REPRODUCTIVE IMPORTANCE OF DOMINANT MALE GREATER PRAIRIE CHICKENS

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THE breeding display of Greater Prairie Chickens (*Tympanuchus cupido pinnatus*) has been described by several authors (Breckenridge 1929, Bent 1932, Hamerstrom 1941, Schwartz 1945, Hamerstrom and Hamerstrom 1960, Robel 1964). All mentioned the importance of aggressive behavior and territoriality during the display season.

Previous research on Prairie Chickens in Kansas has shown that socially dominant males are responsible for most copulations on booming grounds (Robel 1970). Mating success of males has been correlated with social rank, which was characterized by different levels of aggression (i.e. dominant males highly aggressive).

During 1970 and 1971 we studied the importance of dominant males within a stabilized booming ground social organization, especially as related to reproductive success. Our study involved observing male and female behavior both before and after the removal of dominant males from a booming ground.

METHODS

The study area is 15 km east of Junction City in Geary County, Kansas, on the western edge of the Flint Hills where the dominant vegetation consists of big bluestem (*Andropogon gerardi*) and little bluestem (*Andropogon scoparius*). For descriptions of vegetation and topography see Robel et al. (1970).

We watched a booming ground from a blind about three mornings per week during the springs of 1970 and 1971. Our observations began approximately 1 hour before sunrise and lasted 2 to 3 hours, depending on bird activity.

Male Prairie Chickens were live-trapped on the booming ground with cannon nets. For descriptions of trapping techniques see Silvy and Robel (1967, 1968). Captured males were marked with colored plastic leg bands to facilitate individual recognition. Age of captured males was ascertained by examining the wear on primary tips (Ammann 1944). We referred to captured adult males as AM-(band number), captured juvenile males as JM-(band number), and males we did not capture and therefore could not age as M-(number). Uncaptured males were identified by plumage character and their location on the booming ground.

Each spring was classified as a separate experiment: Experiment I for 1970 and Experiment II for 1971. Each experiment was then classified into separate phases, based upon removal dates and changes in behavior: Experiment I into four phases and Experiment II into three phases.

Male attendance was classified as regular and irregular. Regular attendance occurred when a male established a territory and was present for at least 3 continuous observation days. Irregular attendance occurred when an individual failed to establish a territory and/or remained on the ground for less than 3 continuous observation days.

We recorded numbers of males, female visits, copulation attempts, aggressive encounters, and individual behavioral characteristics during each phase. Each male's territory was determined by recording its position at 15-minute intervals, then plotting the smallest area containing 70% of the sightings. Robel (1966) used 50, 70, and 90% of each bird's location record to plot territories. As he found a relationship between each of the percentages plotted and mating success, we chose the 70% figure to simplify presentation in this paper. Because time limitations prevented our recording territory sightings on all of the regular males present, we chose birds that appeared to be important to the analysis. Territories of birds for which we had relatively few location sightings are hand drawn on territory maps to illustrate the booming ground organization.

We used territory size and position, number of aggressive encounters and males encountered, and individual behavioral characteristics as indices of a bird's standing in the social organization. We classified males as alpha, beta, or gamma depending upon combinations of the above criteria. We tallied an aggressive encounter whenever two males met and exhibited fighting tendencies. An aggressive encounter includes ritualizations that in most instances resulted in active combat. Social organizations refers to the male hierarchy and the spatial arrangement of territories.

The number of successful copulations per male was our index of mating success. We were able to ascertain the difference between successful and unsuccessful copulations by noting both male and female behavior (Ballard 1971). During successful copulations the male usually spent 10 to 15 seconds on the female, whereas during unsuccessful attempts the male was knocked off upon mounting. Following successful copulations, females spent 20 to 30 seconds ruffling their feathers, after which they left the ground within 5 minutes. In contrast, following unsuccessful attempts, hens did not ruffle feathers nor did they leave the ground, but stayed for more courting activity.

RESULTS

EXPERIMENT I

Phase I.—During this phase (26 March to 3 April 1970, 7 observation days) behavioral traits were recorded to ascertain alpha and beta individuals. Nine regular males were present during Phase I; irregulars varied from zero to three.

We recorded 186 territory-location sightings and 150 aggressive encounters (Table 1). Territories for regular males are shown in Figure 1. Bird AM-10 had the largest number of aggressive encounters, interacted with five other males, had the third largest and most central territory, and was considered the alpha male. Bird AM-17 was determined to be the beta male.

Prior to and during Phase I, two irregular males (AM-8 and JM-9) attempted to establish territories, but were repeatedly driven off. Bird JM-9's last attempt to establish a territory was on 22 March, while AM-8 continued to attempt territory establishment throughout Phase I.

We witnessed 14 female visits during Phase I, but saw no attempted copulations. Females appeared unreceptive to courting males.

The alpha and beta males were shot on 3 April, initiating Phase II.

TABLE 1

MALE PRAIRIE CHICKENS ENCOUNTERED REGULARLY DURING EXPERIMENT I

Bird number	Number of location sightings	Territory area (m^2)	Number of males encountered	Number of aggressive encounters
Phase I				
AM-10	38	122.5	5	65
AM-11	29	87.5	6	55
AM-12	31	105.0	7	40
AM-13	32	130.0	5	28
AM-14	—	—	3	6
AM-15	—	—	2	5
AM-17	29	195.0	8	35
M-18	27	62.5	5	55
M-19	—	—	5	11
	186			300
Phase II				
AM-8	39	27.5	5	93
AM-11	30	107.5	3	59
AM-12	36	77.5	7	71
AM-13	26	125.0	5	40
AM-14	—	—	5	51
AM-15	16	185.0	5	23
M-18	—	—	8	49
M-19	31	440.0	9	90
	178			476
Phase III				
AM-8	61	70.0	3	258
AM-11	52	92.5	7	153
AM-13	—	—	4	22
AM-14	59	157.5	7	273
AM-15	52	258.8	6	179
M-18	56	147.5	7	328
M-19	62	86.3	5	327
M-20	52	133.8	5	148
	394			1688
Phase IV				
AM-8	28	50.0	4	99
AM-11	22	80.0	5	36
AM-14	51	310.0	7	159
AM-15	40	152.5	6	131
M-18	39	225.0	8	159
M-19	36	82.5	6	137
M-20	29	180.0	3	68
M-35	25	117.5	4	63
	270			852

Phase II.—After the shots the remaining males flushed from the ground, but returned within 10 minutes. A void space was evident on the ground on their return. Remaining males did not enter into the empty territories. Bird AM-8, which had been attempting to establish a territory during Phase I, was now allowed to display on the ground. We continued watching the ground from 7 to 15 April (6 observation

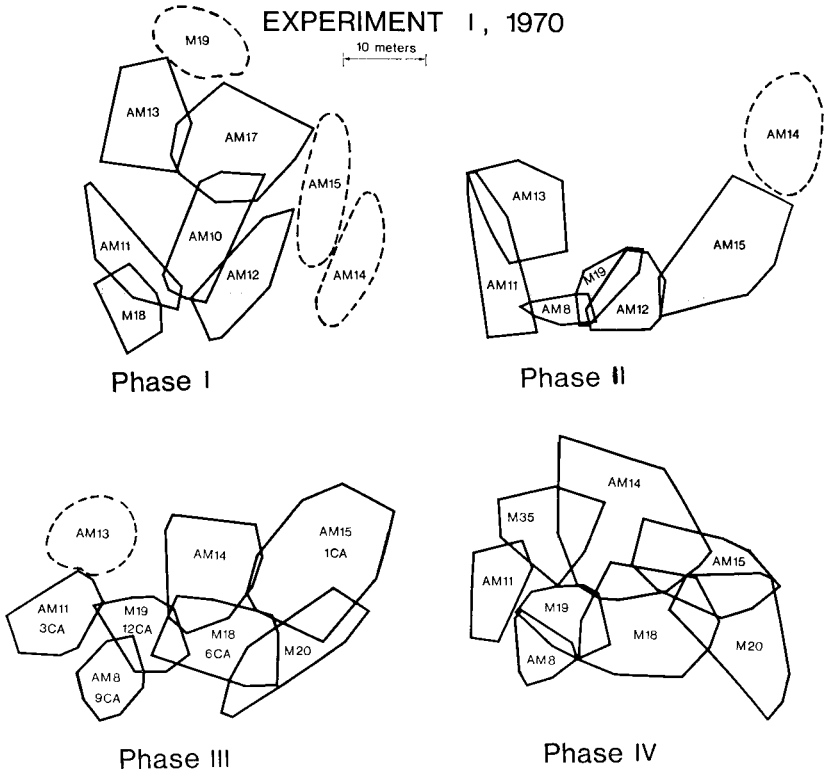

Figure 1. Relative sizes and locations of territories and numbers of copulations attempted (CA) by male Prairie Chickens on a booming ground during the four phases of Experiment I, 1970. Two males (AM-10 and AM-17) were removed from the booming flock at the end of Phase I, and an additional male (AM-12) was removed at the end of Phase II. Dashed lines indicate approximate sizes and locations of territories for which little specific data were collected.

days). Nine males, consisting of seven regulars, one new regular (AM-8), and one irregular, were present. Birds AM-8, AM-12, and M-19 established territories in portions of the void area created by the removal of the alpha and beta males (Figure 1).

During Phase II we recorded 178 territory-location sightings and 238 aggressive encounters (Table 1). Birds AM-8, AM-12, and M-19 had the largest numbers of aggressive encounters but maintained the smallest territories. On the basis of territory size and position, bird AM-12 was the new alpha male.

We counted 21 female visits, but saw no attempted copulations, though females seemed more receptive to courting males than during Phase I.

Bird AM-12 was shot on 15 April, initiating Phase III.

Phase III.—This phase lasted from 16 April to 11 May (12 observation days). Bird M-20 became an established regular territory holder, while AM-13 abandoned its territory on 23 April. Visits by irregular males declined to zero after removal of AM-12, but returned to three males by the end of Phase III.

We recorded 394 territory-location sightings and 844 aggressive encounters (Table 1). Bird M-18 had the third largest territory. Figure 1 shows that although M-19 retained a middle position on the ground, birds M-18 and AM-14 shared the removed bird's area.

We noted 34 female visits and recorded 31 attempted copulations (Figure 1), of which only 3 were successful. Bird M-19 accounted for two successful copulations, AM-15 for the other. Of the 28 unsuccessful copulation attempts, birds AM-11, M-18, AM-8, and M-19 accounted for 3, 6, 9, and 10, respectively.

During Phase III we were unable to pick an alpha male. Four males (AM-14, AM-15, M-18, and M-19) appeared equally aggressive and shared a middle position on the ground. Phase III ended when a change in the social hierarchy became evident.

Phase IV.—This phase lasted from 12 to 26 May (6 observation days). Eight regular territory owners and four irregulars were present.

We recorded 270 territory-location sightings and 426 aggressive encounters (Table 1). Bird AM-14 had the largest territory, while M-18 had the second largest. Birds AM-14 and M-18 also had the largest numbers of aggressive encounters. A large portion of bird AM-14's territory was located between four other territories (Figure 1). We witnessed five female visits but recorded no attempted copulations.

During Phase IV bird AM-14 was the new alpha male. On 9 May a new male (M-35) established a territory between AM-11 and AM-14. After this date AM-14 appeared to be more aggressive, at least more so than the remaining males. We stopped watching the ground on 26 May because booming ground activity was declining.

Experiment II

Phase I.—During this phase, which extended from 19 March to 4 April 1971 (6 observation days), seven regular males and one irregular male were present.

We recorded 250 territory-location sightings and 323 aggressive encounters (Table 2). Bird M-39 had the largest territory, but only the fifth largest number of aggressive encounters, while bird M-38 had the third largest territory and the largest number of aggressive encounters. Bird M-38's territory was located in the middle of the ground, while

TABLE 2
MALE PRAIRIE CHICKENS ENCOUNTERED REGULARLY DURING EXPERIMENT II

Bird number	Number of location sightings	Territory area (m^2)	Number of males encountered	Number of aggressive encounters
Phase I				
AM-11	42	112.5	5	134
AM-15	34	80.0	4	106
AM-16	34	152.5	4	106
M-38	51	197.5	6	151
M-39	40	390.0	5	89
M-40	26	127.5	4	31
M-41	23	212.5	3	29
	250			646
Phase II				
AM-11	36	72.5	4	75
AM-15	—	—	4	40
AM-16	50	115.0	4	134
M-39	46	127.5	5	123
M-40	32	95.0	3	99
M-41	24	80.0	2	21
	188			492
Phase III				
AM-11	22	72.7	4	60
AM-16	30	70.0	4	110
M-40	28	71.4	2	64
M-41	25	76.0	2	52
	105			286

M-39 occupied a position near the end of the ground (Figure 2). Bird M-38 was determined to be the alpha male, while M-39 was considered the beta male.

During Phase I an irregular male (M-42) attempted to establish a territory between birds M-38 and M-39, but was repeatedly driven off.

We noted two female visits but saw no attempted copulations. During female visits bird M-42 followed females on and off the ground, and frequently intruded into other territories disrupting courting activities.

Alpha male (M-38) was shot on 5 April 1971, initiating Phase II.

Phase II.—When M-38 was removed the remaining males flushed from the ground but returned within 20 minutes. Upon their return, bird M-42 tried to establish a territory in the vacated area but was attacked by M-29 and AM-16. We thought M-42 was dead as it lay on its back for 15 minutes, but it recovered, left the ground with an injured wing, and did not return during the remainder of the study.

During this phase, which lasted from 5 to 18 April (7 observation days), six regular males were present until 14 April when AM-15 failed to appear. Bird AM-15 was later found adjacent to the ground, an

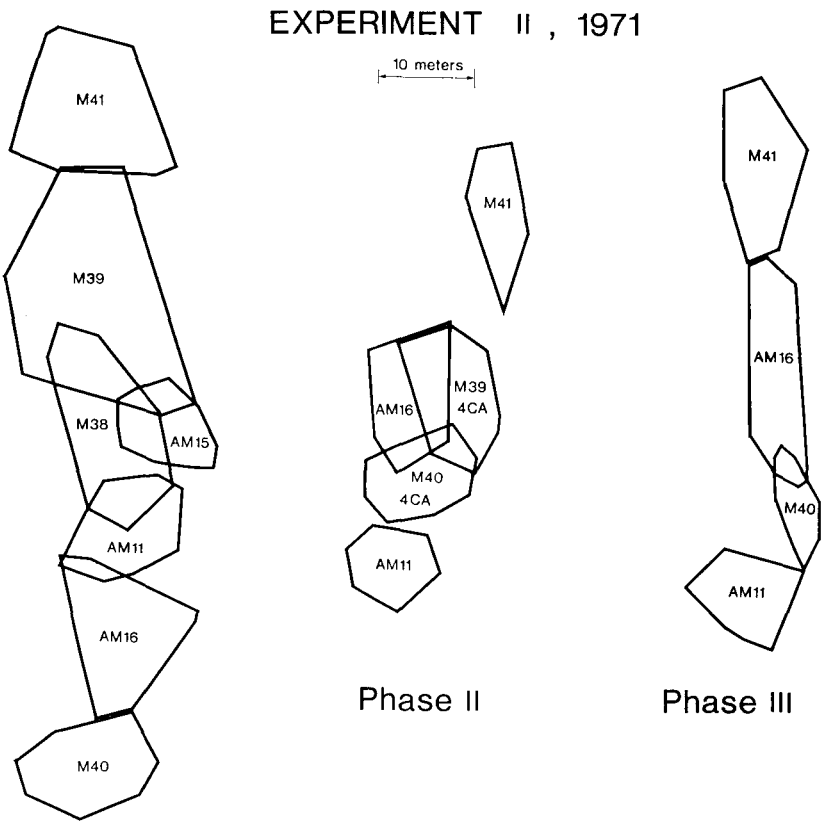

Figure 2. Relative sizes and locations of territories, and numbers of copulations attempted (CA) by male Prairie Chickens on a booming ground during the three phases of Experiment II, 1971. One male (M-38) was removed from the booming flock at the end of Phase I and another (M-39) was removed at the end of Phase II; one male (AM-15) was found dead during Phase II.

apparent victim of predation. No irregular male visits were registered during this phase.

We recorded 188 territory-location sightings and 246 aggressive encounters (Table 2). Bird M-39 had the largest territory and the second largest number of aggressive encounters. Bird AM-16 had the second largest territory and the largest number of aggressive encounters. Bird M-39's territory was located in the middle of the ground with AM-16, who occupied a different position than that held during Phase I (Figure 2). Birds M-39 and M-40 each accounted for one successful copulation

and three unsuccessful copulation attempts (Figure 2). Bird AM-16 was the aggressor in five of the unsuccessful attempts, while female aggression was responsible for one of the failures.

Bird M-39 was shot on 19 April, causing the remaining males to flush, but they returned within 15 minutes, initiating Phase III.

Phase III.—Field studies extended from 19 April to 17 May (8 observation days). On the morning following removal, we noted marked changes in behavior. Regular male attendance dropped to three males on 21 April, while irregular attendance fluctuated between one and two throughout the phase. After 29 April, attendance by regulars and irregulars became erratic.

We recorded 105 territory-location sightings before 29 April and saw 143 aggressive encounters throughout Phase III (Table 2). Bird AM-16 had both the largest territory and the largest number of aggressive encounters. Bird M-40 had the fourth largest territory and the second largest number of aggressive encounters. Bird AM-16 retained its middle position on the ground while extending its territory to the edge of M-41's territory (Figure 2). No other changes in position were evident.

We noted one female visit during Phase III, but saw no attempted copulations.

From 29 April through the remainder of the study, bird attendance on the ground became erratic. The decline in activity this early in the season seemed abnormal but limited observations on a different undisturbed ground showed similar trends (Ballard 1971). Field studies ended on 17 May 1971.

DISCUSSION

Following the removal of dominant males, the lower-ranking birds shifted their territories toward the vacated areas. After the shift in territory locations, we noted an abnormal increase in aggressive encounters. Limited observations on an undisturbed ground showed no increase in aggressive encounters during the same period (Ballard 1971). Thus, possibly because of increased competition among remaining males, birds moving into the vacated areas may not have been able to control large territories successfully.

After the removal of alpha and beta males, the remaining males did not maintain distinct territory boundaries or positions during female visits. When females visited the ground, the entire group of regular males moved in the direction of female movement. Females were confused by this movement and wandered from one side of the ground to the other. In contrast, males on a different undisturbed booming ground maintained a fairly rigid territorial system throughout the study, and the

females visiting that ground usually stayed within the alpha male's territory (Ballard 1971).

Several authors have mentioned the importance of the center position in lekking grouse (Lack 1939, Hamerstrom 1941, Scott 1942, Schwartz 1945, Lumsden 1965). Birds in center or middle positions have been described as being the most aggressive males on the ground. Both age and fighting ability have been deemed important factors in determining the social status of lekking tetraonid males. All alpha and beta males on the experimental ground during the 6 years prior to our study (Robel 1972) and all males removed during our study were at least 2 years of age. Following removal of dominant males, at least 4 of 7 males that attempted copulation were at least 2 years of age.

Wynne-Edwards (1962) postulated that the lek system regulates the number of breeding males in the population by forcing "surplus" males that cannot establish territories to disperse elsewhere and thereby suffer greater mortality. He implied that territory ownership was a prerequisite for successful reproduction. During our study we witnessed several males being turned away from the ground by regular territory holders. Whether or not these males would have suffered greater mortality is speculative, but only after the removal of dominant males were surplus males able to establish territories and participate in courtship.

During our study we saw 39 attempted copulations, of which only 5 were successful. During the previous 6 years (1964–1969) an average of 34 successful copulations per year were recorded on the experimental ground (Robel 1967, 1972). Mating success during that period averaged 92% in contrast to the 13% observed during this study. During 1970, limited observations at an undisturbed booming ground 4 miles from the study ground disclosed mating success comparable to that observed on the experimental ground prior to 1970 (Ballard 1971). Therefore removal of dominant males reduced the mating success of the entire booming ground. Whether the reduction in mating success was a result of an upset in the social organization or to the loss of those males that normally would be physiologically competent to mate is subject to speculation, for we did not know the physiological state of the remaining males.

Removal of dominant males may reduce the differential of mating attempts. Robel (1970) reported that from 1964 to 1967, 108 of 121 (89%) copulations were conducted by alpha and beta males. Only two interruptions per year were observed. In contrast, of the 31 attempted copulations recorded in 1970 (only 3 successful), bird M-19 accounted for 39%, bird AM-8 for 29%, bird M-18 for 19%, bird AM-11 for 10%, and bird AM-15 for 3%. In 1971 birds M-39 and M-40 each accounted for 50% of the observed attempted copulations (2 of 8 were successful).

Our study of male reproductive behavior in a natural population of Prairie Chickens may shed some light on the potential role of lekking behavior in population regulation, for which supporting data are not plentiful in the literature (Brown 1969). First, under the control of a strong, stable social organization, lower ranking males are not permitted to court or mate with hens on the booming ground. Secondly, regular territory owners do not permit surplus males to establish territories, but upon removal of dominant males, nonterritory owners do establish territories. Thirdly, removal of dominant males radically reduces mating success on the booming ground.

Our study, although by no means proving the importance of lekking behavior in population regulation, does provide some supporting experimental data and provides a basis for further investigations.

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SUMMARY

Dominant male Prairie Chickens were removed from a booming ground during the springs of 1970 and 1971. Notes were kept on female visits, numbers of males present, numbers of aggressive encounters, numbers of copulations, territoriality, and individual male and female behavior before and after the removal of dominant males.

Prior to removal, dominant males had large territories and occupied middle positions on the booming ground. Following removal, aggressive males of lower social status moved into the vacated positions and occupied relatively small territories. Surplus males established territories following the removal of dominant males.

During 1970 and 1971, only 5 of 39 (13%) observed copulation attempts were successful. The 39 attempts were performed by seven different males. In contrast, of 132 attempted copulations seen on the same booming ground in previous years, 121 (92%) were successful. Of the 121 successful copulations, 108 (89%) were by alpha and beta males. The function of the booming ground social organization appeared to be one of stabilization during reproduction, which allowed successful reproduction by dominant males and, therefore, possible selection for social aggressiveness in the population.

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