

Geographic variation among Sage Grouse in Colorado.—Sage Grouse (*Centrocercus urophasianus*) occur only in the sagebrush (*Artemisia*) ecosystem of western North America. The species is entirely dependent upon sagebrush for seasonal cover and winter forage (Eng and Schladweiler 1972, Wallestad 1975, Remington and Braun 1985), and except during summer, does not occur in areas where sagebrush is absent. Geologic features, areas of unsuitable soil, and natural and human perturbations have created discontinuities in the sagebrush ecosystem. Consequently, the distribution of Sage Grouse is not continuous (Fig. 1), and some populations are separated by areas of unsuitable habitat. Morphological differences may exist among allopatric populations of Sage Grouse if areas of unsuitable habitat have created barriers to gene flow.

In Colorado, Sage Grouse occur in several montane basins. Typically, sagebrush dominates the basin floors. The surrounding mountains are dominated by subalpine or alpine vegetation that may inhibit movement of Sage Grouse. Sage Grouse wings obtained from hunters suggested that Sage Grouse in the Gunnison Basin (Gunnison and Saguache counties) in southern Colorado were smaller than grouse in other populations in the state (Braun, unpubl. data). To determine if phenotypic differences existed among allopatric populations, we compared morphological features of Sage Grouse in the Gunnison Basin to those of Sage Grouse in North Park (Jackson County) in northern Colorado. Because both populations occur within the range of *C. u. urophasianus* (Aldrich 1963), phenotypic differences could indicate that subspecific classification of Sage Grouse should be reevaluated.

Methods.—Both study areas are montane basins in which sagebrush dominates large areas (>1600 km²) between 2300 and 2900 m in elevation (Beck 1977, Hupp and Braun 1989a). Surrounding mountains are approximately 3100 to 4200 m in elevation. The two populations are about 200 km apart, although Sage Grouse occupy other montane basins between North Park and the Gunnison Basin.

Morphological measures were obtained from two sources in each population for four categories of age and sex; adult (>21 months of age), yearling (9–11 months of age), males, and females. The first was a sample of 97 adult males collected on leks from 1984 to 1986 for analysis of body composition (Hupp and Braun 1989a). With the exception of 1986, adult males were collected in time periods that corresponded to early and late courtship in April and May, respectively. Data for other categories of sex and age were from individuals trapped, marked, and released between March and June, 1983–1985 in North Park and 1984–1985 in the Gunnison Basin. Birds were usually trapped by spotlighting on or near leks (Giesen et al. 1982).

We measured live body mass (± 5 g) and body mass minus ingesta in the digestive tract of collected males. We also measured lengths of the tarsus (base of the middle toe to the proximal end of the tarsus), culmen (straight line from tip of the upper mandible to the insertion of feathers above the mandible), and carpal (wrist to tip of the longest primary with the wing slightly flattened). We recorded live body mass of females and yearling males that were captured and marked. We also measured carpal, tarsus, and culmen lengths of females and yearling males captured in the Gunnison Basin, and also obtained the same data from a small sample of yearling males collected on leks in North Park during April 1984. Carpal lengths of females and yearling males in North Park were measured in 1983.

Body mass of adult male Sage Grouse varies both seasonally and annually due to fluctuations in lipid reserves (Beck and Braun 1978, Hupp and Braun 1989b). Comparisons of body mass of adult males in different populations should be made cautiously to insure that temporal variation is not mistaken for geographic differences. We evaluated within- and



FIG. 1. Current distribution of Sage Grouse in North America (Western States Sage Grouse Comm. 1985:19).

among-year variation of morphological features of adult males. We used analysis of variance (ANOVA) to test for differences between early and late periods of courtship (nested within years and populations) for those years (1984–1985) in which birds were collected in the two time periods. Data from different collection periods were pooled within years when analyses indicated no differences. A second ANOVA assessed differences among years (1984–1986, nested within populations) and between populations.

Morphological features of female and yearling male Sage Grouse were compared between populations by Mann-Whitney tests (Conover 1980:216) due to small sample sizes in the Gunnison population. We pooled data among years because of small sample sizes and made no attempt to assess variation within or among years for females and yearling males.

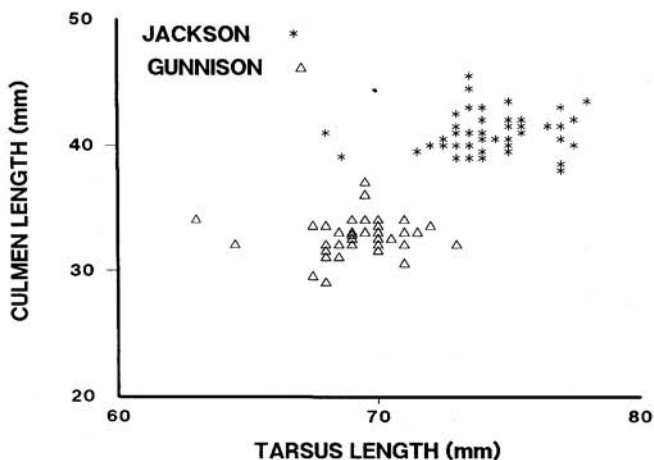


FIG. 2. Comparative tarsus and culmen lengths of 97 adult male Sage Grouse in Gunnison and Jackson counties, Colorado, 1984–1986. Some points represent >one individual.

Results.—There were no differences ($P > 0.11$) in morphological features of adult males between early and late periods of courtship in 1984 and 1985. Because morphological characteristics did not vary between collection periods, data from adult males were pooled within years in each population.

Morphological features of adult males differed ($P < 0.0001$) between populations (Table 1). Body mass (minus ingesta) differed ($P = 0.003$) among years but in each year adult males in the Gunnison population weighed an average of 27% (688–736 g) less than adult males in North Park (Table 1). Body mass with ingesta was 26–28% (788–818 g) less for males in the Gunnison Basin. Carpal lengths also differed among years ($P < 0.001$) but were 10–12% shorter for adult males in Gunnison. There were no annual differences in tarsus and culmen lengths ($P = 0.22$ and 0.38 , respectively). Tarsus and culmen lengths (pooled among years) were 7% and 23% shorter, respectively for males in the Gunnison Basin. A bivariate plot of culmen vs tarsus lengths indicated virtually complete separation between populations (Fig. 2).

Differences in body size were also apparent among females and yearling males (Table 2). Among these categories of age and sex, average live mass of Gunnison Sage Grouse was 26–30% lighter and carpal lengths were 8–11% shorter ($P < 0.001$) than for grouse in Jackson County. Tarsus and culmen lengths of yearling males were 8% and 20% shorter ($P < 0.002$) respectively, for grouse in the Gunnison Basin.

We examined data from other populations in Colorado to learn if morphological features of Sage Grouse in other areas more closely resembled grouse in North Park or the Gunnison Basin or if intermediate forms existed. Data on body mass were not available for most populations. However, measures of primary lengths of hunter-shot birds were available from seven areas of the state (Braun, unpubl. data). We compared average lengths of the outer and inner two primaries of adults of each sex with the Student-Newman-Keuls procedure. The primaries of both sexes were shorter ($P < 0.05$) in the Gunnison population relative to other areas. Primary lengths of females in other populations were similar to those of grouse in North Park. Primaries of males in Moffat County and the Piceance Basin were

TABLE 1
MORPHOLOGICAL MEASURES ($\bar{x} \pm SD$) OF ADULT MALE SAGE GROUSE IN JACKSON AND GUNNISON COUNTIES, COLORADO, APRIL AND MAY, 1984-1986

Area	Year	N	Live mass (g)	Carcass mass (g)*	Tarsus (mm)	Culmen (mm)	Carpal (mm)
Jackson	1984	20	2885 ± 188	2561 ± 164	73.8 ± 2.6	41.0 ± 1.7	339 ± 8.0
	1985	20	2903 ± 156	2676 ± 150	74.5 ± 1.6	41.1 ± 1.5	340 ± 6.5
	1986	10	3005 ± 135	2718 ± 159	75.4 ± 1.6	41.0 ± 1.6	344 ± 5.8
Gunnison	1984	19	2070 ± 133	1873 ± 124	69.5 ± 1.1	32.9 ± 1.9	299 ± 5.8
	1985	18	2085 ± 133	1964 ± 101	68.9 ± 1.9	31.9 ± 1.2	304 ± 6.2
	1986	10	2217 ± 77	1982 ± 78.9	69.0 ± 2.3	32.8 ± 0.8	311 ± 2.6

* Live mass minus ingesta in the digestive tract.

TABLE 2
MORPHOLOGICAL MEASURES ($\bar{x} \pm SD$) OF YEARLING MALE AND FEMALE, AND ADULT FEMALE SAGE GROUSE TRAPPED AND COLLECTED IN JACKSON AND GUNNISON COUNTIES, COLORADO 1983-1985

Age and sex	Area	Live mass (N)	Carpal (N)	Tarsus (N)	Culmen (N)
Yearling male	Jackson	2531 ± 182 (260)	328 ± 10 (151)	73.8 ± 3.8 (6)	38.9 ± 2.0 (6)
	Gunnison	1778 ± 133 (33)	293 ± 11 (35)	67.8 ± 2.0 (35)	31.1 ± 1.6 (35)
Yearling female	Jackson	1475 ± 118 (168)	277 ± 5 (29)	—	—
	Gunnison	1067 ± 77 (5)	251 ± 5 (5)	58.1 ± 1.2 (5)	27.8 ± 0.8 (5)
Adult female	Jackson	1626 ± 114 (143)	284 ± 6 (35)	—	—
	Gunnison	1210 ± 81 (13)	260 ± 9 (13)	58.6 ± 2.2 (13)	27.5 ± 1.2 (13)

TABLE 3
 SPRING (FEB.–MAY) BODY MASS (KG) OF ADULT MALE SAGE GROUSE IN WESTERN NORTH AMERICA

Location	Source	Body mass (N)
Gunnison Co., Colorado	This study	2.1 (47)
Jackson Co., Colorado	This study	2.9 (50)
Jackson Co., Colorado	Beck and Braun (1978)	3.2 (465)
Moffat Co., Colorado	Braun (unpubl. data)	2.8 (39)
Eastern Idaho	Dalke et al. (1963)	2.5 (25)
Eastern Idaho	Autenrieth (1981)	2.6 (10)
Eastern Idaho	Autenrieth (1981)	2.5 (11)
Central Montana	Wallestad (1975)	2.9 (80)
Central Montana	Eng (1963)	2.9 (28)
Southwest Wyoming	Patterson (1952)	2.7 (31)

slightly shorter than those of birds in North Park but longer than those of males in the Gunnison Basin.

Discussion.—A seasonal difference in body mass was less apparent in our sample than in the larger sample of Beck and Braun (1978). However, in both populations, body mass changed annually. Winter severity affects body condition of Sage Grouse and may cause body mass to vary. The winter of 1983–1984 was especially severe in Colorado, and lipid reserves (Hupp and Braun 1989b) and body mass of adult males were lower than in other years. Carpal length also varied among years and suggests that growth and wear of Sage Grouse remiges may be influenced by environmental conditions (Pehrsson 1987).

We accounted for temporal differences in morphological measures of adult males and found the magnitude of variation within a population was much less than the difference between the two populations. We were unable to assess temporal differences in morphological measures for other categories of age and sex. However, differences between areas for adult females and yearlings of both sexes were comparable to those observed for adult males. Sage Grouse in all sex and age categories were significantly smaller in the Gunnison Basin than in North Park. Based on wing measurement data, Gunnison Sage Grouse are also smaller than grouse in other studied populations in Colorado. Comparisons based on primary lengths should be interpreted cautiously due to small sample sizes in some areas, and because primary length can vary among years (Table 1). However, these results suggest that Sage Grouse in other studied regions of Colorado most closely resemble birds in the North Park population and that intermediate forms do not occur.

We compared our data on body mass of adult males with that from studies of *C. u. urophasianus* in other regions (Table 3). Differences were apparent among regions, although we do not have estimates of variance for most populations. We could not account for temporal variation in estimates from other states; however, these data suggest that adult male Sage Grouse in the Gunnison Basin weighed approximately 400–800 g less than males in other populations of *C. u. urophasianus*.

In addition to the difference in body size that we observed between North Park and the Gunnison Basin, J. R. Young (unpubl. data) noted that acoustical and visual components of male displays on leks differed between these two populations. Acoustical elements of male displays in North Park were similar to those of populations in Montana and Wyoming

(Wiley 1973) and California (Gibson and Bradbury 1985), while displays of males in the Gunnison Basin differed from other studied populations.

The phenotypic differences of Sage Grouse in the Gunnison Basin are of interest, given the relatively close proximity (<100 km) of larger-bodied populations. Smaller body size of Sage Grouse in the Gunnison Basin may be due to random divergence of a genetically isolated population. We do not know if the Gunnison population is truly insular. While mountains surrounding the Gunnison Basin may create a barrier to gene flow, Sage Grouse have been observed in alpine areas (Hoffman and Cade 1982). Gene flow may occur between the Gunnison Basin and other unstudied populations that as a group are isolated from larger-bodied Sage Grouse.

We also do not know if there is an adaptive significance to smaller body size of Sage Grouse in the Gunnison Basin. It is unlikely that variation in body size is due to climatic differences between North Park and the Gunnison Basin as seasonal mean temperatures and precipitation are similar between areas (Natl. Oceanic and Atmos. Admin. 1983-1986). Differences in body size may have a nutritional basis as Sage Grouse in North Park and the Gunnison Basin feed on different subspecies of sagebrush that have dissimilar chemical composition (Remington and Braun 1985, Hupp 1987).

Insular populations of Sage Grouse may exist if individuals are unlikely to cross large areas that lack suitable sagebrush habitat. Morphologic divergence of isolated populations is possible. Populations in the southern portion of the Sage Grouse range have been studied less and appear to be more fragmented than populations in northern areas (Fig. 1). Morphological features and genetic divergence of populations of Sage Grouse in southern Utah and southwestern Colorado need to be examined and the extent of geographic variation determined for this species.

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