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CARCASS COMPOSITION AND ENERGY RESERVES OF SAGE GROUSE DURING WINTER[1]

T. E. REMINGTON AND C. E. BRAUN
Colorado Division of Wildlife, Research Center, 317 West Prospect Road, Fort Collins, CO 80526

Abstract. Carcass composition of Sage Grouse (*Centrocercus urophasianus*) was measured to assess the size and variation of energy reserves during winter in North Park, Colorado. Fat content ranged from 0.8 to 8.4%. Adults had higher ($P = 0.001$) fat content than yearlings (4.7 vs. 2.9%); birds collected in 1982 had more ($P < 0.05$) fat than birds collected in 1981. Estimated fat content was higher ($P < 0.05$) when diethyl ether, rather than petroleum ether, was used as a solvent (4.0 vs. 3.6%). Fat comprised 85 to 93% of estimated energy reserves which equaled 9.6, 5.1, 7.0, and 5.3 times standard metabolic rate for adult and yearling males and adult and yearling females, respectively. All age and sex classes gained or maintained weight and fat over winter. Relatively small energy reserves of Sage Grouse are probably most important during breeding and nesting activities.

Key words: Sage Grouse; carcass composition; Centrocercus urophasianus; *Colorado; fat content; energy reserves; winter.*

INTRODUCTION

Avian energetic studies have demonstrated that birds can prepare for periods of high energy demand by accumulating reserves of lipids, glycogen, and labile protein. Lipids are the primary endogenous source of energy used by birds during periods of high energy demand such as migration (Odum and Connell 1956, King and Farner 1963, Blem 1976, McLandress and Raveling 1981), reproduction (Ankney and MacInnes 1978, Raveling 1979, Krapu 1981, Drobney 1982, Reinecke et al. 1982), or over winter (King and Farner 1966, Reinecke et al. 1982, Mortensen et al. 1983). Most grouse have relatively small energy reserves; during periods of high energy demand, energy balance is maintained by continuous feeding, large intakes, and high passage rates of food (Thomas et al. 1975, Thomas and Popko 1981, Brittas and Marcstrom 1982, Thomas 1982). Labile protein and glycogen make up significant proportions of energy reserves within grouse (Grammeltvedt 1978, Thomas and Popko 1981, Thomas 1982).

To measure the importance of energy reserves to survival, reproductive success, or other attributes of fitness, it is necessary to know whether high energy demands are met with endogenous reserves (and if so, whether from fat, protein, and/or glycogen) or from exogenous sources. The importance of endogenous reserves can be evaluated in a general way by their relative size and variability among seasons and individuals.

The objectives of this study were to assess the extent, composition, age and sex variation, and variation over winter of Sage Grouse (*Centrocercus urophasianus*) energy reserves.

METHODS

Sage Grouse were collected in North Park, Jackson County, Colorado. North Park is a large (1,870 km^2) intermountain basin that supports a locally migratory population of Sage Grouse (Beck 1977). Physiographic and vegetative characteristics of North Park have been described by Robertson et al. (1966), Smith (1966), Beck (1977), and Emmons and Braun (1984). The climate of North Park is cold, dry, and windy, with an average frost-free period of only 46 days (U.S. Dep. Commerce 1979). All collections were made between January and April 1981 to 1982. Average monthly temperatures during this period in 1981 and 1982 were −4.8, −4.7, −1.8, 4.8, and −7.1, −6.9, −1.8, and 0.4°C, respectively.

Sage Grouse were shot with a shotgun or .22 caliber rifle. Each bird was classified to sex by internal examination and age following Eng (1955) and Beck et al. (1975). Carcasses were kept frozen until necropsied. Data were collected on total body weight, and weight of liver, pectoralis, and supracoracoideus. Carcasses were plucked, then the feet, outer portions of wings (distal to radiale/ulnare), and the head were removed and the digestive tract emptied prior to homogenizing. Carcasses from birds collected in

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1981 were passed through a small hand-driven meat grinder six to eight times. Two 100-g subsamples of each homogenized carcass were dried at 80°C for 24 hr and ground to a fine powder in a mortar and pestle. Kerr et al. (1982) found that drying carcass samples at temperatures up to 120°C did not cause loss of fat. Fat was extracted (6 hr) from duplicate 10-g samples of the dried and crushed material in a Soxhlet apparatus with diethyl anhydrous ether as solvent. Sample preparation techniques were altered for birds collected in 1982 to reduce sample preparation time and increase precision of the technique. Carcasses were ground while still partially frozen with a large electric meat grinder seven times. The entire homogenate was then dried at 75°C for 24 hr in convection ovens. Dried samples were ground in a Wiley Mill until they passed through a 2-mm screen. Fat was extracted as in 1981. Petroleum and diethyl ether (separately) were used as solvents on duplicate samples from each bird. Ten replicate samples from one bird were extracted to determine precision of this method.

The analysis of variance procedure in the SPSS (Nie et al. 1975) was used to test for significant ($P < 0.05$) differences in fat content among sex and age classes, and between years. Julian date of collection was entered as a possible explanatory covariate. Changes in fat content within winter were evaluated by comparing fat content of birds collected in January and February to that of birds collected in March and April using the Mann-Whitney-Wilcoxon's test (Gibbons 1985).

RESULTS

Petroleum ether extracted less (paired t-test, $P < 0.001$) fat than diethyl ether (3.6 vs. 4.0%, $n = 21$). Diethyl ether extract could be predicted from petroleum ether extract ($\hat{y} = 0.934x + 0.678$, $r^2 = 0.98$).

Fat content varied greatly among and within sex and age classes of Sage Grouse, ranging from 0.8 to 8.4% of live weight (Tables 1, 2). This variability reflects differences in fat reserves among individuals, since fat extraction methodology provided precise ($\bar{x} \pm$ SD of 10 replicates = 2.85 ± 0.018%) estimates of fat content. Age and year of collection explained significant amounts of variation, while sex and Julian date of collection did not. Multiple classification analysis indicated that age accounted for approximately twice as much variability in fat content as did year of collection. Adults had higher fat content than yearlings (4.7 vs. 2.9%), and birds collected in 1982 had more fat than birds in 1981 (4.0 vs. 3.4%). Differences between years were most pronounced in the yearling age class, particularly among males (Table 2). Changes in fat content over winter were evaluated by comparing fat levels of adults and yearlings collected during early (January to February) and late (March to April) winter of 1981 and 1982. There were no differences ($P > 0.05$) in fat content between early and late winter of either year for adults or yearlings. Sexes were combined because sex was not a significant factor in the variance in fat content.

Information on the carcass composition of Sage Grouse can be used to profile the extent and composition of energy reserves during winter. To convert the mass of fat, glycogen, and protein into an estimate of energy reserves we assumed: (1) complete oxidation of fat reserves; (2) catabolism of 49 and 45% of wet weight of pectoralis and supracoracoideus with a DM of 26.4% which is 100% protein, respectively; and (3) complete oxidation of glycogen which comprises 0.43 and 0.38% of the wet weight of breast muscles and liver, respectively (Thomas et al. 1975). Energy from catabolism of leg muscles was not included. Caloric equivalents of fat, protein, and glycogen were assumed to be 9.3, 4.4, and 4.2 Kcal/g, respectively (Dargolts 1973).

Average energy reserves of adults were larger than those of yearlings, and males had larger reserves than females within age classes (Fig. 1). Because of the large variation in body size among sex and age classes, it is more meaningful to compare energy reserves relative to standard metabolic rate (SMR) computed as SMR (Kcal/bird-day) ± 15.3 = 72.6 [body wt. (kg)$^{0.698}$] (Zar 1968). Energy reserves were 10.2, 5.7, 7.6, and 5.9 times SMR for adult and yearling males and adult and yearling females, respectively (Fig. 1). Energy in fat reserves comprised from 77 to 88% of total energy reserves. Breast muscle protein contributed 15 to 22% to energy reserves and glycogen from all sources only 0.4 to 0.8%.

DISCUSSION

Estimates of fat content derived using petroleum and diethyl ether as solvents resulted in differences of 7 to 13% in estimated energy reserves. Petroleum and diethyl ether extracted equal amounts of fat from Snow Geese (*Chen caeru-*

TABLE 1. Average weights (g) of selected Sage Grouse body components (±SE). Sample size is in parentheses.

Sex Age	Total	*M. pectoralis*	*M. supra-coracoideus*	Liver	Fat	Carcass DM[a]
Males						
Adult	3,006 ± 84 (11)	262.1 ± 11.3 (11)	60.4 ± 2.4 (11)	33.6 ± 1.2 (8)	150.9 ± 18.9 (10)	33.9 ± 0.6 (10)
Yearling	2,370 ± 60 (14)	244.1 ± 6.3 (14)	54.8 ± 1.7 (14)	29.3 ± 1.4 (11)	63.0 ± 9.3 (13)	32.4 ± 0.2 (13)
Females						
Adult	1,532 ± 49 (10)	153.1 ± 3.9 (10)	38.2 ± 1.3 (10)	19.4 ± 1.5 (7)	67.6 ± 8.0 (10)	35.1 ± 0.7 (10)
Yearling	1,409 ± 42 (9)	143.6 ± 4.7 (9)	34.0 ± 1.4 (9)	20.8 ± 1.2 (7)	46.4 ± 7.8 (9)	33.3 ± 0.5 (9)

[a] Carcass dry matter expressed as a percentage.

lescens) carcasses (29.1 vs. 30.1%, Dobush et al. 1985). Examination of their data suggests that significant differences could have been identified using a more powerful test such as a paired *t*-test.

Fat comprised 77 to 88% of estimated reserves of Sage Grouse. Using the same assumptions on data from Willow Ptarmigan (*Lagopus lagopus*) (Thomas 1982), Ruffed Grouse (*Bonasa umbellus*) (Thomas et al. 1975), and Rock Ptarmigan (*Lagopus mutus*) (Thomas and Popko 1981), lipids comprise 51, 52, and 67%, respectively, of available energy reserves. Fat makes up a higher percentage of reserves in Sage Grouse because they have a relatively high percentage of body fat and relatively small breast muscles (10 to 12% of body weight vs. about 30% for Ruffed Grouse and Rock and Willow ptarmigan).

Sage Grouse fat content as a percentage of live weight is generally equal to or slightly higher than values reported for Ruffed Grouse (2 to 3%, Thomas et al. 1975), Rock Ptarmigan (3.7 to 4.0%, Thomas and Popko 1981), Willow Ptarmigan (1.5 to 2.0%, Thomas 1982; 3.5 to 4.1%, Brittas and Marcstrom 1982), and Eurasian Black-Grouse, *Lyrurus tetrix* (1.1 to 2.6%, Ijas et al. 1978), collected during winter. These values are substantially lower than maximal values for Spitzbergen Rock Ptarmigan, which store as much as 32% of their body weight as fat prior to the onset of the continuous winter night (Mortensen et al. 1983).

Differences in fat content among adult and yearling Sage Grouse probably reflect diversion of excess dietary calories to growth, rather than fat, in yearlings. Male Sage Grouse do not reach maximum body size until 22 months of age and increase from 80 to 88% of adult weight over winter (Beck and Braun 1978).

The higher fat content of birds in 1982 is not

TABLE 2. Total body fat content of Sage Grouse collected in North Park, Colorado, January to April 1981 to 1982.

	Total body fat (% live weight)							
	Males				Females			
	Adult		Yearling		Adult		Yearling	
	1981	1982	1981	1982	1981	1982	1981	1982
	2.6	2.8	0.8	2.7	2.9	3.8	1.8	1.4
	2.9	5.0	0.9	2.8	3.0	4.0	2.1	2.9
	4.4	5.3	1.0	2.9	3.1	5.7	3.5	3.4
	5.8	6.1	1.1	2.9	3.4		4.7	3.7
	6.9	8.4	3.6	3.0	5.4			6.2
				3.1	5.7			
				4.2	6.1			
				4.4				
$\bar{x}$	4.5	5.5	1.5	3.2	4.2	4.5	3.0	3.5
SE	0.8	0.9	0.5	0.2	0.5	0.6	0.7	0.8

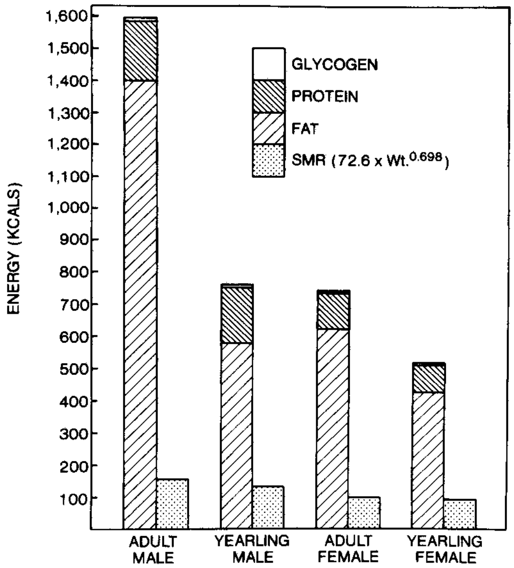

FIGURE 1. Energy reserves and standard metabolic rates (SMR) of Sage Grouse, North Park, Colorado.

readily explainable by obvious environmental parameters. Average temperatures were warmer in 1981 than in 1982. Snow cover could impede access to food or increase search costs. However, there was little (≤10 cm) snow cover on 150 of the 151 days from November to March, 1980 to 1981, but snow cover of this magnitude occurred on 48 of these 151 days in 1981 to 1982. Differences in fat content between years may be related to environmental conditions prior to winter.

Since Sage Grouse maintain or increase weight (Beck and Braun 1978) and maintain fat content over winter, caloric intake must be sufficient to meet metabolic needs during this period. By contrast, food consumption of Spitzbergen ptarmigan declined by 80% during winter; caloric deficits were made up by catabolism of large fat reserves (Mortensen et al. 1983). The relatively small energy reserves of Sage Grouse may buffer short-term periods of low caloric intake or high caloric expenditures such as during severe snowstorms. Sage Grouse energy reserves may be most important during breeding and nesting activities, periods of high energy demands, weight loss (Beck and Braun 1978), and presumably low food intake. Beck and Braun (1978) reported weight losses over the display period of 153 and 64 g for adult and yearling male Sage Grouse, respectively. This compares well with average fat contents of 151 and 63 g, respectively, for adult and yearling males (Table 1). The low fat content of yearling males may explain their infrequent lek attendance and subdued display activity (Wiley 1974, Emmons and Braun 1984). Energy deficits in females would presumably be greatest during egg laying and incubation.

Variation in fat content within sex and age classes appears to be large (Table 2). If fat reserves in Sage Grouse are used as energy sources during display or egg laying/incubation, then the ability of individuals with lower fat levels to complete these activities is questioned. Future research should concentrate on quantifying the energetic costs of these activities and describing the relationship between energy reserves and performance.

These findings are meaningful only if the assumptions used are realistic. Two assumptions are critical and are also somewhat subjective: (1) complete use of fat reserves, and (2) catabolism of 49 and 45% of the pectoralis and supracoracoideus, respectively. These assumptions were derived from data obtained on three Sage Grouse held in captivity for other studies. All three birds refused food for 2 days after capture and lost weight rapidly. Food consumption then began and increased slowly while rate of weight loss declined and then stabilized. A yearling female died 14 days after capture after losing 42% of her initial weight. The other birds were released in apparent good condition after 26 and 22 days in captivity and weight losses of 34 and 23%, respectively. The starved bird contained only 2 g of fat (0.3% of live weight); this is not a meaningful deviation from the first assumption. These data suggest that allowable body weight losses for Sage Grouse may be as much as 34% in extreme situations, but are less than 42%. Willow Ptarmigan died after weight losses of 35 to 45% after being starved for 8 to 12 days (Gjerstad and Hanssen 1984). A reasonable value for a ceiling on weight loss thus appears to be about 35%. The corresponding weight change in breast muscles given 35% body loss was estimated by comparing muscle weights of the starved grouse (42% weight loss) to muscle weights of two birds of comparable initial size and correcting to 35% weight loss. These values, 49 and 45% for pectoralis and supracoracoideus, respectively, compare well to the 25 and 19% weight loss of these muscles in Willow Ptarmigan at 20% total body loss (Grammeltvedt 1978).

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LITERATURE CITED

ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459–471.

BECK, T.D.I. 1977. Sage Grouse flock characteristics and habitat selection in winter. J. Wildl. Manage. 41:18–26.

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. Colorado Div. Wildl., Game Inf. Leafl. 49 (Revised).

BLEM, C. R. 1976. Patterns of lipid storage and utilization in birds. Am. Zool. 16:671–684.

BRITTAS, R., AND V. MARCSTROM. 1982. Studies in Willow Grouse *Lagopus lagopus* of some possible measures of condition in birds. Ornis Fenn. 59: 157–169.

DARGOLTS, V. G. 1973. An analysis of constants used in indirect calorimetry of birds and mammals. Sov. J. Ecol. (Engl. transl. Ekologiya) 4:68–74. Transl. from 1975 Consultants Bureau, Div. Plenum Publ. Corp., New York.

DOBUSH, G. R., C. D. ANKNEY, AND D. G. KREMENTZ. 1985. The effect of apparatus, extraction time, and solvent type on lipid extractions of Snow Geese. Can. J. Zool. 63:1917–1920.

DROBNEY, R. D. 1982. Body weight and composition changes and adaptations for breeding in Wood Ducks. Condor 84:300–305.

EMMONS, S. R., AND C. E. BRAUN. 1984. Lek attendance of male Sage Grouse. J. Wildl. Manage. 48: 1023–1028.

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

GIBBONS, J. D. 1985. Nonparametric methods for quantitative analysis. 2nd ed. Am. Sci. Press, Columbus, OH.

GJERSTAD, K. O., AND I. HANSSEN. 1984. Experimental lead poisoning in Willow Ptarmigan. J. Wildl. Manage. 48:1018–1022.

GRAMMELTVEDT, R. 1978. Atrophy of a breast muscle with a single fibre type (*M. pectoralis*) in fasting Willow Grouse, *Lagopus lagopus* (L.). J. Exp. Zool. 205:195–204.

IJAS, L., I. NUUJA, R. PALOKANGAS, J. SOIMAJARVI, AND P. VALKEAJARVI. 1978. Body lipid composition in the winter fed and control populations of the wild male Black Grouse (*Lyrurus tetrix* L.) in autumn and spring. Comp. Biochem. Physiol. 60: 313–317.

KERR, D. C., C. D. ANKNEY, AND J. S. MILLAR. 1982. The effect of drying temperature on extraction of petroleum ether soluble fats of small birds and mammals. Can. J. Zool. 60:470–472.

KING, J. R., AND D. S. FARNER. 1963. The relationship of fat deposition to *Zugunruhe* and migration. Condor 65:200–223.

KING, J. R., AND D. S. FARNER. 1966. The adaptive role of winter fattening in the White-crowned Sparrow with comments on its regulation. Am. Nat. 100:403–418.

KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. Auk 98:29–38.

MCLANDRESS, M. R., AND D. G. RAVELING. 1981. Changes in diet and body composition of Canada Geese before spring migration. Auk 98:65–79.

MORTENSEN, A., S. UNANDER, M. KOLSTAD, AND A. S. BLIX. 1983. Seasonal changes in body composition and crop content in Spitzbergen ptarmigan *Lagopus mutus hyperboreus*. Ornis Scand. 14:144–148.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. Statistical package for the social sciences. McGraw-Hill Book Co., New York.

ODUM, E. P., AND C. E. CONNELL. 1956. Lipid levels in migrating birds. Science 123:892–894.

RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk 96:234–252.

REINECKE, K. J., T. L. STONE, AND R. B. OWEN, JR. 1982. Seasonal carcass composition and energy balance of female Black Ducks in Maine. Condor 84:420–426.

ROBERTSON, D. R., J. L. NIELSEN, AND N. H. BARE. 1966. Vegetation and soils of alkali sagebrush and adjacent big sagebrush ranges in North Park, Colorado. J. Range Manage. 19:17–20.

SMITH, E. L. 1966. Soil vegetation relationships of some *Artemisia* types in North Park, Colorado. Ph.D.diss., Colorado State Univ., Fort Collins.

THOMAS, V. G. 1982. Energetic reserves of Hudson Bay Willow Ptarmigan during winter and spring. Can. J. Zool. 60:1618–1623.

THOMAS, V. G., H. G. LUMSDEN, AND D. H. PRICE. 1975. Aspects of the winter metabolism of Ruffed Grouse (*Bonasa umbellus*) with special reference to energy reserves. Can. J. Zool. 53:434–440.

THOMAS, V. G., AND R. POPKO. 1981. Fat and protein reserves of wintering and prebreeding Rock Ptarmigan from south Hudson Bay. Can. J. Zool. 59: 1205–1211.

U.S. DEPARTMENT OF COMMERCE. 1979. Climatological data: annual summary, Colorado. Natl. Oceanic and Atmospheric Admin. 84(13).

WILEY, R. H. 1974. Evolution of social organization and life-history patterns among grouse. Q. Rev. Biol. 49:201–227.

ZAR, J. G. 1968. Standard metabolism comparisons among orders of birds. Condor 70:278.