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Body mass and primary molt patterns of Greater Sage-Grouse in Colorado

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Abstract.—Patterns in body mass and molt provide useful information about how birds interact with their environment and act as potential explanatory variables in behavioral and demographic differences among sex and age classes. We collected population data for Greater Sage-Grouse (*Centrocercus urophasianus*) in Jackson and Moffat counties, Colorado, from 1973 to 1993 prior to consideration of federal listing of the species under the Endangered Species Act. Using spotlights and long-handled nets, we located and captured Greater Sage-Grouse while they roosted (primarily at night). Each captured bird was banded and released near the site of capture. We recorded the molt status of the primary flight feathers (1–10) and measured body mass. Most birds were captured prior to and during breeding (March–May) and during the brood-rearing period (July–September). Replacement of primary (P) flight feathers was initiated in May, starting with the first primary (P1), and was completed at the last primary (P10) by late September for adult (ASY) and subadult (SY) males, and by October for hatch-year males (young of the year, HY). Adult and subadult females did not replace primary flight feathers until after nesting was completed, starting in June. Primaries 1–3 were replaced within a week of the hen leaving the nest site, with or without chicks. Primary replacement then was similar to that of adult and subadult males and was completed before early October. A few late-nesting hens retained P10 and P9 into early October. Young of the year rarely replaced juvenal P9 and P10 in the year of hatching. Body mass of males peaked ($\bar{x}$ = 3000 g for adults, and 2200 g for yearlings) in March–April when birds were primarily feeding on sagebrush and then decreased to late May and reached seasonal lows ($\bar{x}$ = 2200 g) in July–August. Mass of females peaked in April ($\bar{x}$ = 1640 g) and decreased to 1250 g in August.

Resumen.—Los patrones de muda y cambios en masa corporal aportan información útil sobre cómo las aves interactúan con su entorno, además de servir como posibles variables explicativas en las diferencias demográficas y de comportamiento según el género y la edad. Entre 1973 y 1993, recolectamos datos sobre la población del urogallo de las artemisas (*Centrocercus urophasianus*) en los condados de Jackson y Moffat, Colorado, antes de que esta especie se incluyera en la lista federal de Especies en Peligro de Extinción. Se localizaron y capturaron urogallos de las artemisas en sus nidos, principalmente de noche, utilizando reflectores y redes de mango largo, posteriormente fueron anillados y liberados cerca del sitio de captura. Registramos el estado de la muda de las plumas primarias de vuelo (1–10) y la masa corporal. La mayoría de las aves fueron capturadas antes y durante el período de reproducción (marzo–mayo) y durante el período de crianza (julio–septiembre). El reemplazo (muda) de las plumas primarias (P) de vuelo se inició en mayo, comenzando con la primera pluma primaria (P1) y se completó con la última pluma primaria (P10) a fines de septiembre en los machos adultos (ASY, por sus siglas en inglés) y subadultos (SY, por sus siglas en inglés). Mientras que la muda del plumaje de los machos menores de un año (nacidos en el último año, HY, por sus siglas en inglés) se completó en octubre. Las hembras adultas y subadultas no reemplazaron sus plumas primarias de vuelo hasta completar el período de anidación (a partir de junio). Las plumas primarias 1–3 se reemplazaron durante la semana posterior a que la gallina abandonara el nido, con o sin polluelos. La muda fue similar a la de los machos adultos y subadultos y se completó durante los primeros días de octubre. Algunas hembras que anidaron tardiamente retuvieron las últimos plumas P10 y P9 hasta principios de octubre. Las crías menores a un año rara vez reemplazaron sus plumas P9 y P10 durante el año en el que eclosionaron. La masa corporal de los machos alcanzó su punto máximo (promedio = 3000 g en adultos, 2200 g en los jóvenes) entre marzo y abril, cuando se alimentaron principalmente en las artemisas y fue disminuyendo hacia finales de mayo hasta alcanzar los mínimos estacionales (promedio = 2200 g) entre julio y agosto. La masa corporal de las hembras alcanzó su punto máximo en abril (promedio = 1640 g) y disminuyó a 1250 g en agosto.

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Greater Sage-Grouse (*Centrocercus urophasianus*) (hereafter sage-grouse) historically were widely distributed in western North America (Schroeder et al. 2004). They were once a major component of the avifauna of the sagebrush (*Artemisia* spp.) steppe but have been decreasing in abundance and distribution for many years (Connelly and Braun 1997, Braun 1998). Sage-grouse are sexually dimorphic and both females and males can be sexually mature as yearlings (SY) (the spring after hatching) (Dalke et al. 1963, Eng 1963). Females are more common in the yearling and adult (ASY) age classes, likely because of differences in survival between sexes (Swenson 1986, Braun et al. 2015).

Male sage-grouse are markedly larger than females and may have energy constraints for molting during breeding that are different from those of females. Generally, body mass of birds is reduced during molt, and the energy costs of avian molt are well documented (Swaddle and Witter 1997, Rohwer et al. 2009). Sage-grouse have been studied intensively throughout their range using capture-recapture and radio-telemetry monitoring methodologies. But data on the timing of gain and loss in body mass has not been related to timing of breeding and molt of primary flight feathers by sex or age class. Data from banding studies have revealed that differences in survival and productivity depend largely on the demographic age and sex class to which individuals belong, with males having lower survival than females (Zablan et al. 2003, Hagen et al. 2018). The ability to accurately classify age of captured grouse depends heavily on molt patterns (breeding-age classes), while mass is distinctly different and useful for accurately classifying sex. Thus, understanding molt and body mass patterns is also important from an applied standpoint, as reported also by Bendell (1955) for Sooty Grouse (*Dendragapus fuliginosus*) on Vancouver Island, British Columbia.

The overall general pattern of the primary flight feather molt of sage-grouse has been described (Eng 1955, Schroeder et al. 1999), as has body mass in localized areas (Beck and Braun 1978) and for young (HY) after hatching (Pyrah 1963, Petersen 1980). Replacement of primary flight feathers is sequential from inner to outer (Braun and Schroeder 2015), but timing of molt has not been compared with body mass.

Changes in body mass in relation to timing of flight feather replacement of sage-grouse are poorly reported in the literature. Beck and Braun (1978) reviewed the available literature at that time. Despite multiple studies that included capture and banding of sage-grouse reported in the literature (Knick and Connelly 2011), we found no recent published data on these biological parameters across the range of the species. We captured and banded sage-grouse in Jackson (Zablan et al. 2003) and Moffat counties (Dunn and Braun 1986, Hagen et al. 2018), Colorado, during 1973 through 1993 and recorded body mass and replacement of primary flight feathers. Changes in body mass were expected because of the breeding behavior of male sage-grouse and the egg development and nesting behavior of female sage-grouse. We hypothesized that knowledge of the replacement sequence of primary flight feathers would be helpful in understanding timing of changes in body mass as well as for identifying age classes of birds in the harvest (Dalke et al. 1963, Eng 1963) and in banding programs.

The objectives of this paper are (1) to document changes in body mass between age classes—i.e., from hatching (HY) to yearling (SY) and from yearling to adult (ASY)—by age and sex; and (2) to relate the timing of primary flight feather replacement to changes in body mass through a calendar year.

Methods

Study Areas

Sage-grouse were captured throughout north-central (Jackson County) and northwestern (Moffat County) Colorado from 1973 to 1993. Jackson County is east of the Continental Divide in an intermountain basin adjacent to Wyoming, with high (>3000 m) mountains to the south, east, and west. The area is characterized by low rolling benches with wet drainages and is dominated by sagebrush and native forbs and bunchgrasses (Beck 1977). Streamside areas, formerly dominated by willows (*Salix* spp.), have been mostly cleared and converted to native hay crops. The growing season is about 40 days, and there are no cultivated crops. Livestock production is the primary land use, with some areas affected by oil/gas/coal production. The area is generally at an elevation of 2200–2400 m.

Moffat County is in northwest Colorado, west of the Continental Divide, and is bordered by Utah on the west and Wyoming on the north. The area has low rainfall except at higher elevations near adjacent Utah and Wyoming. The growing season is sufficiently long for crops such as wheat, oats, barley, and alfalfa in low-elevation areas and along stream courses. The topography is rolling, with most of the native vegetation once dominated by sagebrush, native forbs, and bunchgrasses. Elevation varies from 1500 m along riverine systems to 2400 m near the higher forested areas (Braun et al. 2015). Sage-grouse historically occurred throughout the county, but their distribution is now highly fragmented by cultivated fields and areas used for coal and oil/gas production. All of the area is at least seasonally grazed by domestic livestock, and public lands are managed by the Bureau of Land Management for livestock grazing and energy development (coal, gas, and oil).

Captures

In January through March, sage-grouse were located at night using spotlights from vehicles along roads and trails where the birds had been observed foraging. Efforts from April into May focused on and near leks, and along trails where sage-grouse were known to roost at night. Brood-use areas near daily foraging sites were checked from July into September at night to locate hens with chicks as well as groups of males and unsuccessfully nesting hens. After being spotlighted while roosting, most birds were captured with long-handled nets as described by Giesen et al. (1982). Some birds were captured in spring and summer using cannon nets mounted on a vehicle (Lacher and Lacher 1964) or on the ground as described by Braun (1976) near livestock watering ponds or sites used for salting livestock. Some chicks and hens were captured in drive traps in meadows as reported by Patterson (1952).

Captured birds were placed separately in loose mesh burlap sacks until they were weighed on a balance or electronic scale. Age (HY, SY, or ASY) was assigned to each bird captured based on the appearance of primaries 9 and 10 in comparison to primaries 8–6 following Braun and Schroeder (2015). Primary flight feather replacement of primaries 1–10 of SY and ASY birds was checked and recorded as 0 (none replaced), 1, 2, etc., through primary 10, if P10 was being replaced (sage-grouse have 10 primary flight feathers). Chicks (HY) younger than 3–4 weeks of age were not banded because they were not able to retain a band. Age of chicks was based on retention of juvenile secondary (S)1 and replacement of juvenile primaries by adult primaries starting at primary 1. We examined replacement of juvenile secondary feathers until molt of S1, which was the last to be replaced (next to P1, which was the first primary flight feather to be replaced). Length of the most recently replaced growing primary was recorded for all chicks up to 1 September. Primary molt was checked for both wings if there were missing flight feathers.

Sage-grouse rarely were missing primary flight feathers from the normal sequence (starting at P1 and going through P10 for adults and yearlings). Gaps not in synchrony in the replacement sequence were thought to be the result of flying into a fence or power line or possibly encountering predators. We noted the few observations but did not include birds with obvious injuries in the data set.

Sex of adults and yearlings was based on size or, when in doubt, by length of primaries 10, 9, and 1 (Braun and Schroeder 2015). Sex of chicks in July and August was based on length of fully grown juvenile primaries or length of fully grown adult primaries starting at P1. All birds captured were released near the capture sites after processing.

Data were recorded and stored separately by area and by year. All values were entered into Microsoft Excel files, checked against the original data sheets, and sorted to identify problematic values. Those birds with values that could not be verified were deleted. Means and standard errors were calculated for body mass of each age and sex class.

Results

We recorded body mass (Fig. 1) and primary molt (Fig. 2) for 8705 sage-grouse captured in Jackson and Moffat Counties, Colorado, during 1973–1993. This total included 3008 adult (2+ years = ASY) and 2255 yearling (in first year of life = SY) males, 1063 adult (ASY) and 1009 yearling (SY) females, and 678 males and 692 females banded as young of the year (hatched after 1 June and captured prior to 1 November in their first year of life). Body

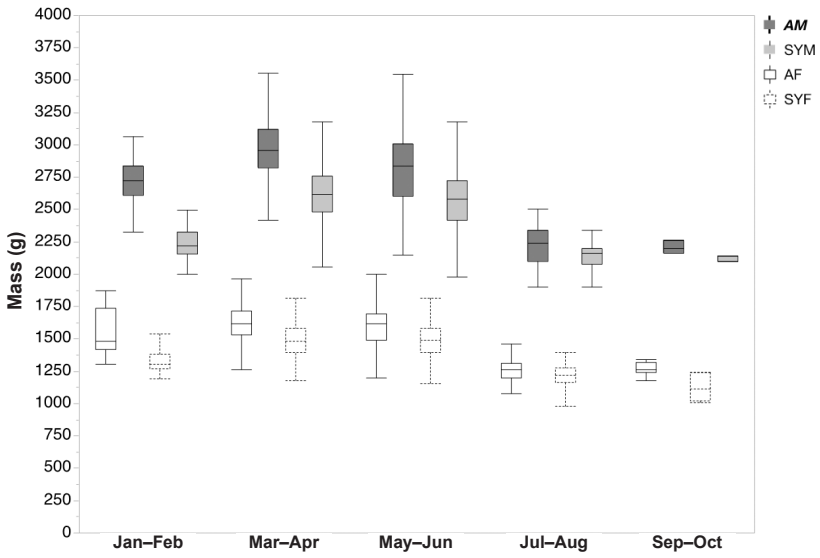

Fig. 1. Body mass (g) of adult and second-year (yearling) Greater Sage-Grouse in Colorado. Both males and females of each age class reach their peak body mass in spring (March–April). AM = adult male, SYM = second-year (yearling) male, AF = adult female, and SYF = second-year (yearling) female. Boxes indicate the 25th, 50th, and 75th percentiles. Whiskers indicate 10th and 90th percentiles.

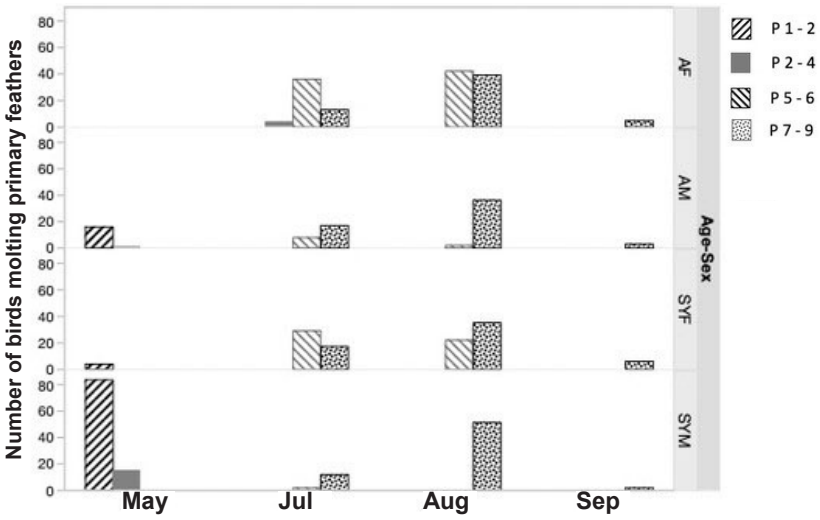

Fig. 2. Molt of adult and second-year (yearling) Greater Sage-Grouse in Colorado. AF = adult female, AM = adult male, SYF = second-year (yearling) female, and SYM = second-year (yearling) male. P = primary flight feather.

mass of chicks changes rapidly throughout the first 6 weeks after hatch, and averaging body mass across chicks of varying age would not be particularly meaningful. Therefore, we only report primary molt for chicks.

Body mass of adults and yearlings increased from January into April (Fig. 1), with females peaking slightly after males. Adult and SY males weighed an average of 2976 g (SD = 233 g, n = 2184) and 2617 g (SD = 229 g, n = 1662), respectively, in March–April. Adult and SY females weighed an average of 1628 g (SD = 142 g, n = 949) and 1496 g (SD = 133 g, n = 853), respectively, in March–April. The

gain in mass over winter was the result of males preparing for displaying (development of air sacs) on leks and females preparing for egg laying. There was no replacement of primary flight feathers during this period.

Sage-grouse did not initiate replacement (molt) of primary flight feathers until early to mid-May for adult and yearling males when most had ceased active display on leks (some were still loosely associated with leks depending upon weather conditions during the reproductive period). Thus, the general male replacement pattern was primaries 1–3 in mid- to late May (trapping was minimal in June), primaries 6–7 by late July, 7–8 by late August, 8–9 by mid-September, with complete replacement (P10) by the end of September (Fig. 2). Females did not start replacing primary flight feathers until they either hatched a clutch or had lost their nesting attempt and did not renest. However, we documented rapid replacement of primaries of unsuccessfully nesting hens in June and July (primaries 4–7) versus hens with chicks (primaries 1-2-3 in June), 4–8 in July, 5–8 in August, and 8–10 in September. We had few captures of sage-grouse in October–December.

Sage-grouse chicks are precocial but cannot fly at hatch. They have 8 short primary quills by day 2, and the growing juvenile primaries allow weak flight at day 10–14. Adult P1 replaces juvenile P1 at 21–24 days of age. Adult P2 emerges (quill) by 28–30 days of age, as does emergence of juvenile P9 followed by juvenile P10. Juvenile P9 and P10 are not completely fully grown until mid- to late September.

Chicks (HY) replaced primaries starting with P1 at 3 weeks of age and then at the rate of 1 primary every 7–10 days through P8. Primaries 9–10 of first-year sage-grouse normally are replaced while primaries 6–8 are actively growing. These 2 outer juvenal primaries are normally retained until late summer and fall of the next year. Replacement of primary flight feathers started for adult and yearling males in May with loss of P1 and proceeding to P2 and P3 in early June. Primary molt of yearlings slightly preceded that of adults. There was no replacement of primaries by females of either age class in May. Primary replacement started slightly earlier for yearling than for adult females, possibly because of nest failure. Primary 1 was replaced once hens had ceased nesting (defined as nest failure or successful completion of nesting and initiation of brood-rearing). Replacement of primaries 2 and 3 followed quickly and then at 10- to 14-day intervals during July and August. By early September, hens with broods were replacing primaries 6–7, while those captured without broods were replacing primaries 8–9. By mid-September, apparently broodless (i.e., captured at night without a brood) females were replacing primary 10 (full molt of all primaries).

Yearling males completed replacing P10 by 20–25 September (or even earlier), and those with fully completed primary flight feather molt could not be separated from adults. Adult males completed replacement of primary flight feathers by 15–20 September, slightly later than yearling males. Once primary 10 was replaced, adult and yearling males could not be distinguished.

Discussion

Body mass of all sage-grouse increased during winter (November to March) and was highest for adult males in early to mid-April. Body mass was highest for yearling males in mid- to late April, and for both adult (slightly earlier) and yearling females by late April to early May. These increases in body mass occurred when the diet was primarily sagebrush (Remington and Braun 1985, Hupp and Braun 1989) and birds were preparing for courtship and nesting (i.e., egg development and laying). There was no replacement of primary flight feathers during this period, consistent with the hypothesis that breeding and molt are usually mutually exclusive events (Payne 1972).

Replacement of primary flight feathers commenced at the end of the breeding period for all adult and yearling males (late May to early June) and for all adult and yearling females once nesting activities had ceased (early June to early July). Replacement of all primaries was in sequence from 1 through 10 and ended for males by late September and for females by early October, with few exceptions. Petrides (1945) reported that gallinaceous birds typically retain Juvenile P9 and 10 during the first prebasic molt (terminology follows Humphrey and Parkes 1959), but Wild Turkeys (*Meleagris gallopavo*) (reviewed

by Lewis 1967) do not. Schmutz and Hoffman (1991) reported that Wild Turkeys in Colorado did not uniformly retain Juvenile P9 and 10 through their first year and suggested that the variation between individuals might be related to body mass and possibly hatch dates, which are subject to proximate environmental factors. Molt and replacement of primary flight feathers of adult and yearling sage-grouse occurred as body mass decreased. Molt of primaries of all juveniles occurred as body mass increased. This is similar to what was reported for Sooty Grouse (Bendell 1955).

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