

SEXUAL SELECTION AND MATING CHRONOLOGY OF LESSER PRAIRIE-CHICKENS

ADAM C. BEHNEY,^{1,5,7} BLAKE A. GRISHAM,¹ CLINT W. BOAL,²
HEATHER A. WHITLAW,^{3,6} AND DAVID A. HAUKOS⁴

ABSTRACT.—Little is known about mate selection and lek dynamics of Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*). We collected data on male territory size and location on leks, behavior, and morphological characteristics and assessed the importance of these variables on male Lesser Prairie-Chicken mating success during spring 2008 and 2009 in the Texas Southern High Plains. We used discrete choice models and found that males that were less idle were chosen more often for mating. Our results also suggest that males with smaller territories obtained more copulations. Morphological characteristics were weaker predictors of male mating success. Peak female attendance at leks occurred during the 1-week interval starting 13 April during both years of study. Male prairie-chickens appear to make exploratory movements to, and from, leks early in the lekking season; 13 of 19 males banded early (23 Feb–13 Mar) in the lekking season departed the lek of capture and were not reobserved (11 yearlings, 2 adults). Thirty-three percent (range = 26–51%) of males on a lek mated (yearlings = 44%, adults = 20%) and males that were more active experienced greater mating success. Received 2 May 2011. Accepted 28 July 2011.

Males in lek mating systems aggregate on arenas (leks) which females visit for breeding; males provide no parental care or resources to females, other than genetic material (Höglund and Alatalo 1995). Sexual selection is typically strong in lek mating systems where some individuals obtain many mating opportunities while others obtain none (Robel 1966, Gibson and Bradbury 1985, McDonald 1989) and, in many species, males have evolved elaborate courtship displays and ornaments. Females are thought to select the highest quality males to maximize direct (survival or clutch size) or indirect benefits (good genes) (Bradbury and Gibson 1983, Reynolds and Gross 1990).

Vocal, morphological, territorial, and behavioral characteristics have been examined among lekking grouse species with regard to mate choice (e.g., Robel 1966, Gibson and Bradbury 1985,

Gibson et al. 1991, Gibson 1996, Höglund et al. 1997, Nooker and Sandercock 2008). Correlates of male mating status (mated vs. non-mated) for Greater Sage-Grouse (*Centrocercus urophasianus*) included display rate, lek attendance, and a vocal component (Gibson and Bradbury 1985). Gibson et al. (1991) found that female choice in Greater Sage-Grouse was related to male vocalization performance, previous mating locations of females, and choices of other females. Specifically, initial attraction of female Greater Sage-Grouse to males was based on vocalizations while probability of mating was related to male display rate (Gibson 1996). Male Sharp-tailed Grouse (*Tympanuchus phasianellus*) holding central territories obtained more copulations than peripheral males (Gratson et al. 1991), although Gratson (1993) concluded that dance time and auditory characteristics were better predictors of mating success than territory location. Alternatively, display and aggressive behaviors were better predictors of male mating success for Greater Prairie-Chickens (*T. cupido*) than territory characteristics (Nooker and Sandercock 2008).

Lesser Prairie-Chickens (*T. pallidicinctus*) are a lek-mating grouse, inhabiting short and mixed-grass prairies of the southern Great Plains. Significant population declines throughout much of their historic range (Hagen and Giesen 2005) have resulted in their designation as a 'candidate' for protection under the Endangered Species Act (USDI 2008). Little is known about sexual selection and lek dynamics of Lesser Prairie-Chickens, and future research and conservation could benefit from information on when prairie-chickens mate, how

¹Texas Cooperative Fish and Wildlife Research Unit, Department of Natural Resources Management, Texas Tech University, Lubbock, TX 79409, USA.

²U.S. Geological Survey, Texas Cooperative Fish and Wildlife Research Unit, Department of Natural Resources Management, Texas Tech University, Lubbock, TX 79409, USA.

³Texas Parks and Wildlife Department, Texas Tech University, Lubbock, TX 79409, USA.

⁴U.S. Fish and Wildlife Service, Texas Tech University, Lubbock, TX 79409, USA.

⁵Current address: Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, IL 62901, USA.

⁶Current address: U.S. Fish and Wildlife Service, Texas Tech University, Lubbock, TX 79409, USA.

⁷Corresponding author; e-mail: abehney@siu.edu

many males mate, and what characteristics influence male mating success. The objectives of our study were to (1) assess the roles of behavioral, territorial, and morphological characteristics for Lesser Prairie-Chicken mate choice, (2) report dates of peak female attendance and copulations, and (3) assess the extent of mating skew on prairie-chicken leks.

METHODS

Study Area.—Our study occurred on private lands in Cochran and Yoakum counties in the Texas Southern High Plains Ecoregion (Llano Estacado). The area consists of a matrix of grassland and cropland (Wu et al. 2001) among a level to gently undulating landscape with small vegetated dunes providing infrequent topographical relief. The dominant vegetation was shinnery oak (*Quercus havardii*) intermixed with sand sagebrush (*Artemisia filifolia*), grasses, and forbs (Pettit 1979, Woodward et al. 2001).

The mean annual precipitation was 48.3 cm for the period 2000–2009 (50.3 and 45.2 cm in 2008 and 2009, respectively) with average summer (Jun–Aug) and winter (Dec–Feb) temperatures of 25.4 and 5.4°C, respectively. Extreme high and low temperatures were 39.5 and –13.4°C, respectively (U.S. Department of Commerce 2010). The average elevation of the study area is ~1,100 m.

Field Methods.—We conducted this study on four different leks during spring 2008 and 2009. Two leks were sampled in 2008 and three in 2009 with one sampled in both years. Grass cover on some leks was too high and dense to see the birds' legs continuously. Thus, we selected leks for this study based on vegetation characteristics that facilitated identification of color bands on legs of prairie-chickens.

We captured male Lesser Prairie-Chickens using walk-in-funnel traps (Haukos et al. 1990, Schroeder and Braun 1991) early in the lekking season (late Feb–early Mar). We also captured males opportunistically with a bownet throughout the lekking season. We did not attempt to capture males with the bownet while females were present on a lek. Each captured male was fitted with a unique color band combination (Association of Field Ornithologists, Manomet, MA, USA) and a numbered aluminum Texas Parks and Wildlife Department band (size 6). We measured mass (g), right pinnae length (mm), right tarsus length (mm), and right unflattened wing cord length from

bend of wing to tip of longest primary (mm) for each captured male. We classified prairie-chicken age as either adult or yearling based on plumage characteristics. Yearlings exhibited frayed tips of the ninth and tenth primaries and spotting within 2.5 cm of the tip of the tenth primary whereas adults lacked frayed primaries and had no spotting within 2.5 cm of the tip of the tenth primary (Copelin 1963). Four males (2 yearlings, 2 adults) were marked with necklace style radio transmitters.

We placed a grid of points centered on the activity center of each study lek to facilitate mapping of male territories. Grid points consisted of numbered, orange-colored, blocks of wood (7.6 × 5.1 × 5.1 cm), placed every 5 m encompassing the entire lek area. Some leks were sufficiently small to be covered with a 5 × 8 grid (20 × 35 m) while others required a 10 × 10 grid (45 × 45 m). Grids were placed on leks in February before birds started attending leks.

We conducted observations from a blind (Primos Ground Max, Flora, MS, USA) placed within 10 m of the edge of the lek during morning and evening lekking periods. We used binoculars and spotting scopes to identify males, and assess locations and behavior. We used the grid points as a reference to plot locations of males onto a corresponding paper copy of the grid during 10-min interval scan samples. Lek observations were not conducted if a lek had walk-in-funnel traps present or after the bownet had been triggered. Observations were made 2–3 days/week from 24 February to 21 May 2008 and 5 March to 10 May 2009. The order of leks to be monitored was randomly selected, weekly. Leks were not observed when lightning was present or winds exceeded ~45 km/hr.

We recorded a description of male Lesser Prairie-Chicken behavior every time a location was plotted. Behavioral categories included display, moving, face off, fighting, and idle. Display involved erecting pinnae, enlarging eye-combs, elevating tail, drooping wings, extending head and neck forward, stamping feet, inflating esophageal air sacs, and emitting booming vocalization (Hagen and Giesen 2005). Moving was when the male was walking or running but not displaying. Face off consisted of two males in close proximity (<1 m), facing each other at a territory boundary, typically in a semiprone position, but not displaying, moving, or fighting (Hagen and Giesen 2005). Fighting consisted of two males actively fighting each other

with one typically charging the other with rapid aggressive movements. Idle was recorded when a male was not doing any of the other behaviors.

We noted the male that performed any copulation attempt and the location. A copulation attempt was defined as anytime a male was able to put at least one foot on the female's back. Most copulation attempts were interrupted by other males at varying times throughout the attempt. We classified copulation attempts as successful when females vigorously ruffled their feathers and departed the lek after copulating (Hagen and Giesen 2005).

Statistical Analyses.—We used Skew Calculator 2003 (Nonacs 2003) to analyze mating skew on leks. We used two indices of mating skew: λ and B (Binomial Skew Index). Lambda values ranged from 0 to 1 with larger values indicating greater skew (Kokko and Lindström 1997). Positive values of B indicate some monopolization of matings (skew), while 0 indicated random mating, and negative values indicated a more equal distribution (Nonacs 2000). B -values, generally, ranged from -1 to 1 , although it is possible to obtain values >1 . Confidence intervals and P -values can be calculated for B (Nonacs 2000). Lek attendance rates were calculated as the number of days a male was observed on the lek divided by the number of days the lek was observed and at least one male was present.

We assessed two characteristics of territories: size and distance to center of lek activity. We calculated two measures of territory size, 95% kernel and 95% minimum convex polygon (MCP) estimates, using plotted male locations with ≥ 24 locations/behavioral observations. Both metrics were computed in the ADEHABITAT package (Calenge 2006) of Program R (R Development Core Team 2008). Lesser Prairie-Chickens appear to spend a disproportionate amount of time at territory boundaries and we suspect that kernel estimators overestimated territory size. MCPs only outline the outer points of a distribution and may be more accurate in assessing individual territory sizes of lekking prairie-chickens. Thus, only MCP estimates of territory size were used for modeling. We report kernel estimates of territory size for comparative purposes with other studies of lekking grouse (e.g., Nooker and Sandercock 2008). Kernel estimates were correlated with MCP estimates ($r = 0.98$). A male's center of activity was computed as the centroid of all its locations. Each

male's centroid was averaged to ascertain the center of activity for the lek.

Discrete choice models (DCM) allow inference to be drawn about resource preferences based on the attributes of the resource (Cooper and Millsbaugh 1999). These models predict the probability that an individual will select a certain resource as opposed to any of the other available resources and assume that individuals make choices that will maximize utility (Cooper and Millsbaugh 1999). DCMs are used more frequently in habitat selection studies (e.g., Lesmeister et al. 2008, Vanak and Gompper 2010). We followed the example of Nooker and Sandercock's (2008) studies of Greater Prairie-Chickens and used DCMs (PROC MDC, SAS Version 9.1, Cary, NC, USA) to assess correlates of male mating success for Lesser Prairie-Chickens. Each copulation attempt represents one sample in the DCM. A female chooses one male to mate with among a group of males, which is considered the choice set. DCMs allow the choice set to vary by sample, which is necessary when multiple leks are involved. The males (or sample of males) on one lek compose the choice set for each copulation attempt on that lek. We had to collect ≥ 24 location/behavior points on the male involved in the copulation attempt for it to be included in this analysis. Not every male on a lek was included in the analysis, but we believe our sample is representative of all males attending the lek. We trapped across the entire lek area and did not focus trapping efforts on central or peripheral males.

Behavioral variables included the proportion of observations recorded as each behavior category: display, face off, fighting, idle, and moving. Morphological variables included wing cord length (cm), tarsus length (cm), pinnae length (cm), and mass (g). Territorial variables included distance to lek center (m), and territory size (MCP, m^2). We did not use all variables in discrete choice models due to small sample sizes. We selected the behavioral variables display and idle to use in models because they were uncorrelated ($r = -0.1$, $P = 0.59$) and represented what we hypothesized to be important in mate choice. We selected the morphological variables mass and pinnae length because they were uncorrelated ($r = 0.1$, $P = 0.59$) and represent a size component (mass) and a secondary sexual characteristic (pinnae). We also included territory size, distance to lek center, and age in models.

Variables were standardized by replacing each observation by $(x_j - \bar{x}_j) / s_{x_j}$ for each lek to facilitate direct comparison of parameter estimates as effect sizes (Gratson et al. 1991, Agresti 2002, Nooker and Sandercock 2008). The sign of the slope coefficients indicate if that variable is positively or negatively correlated with male mating success and the magnitude of coefficients are directly comparable indices of effect size. We used Akaike's Information Criterion corrected for small samples (AIC_c) and model averaged slope coefficient estimates across all models in the model set to avoid basing inference on a single model (Anderson 2008).

We only considered models with ≤ 3 variables due to small sample sizes. Each variable appeared an equal number of times in the model set to facilitate model averaging and calculating relative importance values (Anderson 2008). We evaluated models based on all copulation attempts regardless of whether it was successful, and only successful copulation attempts. We also calculated Pearson's correlation coefficient (r) between each variable and the proportion of all and successful copulations each male obtained on its' respective lek.

It is generally not good practice to use all possible models but we believe it was justified due to the exploratory nature of this type of analysis. Previous studies have not examined sexual selection of Lesser Prairie-Chickens and our goal was to provide a baseline for more in-depth future experimental work. All models were biologically and theoretically possible and we used model averaging to derive parameter estimates as indices of effect sizes so inference was not placed on any single model (Anderson et al. 2000, Anderson 2008).

RESULTS

We spent 272.5 hrs observing Lesser Prairie-Chicken behavior at leks during spring 2008 and 2009 (mean \pm SE = 47.9 ± 6.9 hrs/lek/yr). Study leks averaged 10.5 males/morning (range = 4.4–16.0) during the spring lekking season. We captured 22 and 14 birds in 2008 and 2009, respectively. Thirteen of nineteen males (11 yearlings, 2 adults) captured during early trapping sessions between 23 February and 13 March 2008, were not reobserved even after extensively searching within 4 km of the leks of capture. These 13 birds were not included in the analyses. Additionally, two males in 2008 and 2009 were

banded but we were unable to collect all morphological measurements. This left us with 7 and 12 individuals, respectively, in 2008 and 2009 with complete morphological measurements to use for analysis.

Mean \pm SE lek attendance rate of marked males that were reobserved on study leks at least once was 0.88 ± 0.04 . We noted 163 and 76 female observations on leks in 2008 and 2009, respectively. Female lek attendance peaked during the 7-day interval starting 13 April in both years (Fig. 1A). The maximum number of females observed on a lek simultaneously was 17. We observed females on leks during evening display periods on one and two occasions in 2008 and 2009, respectively, and in 2008 we observed four copulation attempts during evening lekking.

Overall, male mating success was skewed ($\lambda = 0.60$; B -value = 0.30, $P < 0.001$). We observed 62 copulation attempts on leks in 2008, 30 of which were deemed successful. Copulation attempts peaked during the 7-day interval starting 27 April (Fig. 1B). Four males were responsible for all copulation attempts on lek B1, which averaged 15.2 males per morning ($\lambda = 0.54$; B -value = 0.27, $P < 0.001$). Three males were responsible for 97% of copulation attempts, two of which were responsible for 82% of all copulation attempts. Five males were responsible for all copulation attempts on lek B2, which averaged 16.0 males per morning ($\lambda = 0.77$; B -value = 0.53, $P < 0.001$). Three males were responsible for 93% of all copulation attempts, one of which performed 79% of all copulation attempts. We observed 29 copulation attempts in 2009, 12 of which were deemed successful. Copulation attempts peaked during the interval starting 13 April (Fig. 1B). We only observed one copulation attempt on lek B1, and this lek was removed from the skew analysis. Three males were responsible for all copulation attempts on lek B4, which averaged 9.2 males per morning ($\lambda = 0.58$; B -value = 0.24, $P < 0.001$). Two males were responsible for 88% of all copulation attempts. Four males performed all copulation attempts on lek R5, which averaged 7.8 males per morning ($\lambda = 0.52$; B -value = 0.15, $P = 0.006$) with two of the males performing 82% of all copulation attempts. The percentage of adult and yearling marked birds that attempted ≥ 1 copulation was 20 and 44%, respectively. The mean \pm SE percentage of copulations obtained on a lek for adults and yearlings was 0.09 ± 0.06 and 0.18 ± 0.05 , respectively.

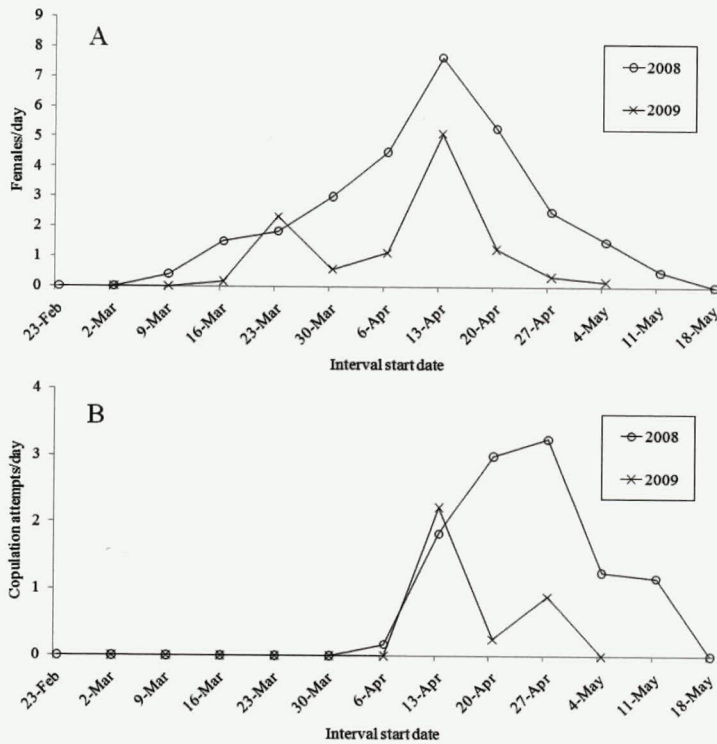


FIG. 1. Distribution of female attendance (A) and copulation attempts (B) at leks throughout the Lesser Prairie-Chicken spring lekking season in the Texas Southern High Plains at two leks in 2008 and three leks in 2009.

Overall, morphological traits contained the least variability (mean CV = 6.72%; Table 1). Pinnæ length exhibited the most variation of the morphological traits. Mean CV for behavioral traits, excluding proportion of time fighting, was 44.05%. We did not observe fighting often ($n = 14$ occurrences by 8 males) while recording location points, which could explain the greater variation in this variable. Other behavioral traits exhibited little heterogeneity. Territory characteristics (distance to lek center and size of territory) was the most variable parameter (mean CV = 70.35%, Table 1).

Males displayed strong fidelity to specific territory position on the lek within a season after initial territory establishment. The only marked male that was observed during both years of the study occupied the same territory. Males occupied the same territories between morning and evening lekking periods. All locations obtained during the evening lekking period were consistent with locations in morning periods.

Percent of time spent idle had the strongest (negative) correlation with the proportion of all ($r = -0.6$, $P = 0.005$) and successful ($r = -0.5$,

$P = 0.04$) copulations obtained by males (Fig. 2). Percent of time engaged in face off behavior was also correlated (positive) with proportion of all copulations obtained ($r = 0.5$, $P = 0.03$), although marginally with proportion of successful copulations ($r = 0.4$, $P = 0.06$). The other characteristics were not significantly correlated ($P > 0.1$) with proportion of copulations obtained.

The most parsimonious model, considering all copulation attempts ($n = 52$ copulation attempts, 19 males), included percent of time spent idle and MCP, and obtained 39% of the Akaike weight (Table 2). All models containing idle were ranked higher than those not containing idle, which also had the greatest model averaged slope coefficient (Fig. 3). The third and fourth best models appeared competitive but contained pretending variables, which contribute little to model fit as evidenced by similar deviance values. Relative importance values for idle, MCP, age, pinnæ, display, distance, and mass were 1.00, 0.52, 0.47, 0.13, 0.12, 0.00, and 0.00, respectively.

The most parsimonious model, considering only successful copulation attempts ($n = 30$ copulations,

TABLE 1. Characteristics measured for male Lesser Prairie-Chickens observed at two leks in 2008 and three leks in 2009 in the Texas Southern High Plains.

Category	Trait	Mean \pm SE		CV ^a
		Adult (<i>n</i> = 10)	Yearling (<i>n</i> = 9)	
Behavior ^b	Display	0.29 \pm 0.02	0.30 \pm 0.03	36.57
	Face off	0.33 \pm 0.03	0.35 \pm 0.04	41.63
	Fighting	0.00 \pm 0.00	0.01 \pm 0.00	295.55
	Idle	0.25 \pm 0.03	0.19 \pm 0.02	53.36
	Moving	0.13 \pm 0.02	0.15 \pm 0.01	44.64
Territory	Distance to lek center (m)	12.66 \pm 1.40	11.09 \pm 1.75	56.44
	Kernel size (m ²)	245.07 \pm 41.26	109.68 \pm 10.73	81.92
	MCP size (m ²)	108.50 \pm 17.49	43.29 \pm 5.46	84.27
Morphology	Wing cord (cm)	21.69 \pm 0.12	21.54 \pm 0.09	2.17
	Tarsus (cm)	5.83 \pm 0.06	5.47 \pm 0.11	7.42
	Pinnae (cm)	6.64 \pm 0.13	6.88 \pm 0.22	11.08
	Mass (g)	783.10 \pm 9.03	780.22 \pm 13.65	6.20

^a Coefficient of Variation values computed from pooled adult and yearling values.

^b Behavior variables are proportion of observations in each behavior category for an individual male.

19 males), included idle and MCP but obtained an Akaike weight of only 23% (Table 3). All models containing idle outperformed those not containing the variable and it had the greatest model averaged slope coefficient (Fig. 3). Relative importance values for idle, MCP, age, mass, pinnae, display, and distance were 1.00, 0.43, 0.39, 0.27, 0.17, 0.08, and 0.05, respectively.

DISCUSSION

We found significant skew in male mating, similar to those reported for Greater Prairie-Chickens (Nooker and Sandercock 2008). It is clear that male Lesser Prairie-Chickens that are less idle experience greater mating success. Yearling males with smaller territories also tended to be selected more often for mating in our study. Morphological characteristics exhibited weaker

effects on male mating success. Males displayed high territory fidelity within a season (after initial territory establishment).

Males that were less idle were more likely to mate which we interpret to indicate that males that are generally more active experience greater mating success. It has been repeatedly found that males that display more, mate more (Gibson and Bradbury 1985, Höglund and Lundberg 1987, Nooker and Sandercock 2008). Being idle likely requires less energy than participating in other behaviors and Gibson and Bradbury (1985) suggest that energetic factors may have a role in observed variation in display rates. A host of reasons exist for female choice based on behavioral characteristics including direct survival benefits for the female or indirect genetic benefits for her offspring. For example, males that do not

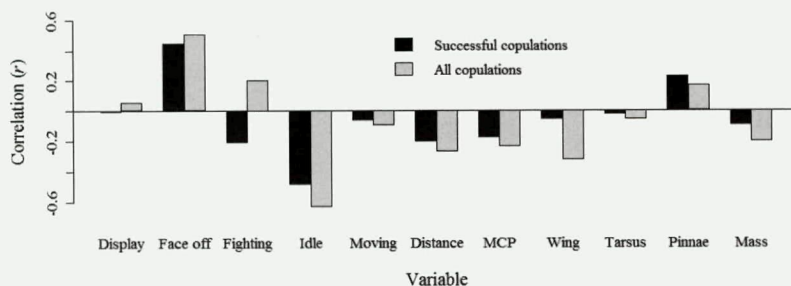


FIG. 2. Pearson's correlation coefficient (*r*) between male Lesser Prairie-Chicken characteristics and percent of all (light gray) and successful (dark gray) copulations obtained on leks in the Texas Southern High Plains during 2008 and 2009. Display, face off, fighting, idle, and moving are the proportion of behaviors recorded in each behavior category. Distance = distance from territory center to lek center. MCP = territory size (minimum convex polygon). Wing, tarsus, pinnae, and mass are morphological characteristics.

TABLE 2. Top ($\Delta < 20$) conditional logit discrete choice models of male Lesser Prairie-Chicken mating success in the Texas Southern High Plains during 2008 and 2009 incorporating 19 males and 52 copulations regardless of success.

Model ^a	k	Deviance	AIC _c	Δ AIC _c	w _i
Idle + MCP	2	60.95	65.17	0.00	0.40
Idle + Age	2	61.17	65.38	0.21	0.36
Idle + MCP + Pinnae	3	60.95	67.40	2.22	0.13
Idle + Age + Display	3	61.14	67.58	2.41	0.12
Idle + Dist + Mass	3	72.80	79.24	14.07	0.00
Idle + Pinnae	2	75.58	79.79	14.62	0.00
Idle + Mass	2	77.32	81.53	16.36	0.00
Idle + Dist + Pinnae	3	75.21	81.66	16.48	0.00
Idle	1	81.47	83.54	18.37	0.00

^a Idle = proportion of time spent idle; Display = proportion of time spent displaying; Dist = distance from territory center to lek center; MCP = territory size (minimum convex polygon); Pinnae and Mass are morphological measurements; Age = yearling or adult.

display often may indicate a poorer physiological condition and inability to acquire sufficient food resources compared to other males.

Males with smaller territories tended to mate more, as reported by others (Wiley 1973, Hovi et al. 1994). Our finding of distance to lek center having little to no effect on mating success is in contrast to most previous research (Ballard and Robel 1974, Kruijt and de Vos 1988, Gratson et al. 1991, Rintämäki et al. 1995) although Gibson and Bradbury (1985) and Nooker and Sandercock (2008) also found that territory location was not important in mate choice. Our correlation analysis suggested that males closer to the center of the lek mated more than peripheral males. Smaller territories are typically associated with areas on the lek with higher male density (Wiley 1973). Areas of high male density are thought to be a result of males relocating their territories around successful males and intruding into their territories in hope of gaining copulations (Landel 1989). Rintämäki et al.

(1995) noted this phenomenon as the 'spatial spill' hypothesis (hotshot hypothesis, Arak 1984), whereas males cluster around dominant males in hope of gaining copulations. Rintämäki et al. (1995) speculated the reason for these 'spillover' copulations may include a surplus of females attempting to copulate with the dominant male and competition for that male may cause females to mate with adjacent males. The dominant male may be limited by sperm depletion or adjacent males may steal copulations from a preoccupied dominant male (Rintämäki et al. 1995). Females may experience difficulties in comparing males and mistakenly mate with an adjacent, potentially poorer quality, male. It is not clear whether territory size or location is a cause or effect of being a dominant male (Gratson et al. 1991).

It is possible that radio transmitters affected reproductive performance of prairie-chickens. The four radio-marked males were all on the same lek and included two adults and two yearlings. Only

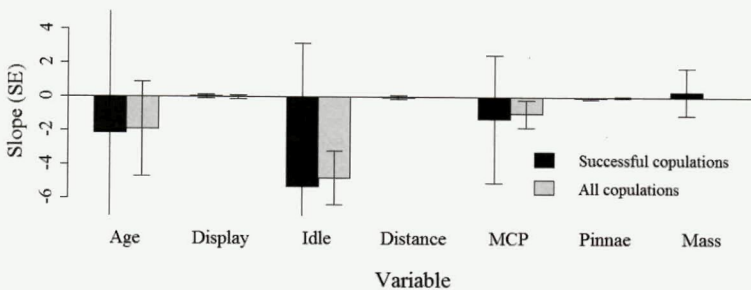


FIG. 3. Model averaged slope coefficients (plus or minus unconditional SE) of standardized variables from discrete choice models describing effect of male Lesser Prairie-Chicken characteristics on obtainment of any copulation attempt (light gray) and only successful copulations (dark gray) in the Texas Southern High Plains during 2008 and 2009. Age is categorical adult or yearling. Display and idle are the proportion of behaviors recorded as each behavior category. Distance is distance from territory center to lek center. MCP is territory size (minimum convex polygon). Pinnae and mass are morphological characteristics. Error bars extending outside the region 5 to -7 are not shown completely.

TABLE 3. Top ($\Delta < 10$) conditional logit discrete choice models of male Lesser Prairie-Chicken mating success in the Texas Southern High Plains during 2008 and 2009 incorporating 19 males and 30 successful copulations.

Model ^a	k	Deviance	AIC _c	Δ AIC _c	w _i
Idle + MCP	2	22.96	27.41	0.00	0.24
Idle + Age	2	23.10	27.54	0.13	0.22
Idle + MCP + Mass	3	22.06	28.98	1.57	0.11
Idle + Age + Mass	3	22.34	29.27	1.86	0.09
Idle + MCP + Pinnae	3	22.58	29.50	2.10	0.08
Idle + Age + Display	3	23.01	29.93	2.52	0.07
Idle + Pinnae	2	25.60	30.04	2.63	0.06
Idle + Mass	2	26.35	30.80	3.39	0.04
Idle + Dist + Mass	3	25.15	32.08	4.67	0.02
Idle + Dist + Pinnae	3	25.59	32.51	5.11	0.02
Idle	1	30.64	32.78	5.38	0.02
Idle + Display	2	29.63	34.08	6.67	0.01
Idle + Dist	2	30.58	35.02	7.62	0.01

^a Idle = proportion of time spent idle; Display = proportion of time spent displaying; Dist = distance from territory center to lek center; MCP = territory size (minimum convex polygon); Pinnae and Mass are morphological measurements; Age = yearling or adult.

one of the radio-marked males mated (a yearling). Little information is available on the effects of radio transmitters on male grouse reproductive performance although Boag (1972) reported radio-marked captive Red Grouse (*Lagopus lagopus scotica*) were less active than controls. The small sample of radio-marked males in our study prevented any test of effects.

Territory occupancy stabilized ~13 March in 2008. Males captured after 13 March during both years of study were reobserved on the lek of capture whereas in 2008, many males captured before 13 March were not reobserved. In contrast, Haukos (1988) reported that, within the same study area, territories were unstable and he did not observe any copulation attempts on leks whereas we observed 91. We suspect this inconsistency may be due to differences in vegetation on leks between the two studies. Haukos (1988) reported vegetation on the leks was sparse, if present at all, and physical structure was frequently altered by wind. Our study occurred 20 years later and succession of vegetation had covered leks with shortgrass and small shrub cover.

We banded numerous males on leks early in the lekking season that did not establish territories at these sites. Unfortunately, we did not radiomark these individuals. Thus, fate of the males that departed their lek of capture and were not reobserved is unknown. Hagen et al. (2005) found that some yearling (20%) and adult (8%) males switched leks between years with an average distance traveled of 3.3 and 3.1 km, respectively. This was well within our search areas but we failed

to relocate any of the males at other leks. Haukos and Smith (1999) observed similar patterns of male movements and satellite lek formation just prior to female attendance. Our data, and those of Haukos and Smith (1999) and Hagen et al. (2005) suggest that estimates of population size from lek counts may be biased if these males did not establish territories on a lek (Walsh et al. 2010). Research using early season radiomarking to examine early season dispersal and inter-lek movements within a season could prove valuable for understanding lek dynamics and gene flow, and facilitate better estimates of population size.

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