EFFECTS OF MICROHABITAT AND MICROCLIMATE SELECTION ON ADULT SURVIVORSHIP OF THE LESSER PRAIRIE-CHICKEN

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Abstract: Populations of the lesser prairie-chicken (*Tympanuchus pallidicinctus*), an endemic grouse of the south-central United States, have declined precipitously. This species occurs in short- and mixed-grass prairies with sandy soils. Apart from perennial grasses of short stature, prairie-chicken habitat is characterized by dryland shrubs of the sand shinnery community, particularly the shinnery oak (*Quercus havardii*) and sand sagebrush (*Artemisia filifolia*). We measured microhabitat and microclimate characteristics at bird-centered and random points at the southwestern (New Mexico) and northeastern (Oklahoma) edges of the species' range. We estimated survival by locating radio-tagged prairie-chickens ($n = 544$) from April 1999 to June 2003. We found that lesser prairie-chickens used sites within the sand shinnery community that had a higher cover and greater density of shrubs (ANOVA: $P < 0.0001$). Microclimate differed substantially between occupied and random sites (MANOVA: $P < 0.0001$), and prairie-chicken survival was higher in microhabitat that was cooler, more humid, and less exposed to the wind. Survivorship was higher for adults that chose microhabitat with a higher cover of shrubs and grasses and a higher density of vegetation. Survivorship was higher for prairie-chickens that used sites with >20% cover of shrubs than for those choosing 10–20% cover; in turn, survivorship was higher for prairie-chickens choosing 10–20% cover than for those choosing <10% cover (Cox regression: $P < 0.05$). Whereas vegetation may recover following moderate habitat disturbance, land managers applying herbicides or otherwise removing shrubs should understand the potentially negative effects of reduced shrub cover on adult survivorship of lesser prairie-chickens.

JOURNAL OF WILDLIFE MANAGEMENT 69(3):1270–1278; 2005

Key words: habitat selection, lesser prairie-chicken, microclimate, New Mexico, Oklahoma, sand shinnery, survivorship, *Tympanuchus pallidicinctus.*

The lesser prairie-chicken is rare, declining, and occupies a small range (Johnsgard 2002). This species is confined to the south-central United States; its distribution centers on the Llano Estacado, a high, flat plain in the shortgrass prairie province of the southwestern Great Plains (Taylor and Guthery 1980). The lesser prairie-chicken is a relatively large bird that wanders widely, making it a good focal species (Abell 2002) for terrestrial ecosystems. Accordingly, an understanding of its ecology and demography is critical to our understanding of the sand shinnery ecosystem and potential impacts to the species, whether from changes in land use or in climate (Whitford 1997). Apart from the recently described Gunnison sage-grouse (*Centrocercus minimus*), the lesser prairie-chicken has the smallest population and most restricted range of any North American grouse (Sands 1968, Giesen 1998, Johnsgard 2002). Since the 1950s, lesser prairie-chicken populations have declined in New Mexico (Bailey and Williams 2000) and Kansas (Jensen et al. 2000) and markedly so in Oklahoma (Horton 2000), Colorado (Giesen 2000), and Texas (Sullivan et al. 2000). Since European settlement of the plains, the lesser prairie-chicken's range and population size have each declined by over 90% (Taylor and Guthery 1980). Causes of the decline are elusive but could include excessive grazing by cattle and sheep, excessive cultivation, increased proportion of trees (especially the eastern red cedar [*Juniperus virginiana*]), increased populations of predators, and increased energy development (Crawford and Bolen 1976, Taylor and Guthery 1980, Applegate and Riley 1998, Giesen 1998).

As part of a long-term study on the ecology and demography of the lesser prairie-chicken, we quantified habitat use of radiotagged birds. Our goal was to identify fine scale habitat use beyond the broad scale already known for the species (Jones 1963, 1964; Taylor and Guthery 1980; Cannon and Knopf 1981). We also explored the ramifications of this habitat use in 3 ways: (1) How does selection for microhabitat correspond to differences in microclimate? (2) Does microhabitat selection correlate with increased adult sur-

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vivorship? By corollary, (3) how does land use affect microhabitat and microclimate? The answers to these questions will help guide more specific plans to conserve remaining lesser prairie-chicken populations.

STUDY AREA

In April 1999, the Sutton Avian Research Center established lesser prairie-chicken study areas in east-central New Mexico and northwestern Oklahoma, USA. The areas were positioned on either side of the Llano Estacado, where natural vegetation was characterized by a sand shinnery community (Peterson and Boyd 1998) co-dominated by shinnery oak, sand sagebrush, and various perennial grasses (Dhillion et al. 1994). Common forbs in this community included buckweed (*Eriogonum annuum*), plains blackfoot (*Commelina erecta*), and non-native Russian thistle (*Salsola tragus*). Other common shrubs included plains (*Yucca campestris*) and soapweed (*Y. glauca*) yuccas, honey mesquite (*Proposis glandulosa*), broom snakeweed (*Gutierrezia sarothrae*), and Chickasaw (*Prunus angustifolia*) and Oklahoma (*P. gracilis*) plums (Dhillion et al. 1994, Peterson and Boyd 1998). There was a natural gradient across the llano of increased shinnery oak to the west (eastern New Mexico) and increased sand sagebrush to the east (western Oklahoma).

The New Mexico study area (~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 area supported native shortgrass prairie dominated by shinnery oak. Some sites on 1 private ranch were treated with tebuthiuron, an herbicide designed to thin or kill stands of shinnery oak and other shrubs. The Oklahoma study area (~56,175 ha) supported a mixture of native short- and mixed-grass prairie dominated by sand sagebrush and plums (~59%), and Conservation Reserve Program (CRP) fields were dominated by Old World bluestems (*Bothriochloa* spp.), weeping lovegrass (*Eragrostis curvula*), or native-mix (~21%). Roughly half of each study area was subjected to moderate cattle grazing.

At both sites climate was arid and strongly seasonal, with hot, wet summers and cold, dry winters. Mean annual rainfall (New Mexico, 44.0 ± 13.2 cm [17.3 ± 5.2 inches]; Oklahoma, 56.1 ± 14.8 cm [22.1 ± 5.8 inches]) was similar, as were mean temperatures in July (New Mexico, 25.4°C; Oklahoma, 26.8°C) and January (New Mexico, 3.7°C; Oklahoma, 0.1°C). At each site, summer (late May–Sep) rainfall accounted for >50% of the annual total; however, winter (Nov–Feb) rainfall accounted for only ~15%.

METHODS

Trapping and Radiotracking

We trapped prairie-chickens principally on spring leks; peak lekking activity occurred in March and April, but we trapped into May. We also trapped a few leks in September and October. We trapped a given lek 5–10 consecutive days. We captured birds using walk-in funnel traps patterned after Schroeder and Braun's (1991) design for the greater prairie-chicken (*T. cupido*). We fitted each bird with an aluminum leg band. We placed a bib-mounted radio transmitter (Telemetry Solutions, 1130 Burnett Avenue, Suite J, Concord, California 94520, USA, or Wildlife Materials, Inc., 1031 Autumn Ridge Road, Carbondale, Illinois 62901, USA) on all females and on all (1999–2001) or up to 5 (2002–2003) males per lek. Transmitters were glued or sewn onto vinyl-coated nylon bibs (Amstrup 1980); they weighed 14–15 g or ~2% of an adult's body weight. The mounting system and a tuned-loop antenna were designed to minimize adverse effects on the birds (Amstrup 1980, Cotter and Grotto 1995). Each transmitter had a 12-hr mortality switch.

We tracked birds from the ground as often as possible, with efforts extending throughout the day (1 hr before sunrise to 2 hr after sunset). We used 3 types of receivers (AVM® LA12Q, ATS® R2000, ATS® R4000) equipped with either a 5-element Yagi or an omnidirectional antenna. We tracked many (60–70%) birds several times per week and almost all birds (>90%) at least once every 2 weeks. To locate birds we could not find on the ground for 2–3 weeks, we flew aerial transects (Gilmer et al. 1981) twice per month from May to June and once every 2 months the rest of the year.

Vegetation and Microclimate Sampling

Beginning in October 2000, we sampled vegetation at 2 types of points: occupied, meaning a location at or near a radiotracked prairie-chicken, and random, meaning a location selected a priori then located in the field (i.e., not bird-centered). For occupied sites, we sampled vegetation along a transect anchored at the location of a tracked prairie-chicken. To avoid flushing or disturbing a roosting or foraging bird, we extended sampling transects at occupied sites from a point in like habitat (e.g., if the bird was in dense native-mix CRP, our point was in dense native-mix CRP) <50 m (<20 m in 95% of cases) from the bird at a bearing of 45° or 225°, whichever led us away from the bird. We thus sacrificed some accuracy for the welfare of the birds (75–80% of which did not flush during vegetation sampling), but because we chose alternate points indiscriminately, they should not be biased systematically. Each month we sampled 60–90 randomly centered transects. We generated random locations using a standard algorithm, and then located them in the field with a Global Positioning System (GPS) unit. These points could fall anywhere within the study area, but we excluded roads, ditches, ranch yards, and other clearly unsuitable locations. We oriented transects at random sites at a bearing of 45–225° (to be consistent with occupied transects) centered on the predetermined GPS point. We sampled occupied sites while tracking a bird and random sites in between tracking efforts; we gathered data throughout the day for either type of site.

Vegetation sampling procedures were the same for occupied and random sites. We avoided sampling on days with heavy or steady rain or wind exceeding 30 km/hr. As a measure of relative cover, we tallied canopy (i.e., the tallest plant >20 cm above ground) contacts on a vertical rod at 1-m intervals along the 10-m transect; this yielded 11 samples, 1 each from meters 0–10. As a measure of density, at the transect's zero point we tallied rod contacts at <10 cm, 10–50 cm, and >50 cm above ground, and we recorded the height of the canopy at the rod and the maximum height within a 1-m radius of the rod. At this same point, we tallied the number of woody stems contacting a 0.5-m radius chain, though only if the shrub's base was within the 0.5-m radius (i.e., the rooted density). We recorded separate estimates of density for shinnery oak, sand sagebrush, plums, mesquite, tallgrass (e.g., *Andropogon*, *Bothriochloa*, *Bouteloua curtipendula*, *Digitaria*, *Eragrostis*, *Lolium*, *Panicum*, *Schizachyrium*, *Sorghastrum*, *Sorghum*, *Sporobolus*, *Tripsacum*, *Triticum*), and shortgrass (e.g., *Aristida*, *Bouteloua gracilis*, *hirsute*, and *oligostachya*, *Buchloe*, *Chloris*, *Muhlenbergia*, *Setaria*, *Stipa*).

We also gathered microclimate data at each vegetation sampling point. Using handheld Kestrel® 3000 data loggers, we recorded temperature (°C), relative humidity (%), and wind speed (km/hr) at the ground and at 2 m above the ground.

Statistical Analyses

We collected data on occupied sites fortuitously (i.e., whenever a radiocollared bird was detected), so we tracked some individual birds more frequently than others. These habitat data were clearly autocorrelated temporally and were thus pseudoreplicated. We effectively eliminated autocorrelation by collapsing vegetation data to means per bird, per month. This reduced data set included 2,692 sites occupied by 544 individual lesser prairie-chickens and 3,791 random sites sampled from October 2000 to June 2003. Associated vegetation data included: (1) a series of canopy measures, classified as shrub (all shrub species), grass (all grass species), shinnery oak, sand sagebrush, or other shrub species and (2) a series of density measures at the 0-m point of the transect, either irrespective of species (density <10 cm, 10–50 cm, and >50 cm above ground) or for shinnery oak, sand sagebrush, or other shrubs.

We hypothesized that occupied habitat would differ from a random sampling of available sand shinnery habitat. We tested this hypothesis separately by state, using the reduced data set in a series of mulitvariate analyses of variance (MANOVA; PROC GLM, SAS version 8.0, SAS Institute). Survey type (i.e., random vs. occupied) was a main effect, month a covariate, and type × month an interaction term. Because climate was similar between study areas, we did not include a year effect. We also treated tebuthiuron application as a main effect for New Mexico plots; tebuthiuron was not used on our Oklahoma plots. We ran separate MANOVAs for 3 combinations of response variables: (1) canopy density of all shrubs, all grasses, shinnery oak, sand sagebrush, and other shrub species; (2) density at the 0-point <10 cm, 10–50 cm, and >50 cm above ground, height at the 0-point, and maximum height within a 1-m radius of this point; and (3) ambient temperature, relative humidity, and wind speed at ground level. For the last set of analyses, we excluded all data from night roosts.

We further tested for differences between random and occupied sites by even more conservative means. We constructed a data set in which random sites were represented by monthly means within year (n = 66) and occupied sites by within-bird means (n = 389). We then applied a multiresponse permutation procedure (MRPP; PC-ORD ver. 4.0, MjM Software), which is essentially a nonparametric discriminant function analysis, with Euclidean distances and natural weighting (Zimmerman et al. 1985), to this greatly reduced data set. We judged any short- or mixed-grass prairie with an infusion of shinnery oak and/or sand sagebrush to be suitable for the lesser prairie-chicken. We predicted that, in multivariate space, occupied sites would be subsets of random sites. The clearest manifestation of nestedness would be that variance around occupied sites was much less than variance around random sites. We tested this prediction by means of a variance ratio test (Sokal and Rohlf 1995:189). Last, we constructed a canonical discriminant function (PROC DISCRIM, SAS version 8.0) to create a heuristic graphical representation of the 4 groups.

We used failure-time analyses to explore patterns of adult survivorship and their relationship with microhabitat. Estimates of survival time can be biased in radiotracking studies (Burger et al. 1991), but we used the same technique throughout our study area, so biases should be spread evenly across state, sex, vegetation, and microclimate. The effects of potential bias should be minimal other than increasing overall error, which reduces power of statistical tests. We used the product-limit (Kaplan-Meier) estimator to build survival curves by state and by sex. Right-censored data accounted for 50–55% of the all data. We tested for differences in survival times between states and sexes with likelihood-ratio χ^2 tests (PROC LIFETEST, SAS version. 8.0). We used Cox's proportional hazards regression model to examine how vegetation structure and microclimate were associated with survival time (PROC PHREG, SAS version 8.0).

RESULTS

Although the effect size tended to be small (**d** < 0.2), we could distinguish between occupied and random sites consistently. Relative to random sites, vegetative cover and density were significantly higher on occupied sites in New Mexico (Wilks' $\Lambda = 0.98$, $P < 0.0001$) and Oklahoma (Wilks' $\Lambda = 0.92$, $P < 0.0001$), though the amount of grass cover did not contribute to the result (Table 1). Nearly half (47.5%) of our sampling points were grazed, yet grass cover did not differ between occupied and random sites (Table 1) even when controlling for grazing (ungrazed: $F_{1,11} = 1.72$, $P > 0.20$; grazed: $F_{1,11} = 0.77$, $P > 0.35$). Shinnery oak cover was significantly higher on occupied sites in New Mexico (**d** = 0.21); however, the amount of sand sagebrush was significantly higher on occupied sites in Oklahoma (**d** = 0.19; Table 1). At both sites the amount of cover by other shrub species, principally broom snakeweed, mesquite (in New Mexico), and plums (in Oklahoma), was also significantly higher on

Table 1. Differences in vegetative cover between sites occupied by radiotagged lesser prairie-chickens (*Tympanuchus pallidicinctus; n* = 2,692) and sites sampled at random (*n* = 3,791) in Roosevelt County, New Mexico, USA, and Harper, Ellis, and Beaver counties, Oklahoma, USA, Oct 2000–Jun 2003.

Study area	Cover type[a]	Occupied mean	Random mean	Significant?[b]
	shrub	2.07	1.79	yes
	grass	1.45	1.41	no
New Mexico	shinnery oak	22.52	19.56	yes
	sand sagebrush	0.11	0.10	no
	other shrubs	0.55	0.35	yes
	shrub	0.92	0.48	yes
	grass	1.78	1.64	no
Oklahoma	shinnery oak	0.0002	0.00	no
	sand sagebrush	0.18	0.11	yes
	other shrubs	0.50	0.27	yes

[a] Shrub and grass signify the amount of those vegetation types along a 10-m transect. Other measures signify the density of particular shrubs along the transect. Other shrubs most often refers to broom snakeweed (*Gutierrezia sarothrae*), *Yucca* spp., mesquite (*Prosopis* spp.), and plum (*Prunus* spp.).
[b] Per post-hoc tests (Tukey's HSD) controlling experiment-wise α at 0.05.

Table 2. Differences at the transect's center in vegetation density and height between sites occupied by radiotagged lesser prairie-chickens (*Tympanuchus pallidicinctus; n* = 2,692) and sites sampled at random (*n* = 3,791) in Roosevelt County, New Mexico, and Harper, Ellis, and Beaver counties, Oklahoma, USA, Oct 2000–Jun 2003.

Study area	Measure[a]	Occupied mean	Random mean	Significant?[b]
	<10 cm	0.87	0.79	no
New Mexico	10–50 cm	1.15	1.00	yes
	>50 cm	0.06	0.05	no
	height (cm)	13.35	12.03	yes
	<10 cm	1.83	1.67	yes
Oklahoma	10–50 cm	1.38	0.80	yes
	> 50 cm	0.06	0.05	no
	height (cm)	13.03	10.06	yes

[a] The first 3 measures are of density as determined by the number of contacts on a vertical rod within 10 cm of the ground, between 10 and 50 cm above ground, and over 50 cm above ground.
[b] Per post-hoc tests (Tukey's HSD) controlling experiment-wise α at 0.05.

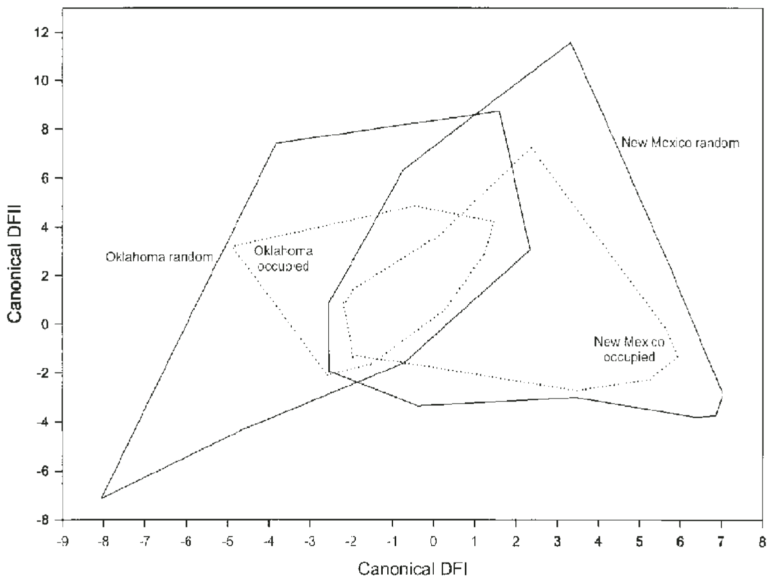

Fig. 1. Comparison of sites occupied (n = 2,692) by the lesser prairie-chicken (*Tympanuchus pallidicinctus*) and those measured randomly (n = 3,791) in Roosevelt County, New Mexico, and Harper, Ellis, and Beaver counties, Oklahoma, USA, Oct 2000–Jun 2003. As expected, occupied sites were a subset of the random sites.

occupied sites (0.20 < **d** < 0.26). For New Mexico (Wilks' Λ = 1.00, P < 0.02) and Oklahoma (Wilks' Λ = 0.96, P < 0.0001), measures of density and height at the 0-point had a similar pattern, with density 10–50 cm above ground and vegetation height being significantly higher on occupied sites (Table 2). In every case the amount of variation explained by a given vegetation measure was low; all R^2 values were below 0.16 and typically 0.05 < R^2 < 0.10.

Using MRPP on the aforementioned conservative data set, we distinguished between occupied and random sites in New Mexico (T = –3.51, P < 0.01) and Oklahoma (T = –15.25, P < 0.0001); however, as with the MANOVAs, the effect size was small (A = 0.01 and A = 0.04, respectively). An overall MRPP on the 4 groups (occupied and random in each state) yielded a much higher effect size (A = 0.28, t = –140.05, P < 0.0001), but most of the effect was from differences between the states (A = 0.40 for New Mexico vs Oklahoma random, A = 0.26 for New Mexico vs Oklahoma occupied). Nonetheless, as predicted, for New Mexico ($F_{1811,1428}$ = 1.91, P < 0.001) and Oklahoma ($F_{1714,1497}$ = 1.81, P < 0.001) the variance around random points was significantly higher than the variance around occupied points. That occupied sites are a subset of random sites is apparent in multivariate space (Fig. 1).

Small differences in vegetation cover and density between occupied and random sites translated to larger differences in microclimate. Lesser prairie-chickens chose sites markedly cooler (**d** = 0.33 in New Mexico, **d** = 0.12 in Oklahoma), more humid (**d** = 0.24 in each state), and, in Oklahoma, less exposed to wind (**d** = 0.14) than random sites (Table 3; New Mexico: Wilks' Λ = 0.96, P < 0.001; Oklahoma: Wilks' Λ = 0.97, P < 0.001). Moreover, differences in vegetation cover and density between occupied and random sites translated to differences in survivorship. Survival times did not differ between New Mexico and Oklahoma (Fig. 2; χ^2 = 0.42, P > 0.50) and did not differ between males and females (Fig. 3; χ^2 = 0.09, P > 0.75). But survival times were positively associated with increased vegetative cover (χ^2 = 11.71,

Table 3. Differences in microclimate between sites occupied by radiotagged lesser prairie-chickens (*Tympanuchus pallidicinctus*; n = 2,692) and sites sampled at random (n = 3,791) in Roosevelt County, New Mexico, USA, and Harper, Ellis, and Beaver counties, Oklahoma, USA, Oct 2000–Jun 2003.

Study area	Measure	Occupied mean	Random mean	Significant?[a]
	temperature (°C)	22.7	26.0	yes
New Mexico	relative humidity (%)	30.4	26.6	yes
	wind speed (km/hr)	2.74	2.39	no
	temperature (°C)	18.9	20.0	no[b]
Oklahoma	relative humidity (%)	38.3	34.3	yes
	wind speed (km/hr)	1.89	2.37	yes
	temperature (°C)	20.7	22.6	yes
Combined	relative humidity (%)	34.6	31.0	yes
	wind speed (km/hr)	2.29	2.38	no

[a] Per post-hoc tests (Tukey's HSD) controlling experimentwise α at 0.05.
[b] 0.05 < P < 0.10.

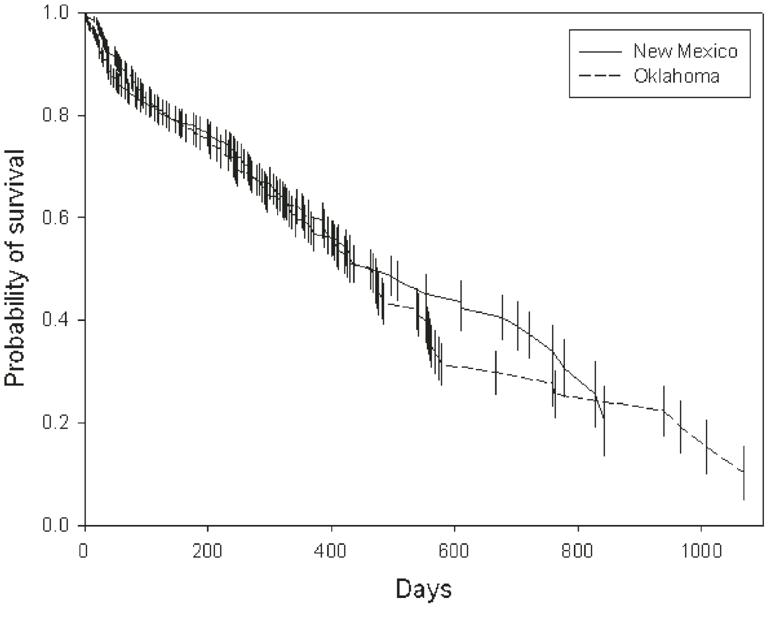

Fig. 2. Adult survivorship of the lesser prairie-chicken (*Tympanuchus pallidicinctus*) in Roosevelt County, New Mexico, USA, and Harper, Ellis, and Beaver counties, Oklahoma, USA, Oct 2000–Jun 2003. The curves do not differ statistically.

$P < 0.01$), whether shrubs ($\chi^2 = 10.11$, $P < 0.01$) or grasses ($\chi^2 = 6.49$, $P < 0.02$). For example, birds occupying sites with high (>20%) shrub cover survived longer than those occupying sites with moderate (10–20%) or low (<10%) shrub cover (Fig. 4; $\chi^2 = 6.86$, $P < 0.05$). Survival times were likewise positively associated with increased vegetative density at the 0-point of the transect ($\chi^2 = 43.91$, $P < 0.0001$). Increased survival time was also associated with microclimate ($\chi^2 = 19.54$, $P < 0.001$), particularly lower temperature ($\chi^2 = 11.10$, $P < 0.001$) and higher relative humidity ($\chi^2 = 10.33$, $P < 0.01$).

DISCUSSION

Habitat Selection and Its Consequences

Habitat selection has consequences for a species' demography and other aspects of its life history (Block and Brennan 1993). Accordingly, a species may use specific portions of a particular habitat, choosing sites on the basis of physiognomy, floristic composition, or microclimate (Price 1978, Rotenberry 1985). Lesser prairie-chickens do not occupy the sand shinnery vegetation community uniformly but choose specific sites within that community. We found differences between occupied and random sites despite their potential overlap (i.e., a random site could have been occupied, at some point, by a bird we failed to detect). Yet within the sand shinnery community, occupied sites were characterized by greater cover and density of shrubs and a higher proportion of shrubs, whether shinnery oak in New Mexico or sand sagebrush in Oklahoma. The lesser prairie-chicken also prefers taller, denser habitat for nesting (Giesen 1994). Habitat selection in the species therefore appears to be driven more by physiognomy than by floristic composition (compare Rotenberry 1985), suggesting a common mechanism that does not vary geographically.

On average, lesser prairie-chickens avoided sites that were hotter, drier, and more exposed to the wind, suggesting that, like the northern bobwhite (*Colinus virginianus*; Forrester et al. 1998), the lesser prairie-chicken sees its habitat as patchy with regard to microclimate. Temperature played a bigger role in New Mexico, which is drier than Oklahoma. Conversely, avoidance of exposure to the wind played a bigger role in Oklahoma, where shrub cover is lower than in New Mexico. Temperature and wind affect metabolic rate (Sherfy and Pekins 1995), whereas the effects of relative humidity are manifested perhaps through osmoregulation. The larger difference among measures of microclimate at occupied vs. random sites suggests that birds selected vegetation structure at a scale finer than we measured it. Nonetheless, we uncovered consistent differences in structure, so we could identify the importance of specific habitat parameters that influenced choice.

The lesser prairie-chicken's selection of microhabitat with a greater cover and density of vegetation, especially of shrubs, may be related to predator avoidance as much as it is to thermoregulation, as other gallinaceous birds also prefer higher cover to avoid raptors (Kopp et al. 1998). And other factors may drive selection of cooler, moister microhabitat. The lesser prairie-chicken may choose sub-

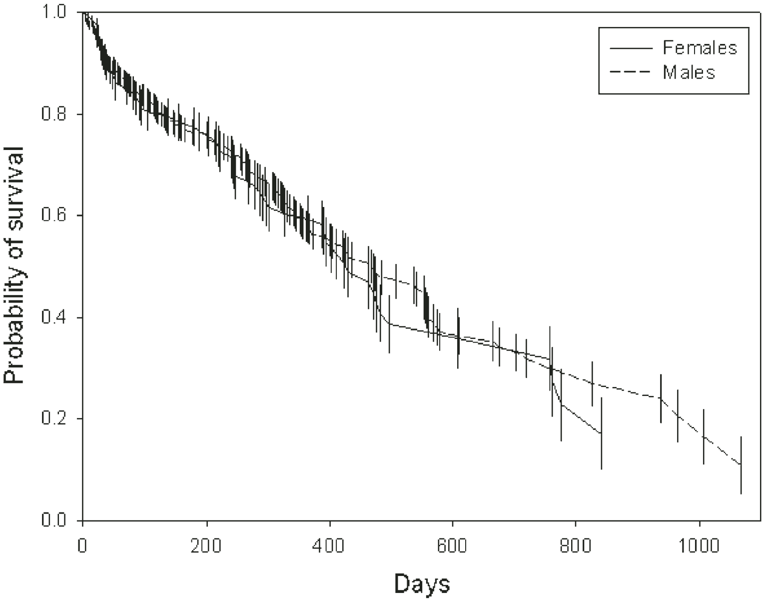

Fig. 3. Survivorship of adult male and adult female lesser prairie-chickens (*Tympanuchus pallidicinctus*) in Roosevelt County, New Mexico, USA, and Harper, Ellis, and Beaver counties, Oklahoma, USA, Oct 2000–Jun 2003. The curves do not differ statistically.

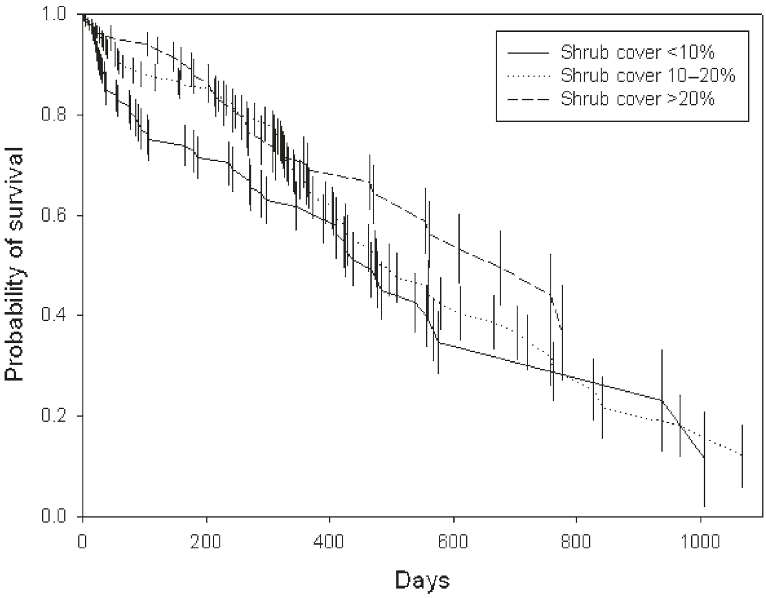

Fig. 4. Adult survivorship of the lesser prairie-chicken (*Tympanuchus pallidicinctus*) in relation to shrub cover in Roosevelt County, New Mexico, USA, and Harper, Ellis, and Beaver counties, Oklahoma, USA, Oct 2000–Jun 2003. Survivorship increases as shrub cover increases ($\chi^2 = 6.86$, $P < 0.05$).

sets of habitat with higher abundances of arthropods (Jamison et al. 2002), and acorns of the shinnery oak may be an important source of food (Doerr and Guthery 1983). Of course, these factors are not mutually exclusive. Regardless of the motivations for habitat selection, a substantial reduction of shrub cover and density, which can occur in the wake of mechanical disturbance or herbicide application or burning, could prove detrimental to individual prairie-chickens by hindering a bird's ability to thermoregulate or escape detection by a predator.

Survivorship and Prospects for Conservation

Populations of the lesser prairie-chicken continue to decline through the species' range (Giesen 1998, Johnsgard 2002). Despite potential differences in population stability in each state, adult survivorship is the same between New Mexico and Oklahoma. Our results therefore do not clearly implicate adult survivorship as a major factor in long-term declines, unless similar problems (e.g., habitat degradation) affect the species range wide. Even so, as with the greater prairie-chicken (Wisdom and Mills 1997), it seems likely that nest success and brood survival are the life-history stages exerting the greater influence on population persistence. But if adult survivorship is reduced even slightly, it may directly affect total nest production, the ability to find mates, and, ultimately, the persistence of populations.

Our study links survivorship to specific characteristics of microhabitat and microclimate. Even though we could not detect differences in grass cover between occupied and random sites, regardless of grazing activity, our data show that lesser prairie-chickens survive longer when selecting sites with higher grass cover. We thus infer that there is a point on the shrub cover to grass cover continuum that is ideal for lesser prairie-chicken survivorship. Our data suggest that adult survivorship was maximized when shrub cover was 20%. We could not identify an upper limit, but among all 9,087 occupied sites, only ~2.5% (223) had shrub cover >50%, suggesting the limit is at or below that figure.

Fire is a natural component of the Great Plains ecosystems and was surely 1 of 2 key factors maintaining the balance between shrub and grass cover as the ecosystem evolved. The other key factor was heavy, infrequent grazing by large ungulates, particularly the American bison (*Bison bison*). Over the past century, the combined effects of fire suppression and heavy, continuous grazing by cattle have greatly altered the composition of the plains ecosystems, allowing for an increase in trees and shrubs at the expense of native perennial grasses. Boyd and Bidwell (2001) felt that prescribed fire is the best means to restore a healthy prairie ecosystem. Short of that, the limited application of herbicides may be useful for thinning stands of shinnery oak and sand sagebrush and facilitating recruitment of native prairie grasses. Even so, our study shows that shrub cover and density can be thinned too much.

MANAGEMENT IMPLICATIONS

We recommend that managers striving to conserve the lesser prairie-chicken manage for the species' specific microhabitat requirements. Biologists have long known that the species requires sand shinnery vegetation, but our study identified an important subset of that vegetation. We recommend that shrub cover be retained or restored at or above 20% of the total vegetation. Herbicides, plowing, and grazing thin oak cover directly and thus may thin prairie-chicken populations indirectly. Although densities of the lesser prairie-chicken may not differ between habitats untreated and treated with herbicide (Olawsky and Smith 1991), females prefer to nest in untreated areas (Haukos and Smith 1989) and, as we have shown, survivorship is higher in areas with greater shrub cover. Yet minimizing the application of herbicides (Applegate and Riley 1998) may not elevate prairie-chicken populations. By reducing the extent of shinnery oak or sand sagebrush cover, herbicide allows for an increase in grass cover (Donaldson 1969, Doerr and Guthery 1983, Haukos and Smith 1989), but management practices that lead to a reduction of shrub cover below 20% should be avoided or minimized. Moreover, because survivorship increases as grass cover increases, intensive grazing likely has a negative impact on the species.

ACKNOWLEDGMENTS

We thank the many field crew members who gathered data. We also thank various land owners, particularly J. D. Weaver in New Mexico and D. O'Hair in Oklahoma, for allowing access to their property. Our work was funded by the U.S. Fish and Wildlife Service, New Mexico Department of Game and Fish, Oklahoma Department of Wildlife Conservation, National Fish and Wildlife Foundation, Western Governors' Association, High Plains Resource Conservation & Development, Grasslands Foundation, Wolf Creek Charitable Foundation, K. S. Adams Foundation, University of Oklahoma, ConocoPhillips, World Publishing, Bank of Oklahoma, Arrow Trucking, Riggs-Abney Attorneys, and many private donors, including J. Brock, S. Daniel, C. McGraw, J. McGraw, H. and S. Price, and G. Records. D. M. Davis, W. C. Dunn, W. R. Gould, S. L. Harmon, B. Palmer, and an anonymous referee provided helpful assessments of a draft of our manuscript.

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Associate Editor: Palmer.