

TERRITORIAL POSITION IN SHARP-TAILED GROUSE LEKS:
THE PROBABILITY OF FERTILIZATION¹

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Alexander (1975) described a nonresource-based mating system as one where males offer mates and young only gametes. Studies of nonresource-based mating systems are important in understanding mate choice and evolution because complicating variables are not involved. In this system, female choice is theoretically based only on benefits derived from males.

Sharp-tailed Grouse (*Tympanuchus phasianellus*) exhibit a nonresource-based mating system. During the breeding season, males display on leks (Lumsden 1965, Hjorth 1970) with females preferring males with territories located centrally in the lek (Lumsden 1965, Hjorth 1970).

We examined why females prefer to mate with central males on the lek. Specifically, do females that choose central males benefit by increased probability of fertilization (Avery 1984)? We relate increased probability of fertilization to sperm availability (Eng 1963) and sperm number (David et al. 1979). Sperm must be available at the appropriate time (i.e., when females are receptive) and in adequate quantity to ensure fertilization of ova. If sperm are inadequate in quantity, females risk reproductive success for the year, as females of lekking grouse species typically copulate only once (Kruijt and Hogan 1967, Wiley 1973).

METHODS

We examined portions of 13 male Sharp-tailed Grouse taken by native North Americans from three leks in March–April 1991, near Fort Albany, Ontario (52.15°N; 81.35°W). Juveniles were distinguished from adults using characteristics of feather wear (Ammann 1944). Males were scored as those occupying central or peripheral territories by LJST at the time of collection. Central territories were defined as those surrounded on all sides by other territories while peripheral territories had at least one side unbounded (Hogan-Warburg 1966, Kruijt and Hogan 1967).

Body mass was measured to the nearest gram using either a spring scale or triple-beam balance. Testis size

was used as an indicator of the number of spermatozoa produced by an individual (Johnson et al. 1980). We removed, separated and measured left testes to the nearest 0.1 mm (length and width) using calipers. Testis volume was used as a measure of testes size, with volume estimated following Rising (1987).

Because of small sample sizes, data were pooled from the three leks. Data for testes were subject to a Wilcoxon rank sum test between central and peripheral males. Spearman rank correlation analysis (r_s) was used to determine the relationship between testis volume and body mass.

RESULTS

Two individuals were juveniles with both being scored as peripheral males.

Testis volume was larger ($z = -2.5$, $P < 0.05$) in central males than peripheral individuals (central males: $n = 7$, $\bar{x} = 154.4$, $SD = 64.5$; peripheral males: $n = 6$, $\bar{x} = 95.3$, $SD = 15.2$).

Furthermore, there was a positive relationship ($r = 0.76$, $P < 0.01$) between testis volume and body mass (Fig. 1).

DISCUSSION

Younger males of lekking grouse species typically reside in peripheral territories (e.g., Rippen and Boag 1974, Kruijt and Hogan 1967). Further, Eng (1963) has shown that in juvenile male Sage Grouse (*Centrocercus urophasianus*), the physiological capacity to breed was not attained until after most females had mated, while adult males reach maximum capacity to breed during the peak in female attendance at the lek. If the delay in reproduction maturation observed in juvenile Sage Grouse males is true of other lekking grouse species (Wiley 1974), then female Sharp-tailed Grouse may increase the probability of fertilizing their ova by selecting males that have sperm available at the appropriate time (i.e., central males).

In bird species that lack true intromittent organs (Lofts and Murton 1973), there is no assurance that the total volume of ejaculate will reach the female's internal reproductive tract. Thus, the volume of semen and amount of sperm in an ejaculate may be of importance in ensuring fertilization of ova. Also, large testes decrease the "sperm depletion" effect seen in individuals that perform frequent copulations as a pre-

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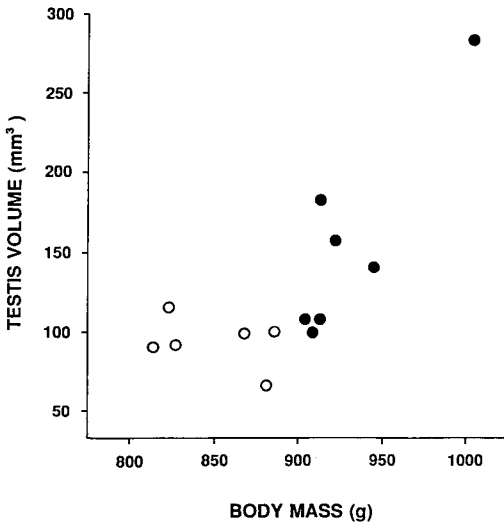


FIGURE 1. Relationship between testis volume and body mass of lekking Sharp-tailed Grouse for central (●) and peripheral (○) males.

ferred male may have to copulate with several females in a short period of time (Cartar 1985). Indeed, levels of testicular sperm in Sharp-tailed Grouse were found to be greater in central males compared to peripheral males (Nitchuk and Evans 1978).

The positive relationship between testis volume and body mass was not unexpected as measures of body and organ size generally scale positively (Calder 1984). Thus, a female may use the body mass of a male as a further cue to assess the probability that sperm from a potential mate will fertilize all ova.

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LITERATURE CITED

ALEXANDER, R. D. 1975. Natural selection and specialized chorusing behavior in acoustical insects, p. 35-77. In D. Pimental [ed.], *Insects, science, and society*. Academic Press, New York.

- AMMANN, G. A. 1944. Determining the age of Pinnated and Sharp-tailed Grouse. *Auk* 8:170-171.
- AVERY, M. I. 1984. Lekking in birds: choice, competition and reproductive constraints. *Ibis* 126:177-187.
- CALDER, W. A. 1984. *Size, function and life history*. Harvard University Press, Cambridge, MA.
- CARTAR, R. V. 1985. Testis size in sandpipers. *Naturwissenschaften* 72:157-158.
- DAVID, G., P. JOUANNET, A. MARTIN-BOYCE, A. SPIRA, AND D. SCHWARTZ. 1979. Sperm counts in fertile and infertile men. *Fertil. Steril.* 31:453-455.
- ENG, R. L. 1963. Observations on the breeding biology of male Sage Grouse. *J. Wildl. Mgmt.* 27:841-846.
- HJORTH, I. 1970. Reproductive behaviour in Tetraonidae. *Viltrevy* 7:282-525.
- HOGAN-WARBURG, A. J. 1966. Social behavior of the Ruff, *Philomachus pugnax* (L.). *Ardea* 54:109-229.
- JOHNSON, L., C. S. PETTY, AND W. B. NEAVES. 1980. The relationship of biopsy evolutions and testicular measurements to over-all daily sperm production in human testes. *Fertil. Steril.* 34:36-40.
- KRUIJT, J. P., AND J. A. HOGAN. 1967. Social behavior on the lek of the Black Grouse, *Lyrurus tetrix tetrix* (L.). *Ardea* 55:203-240.
- LOFTS, B., AND R. K. MURTON. 1973. Reproduction in birds, p. 1-107. In D. S. Farner and J. R. King [eds.], *Avian biology*, Volume 3. Academic Press, New York.
- LUMSDEN, H. G. 1965. Displays of the Sharp-tailed Grouse. Res. Rep. 66. Ontario Department of Lands and Forests, Research Branch, Toronto, Ontario.
- NITCHUK, W., AND R. EVANS. 1978. A volumetric analysis of Sharp-tailed Grouse sperm in relation to dancing ground size and organization. *Wilson Bull.* 90:460-462.
- RIPPEN, A. B., AND D. A. BOAG. 1974. Spacial organization among Sharp-tailed Grouse on arenas. *Can. J. Zool.* 52:591-597.
- RISING, J. D. 1987. Geographic variation in testis size in Savannah Sparrows (*Passerculus sandwichensis*). *Wilson Bull.* 99:63-72.
- WILEY, R. H. 1973. Territoriality and non-random mating in Sage Grouse, *Centrocercus urophasianus*. *Anim. Behav. Monogr.* 6:85-169.
- WILEY, R. H. 1974. Evolution of social organization and life history patterns among grouse. *Quart. Rev. Biol.* 49:201-227.