Diet and Internal Anatomy of Male Sharp-tailed Grouse, *Tympanuchus phasianellus*, as Related to Age and Position on the Lek

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Heart weight, gizzard weight, and caeca length of male Sharp-tailed Grouse (*Tympanuchus phasianellus*) that occupied central territories on four leks near Fort Albany, Ontario, were significantly but not disproportionately larger compared to peripheral individuals (and yearlings). Thus, relative heart size did not explain higher levels of activity maintained by central males and adults on the lek. No advantage in digestive efficiency between the classes studied was found using digestive morphology as the criterion. Further, no differences were found between age and lek location in type and energy content of diet. Perhaps differences in body condition between the classes, as has been shown previously, can be related to differences in gastro-intestinal microflora.

Key Words: Sharp-tailed Grouse, *Tympanuchus phasianellus*, age, territorial position, spring foods, internal anatomy.

Male Sharp-tailed Grouse, *Tympanuchus phasianellus*, occupying central territories on leks are preferred by females as mates and expend more energy on lek attendance and territorial defense than individuals in peripheral territories (e.g., Kermott 1982). Furthermore, male sharptails in central territories are in better body condition than peripheral males, as are adults compared to yearlings (Tsuji et al. 1994). Body condition, or the ability to maintain body condition, in grouse appears to be related to mate choice (based on activity level) and may be related to individual differences in digestive tract morphology or energy content of diet. Relative heart size also may be of importance in relation to activity levels of individuals at the lek. Heart size in birds has been related to activity, with an increase in size being correlated with an increase in activity level (Hartman 1955). In the present study of lekking Sharp-tailed Grouse, we compare territorial position (important in mate choice) and age to variation in heart size, digestive morphology, and diet (type and energy content).

Methods

Study sites were in muskeg on the western shore of James Bay, near Fort Albany, Ontario (52°15′N; 81°35′W: see Hanson 1953 for a detailed habitat description). Forty-nine male Sharp-tailed Grouse were "harvested" by native Canadians from four separate leks during the 1992-1993 breeding seasons. Shape and feather wear of outer primaries were used to distinguish between yearlings and adults (Ammann 1944). Males were classified prior to collection as those possessing either central or peripheral territories (Tsuji et al. 1992).

Three morphological variables were measured on each specimen: body mass, fresh weight following collection; heart, following Hartman (1955); and gizzard, after removal of contents. All were measured to the nearest 0.1 gram on a triple-beam balance. A subset of 23 individuals from two leks was processed following Fenna and Boag (1974) to determine caeca lengths (to the nearest 0.5 cm) for each individual.

Data were analyzed using procedures contained in SAS (SAS Institute 1982). Morphological variables were transformed to natural logarithms, samples from central and peripheral males along with samples for adults and yearlings were found to be normally distributed (Sharpiro-Wilk's test: Shapiro and Wilk 1965). Variation in character means between central and peripheral males and between adults and juveniles were assessed by single-classification analysis-of-variance (ANOVA). For peripheral birds, data for heart and gizzard were subject to a Wilcoxon rank-sum test between adults and yearlings. Linear-regression analysis was used to examine the relationship between heart and body mass, gizzard and body mass, and caeca length and body mass among individuals.

Energy content of diet (i.e., gross energy, kJ/gram of dry matter) was assessed by drying gizzard contents at 60°C for three days, grinding and pulverizing the dried material, and then completely oxidizing approximately one gram of dry matter in an oxygen bomb calorimeter (Evans and Dietz 1974). Diet data were not normally distributed for the classes examined. Wilcoxon rank-sum tests between central and peripheral individuals, and between yearlings and adults were performed.

TABLE 1. Morphometric characters and ANOVAs between juvenile and adult males, and males occupying peripheral and central territories on leks, of Sharp-tailed Grouse.

	Heart weight, g			
	N	$\bar{X}$	SD	F[a]
Peripheral	26	11.1	1.0	8.83**
Central	19	12.0	0.9	
Adult	23	12.0	0.9	12.59***
Juvenile	22	11.0	1.0	
	Gizzard weight, g			
	N	$\bar{X}$	SD	F[a]
Peripheral	28	21.3	0.9	11.87***
Central	21	22.5	1.4	
Adult	26	22.3	1.3	9.08**
Juvenile	23	21.3	0.9	
	Caeca length, cm			
	N	$\bar{X}$	SD	F[a]
Peripheral	16	47.1	2.1	20.13***
Central	7	50.9	0.8	
Adult	7	50.9	0.8	20.13***
Juvenile	16	47.1	2.1	

[a] Significance of F: **, $P < 0.01$; ***, $P < 0.001$.

Results

Of the 49 specimens, 26 were adults and 23 were yearlings. Only adults occupied central territories (N = 21) whereas peripheral males consisted of five adults and 23 yearlings. Central males had significantly larger hearts, gizzards, and caeca than peripheral individuals (Table 1). Also, adults had larger organs compared to yearlings (Table 1). Among peripheral birds, no significant differences for heart ($P = 0.13$) and gizzard ($P = 0.63$) were found between adults (heart, N = 4, $\bar{X}$ = 11.9, SD = 1.1; gizzard, N = 5, $\bar{X}$ = 21.5, SD = 0.7) and yearlings (heart, N = 22, $\bar{X}$ = 11.0, SD = 1.0; gizzard, N = 23, $\bar{X}$ = 21.3, SD = 1.0).

There were significant relationships between heart weight and body mass ($r = 0.57$, $P = 0.0001$; Figure 1), gizzard weight and body mass ($r = 0.54$, $P = 0.0001$; Figure 2), and caeca length and body mass ($r = 0.82$, $P = 0.0001$; Figure 3). Fifty-five percent of central males and 57% of adults had heart weights greater than those predicted by the regression equation and 52% of the peripheral males and 50% of the yearlings had values higher than expected. Similar positional and age trends were noted for gizzard weights and caeca lengths.

There was no relationship in residual variation between peripheral and central males for heart weights, gizzard weights, and caeca lengths ($F = 0.01$, $P = 0.9063$; $F = 0.43$, $P = 0.5136$; $F = 1.08$, $P = 0.3095$; respectively). Non-significant results were also evident for an ANOVA of residual variation between yearlings and adults for heart weights, gizzard weights, and caeca lengths ($F = 0.06$, $P = 0.8125$; $F = 0.01$, $P = 0.9374$; $F = 1.08$, $P = 0.3095$; respectively). Thus, central males and adults did not possess disproportionately

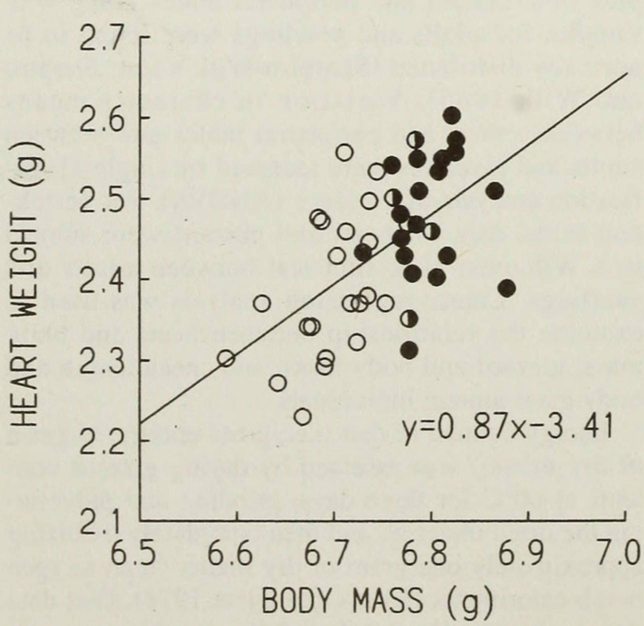

FIGURE 1. Relationship between the natural log of heart weight and body mass of 45 male Sharp-tailed Grouse. Adults in central territories are represented by solid symbols; adults in peripheral territories by half-filled symbols; and yearlings in peripheral territories by open symbols.

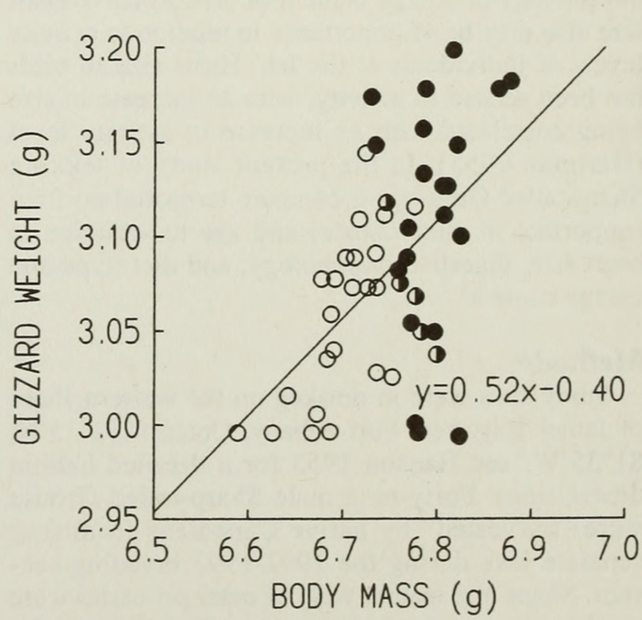

FIGURE 2. Relationship between the natural log of gizzard weight and body mass of 49 male Sharp-tailed Grouse. Adults in central territories are represented by solid symbols; adults in peripheral territories by half-filled symbols; and yearlings in peripheral territories by open symbols.

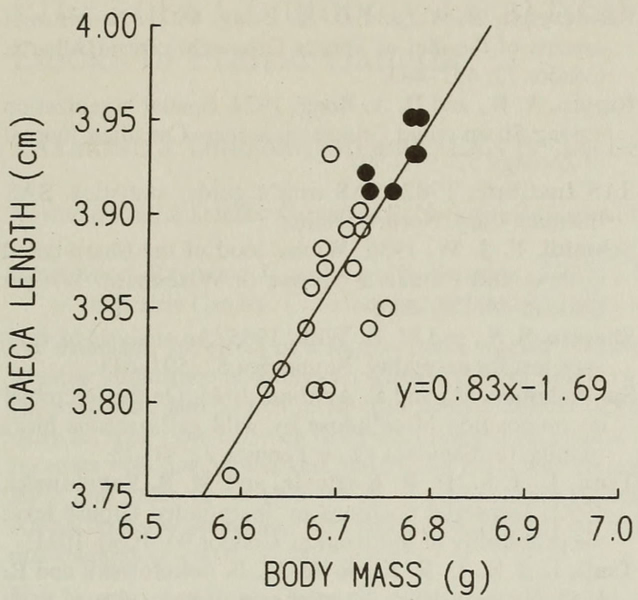

FIGURE 3. Relationship between the natural log of caeca length and body mass of 23 male Sharp-tailed Grouse. Adults in central territories are represented by solid circles and yearlings in peripheral territories by open circles.

large hearts, gizzards, and caeca compared to peripheral individuals and yearlings, respectively.

The gizzard contents of all individuals examined consisted mainly of buds and twigs of Tamarack (*Larix laricina*) and some of willow (*Salix* spp.). The seeds of the wild rose (*Rosa* spp.) were also present to a lesser extent. No differences in energy content of diet were found for; yearlings versus adults, and peripheral versus central males (Table 2).

Discussion

Older males of lekking Sharp-tailed Grouse have been shown typically to occupy central territories, with peripheral territories occupied by adults and yearlings (e.g., Rippin and Boag 1974; this study). Older males also tend to expend more energy on courtship activities than yearlings (e.g., Kermott 1982). However, relative heart size does not explain the higher level of activity maintained by central males and adults on the lek. Moreover, Tsuji et al. (1994) showed that male sharptails occupying central territories on the lek were in better body condition than their peripheral counterparts, and that adults were in better condition than yearlings. The differences in condition between these groups of birds cannot be attributed to anatomical differences in the gizzard and caeca. Although gizzard weight and caeca length in centrally located males and adults were significantly heavier and longer compared to peripherally located individuals and yearlings, respectively, these organs were not disproportionately larger. Thus, no gastro-intestinal advantage (anatomical) can be attributed to positional or age factors.

It is not surprising there were no positional or age effects with regards to diet (type and energy content), as the main plant foods in the Sharp-tailed Grouse diet are omnipresent on the muskeg (Hanson 1953). Further, sharptails rarely dig or scratch for food; therefore, it appears that snow depth, not behavioral differences, determines availability of winter and early spring food (Schmidt 1936; Marshall and Jenson 1937).

Differences in body condition in sharptails were not related to any of the variables measured. However, individual differences in condition may be related to differences in the microorganisms present. Indeed, Suomalainen and Arhimo (1945) found that microorganisms cultured from the gastro-intestinal tract (i.e., gizzard and caeca) of young galliforms had the ability to digest cellulose, but activity levels were low relative to cultures from adults. The difference in microbial activity between yearlings and adults may be related to the seasonal switch in diet common to galliforms (Pendergast and Boag 1971). During the late spring to early autumn, a highly digestible diet of berries and insects make up the sharptails' diet (Mitchell and Riegert 1994), whereas late autumn and winter bring a low quality diet of browse which is high in cellulose (Schmidt 1936; Marshall and Jenson 1937). Yearling galliforms do not appear to be able to adapt physiologically to the winter diet of browse as easily as adults (Pendergast and Boag 1971), probably due to differences in their intestinal fauna.

TABLE 2. Energy content of diet and Wilcoxon rank-sum tests between juvenile and adult males, and males occupying peripheral and central territories on leks, of Sharp-tailed Grouse.

	Quality of diet (kJ/g)		
	N	$\bar{X} \pm$ SD	Z[a]
Age			
Juveniles	22	24.2 ± 3.6	0.43^{NS}
Adults	15	24.1 ± 3.5	
Position			
Peripheral males	24	24.1 ± 3.5	0.80^{NS}
Central males	13	24.3 ± 3.7	

[a]Significance of Z: ^{NS}, $P > 0.42$.

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