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RELATIONSHIP OF BODY SIZE OF MALE SHARP-TAILED GROUSE TO LOCATION OF INDIVIDUAL TERRITORIES ON LEKS

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ABSTRACT.—We examined size differences in four morphometric characters of 52 male Sharp-tailed Grouse (*Tympanuchus phasianellus*) occupying central and peripheral territories on six leks near Fort Albany in northeastern Ontario. Univariate and multivariate analyses showed that central males, which were all adults, were significantly larger than peripheral individuals, some of which were juveniles. Central males were disproportionately heavier for their body size than peripheral males. Differences in body condition may permit central males to attend the lek for longer periods of time and display more than their peripheral neighbors. Body size as well as body condition may be important in male-male interactions involving territory acquisition and maintenance on the lek. *Received 18 May 1993, accepted 21 Sept. 1993.*

Sharp-tailed Grouse (*Tympanuchus phasianellus*) exhibit lekking behavior in which males establish territories in aggregates and display within sight of each other on open, relatively flat habitat (Hjorth 1970, Hoglund 1989). These territories are maintained by males on an infrequent basis for most of the year but are visited on a daily basis during the breeding season (Moyles 1977, Kermott 1982). Females visit the mating arena for the sole purpose of mating (Bradbury 1977, 1985); they show a marked preference for males occupying centrally-located territories on the lek (Lumsden 1965, Evans 1969, Hjorth 1970).

Individual males of the lek get central territories sequentially; juvenile males first establish territories on the lek periphery and move centripetally as vacancies become available (Evans 1969, Rippen and Boag 1974, Kermott 1982). Thus, older males occupy central territories and more peripheral territories are occupied by younger individuals (Rippen and Boag 1974). Although chance events (e.g., death) can have a major role in gaining a central territory, occupancy of a preferred central territory can be maintained only by daily visits to the lek to display and defend territorial boundaries (Kruijt et al. 1972, Wiley 1973, DeVos 1983). It has been hypothesized that male-male interactions, such as in territorial defense, competitive ability of an individual can be enhanced through an increase in body size (Clutton-Brock et al. 1977). Here we examine morphological variation of males on leks of Sharp-tailed

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Grouse and relate male age and body size to territorial position in the lek.

STUDY AREA AND METHODS

Study sites were in areas of muskeg near Fort Albany, Ontario (52°15′N, 81°35′W), on the west shore of James Bay (Hanson 1953). One of us (L.J.S.T.) accompanied several native North Americans on their spring hunt for Sharp-tailed Grouse in the above area and examined birds killed on these hunts.

A total of 52 males was examined from six separate leks during the 1990–1992 breeding seasons. Adults were distinguished from juveniles on the basis of appearance and wear of primary feathers (Ammann 1944). At the time of collection, L.J.S.T. scored males as those possessing either central or peripheral territories. Central differed from peripheral territories by having neighboring territories on all sides (Hogan-Warburg 1966, Kruijt and Hogan 1967).

Four morphological variables were measured on each bird as follows: bill length, measured from the anterior edge of the nostril to the bill tip; wing length, the flattened wing length from the bend in the wing to the tip of the longest primary; tarsometatarsus length, the bone measurement from the tip of the intercondylar prominence to trochlea for digit III; body mass, fresh weight taken immediately following collection of specimens. Linear measurements were made with vernier calipers to the nearest 0.05 mm except wing length which was taken with a ruler to the nearest 1.0 mm. Body mass was measured to 1.0 g with either a spring scale or triple-beam balance.

The data were analyzed by multivariate and univariate procedures (SAS Inst. 1982). Variables were transformed to natural logarithms and samples for central and peripheral males were normally distributed at the $\alpha = 0.01$ level (Shapiro-Wilk's test, Shapiro and Wilk 1965). Variation in character means between central and peripheral males was assessed multivariately by single-classification multivariate analysis of variance (MANOVA) and univariately by single-classification analysis of variance (ANOVA). The structure of covariation among the characters was determined using principal component (PC) analysis. The first three PCs and associated eigenvalues were extracted from a total correlation matrix of the four characters. Bootstrapping (Efron 1982) was used to avoid making a subjective interpretation of the "meaning" of the principal components. Data were randomly sampled 1000 times with replacement and 95% confidence limits determined for estimates of PC coefficients and eigenvalues using the percentile method (Efron 1981). PC scores were calculated for each individual on the first component and compared between central and peripheral birds by ANOVA. The relationship between body mass and body size among individuals was assessed by linear regression analysis.

RESULTS

Age, morphological variation, and territorial position.—Of 52 birds examined, 40 (76.9%) were adults, while 12 (23.1%) were juveniles. Age of males was highly (χ^2 adjusted for continuity = 13.1, $P < 0.0001$) related to position of territory (i.e., peripheral or central). Only adult males (N = 26) occupied central territories. Fourteen (46.2%) adult males held peripheral territories, with the remaining 12 used by juveniles.

MANOVA of the four measured characters indicated a significant dif-

TABLE 1
MORPHOMETRIC CHARACTERS, AND ANOVA BETWEEN MALES OCCUPYING PERIPHERAL AND CENTRAL TERRITORIES OF SHARP-TAILED GROUSE

Character	Peripheral males (N = 26) $\bar{x} \pm$ SD	Central males (N = 26) $\bar{x} \pm$ SD	F^a
Body mass, g	847.27 ± 33.41	912.14 ± 29.90	54.62***
Tarsometatarsus length, mm	45.80 ± 0.89	46.89 ± 0.77	22.18***
Wing length, mm	215.15 ± 4.03	219.04 ± 6.30	7.01*
Bill length, mm	12.50 ± 0.35	13.02 ± 0.45	21.50***

[a] Significance of F: * = $P < 0.05$; *** = $P < 0.001$.

ference (F approximation of Wilk's lambda = 19.51, df = 4 and 47, $P < 0.0001$) between males on peripheral and central territories. Similarly, a significant difference (F approximation of Wilk's lambda = 10.54, df = 4 and 35, $P < 0.0001$) between adults on peripheral and central territories was noted. Further, among peripheral individuals, a significant difference (F approximation of Wilk's lambda = 6.45, df = 4 and 21, $P = 0.0015$) between adults and juveniles was shown. ANOVA of each character showed that males on central territories were significantly heavier and had larger tarsometatarsus, wing, and bill than males on peripheral territories (Table 1). Among adults, significant differences ($P < 0.037$) between central and peripheral males were found for body mass, tarsometatarsus length, and bill length but not for wing length ($P = 0.1339$). For peripheral birds, adults exceeded juveniles significantly only in mass (Table 2).

Character covariation.—Boot-strapped coefficients of the first three principal components (PC), their associated eigenvalues, and estimated 95% confidence intervals varied (Table 3). The PCs combined accounted

TABLE 2
MORPHOMETRIC CHARACTERS, AND ANOVA BETWEEN JUVENILES AND ADULT MALES OCCUPYING PERIPHERAL TERRITORIES OF SHARP-TAILED GROUSE

Character	Juvenile males (N = 12) $\bar{x} \pm$ SD	Adult males (N = 14) $\bar{x} \pm$ SD	F^a
Body mass, g	823.13 ± 26.59	867.97 ± 23.42	20.89***
Tarsometatarsus length, mm	45.46 ± 0.79	46.09 ± 0.89	3.63
Wing length, mm	213.92 ± 4.29	216.21 ± 3.60	2.25
Bill length, mm	12.40 ± 0.31	12.59 ± 0.37	1.85

[a] Significance of F: *** = $P < 0.001$.

TABLE 3

BOOTSTRAPPED PRINCIPAL COMPONENTS AND ASSOCIATED EIGENVALUES (λ) OF MORPHOMETRIC CHARACTERS OF SHARP-TAILED GROUSE

	PC1		PC2		PC3	
Character	Coeff.	95% CI	Coeff.	95% CI	Coeff.	95% CI
Body mass	0.849	0.751, 0.917	−0.191	−0.498, 0.160	−0.092	−0.420, 0.394
Tarsometatarsus length	0.816	0.651, 0.908	−0.154	−0.527, 0.357	−0.098	−0.597, 0.632
Wing length	0.449	−0.023, 0.752	0.685	−0.603, 0.988	0.180	−0.573, 0.717
Bill length	0.689	0.416, 0.839	0.058	−0.622, 0.849	0.138	−0.680, 0.755
λ	2.122	1.771, 2.505	0.924	0.725, 1.098	0.637	0.439, 0.839

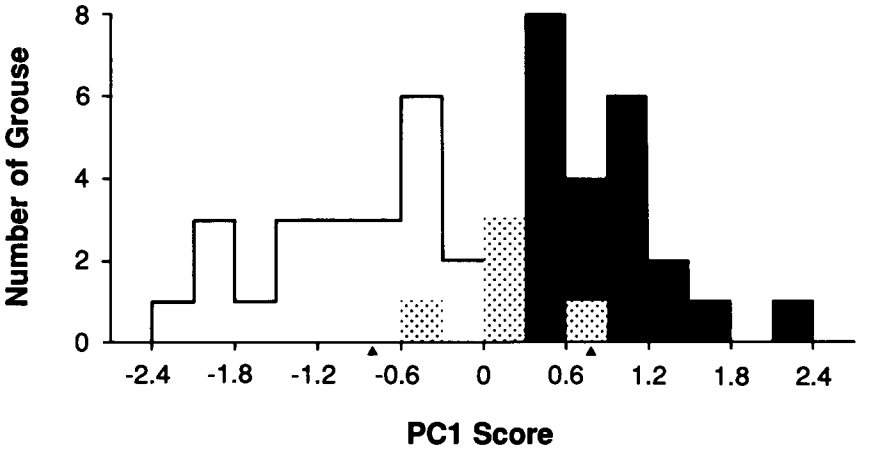

FIG. 1. Frequency distribution of individual scores on the first principal component (PC1) based on four morphometric characters of Sharp-tailed Grouse on peripheral (open histogram) or central (solid histogram) territories in six leks. Overlap in histograms is shown by the stippled areas. Triangles indicate multivariate means for each sample.

for 92.1% of the total variation. Confidence intervals that do not include zero identified coefficients significant at the $\alpha = 0.05$ level. Significant coefficients were identified only on PC1, which explained variation in body mass and lengths of tarsometatarsus and bill. Frequency distributions of individual scores along PC1 illustrate the distinctiveness between peripheral and central males in terms of multivariate size (Fig. 1). Large central males had correspondingly high values on PC1 relative to peripheral males. ANOVA showed a significant difference ($F = 74.40$, $P < 0.001$) in PC1 scores between the two groups.

Relationship between body mass and body size.—Length of tarsometatarsus was used as a measure of body size in comparing variation in body mass of males occupying peripheral vs central territories. Linear regression analysis showed that 39.1% ($r = 0.62$, $P < 0.0001$) of the variation in body mass was attributable to variation in tarsometatarsus length (Fig. 2). Among central males, 73.1% had values of body mass that exceeded those predicted by the regression equation, while 69.2% of peripheral males had values of body mass lower than predicted. ANOVA of residual variation between peripheral and central males was significant ($F = 15.10$, $P = 0.0003$). Thus, central males were disproportionately heavy for their body size when compared to their peripheral counterparts.

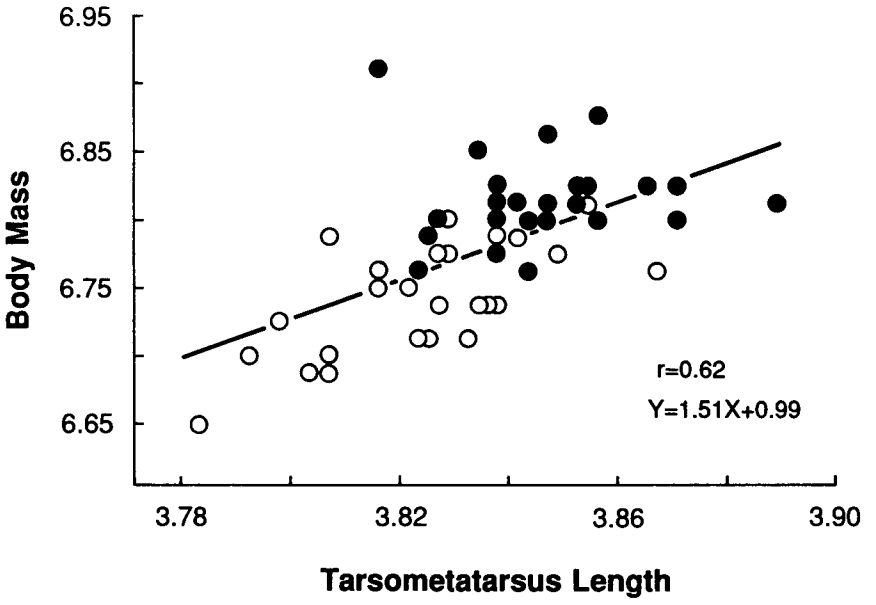

FIG. 2. Relationship between the natural log of body mass and tarsometatarsus length of 52 Sharp-tailed Grouse occupying peripheral (○) and central (●) territories in six leks.

DISCUSSION

Only adult Sharp-tailed Grouse males occupied central territories while peripheral territories contained approximately equal numbers of juveniles and adults. This supports previous findings that most males gradually move centripetally on the lek filling vacancies that occur naturally (Moyles 1977, Kermott 1982). Central territories are only rarely acquired by direct aggressive behavior; however, survivorship, site fidelity, and aggressiveness are of importance in acquiring preferred territories (Moyles 1977, Kermott 1982).

In male Sharp-tailed Grouse, large body size is of known importance when territories initially are established on the periphery of the lek (Moyles 1977, Gratson 1989). Furthermore, Nitchuk (1969) found that males occupying the preferred central territories were larger than individuals at the periphery; however, differences in mean body mass were not significant. In the present study, coefficients on PC1 all had positive, mainly large values with PC1 being interpreted as a multivariate measure of overall size (Jolicoeur and Mosimann 1960, Blackith and Reyment 1971). The observation that central males are larger than peripheral individuals is consistent with the competitive hypothesis (Clutton-Brock et

al. 1977). Furthermore, all differences were not attributable to age, because adults occupying peripheral territories were significantly smaller compared to their central counterparts.

Although absolute body size may be important in male-male combat and obtaining territories (Emlen 1976), health of an individual is also of importance in maintaining a preferred territory because daily attendance at the lek by males is required to maintain territorial boundaries (Kermott 1982, DeVos 1983). Relative body mass as related to body size is a good indicator of general health (Vehrencamp et al. 1989). Adult males in peripheral territories, although not significantly different from juveniles in linear measures of body size, were significantly larger in body mass and therefore may have physiological advantages over juveniles. Increased mass may enhance length of fasting in seasonal environments. On cold days when thermoregulatory demands increase (Gibson and Bradbury 1985), large males may be able to attend the lek for longer periods and display more than smaller peripheral males. Also, endogenous reserves may be of importance during short periods of high energy demands (Hupp and Braun 1989), for example, during peaks of attendance of females at the lek, when male display rates are greatest (Kermott 1982).

Occupancy of a central territory does not by itself guarantee mating success, as some centrally located males on a lek do not mate (Hartzler 1972). It appears that occupying a central territory allows an individual to be part of a subset of males at the lek that are preferentially examined by females with actual mating preference depending on some other variable. In Sage Grouse (*Centrocercus urophasianus*), display rates among territorial males have been shown to be positively correlated with mating success (e.g., Hartzler 1972). Furthermore, males that display most actively on a lek lose less mass per day compared to males that display less vigorously (Vehrencamp et al. 1989). Condition or the ability to maintain condition may be the actual variable of importance in female mating preference at the lek.

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