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SEASONAL LEKKING BEHAVIOR OF THE GREATER PRAIRIE-CHICKEN IN ILLINOIS

(TITLE)

BY

SCOTT A. SIMPSON

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER OF SCIENCE

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

1984
YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING
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SEASONAL LEKKING BEHAVIOR OF THE GREATER PRAIRIE-CHICKEN IN ILLINOIS

Scott A. Simpson

Abstract: Spring behavior of prairie-chickens (Tympanuchus cupido) has been studied extensively, however there is little information on fall-winter lekking activity. Greater prairie-chickens were observed weekly on a lek from 25 September 1982 to 23 June 1983 during morning and evening hours in Jasper County, Illinois. The peak number of prairie-chicken males on the lek occurred in February although hen attendance did not occur until 10 March 1983. All spring lekking activities were higher compared to that of the fall-winter period. Fall-winter lek activity was centered on brief, less intense male aggression which probably establishes or maintains territorial boundaries. Imperfect booming performances were common during the fall-winter with each display being best developed and most intense during hen attendance.

The AM period was: less variable in daily attendance; significantly higher in time spent on the lek, Activity Index (i.e. Indice which incorporates time spent on the lek, mean encounters per cock, number of males involved in aggression and attendance on the lek; used to evaluate male behavior) and numbers of males on the lek; compared to that of the PM. The PM period was more affected by

cloud cover (51-100%) and was associated with significantly less time spent on the lek, earlier departure times and a lower Activity Index.

The northern harrier (Circus cyaneus) accounted for 97.3% of the interspecific interactions with repeated harassment being the most common behavior observed. Ring-necked pheasant (Phasianus colchicus) interactions were observed, however they appeared to be of little effect on lekking behavior in this study.

Greater prairie-chicken males devote large amounts of time defending territories and performing communal courtship displays on leks (Schwartz 1945, Hjorth 1970, Hamerstrom and Hamerstrom 1973), for the sole purpose of mating. Mating takes place in the spring, usually during the morning, however competition among males occurs from fall throughout the winter (Schwartz 1945, Mohler 1952, Hamerstrom and Hamerstrom 1955) and into spring during evenings (Yeatter 1943, Schwartz 1945) as well as mornings. Consequently, studies of prairie-chicken lekking behavior have largely been limited to the morning period in the spring. The evolution of lek activity at other periods of the year is problematic. It can be assumed that territories will only be defended as long as the benefit of defending them is not outweighed by the

costs (De Vos 1979). Fall, winter and evening lekking activity must provide some reproductive benefits or the expenditure of this energy would not have evolved.

There is some evidence that lek attendance in fall and and winter may significantly influence several aspects of reproductive behavior in spring. Moyles and Boag (1981) found that individual sharp-tailed grouse (Tympanuchus phasianellus), which also establish and maintain territories in autumn and winter, may have a selective advantage in acquiring a territory early in the lekking season and for the life of the individual. The advantage of this strategy appears to increase the possibility of defending a central territory where the chance of copulation is greatest (Robel 1967, Hamerstrom and Hamerstrom 1973).

A second advantage of fall-winter lek attendance is that males can maintain contact with each other with relatively brief, low-intensity encounters in order to reinforce or establish territorial boundaries before the breeding season. Maintenance of territories for long periods of time can be partially explained by the fact that lekking grouse tend to return to the same lek year after year once they have established a territory (Copelin 1963, Hamerstrom and Hamerstrom 1973, Robel and Ballard 1974, De Vos 1983.) De Vos (1983) found that black grouse (Tetrao tetrix) males maintained their territories from spring to autumn and usually remained in possession

of most of the ground that they controlled at the end of spring. Similar multi-seasonal activity in prairie-chickens has been described (Schwartz 1945), but there is little information on the importance of fall and winter lek activity on spring courtship and mating. This is a report of observations on one greater prairie-chicken lek from the initiation of activity in fall through winter and to the termination of lek attendance in the spring. The primary objectives of this study were to determine seasonal trends in; (1) Numbers of males attending the lek (2) Daily attendance to the lek (3) Aggression (4) Display behavior (5) Interspecific interactions.

STUDY AREA

This study was conducted on a lek located on the Donnelley Brothers Prairie-Chicken Sanctuary near Bogota in Jasper County, Illinois. This sanctuary is one of 14 tracts scattered within about 41 km^2 in Jasper County (Fig. 1). The tracts range from the 6.9-ha Cyrus Mark Sanctuary to the 93.9-ha Yeatter-Field-McGraw unit and total 486-ha. The area encompassing the sanctuary system (Fig. 1) contains 53 active farmsteads, one small town and 62.5 km of public roads (Westemeier 1972). The prairie-chicken population in Jasper County during the spring of 1983 numbered 60 cocks and an unknown number of hens (R. L. Westemeier, Illinois Natural History Survey, pers. commun.). The national status and management of

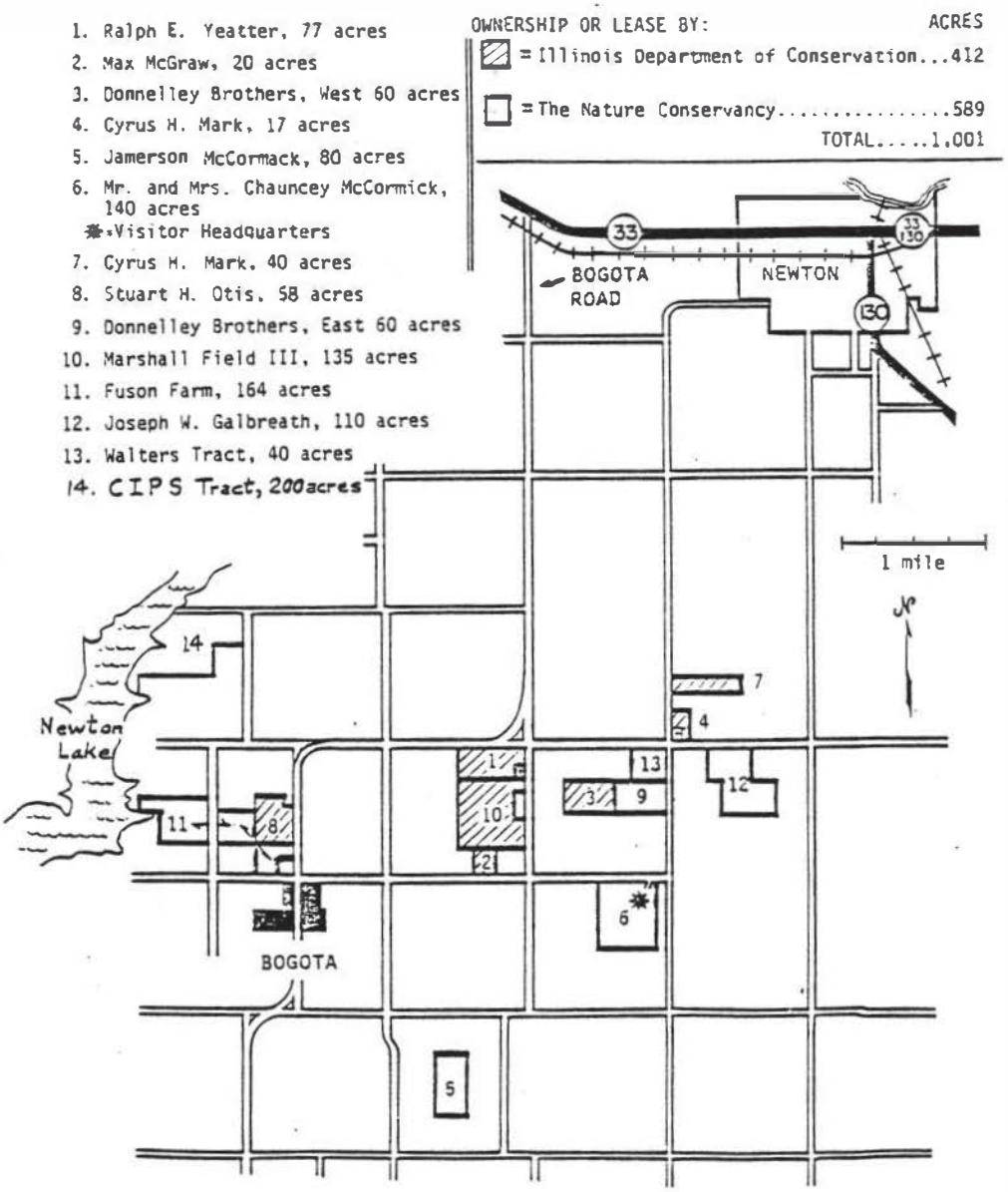

Fig. 1. Map showing the Jasper County Prairie-Chicken Sanctuaries (Courtesy of the Illinois Natural History Survey).

greater prairie-chickens has been described by Westemeier (1980).

The sanctuaries were mostly acquired from 1962 to 1973 by The Prairie Chicken Foundation of Illinois and the Prairie Grouse Committee of the Illinois Chapter of The Nature Conservancy (TNC) (Sanderson et al. 1973). The sanctuaries are currently owned by the TNC, the Illinois Department of Conservation (IDOC), and Central Illinois Public Service Company (CIPS). Management is a cooperative effort between the TNC, the Illinois Natural History Survey (INHS), IDOC, and CIPS.

According to Schwegeman (1973), Jasper County lies in the southern till plain division, with the topography being nearly level to dissected till plain. The soils are light colored and strongly developed with poor internal drainage. Approximately 40% of the southern till plain division supported prairie vegetation at the time of settlement. Today, nearly all the land has been converted into agricultural uses. Jasper County has a total land area of 128,259-ha with 107,650.6-ha (83.9%) of this being in farm land. Corn (Zea mays), soybeans (Glycine max) and wheat (Triticum aestivum) comprise 74.9% of this farm land. The remaining includes other small grains, idle cropland, forage crops and pasture land (U.S. Department of Commerce, 1981).

The lek studied in this investigation was a traditional booming ground on the East Donnelley Brothers

sanctuary (Fig. 1). This 24.3-ha unit was purchased in the summer of 1967 and since that time has had at least one stable lek site on or near it annually (R. L. Westemeier, pers. commun.). This unit along with the adjoining 24.3-ha West Donnelley Sanctuary and 16.2-ha Walter's tract had only one lek during this study. The study lek was located on the south end of a 2.8-ha bean stubble field that measured 70 m by 402 m. Vegetation on the Donnelley sanctuaries was about 88% grass and legume cover consisting primarily of redtop (Agrostis alba), timothy (Phleum pratense), smooth brome (Bromus inermis), and red clover (Trifolium pratense). Two fields of soybeans totaling 5.7-ha were present for the purpose of providing the lek site and renovating old sods. The area was managed by sharecropping, prescribed burning and rotary mowing. Sharecropping by local farmers consists of an 8 - 10 year rotation of grasses and 1 - 2 years of soybeans in most fields. Grass-seed harvesting of redtop and timothy stands is the basic management operation on most sanctuary land. Some late mowing of legume hay is allowed and the combine residue from grass-seed harvests is also baled and removed from fields. Cover on the Walter's tract is about 75% native prairie vegetation and 25% woodland that is managed by prescribed burning at intervals of about three years.

MATERIAL AND METHODS

Prairie-chickens were observed from a blind located on the periphery of the lek during the 1982-83 lekking season. Observations were conducted once a week, both morning and evening, starting 25 September 1982 with harvest of soybeans from the site to the termination of lek attendance on 23 June 1983. For the purpose of this study, fall-winter refers to the time preceding 10 March 1983 at which time hen attendance on the lek became regular, and spring representing the time after 10 March. A total of 80 observation periods and 218 blind hours were made. I entered the blind one hour before sunrise and stayed until departure of birds at mid-morning, then re-entered the blind about two hours before sunset and stayed until the departure of the cocks. The number of males on the lek was recorded at 15 minute intervals. Hens were recorded as they arrived and departed.

Activity on the lek was evaluated by recording the frequency of behavioral traits during five minute time periods at 15 minute intervals beginning with the arrival of males and continuing until their departure (Robel 1964). The number of cocks involved in aggressive encounters was recorded and the levels of aggression were evaluated as strong encounters, weak encounters and confronted crouching. These are defined as follows;

1. Strong encounters involved birds whose fighting included at least one bird flapping its wings

and leaving the ground.

2. Weak encounters include fighting in which the cocks do not leave the ground.
3. Confronted crouching usually occurring at territorial boundaries, involves both cocks facing each other in a squatting fashion.

Evaluation of the activity of prairie chicken cocks on the lek is difficult, because all activitiy levels are influenced by season, daily weather, time spent on the lek, number of males involved in aggressive encounters and lek attendance. Aggression by prairie-chicken cocks on the lek was quantified three ways to represent different aspects of behavior: (1) Activity Index, (2) Encounters/cock, and (3) Daily patterns of aggression. The Activity Index was calculated as monthly summations; Encounters/cock was figured as monthly means; and Daily patterns of aggression were calculated for daily time periods. Each technique is based on weighted means $(F_i \bar{x}_i)$ where:

F_i = total number of cocks exhibiting aggressive behavior during a five minute observation period

$\bar{x}_i$ = total number of aggressive encounters for a five minute observation period/number of cocks involved

The Activity Index (AI) incorporates time spent on the lek by prairie-chicken cocks, mean encounters per cock, number of males involved and attendance on the lek and was calculated for each weekly observation period. AI = daily $\sum (F_i \bar{x}_i)$. These weekly AI were then summed to arrive at monthly (four weeks) totals. Two months (December and March) however, had five weeks of observations so the five AI's for each of these months were summed then divided by five and multiplied by four to provide a comparative monthly value.

Encounters/cock is a measure of male to male aggression regardless of time spent on the lek or of daily attendance on the lek. This measure of aggression was calculated for each weekly observation period as: daily $\sum (F_i \bar{x}_i)$/daily $\sum (F_i)$. These weekly values were then averaged for each month.

Daily patterns of aggression (DPA) evaluated encounters/cock with respect to sunrise or sunset. All aggresive encounters in ten minute blocks before and after sunrise and sunset (e.g. 1-9 min., 10-19 min. after sunrise) were subjected to the encounters/cock formula [DPA = 10 min. period $\sum (F_i \bar{x}_i)$/10 min. period $\sum (F_i)$]. The DPA was calculated for fall-winter and spring.

Quantitative measurements of the booming display were made during each observation period by recording the

presence or absence of those displays common during spring lekking. The following displays described by Hjorth (1970) were considered: flutter jump, upright cackle, forward rush, stamping roll, one, two, or three noted booms, partial or fully inflated air sacs, color of air sac, whoop, nuptial bow, partial or fully expanded eyebrow combs and color.

Interspecific encounters were recorded each time there was a prairie-chicken reaction to a lek visitor. The prairie-chicken responses were categorized using the criteria of Berger et al. (1963), i.e. all flush, some flush, all crouch, some crouch, slow down in activity and no reaction. Slowdown in activity included one or more birds becoming attentive to the visitor and often stopping or slowing down it's display activity. Each visitor to the lek was recorded by species and sex where possible. Northern harriers were sexed by color and size (Berger et al. 1963), however, since juvenile male harriers and all females are brown, juvenile males were included in the female category. A chi-square contingency table was used to analyze reactions of prairie-chickens to either adult male or brown harriers (Schefler 1980).

Meterological data recorded during each weekly observation period were: light intensity at arrival and departure of prairie-chickens; wind velocity and air temperature at arrival and departure of observer, and

cloud cover and wind direction for each weekly observation period.

Students t-tests were used to determine if cloud cover (0-50%, 51-100%) was related to time spent on the lek, aggression levels [$\sum (F_i \bar{x}_i)$ and $\sum (F_i \bar{x}_i) / \sum (F_i)$] and attendance of prairie-chicken cocks on the lek. Matched pairs t-tests were used to determine if aggression indices (Encounters/Cock and Activity Index) were different during PM than AM at times of male attendance to the lek. One-way analysis of variance (ANOVA) was used to determine if cloud cover (0-50%, 51-100%) was related to arrival and departure time (with regard to sunrise and sunset). The level of significance used in all statistical tests was 0.05.

Results

There was less activity on the lek by both males and females during the fall and winter than in the spring. The number of prairie-chicken cocks on the lek, calculated as monthly averages of weekly counts peaked in February in both the AM and PM, followed by a gradual decline throughout the spring (Fig. 2). An attendance low for both AM and PM periods occurred in December. The average monthly PM count was 46% lower than the AM count. This difference dropped to only 30% during the period of hen attendance, compared to 53% before hen attendance. The

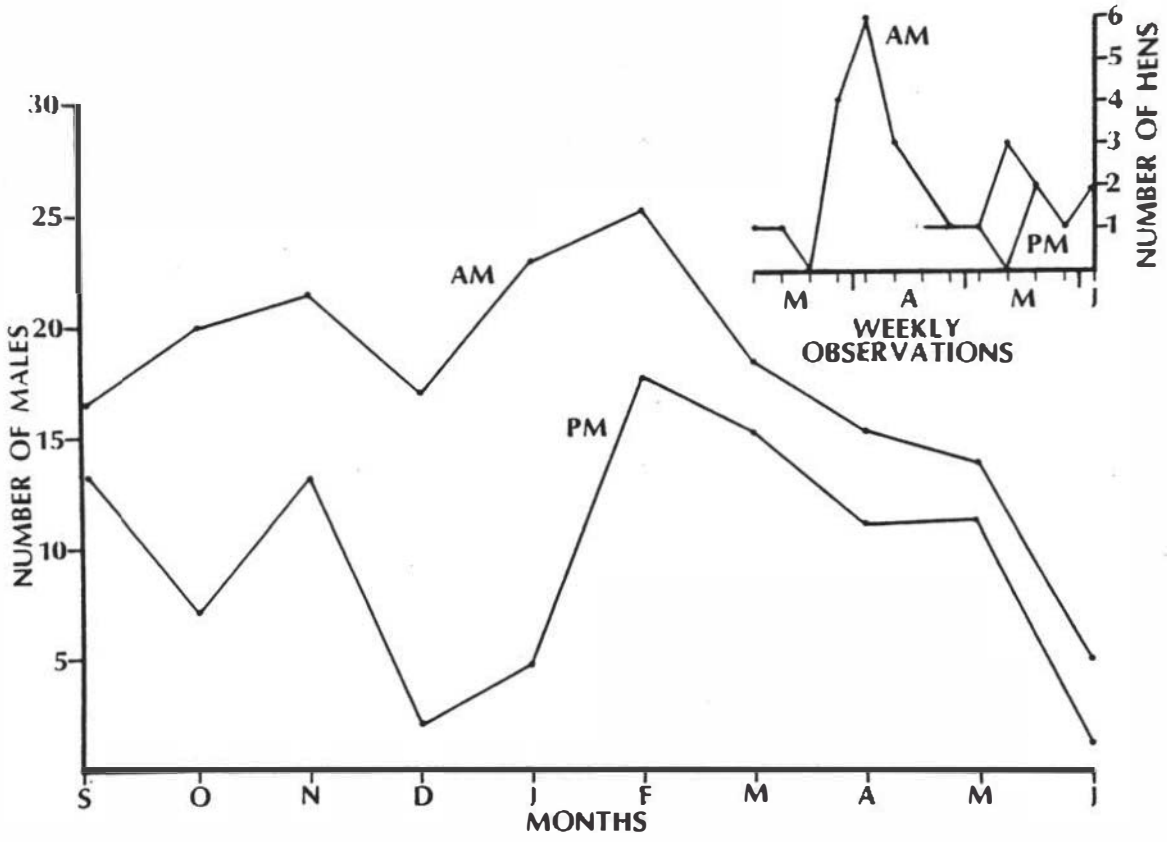

Fig. 2. Peak numbers of prairie-chicken males calculated as monthly averages of weekly counts on the lek, throughout the 1982-83 lekking season, during AM and PM observation periods. The small right-hand graph plots the peak number of hens on the lek during AM and PM weekly observations.

time cocks spent on the lek was longer in AM by an average of 77 minutes/day. However, the fluctuations in time spent on lek between AM and PM throughout the season were very similar (Fig. 3). The activity period during the AM peaked in October and November, declined in December and then increased gradually to May. A similar pattern occurred in the PM, except for a decrease from September to October. The May peak for both AM and PM was 900 (225/day) and 462 (154/day) minutes, respectively.

The AM lek attendance by cocks was regular throughout the season with only two mornings (23 December and 23 June) without males on the booming ground (Fig. 4). The December morning was warm (14°C), windy (16.6 km), cloudy (100%) and with some rain. The June observation was the last of the season, with warm (20.5°C) temperatures and dense vegetative growth on the lek site. In the AM period, male attendance levels, time spent on the lek, the activity index and encounters/cock showed no significant differences between cloud cover (0-50%, 51-100%) for fall-winter, spring or combined. (t-test, $P > 0.05$).

The PM lek attendance was more variable and included 12 (30%) days in which no males attended the lek (Fig. 5) and was significantly less than the AM attendance (t-calc.=5.28, d.f.=76, $P < 0.05$). The fall-winter seasons in the PM accounted for nine absences (75%) with only one (8%) absence during the period of hen attendance.

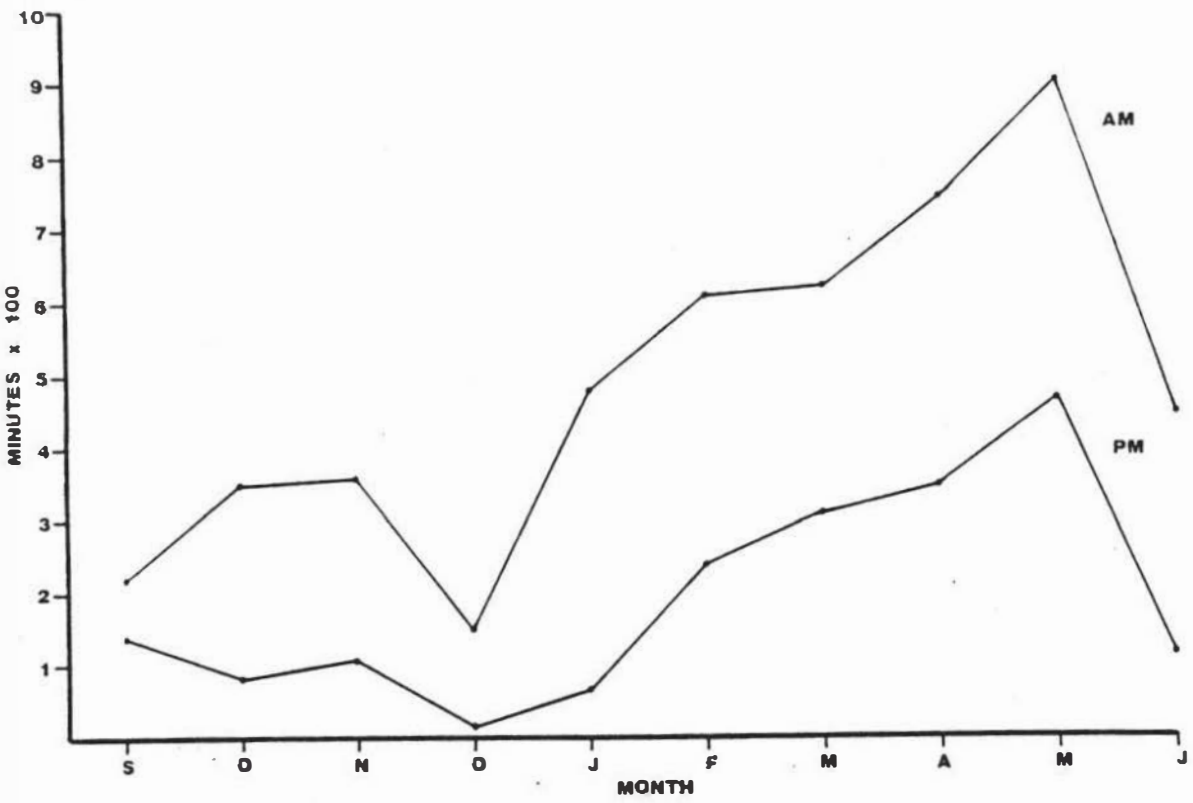

Fig. 3. Number of minutes that prairie-chicken males spent on the lek during the 1982-83 lekking season based on monthly totals of weekly observations.

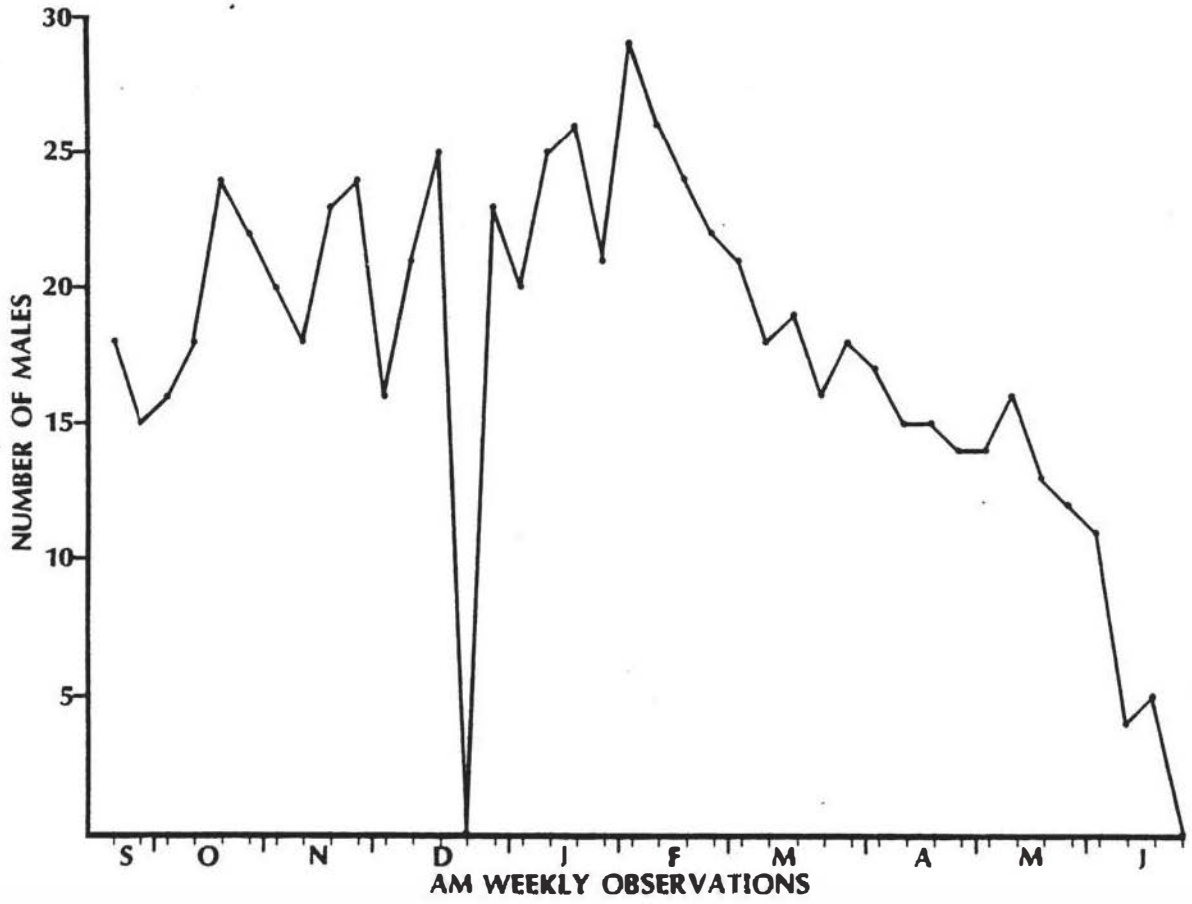

Fig. 4. Peak numbers of prairie-chicken males on the lek during weekly morning observations for the 1982-83 lekking season.

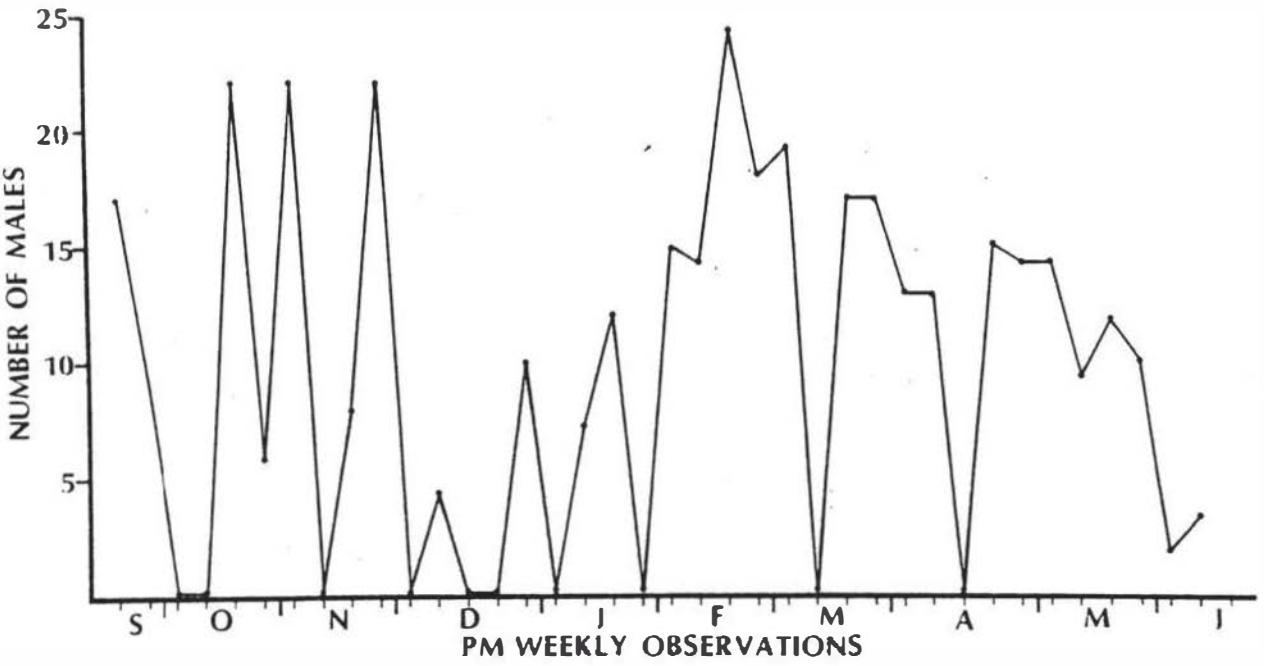

Fig. 5. Peak numbers of prairie-chicken males on the lek during weekly evening observations for the 1982-83 lekking season.

Seven (58%) of the absences during the PM observations were 100% cloudy and five of these were also affected by precipitation. The PM observations appeared to be more affected by weather conditions with significantly less time spent on the lek and a lower Activity Index during periods of cloud cover (51-100%) (t-calc.=2.38, d.f.=34, $P < 0.05$). Attendance level of males and Encounters/Cock were not significantly lower during periods of cloud cover (51-100%). However, differing weather conditions between AM and PM periods in October appeared to cause an AM rise and PM drop in male lek attendance (Table 1). Also, cocks tended to depart from the lek earlier in relation to sunset on cloudy days (51-100% cloud cover) than on clear days (0-50%) (ANOVA, F=13.15, d.f.=1 and 26, $P < 0.05$).

Hens attended the lek in the morning only twice during fall-winter (24 October and 6 November) with one and two females respectively. The hens only stayed a short time foraging in the bean field and the males did not respond to their presence. Hens appeared during 12 weekly AM observation periods from 10 March to 5 June with the peak on 7 April (Fig. 2). These numbers represent actual weekly counts. The PM peak was on 19 May, with hen attendance from 20 April to 19 May on four occasions. Copulations occurred during ten morning observation periods from 31 March to 5 June and in three evening observation periods from 20 April to 19 May.

Table 1. Peak number of prairie-chicken males on the lek during weekly observations in October with regard to weather conditions.

	Date	Cloud cover (%)	Wind (km)	Precipitation	Number of cocks
AM	7 Oct.	100	10.8	Rain	16
	16 "	0	4.1	-	18
	24 "	0	1.6	-	24
	28 "	75	5.8	-	22
PM	6 Oct.	100	8.3	Rain	1
	15 "	50	16.7	-	0
	23 "	0	7.5	-	22
	27 "	40	12.5	-	6

The Activity Index increased steadily from September to a peak in April except for a small decline in December (Fig. 6). Seasonal trends in AM and PM Activity Indices were similar, although the overall PM activity was 70.3% less (t-calc.=3.35, d.f.=57, $P < 0.05$). Fall-winter Activity Index levels for both AM (t-calc.=3.18, d.f.=33, $P < 0.05$) and PM (t-calc.=2.38, d.f.=22, $P < 0.05$) were significantly lower than spring levels. The fall-winter Activity Index averaged 60.26/day for the AM period and increased almost two-fold to 117.95 in the spring. The PM activity index averaged 26.38 and 61.91 for fall-winter and spring, respectively.

Seasonal trends in activity of prairie-chickens as measured by Encounters/Cock (Fig. 7) was similar to the Activity Index (Fig. 6). Both AM and PM Encounters/Cock increased gradually to the spring peak in April. This was followed by sharp declines in May and June. However, the Encounters/Cock in the AM and PM period were not significantly different during periods of lek attendance (matched pairs t-test, $P > 0.05$). The AM mean encounters/cock/daily observation periods were 1.36 and 2.10 while the PM was 1.28 and 2.13 for fall-winter and spring, respectively; both represent significant differences (t-calc=3.38, d.f.=33, $P < 0.05$) for the AM and (t-calc=2.38, d.f.=22, $P < 0.05$) for the PM.

Encounters between males during the fall-winter, although occurring less frequently and less intensively

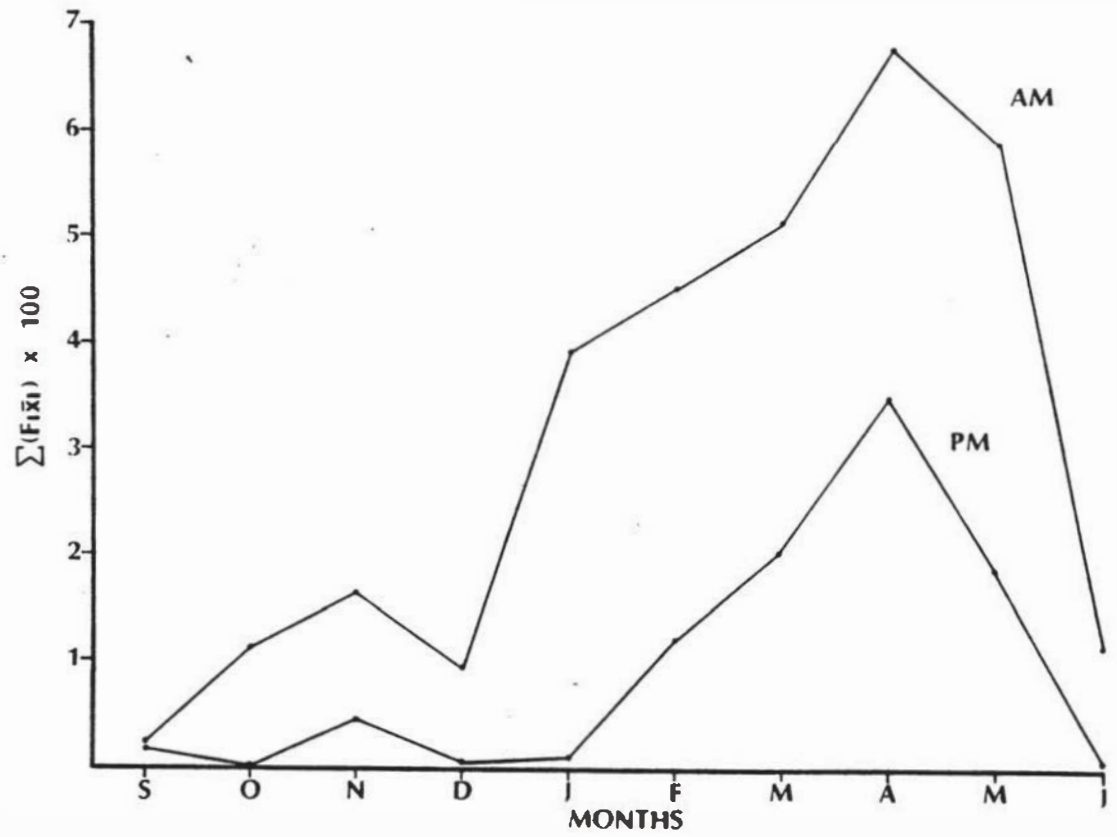

Fig. 6. Activity Index representing monthly summations of $F_i\bar{x}_i$ (see text) over the 1982-83 lekking season.

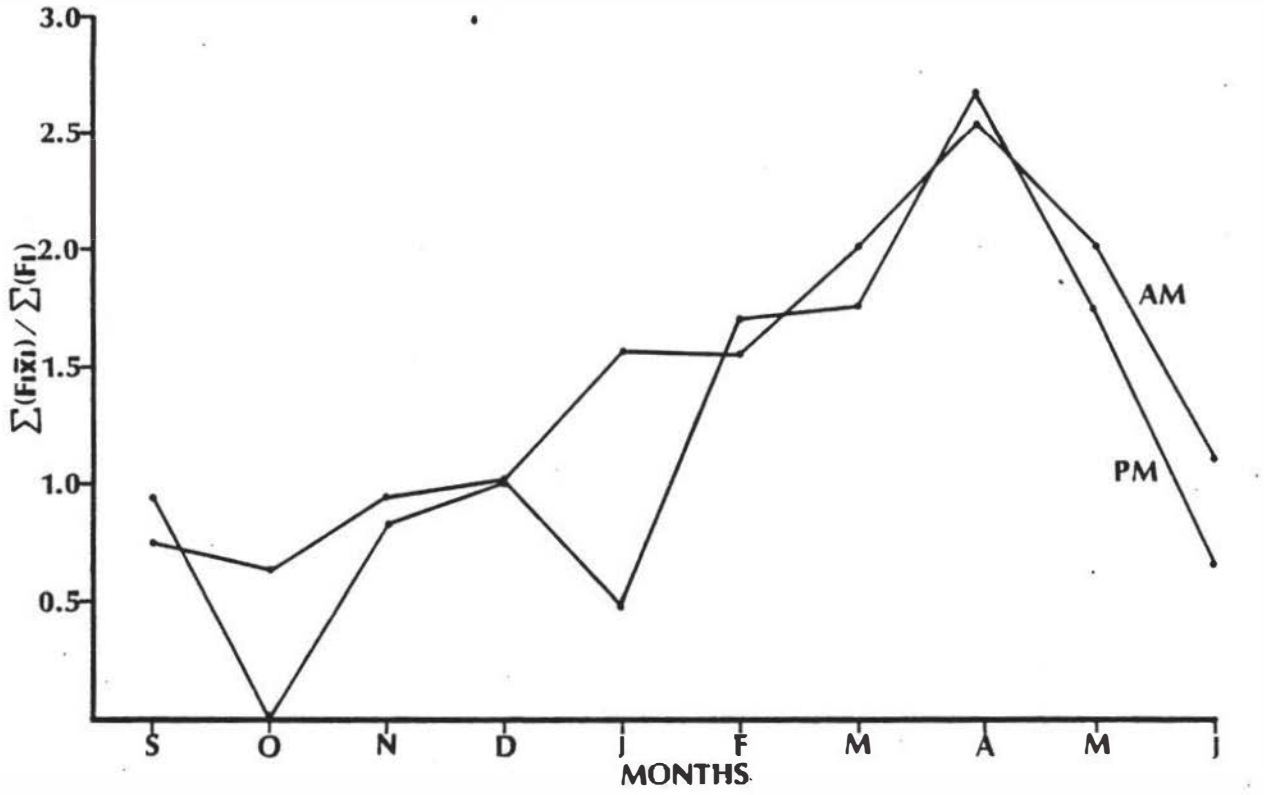

Fig. 7. Morning and evening monthly averages of Encounters/cock of prairie-chicken males on the lek for the 1982-83 lekking season.

than in spring, did include actual fighting with body contact and feather pulling. A major behavior observed at this time involved repeated chasing until the intimidated flew from its opponent. The majority of the lekking activity was from males located in the center of the group. The males toward the periphery were less active, often lethargic and only occasionally displaying. The morning daily Encounters/Cock (DPA) was rather variable for both fall-winter and spring (Fig. 8). The fall-winter included a peak at 1-9 minutes after sunrise based on seven observation periods involving 92 males. A higher peak involving only four observation periods and 12 cocks occurred at 80-89 minutes after sunrise. The spring peak involving the most observation periods and numbers of cocks occurred at 1-9 minutes after sunrise. The two highest peaks occurred at 130-139 and 180-189 minutes after sunrise, however these peaks were based only on 16 cocks/three observation periods and six cocks/one observation period, respectively. The evening daily Encounters/Cock for the spring revealed three distinct peaks (Fig. 9). The spring peak based on the most cocks (32) and observation periods (5) was at 50-59 minutes before sunset. The fall-winter evening peak with the largest number of observations (5) and cocks (38) occurred at 20-29 minutes before sunset.

The time males arrived and departed from the lek varied seasonally with respect to sunrise (Fig. 10),

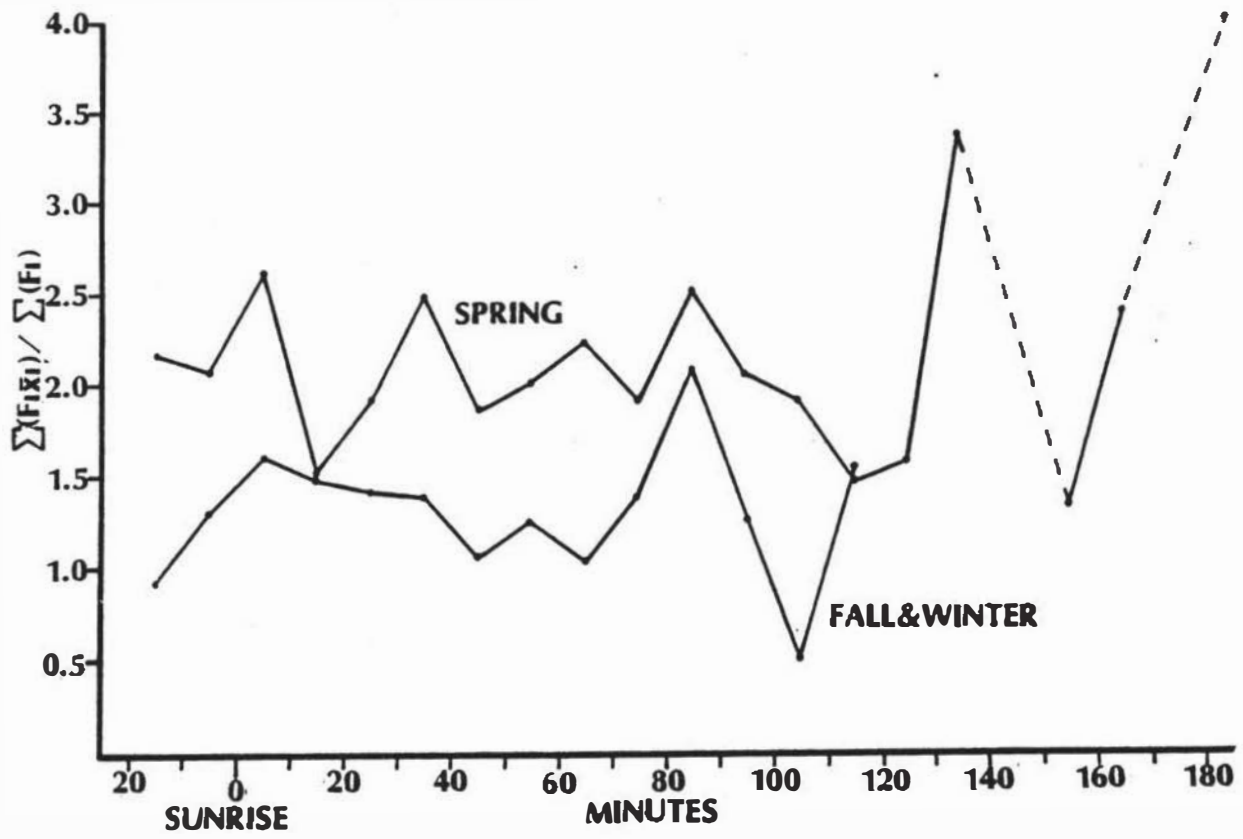

Fig. 8. Daily patterns of aggression (DPA) of males on the lek for ten-minute time blocks before and after sunrise during the 1982-83 lekking season. Dashed lines connect ten-minute time blocks, with no data between.

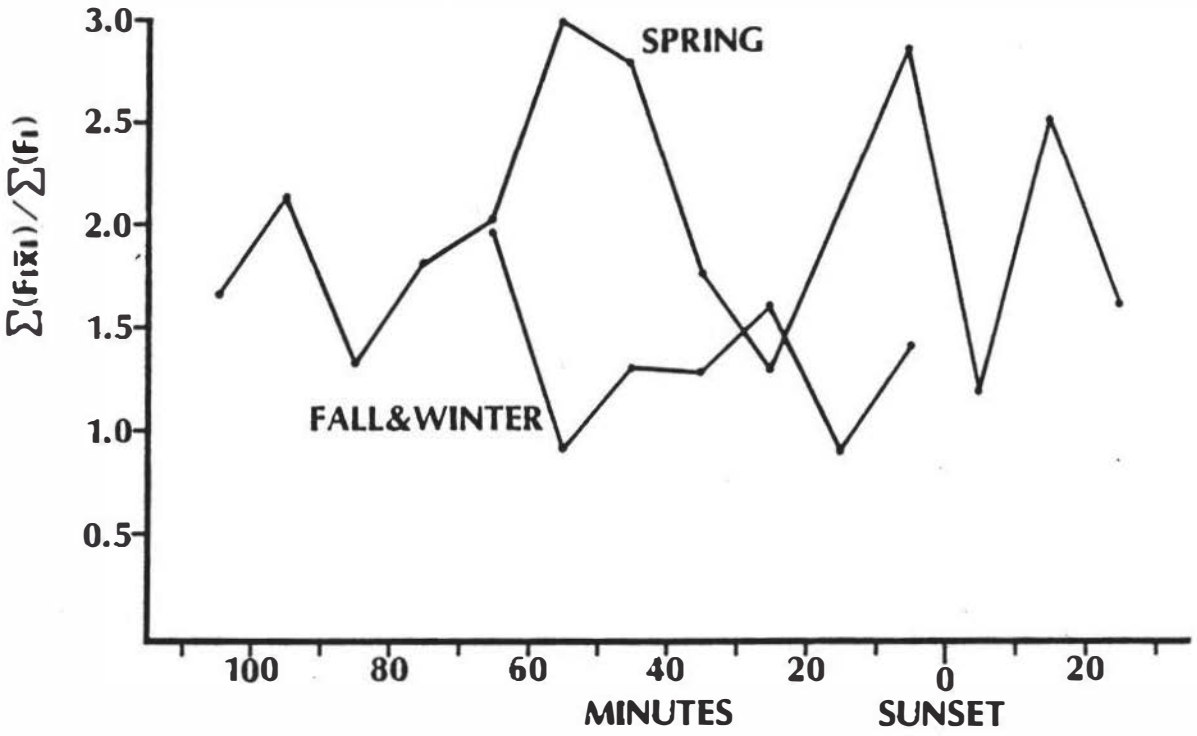

Fig. 9. Daily patterns of aggression (DPA) of males on the lek for ten-minute time blocks before and after sunset during the 1982-83 lekking season.

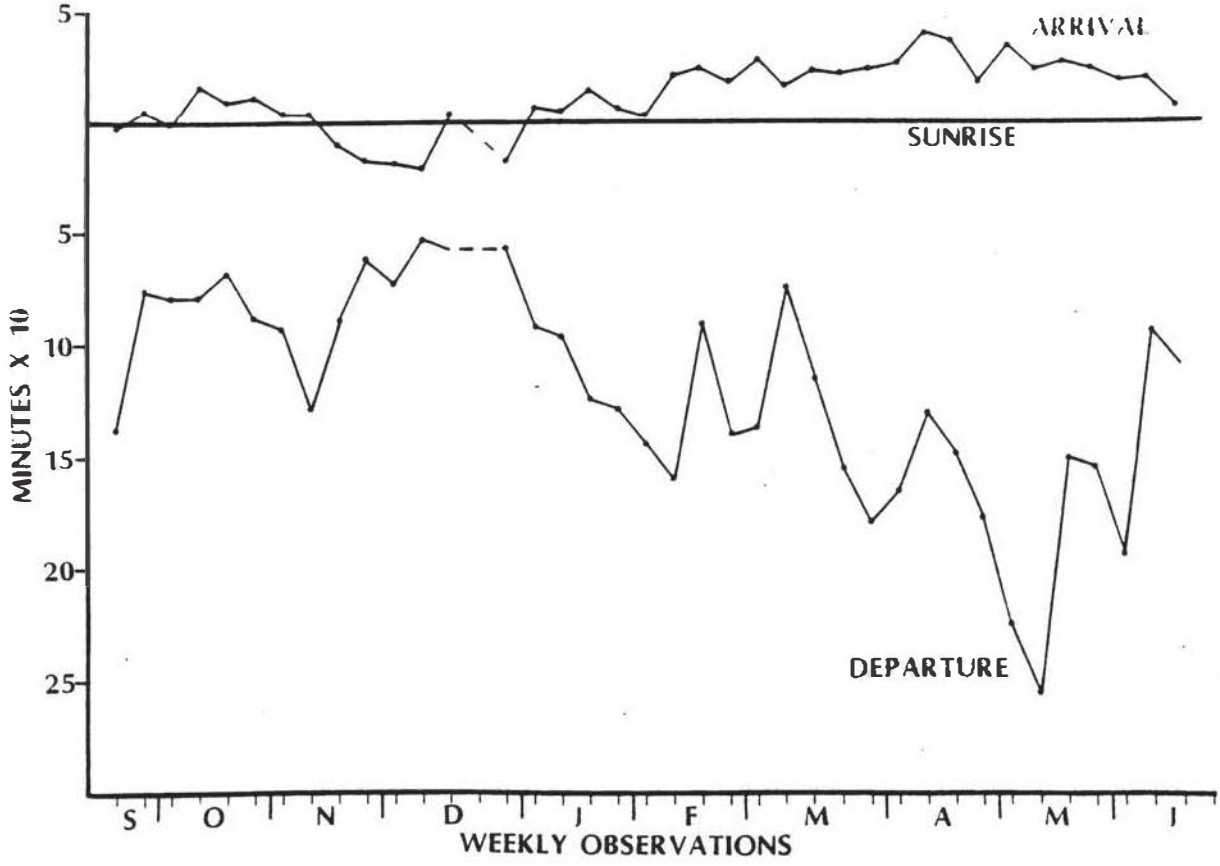

Fig. 10. Morning arrival and departure times (minutes before or after sunrise) of males to the lek during weekly observations over the 1982-83 lekking season. The dashed lines represent weekly observations without males in attendance on the lek.

sunset (Fig. 11) and also appeared to be correlated with the photoperiod (Fig. 12). Fall-winter arrival times often occurred near or after sunrise with the shortest photoperiods. During the spring with increased photoperiods they consistently arrived 20-40 minutes before sunrise. The amount of time spent on the lek increased to a peak in May. Since arrival times remained relatively stable, the departure times became progressively later through the spring. During the longest photoperiods in June, arrival and departure times again begin to narrow. The PM arrival times (Fig. 11), although more variable than AM arrival times, also appear to be associated with photoperiod that is, arrival times in the PM were earlier as the photoperiod lengthened.

Cloud cover affected arrival and departure times at the lek for both morning and evening. Average morning arrival times occurred 14.05 and 9.23 minutes before sunrise for clear (0-50% cloud cover) and cloudy (51-100% cloud cover) days, respectively. Mean departure times for the AM period were 115.76 and 125.09 minutes after sunrise for clear and cloudy days, respectively. However, these differences were not significant (ANOVA, $P > 0.05$). Average evening arrival times were 73.28 and 58 minutes before sunset for clear and cloudy days, respectively (not significant, ANOVA, $P > 0.05$). Evening departure times are significantly earlier with 51-100% cloud cover (average of 2.8 min before sunset) than on days with 0-50%

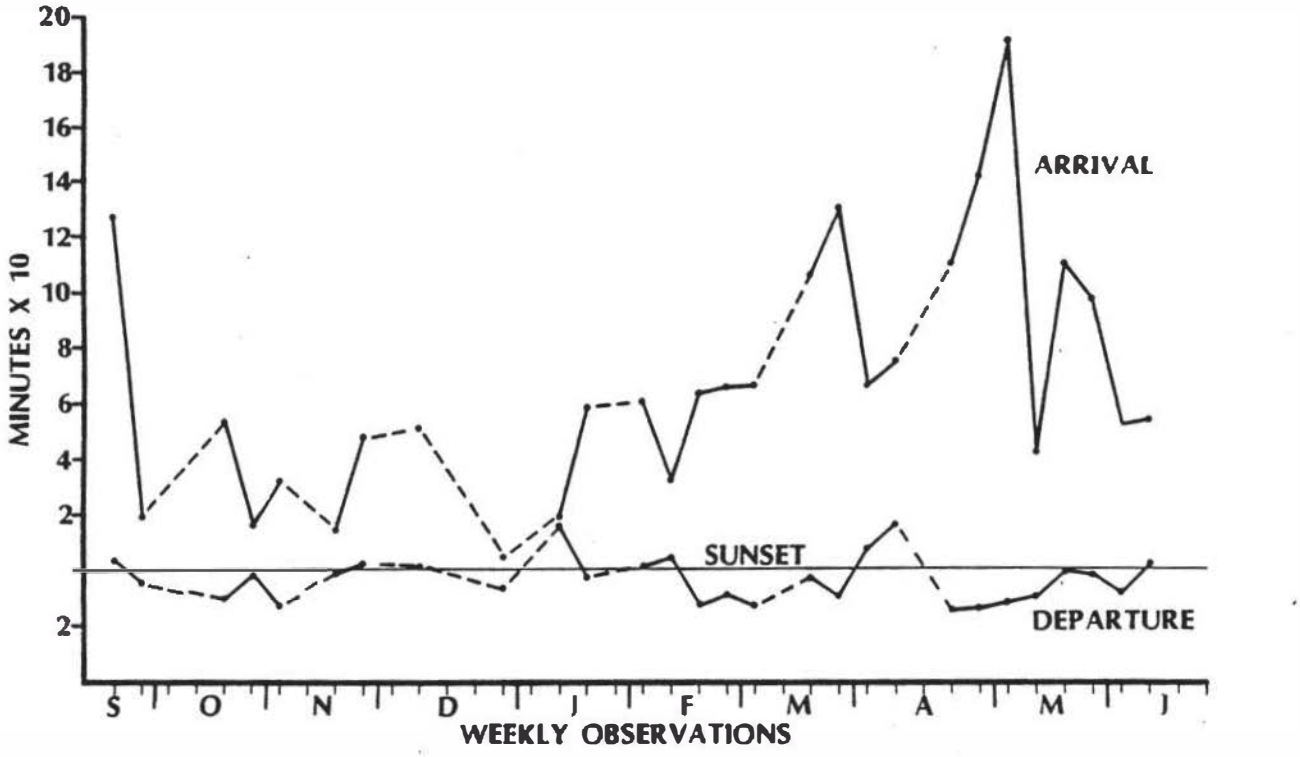

Fig. 11. Evening arrival and departure times (minutes before or after sunset) of males to the lek during weekly observations over the 1982-83 lekking season. The dashed lines connect dates that are more than one week apart, due to no male attendance.

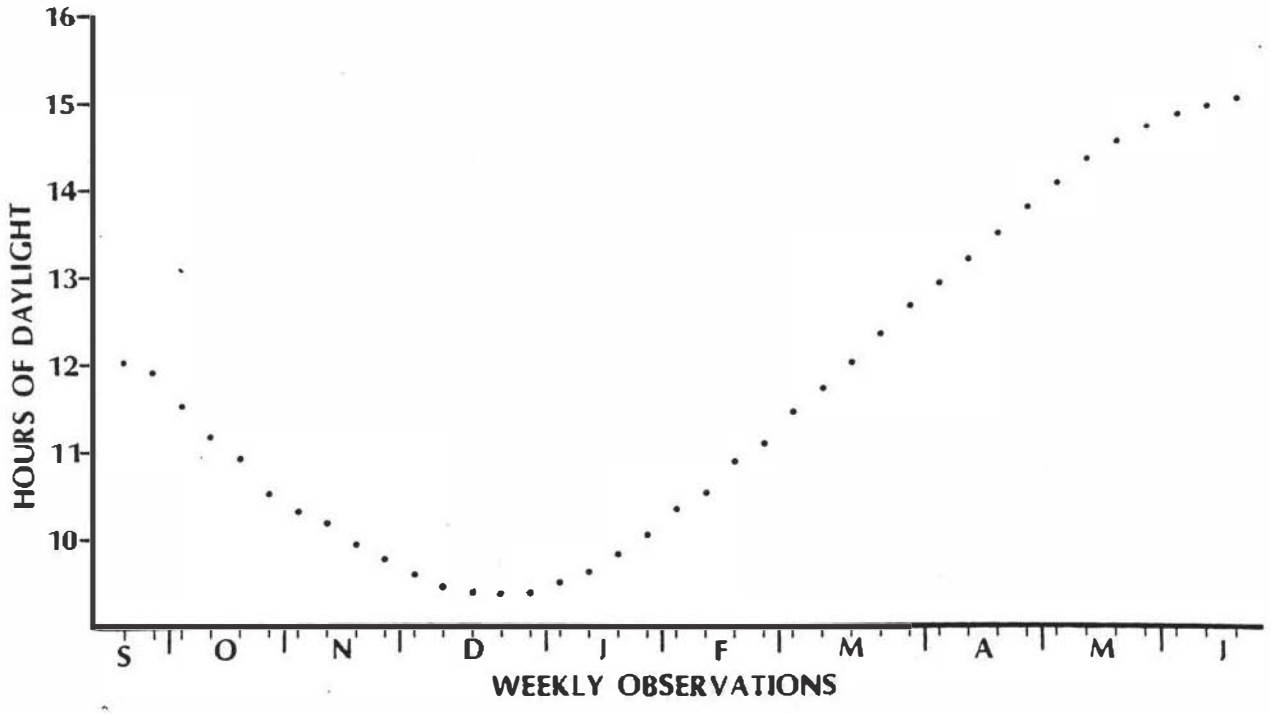

Fig. 12. Photoperiod for each weekly observation period throughout the 1982-83 lekking season.

cloud cover (average of 7.05 min. after sunset) (ANOVA, $F=13.15$, d.f.=1 and 26, $P < 0.05$).

Display Behavior

The fall lek display was similar to that of spring except it appeared to be less developed. Displays and calls characteristic of spring develop as the season progresses (Table 2). The fall booming consisted of only one note of the normal spring three-noted booming sequence. The first three-noted boom was heard on 24 October 1982, with only a few males participating, then by 7 November 1982 the majority were uttering the three-noted sequence. However, this complete sequence was less intense and not as distinct or resonant as that of spring. During the fall-winter, males commonly boomed in an upright position with the pinnae not fully erected. Forward booming postures with erect pinnae were also seen during fall-winter, but they occurred less frequently and only during periods of peak activity. The characteristic sound of spring booming was reached gradually with booming becoming more pronounced in February and by the first of March it was very similar to that of spring.

The fall apteria was smaller and peachy in color; it had changed to pale orange by approximately 5 January. The bright orange characteristic of spring was not prevalent until about 19 February. Initially the males

Table 2. Progressive establishment of displays and calls that are characteristic of spring behavior throughout the 1982-83 lekking season.

Display or call	Time first observed	
	AM	PM
Upright cackle	7 November	24 November
Tail flicking	7 November	7 November
Stamping roll	29 December	19 February
Whoop	5 February	19 February
Flutter jump	19 February	24 March
Forward rush	3 March	21 April
Nuptial bow	31 March	21 April
Booming		
1 note	25 September	25 September
2 "	16 October	24 October
3 "	24 October	24 October
Apterial		
partial	25 September	25 September
full	5 February	10 February
Eyebrow combs		
partial	19 January	19 January
full	24 February	3 March

were not fully molted, however, by 7 October some tails were completely molted and by 16 October all tails were molted. The pinnae molting was largely completed by 24 October.

INTERSPECIFIC ENCOUNTERS

Prairie-chickens were observed to interact with five avian species during this study: northern harrier, rough-legged hawk (Buteo lagopus), American kestrel (Falco sparverius), American crow (Corvus branchyrhynchos) and the ring-necked pheasant. Although common in the area, short-earred owls (Asio flammeus), great horned owls (Bubo virginianus) and red-tailed hawks (Buteo jamaicensis) were not seen near the lek. Prairie-chickens were also observed turning around rapidly as a flock of mourning doves (Zenaida macroura) and barn swallows (Hirundo rustica) flew over the lek on 4 May 1983. Mammals were not seen interacting with prairie-chickens on the lek. The northern harrier accounted for 97.3% of the total interactions observed (Table 3). Northern harriers invoked a response 260 times throughout this study, 196 (75%) in the morning and 64 (25%) in the evening. I also observed 32 additional flushes by northern harriers from roost sites and feeding areas near the lek. The peak of harrier vs. prairie-chicken interactions was February with a smaller

Table 3. Prairie-chicken responses to avian visitors of other species on the lek during the 1982-83 lekking season.

	Northern Harrier					American Crow	Rough-legged Hawk	American Kestrel	Ring-necked Pheasant	Barn Swallow	Mourning Dove
	AM			PM							
	Male	"Female"	?	Male	"Female"	?						
All flush	5	34	2	0	1	-	2	-	-	-	-
Some flush	24	89	1	11	25	1	-	1	-	-	-
All squat	-	1	-	-	-	-	-	-	-	-	-
Some squat	2	-	-	4	-	-	-	-	-	-	-
Weak reaction	16	12	2	8	9	1	-	-	2	1	1
No reaction	3	5	-	-	-	2	-	-	5	-	-
	50	141	5	23	35	4	2	1	7	1	1

fall peak in November for both morning and evening observations (Fig. 13). The majority (80%) of the interactions occurred before the first hen attendance on 10 March 1983.

Harriers were never seen to make contact with a prairie-chicken although they did extend their talons on several occasions. The typical harrier behavior was to "dive-bomb" or swoop at the displaying or loafing prairie-chicken males, often repeating this action until all the males had flushed from the lek. Harriers also pursued prairie chicken males, and with repeated harassment often flushed them over 0.4 km from the lek. Prairie-chicken males would also flush at the sight of a harrier as it flew non-aggressively over the booming ground. Prairie chickens responded more strongly to harriers in the fall-winter than in the spring (chi-square calc.=10.82, d.f.=3, $P < 0.05$). In the fall-winter there were more "all flush" and "weak reaction" responses, with less "some flushes", "no reactions", "all and some squats". Prairie-chickens appear to respond differently to "female" and male northern harriers' harassment (Table 3). "Female" encounters ended with all or some flush, 85% of the time, while only 55% of the male encounters ended with these responses. "Females" were responsible for 87.5% of the 40 "all flush" responses in this study. When the four responses, all flush, some flush, weak reaction and no reaction are considered between male and "female"

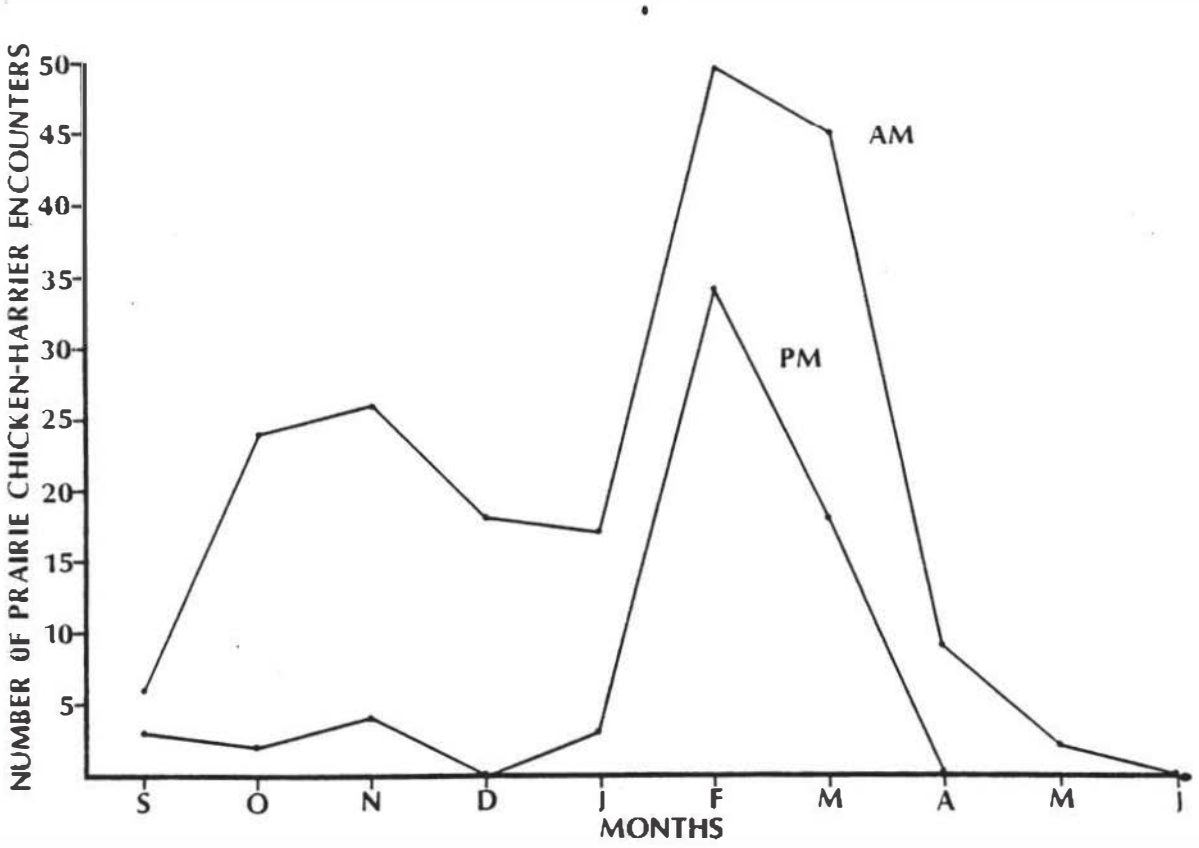

Fig. 13. Monthly total number of prairie-chicken vs. northern harrier encounters over the 1982-83 lekking season for both morning and evening.

harriers, there was significantly more reaction to the "female" (chi-square calc.=20.78, d.f.=3, $P < 0.05$). In certain instances, prairie-chicken cocks refused to flush and fought back by alternating squatting with jumping at the swooping harrier. Prairie-chickens exhibited this behavior on four occasions to male harriers and twice to "female" harriers, with the "female" harrier hoovering over the fighting male prairie-chicken.

Crows, although not a potential predator, also were observed harassing prairie-chickens (Table 3). Crows swooped three times at displaying males causing them to be in an alert upright position. A crow showing no aggressive behavior as it flew over the lek caused one male prairie-chicken to flush.

Cock pheasants disturbed prairie-chicken males on the booming ground on two of the seven days pheasants were known to be present during the 1982-83 lekking season. Six of the seven visits by cock pheasants and the two confrontations occurred during the fall-winter. Cock pheasants were seen near prairie-chickens on three occassions with no apparent reaction from either bird species. In one instance the distance between birds of the two species was only 2 m. In another instance, two cock pheasants were feeding unaggressively within 4 m of a prairie-chicken; however, when the prairie-chicken began to run away, one pheasant pursued until the prairie-chicken stopped. An interaction on the morning of

25 September 1982 resulted in the prairie-chicken dominating the encounter:

> 0758: The pheasant cock ran between three prairie-chicken males. One of the prairie-chicken males advanced toward the pheasant on three occasions, each time the pheasant jumped up and back. The pheasant then lowered his head, raised his tail and ran approximately three meters away from the prairie-chickens, then repeated the same head lowering, tail raising behavior several times in close proximity to a displaying male prairie-chicken.
> 0802: Another confrontation occurred much in the same manner as before, except that the pheasant retreated to the edge of the bean field and left the lek at 0804.
> 0816: The same pheasant returned to the lek and was feeding near the prairie-chickens.
> 0818: One male prairie-chicken ran directly at the pheasant, it jumped up and flew about 3 meters. The prairie-chicken advanced again and the pheasant flew from the area.

Discussion

Wittenberger (1978), DeVos (1979), Wrangham (1980), and Bradbury (1981) have postulated that the evolution of lek mating systems in grouse is partially based on the

intersexual selection component of sexual selection. Theories of female choice assume that males are selected on the basis of phenotypic traits which reflect genetic quality (Fisher 1958). It is reasonable to assume that female mating preference for the center of the lek (Robel 1967, Hamerstrom and Hamerstrom 1973, DeVos 1983) and intense competition by males for these sites are related. Social dominance and competitive vigor of males affect their place on the lek and only the most dominant males occupy the critical central territories (DeVos 1979). This limited chance for reproductive success has likely resulted in strong lek site attachment. Prairie-chicken males in this study spent approximately 24% of the daylight hours from mid-September to mid-June on the lek during the 1982-83 lekking season. Moyles and Boag (1981) and DeVos (1983) consider territory establishment and maintenance as primary reasons for fall-winter lek site attachment. I found that activity centered on male to male interactions during the fall-winter. Except for male to female interactions, all spring behavioral traits were exhibited in fall-winter although generally at lower intensities. The data on amount of time spent on the lek and on levels of aggression suggests that it is advantageous for males to attend the lek throughout fall-winter or the expenditure of this energy would have not evolved.

Schwartz (1945) found that the number of males occupying a booming ground was not constant throughout the season, but that attendance at both daily periods was less regular early and late in the season. Similar patterns were seen in this study with irregular attendance being observed for both AM and PM in the fall-winter (Figures 4 and 5). Spring, however, resulted in a more constant number of males on the AM and PM lek. Schwartz (1945) also reported the maximum number of males using a booming ground was most accurately indicated by the number observed around sunrise during the peak of the season. However, this study and that of Robel (1966, as cited by Hjorth 1970) indicated the maximum number of males occurred early in the season (Fig. 2). The numbers during April were 40% less than those in February, presumably due to the dispersal of males associated with the formation of additional booming grounds.

Activity of prairie-chicken males on the lek is complex and difficult to quantify accurately. Factors influencing competeting males include: time spent on the lek, encounters/cock, number of males involved in aggressive encounters and daily attendance. Although the number of encounters/cock may remain constant over days, the time on the lek may increase indicating a stronger lek site attachment. The Activity Index that I constructed incorporates these factors and is an attempt to show seasonal trends of overall activity. The Activity Index

was largely affected by time and daily attendance since similar seasonal fluctuations occurred between the Activity Index and time spent on the lek (Figures 3 and 6). The decline in time spent on the lek in December (Fig. 3) also resulted in a decline in the Activity Index. Sporadic and low evening cock attendance caused both time spent on the lek and the Activity Index to be low. However, the maximum hen attendance in April increased the male aggressive levels enough to cause an April peak in the Activity Index, despite lower levels of time spent on the lek in April.

The number of Encounters/Cock was also used as a measure of activity to represent male-to-male aggression seen during the observation periods regardless of time spent on the lek, daily attendance and total number of males participating. The AM Encounters/Cock did not fluctuate with time spent on the lek or with daily attendance, but increased gradually from September to April. The seasonal increase of the Activity Index was greater (Fig. 6) than that of the Encounters/Cock (Fig. 7) indicating that fall-winter aggression is high relative to the amount of time and daily attendance levels on the lek. Despite these differences both the Activity Index and Encounters/Cock indices peaked in April, the same time period when the number of hens on the lek peaked. This indicates that the presence of females increases male activity, even though there were fewer males on the lek

during April. Schwartz (1945), Robel (1964), and Hamerstrom and Hamerstrom (1973) also report peak male activity during hen attendance. DeVos (1983) stated that the time black grouse spent on the territory/day was greatest during periods of peak hen attendance, because at this time the chance of copulating is highest. I found the maximum number of hens on the lek on 7 April which did not coincide coincide with the peak time males spent on the lek/day (Fig. 3). These data suggest that males are increasing time on the lek, but are decreasing costly aggression in response to low hen numbers. The territorial boundries are so well defined by this time that fighting was replaced by ritualized display-fighting (Hamerstrom and Hamerstrom 1960). Some of these behaviors were not recognized or recorded as aggression in this study. It might be evolutionarily beneficial for males to increase their time on the lek later in the season to ensure fertilization of late and re-nesting females.

The importance of PM lek activity by prairie-chicken males is questionable since attendance and the Activity Index were significantly less than the AM (matched pairs, t-calc.=7.45, d.f.=37, $P < 0.05$). Schwartz (1945) found evening copulations occurred during spring and that fall evening lek attendance was never as regular as in the spring, however, he makes no mention of PM activity levels compared to that of AM. I found that fall-winter PM lek attendance levels were also more variable than that in the

AM, however, Encounters/Cock were not significantly less in the PM throughout the year at times when males attended the lek (matched pairs t-test, $P > 0.05$) (Fig 7). This suggests that the males attending the PM lek, although lower in number and variable in daily attendance, appear to be the more aggressive males associated with central territories. Robel (1970) found that the most aggressive males controlled the central territories and were responsible for a large percentage of the copulations. These males were at least two and one-half years old. The PM lek may be attended by those males who defend central territories from marginal males. The majority (75%) of the days with no males on the lek were in the fall-winter period when hens were not on the lek either AM or PM. Eight percent of days without males on the PM lek were in spring when females were present in the AM. Robel et al. (1970) noted a lower evening preference index for the lek attendance during the spring, but he found no fall-winter evening lek attendance. I saw hens in the evening period only during the spring. The PM period appears to be highly associated with reproductive success if attended by only older more aggressive males during periods of hen attendance. The cost of both morning and evening lek attendance may exceed benefits if chances of reproductive success are low. Therefore, PM attendance may be forfeited by marginal or non-territorial males unlikely to

copulate and by reproductively successful males during periods of unlikely hen attendance.

Schwartz (1945) and DeVos (1983) state that fall-winter lekking activity is largely affected by climatic conditions, with no lek attendance during extended periods of severe weather. The weather during the winter (December, January, and February) of this study was unseasonably mild, with above normal temperatures and little snowfall (U.S. Weather Bureau, 1971-83). Males did visit the lek almost on a daily basis from 25 September 1982 to 23 June 1983, although precipitation and cloud cover affected some aspects of lekking activity during the evening period. Most activity levels were lower during the PM period under ideal weather conditions (Figures 2, 3, and 6), consequently, during unfavorable weather these levels were drastically lowered. For example in October, the monthly mean for the number of males in the PM dropped in contrast to a raise in the AM (Fig. 2), possibly a result of differing weather conditions (Table 1). In December all but three observation periods had 100% cloud cover and a large amount of rain, thus lowering both AM and PM cock counts. Significantly less time spent and earlier departure time from the PM lek occurred during days with cloud cover (51-100%).

The higher and more consistent levels of activity during the AM compared to the PM, appear to be less affected by weather. However, censuses by the INHS have

traditionally shown lower AM cock counts during the severe winter weather of December than during the fall or subsequent winter or spring periods (R. L. Westemeier, pers. commun.). Ideal conditions for spring prairie-chicken activity, according to Hamerstrom and Hamerstrom (1973), are clear, still, and frosty mornings; the ideal temperature range is about 25-40°F (-3.8 to 4.4°C). They state that warm, windy and rainy mornings decrease overall activity and may deter it completely. The only winter morning with no males in my study, was similar i.e. warm (11.7°C) 100% cloud cover and rainy. Although other mornings of 100% overcast and rain were attended by males and were associated with delayed arrival and extended departure times resulting on days with 51-100% cloud cover, but not at significant levels. The division of cloud cover into 0-50% and 51-100% and my tendency to avoid periods of severe weather during flexible, weekly observations probably resulted in the AM period showing no significant activity decreases with cloud cover 51-100%.

Robel (1964) concluded that "booming activity" of greater prairie-chickens increased as the photoperiod lengthened, and then decreased as temperatures rose above 18°C to 20°C. The Activity Index in this study likewise increased to April (Fig. 6) and the time spent on the lek increased through May; both factors parallel the increase in the photoperiod (Fig. 12). Also, arrival and

departure times became earlier and later, respectively as the photoperiod increased. Time spent on the lek then decreased from May to June with rising temperatures (10.8oC to 17oC and 18.3oC to 21.7oC for the mean low and high temperatures, respectively). The wet spring of 1983 delayed tillage practices and annual weed growth as tall as 60 cm was common. Prairie-chicken males prefer short cover or no cover for booming (Schwartz 1945). It appears that several factors appear to be involved in the termination of lek attendance.

Schwartz (1945) and Hjorth (1970) describe imperfect greater prairie-chicken booming performances during situations when tendencies to display are low or when the structure of the reproductive organs are not fully developed. These are most likely to occur at the beginning and end of the season, at the end of the morning period, during the middle of the day, and at the beginning of the evening period. Each display is best developed and most intense in the spring (Hamerstrom and Hamerstrom 1955) and even then only after hens attend the lek. I found that fall-winter booming performances were imperfect or "listless" and developed slowly. It is difficult to quantify lek display behavior, but it is possible to record dates these behaviors were first seen (Table 2). There was also individual variation among these traits with some males displaying more normal behaviors than others.

Schwartz (1945) reports that the tempo of lekking activity increases rapidly to a peak about sunrise and at the height of the season it is maintained with little diminuation until the end of the AM period. A similar pattern in this study demonstrated peaks for both fall-winter and spring during the time period of 1-9 minutes after sunrise. This level was relatively constant with minor fluctuations and was maintained for about two hours. Activity during the evening, rather than peaking at sunset as reported by Schwartz (1945), had three distinct peaks : before, near, and after sunset. These males are aggressive upon arrival to the lek, then a semi-lethargic period follows until near sunset, at which time the aggression increased.

Prairie-chicken male activity can be influenced throughout the daily booming periods by hen arrivals and or by the presence of raptors in the area. The tempo of activity usually increases as hens arrive, although it fluctuates as males depart from and return to the lek during periods of raptor harassment. Berger et al. (1963) report that rough-legged hawks pose virtually no threat to adult prairie-chickens, but they respond to them as strongly as they do to red-tails due to the similar size of the two raptor species. Two such instances occurred in this study as an "all flush" response occurred as a rough-legged hawk flew high and at a considerable distance (50 m) from the booming ground. American kestrels are also

known to elicit responses by prairie-chickens (Berger et al. 1963, Sparling and Svedarsky 1978). One "some flush" response elicited by a kestrel was noted in this study. Northern harriers are not considered serious predators of adult prairie-chickens on or off the the lek during the spring [Yeatter (1943), Schwartz (1945), Berger et al. (1963), Anderson (1969) or Sparling and Svedarsky (1978)]. However, most of them report persistent harassment of prairie-chickens by harriers on the booming ground; these results are largely congruent with their observations. Although uncommon, Berger et al. (1963) report that harrier harassment was severe enough to interfere with breeding behavior. The frequent harassment on and off the booming ground throughout the year is not likely to lower the reproductive success of the prairie-chicken, however, it seems reasonable to assume that there is an energy cost to both species. In general, the results of this study agree with previous research on northern harrier encounters with prairie-chickens, however, several noteable differences did occur. I found, for example, 3.25 encounters per blind sitting which was higher than Berger et al. (1963), Anderson (1969) and Sparling and Svedarsky (1978) (Table 4). The considerable difference I observed could have resulted, in part, from differences in methodology used in recording data. I recorded prairie-chicken responses to each aggressive move by the harrier (i.e. one interaction = each swoop or dive by the

Table 4. Comparison of data from studies of prairie-chicken vs. northern harrier encounters.

	Berger et. al. (1963)	Anderson (1969)	Sparling and Svedarsky (1978)	This study
Number of encounters	881	661	34	260
Years of data	21	7	2	1
Blind sittings	4745	2115	-	80
Additional man mornings observing at greater distances	400	50	-	-
Hours of observations	-	-	673	218
Encounters/blind sitting	0.17	0.30	-	3.25[a]

a The large difference with previous studies may, in part, be due to differences in methodology.

harrier which elicited a response or if the harrier flew near the lek and caused a response). Berger et al. (1963) considered an encounter to be any raptor presence on or above the booming ground close enough to have an effect in behavior. Sparling and Svedarsky (1978), however, recorded an encounter to be any time a visitor was observed within a quarter of a mile of the display ground at altitudes of less than twenty feet and which affected grouse behavior. There is no mention of how each swoop or dive are recorded.

The increased northern harrier vs. prairie-chicken encounter rate that I observed was probably also enhanced by the inclusion of fall-winter observations to those made in spring. Schwartz (1945) reports that in the fall season, prairie-chickens are more frequently flushed by marsh hawks and crows. The fall-winter observations accounted for 80% of the encounters in my study, and 25% of the total interactions were seen during the evening observations. The males during the fall-winter were more likely to respond by "all flushing" rather than some flush, or they remained on the booming ground in a squatting fashion. It is interesting to note that Sparling and Svedarsky (1978) report males are less likely to flush while females are on the lek.

Raptor mirgration patterns also influcence rates of prairie-chicken harassment. The peaks of harassment in November and February (Fig. 13) coincide with fall and

spring migration of the northern harrier through east-central Illinois (L. B. Hunt, Eastern Illinois University, pers. commun.). The mild weather and light snowfall probably enhanced the number of harriers that wintered on the sanctuaries, thus prompting an increase in interactions.

Prairie-chickens responded differently to male and "female" harriers, which are dimorphic in size. Adult female harriers weigh approximately 50 percent more than adult males (Berger et al. 1963). The "females" elicited stronger responses, since they are potentially more dangerous as a predator. I found that of 40 "all flush" reactions 87.5% were to "females", which was higher than those observed by Berger et al. (1963) and Anderson (1969) who indicated that 67.9% and 72% respectively of their "all flush" responses were to "females".

Vance and Westemeier (1979) indicate that harassment of prairie-chickens by pheasants is greatest during the spring when both species are defending territories, often disrupting breeding activities on the booming ground. Pheasants usually dominate prairie-chickens in aggressive encounters (Harger 1956, Sharp 1957, Anderson 1969, Vance and Westemeier 1979). I found the presence of pheasants on the study lek occurred primarily (85%) during the fall and winter. Cock pheasants were common around the study lek; they were seen or heard on 53 (66%) of the observation periods. However, presence of, and harassment by

pheasants should be considered as sporadic throughout the year and from my weekly observations, harassments of prairie-chickens on the study lek appeared to be of little consequence.

This study was not able to evaluate data on individual prairie-chicken males or on reproductive success by age class, or seasonal territorial shifts within the lek, since the birds could not be banded due to their endangered status. It is reasonable to assume that the significance of multi-seasonal lek attendance is highly correlated with territorial establishment and maintenance, which eventually leads to increased reproductive success by those prairie-chicken males at the top of the dominance hierarchy. Additional research involving banded males is needed to determine the ultimate role of why prairie-chicken males devote large amounts of time and energy exhibiting territorial behavior over an extended time period when the actual breeding takes place within a relatively narrow time frame.

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