of a hunted Sage Grouse population in Colorado, U.S.A. Int. Grouse Symp. 3:148-162.

Braun, C. E., and T. D. I. Beck. 1985. Effects of changes in hunting regulations on Sage Grouse harvest and populations. Game Harvest Manage. Symp. 3:335-343.

Byrne, M. W. 2002. Habitat use by female greater sage grouse in relation to fire at hart Mountain National Antelope Refuge, Oregon. M.Sc. thesis, Oregon State University.

Call, M. W., and C. Maser. 1985. Wildlife habitats in managed rangelands--the great basin of southeastern Oregon. Sage Grouse. U.S. Dep. Agric., For. Serv. Gen. Tech. Rep. PNW-187.

Connelly, J. W., Jr. 1982. An ecological study of Sage Grouse in southeastern Idaho. Ph.D. diss., Washington State Univ., Pullman.

Connelly, J. W., and I. J. Ball. 1978. The ecology of Sage Grouse on the Idaho National Engineering Laboratory Site. Pp. 224-234 in Ecological studies on the Idaho National Engineering Laboratory Site. Prog. Rep, Pocatello, ID.

Connelly, J. W., and O. D. Markham. 1983. Movements and radionuclide concentrations of Sage Grouse in southeastern Idaho. J. Wildl. Manage. 47:169-177.

Connelly, J. W., W. J. Arthur, and O. D. Markham. 1981. Sage Grouse leks on recently disturbed sites. J. Range Manage. 34:153-154.

Connelly, J. W., H. W. Browers, and R. J. Gates. 1988. Seasonal movements of Sage Grouse in southeastern Idaho. J. Wildl. Manage. 52:116-122.

Connelly, J. W., W. L. Wakkinen, A. P. Apa, and K. P. Reese. 1991. Sage Grouse use of nest sites in southeastern Idaho. J. Wildl. Manage. 55:521-524.

Connelly, J. W., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting by Sage Grouse in southeastern Idaho. Condor 95:1041-1043.

Connelly, J. W., K. P. Reese, W. L. Wakkinen, M. D. Robertson, and R. A. Fischer. 1994. Sage Grouse ecology. Study I: Sage Grouse response to a controlled burn. Idaho Dep. Fish and Game, Boise. P-R Proj. W-160-R-21.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies Report. Cheyenne, Wyoming.

Crawford, J. E., Jr. 1960. The movements, productivity, and management of Sage Grouse in Clark and Fremont counties, Idaho. M.S. thesis, Univ. Idaho, Moscow.

Crunden, C. W. 1963. Age and sex of Sage Grouse from wings. J. Wildl. Manage. 27:846-850.

Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1960. Seasonal movements and breeding behavior of Sage Grouse in Idaho. Trans. North Am. Wildl. Conf. 25:396-407.

Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of Sage Grouse in Idaho. J. Wildl. Manage. 27:811-841.

Drut, M. S. 1992. Habitat use and selection by sage grouse broods in southeastern Oregon. -M.Sc. thesis, Oregon State University, Corvallis, USA. 44 pp.

Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994a. Brood habitat use by Sage Grouse in Oregon. Great Basin Nat. 54:170-176.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994b. Diets and food selection of Sage Grouse chicks in Oregon. J. Range Manage. 47:90-93.

Dunn, P. O., and C. E. Braun. 1985. Natal dispersal and lek fidelity of Sage Grouse. Auk 102:621-627.

Dunn, P. O., and C. E. Braun. 1986a. Late summer-spring movements of juvenile Sage Grouse. Wilson Bull. 98:83-92.

Dunn, P. O., and C. E. Braun. 1986b. Summer habitat use by adult female and juvenile Sage Grouse. J. Wildl. Manage. 50:228-235.

Eng, R. L. 1952. A two-summer study of the effects on bird populations of chlordane bait and aldrin spray as used for grasshopper control. J. Wildl. Manage. 16:326-337.

Eng, R. L. 1955. A method for obtaining Sage Grouse age and sex ratios from wings. J. Wildl. Manage. 19:267-272.

Eng, R. L. 1963. Observations on the breeding biology of male Sage Grouse. J. Wildl. Manage. 27:841-846.

Eng, R. L. 1971. Two hybrid Sage Grouse x Sharp-tailed Grouse from central Montana. Condor 73:491-493.

Eng, R. L., and P. Schladweiler. 1972. Sage Grouse winter movements and habitat use in central Montana. J. Wildl. Manage. 36:141-146.

Enyeart, G. W. 1956. Responses of Sage Grouse to grass reseeding in the Pines Area, Garfield County, Utah. M.S. thesis, Utah State Agric. Coll., Logan.

Evans, C. C. 1986. The relationship of cattle grazing to Sage Grouse use of meadow habitat on the Sheldon National Wildlife Refuge. M.S. thesis, Univ. Nevada, Reno.

Fischer, R. A. 1994. The effects of prescribed fire on the ecology of migratory sage grouse in southeastern Idaho. - PhD thesis, University of Idaho, Moscow, USA. 150 pp.

Fischer, R. A., K. P. Reese, and J. W. Connelly. 1996a. An investigation on fire effects within xeric Sage Grouse habitat. J. Range Manage. 49:194-198.

Fischer, R. A., K. P. Reese, and J. W. Connelly. 1996b. Influence of vegetal moisture content and nest fate on timing of female Sage Grouse migration. Condor 98:868-872.

Fischer, R. A., W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1997. Effects of prescribed fire on movements of female Sage Grouse from breeding to summer ranges. Wilson Bull. 109:82-91.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1993. Nesting-area fidelity of Sage Grouse in southeastern Idaho. Condor 95:1038-1041.

Gibson, R. M. 1989. Field playback of male display attracts females in lek breeding Sage Grouse. Behav. Ecol. Sociobiol. 24:439-443.

Gibson, R. M. 1990. Relationships between blood parasites, mating success and phenotypic cues in male Sage Grouse Centrocercus urophasianus. Am. Zool. 30:271-278.

Gibson, R. M. 1992. Lek formation in Sage Grouse: the effect of female choice on male territorial settlement. Anim. Behav. 43:443-450.

Gibson, R. M. 1996a. A re-evaluation of hotspot settlement in lekking Sage Grouse. Anim. Behav. 52:993-1005.

Gibson, R. M. 1996b. Female choice in Sage Grouse: the roles of attraction and active comparison. Behav. Ecol. Sociobiol. 39:55-59.

Gibson, R. M., and J. W. Bradbury. 1985. Sexual selection in lekking Sage Grouse: phenotypic correlates of male mating success. Behav. Ecol. Sociobiol. 18:117-123.

Gibson, R. M., and J. W. Bradbury. 1987. Lek organization in Sage Grouse: variations on a territorial theme. Auk 104:77-84.

Gibson, R. M., J. W. Bradbury, and S. L. Vehrencamp. 1991. Mate choice in lekking Sage Grouse revisited: the roles of vocal display, female site fidelity, and copying. Behav. Ecol. 2:165-180.

Gill, R. B. 1965. Distribution and abundance of a population of Sage Grouse in North Park, Colorado. M.S. thesis, Colorado State Univ., Fort Collins.

Gill, R. B. 1967. Sex, age determination of Sage Grouse from plumage characteristics. Colorado Game, Fish and Parks Dep., Denver. Game Info. Leafl. 49.

Girard, G. L. 1937. Life history, habits and food of the Sage Grouse, Centrocercus urophasianus Bonaparte. Univ. Wyoming, Laramie. Publ. 3.

Gray, G. M. 1967. An ecological study of Sage Grouse broods with reference to nesting, movements, food habits, and sagebrush strip spraying in the Medicine Lodge drainage, Clark County, Idaho. M.S. thesis, Univ. Idaho. Moscow.

Gregg, M. A. 1991. Use and selection of nesting habitat by sage grouse in Oregon. - M.Sc. thesis, Oregon State University, Corvallis, USA. 46 pp.

Gregg, M. A., J. A. Crawford, and M. S. Drut. 1993. Summer habitat use and selection by female Sage Grouse (Centrocercus urophasianus) in Oregon. Great Basin Nat. 53:293-298.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetative cover and predation of Sage Grouse nests in Oregon. J. Wildl. Manage. 58:162-166.

Griner, L. A. 1939. A study of the Sage Grouse (Centrocercus urophasianus), with special reference to life history, habitat requirements, and numbers and distribution. M.S. thesis, Utah State Agric. Coll., Logan.

Hanf, J. M., P. A. Schmidt & E. B. Groshens. 1994. Sage grouse in the high desert of central Oregon: results of a study, 1988-1993. - Bureau of Land Management. Portland, Oregon, USA. 67 pp.

Hausleitner, D. 2003. Population dynamics, habitat use and movements of greater sage-grouse in Moffat County, Colorado. - M.Sc. thesis, University of Idaho, Moscow, USA. 162 pp.

Heath, B. J., R. Straw, S. H. Anderson, J. Lawson & M. J. Holloran. 1998. Sage-grouse productivity, survival, and seasonal habitat use among three ranches with different

livestock grazing, predator control, and harvest management practices. - Project Completion Report, Wyoming Game and Fish Department, Cheyenne, USA. 71 pp.

Hofmann, L. A. 1991. The western Sage Grouse (Centrocercus urophasianus phaios) on the Yakima Training Center in central Washington. A case study of a declining species and the military. M.S. thesis, Central Washington Univ., Ellensburg.

Holloran, M. J. 1999. Sage grouse (*Centrocercus urophasianus*) seasonal habitat use near Casper, Wyoming. - M.Sc. thesis, University of Wyoming, Laramie, USA. 123 pp.

Hupp, J. W., and C. E. Braun. 1991. Geographical variation among Sage Grouse in Colorado. Wilson Bull. 103:255-261.

June, J. W. 1963. Wyoming Sage Grouse population measurement. Proc. West. Assoc. State Game and Fish Comm. 43:206-211.

Knerr, J. S., and T. A. Messmer. 2006. Greater sage-grouse (Centrocercus urophasianus) ecology in western Box Elder County, Utah. Report. Utah State University, Logan, UT.

Klebenow, D. A. 1969. Sage Grouse nesting and brood habitat in Idaho. J. Wildl. Manage. 33:649-662.

Klebenow, D. A. 1985. Habitat management for Sage Grouse in Nevada. World Pheasant Assoc. J. 10:34-46.

Klebenow, D. A., and G. M. Gray. 1968. Food habits of juvenile Sage Grouse. J. Range Manage. 21:80-83.

Klott, J. H., and F. G. Lindzey. 1990. Brood habitats of sympatric Sage Grouse and Columbian Sharp-tailed Grouse in Wyoming. J. Wildl. Manage. 54:84-88.

Klott, J. H., R. B. Smith & C. Vullo. 1993. Sage grouse habitat use in the Brown's Bench area of south-central Idaho. - United States Department of Interior, Bureau of Land Management, Idaho State Office, Technical Bulletin 93-4, Boise, Idaho, USA. 14 pp.

Lords, J. L. 1951. Distribution, ecology, and population dynamics of the Sage Grouse in Utah. M.S. thesis, Univ. Utah, Salt Lake City.

Lyon, A. G. 2000. The potential effects of natural gas development on sage grouse near Pinedale, Wyoming. - M.Sc. thesis, University of Wyoming, Laramie, USA. 121 pp.

Martin, N. S. 1965. Effects of sagebrush manipulation on Sage Grouse. M.S. thesis, Montana State Univ., Bozeman.

Martin, N. S. 1970. Sagebrush control related to habitat and Sage Grouse occurrence. J. Wildl. Manage. 34:313-320.

Martin, N. S. 1976. Life history and habitat requirements of Sage Grouse in relation to sagebrush treatment. Proc. West. Assoc. State Game and Fish Comm. 56:289-294.

Martin, R. C. 1990. Sage Grouse responses to wildfire in spring and summer habitats. M.S. thesis, Univ. Idaho, Moscow.

Musil, D. D., J. W. Connelly, and K. P. Reese. 1993. Movements, survival, and reproduction of Sage Grouse translocated into central Idaho. J. Wildl. Manage. 57:85-91.

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 Nat. 54:228-233.

Myers, O. B. 1992. Sage Grouse habitat enhancement: effects of sagebrush fertilization. Ph.D. diss., Colorado State Univ., Fort Collins.

Nelson, O. C. 1955. A field study of Sage Grouse in southeastern Oregon with special reference to reproduction and survival. M.S. thesis, Oregon State Coll., Corvallis.

Oakleaf, R. J. 1971. Relationship of Sage Grouse to upland meadows in Nevada. M.S. thesis, Univ. Nevada, Reno.

Oyler-McCance, S. J., S. E. Taylor, T. W. Quinn. 2005. A multilocus population genetic survey of the greater sage-grouse across their range. Molecular Ecology 14:1293–1310.

Oyler-McCance, S. J., N. W. Kahn, K. P. Burnham, C. E. Braun, T. W. Quinn. 1999. A population genetic comparison of large- and smallbodied sage-grouse in Colorado using microsatellite and mitochondrial DNA markers. Molecular Ecology, 8, 1457–1465.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Sage Books, Inc., Denver, CO.

Petersen, B. E. 1980. Breeding and nesting ecology of female Sage Grouse in North Park, Colorado. M.S. thesis, Colorado State Univ., Fort Collins.

Popham, G. P. & R. J. Gutiérrez. 2003. Greater sage-grouse *Centrocercus urophasianus* nesting success and habitat use in northeastern California. - Wildlife Biology 9:327-334.

Pyle, W. H., and J. A. Crawford. 1996. Availability of foods of Sage Grouse chicks following prescribed buring in sagebrush-bitterbrush. J. Range Manage. 49:320-324.

Pyrah, D. B. 1954. A preliminary study toward Sage Grouse management in Clark and Fremont Counties based on seasonal movements. M.S. thesis, Univ. Idaho, Moscow.

Pyrah, D. B. 1963. Sage Grouse investigations. Idaho Fish and Game Dep., Boise. P-R Proj. W-125-R-2.

Rasmussen, D. I., and L. A. Griner. 1938. Life history and management studies of the Sage Grouse in Utah, with special reference to nesting and feeding habits. Trans. North Am. Wildl. Conf. 3:852-864.

Remington, T. E., and C. E. Braun. 1988. Carcass composition and energy reserves of Sage Grouse during winter. Condor 90:15-19.

Robertson, M. D. 1991. Winter ecology of migratory Sage Grouse and associated effects of prescribed fire in southeastern Idaho. M.S. thesis, Univ. Idaho, Moscow.

Rogers, G. E. 1964. Sage Grouse investigations in Colorado. Colorado Game, Fish and Parks Dep., Denver. Tech. Pub. No. 16.

Rothenmaier, D. 1979. Sage Grouse reproductive ecology: breeding season movements, strutting ground attendance and site characteristics, and nesting. M.S. thesis, Univ. Wyoming, Laramie.

Savage, D. E. 1968. The relationship of Sage Grouse to upland meadows in Nevada. M.S. thesis, Univ. Nevada, Reno.

Schoenberg, T. J. 1982. Sage Grouse movements and habitat selection in North Park, Colorado. M.S. thesis, Colorado State Univ., Fort Collins.

Schroeder, M. A. 1997. Unusually high reproductive effort by Sage Grouse in a fragmented habitat in north-central Washington. Condor 99:933-941.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. Diebert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson & S. J. Stiver. 2004. Distribution of sage-grouse in North America. - Condor 106: 363-376.

Sime, C. A. 1991. Sage Grouse use of burned, non-burned, and seeded vegetation on the Idaho National Engineering Laboratory, Idaho. M.S. thesis, Montana State Univ., Bozeman.

Slater, S. J. 2003. Sage-grouse (*Centrocercus urophasianus*) use of different-aged burns and the effects of coyote control in southwestern Wyoming. - M.Sc. thesis, University of Wyoming, Laramie, USA. 177 pp.

Smith, J. T. 2003. Greater sage grouse on the edge of their range: leks and surrounding landscapes in the Dakotas. M.Sc. thesis, South Dakota State University, Brookings, South Dakota.

Stanton, D. C. 1958. A study of breeding and reproduction in a Sage Grouse population in southeastern Idaho. M.S. thesis, Univ. Idaho, Moscow.

Sveum, C. M. 1995. Habitat selection by Sage Grouse hens during the breeding season in south-central Washington. M.S. thesis, Oregon State Univ., Corvallis.

Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998a. Nesting habitat selection by Sage Grouse in south-central Washington. J. Range Manage. 51:265-269.

Sveum, C. M., J. A. Crawford, and W. D. Edge. 1998b. Use and selection of brood-rearing habitat by Sage Grouse in south central Washington. Great Basin Nat. 58:344-351.

Taylor, S. E., and J. R. Young. 2006. A comparative behavioral study of three greater sage-grouse populations. Wilson Journal of Ornithology 118:36-41.

Wakkinen, W. L. 1990. Nest site characteristics and spring-summer movements of migratory Sage Grouse in southeastern Idaho. M.S. thesis, Univ. Idaho, Moscow.

Wakkinen, W. L., K. P. Reese, and J. W. Connelly. 1992. Sage Grouse nest locations in relation to leks. J. Wildl. Manage. 56:381-383.

Wallestad, R. O. 1971. Summer movements and habitat use by Sage Grouse broods in central Montana. J. Wildl. Manage. 35:129-136.

Wallestad, R. O. 1975. Life history and habitat requirements of Sage Grouse in central Montana. Montana Dep. Fish, Game, and Parks, Helena.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of Sage Grouse hens in central Montana. J. Wildl. Manage. 38:630-633.

Wallestad, R. O., and P. Schladweiler. 1974. Breeding season movements and habitat selection of male Sage Grouse. J. Wildl. Manage. 38:634-637.

Welch, B. L., F. J. Wagstaff, and R. L. Williams. 1990. Sage Grouse status and recovery plan for Strawberry Valley, Utah. U.S. Dep. Agric., For. Serv. Res. Pap. INT-430.

Welch, B. L., F. J. Wagstaff, and J. A. Roberson. 1991. Preference of wintering Sage Grouse for big sagebrush. J. Range Manage. 44:462-465.

Welch, B. L., C. L. Cox, and T. K. Sales. 1995. Strutting sounds and strutting posturing of two Utah Sage Grouse populations. U.S. Dep. Agric., For. Serv. Res. Pap. INT-RP-485.

Wik, P. A. 2002. Ecology of greater sage-grouse in south-central Owyhee County, Idaho. - M.Sc. thesis, University of Idaho, Moscow, USA. 141 pp.

Wiley, R. H., Jr. 1973. The strut display of male Sage Grouse: a "fixed" action pattern. Behavior 47:129-152.

Young, J. R. 1994. The influence of sexual selection on phenotypic and genetic divergence among Sage Grouse populations. Ph.D. diss., Purdue Univ., West Lafayatte, IN.

Young, J. R., J. W. Hupp, J. W. Bradbury, and C. E. Braun. 1994. Phenotypic divergence of secondary sexual traits among Sage Grouse, Centrocercus urophasianus, populations. Anim. Behav. 47:1353-1362.

Zablan, M. A. 1993. Evaluation of Sage Grouse banding program in North Park, Colorado. M.S. thesis, Colorado State Univ., Fort Collins.

Zunino, G. W. 1987. Harvest effect on Sage Grouse densities in northwest Nevada. M.S. thesis, Univ. Nevada, Reno.