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Non-random mating in classical lekking grouse species: seasonal and diurnal trends

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Abstract This paper is the first to integrate both field and theoretical approaches to demonstrate that fertility benefits can be a direct benefit to females mating on the classical lek. Field data collected for male sharp-tailed grouse (*Tympanuchus phasianellus*), a classical lekking species, revealed potential fertility benefits for selective females. Adult males and individuals occupying centrally located territories on the lek were found to have significantly larger testes than juveniles and peripheral individuals. Further, using empirical data from previously published studies of classical lekking grouse species, time-series analysis was employed to illustrate that female mating patterns, seasonal and daily, were non-random. We are the first to show that these patterns coincide with times when male fertility is at its peak.

Key words Grouse · Fertility · Time-series analysis

Introduction

A lek can be defined as an area used for mating that contains limited resources, and where males establish territories to form an aggregate. Females of the species visit the lek for the sole purpose of mating. The male apparently offers the female and young nothing more than his gametes (Alexander 1975). The outline of a lek can be approximated by a circle, the area of the lek being divided basically into a central and peripheral portion (Schwartz 1945; Lumsden 1965; Wiley 1973; DeVos 1978, 1983). Central territories are defined as those surrounded on all sides by other territories while peripheral territories have at least one side unbounded (Kruijt and Hogan 1967). Individual males of a lek species usually gain centrally located territories through occupation of vacant territories over time, but when there are no vacancies, males typically occupy the same territory over the year and from one year to the next (Lumsden 1965; Tsuji et al. 1994). The centripetal movement begins when juvenile males establish territories on the lek periphery with the older males usually occupying the central territories. As vacancies arise during the current or subsequent breeding season, peripheral individuals begin to occupy more centralized territories (Kruijt and Hogan 1967; Wiley 1973; DeVos 1978, 1983). As a result, older males typically occupy more central positions while younger ones reside in more peripheral territories (Tsuji et al. 1994).

Classical lekking grouse are bird species that display in open, relatively flat habitat with members of the lek being within sight of each other (Hjorth 1970). Such grouse species include the black grouse (*Tetrao tetrix*), the sharp-tailed grouse (*Tympanuchus phasianellus*), the lesser and greater prairie chicken (*Tympanuchus pallidicinctus* and *Tympanuchus cupido*) and the sage grouse (*Centrocercus urophasianus*) (Lumsden 1965; Wiley 1973; DeVos 1978, 1983). An interesting phenomenon associated with classical lekking grouse species is the observation that a disproportionate number of matings involve males that occupy centrally located territories (see, e.g., Kruijt and Hogan 1967; DeVos 1978, 1983). It should also be stressed that females typically copulate only once during a breeding season (Tsuji 1996).

The probability of fertilization can be related to three basic factors in birds, since male birds do not possess accessory reproductive organs (Lake 1971). These factors are sperm availability, quantity, and quality. In order to ensure fertilization, females must mate when gametes are available at the appropriate time, in sufficient quantity,

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and of good quality. The female, it is assumed, has the opportunity of realizing her full reproductive potential for the year, that is, all her ova are fertilized.

In the work described in this paper, we merged field and theoretical approaches to study non-random mating in classical lekking grouse species. In the field portion of the paper, new data are presented (i.e., testis volume as related to age and territorial position and the relationship between testis volume and body mass) that augment previous fertility studies of the sharp-tailed grouse. In the theoretical section, previously published data from empirical studies are examined by time-series analysis. Incorporating this approach, we show for the first time that females of classical lekking grouse species mate non-randomly with respect to time, not only during the breeding season but also within the male daily display period, coinciding with times of optimal male sperm production.

Materials and methods

Field study

We examined portions of 37 male sharp-tailed grouse taken by Native North Americans from five leks during the 1991–1992 breeding seasons (date of collection was recorded). Leks were located near Fort Albany, Ontario, Canada (52.15°N; 81.35°W). Juveniles and adults were separated on the basis of feather wear (Ammann 1944). Males were scored in the field as those occupying central or peripheral territories at the time of collection.

Body mass was measured on a spring-scale or triple-beam balance, to the nearest gram. The left testis was removed, separated, and measured (length and width) using calipers, to the nearest 0.1 mm. Testis volume was estimated according to the method of Rising (1987) and used as a measure of testis size.

Data for testes were first placed into categories related to the time of collection (a factor known to influence testis size), prior to Wilcoxon rank-sum tests being performed comparing adults and juveniles. Non-parametric statistics were used because data did not meet the assumptions of parametric statistics. In addition, 1992 testes data were subject to a Wilcoxon rank-sum test comparing central and peripheral individuals. Testes data for 1991 (central versus peripheral) have been published previously (Tsuji et al. 1992). Spearman rank-correlation analysis (r_s) was used to determine the relationship between testis volume and body mass for 1992 data from leks 1 and 2. The relationship with respect to 1991 data has been reported previously (Tsuji et al. 1992).

Time series analysis

Although males of classical lekking grouse display throughout a breeding season that lasts approximately 4 months (see, e.g., Kruijt and Hogan 1967; Hartzler 1972; Svedarsky 1979; Kermott 1982), mating is concentrated into a short period of time, the mating peak (e.g., Schwartz 1945; Evans 1961; Dalke et al. 1963). To determine whether matings occurred non-randomly within the breeding season for four empirical studies (Kruijt and Hogan 1967; Hartzler 1972; Svedarsky 1979; Kermott 1982), a time-series analysis was employed. In addition, diurnal trends in copulations were examined by time-series analysis for three studies containing appropriate data (Evans 1961; Lumsden 1965; Hartzler 1972). We assume copulations off the lek to be rare (see, e.g., DeVos 1978; Sexton 1979; cf., Kruijt et al. 1972).

Randomness or a departure from random expectation can be ascertained from the ratio

$$R=r_A/r_E, \tag{1}$$

where

$$r_A=\frac{\sum_{i=1}^{N}}{N}r_i \tag{2}$$

and

$$r_E=\frac{N+2}{N+1}\cdot\frac{D}{2N}. \tag{3}$$

The term r_A is defined as the observed mean distance between nearest neighbours and N is the number of events scored at a distance r_i from the nearest neighbour (for all i=1, N). The expression r_E was derived by Tsuji (1992) and is the expected mean distance for a random population where D is the length of time chosen for observation. When events in a time series are random, R=1. When R=0, the maximum clumping of events has occurred. When events are more evenly spaced, R becomes greater than 1 with an upper limit of 2.15 (Clark and Evans 1954; Tsuji 1992).

Results and discussion

Sperm availability: time of year

Eng (1963) and Hannon et al. (1979) have found in *C. urophasianus* and blue grouse (*Dendragapus obscurus*) that, even though juveniles were capable of producing viable sperm during the breeding season, their testis development was delayed and testis volume was smaller than that of adults. In *T. phasianellus*, testis development also appears to be delayed in juveniles (Nitchuk 1969) and the testes are smaller than in adults (Table 1). Thus, *T. phasianellus* and *C. urophasianus* females may increase the probability of fertilizing their entire clutch by mating with adults who have sperm available at the appropriate time.

Results from a time-series analysis (Table 2) illustrate that, within the breeding season, matings are non-random and sometimes clumped. Further, mating peaks within the breeding season (Fig. 1) coincide with times of greatest testes development [in *C. urophasianus*, early to

Table 1 Descriptive statistics of testis volume and results from a Wilcoxon rank-sum test for *T. phasianellus*

Time of collection	Testis volume (mm^3) Adults: $\bar{x}$±SD, range, (N)	Juveniles: $\bar{x}$±SD, range, (N)	P
Last week March – first week April[a]	133.14±59.01 70.19 – 283.05 (11)	94.27±0.89 93.64 – 94.90 (2)	–
Second week April[b]	236.07±52.54 158.66 – 321.38 (8)	151.00±46.54 63.82 – 181.04 (6)	0.002
Third week April[c]	419.33±95.47 277.48 – 611.78 (9)	282.33 282.33 (1)	–

[a] Data from three leks, 1991
[b] Data from lek 1, 1992
[c] Data from lek 2, 1992

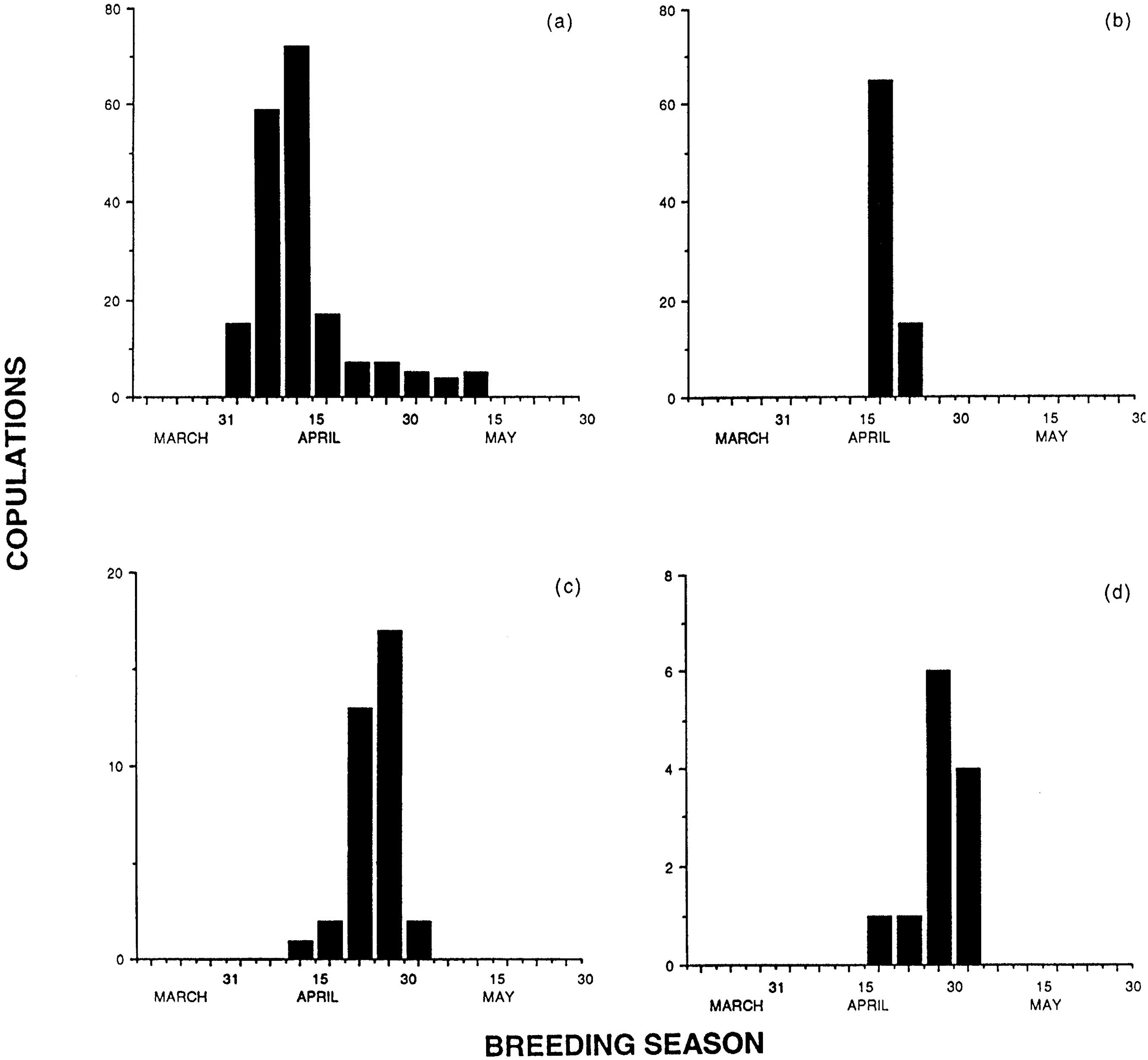

Fig. 1a–d Graphical representation of the number of copulations (and mating peak) within a single breeding season for several classical lekking grouse species. **a** 1971 data for *C. urophasianus* (Hartzler 1972); **b** 1977 data for *T. cupido* (Svedarsky 1979); **c** 1963 data for *Tetrao tetrix* (Kruijt and Hogan 1967); **d** 1973 data for *T. phasianellus* (Kermott 1982)

Table 2 Time-series analysis of matings within a single breeding season on the classical lek

Species	*R*	Source
Tetrao tetrix	0.30	Kruijt and Hogan (1967)[a]
C. urophasianus	0.17	Hartzler (1972)[b]
T. cupido	0.00	Svedarsky (1979)[c]
T. phasianellus	0.23	Kermott (1982)[d]

[a] Observational data from 1963 of a single lek
[b] Data from 1971 of a single lek
[c] Data from 1977 of a single lek
[d] Data from 1973 of a single lek

the middle of April (Eng 1963); in *T. phasianellus*, middle to late April (Nitchuk 1969); in *T. cupido*, early to the middle of April (Schwartz 1945)]. The availability of sperm appears to be related to the period during which females mate (Peterle 1954; Evans 1961; Eng 1963; Nitchuk 1969).

Sperm availability: time of day

Langford and Howarth (1972) have shown a diurnal rhythm of testicular temperature and spermatogenic activity in *Gallus*. Spermatogenic activity was found to be greatest between 2400 hours and 0200 hours when body and testicular temperature were lowest, and minimal between 0700 hours and 0900 hours when body and testic-

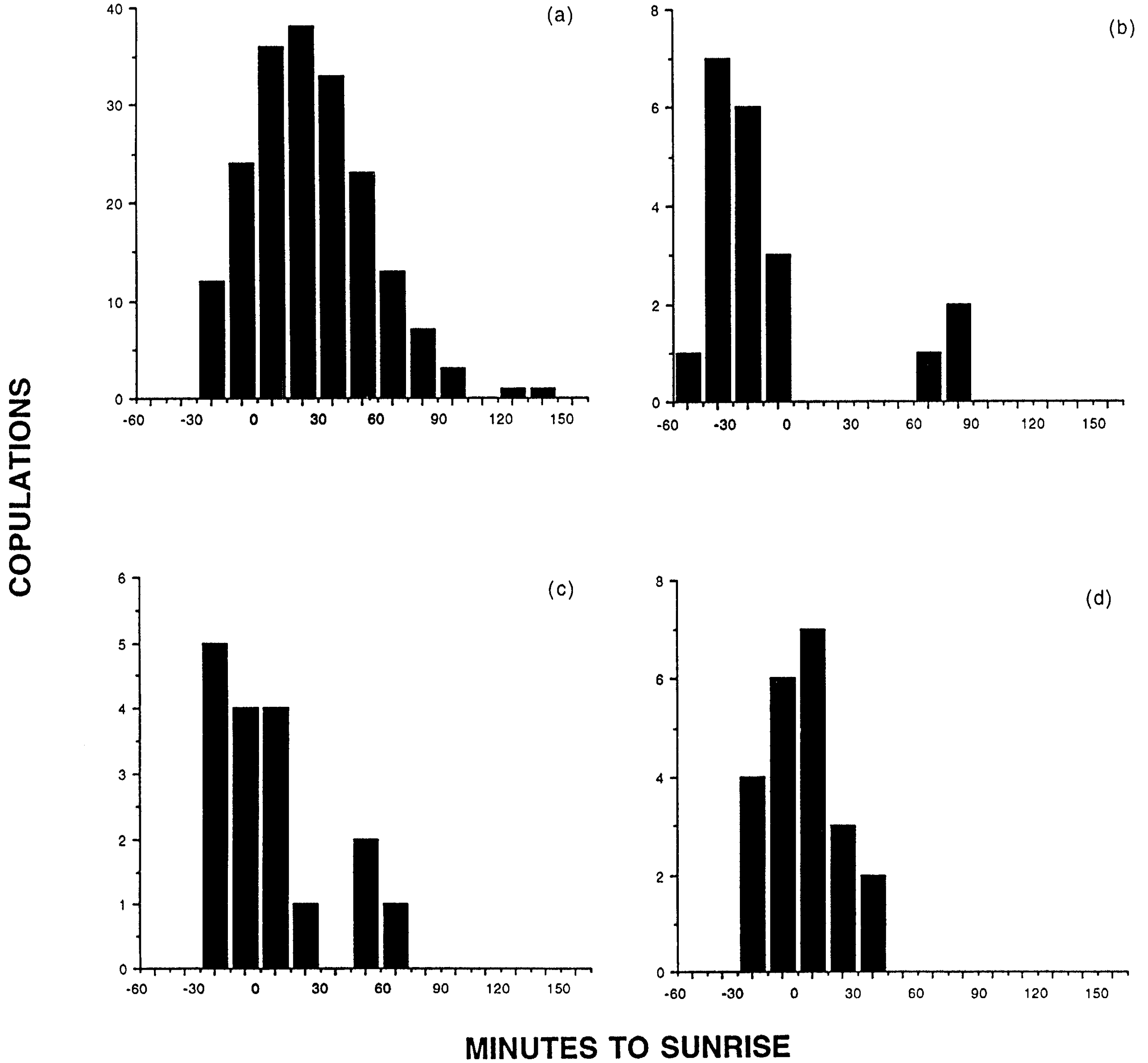

Fig. 2a–d Graphical representation of the number of copulations (with respect to sunrise) within a single breeding season that were observed at a single lek for several classical lekking grouse species. **a** 1971 data for *C. urophasianus* (Hartzler 1972); **b** 1960 data for *T. phasianellus* (Evans 1961); **c** 1964 data for *T. phasianellus* (Lumsden 1965); **d** 1963 data for *Tetrao tetrix* (Kruijt and Hogan 1967)

ular temperatures were rapidly rising (Langford and Howarth 1972). Further, Lake and Wood-Gush (1956) have suggested that mating activity should be greatest when semen yields are best. Thus, it is not surprising that classical lekking females have been found to mate preferentially around sunrise (e.g., Scott 1942; Landel 1989; Fig. 2) before body and testicular temperatures of lekking males have risen appreciably. Indeed, female copulations during the afternoon (Svedarsky 1979; Kermott 1982) and evening (Hartzler 1972; Landel 1989) display periods have been reported as rare.

Time-series analysis of the times of copulation for several empirical studies revealed a non-random trend, with most matings occurring around sunrise (Table 3). After sunrise, body and testicular temperatures increase, resulting in a decrease in spermatogenic activity.

Sperm quantity

An increase in sperm number has often been related to an increase in fertility (e.g., Martin and Dziuk 1977; Wall and Jones 1977). Furthermore, body mass has been positively associated with testis size in galliformes (e.g., Parker et al. 1942; Tsuji et al. 1992; Fig. 3) and larger testes are known to produce greater volumes of semen (e.g., Burrows and Titus 1939; Brillard and deReviers 1985) with more sperm per ejaculate (Brillard and deReviers 1985). Thus, females mating with the larger

Table 3 Time-series analysis of matings within the morning display period on the classical lek

Species	*R*	Source
T. phasianellus	0.69	Evans (1961)[a]
T. phasianellus	0.48	Lumsden (1965)[b]
C. urophasianus	0.49	Hartzler (1972)[c]

[a] Observational data from 1960 of a single lek
[b] Data from 1964 of a single lek;
[c] Data from 1971 of a single lek

Table 4 Descriptive statistics of testis volume and results from Wilcoxon rank-sum tests comparing males occupying peripheral and central territories on leks of *T. phasianellus*. Data from the 1992 breeding season

Lek	Testis volume (mm^3)		*P*
	Central males	Peripheral males	
	$\bar{x}$±SD (*N*)	$\bar{x}$±SD (*N*)	
1	247.13±45.46 (7)	152.12±42.59 (7)	0.002
2	465.46±78.56 (6)	315.89±41.86 (4)	0.014

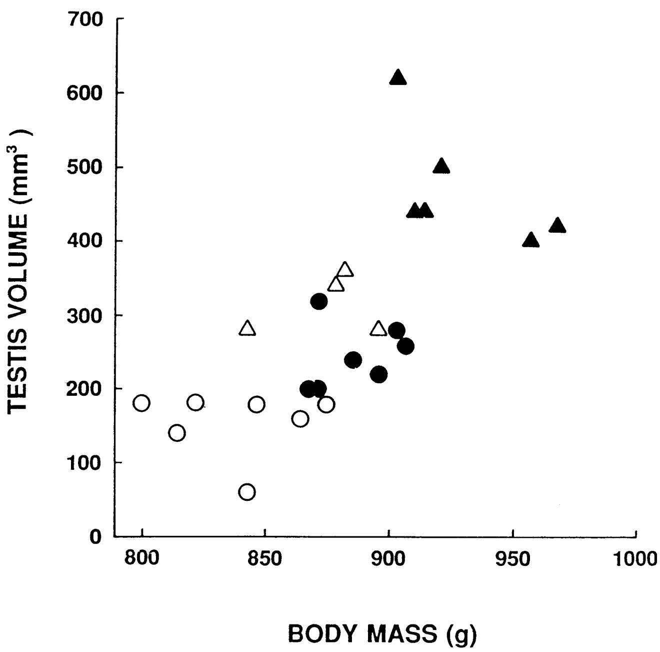

Fig. 3 Relationship between testis volume and body mass for central (●, ▲) and peripheral (○, △) males (*T. phasianellus*). Data were gathered during the 1992 breeding season. ○, ● Birds from lek 1 (r_s=0.75, *P*=0.002); and △, ▲ birds from lek 2 (r_s=0.56, *P*=0.090)

males on the lek would increase the probability of fertilizing their entire clutch.

In *C. urophasianus*, Eng (1963) found that adult males were considerably heavier and had larger testes than juvenile males throughout the breeding season. Tsuji et al. (1994) reported both an age and a positional effect in *T. phasianellus*, where adults and centrally located males were significantly larger than juveniles and peripherally located individuals (cf., Gratson 1993). Furthermore, in this species of grouse, it has been reported that central males have significantly larger testes (Tsuji et al. 1992; Table 4) and greater levels of testicular sperm (Nitchuk and Evans 1978) than peripheral individuals. Thus, females mating with central males would increase their probability of fertilizing their entire clutch for the year. Indeed, yearlings (Wiley 1973; Kermott 1982) and peripheral males (Lumsden 1968; Hartzler 1972; Gibson and Bradbury 1985; Alatalo et al. 1991) have rarely been reported to mate. Successful males have been described qualitatively, as larger and heavier than others on the lek (Lumsden 1968; Hjorth 1970).

Sperm quality

In galliformes, males require an adequate food supply in order to maintain a healthy reproductive state (Lake 1971). A decrease in food supply and/or quality can act directly on the gonads or indirectly on the hormonal system controlling the reproductive organs (Huxley 1976). Thus, deficiencies in diet can often lead to decreases in sperm quality and consequently a decrease in fertility (Arscott and Parker 1967; Boone et al. 1967; Edwards 1967; Lillie and Menge 1968). Diseases can also lead to striking decreases in sperm quality (Munro 1938).

Condition or the ability to maintain condition, during the entire breeding season, appears to be important in territorial defence and maintaining a preferred territory on the lek (Tsuji et al. 1994). When centrally located males become weakened with a subsequent loss of condition through fatigue, illness or injury, these individuals are forced from their preferred territories (i.e., central) to more peripheral locations (Hartzler 1972; Kruijt et al. 1972; DeVos 1978, 1983; Kermott 1982). Although previously successful males have been observed still to inhabit the lek, no reports of the displaced individuals again being successful in mating have been reported (e.g., Hartzler 1972; DeVos 1983).

Conclusion

It has often been assumed that males of classical lekking grouse species produce unlimited quantities of sperm; however, sperm may be limited not only during the breeding season but also within the daily display periods. Males may be limited to a set number of fertile ejaculates and need time to replenish depleted reserves (Dewksbury 1982; Birkhead 1991). Since females of classical lekking grouse species mate only once during a single breeding season, the importance of mating with a fertile male cannot be overemphasized. The present study suggests that the maximum sperm output of males (seasonal cycle in testis development and diurnal rhythm of sperm production), coincides with the seasonal mating pattern of females.

However, in a limited fertility experiment carried out by Gratson (1989), no differences in egg fertility were found between renesting clutches laid by *T. phasianellus* females that had remated with previously highly successful mated males and those that remated with previously unsuccessful males. Preferred males at some, but not all, leks had been removed prior to the females being forced to remate (Gratson 1989). Although Gratson (1989) states that preferred males did not provide fertility benefits to the females, a closer examination of this experiment does not support this claim. One problem arises in the classification of "unsuccessful males" as males that did not breed at all and those that obtained only one copulation during the initial breeding season (Gratson 1989). Only non-breeders (i.e., no copulations) should have been classed as "unsuccessful males" because males achieving only one copulation may still have provided fertility benefits compared to those that did not breed at all. In addition, the remating experiment was conducted later in the breeding season, which is of importance in terms of fertility because it is known that juvenile grouse show a delay in testis development (Eng 1963; Hannon et al. 1979); that is, juveniles may be more fertile at one time than at another. To assess fertility benefits properly, one must examine mating parameters only within the peak of female mating, because testes and sperm characteristics change throughout the breeding season.

It should be emphasized that, although we have argued that fertility parameters are an important factor affecting when mating occurs, other ecological factors that affect chick survival may also influence the timing of mating, within the breeding season.

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