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FINE-SCALE SELECTION OF HABITAT BY THE LESSER PRAIRIE-CHICKEN

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Abstract—Proper management of grasslands and shrublands requires an understanding of the factors that influence the persistence of organisms. We compare differences in vegetation between sites occupied by the lesser prairie-chicken (*Tympanuchus pallidicinctus*) and random sites to investigate composition of grasses and forbs and the importance of cover. We observed that birds selected habitat, at least in part, based on composition of grasses and forbs. There was generally a larger variance in diversity of plants for random sites compared to sites associated with presence of lesser prairie-chicken. The role of vegetative cover in selection of habitat is important for avoidance of predators, but use of cover also is a means of thermoregulation. Risk-sensitive behavior is a trade-off between avoiding predation and suitable microclimate. We report evidence that the lesser prairie-chicken consistently seeks to limit the risk of predation and selects locales with a favorable microclimate; birds select sites more or less exposed depending on apparent temperature. We infer that selection of habitat by the lesser prairie-chicken is the result of composition of species of plants, avoidance of predators, and thermoregulation, with the lekking mating system of this bird also playing a role. This declining species might face increasing threats as some practices of land management alter structure of vegetation and reduce shrub cover.

Resumen—El manejo adecuado de los pastizales y matorrales requiere una comprensión de los factores que influyen en la persistencia de los organismos. Se comparan las diferencias de vegetación entre sitios ocupados por el pollo de la pradera menor (*Tympanuchus pallidicinctus*) y sitios al azar para investigar la composición de pastos y hierbas y la importancia de la cubierta. Observamos que las aves seleccionaron el hábitat, al menos en parte, basándose en la composición de pastos y hierbas. En general hubo una variación mayor en la diversidad de la vegetación de los sitios al azar en comparación con los sitios asociados con la presencia del pollo de la pradera menor. El papel de la cubierta vegetal en la selección de hábitat es importante para evitar a los depredadores, pero el uso de la cubierta es también un medio de termorregulación. El comportamiento sensible al riesgo es una concesión mutua entre evitar la depredación y conseguir un microclima adecuado. Se presenta evidencia de que el pollo de la pradera menor constantemente trata de limitar el riesgo de depredación y de seleccionar lugares con un microclima favorable; las aves seleccionan los sitios más o menos expuestos dependiendo de la temperatura ambiental. Se infiere que la selección del hábitat del pollo de la pradera menor es el resultado de la composición de especies de plantas, de evitar a los depredadores, y de la termorregulación, con el sistema de apareamiento lek de esta ave también jugando un papel importante. Esta especie en declive puede encontrar amenazas crecientes debido a que algunas prácticas de manejo de la tierra alteran la estructura de la vegetación y reducen la cobertura de arbustos.

Temperate grasslands and shrublands are among the most endangered ecosystems and have the lowest rate of protection of all the Earth's biomes (Brennan and Kuvlesky, 2005; Basurto and Hadley, 2006). Among these grasslands and shrublands, the prairies of the Great Plains in the United States have been severely altered and diminished (Samson and Knopf, 1994; Samson et al., 2004), harming a myriad of species that depend on them. This includes elimination of prairie-specialist mammals (Benedict et al., 1996) and substantial overall declines in populations of many avian species (Askins et al., 2007). It is important to understand what factors affect an organism's ability to survive and reproduce. This understanding requires study of selection of habitat at different levels as well as assessment of various hypotheses about why an organism selects or avoids a particular habitat.

In terms of vegetation, animals select a habitat on the basis of taxonomic composition (floristics) and structural features (physiognomy), although their relative importance is a matter of debate (Rotenberry, 1985; Mac Nally, 1990; Müller et al., 2010). Beyond vegetation, terrestrial species in open habitats, including desert and prairie, often use features of the landscape such as rocks and mounds for cover. The various factors that determine selection of habitat are frequently in flux due to human activities. Agriculture, development of energy, suppression of fire, and livestock operations have fragmented and converted the native structure of prairies.

One of the icons and umbrella-species of the prairie of the southcentral United States is the lesser prairie-chicken (*Tympanuchus pallidicinctus*), an endemic grouse that has experienced a precipitous decline in population size in the past decades, chiefly because of large-scale conversions and loss of habitat (Woodward et al., 2001; Fuhlendorf et al., 2002; Samson et al., 2004; Pruett et al., 2009*a*; C. A. Hagen and K. M. Giesen, http://bna.birds.cornell.edu.ezproxy.lib.ou.edu/bna/species/364). Besides conversion of habitat due to development and agriculture, the extent of heterogeneous habitat with native grasses and forbs, and cover of intermixed shrubs, in which lesser prairie-chicken evolved, has been reduced with traditional practices of rangeland management (Fuhlendorf et al., 2006). Excessive grazing renders nesting cover insufficient (Riley et al., 1992), and suppression of fire has allowed encroachment by trees, a major contributor to reduction of the size of populations of the lesser prairie-chicken (Fuhlendorf et al., 2002). Collisions with low fences, which proliferate in the prairie following settlement by humans, also have become a major source of mortality (Patten et al., 2005*a*; Wolfe et al., 2007). This lekking species requires open areas when displaying and choosing mates; there also is evidence that the lesser prairie-chicken selects habitats with a favorable microclimate, one associated with higher survival of adults (Patten et al., 2005*b*) and broods (Bell et al., 2010).

Our effort goes beyond traditional studies of use of habitat in that we examine selection of microhabitat and how it affects mortality from predation. The specific predator-cover tactics of species of grouse are considered major determinants of annual rates of mortality, mostly independent of fecundity and density (Bergerud and Gratson, 1988). Grasses, forbs, and shrubs are integral parts of the habitat of the lesser prairie-chicken; we wished to determine how floristics and physiognomy at this fine scale influenced selection of habitat. We generated predictions based on the view that use of cover is predicated on a mix of avoidance of predators, thermoregulation, and reproductive requirements (Table 1). To avoid aerial predators, extent of cover at occupied sites always ought to exceed that available at random sites in that same habitat. We expect mammalian predation to occur chiefly with the use of scent at night, but cover affects dispersion of scent (Bergerud and Gratson, 1988; Conover and Borgo, 2009; Conover et al., 2010). To thermoregulate, extent of cover used should be higher when temperature is high (i.e., cover provides shade) but lower when temperature is low (i.e., birds seek solar radiation for warmth to avoid hypothermia). During the reproductive season, cover should be sacrificed when lekking or searching for suitable nest sites (March–June) but prioritized otherwise. Only if predators, temperature, and reproduction jointly drive cover-seeking behavior did we expect to find evidence in support of all three predictions, which would imply that selective pressures on the species converge sometimes (e.g., exposure and associated predation should be lowest in autumn) but conflict at others, leading to tradeoffs under certain climatic conditions. Our objectives are to describe selection of habitat by lesser prairie-chicken by determining associations between choice of site and flora, physical exposure in different seasons and microclimate, and whether mortalities from predation change with amount of exposure.

Materials and Methods—Our two study areas were located in the mixed and shortgrass prairies of the southwestern Great Plains, in Beaver, Harper, and Ellis counties in northwestern Oklahoma, and Roosevelt County in eastern New Mexico. Natural vegetation was characterized by a community of sand shinnery oak (*Quercus havardii*) or sand sagebrush (*Artemisia filifolia*; Dhillion et al., 1994; Peterson and Boyd, 1998) on predominantly sandy soil or sandy clay loam. The study area in Oklahoma (56,175 ha) supported native prairie (59%) dominated by sand sagebrush and plums (*Prunus*) and fields of the Conservation Reserve Program (21%) dominated by Old World bluestems (*Bothriochloa*), lovegrass (*Eragrostis*), or native-mix, with numerous forbs and grasses (Appendix 1). There was a natural gradient with increased sand sagebrush in the east (western Oklahoma) and increased shinnery oak in the west (eastern New Mexico). The study area in New Mexico (42,150 ha) included the New Mexico Department of Game and Fish's North Bluit and Milnesand Prairie-Chicken Areas and portions of private ranches. The habitat in this area was analyzed through geographic information system for planning conservation of the lesser prairie-chicken by Johnson et al. (2006). The dominant sand-shinnery-oak communities were fragmented by cultivation, and some sites on one private ranch were treated with tebuthiuron, an herbicide designed to thin or kill stands of shinnery oak and other shrubs (Patten and Kelly, 2010). Other common shrubs and subshrubs at the study site in New Mexico included honey mesquite (*Prosopis glandulosa*), tree cholla (*Cylindropuntia imbricata*), broom snakeweed (*Gutierrezia sarothrae*), and soapweed yucca (*Yucca glauca*). Common grasses were sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), blue grama (*Bouteloua gracilis*), black grama (*Bouteloua eriopoda*), sideoats grama (*Bouteloua curtipendula*), sand dropseed (*Sporobolus cryptandrus*), and purple threeawn (*Aristida purpurea*). Common forbs were western ragweed (*Ambrosia psilostachya*), annual buckwheat (*Eriogonum annuum*), and camphorweed (*Heterotheca subaxillaris*; Bell et al., 2010). Approximately half of each study area was subjected to grazing by cattle.

Climate at both study sites was semiarid continental with hot summers and cold, dry winters with a frost-free growing period extending from mid-April to late October (Wright, 2003). Mean (± 1 *SD*) annual precipitation (New Mexico, 45.4 ± 15.5 cm;

Table 1—Predictions about the relationship between use of protective cover and three key aspects of needs for survival, maintenance, and reproduction of lekking grouse.

Consideration	Predicted cover	Predicted seasonality
Avoidance of predators	High always	Throughout year
Thermoregulation	High when warm; low when cold	Varies from summer peak to winter nadir (intermediate in spring and autumn)
Breeding	Low when lekking or choosing nest site; higher otherwise	Nadir in spring (except for females on nests)

Oklahoma, 54.1 ± 9.4 cm) was similar, as were mean (±1 *SD*) temperatures in January (New Mexico, 3.0 ± 2.3°C; Oklahoma, 1.8 ± 1.6°C) and July (New Mexico, 25.4 ± 1.3°C; Oklahoma, 26.9 ± 1.4°C). Actual rainfall during our studies was 32.5 cm in 2003 and 73.2 cm in 2004 at Clovis near the study site in New Mexico (Western Regional Climate Center, http://www.wrcc.dri.edu/) and 57.9 cm in 2003, 73.0 cm in 2004, and 63.4 cm in 2007 at Slapout near the study site in Oklahoma (Oklahoma Climatological Survey, http://www.mesonet.org/). At each site, summer (late May–September) rainfall accounted for >50% of the annual total often occurring during high-intensity thunderstorms; winter (November–February) precipitation accounted for only 15–20% (United States Department of Agriculture National Resources Conservation Services, http://soils.usda.gov/MLRAExplorer).

We used walk-in funnel traps to capture lesser prairie-chickens principally on spring leks (March–May; methods in Schroeder and Braun, 1991; Wolfe et al., 2007). We placed a bib-mounted radio transmitter (Telemetry Solutions, Inc., Concord, California, and Wildlife Materials, Inc., Murphysboro, Illinois) on all captured females and most captured males (due to higher capture rates of males because they attended the leks more regularly than did females). Transmitters had a 12-h mortality switch, and we examined the carcass of each bird found dead to determine cause of mortality (methods in Wolfe et al., 2007). We tracked the birds at different times of the day throughout the year, typically ranging from 1 h before sunrise to 2 h after sunset and several times per week and almost always at least once every 2 weeks (Patten et al., 2005*a,* 2005*b*). We only analyzed locations where the tracker was able to home in on the birds. We excluded triangulated positions because these locations were found on private land where we did not have access for surveys of vegetation.

We surveyed 737 vegetation plots in 2007 at the study site in Oklahoma (we were not using our study site in New Mexico at that time) to determine associations between choice of site and flora. These surveys entailed estimating ground cover as percentage of each genus, as well as species when identifiable, of grasses and forbs in a 1-m^2 square grid at the lowest stratum (the basal cover). Nomenclature follows United States Department of Agriculture Natural Resources Conservation Services PLANTS database (http://plants.usda.gov/). We also estimated cover of shrubs, bare ground, or rock. The surveys of vegetation were completed either at a priori randomly chosen sites or at sites occupied recently by a lesser prairie-chicken, as determined from ongoing radiotracking, to allow comparisons of composition of vegetation. Sites of nests or hens with broods were not included. We did include additional sites where the technician had flushed lesser prairie-chickens while surveying vegetation. We located survey sites with a Global Positioning System (GPS) unit in the field but excluded random locations that were in unsuitable habitats such as roads, ditches, or ranch yards. We tested for independence-association in the amount of coverage in occupied and random sites based on each species of plant and based on species combined into types of vegetation (grasses, forbs, shrub, or bare ground). These tests were analyzed for the total data as well as per season and month using chi-square. We standardized and ranked differences between observed and expected coverage of the species of plants. We used nonmetric multidimensional scaling to test whether variance differed in composition of species between the sites and to illustrate the distribution as an ordination graph. We applied rarefaction to compare the number of species found between the sites while correcting for sample-size bias using EstimateS (R. K. Colwell, http://purl.oclc.org/estimates). We calculated Shannon's evenness for each plot (J'; Shannon, 1948) and compared the occupied and random sites with a t-test assuming unequal variances. Unidentified species, rock, bare ground, and shrub cover were not included, thereby excluding some sites that only consisted of these types in the analyses of diversity.

We estimated vegetative cover with the cone of vulnerability (Kopp et al., 1998) at both study sites in 2003 and 2004 to determine whether exposure differs with microclimate and among seasons. In each cardinal direction, we measured the angle (θ) between perfectly vertical and the nearest point at which vegetative cover contacted a rod. The visual obstruction decreased with a larger angle, meaning that the exposure would be highest at 90° (no vegetation interfering with line of sight). We collected data at points where birds were tracked and at points selected randomly and located by GPS in the field. For each point, we calculated the arithmetic difference between measured angle and horizontal (i.e., $90° - \theta$) and the harmonic mean across these four directions to obtain a single exposure angle. If the same individual was sampled more than once, we calculated a grand mean for that bird and used this mean in analyses.

Temperature, wind speed, and relative humidity were measured at ground level with a Kestrel meter (Nielsen-Kellerman, Boothwyn, Pennsylvania) at the time birds were tracked. Rather than rely on ambient temperature for assessment of thermoregulation, we estimated a biologically meaningful temperature. We used direct readings of ambient and ground temperatures to calculate apparent temperature (T′) in shade as:

$$T' = -2.7 + 1.04T + 2.0e - 0.65v \quad (1)$$

(Steadman, 1984), where T is ambient temperature (°C), e is vapor pressure (kPa), and v is wind speed (m/s). We calculated vapor pressure as:

$$e = e_s(T)(RH/100) \quad (2)$$

where RH is relative humidity (%) and $e_s(T)$ is saturation vapor pressure (kPa) at ambient temperature T:

$$e_s(T) = 0.6108 \exp^{17.27T/(T+237.3)} \quad (3)$$

(Tetens, 1930). Transformation (1) thus corrects ambient and ground temperature readings for relative humidity and wind speed, of which the former increases and the latter decreases apparent temperature.

We used a nested analysis of variance (ANOVA; bird nested with state, month nested within bird) to assess the extent to which mean exposure angle differed by study site and repeated-measures ANOVA to determine if angle varied with season or by individual. Each season comprised 3 months with spring starting in March. We constructed a correlation matrix to determine if there was a significant temporal autocorrelation from month to month.

RESULTS—We identified a total of 48 grasses and forbs to the genus and an additional 127 species of grasses and forbs (Appendix 1). Of the 737 plots surveyed, 479 had been occupied by lesser prairie-chickens and 258 were random. A total of 142 genera or species of plants was recorded at the occupied sites, and 113 taxonomic units (i.e., genera or species) were recorded at the random sites. The confidence intervals of the rarefaction curves did not overlap (Fig. 1), meaning the number of species found at occupied sites was smaller than at random sites. Rarefaction showed that the random sample was richer (mean ± 95% confidence interval = 112.8 ± 0.1 taxonomic units) than the occupied sites (107.7 ± 1.3 taxonomic units). Variance in species composition among random sites was higher than that at occupied sites (Fig. 2; $F = 1.42$, $P < 0.001$, $df = 240, 471$). Evenness was similar, with a slightly lower value at random sites (mean $J'_{bird} = 0.136$, mean $J'_{random} = 0.131$, $t = 0.56$, $P = 0.578$, $df = 416$).

Amount of grass and forb cover differed between random and occupied sites ($\chi^2 = 1806$, $P < 0.001$, $df = 2$); relative to random sites, occupied sites had a higher percentage of grass cover (66.6 versus 56.2%) and forb cover (16.0 versus 12.8%), although the relative amount of grass-to-forb cover was similar between the sites. There was less bare ground and shrub cover at occupied sites compared to random sites. Composition of plants also differed between sites; lesser prairie-chickens chose sites that contained certain species of grasses and forbs but appeared to avoid other species, and this pattern was evident in all seasons and months surveyed (Table 2; $P <$ 0.001 for all tests). When we reduced the dataset by removing species that covered little ground area from the analysis and concentrating on plants that covered $\geq$1 m^2 of the total area surveyed (species within a genus that would cover >1 m^2 together were lumped by genus), the top five plants found more often than expected through all seasons (Table 2) were windmill grass (*Chloris verticillata*), Illinois bundle flower (*Desmanthus illinoensis*), tumblegrass (*Schedonnardus paniculatus*), dropseed (*Sporobolus*), and alfalfa (*Medicago*). The bottom five plants found less often than expected were broom snakeweed, Indian blanket (*Gaillardia pulchella*), sorghum (*Sorghum*), johnsongrass (*Sorghum halepense*), and hairy grama (*Bouteloua hirsuta*). The rankings among the seasons varied to some extent, as can be expected due to differences in growing conditions and phenology, as well as requirements of the birds for food and cover. Plants determined as having the greatest or least association with occurrence of lesser prairie-chicken were not among the most abundant; there were 18 genera or species of plants that covered $\geq$5 m^2 of the total area surveyed (Table 3). When coverage was not partitioned according to season, hairy grama had less association with sites of lesser prairie-chicken than did wheat (*Triticum*), whereas alfalfa had the most association, followed by sand dropseed.

Mean exposure angle did not differ between the states of Oklahoma and New Mexico either by bird (nested ANOVA: $F = 3.41$, $n_{Oklahoma} = 99$, $n_{New\ Mexico} = 111$, $P >$ 0.05, $df = 1, 209$) or by season (repeated-measures ANOVA: $F = 1.78$, $P > 0.15$, $df = 1, 36$). Among birds sampled in each season ($n = 38$), there was a significant effect of individual (repeated-measures ANOVA: $F =$ 10.36, $P < 0.0001$, $df = 3, 108$) but no individual × state interaction ($F_{3,108} = 0.57$, $P > 0.50$, $df = 3, 108$). In only one case (of 66 paired comparisons) was there a significant correlation in successive months, implying results were not temporally autocorrelated. Across all months of our study ($n = 16$), lesser prairie-chickens consistently occupied sites with greater cover than what was available to them (Fig. 3); i.e., sites were less exposed than they would be had site occupancy been random. Relative to apparent temperature, exposure traces a mirror-image path (Fig. 4). When hotter, lesser prairie-chickens were less exposed (more shaded); when colder, they were more exposed (less shaded). Mean exposure angle was itself correlated with predation rate (Fig. 4; $r =$ 0.83, $P < 0.05$, $df = 4$).

DISCUSSION—Whether structure of vegetation (physiognomy) and composition of species (floristics) play competing or complementary roles in habitat selection has not been resolved fully (Rotenberry, 1985; Rodewald and Abrams, 2003; Walker, 2008; Müller et al., 2010), and the pattern may vary among systems (Fleishman et al., 2003). The lesser prairie-chicken selects habitat, at least in part, on the basis of floristics, in that we found associations between site chosen and particular species of grasses and forbs. Yet, from our estimates of physical exposure, we infer that selection of habitat by this species also is the result of a compromise among avoidance of predators, thermoregulation, and reproductive needs; so, the structure of vegetation also matters. We conclude that the lesser prairie-chicken needs specific floristics and a

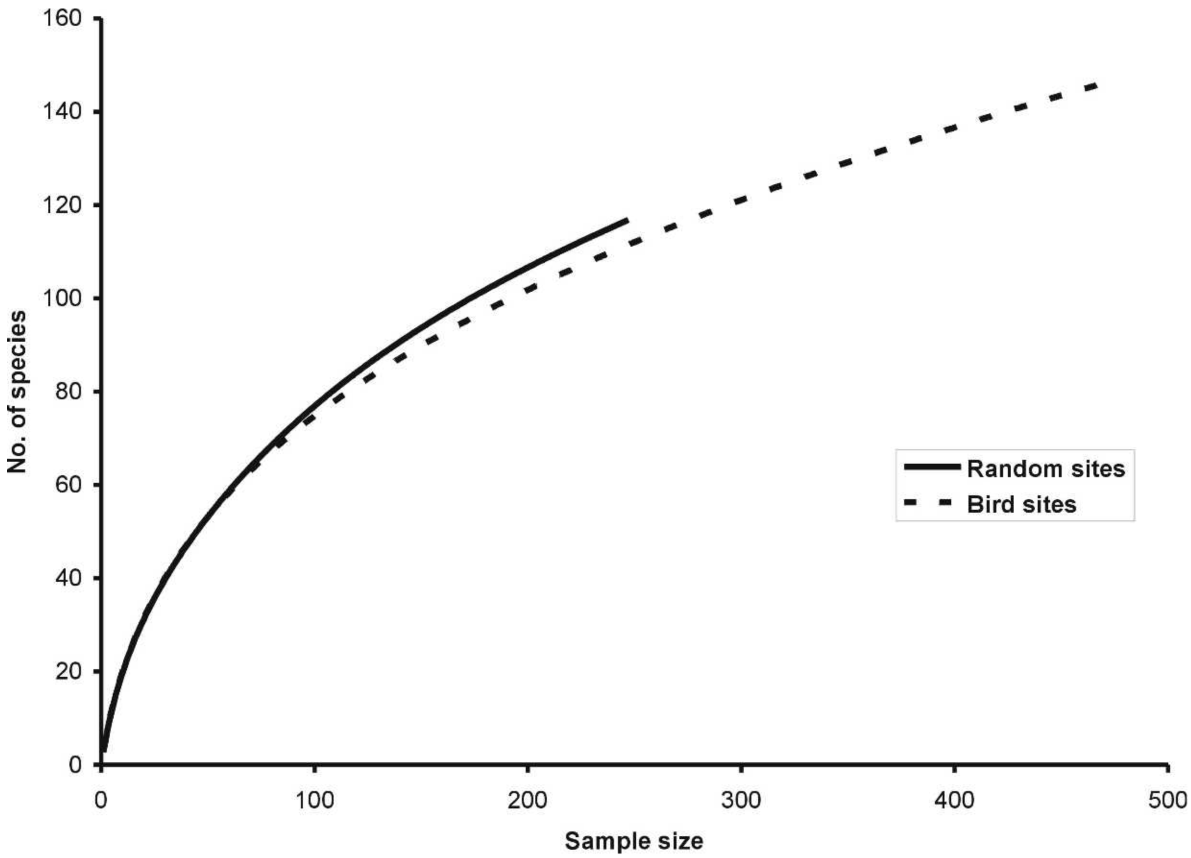

Fig. 1—Rarefaction curves estimating species richness for a subsample based on the pooled total species richness for the random sites (solid line) and sites that had been occupied by lesser prairie-chicken, *Tympanuchus pallidicinctus* (dashed line) in northwestern Oklahoma.

specific physiognomy in the prairie biome to which it is endemic.

Ordination plots imply selectivity because occupied sites by the lesser prairie-chicken cluster together more and exhibit less variance than random sites do (Fig. 2). Composition of plants differed significantly between occupied and random sites across seasons. Mechanistic reasons for selectivity require additional study, but we suggest that reasons are twofold. First, particular species of plants have growth forms that correspond to the physiognomy selected by the species. Second, plants associated with occurrence of lesser prairie-chicken provide food, themselves (Jones, 1963*a,* 1963*b,* 1964; Riley et al., 1993) and as habitat for palatable arthropods in warmer months. Coleoptera (beetles and weevils) and Orthoptera (grasshoppers and crickets) are seasonally primary food sources for the lesser prairie-chicken, especially for the young (Jones, 1963*a*; Jamison et al., 2002; Hagen et al., 2005). Jamison et al. (2002) were not able to separate selection by lesser prairie-chickens for areas of forb cover from selection of areas with greater invertebrate biomass associated with forb cover. Diversity of arthropods has been shown to be strongly related to diversity of plants (Haddad et al., 2009), and composition of local plants may be the most effective predictor of the composition of assemblages of arthropods (Schaffers et al., 2008), leaving open the question of whether sites are chosen because of the plants themselves or the food (insects) on them. Activity and abundance of arthropods are influenced by moisture, particularly in arid regions (Wenninger and Inouye, 2008), suggesting a role for climate, and the configuration of vegetation and cover provided by plants might influence occupancy (Müller et al., 2010).

We found broom snakeweed to be least associated with occurrence of lesser prairie-chicken although the plant has been identified as a food source for the species during winter (Jones, 1963*a,* 1963*b*). Broom snakeweed is a subshrub or large forb whose growth was relatively stunted at our study area in Oklahoma. It is considered an indicator of disturbed vegetation and has been positively associated with leks of lesser prairie-chicken in New Mexico (Hunt and Best, 2010). We found a positive correlation between broom snakeweed and occupancy by lesser prairie-chicken during winter, but that correlation was calculated across a small cumulative area (100 cm^2). Two other species of plants with a negative association, Indian blanket and sunflower (*Helianthus*), occur in disturbed habitats along roadsides and fences, which might explain why sites with these plants appeared to be

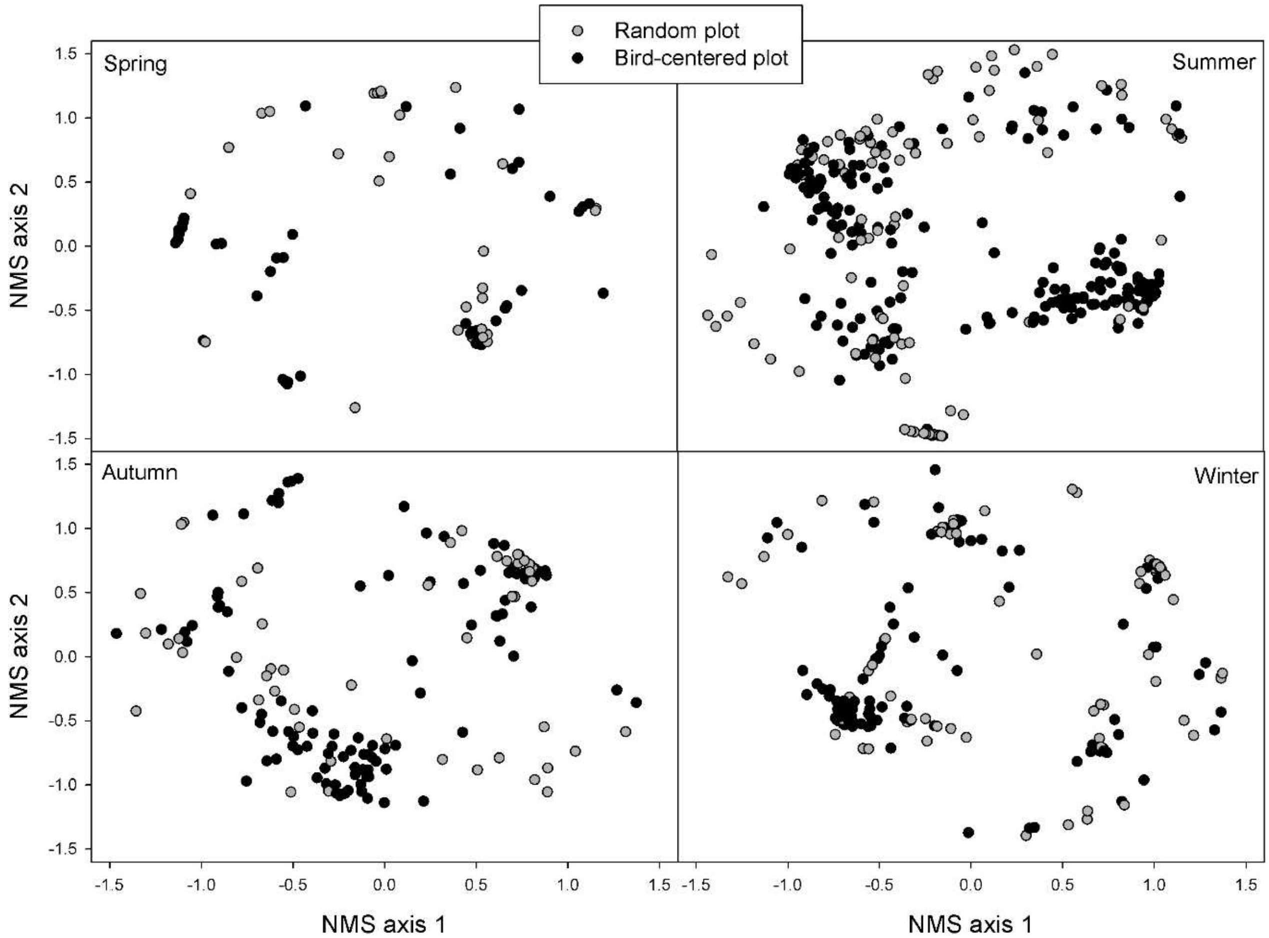

FIG. 2—Ordination analyses (nonmetric multidimensional scaling) using plant species coverage for sites that had been occupied by lesser prairie-chicken, *Tympanuchus pallidicinctus* (black), and random sites (gray) in northwestern Oklahoma (Beaver, Harper, and Ellis counties) during the different seasons.

avoided. Research has shown that objects in otherwise suitable habitat, such as roads, vertical objects, and anthropogenic structures, rather than the plants can explain why lesser prairie-chickens avoid some sites (Pitman et al., 2005; Pruett et al., 2009*b*; Patten and Kelly, 2010; Hagen et al., 2011). Johnsongrass is a nonnative species that spreads quickly in disturbed and cultivated fields. Lesser prairie-chickens feed occasionally in cultivated fields (Salter et al., 2005), including sorghum and wheat, but birds are likely to have lower survival if shrub cover is reduced (Patten et al., 2005*b*). Wheat was associated negatively with occupancy across the year, but the association was positive during the autumn, when availability of arthropods diminished and grains could provide food (Table 2).

Among the more abundant species of plants recorded on our surveys, alfalfa and sand dropseed were the most highly associated with occurrence of lesser prairie-chicken and wheat and three species of *Bouteloua* were the least associated (Table 3). We suggest that the negative association with some native grasses might be an effect of physiognomy, especially in areas where suppression of fire (Fuhlendorf and Engle, 2001) allows ground-level vegetation to grow dense and thereby hinders terrestrial movements by lesser prairie-chickens. As an example (although confidence intervals overlap, likely as a result of small sample sizes), average ground coverage of big bluestem was 29% at occupied sites but ground coverage was 54% at random sites. In the case of the positive association with alfalfa, we posit that the alfalfa attracts birds because of its moisture. Among common crops, alfalfa has a relatively high demand for water (Moore et al., 1994; Herrero and Casterad, 1999).

Regardless of season, birds selected sites with more cover than was available across the landscape. This pattern is consistent with the prediction of the predation hypothesis. Aerial predators depredate lesser prairie-chickens, particularly during migration of raptors (Wolfe et al., 2007). That mortality from predation rises during seasons when birds are more exposed lends credence to this interpretation. At the least, the pattern suggests a plausible selection pressure for refining choice of habitat. We also infer (from the alternate cycling of apparent temperature and mean exposure; Fig. 4) that the lesser

Table 2—Coverage of plants at locations of the lesser prairie-chicken (*Tympanuchus pallidicinctus*) and at random locations in Beaver, Harper, and Ellis counties in northwestern Oklahoma. Standard differences in observed versus expected coverage of selected genera and species of plants (with total cover > 1 m^2; negative value = less coverage than expected) at locations of birds. The absolute (negative and positive) largest differences are noted by an asterisk.

	Coverage (dm^2)		Standardized difference in observed and expected coverage					
Taxon	Locations of birds	Random locations	December–March	April–May	June–September	October–November	Total difference	Mean difference
Ambrosia	557	218	0.26	0.35[a]	−0.03	−0.30	0.03	0.03
Andropogon gerardii	410	321	0.29*	−0.65[a]	−0.27	−0.24	−0.13	−0.13
Aristida	765	378	0.10	−0.21*	0.10	−0.28	−0.02	−0.02
Bothriochloa ischaemum	9,064	2,835	−0.04	0.34[a]	0.19	−0.15	0.07	0.06
Bothriochloa saccharoides	1,051	395	−0.07	−0.38[a]	0.09	0.16	0.04	0.03
Bouteloua curtipendula	9,004	2,193	0.14	−0.10[a]	0.07	0.25	0.11	0.12
Bouteloua dactyloides	1,433	1,383	0.03	−0.44*	−0.21	−0.17	−0.18	−0.17
Bouteloua gracilis	797	927	−0.15	0.00	−0.37	−0.63*	−0.23	−0.20
Bouteloua hirsuta	340	730	−0.20	0.35*	−0.52*	−0.65*	−0.37	−0.38
Bromus arvensis	2,387	703	0.25[a]		0.04	0.09	0.08	0.06
Bromus	519	125		0.19	0.01		0.11	0.13
Chloris verticillata	120		0.35[a]		0.28*	0.32*	0.31*	0.29*
Cirsium	246	81	0.21	−0.01[a]	0.02	0.17[a]	0.06	0.04
Convolvulus	91	65	0.35[a]	0.25*	−0.35	0.32[a]	−0.11	−0.11
Dalea	89	28		0.35[a]	−0.22	0.24	0.07	0.06
Desmanthus illinoensis	482	7	0.35*		0.26	0.30	0.29*	0.29*
Eragrostis	85	131	−0.29		0.28[a]	0.32[a]	−0.30	−0.26
Eriogonum annuum	56	75	−0.65*		0.28*	0.01	−0.26	−0.25
Gaillardia pulchella	46	127	−0.65[a]		−0.44	−0.68[a]	−0.43*	−0.46*
Grindelia	244	110	0.25		−0.07	−0.06	0.00	−0.01
Gutierrezia sarothrae	44	306	0.35[a]		−0.60*	−0.62	−0.57*	−0.58*
Helianthus	114	226	−0.28[a]		−0.44	−0.15	−0.36	−0.38
Heterotheca	1,276	501	−0.45[a]		−0.08	0.13	0.03	0.01
Medicago	1,054	110	0.35[a]		0.15	0.32*	0.21	0.19
Melilotus	148	33	0.35[a]	0.21	0.05	0.32[a]	0.13	0.13
Panicum	537	170	−0.37		0.28*	0.09	0.07	0.06
Pascopyrum smithii	90	35			0.22	−0.68*	0.03	0.01
Plantago	282	89		0.35[a]	0.09	−0.30	0.07	0.04
Salsola	649	137	−0.05	0.35[a]	−0.06	0.24	0.13	0.14
Schedonnardus paniculatus	130				0.28*	0.32[a]	0.31*	0.28*
Schizachyrium scoparium	1,588	1,430	−0.04	−0.54[a]	−0.35	−0.07	−0.17	−0.15
Setaria	160	30	0.35*		0.01	0.12	0.15	0.15
Sorghastrum nutans	435	180	0.35[a]		0.02	−0.09	0.02	0.00
Sorghum halepense	140	345	−0.40		−0.35	−0.40	−0.40	−0.39*
Sorghum	67	180	−0.42*		0.28[a]		−0.42*	−0.39
Sporobolus	955	80	0.21	0.30*	0.28[a]	−0.28[a]	0.23	0.27
Symphyotrichum	159	29	0.07		0.21	0.12	0.15	0.15
Triticum	760	1,505	−0.65*	−0.32*	−0.59*	0.32*	−0.36	−0.36

[a] Sample size was <10% of total coverage of that species; therefore, the difference was not included in ranking.

prairie-chicken selects more-exposed or less-exposed sites depending on temperature. In this case, and as predicted, when it is cold, birds occur more in the open, presumably to avoid hypothermia; conversely, when it is hot, birds occur less in the open, presumably to avoid hyperthermia. The northern bobwhite (*Colinus virginianus*) also selects warmer locations at cooler temperatures and avoids exposed areas during warmer temperatures (Guthery et al., 2005). Other avian species, including grouse, have been reported to decrease energetic expenditure by selecting favorable microhabitat (Pekins et al., 1997). This tendency to seek thermally favorable sites may conflict with selection for avoidance of predators, setting up a tradeoff across seasons.

Other aspects of the life history of the lesser prairie-chicken exert additional selection pressures and, accordingly, influence selection of habitat. Two key aspects relate to the species' breeding system. Males gather on leks each spring to display for females, and during that time they must remain in the open, else they run the risk of not mating. Peak mortality of males coincides with spring lekking (Patten et al., 2005*a*), when they are

TABLE 3—Standard differences in total observed versus expected coverage of genera and species of plants with abundance > 5 m^2 at locations of the lesser prairie-chicken (*Tympanuchus pallidicinctus*) in Beaver, Harper, and Ellis counties in northwestern Oklahoma. Negative value = less coverage than expected.

Rank	Taxon	Common name	Standardized difference between total observed and expected coverage
1	*Medicago*	Alfalfa	0.205
2	*Sporobolus cryptandrus*	Sand dropseed	0.187
3	*Salsola*	Russian thistle	0.131
4	*Bouteloua curtipendula*	Sideoats grama	0.104
5	*Bromus arvensis*	Japanese brome	0.076
6	*Bothriochloa ischaemum*	Old world bluestem	0.068
7	*Ambrosia*	Ragweed	0.044
8	*Panicum virgatum*	Switchgrass	0.032
9	*Heterotheca villosa*	Hairy false goldenaster	0.028
10	*Bothriochloa saccharoides*	Silver bluestem	0.026
11	*Sorghastrum nutans*	Indiangrass	0.007
12	*Aristida purpurea*	Purple threeawn	−0.011
13	*Andropogon gerardii*	Big bluestem	−0.140
14	*Schizachyrium scoparium*	Little bluestem	−0.174
15	*Bouteloua dactyloides*	Buffalograss	−0.192
16	*Bouteloua gracilis*	Blue grama	−0.238
17	*Triticum*	Wheat	−0.365
18	*Bouteloua hirsuta*	Hairy grama	−0.383

exposed frequently to predators. Before choosing a mate, a female typically travels among leks, which are seldom <1 km apart; after mating, a female typically moves a considerable distance in search of a suitable nest site (mean distance between a nest and the lek of capture at the study site in Oklahoma was 3–4 km, with a maximum distance of 22 km; Sutton Avian Research Center, in litt.). Variation in movements from lek of capture to nest site

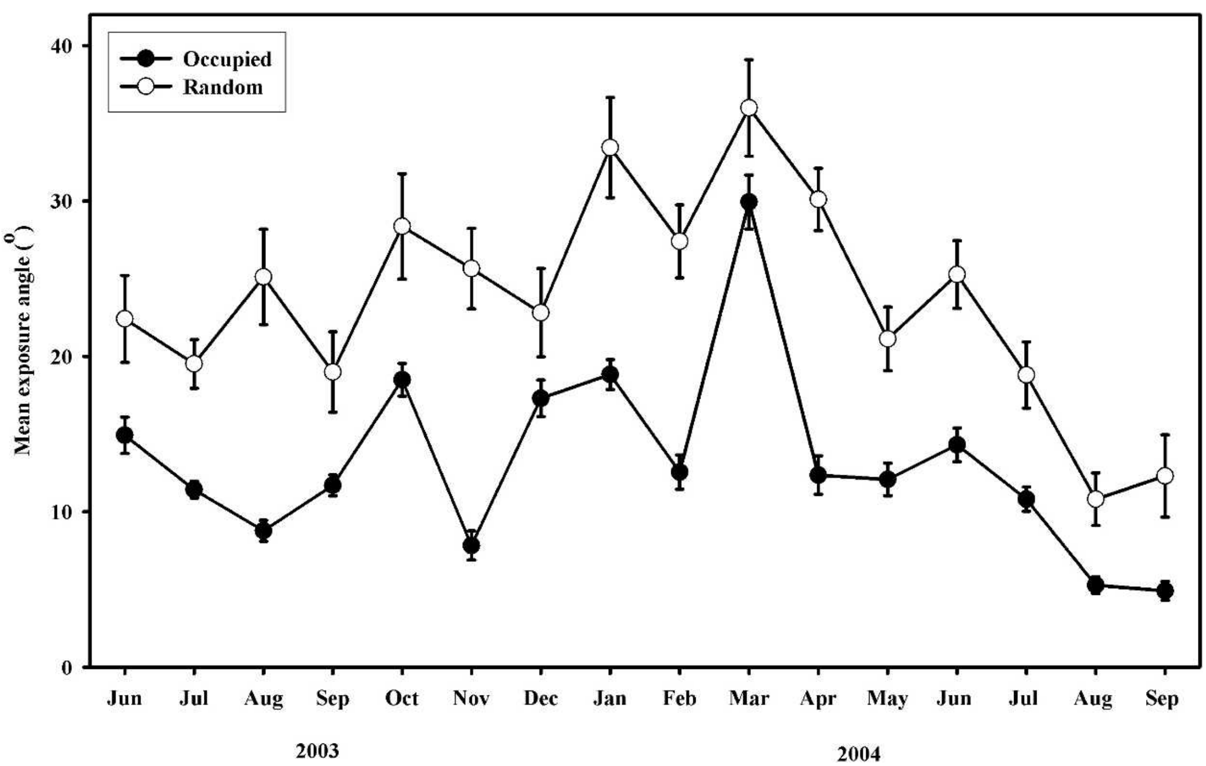

FIG. 3—Mean (per bird) exposure angle at sites chosen randomly and those occupied by lesser prairie-chicken (*Tympanuchus pallidicinctus*) in northwestern Oklahoma and eastern New Mexico.

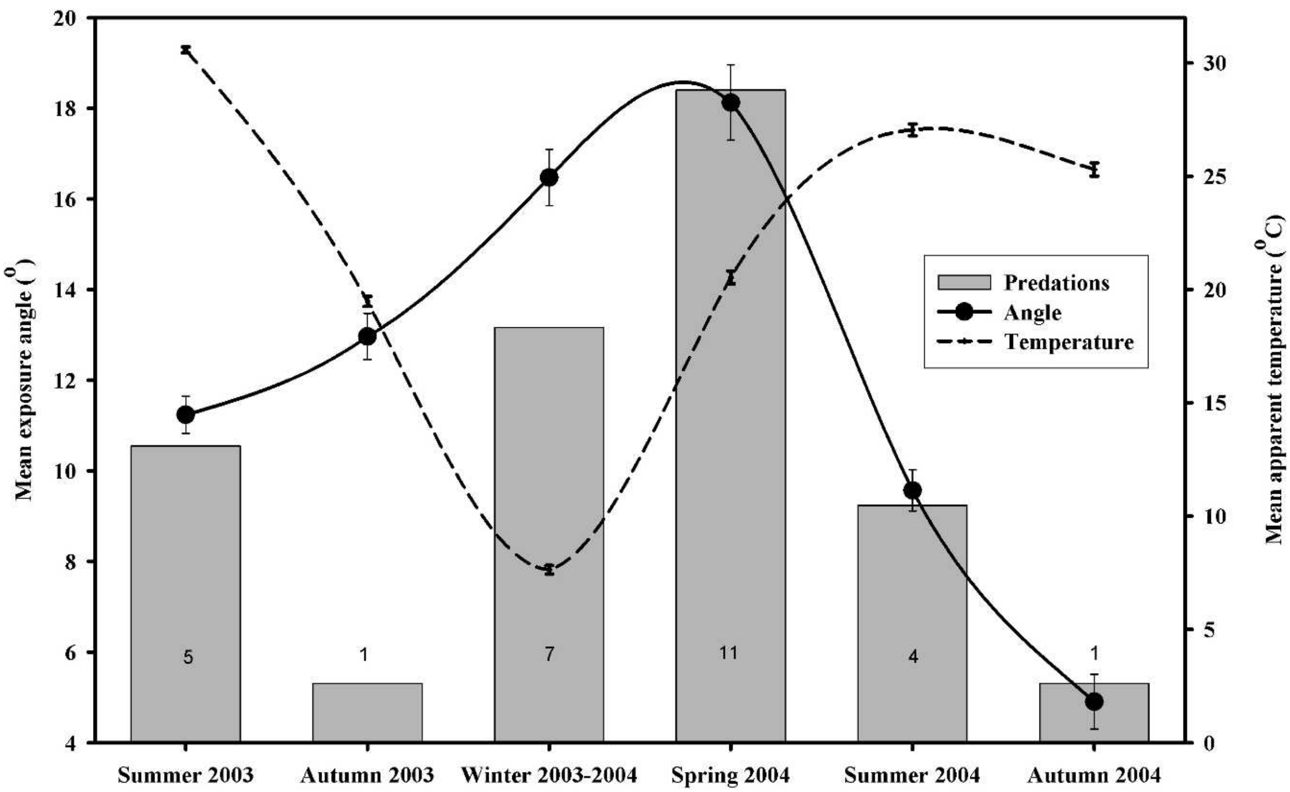

Fig. 4—Mean (per bird) exposure angle in relation to mean apparent temperature for lesser prairie-chicken (*Tympanuchus pallidicinctus*) in northwestern Oklahoma and eastern New Mexico. Counts of mortalities known to be the result of predation are given within or above bars.

has been attributed to quality of habitat and weather (Giesen, 1994). During both periods, the female is necessarily more exposed, and peak mortality of females coincides with their peak vagility (Patten et al., 2005*a*; Hagen et al., 2007). That predation is lowest in autumn, as predicted, lends key support to three factors acting simultaneously, avoidance of predators, thermoregulation, and breeding activities.

Conservation Recommendations—Patten et al. (2005*b*) previously reported an association between microhabitat and survival in the lesser prairie-chicken, birds that occupied, on average, areas with higher percentage of shrub cover tended to survive longer (also see Hagen et al., 2009). Moreover, females placed nests at sites with higher vegetative cover (Pitman et al., 2006; Davis, 2009; Patten and Kelly, 2010), presumably to lessen the probability of predation, and led broods into areas with more cover for thermoregulation (Bell et al., 2010). We conclude that availability of cover translates into high survival value; yet, this declining species faces direct and indirect threats related to the availability of cover. Key among direct threats is conversion of native grasslands and application of herbicides such as tebuthiuron (Johnson et al., 2004; Patten and Kelly, 2010) to increase forage for livestock. Potential indirect threats include increased ambient temperature as a result of global climate change, which is predicted to have especially adverse effect on avifauna of the Great Plains (Peterson, 2003), a region sensitive to drought associated with climate cycles (Clark et al., 2002). Invasive plants in the southern Great Plains (e.g., Crawford and Hoagland, 2009), especially exotic grasses, also may affect habitat selection, particularly if a successful invader is avoided by the lesser prairie-chicken. Our results demonstrate that selection of habitat by the lesser prairie-chicken is driven by composition of the vegetation to a greater extent than previously known. Lesser prairie-chicken tends to occur where specific species of plants are abundant and tends to avoid stands of other species of plants.

We recommend that the vegetation in the range of the lesser prairie-chicken is optimally maintained as native grasslands with a moderate amount (20–30%) of shrub cover available (Patten et al., 2005*b*). On the basis of variation among the seasons in associations of species of plants and extent of vegetative cover, it is clear that heterogeneity in vegetation is essential to the species. Height of vegetation and variation in its density should be maintained to provide thermal diversity. An increase in the importance of microclimatic refugia can be expected with climate changes (Suggitt et al., 2011). If recovery of dwindling populations of the lesser prairie-chicken is the objective of management, our results point to specific species of plants that should be restored and others that should be avoided (keeping physiognomy in mind). We reiterate (see Patten et al., 2005*b*; Patten and Kelly, 2010) the importance of shinnery-oak or sand-sagebrush cover that affects survivorship of lesser prairie-chicken as well.

Land management for the lesser prairie-chicken should target restoration of specific grasses and forbs favored by the species and maintenance of sufficient shrub-cover to allow the species to avoid predators and thermoregulate. Gill et al. (2006) demonstrated that complex ecosystems of native grassland can be reassembled on heavily degraded lands through management within a relatively short time frame. They concluded that conservation efforts with proper establishment and management of grasslands (such as Conservation Reserve Programs) have great potential to benefit high-priority, grassland obligates. The long-term persistence of the lesser prairie-chicken is imperiled unless important features of the habitat are maintained, a prospect growing increasingly dim (e.g., Samson et al., 2004; Pruett et al., 2009*b;* Jarnevich and Laubhan, 2011).

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Appendix 1—Ground coverage (dm^2) and species of forbs and grasses identified in surveyed plots in Beaver, Harper, and Ellis counties in northwestern Oklahoma during a study of lesser prairie-chicken (*Tympanuchus pallidicinctus*). Surveyed plots contained 12,471 dm^2 of bare ground and 110 dm^2 of rock.

Taxon	Common name	Type of vegetation	Total coverage (dm^2)
Acacia angustissima	Prairie acacia	Forb	7
Achillea millefolium	Yarrow	Forb	18
Agalinis	Foxglove	Forb	5
Ambrosia artemisiifolia	Annual ragweed	Forb	95
Ambrosia psilostachya	Western ragweed	Forb	656
Ambrosia	Ragweed	Forb	79
Amphiachyris dracunculoides	Prairie broomweed	Forb	20
Andropogon gerardii	Big bluestem	Grass	731
Andropogon hallii	Sand bluestem	Grass	5
Aphanostephus skirrhobasis	Arkansas dozedaisy	Forb	42
Aristida oligantha	Prairie threeawn	Grass	360
Aristida purpurea	Purple threeawn	Grass	653
Aristida	Threeawn	Grass	130
Artemisia carruthii	Carruth's sagewort	Forb	3
Artemisia ludoviciana	Sagewort	Forb	5
Artemisia	Sagebrush	Forb	12
Astragalus gracilis	Slender milkvetch	Forb	4
Astragalus mollissimus	Woolly locoweed	Forb	17
Astragalus	Milkvetch	Forb	18
Bothriochloa ischaemum	Old world bluestem	Grass	12,243
Bothriochloa saccharoides	Silver bluestem	Grass	1,446
Bouteloua curtipendula	Sideoats grama	Grass	11,197
Bouteloua dactyloides	Buffalograss	Grass	2,816
Bouteloua gracilis	Blue grama	Grass	1,724
Bouteloua hirsuta	Hairy grama	Grass	1,070
Bouteloua	Silver grama	Grass	10
Bromus arvensis	Japanese brome	Grass	3,145
Bromus catharticus	Rescuegrass	Grass	65
Bromus	Brome	Grass	135
Bromus tectorum	Cheatgrass	Grass	444
Buglossoides arvensis	Corn gromwell	Forb	10
Callirhoe involucrata	Purple poppymallow	Forb	10
Callirhoe	Poppymallow	Forb	10
Calylophus hartwegii	Hartweg's sundrops	Forb	5
Calylophus serrulatus	Yellow sundrops	Forb	35
Castilleja sessiliflora	Downy paintedcup	Forb	10

Appendix 1—Continued.

Taxon	Common name	Type of vegetation	Total coverage (dm^2)
Cenchrus spinifex	Sandbur	Grass	10
Chamaesaracha coniodes	Gray five eyes	Forb	3
Chamaesyce maculata	Spotted sandmat	Forb	20
Chamaesyce prostrata	Prostrate sandmat	Forb	10
Chamaesyce	Sandmat	Forb	1
Chamaesyce stictospora	Slimseed sandmat	Forb	1
Chenopodium album	Lambsquarters	Forb	5
Chenopodium ambrosioides	Mexican tea	Forb	1
Chloris verticillata	Windmill grass	Grass	120
Chrysopsis pilosa	Soft goldenaster	Forb	75
Cirsium ochrocentrum	Yellowspine thistle	Forb	5
Cirsium	Thistle	Forb	12
Cirsium undulatum	Wavyleaf thistle	Forb	315
Commelina communis	Asiatic dayflower	Forb	2
Convolvulus arvensis	Field bindweed	Forb	95
Convolvulus	Bindweed	Forb	61
Conyza canadensis	Canadian horseweed	Forb	93
Croton	Croton	Forb	58
Croton texensis	Texas croton	Forb	2
Cyperus	Sedge	Grass	2
Dalea candida	White prairie clover	Forb	3
Dalea enneandra	Nineanther prairie clover	Forb	72
Dalea purpureum	Purple prairie clover	Forb	41
Dalea	Prairie clover	Forb	11
Descurainia pinnata	Western tansymustard	Forb	29
Desmanthus illinoensis	Illinois bundle flower	Forb	489
Dichanthelium oligosanthes	Heller's rosette grass	Grass	5
Elymus canadensis	Canada wildrye	Grass	40
Engelmannia peristenia	Engelmann's daisy	Forb	10
Eragrostis cilianensis	Stinkgrass	Grass	7
Eragrostis secundiflora	Red lovegrass	Grass	114
Eragrostis sessilispica	Tumble lovegrass	Grass	10
Eragrostis	Lovegrass	Grass	5
Eragrostis trichodes	Sand lovegrass	Grass	80
Erigeron tenuis	Slenderleaf fleabane	Forb	3
Eriogonum annuum	Annual buckwheat	Forb	131
Erysimum asperum	Western wallflower	Forb	15
Erysimum repandum	Spreading wallflower	Forb	7.5
Euphorbia marginata	Snow on the mountain	Forb	2
Evax	Pygmy cudweed	Forb	5
Evolvulus nuttallianus	Shaggy dwarf morning-glory	Forb	12
Gaillardia pulchella	Indian blanket	Forb	173
Gaura coccinea	Scarlet beeblossom	Forb	7
Gaura	Beeblossom	Forb	5
Glandularia	Mock vervain	Forb	20
Grindelia	Gumweed	Forb	117
Grindelia squarrosa	Curlycup gumweed	Forb	237
Gutierrezia sarothrae	Broom snakeweed	Forb	350
Haplopappus	Haplopappus	Forb	11
Helianthus	Sunflower	Forb	340
Heliotropium tenellum	Pasture heliotrope	Forb	1
Heterotheca	False goldenaster	Forb	65
Heterotheca subaxillaris	Camphorweed	Forb	60
Heterotheca villosa	Hairy false goldenaster	Forb	1,682
Hordeum pusillum	Little barley	Grass	5
Hymenopappus	Hymenopappus	Forb	21
Kochia scoparia	Fireweed	Forb	40

Appendix 1—Continued.

Taxon	Common name	Type of vegetation	Total coverage (dm^2)
Lactuca serriola	Prickly lettuce	Forb	35
Lactuca	Lettuce	Forb	1
Lepidium densiflorum	Common pepperweed	Forb	12.5
Lepidium oblongum	Veiny pepperweed	Forb	15
Lepidium	Pepperweed	Forb	17
Lesquerella gordonii	Gordon's bladderpod	Forb	20
Liatris punctata	Dotted blazing star	Forb	11
Liatris pycnostachya	Prairie blazing star	Forb	26
Linum perenne	Blue flax	Forb	5
Linum	Flax	Forb	2
Lomatium foeniculaceum	Desert biscuitroot	Forb	20
Medicago	Alfalfa	Forb	1,164
Melilotus officinalis	Yellow sweetclover	Forb	26
Melilotus	Sweetclover	Forb	155
Mimosa microphylla	Catclaw sensitivebriar	Forb	2
Monarda pectinata	Plains beebalm	Forb	17
Muhlenbergia	Muhly	Grass	10
Oenothera	Evening primrose	Forb	5
Opuntia	Prickly pear	Forb	10
Oxalis	Woodsorrel	Forb	5
Panicum capillare	Witchgrass	Grass	17
Panicum hallii	Hall's panicgrass	Grass	10
Panicum havardii	Havard's panicgrass	Grass	5
Panicum obtusum	Vine mesquite	Grass	90
Panicum	Panicgrass	Grass	5
Panicum virgatum	Switchgrass	Grass	580
Paronychia jamesii	James' nailwort	Forb	22
Paronychia sessiliflora	Creeping nailwort	Forb	5
Pascopyrum smithii	Western wheatgrass	Grass	125
Pediomelum cuspidatum	Largebract Indian breadroot	Forb	25
Pediomelum	Indian breadroot	Forb	1
Physalis angulata	Cutleaf groundcherry	Forb	5
Physalis	Groundcherry	Forb	13
Plantago aristata	Bracted plantain	Forb	138
Plantago patagonica	Woolly plantain	Forb	69
Plantago rhodosperma	Redseed plantain	Forb	3
Plantago	Plantain	Grass	10
Plantago virginica	Virginia plantain	Forb	10
Plantago wrightiana	Wright's plantain	Forb	145
Polygala alba	White milkwort	Forb	32
Pseudognaphalium obtusifolium	Rabbit-tobacco	Forb	3
Psoralidium	Scurfpea	Forb	45
Psoralidium tenuiflorum	Slimflower scurfpea	Forb	10
Quincula lobata	Chinese lantern	Forb	5
Ratibida columnifera	Upright prairie coneflower	Forb	24
Rumex	Dock	Forb	10
Salsola	Russian thistle	Forb	786
Schedonnardus paniculatus	Tumblegrass	Grass	130
Schizachyrium scoparium	Little bluestem	Grass	3,018
Scutellaria resinosa	Sticky skullcap	Forb	5
Senecio riddellii	Riddell's ragwort	Forb	5
Setaria geniculata	Knotroot bristlegrass	Grass	80
Setaria pumila	Yellow foxtail	Grass	65
Setaria	Bristlegrass	Grass	45
Shrub	Shrub		3,389
Solanum elaeagnifolium	Silverleaf nightshade	Forb	29
Solanum	Nightshade	Forb	3
Solidago canadensis	Canada goldenrod	Forb	10

Appendix 1—Continued.

Taxon	Common name	Type of vegetation	Total coverage (dm^2)
Solidago	Goldenrod	Forb	2
Sonchus asper	Spiny sowthistle	Forb	2
Sorghastrum nutans	Indiangrass	Grass	615
Sorghum halepense	Johnsongrass	Grass	485
Sorghum	Sorghum	Grass	247
Sporobolus compositus	Composite dropseed	Forb	10
Sporobolus cryptandrus	Sand dropseed	Grass	575
Sporobolus	Dropseed	Grass	450
Stenaria nigricans	Diamondflower	Forb	10
Stenosiphon linifolius	False gaura	Forb	10
Symphyotrichum ericoides	Heath aster	Forb	123
Symphyotrichum fendleri	Fendler's aster	Forb	15
Symphyotrichum	Aster	Forb	50
Tetraneuris scaposa	Stemmy four-nerve daisy	Forb	10
Thelesperma megapotamicum	Hopi tea greenthread	Forb	39
Thelesperma	Greenthread	Forb	6
Tradescantia bracteata	Longbract spiderwort	Forb	5
Tragopogon dubius	Yellow salsify	Forb	10
Tragopogon pratensis	Goatsbeard	Forb	5
Tridens	Tridens	Grass	10
Triticum	Wheat	Grass	2,265
Unidentified	Unidentified		3,239
Vernonia baldwinii	Baldwin's ironweed	Forb	3
Veronica peregrina	Neckweed	Forb	2
Vulpia octoflora	Sixweeks fescue	Grass	45
Zea mays	Yellow sweet corn	Forb	4
Total			73,700