

# MOVEMENT AND LEK VISITATION BY FEMALE GREATER PRAIRIE-CHICKENS IN RELATION TO PREDICTIONS OF BRADBURY'S FEMALE PREFERENCE HYPOTHESIS OF LEK EVOLUTION,

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**ABSTRACT.**—Evolution of lek behavior has been explained by the female preference hypothesis in which females select large clusters of males for mating. I tested predictions that females should have spring home-range diameters equal to inter-lek distances and that most females should visit only one lek during the breeding season in a population of Greater Prairie-Chickens (*Tympanuchus cupido*) in northeastern Colorado. Nest-to-lek distances were used as an indirect measure of home-range size. Contrary to predictions, 66 of 89 females (74%) nested closer to a lek other than where captured, which indicated that most home ranges encompassed >1 lek. In addition, home-range diameters were greater than inter-lek distances. Furthermore, at least 67 of 79 females (85%) visited >1 lek during the breeding season. Bradbury's female preference hypothesis may not be applicable to Greater Prairie-Chickens in northeastern Colorado. Received 29 October 1990, accepted 3 May 1991.

NUMEROUS hypotheses have been proposed to illuminate the direct and indirect role of female choice in evolution of lek behavior (Emlen and Oring 1977, Wrangham 1980, Bradbury 1981, Bradbury and Gibson 1983, Beehler and Foster 1988). Although hypotheses differ with respect to the importance they attribute to behavior of males and females, increased opportunities for females to select males, leks, or both is often considered an initial process in the evolution of lek behavior from territoriality, its hypothesized precursor.

Bradbury (1981) argued that increased home-range size for females leads to their increased ability to select males, leks, or both. Hence, variation in female home-range size may explain the continuum between lek and territorial species. In Bradbury's "female preference" hypothesis, unanimity of female choice for certain males or leks would lead to a characteristic distribution of females and leks. Most females should have spring home ranges that include only 1 lek. Bradbury (1981) predicted specifically that diameter of female home ranges should be less than inter-lek distances and that most females should visit only 1 lek. The validity of the specific predictions were examined by Beehler and Foster (1988).

I tested Bradbury's (1981) predictions for the female preference hypothesis by examining lek visitation, home-range size, and lek-to-nest distances (an indirect measure of home-range size) of female Greater Prairie-Chickens (*Tympanu-*

*chus cupido*). If most females visit >1 lek or have home ranges that include >1 lek, Bradbury's female preference hypothesis can be rejected. Although *most* was not defined by Bradbury, I conservatively defined *most* as  $\geq 50\%$ .

## METHODS

I studied Greater Prairie-Chickens in 1986–1988 on a 301-km<sup>2</sup> area centered (40°11'N, 102°22'W) 10 km NE of Eckley, Colorado (Fig. 1). The area consisted of grassland, sand sagebrush (*Artemisia filifolia*), and small soapweed (*Yucca glauca*) intermixed with irrigated fields of agriculture, primarily corn.

Locations of leks ( $\geq 2$  displaying males) and maximum male attendance at each lek each year were based on at least 2 observations. Although some leks appeared permanent on a year-to-year basis and others temporary, variation in lek stability within each breeding season was minimal (Schroeder 1990).

Trapping was concentrated on a core area of approximately 100 km<sup>2</sup>. I captured female Greater Prairie-Chickens at winter feeding sites and on leks; I used walk-in traps baited with corn at feeding sites, and walk-in traps and cannon nets on leks (Fig. 1). Captured females were banded with a numbered aluminum band and a unique combination of 3 colored plastic bands, and fitted with battery- or solar-powered radio transmitters attached to collars (Amstrup 1980). Radio weights ranged between 1.8 and 2.3% of each bird's body weight. I classed birds as yearlings (first breeding year) or adults (>1 breeding year) (Ammann 1944).

I placed radio transmitters on 36 adult and 56 yearling female Greater Prairie-Chickens during the 1986–1988 breeding seasons (classed as *late-captured*). Be-

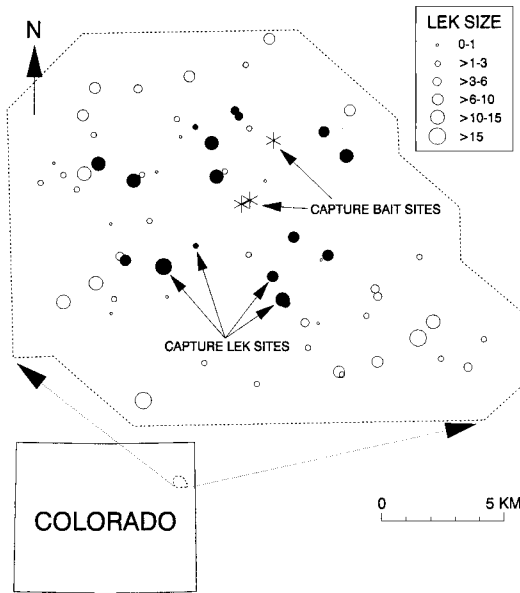


Fig. 1. Locations of leks and capture sites on Great Prairie-Chicken study area in 1986–1988 (301 km<sup>2</sup> outlined by dashed boundary) in northeastern Colorado.

cause spring capture techniques potentially disturb females, data from an *early-captured* sample of 12 adults and 7 yearlings captured at feeding sites during winter 1987/1988 were examined as a control.

I used a portable receiver and 3-element Yagi antenna to locate radio-marked Greater Prairie-Chickens. I observed birds at least once every 3 days during early (15 February to 31 March) and late (1 April to 15 May) spring. Early spring was typically the period before lek visitation by females, and late spring was the period of lek visitation, breeding, and nest initiation (Robel et al. 1970). Observations for each bird were obtained by triangulation; 3 or more azimuths were obtained  $\leq 1.5$  km of target transmitters and at angles-of-incidence  $> 35^\circ$  and  $< 145^\circ$ . I used Universal Transverse Mercator coordinators (UTMs) to record locations (nearest 10-m interval). Examinations of accuracy indicated that 90% of the locations derived by triangulation were within 250 m of actual locations (Appendix 1).

I examined Bradbury's predictions for the female preference hypothesis by identifying lek visitation, home-range size, and lek-to-nest distances (an indirect measure of home-range size) for female Greater Prairie-Chickens. Home-range size for females was estimated in both early (before most lek visitation) and late spring (during lek visitation and nest establishment). Home-range size was estimated as the area within a 75% probability contour generated with harmonic means (grid size of  $25 \times 25$ ) (Dixon and Chapman 1980); this technique was chosen because it is

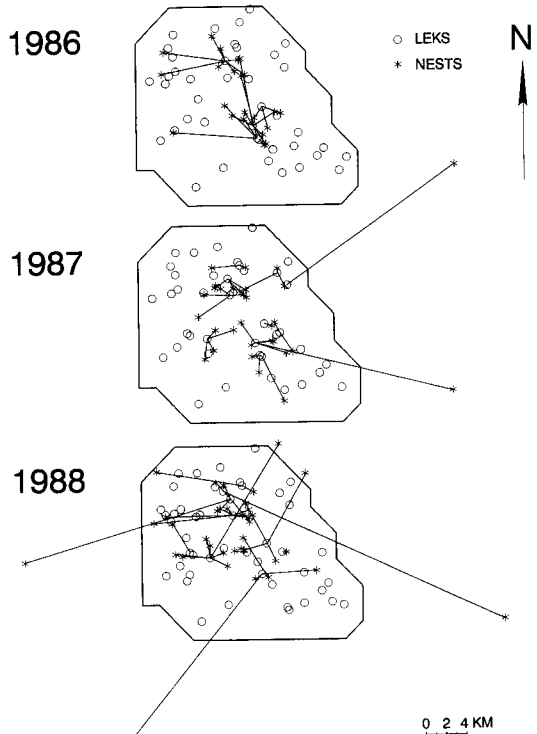


Fig. 2. Distribution of female Greater Prairie-Chicken nests in relation to lek where each female was first observed or captured.

relatively unaffected by sample size (Boulanger and White 1990), and it is conservative.

RESULTS

I found 65 different leks on the study area during 1986–1988; not all leks were active every year. I found 41 in 1986, 42 in 1987, and 47 in 1988. The mean ( $\pm$ SD) distance between a lek and its nearest neighbor was  $1.31 \pm 0.56$  km (median: 1.42) in 1986,  $1.20 \pm 0.70$  km (median: 1.32) in 1987, and  $1.18 \pm 0.62$  km (median: 1.15) in 1988.

*Home-range size.*—Distances between nest locations and the lek where each female was first observed, and distances between nests and the nearest leks, were determined separately for each year (Fig. 2). Females ( $n = 89$ ) nested an average of 3.62 km from leks where they were first observed (Table 1). Some females moved relatively long distances (Fig. 3). Hens ( $n = 81$ ) nested an average of 1.00 km from the nearest

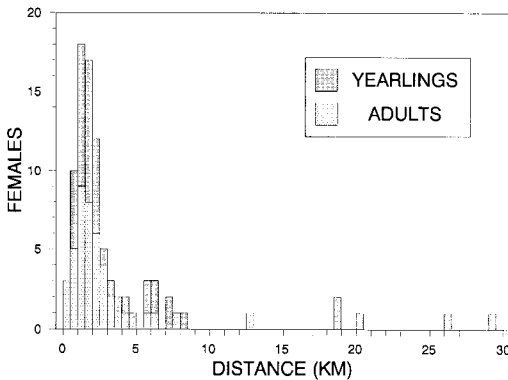


Fig. 3. Distribution of distances between 89 female Greater Prairie-Chicken nest sites and leks where each female was first observed or captured.

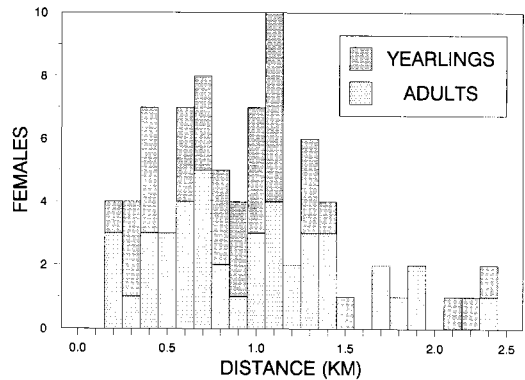


Fig. 4. Distribution of distances between 82 female Greater Prairie-Chicken nest sites and nearest lek.

lek (Table 1) with distances ranging from 0.23 to 2.39 km (Fig. 4). Of 89 females, 8 nested off the study area, and the distance to the nearest lek could not be determined.

There was no difference that could be attributed to year in distance between the lek where each female was first observed and her nest ( $F = 1.35$ ,  $P = 0.265$ ). Yearling females tended to move farther between the lek where first observed and their nest site than adults ( $F = 3.89$ ,  $P = 0.052$ ). The difference may be attributed partially to yearling dispersal. For instance, the 5 females with the longest distances (19–29 km) between their nest and the lek where first observed were yearlings. In addition, 12 of 16 movements  $>5$  km were by yearlings. There was no difference by year ( $F = 0.50$ ,  $P = 0.611$ ) or age ( $F = 0.02$ ,  $P = 0.901$ ) for nest-to-nearest-lek distance (Table 1).

Disturbance may also have been a factor. Females captured during the breeding season (late-captured) had nest sites farther from the lek first visited ( $t = 2.352$ ,  $P = 0.022$ ) than females captured before the breeding season (early-captured). Some early-captured females were marked before migratory movements between seasonal home ranges (Schroeder 1990). Four marked females moved 6–18 km before being observed on leks during the breeding season. In contrast, all late-captured females were observed on leks (by definition), often before making similar long movements. Thus, distances between lek first visited and nest site were biased toward shorter distances for early-captured females. There was no difference for nest-to-nearest-lek distance attributable to capture timing ( $t = 1.660$ ,  $P = 0.113$ ) (Table 1).

Of 89 females, 66 (74%) nested closer to a lek different from the lek where first observed or captured. When compared with a maximum predicted value of 50%, the observed value was higher ( $\chi^2 = 20.775$ ,  $P < 0.001$ ). Late-captured females (76.0%,  $n = 75$ ), did not differ from early-captured females (64.3%,  $n = 14$ ) ( $\chi^2 = 0.845$ ,  $P = 0.431$ ). If disturbance was a factor, late-captured females would be expected to avoid leks where they were captured.

There were no differences in home-range size associated with year ( $F = 2.00$ ,  $P = 0.161$ ), age ( $F = 1.10$ ,  $P = 0.337$ ), and timing of capture ( $F = 0.04$ ,  $P = 0.838$ ) for early spring, and in home-range size associated with year ( $F = 2.43$ ,  $P = 0.131$ ), age ( $F = 0.35$ ,  $P = 0.508$ ), and timing of capture ( $F = 0.51$ ,  $P = 0.483$ ) for late spring (Table 2). However, home-range size during late spring ( $\bar{x} = 624$  ha) was larger ( $t = 2.098$ ,  $P = 0.038$ ) than in early spring ( $\bar{x} = 213$  ha) (Table 2). Home-range size was positively correlated with distances between nest locations and the lek where each female was first observed ( $r = 0.629$ ,  $P = 0.001$ ).

When home-range diameter was calculated as though each home range were a circle, average diameter for home ranges was  $1.51 \pm 0.66$  (SD) in early spring and  $2.24 \pm 1.71$  km in late spring. These estimates were greater ( $t = 2.090$ ,  $P = 0.043$ , early spring;  $t = 5.534$ ,  $P = 0.001$ , late spring) than distances between neighboring leks (mean yearly range of 1.18–1.31, median range of 1.15–1.42).

*Lek visitation.*—I observed 79 radio-marked females on leks at least twice during the breeding season. Of these females, 84.8% (95% C.I. of 75.3 to 91.9%) were observed on  $>1$  lek (Fig. 5) which

TABLE 1. Distances (m) between Greater Prairie-Chicken nests and leks in northeastern Colorado, 1986-1988.

Category	Lek visited first			Lek nearest to nest		
	<i>n</i>	Median	$\bar{x} \pm SD$	<i>n</i>	Median	$\bar{x} \pm SD$
Year						
1986	22	2.09	2.86 ± 2.11	21	0.84	0.96 ± 0.53
1987	31	1.65	2.91 ± 4.34	29	0.78	0.94 ± 0.53
1988	36	1.86	4.71 ± 6.84	31	1.14	1.08 ± 0.47
Age <sup>a</sup>						
Adult	42	1.79	2.28 ± 2.25	38	0.97	0.98 ± 0.51
Yearling	47	2.04	4.82 ± 6.62	43	0.96	1.01 ± 0.52
Status <sup>b</sup>						
Early-captured	14	1.87	2.01 ± 1.87	14	1.05	1.16 ± 0.51
Late-captured	75	1.98	3.92 ± 5.55	67	0.84	0.96 ± 0.50
Totals	89	1.93	3.62 ± 5.19	81	0.96	1.00 ± 0.50

<sup>a</sup> One female of unknown-age was excluded from the sample for nearest lek-nest distances.

<sup>b</sup> Females captured before lek visitation were considered early-captured and those captured on leks during lek visitation were considered late-captured.

was greater ( $\chi^2 = 38.291, P < 0.001$ ) than the hypothesized upper-limit of 50%. Lek visitation did not differ according to female age ( $\chi^2 = 0.040, P = 0.841$ ). In addition, early-captured females (88.2%,  $n = 17$ ) did not differ from late-captured females (83.9%,  $n = 62$ ) in their likelihood to visit >1 lek ( $\chi^2 = 0.197, P = 0.741$ ). If disturbance was a factor, late-captured females should have visited more leks than early-captured females.

As number of lek visits increased, number of visits to different leks generally increased (Fig. 6). For example, 1 female was observed on 6 different leks in 8 lek visits. In contrast to most females, 1 female visited the same lek on 9 consecutive observations.

I examined capture as a possible disturbance factor by compiling data on consecutive lek visits (Fig. 7). If females were adversely affected by capture, they would be expected to avoid the capture lek on their next lek visit. However, there was no difference ( $\chi^2 = 0.192, P = 0.740$ ) in the likelihood to visit a different lek on the second lek visit between late-captured (75.8%) and early-captured females (70.6%). The probability of visiting a different lek on lek visit 2 ( $n = 79, 74.7%$ ) was greater ( $\chi^2 = 7.889, P = 0.005$ ) than in lek visits  $\geq 3$  ( $n = 137$  combined, 55.5%). Hence, the tendency to visit the same lek(s) in later visits may represent female selection of leks, as opposed to effects of capture timing.

TABLE 2. Home-range size (ha) for female Greater Prairie-Chickens in northeastern Colorado 1986-1988.

Category	Early spring			Late spring		
	<i>n</i>	Median	$\bar{x} \pm SD$	<i>n</i>	Median	$\bar{x} \pm SD$
Year						
1986	3	165.0	149.3 ± 115.6	21	252.5	526.9 ± 749.8
1987	2	328.7	328.7 ± 247.9	36	264.4	349.4 ± 287.8
1988	25	156.8	210.9 ± 252.7	40	310.9	921.6 ± 2,861.1
Age						
Adult	22	165.0	175.9 ± 97.2	49	266.0	369.2 ± 304.7
Yearling	8	134.9	313.6 ± 439.2	48	271.0	883.7 ± 2,645.6
Status <sup>a</sup>						
Early-captured	24	160.8	231.3 ± 260.1	19	461.3	625.1 ± 959.1
Late-captured	6	113.1	137.7 ± 111.6	78	260.4	623.5 ± 2,049.0
Totals	30	160.8	212.6 ± 239.3	97	266.0	623.8 ± 1,881.5

<sup>a</sup> Females captured before lek visitation were considered early-captured and those captured on leks during lek visitation were considered late-captured.

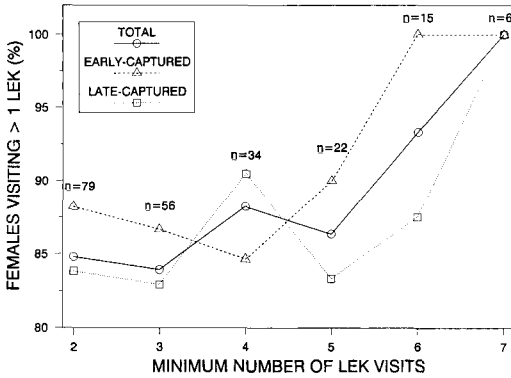


Fig. 5. Proportion of female Greater Prairie-Chickens that visited >1 lek in relation to number of times observed on a lek.

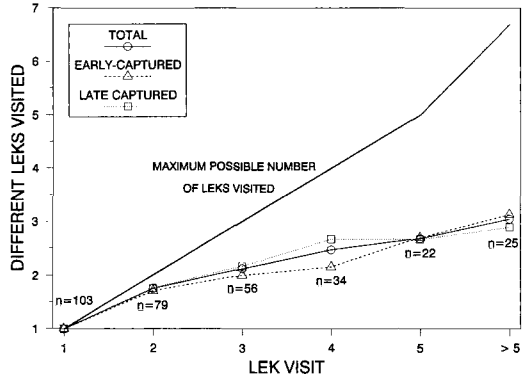


Fig. 6. Number of different leks visited by female Greater Prairie-Chickens in relation to number of times they were observed on leks.

DISCUSSION

Beehler and Foster (1988) discussed problems associated with analysis of lek behavior, including examinations of home ranges. Consequently, I used 3 relatively conservative techniques to examine home ranges for female Greater Prairie-Chickens in northeastern Colorado. First, home-range size was estimated with 75% contours (Dixon and Chapman 1980) as opposed to the 95% or 100% estimates frequently used. Second, diameters of home ranges were determined as though home ranges were circles. Third, distances between nests and leks where each female was captured were used as indirect indications of each female's ability to move. Comparability of the techniques was supported by the strong correlation between home-range size and distance between nests and capture leks.

As with home-range techniques, trapping of female Greater Prairie-Chickens "late" on leks or "early" on feeding sites did not appear to influence their movement and lek visitation. Consequently, I did not consider the capture of females on leks a source of disturbance.

Bradbury (1981) predicted that female choice for certain leks, males, or both, would lead to a characteristic distribution of leks and home ranges. Most females (conservative definition: >50%) would have home ranges that include only 1 lek and most should visit only 1 lek. Although direct examinations of home-range size are difficult, and possibly not interpretable (Beehler and Foster 1988), I estimated home-range sizes to provide an evaluation of the relevancy of Bradbury's (1981) prediction that di-

ameters of home ranges should be less than distances between neighboring leks.

Measures of home-range size in my study were probably conservative. First, home-range size was estimated with 75% contours. Second, it was not logistically feasible to detect all female movements. Third, *detection distance* (distance at which males can be detected readily by females) was not added to the home-range diameter (Bradbury 1981). Despite the conservative estimates of home-range size, average home-range diameter for my study was larger than predicted. In addition, most (74%) female Greater Prairie-Chickens nested closer to a lek other than where captured, an indirect indication that home ranges were larger than predicted.

Svedarsky (1988) found that 11 of 18 (61%)

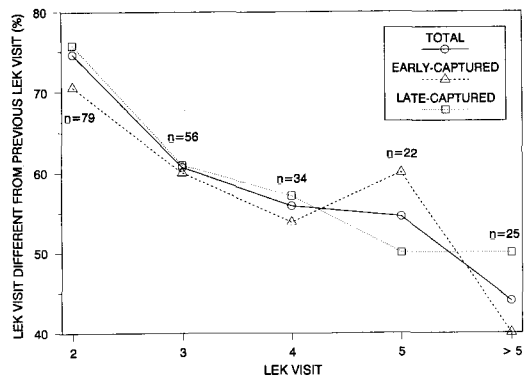


Fig. 7. Likelihood of a female Greater Prairie-Chicken visiting a lek different than the previous lek visited in relation to the consecutive number of her lek visit in northeastern Colorado, 1986-1988.

Greater Prairie-Chicken females in Minnesota nested closer to a lek other than where captured. Similarly, home ranges for 20 female Sage Grouse (*Centrocercus urophasianus*) in California were larger than predicted, and included an average of 2.2 leks (Bradbury et al. 1989). In contrast, home ranges for Great Snipe (*Gallinago media*) were smaller than predicted (Höglund and Robertson 1990).

As with home-range size, it was not feasible to detect all lek visits by females. Therefore, measures of lek visitation were probably conservative. Nevertheless, most (85%) Greater Prairie-Chickens visited >1 lek during the breeding season. Similarly, Great Snipe females also visited >1 lek during a breeding season (Höglund and Robertson 1990). Although only 3 of 55 female Common Capercaillie (*Tetrao urogallus*) visited >1 lek in Norway (Wegge and Rolstad 1986), hens did not necessarily visit the closest lek (Wegge 1985).

These results do not support Bradbury's (1981) predictions that females should visit only 1 lek and have home ranges that include only 1 lek. Thus, Bradbury's female preference hypothesis is rejected for Greater Prairie-Chickens in northeastern Colorado. Despite the rejection, these results appeared to test the "unanimity" of female choice for certain males or leks, rather than the "importance" of female choice in the process of lek evolution. For example, females may have preferences for particular males or leks without the predicted effects on distributions of both females and leks (Höglund and Robertson 1990). Furthermore, the most important aspect of Bradbury's (1981) theory is the relationship between female home-range size and tendencies for males to form leks. My results did not address this relationship.

Size and distribution of female home ranges may provide insights into why some species form leks and others do not. Unfortunately, Bradbury (1981) did not explain clearly how increased home-range size of females could result in the development of lek behavior by males. He did not address why males congregate on leks rather than defending relatively exclusive territories.

The least costly male (Wrangham 1980), female preference (Bradbury 1981), hotspot (Bradbury and Gibson 1983), and hotshot (Beehler and Foster 1988) hypotheses all suggest directly or indirectly that increased tendency for males to form leks is a consequence of increased ability by females to select males, leks, or both.

The primary differences among the hypotheses are that lek size and distribution are caused by unanimity of female choice for males or leks in the least costly male and female preference hypotheses—by maximization of male access to females in the hotspot hypothesis and by male-male interactions in the hotshot hypothesis. Rarely do the theories present a mechanism which could lead to evolution in leks from a dispersed mating system.

Female home-range size during the breeding season has obvious implications for a female's ability to select either leks or males (Bradbury 1981). A consequence of increased female home-range size, without a corresponding decrease in female density, would be an increased probability of encountering conspecifics. Therefore, if territorial females increase the size of their home ranges, the response should be either a decrease in their density or territorial tendencies (Emlen and Oring 1977).

Although large female home ranges during the breeding season would permit increased female choice by allowing females to examine many males, the amount of freedom of female choice for males would be inversely correlated with levels of intrasexual aggression among females. If females were not able to tolerate other females within close proximity, as on a lek, the resulting female dispersion should create additional mating opportunities away from normal display areas. This would tend to decrease rather than increase the aggregation of males. Hence, lek formation could result from increased sociality or tolerance among females, but not directly from large female home ranges in which females still maintain some conspecific intolerance or territoriality.

Large home ranges do not, by themselves, explain why some males give up territories to pursue females into the territory of another male (a likely cause of territory breakdown). The originally selected male would undoubtedly chase any intruding males, as is typical with most territorial animals. Therefore, the change from territoriality to lek mating would come at the point where defense of mates becomes more important than defense of territories, a point which is reached only when >1 female is present within the range of a male. If >1 female is with a male at the same time, other males may be able to encroach on the selected male. Likewise, the number of unselected males will be proportional to the unanimity of female selection (Hammerstein and Parker 1987).

The presence of >1 female would require female tolerance for other females. Whether females arrive on the lek together or alone may not matter. The important consideration is that females tolerate each other within the territorial boundaries of the same male; even if the boundaries are on a lek. Relative differences in tolerance among females may explain why leks vary in dispersion from tight clusters to expanded formations ("exploded leks") (Bradbury 1981).

Tolerance among females may be the key to understanding the evolution of lek mating systems. Female tolerance may provide a testable alternative to the idea that home-range size led to evolution of lek mating systems. Possible reasons for conspecific tolerance may be found in feeding behavior, food requirements (causes for a large home range), or predation risks (possibly reduced by flocking) (Bradbury 1981). When variability in home-range size, intensity of female choice, costs of female travel, and patterns of male settlement are considered in a multivariate approach, realistic explanations for the evolution of lek behavior may incorporate numerous hypotheses (Gibson et al. 1990, Höglund and Robertson 1990).

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APPENDIX 1. Accuracy of triangulation techniques.

I examined the accuracy of the triangulation technique with 13 test transmitters placed on the ground (by another observer) in a relatively hilly 4-km<sup>2</sup> area, 1-2 km from the nearest access points (relatively inaccessible). Five azimuths were obtained for each transmitter from each of 5 locations (4 locations for 3 transmitters). The standard deviation between observed and average azimuths was 2.10° ( $n = 310$ ). In contrast, estimated azimuths deviated an average of 6.97° from actual azimuths (the overall bias was -1.66°). Most of the variation apparently was due to the location where the azimuth was obtained and the transmitter that was being located.

Estimated locations were compared with actual locations of nests, dead birds, and test transmitters (Appendix 2). Approximately 90% of the locations derived by triangulation were within 250 m of actual locations. Although this sample was not affected by problems associated with bird movement, other factors may have adversely affected accuracy; transmitters usually were close to, or on, the ground. Transmitters from dead birds frequently were buried, upside down, or damaged (chewed); transmitters on nesting females were usually in dense vegetation, close to the ground, and shielded by the female.

APPENDIX 2. Distribution of distances between estimated and actual locations of 13 test transmitters, 79 nests, and 44 dead Greater Prairie-Chickens in northeastern Colorado, 1986-1988.

