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ENDOGENOUS RESERVES OF ADULT MALE SAGE GROUSE DURING COURTSHIP[1]

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Abstract. Lipid reserves of 116 adult (>1 year of age) male Sage Grouse (*Centrocercus urophasianus*) were evaluated in two Colorado populations during lek attendance between 1983 and 1986. Lipid reserves following winters (November–March) with snowfalls <124 cm were larger ($P < 0.001$) than reserves following winters with snowfalls >160 cm. Lipid reserves during early courtship were larger than reserves during late courtship ($P < 0.001$). Males catabolized lipids during courtship but did not use breast muscle protein. Catabolism of lipids likely provides <5% of male energetic requirements during courtship. An adaptive advantage to fat deposition before breeding may exist if males primarily mobilize lipids during the peak period of female lek attendance when male reproductive success is determined, or during periods when thermoregulatory costs are high due to low ambient temperatures or wind.

Key words: Avian energetics; breeding behavior; Centrocercus urophasianus; *Colorado; lipids; Sage Grouse.*

INTRODUCTION

The energetic costs of reproduction are high in many avian species. Females may use endogenous reserves to meet energetic demands associated with follicle growth and incubation (Korschgen 1977, Drobney 1980, Ankney 1984). Males of some species also mobilize endogenous reserves during courtship or territory defense (Ankney 1977, 1984; Raveling 1979; Krapu 1981; Brittas 1984; Alisauskas and Ankney 1985; Krapu et al. 1985; Hohman 1986; Servello and Kirkpatrick 1988). However the proportion of male reproductive costs that may be met by use of endogenous reserves is poorly understood for most species.

Species of Tetraoninae that display on leks may provide insights regarding the relationships between male energetic demands and use of endogenous reserves during the breeding season. Elaborate courtship displays and prolonged periods of courtship in lek species (Hjorth 1970) likely result in high energetic costs among males. Endogenous reserves may be used to partially meet these demands. We are unaware of previous studies that examine endogenous reserves of male Tetraoninae during the period of lek display.

We examined fat reserves and breast muscle mass of adult male Sage Grouse (*Centrocercus urophasianus*) in two Colorado populations and tested the hypothesis that males used lipid and protein reserves during the period that they displayed on leks. We also compared differences in endogenous reserves among years to evaluate the effects of winter snow accumulations and ambient temperatures on lipid and protein deposition.

METHODS

We collected adult male Sage Grouse for whole carcass analysis of endogenous reserves. Males were trapped at night on or near leks (Giesen et al. 1982) in Jackson and Gunnison counties. The study areas were in northcentral and southwestern Colorado, respectively and both were high elevation (>2,000 m), sagebrush (*Artemisia*)-dominated intermontane basins. Study areas have been described by Beck (1977), Remington and Braun (1985), and Hupp and Braun (in press). Males were collected annually in Jackson County during two discrete sampling periods (early and late courtship) from 1983 th
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late courtship) from 1983 through 1985. Males in Gunnison County were collected during early and late courtship in 1984 and 1985. Sage Grouse in each population were collected only during early courtship in 1986. Sampling during early courtship occurred during the first 2 weeks that males consistently displayed on leks (usually between 1 and 15 April). This period was prior to or during peak female attendance. Severe winter weather in 1984 delayed courtship initiation in both populations; collection during early courtship did not occur until the final week of April. The late courtship sampling period was between 14 and 22 May in each year. Usually no more than two or three males were obtained from a single lek within a sampling period. Between eight and 10 adult males were collected in each sampling period during all years in both populations. We measured endogenous reserves from a total of 116 adult male Sage Grouse between 1983 and 1986. We assumed that our collection procedure was indiscriminate with regard to an individual's dominance on a lek and that the patterns of lipid use that we observed were a representative sample of population trends.

Following collection, males were weighed (±5 g) then frozen in sealed plastic bags. Before laboratory analysis, carcasses were thawed, then the feathers, head, tarsi, and wings distal from the carpals were removed and discarded. Breast muscles (pectoralis and supracoracoideus) on one side of the body were excised and weighed. Leg muscles (all muscles attached to the femur or tibiotarsus) were excised and weighed in 1985. Internal organs were also removed and weighed. Gut contents (ingesta in the esophagus, gizzard, intestines, and caeca) were removed, weighed, and discarded. Muscles and internal organs were returned to the carcass prior to homogenization in a commercial meat grinder. The homogenate was spread on aluminum foil and dried in a forced air oven at 80°C for 24 hr (Kerr et al. 1982). The dried carcass was further homogenized in a high speed Wiley Mill until it passed through a 2-mm screen. Lipids were extracted from 10-g subsamples of homogenate with diethyl ether for 6 hr in a soxhlet apparatus (Dobush et al. 1985, Remington and Braun 1988).

Lipid reserves were expressed as grams of fat, and as percent of live weight minus the weight of ingesta. Breast muscle mass (the combined weights of the pectoralis and supracoracoideus from one side of the body multiplied by 2) was used as an index of protein reserves. In Sage Grouse, breast muscles are probably the major source of labile protein due to the nonmuscular nature of the gizzard. Moisture content of breast muscles was relatively invariant ($\bar{x}$ = 73.6%, SE = 1.3, n = 10), therefore changes in breast muscle mass were probably indicative of protein mobilization.

Homogeneity of variances was evaluated via Bartlett's test (Zar 1984:181). Null hypotheses of no differences in lipid reserves and breast muscle mass among years (1983–1985) or courtship periods were tested using a two-way analysis of variance (courtship period nested in year) for each population. Sample sizes were similar among collection periods, thus analysis of variance was robust when variances were not homogeneous (Zar 1984:170). Multiple comparisons among all collection periods within a population were made with the Student-Newman-Keuls procedure.

RESULTS

In each population, lipid reserves of male Sage Grouse differed among years ($P < 0.001$) and between early and late courtship ($P < 0.001$). Lipid reserves declined during courtship in all years (Table 1). Lipid reserves of males in Jackson County were lower during early courtship in 1984 and 1986 than during the same period in other years (Table 1). Early courtship reserves of males in Gunnison County were low in 1984 relative to 1985 and 1986. Lipid reserves during late courtship were similar among years (Table 1) for both populations. Variance of lipid reserves was smaller ($P < 0.001$) during late courtship in both populations (Table 1).

In Jackson County, breast muscle mass differed slightly among years ($P = 0.06$) and between early and late courtship ($P = 0.09$). Breast muscle mass during early courtship in 1983 was high relative to other periods (Table 1) and likely accounts for most of the observed variation. Breast muscle mass of male Sage Grouse in Gunnison County did not differ between years ($P = 0.11$) or courtship periods ($P = 0.24$). Variances of breast muscle mass did not vary among collection periods ($P > 0.12$). Among Jackson County males, leg muscle mass ($\bar{x}$ = 123 g, SE = 2.8) during early courtship was similar ($P = 0.14$) to muscle mass during late courtship ($\bar{x}$ = 130 g, SE = 3.3). There were also no differences ($P = 0.94$) between early ($\bar{x}$ = 102 g, SE = 3.0) and late courtship ($\bar{x}$ = 102 g, SE = 2.0) leg

TABLE 1. Physical characteristics of adult male Sage Grouse during early vs. late courtship in Gunnison and Jackson counties, Colorado, 1983–1985.

County Year Period	n	Lipids (%)[a]		Lipids (g)		Breast muscle (g)[b]	
		$\bar{x}$[c]	SE	$\bar{x}$	SE	$\bar{x}$	SE
Jackson							
1983							
Early	9	5.4[1]	0.38	155[1]	10.8	654[1]	8.4
Late	10	1.1[2]	0.20	30[2]	5.3	612[1,2]	13.2
1984							
Early	10	2.3[3]	0.38	59[3]	10.6	597[2]	14.7
Late	10	0.8[2]	0.10	20[2]	3.1	614[1,2]	11.4
1985							
Early	10	5.5[1]	0.29	145[1]	7.6	608[1,2]	13.4
Late	10	0.5[2]	0.10	13[2]	2.3	607[1,2]	10.8
1986							
Early	10	3.6[4]	0.33	99[4]	9.4	653[1]	12.2
Gunnison							
1984							
Early	10	2.2[1]	0.44	42[1]	8.2	437[1]	11.7
Late	9	0.7[2]	0.10	12[2]	1.8	423[1]	7.7
1985							
Early	10	4.1[3]	0.25	82[3]	5.6	458[1]	12.6
Late	8	0.8[2]	0.10	16[2]	1.9	435[1]	8.7
1986							
Early	10	4.2[3]	0.32	82[3]	6.6	488[2]	5.6

[a] Lipids as percent of live weight minus weight of digestive tract contents.
[b] Combined weights of pectoralis and supracorecoideus from one side of breast × 2.
[c] Within populations (counties), means followed by different superscripts were significantly different ($P < 0.05$) from each other.

muscle mass among males from Gunnison County.

DISCUSSION

LIPID DEPOSITION AND WINTER SEVERITY

Lipid reserves at the beginning of courtship were apparently influenced by winter snowfall and ambient temperatures. In Jackson County, lipid reserves during early courtship were highest in 1983 and 1985 but were reduced in 1984. Lipid reserves of males in Gunnison County were also low in 1984. Deep snows (>50 cm) persisted from December 1983 through March 1984 in each study area and temperatures were below 30-year averages (Table 2). Increased thermoregulatory costs and reduced access to sagebrush forage likely resulted in lower lipid deposition during the 1984 winter. In Gunnison County, 93% of the sagebrush vegetation was covered by snow in January 1984 while in the milder 1985 and 1986 winters only 16–22% of sagebrush habitat was snow-covered (Hupp and Braun, in press). In Jackson County, Sage Grouse may have been forced to forage on a nutritionally inferior subspecies of big sagebrush (Remington and Braun 1985). Deep snows probably increased Sage Grouse locomotion costs during feeding. Distances between exposed plants increased in severe winters and, based on track observations in Gunnison County, Sage Grouse usually sank 5–10 cm into soft snow while foraging. Reduced endogenous reserves resulting from winter conditions that limit access to forage resources or increase thermoregulation costs have been observed in other avian species (Dugan et al. 1981, Mortensen et al. 1983, Whyte and Bolen 1984, Heitmeyer 1985).

Collections during early courtship were delayed in 1984 because males did not initiate display activities until late April. It is unlikely that reduced early courtship reserves in 1984 were an artifact of delayed sampling. Live weights of 20 adult males captured in Jackson County in early April ($\bar{x}$ = 2,764 g, SE = 57) were lower (P = 0.03) than live weights of 18 males captured or collected in the final week of the month ($\bar{x}$ = 2,926 g, SE = 46). It is doubtful that lipid reserves were larger in early April when body weights were lower. Delayed courtship in 1984 was likely

TABLE 2. Winter (Novembe
lipid reserves of adult male Sa
1983–1986.

Snowfall (cm)[a]	
Temperature departure (°C)	
Lipids (%[c])	

[a] Data are from National Oceanic and
[b] Snowfall accumulations in December
[c] Lipid reserves expressed as percent o

a response to deep snow co
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Lipid reserves of adult r
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USE OF LIPID RESERVES DURING COURTSHIP

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Use of lipids during cou
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sagebrush leaves were nor
that Sage Grouse consumed

late courtship in Gunnison and

Breast muscle (g)[b]	
$\bar{x}$	SE
654[1]	8.4
612[1,2]	13.2
597[2]	14.7
614[1,2]	11.4
608[1,2]	13.4
607[1,2]	10.8
653[1]	12.2
437[1]	11.7
423[1]	7.7
458[1]	12.6
435[1]	8.7
488[2]	5.6

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TABLE 2. Winter (November–March) snowfall and mean temperature departure from 30-year averages, and lipid reserves of adult male Sage Grouse during early courtship in Gunnison and Jackson counties, Colorado, 1983–1986.

	Jackson				Gunnison		
	1983	1984	1985	1986	1984	1985	1986
Snowfall (cm)[a]	124	163	102	166[b]	186	97	90
Temperature departure (°C)	1.2	−0.7	0.2	1.9	−3.1	1.7	2.3
Lipids (%[c])	5.4	2.3	5.5	3.6	2.2	4.1	4.2

[a] Data are from National Oceanic and Atmospheric Administration Monthly Climatological Data for Colorado, 1983–1986.
[b] Snowfall accumulations in December 1985 are not available for Jackson County.
[c] Lipid reserves expressed as percent of live weight minus weight of digestive tract contents.

a response to deep snow cover on leks. However the possibility that males postponed courtship due to poor physiological condition should also be considered.

Lipid reserves of adult male Sage Grouse in Jackson County were also low during early courtship in 1986. Heavy snow accumulations in November and December 1985 resulted in reduced lipid deposition among males in that population (Table 2). Winter conditions in Gunnison County during 1986 were not severe and early courtship lipid reserves were similar to reserves of males collected following the mild 1985 winter.

USE OF LIPID RESERVES DURING COURTSHIP

In both populations, male Sage Grouse used lipid reserves during courtship. Following mild winters, males in Jackson County mobilized 125–130 g of fat while Gunnison County males used an average of 66 g of lipids. The low mass of lipid reserves among males in Gunnison County reflected the smaller body size of Sage Grouse in that population (Hupp 1987). Reduction in live weight of males during courtship (Beck and Braun 1978) was attributable to loss of body fat.

Lipid reserves were more variable among males collected during the early part of courtship. Some males may have partially used lipids by the time they were collected during early courtship thus introducing greater variation to the sample. Also, individual birds may have differed in their abilities to accumulate fat during winter. Smaller variance at the end of courtship indicated that minimum levels of fat reserves were similar among males.

Use of lipids during courtship could not be attributed to dietary changes. Visual inspection of esophageal and gizzard contents indicated that sagebrush leaves were normally the only food that Sage Grouse consumed. Mobilization of lipids was probably a response to the energetic demands of courtship. Energetic demands of courtship among male Tetraoninae are potentially high. Vehrencamp et al. (in press) estimated that energetic costs of courtship in male Sage Grouse ranged between 2.0 times standard metabolic rate (SMR) for males that did not display on leks, to 4.0 times SMR for individuals that displayed and successfully mated. Daily energetic requirements of male Capercaillie (*Tetrao urogallus*) during courtship were 2.1 times SMR and were higher than winter existence requirements (Linden 1984). Invariant breast and leg muscle mass indicated that male Sage Grouse did not use protein reserves during courtship. During periods of high energetic demand, birds were more likely to mobilize lipids than protein (Reinecke et al. 1982, Mortensen et al. 1983, Whyte and Bolen 1984, Heitmeyer 1985).

THE ADAPTIVE SIGNIFICANCE OF MALE LIPID RESERVES

Among avian species, both the timing of lipid deposition and the size of reserves accumulated are believed to be adaptive (King 1972, Dawson and Marsh 1986, Lima 1986). The timing of lipid deposition among male Sage Grouse and the size of reserves accumulated may affect male fitness. Sage Grouse maintain fat reserves during winter (Remington and Braun 1988) and reserves of adult males are at their maximum size immediately prior to courtship. Maintenance of lipids prior to courtship may assure that endogenous reserves are available during an energetically demanding activity. Avian deposition of endogenous reserves prior to periods of high energetic demand has been widely observed (West and Meng 1968, Mortensen et al. 1983, Gauthier et al. 1984, Krapu et al. 1985, Mainguy and Thomas 1985, Vangilder et al. 1986).

The adaptive significance of the size of lipid

reserves accumulated prior to courtship is of interest. Lipid reserves of male Sage Grouse were not sufficiently large to meet a major proportion of the total energetic costs of courtship. Assuming a caloric conversion of 37.7 KJ/g lipid metabolized (Ricklefs 1974), Jackson and Gunnison county males obtained approximately 4,898 and 2,470 KJ of energy, respectively from lipid catabolism during courtship. Given the early courtship body mass in 1986, daily SMR requirements were approximately 599 and 494 KJ/day for Jackson and Gunnison county males, respectively (Zar 1968). Using the estimate of Vehrencamp et al. (in press) for energetic demands among displaying male Sage Grouse (approximately 4.0 times SMR), total energetic demands during a 6-week display period were approximately 100,632 and 82,992 KJ/male for Sage Grouse in Jackson and Gunnison counties, respectively. Therefore, fat catabolism could provide only a small proportion (<5%) of the total energetic needs of male Sage Grouse during the courtship period. Sage Grouse apparently meet most energetic requirements during courtship by exploiting exogenous forage resources.

An adaptive advantage to lipid deposition may exist even though fat reserves were not adequate to meet a large proportion of total energetic demands during courtship. Male Sage Grouse may mobilize lipids to meet energy requirements during short periods of high energetic demand. Periods of high energetic demand may occur during the relatively short (<1 week) peak of female attendance when males display intensively, or on days when cold temperatures or wind increase thermoregulatory costs. Although endogenous reserves are small, accumulation of lipids prior to breeding may be selectively favored if an individual's ability to display during a period of high energetic demand is influenced by the availability of fat reserves. The availability of fat reserves during peak female attendance may be especially important because male reproductive success is primarily determined during that period. An additional benefit to prebreeding lipid deposition may exist if male foraging time is reduced during female attendance, and males need to mobilize fat to counter a reduced intake of exogenous energy sources. Mobilization of lipids may not be synchronous among males in a population, and thus explain why mean weights of adult males diminish throughout much of the courtship season (Beck and Braun 1978).

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