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The Effects of Shrub Control and Grazing on Habitat Quality and Reproductive Success of Lesser Prairie-Chickens

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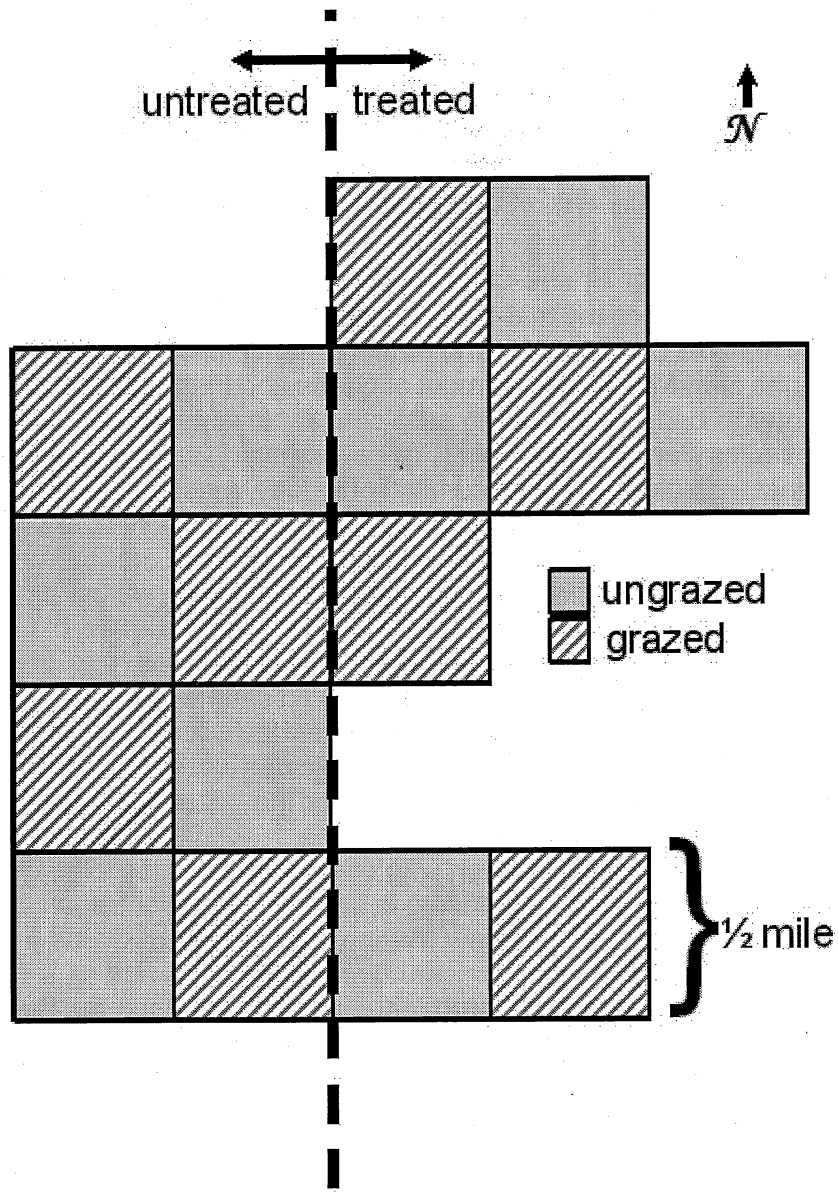
Populations of the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) have declined sharply in New Mexico since the mid-twentieth century (Bailey and Williams 2000). So that there might be feasible conservation and management plans for this species' persistence and recovery, the New Mexico Department of Game and Fish contracted the Sutton Avian Research Center to conduct a study in east-central New Mexico to determine the extent to which this species was affected, if at all, by cattle grazing and application of tebuthiuron, an herbicide that inhibits growth and survival of woody vegetation.

In New Mexico the Lesser Prairie-Chicken occurs in shinnery oak (*Quercus havardii*) grassland, so changes in shrub cover may affect habitat use and reproductive success. It has been hypothesized that in the past century the shinnery oak, a native species, has become more widespread and now occurs in denser stands (Peterson and Boyd 1998). Furthermore, it has been suggested that the increase in oak has reduced grass cover and other forage for cattle (Peterson and Boyd 1998). To counteract this hypothesized effect, land stewards have used a number of techniques to reduce or remove shinnery oak. Among these techniques is the application of herbicides to reduce the amount of oak (and other shrubs) with the goal of improving habitat for the Lesser Prairie-Chicken and other grassland obligates.

One such steward is Jim Weaver, who owns and manages a large ranch in eastern Roosevelt County, New Mexico. Beginning in fall 2000, Weaver began an experiment on his ranch—in coordination with the New Mexico Department of Game and Fish and with the help of the Natural Resources Conservation Service—to reduce shinnery oak cover and thereby increase grass cover. Shrub reduction was implemented through application of tebuthiuron (brand name Spike®).

An important component of this experiment was to determine the effects of shrub reduction on the Lesser Prairie-Chicken. The Sutton Center's prairie-chicken study was therefore focused on the 16 plots established by Dr. Charles Dixon in fall 2000 (Fig. 1). Accordingly, from March 2001 through August 2005 the Center continued its trapping and radiotagging efforts in eastern Roosevelt County (trapping and tracking had begun in April 1999). Herein we report findings of our 4-year study covering 5 breeding seasons. Key results of our study have been published (Patten et al. 2005a,b); these results are reported below. Results from ancillary studies on reticuloendotheliosis virus prevalence (Wiedenfeld et al. 2002), population genetics (Van Den Bussche et al. 2003), and brood survival and chick growth (Bell 2005) are reported elsewhere. Because the study's focus was on the effects of tebuthiuron and associated cattle grazing, herein we typically restrict our results to those obtained in the study plots.

FIGURE 1. Study design for examining the effects of tebuthiuron application ("treated") and cattle grazing on reproductive effort in the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*).



METHODS

The Sutton Center's efforts were manifold. Chief among them was an effort to locate and monitor all nests, but we also tracking tagged birds as often as possible to provide data on movements, survivorship, and habitat use. The last was facilitated by regular vegetation surveys, both standard transects in which vegetation cover and density were sampled and an estimate of the "cone of vulnerability," a measure of microhabitat use as a means of

predator avoidance (Kopp et al. 1998). We also determined cause of death for recovered carcasses and recorded numerous microclimate readings at bird-centered and random locations. Both of these studies lie outside of the goals of the tebuthiuron study, however, so we do not report on them herein (see Patten et al. 2005a,b).

Study Area

The Sutton Center's ~52,000-ha study area was located in eastern Roosevelt County, New Mexico, on the western edge of the Llano Estacado, a region characterized by sandy soils atop caliche bedrock, sand dunes and associated blowouts, and scattered playas (the only naturally occurring surface water). Vegetation is shortgrass prairie dominated by shinnery oak, which occurs principally as clonal shrubs, with a few hybrid mottes reaching 3–4 m in height. Other woody vegetation included sand sagebrush (*Artemisia filifolia*), honey mesquite (*Prosopis glandulosa*), cholla (*Opuntia imbricata*), broom snakeweed (*Gutierrezia sarothrae*), and several *Yucca* species. Common grasses included sand (*Andropogon hallii*), silver (*Bothriochloa laguroides*), and little bluestems (*Schizachyrium scoparium*), dropseeds (*Sporobolus* spp.), grama grasses (*Bouteloua* spp.), and buffalo grass (*Buchloe dactyloides*). Under 10% of the area was cultivated (primarily for cotton), and pads and roads supporting oil production accounted for ~5% of the land area. Most land is private, but the New Mexico Game Commission owns several prairie-chicken management areas that together comprise ~3700 ha of our study area.

Herein we focus on the ~16,500 ha study area centered at the north end of the North Bluitt Prairie-Chicken Area. Tebuthiuron (0.67 kg / ha) was applied to the portions of the study area (Fig. 1) late October–early November 2000. Our focused study began in spring 2001, the first growing season after the treatment. We found that shinnery oak began to die back in May 2001, shortly after the first prairie-chicken nests. As a result, it is possible that some females chose a nesting site that looked suitable to them when it was chosen but that later became unsuitable (e.g., more exposed) because of defoliation once treatment effects became apparent. This potential problem occurred only in the first year of the study; i.e., the effects of tebuthiuron were readily apparent from 2002–2005.

Another important aspect of this study design was to determine the effects of cattle grazing on the Lesser Prairie-Chicken, but grazing treatments on the North Bluitt Prairie-Chicken Area and Weaver Ranch were not implemented until after the 2002 breeding season (W. Heck *in litt.*). By spring 2003, grazing was equal by treatment (Table 1).

TABLE 1. Stocking of cattle in the core study area (Fig. 1) per W. Heck (*in litt.*).

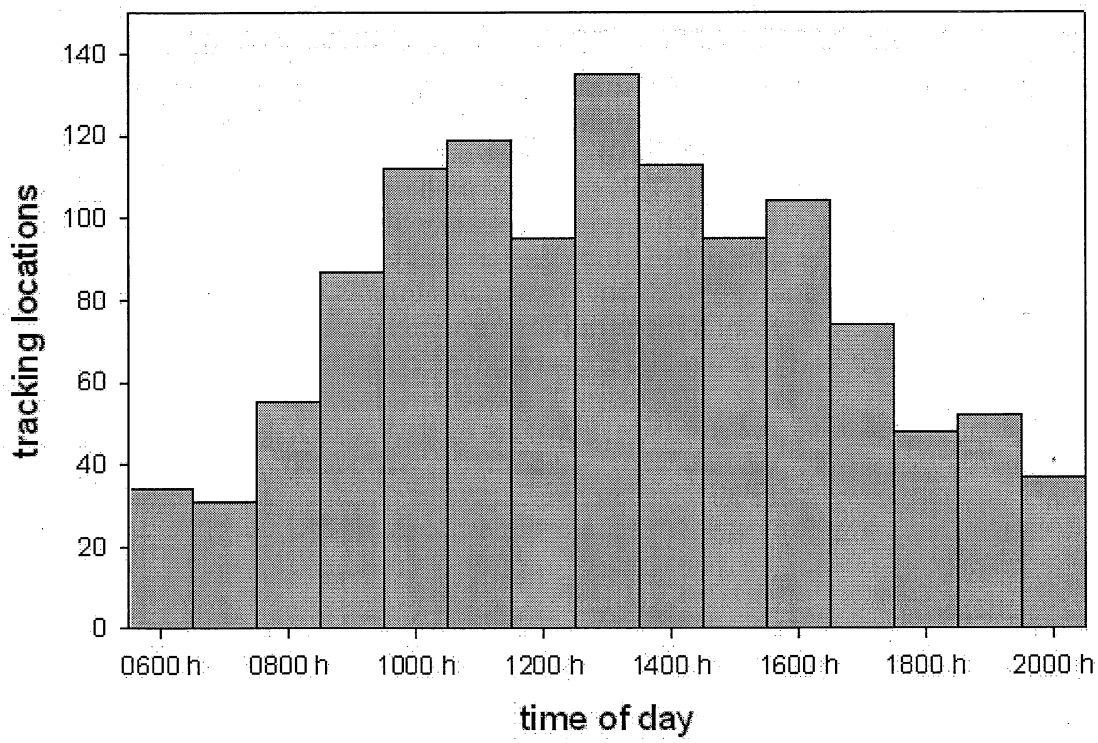
	untreated blocks			treated blocks		
grazing season	steers	cows	heifers	steers	cows	heifers
dormant 2002–2003		175	18		98	
growing 2003	69	41	98	69	41	98
dormant 2003–2004		287			287	
growing 2004	123	26	145	123	26	145
dormant 2004–2005		281			281	
growing 2005	83	104	105	83	104	105

Trapping and Radiotracking

We chiefly trapped Lesser Prairie-Chickens on spring leks. We trapped a given lek 5–10 consecutive days. We captured birds using modified walk-in funnel traps (Schroeder and Braun 1991). We fitted each captured bird with an aluminum leg band and placed a bib-mounted radio transmitter (Telemetry Solutions® or Wildlife Materials®) on all females and ≤5 males / lek. Transmitters were glued and sewn onto vinyl-coated nylon bibs (Amstrup 1980). Each transmitter had a 12-hr mortality switch.

We tracked birds as often as possible, with efforts extending throughout the day (1 hour before sunrise to 2 hours after sunset). We used 3 types of receivers (AVM® LA12Q, ATS® R2000, and 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. We flew aerial transects twice / month from May–June to locate birds not found on the ground for 2–3 weeks. Tracking effort in the morning was concentrated at leks, many of which were outside the study area; therefore, peak tracking numbers in the study area occurred after mid-morning (Fig. 2).

FIGURE 2. Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) tracking locations by time of day (2001–2005, March–August only). Nighttime locations (~85) are excluded. Protocol required that each tagged bird be tracked daily. As a result, once a bird was located tracking effort switched to finding other birds, hence the decline after early afternoon. The morning low was because effort was focused on leks (see text).



Vegetation Sampling

We sampled vegetation at 2 types of points: occupied (a location at or near a radiotracked prairie-chicken) and random (a location selected *a priori* then located in the field). We collected data on occupied sites fortuitously—whenever a radio-collared bird was detected. We sampled vegetation along a transect anchored at the location of the tracked bird. To avoid flushing or disturbing the bird, we extended sampling transects from a point in like habitat <20 m from the bird at a bearing of 45° or 225°, whichever led us away from the bird. We 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 random transects. We generated random locations using a standard algorithm and then located them in the field with a GPS unit. These points could fall anywhere within the study area, but we excluded points without land access and classified clearly unsuitable habitat as "other" (a mere ~1% of samples). We oriented random transects at a bearing of 45°–225° and centered on the GPS point. We sampled occupied sites while tracking a bird and random sites in between tracking efforts; we gathered data throughout the day and year for either type of site.

Vegetation sampling was the same for occupied and random sites. We did not sample on days with heavy or steady rain or wind exceeding 30 kph. As a measure of relative cover we tallied canopy (i.e., the tallest plant >20 cm above ground) and basal contacts against a 6.4-mm vertical rod at 1-m intervals along the 10-m transect (i.e., 11 samples, 1 each from 0 m to 10 m). As an estimate of vegetation density, we tallied the number of times vegetation contacted the rod at three levels: <10 cm, 10–50 cm, and >50 cm above ground. At 5-m intervals we recorded canopy height at the rod and maximum height within a 1-m radius of it, and we counted woody stems contacting a 0.5-m radius chain, but only if the shrub's base lay within the radius. We recorded separate estimates of vegetation density (i.e., vegetation contacts against a vertical rod) for shinnery oak, sand sagebrush, mesquite, and other shrubs, and for tall and short grasses.

We obtained our cone of vulnerability from June 2003–September 2004 at occupied and random points as described above and were likewise the same regardless of the type of point. This measure entailed obtaining an exposure angle at each of the four cardinal directions centered on the bird's location or at a GPS point selected randomly in advance. This angle was measured as that which a 1-m stick leaned until it contacted vegetation. As such, a perfectly covered point yielded an exposure angle of 0°, whereas a perfectly open point yielded an exposure angle of 90°.

For all vegetation points (i.e., both transects and cones), we assigned habitat to one of 16 broad categories: (1) plowed/no growth; (2) wheat, rye, or oats; (3) cotton; (4) alfalfa; (5) sorghum; (6) sunflower; (7) corn; (8) soybean; (9) weeping lovegrass (*Eragrostis curvala*); (10) Asian bluestem (*Bothriochloa* spp.); (11) native mix CRP (conservation reserve program planting); (12) other exotic grasses; (13) fallow; (14) native shortgrass prairie (regardless of tebuthiuron treatment); (15) other CRP; and (16) other/unknown cover ("other" meaning not one of the 15 previously listed categories). Categories reflected the dominant vegetation type at and around the sampling point. For categorical analyses, we further split native (treated vs. not) and lumped farmed and CRP locations (see below).

Nest Monitoring

We followed hens closely from late April through June in anticipation of their nesting. Once a hen was thought to be nesting—i.e., she occupied the same location for consecutive days—we would determine whether she was on a nest. If she was, we placed a marker radio 2 m directly north of the nest. These radios eliminated the need for flagging to relocate a nest, and we could determine from a safe distance (~100 m) whether the hen was still incubating. Nests were monitored once every 2–4 days. If the female flushed, we moved in to examine the nest and record the clutch size. Conversely, we did not obtain clutch size if the female never flushed; i.e., we avoided disturbing the bird solely to obtain this datum. (We have no reason to suspect that such females had different clutch sizes.) After it was confirmed that the hen was no longer incubating—i.e., she was not present for 2 consecutive visits—we used the marker radio to relocate the nest. At this point we photographed the nest and collected egg remains (from which nest success could be evaluated). We returned within 1–2 days to sample vegetation at and around the nest.

Statistical Analyses

We report on habitat use only within the 16 blocks of the study area, but we include year-round data instead of restricting analyses to March–August. However, we did not perform separate analyses with respect to sex or life stage. Random vegetation surveys could occur anywhere in the study area; we assume they provided a suitable index of habitat availability. Our comparison of habitat use relative to tebuthiuron treatment and cattle grazing was restricted to occupied locations in native shortgrass prairie. Tracking locations per block were sufficiently large on average ($\bar{x}$ / cell = 58) to satisfy assumptions of normality, but counts / cell in the treated area were often low. As such, we analyzed tebuthiuron data using a Wilcoxon two-sample test (proc npar1way, SAS ver. 8.0), with herbicide treatment as the classification variable and number of tracking locations as the response. Cattle grazing was not implemented the first two nesting seasons (Table 1); therefore, we used only the last three years of the data (2003–2005) to test its effects. We again analyzed data with the Wilcoxon two-sample test, this time with grazing presence as the classification. Use of cover was determined by calculating monthly means of exposure angle (from the cone of vulnerability measures) throughout the Sutton Center's 52,000-ha study area and throughout the year.

We analyzed habitat specifics conservatively (see Patten et al. 2005b). Because we tracked some birds more frequently than others, habitat data were autocorrelated temporally and therefore pseudoreplicated. We lessened (but likely did not eliminate completely) autocorrelation by collapsing vegetation data to means per bird, per month. This reduced data set included 1415 occupied sites (by 213 individual prairie-chickens) and 1853 random sites sampled from October 2000–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 habitat. We tested this hypothesis using the reduced data set in a series of MANOVAs (proc glm, SAS ver. 8.0). Survey type (i.e. random vs. occupied) was a main effect, month a covariate, and survey type × month an interaction term. We ran separate MANOVAs for 2 combinations of response variables: (1) canopy density of all shrubs, all grasses, shinnery oak, sand sagebrush, and other shrub species, and (2) vegetation 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. We conducted this same analyses with data on basal extent and density from the main study area (Fig. 1). This more focused analysis included 558 occupied sites (averaged by 119 individuals) and 414 random sites.

Despite efforts to reduce this cumbersome data set to a smaller set of more-or-less independent data, the sample size remains large. Accordingly, statistical significance (i.e., $P < 0.05$) may be achieved even though mean differences have little biological meaning; e.g., mean shrub cover could differ statistically significantly between occupied and random sites but the magnitude of the difference may be a <<5% (as in a case where, say, shrub cover was 28.8% at occupied sites and 26.1% at random sites). To avoid misinterpretation of the results, we present simple effect sizes (**d**) as defined by Cohen (1988); i.e., $\mathbf{d} = (\bar{x}_1 - \bar{x}_2)/\sigma$. In Cohen's schema, $\mathbf{d} \approx 0.20$ corresponds to a small effect, $\mathbf{d} \approx 0.50$ to a medium effect, and $\mathbf{d} \approx 0.80$ to a large effect.

The effort to minimize autocorrelation in tracking studies, whether collapsing data to means or using points ≥1 week apart, may never be entirely successful. Treating points separated in time—sometimes by as little as 2 minutes (Root 1967)—as independent has a long history in studies of behavior, and such sequential observations do not necessarily alter results (Morrison 1984, Recher and Gebski 1990), but purists are unlikely to be impressed. Our goal was to examine overall use rather than separately for each bird (or age/sex). As such, had we tested our 16 categories, "If habitat use is combined for all animals, then the chi-square goodness-of-fit is the only [statistical] choice available" (Alldredge et al. 1998:248). Yet this approach has been criticized because of lack of independence, even though it is likely that "with repeat[ed] sampling of the same individual, its proportional use [of a habitat] will stabilize to more or less fixed values" (Guthery et al. 2005:660). A comparable situation allows home ranges to be determined despite spatially autocorrelated data (see Swihart and Slade 1997). Regardless, <2% of tracking locations (62 of 5294) were away from shortgrass prairie, rendering use of techniques unaffected by repeated measures tenuous. Nonetheless, with treated prairie split out and farmed and CRP lands lumped, we applied Johnson's (1980) rank technique—which is amenable to repeated sampling of individuals (Alldredge et al. 1998)—to compare used vs. availability.

We used failure-time analyses to calculate basic survival rate of the Lesser Prairie-Chicken and to how adult survivorship related to shrub cover. As Patten et al. (2005b) noted, "estimates of survival time can be biased in radio-tracking 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. Right-censored data accounted for ~50% of the data. We tested for differences in survival times between three levels of shrub cover (<10%, 10–20%, and >20%) using

a likelihood-ratio χ^2 test (proc lifetest, SAS ver. 8.0), and we used Cox's proportional hazards regression model to examine how vegetation structure were associated with survival time (proc phreg, SAS ver. 8.0).

We also used failure-time analysis (proc lifetest, SAS ver. 8.0) to explore basic patterns of nest survival. Use of this analytic approach can be seen as an extension of the Mayfield's (1961, 1975) widely used technique, which calculates exposure time for a nest irrespective of its initiation. Whatever drawbacks these techniques may have, either approach is vastly superior to a comparison of simple nest success rates (see Thompson et al. 2001); moreover, failure-time analysis has an advantage over Mayfield rates in (a) being able to present heuristic graphics comparing nest success and (b) having a well-established statistical foundation, including the ready incorporation of right-censored data. Even so, use of failure-time analysis for these data requires an assumption that errors are distributed evenly across treatments; i.e., nests were no more or less likely to be found *at a given stage* on any of the treatments or with respect to any other of the comparison variables. We feel that this assumption is met. Because left-censored data will not be incorporated fully, absolute nest survival times will be biased downward; however, with the assumption of equally distributed errors, we can still make valid comparisons between treatments, ages, or other variables of interest.

For tests of nest placement with respect to either tebuthiuron treatment or the presence of cattle grazing, we again used the Wilcoxon two-sample test on nest number / block in the core study area (Fig. 1). We treated each nest as an independent event. Assumptions of normality were not met with the grazing treatment because many nests had to be eliminated with exclusion of the first two years of data (see above and Table 1). As with our Wilcoxon tests for tracking locations, for consistency we used a non-parametric procedure for both of the classification variables. Likewise, *P*-values we report are derived from a *t* approximation.

We used path analysis (proc calis, SAS ver. 8.0) to model potential cause-and-effect pathways in the ecosystem; i.e., with it we could deduce effects of tebuthiuron on fledgling production (hatched chicks / nest). In its essence, path analysis is a generalization of multiple regression. It therefore has the same assumptions as that technique. Differences lie in the ability of path analysis (a) to examine simultaneously effects on more than one response variable (which we did not do) and (b) to build explicit relationships between predictors, allowing some to be dependent on or correlated with other predictors. Beyond the ability to structure such relationships, a key advantage is heuristic: the process begins with construction of a path diagram, a visual representation of the key cause-and-effect relationships in the system under study, including those between predictors. Admittedly, a chief goal for our using path analysis was this heuristic advantage, although the technique also allowed us to model simple relationships between predictors and then to derive a simple model for the effects of tebuthiuron. See Mitchell (1993) and Sokal and Rohlf (1995:634) for complete details on path analysis and its many applications.

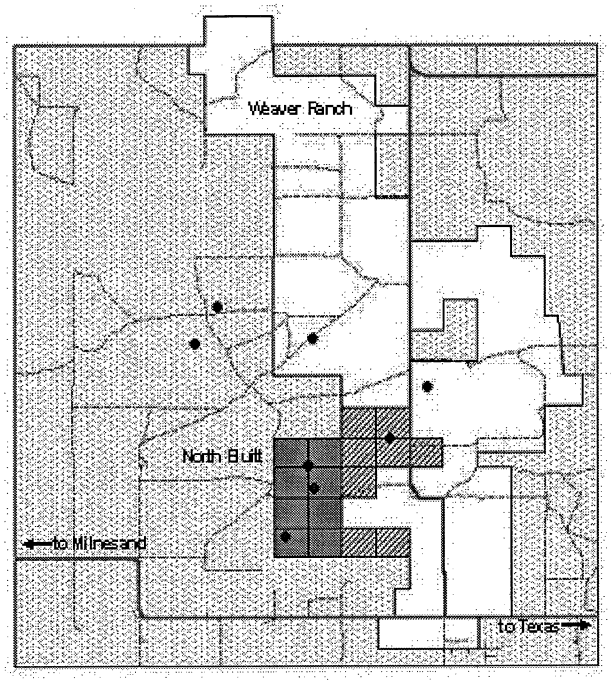
As with the analysis of nest survival, we used all available nests from the 52,000-ha study area to ensure that our sample size was adequate. We treated a path model as "valid" only if the model's χ^2 was non-significant, an indication that the actual and model correlation matrices do not differ (see Mitchell 1993). In the case of multiple "valid" models, we accepted the simplest one (i.e., lowest AIC). Resultant models are not meant

to be a full explanation of all cause-and-effect relationships; rather, they are plausible (simplified) models for the system. The overall effect of tebuthiuron on fledgling production could be calculated through the paths by means of a point-biserial correlation (r_{pb}), which is basically a Pearson's *r* with one variable dichotomous (see Howell 1992:267).

Captures and Tracking

Leks at which birds were trapped centered around the core study area (Fig. 3). Over the course of the focused study (2001–2005), we radiotagged 348 Lesser Prairie-Chickens, 99 (28.4%) of them females ($\bar{x}$ = 69.6 ± 9.8SD total captures / year). The proportion of captured females / lek varied considerably, from a low of 0 (0 of 5) to a high of 0.67 (21 of 31). During the study, we caught an equal number (*n* = 37) of females on North Bluitt and the Weaver Ranch. Because we trapped on leks, non-breeders may not have sampled.

Figure 3. Locations (dots) of Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) leks at which birds were trapped from 2001–2005. The core study area and tebuthiuron treatment on it (see Fig. 1) is in the lower center of the map.



We tracked birds throughout the day (see Fig. 2). During the seasonal window of the focused study (March–August), we obtained 13,164 tracking locations. The number of locations peaked in April (5020), coinciding with our daily monitoring of and trapping at active leks; i.e. lekking males were tracked daily (often multiple times) during this month. Next in line were March (2330) and May (2011), which also coincided with lekking. After May locations declined by nearly half through August. We considered determining survival rates to be an important aspect of the study, so we tracked marked birds year-round, an effort that yielded an additional 6324 locations during the years of the focused study.

HABITAT USE

The Lesser Prairie-Chicken requires an extent of shortgrass prairie to persist (Geisen 1998), yet the species occurs in areas converted to agriculture. To what extent is prairie vital to this species? On the basis of our vegetation surveys at occupied locations, native prairie is used heavily: 98.9% of locations are in prairie. Within the core study area, there is virtually no non-native prairie, so comparisons to availability in this area would not be meaningful. The situation differs little across our 52,000-ha study area.

However, with native prairie divided into untreated and treated with tebuthiuron, we can perhaps examine use vs. availability. As noted above, we did so with 52 birds that had ≥30 tracking locations (on different days or at different coordinates) and five habitat types: farmed (all agricultural categories), CRP, native, treated, and other (as defined above). Availability was estimated per bird. Across the full study area, use and availability differed (Johnson's [1980] technique: $F_{4,48} = 16.62$, $P < 0.0001$), but per Tukey's *post hoc* test this difference is not the result of preference for or avoidance of either untreated prairie or treated prairie. Rather, the difference resulted from an avoidance of agriculture, CRP, and "other" (mostly unsuitable) habitats. Across the 52 birds with sufficient data, there were only 31 (of 2725, or 1.14%) locations away from prairie; therefore, any conclusions drawn from apparent avoidance of these three broad habitat types may be tenuous.

With regard to specific use of habitat, we first analyzed data from occupied versus random vegetation points sampled throughout the Sutton Center's 52,000-ha study area. As reported by Patten et al. (2005b), the Lesser Prairie-Chicken occupied sites that have higher shrub cover (whether shinnery oak or a composite of other shrubs, chiefly *Yucca*, *Prosopis*, and *Gutierrezia sarothrae*), higher vegetation density 10–50 cm above ground, and a taller canopy (Table 2) compared to sites sampled at random in the same habitat. The overall difference was significant (Wilks' $\Lambda = 0.98$, $P < 0.0001$).

TABLE 2. Differences in vegetation cover and density between sites occupied by the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*; $n = 1415$) and sites sampled at random ($n = 1853$) from October 2000–June 2003 (modified from Patten et al. 2005b). *Shrub* and *grass* signify the amount of those vegetation types along a 10-m transect. *Other shrubs* typically refers to *Gutierrezia sarothrae*, *Yucca* sp., and *Prosopis* sp. Density measures are estimated 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. *Post hoc* significance tests (Tukey's HSD) control for experimentwise α at 0.05; significantly larger means are boldfaced. Note the generally small effect sizes.

category	measure	occupied mean	random mean	effect size
	shrub	**2.07**	1.79	0.18
	grass	1.45	1.41	0.02
cover	shinnery oak	**22.52**	19.56	0.21
	sand sagebrush	0.11	0.10	0.06
	other shrubs	**0.55**	0.35	0.26
	<10 cm	0.87	0.79	0.06
density	10–50 cm	**1.15**	1.00	0.08
	>50 cm	0.05	0.06	0.02
height	canopy (cm)	**13.35**	12.03	0.15

A comparison of occupied to random sites in the core study area (Fig. 1) yielded comparable results for density (Table 3; Wilks' $\Lambda = 0.96$, $P < 0.0001$). Results were complex, however, because vegetation densities at mid (10–50 cm) and high (>50 cm) were lower at occupied sites, whereas two of three measures of shrub density—including of shinnery oak, which accounted for the majority of cover and was the only measure with a medium effect size—were higher at occupied sites. Because vegetation density could include grasses as well as shrubs, it may be that the higher density of vegetation at random sites generally reflects a higher density of grass. That maximum vegetation height is significantly higher at random sites ($\bar{x} = 90.96$ cm) than at occupied sites ($\bar{x} = 78.84$ cm) may support this conclusion. Likewise, basal extent, although significant (Wilks' $\Lambda = 0.99$, $P < 0.005$), was lower at occupied sites, an effect of a difference in the extent of grass (i.e., birds occupied sites with a lesser basal extent of grass).

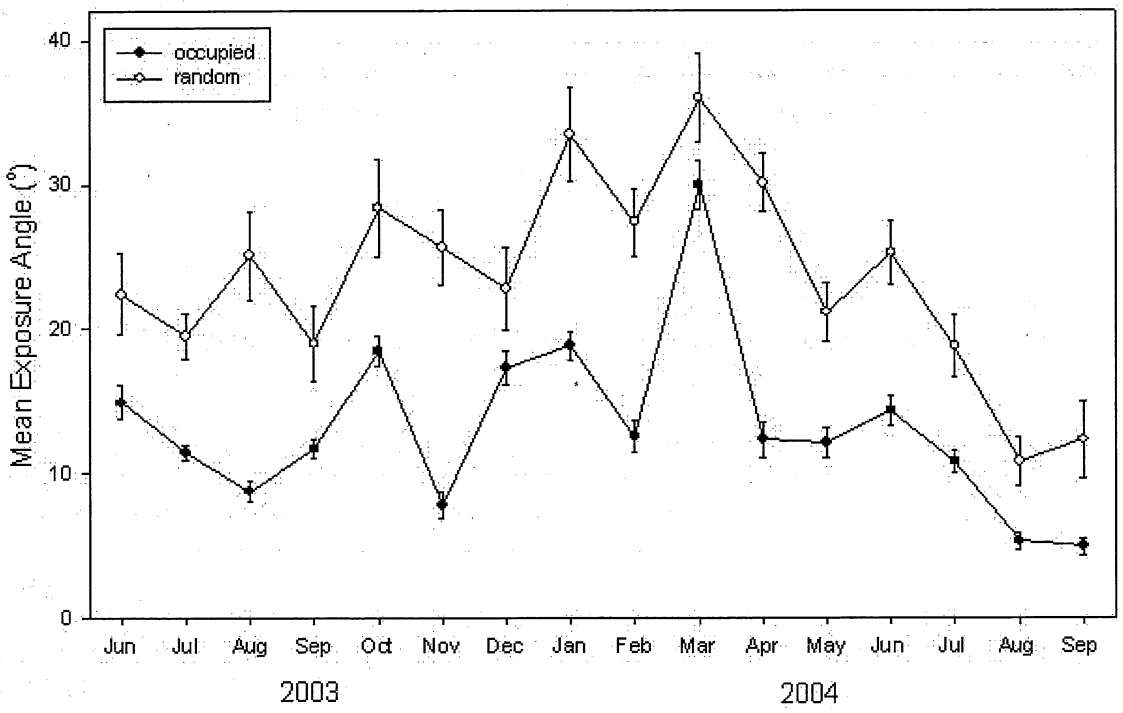
TABLE 3. Differences in basal extent and density of vegetation between sites occupied by Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*; $n = 558$) and sites sampled at random ($n = 414$) in native shortgrass prairie in the core study area (Fig. 1) from March 2001–August 2005. *Shrub* and *grass* signify the amount of those vegetation types along a 10-m transect. *Other shrubs* usually refers to *Gutierrezia sarothrae*, *Yucca* sp., and *Prosopis* sp. Density measures are estimated 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. *Post hoc* significance tests (Tukey's HSD) control for experimentwise α at 0.05; significantly larger means are boldfaced.

category	measure	occupied mean	random mean	effect size
	shrub extent	0.07	0.08	0.04
basal	grass extent	0.46	**0.60**	0.20
	oak extent	0.01	0.03	0.12
	<10 cm	**1.02**	0.71	0.24
	10–50 cm	1.34	**1.75**	0.21
density	>50 cm	0.10	**0.26**	0.28
	shinnery oak	**16.52**	11.62	0.56
	sand sagebrush	0.19	**0.32**	0.27
	other shrubs	**0.37**	0.28	0.12

In general, then, the Lesser Prairie-Chicken appears to occur in areas with higher cover (Table 2) and a higher density of shinnery oak (Table 3), and it may (the effect is small) avoid areas with a higher density or extent of grass (Table 3). The species' occurrence in areas with higher cover is also apparent in a simple description of our cone of vulnerability data: regardless of season and within the larger matrix of prairie, birds occupied sites with more cover (typically shrubs) than what occurred at random (Fig. 4).

Tracking locations in the core study area show another way in which the prairie-chickens distribute themselves non-randomly. We used locations from 113 birds, with each location for a given bird ≥ 1 week apart (to reduce spatial autocorrelation). Birds avoided blocks treated with tebuthiuron (Wilcoxon two-sample test: $C = 100.0$, $P < 0.005$) but were not affected by cattle grazing ($C = 65.0$, $P > 0.75$). If we assume normality of errors, on the basis of an ANOVA herbicide treatment explained nearly 90% ($r^2 = 0.88$) of the variation in occurrence. Also, the percentage of year-round locations in treated blocks declined over time: 25.3% in 2001 → 16.2% in 2002 → 3.1% in 2003 → 1.2% in 2004.

FIGURE 4. Vegetation cover at sites occupied by Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) and at random sites. Exposure was determined as the angle of open space above a center point (the bird's location or a randomly chosen location), as conceptualized by the "cone of vulnerability" (Kopp et al. 1998).

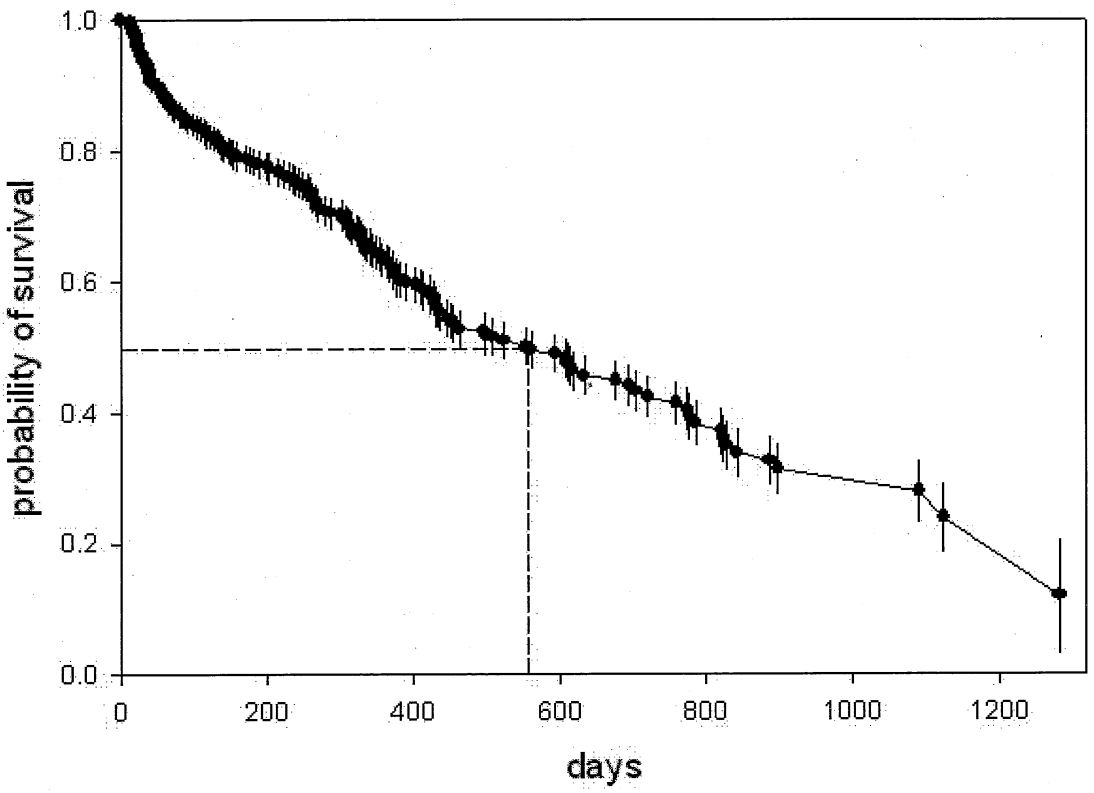


SURVIVAL

Survival of individual Lesser Prairie-Chickens can be parsed into several related sub-topics, such as (a) the basic survival rate, (b) partitioning of survival relative to age and gender, and (c) causes of mortality, the last of which is outside the scope of the focused study. Basic survival rate can be determined by myriad statistical techniques, some of which are more sophisticated than others in that they take into account vagaries in how often a particular individual was tracked; see Morgan and Thomson (2002) for an array of techniques and discussion of their relative merits. Using a simple calculation and discounting those birds tracked less than two weeks (n = 74 birds, 11 of which died in this narrow period), birds eventually found dead (n = 172) survived on average 288 days after being radiotagged.

A more accurate breakdown of daily survival, one that incorporates censored data (52.1% of survival times), suggests that the "half life"—the point at which the probability of survival reaches 50%—of a Lesser Prairie-Chicken is ~560 days (Fig. 5). Our Methuselah was female 476, which lived at least 1478 days after tagging. Her carcass was never found, and she was ~200 days old when initially captured. She likely lived to ~1700 days of age, or until she was just over 4 years old. Most birds live to ~2 years of age.

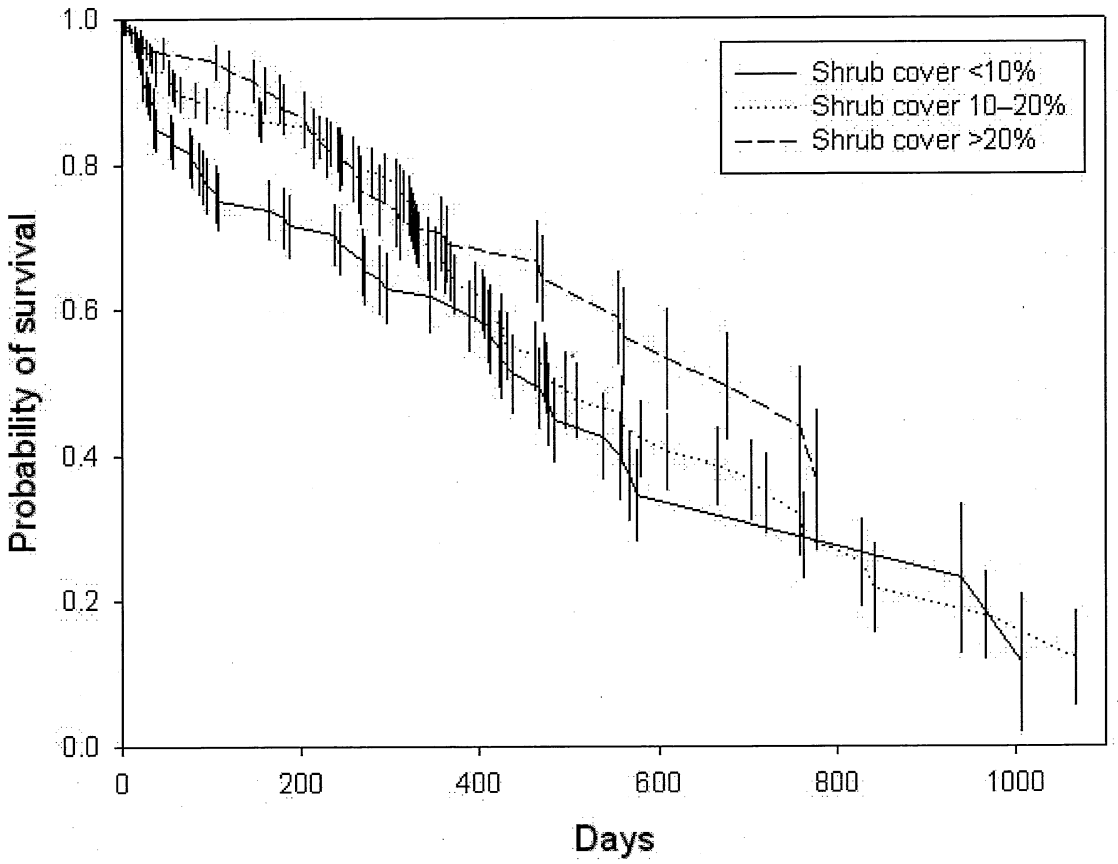
FIGURE 5. Post-radiotagging (n = 359) survival of the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). The "half life" of this species—the point at which survival probability is 50% (dashed line)—is ~560 days.



Survival varies with age and sex. A typical pattern in birds is that the principal time of mortality is during the first year or so of life. The Lesser Prairie-Chicken is no different. Only a small percentage of hatched birds reach adult size (Bell 2005; also see below), and even upon reaching adult size, yearlings succumb more frequently than older birds. After reaching ~1 year of age, sex-for-sex the birds appear to have a relatively constant probability of survival. A bird's gender does play a role in its probability of survival. Even though males display in the open each spring and thus seem to be much more vulnerable to an aerial assault, females are killed at nearly twice the rate of males. Our data show that males are killed more often by predators, but the more motile females are killed much more often as the result of collisions—typically with low fences—and ultimately are killed at a higher rate (see Patten et al. 2005a for details).

As reported by Patten et al. (2005b), survival time was associated positively with increased shrub cover (χ^2 = 10.11, P < 0.01) and increased grass cover (χ^2 = 6.49, P < 0.02). For shrubs, birds occupying sites with high (>20%) cover survived longer than those occupying sites with moderate (10–20%) or low (<10%) cover (Fig. 6; χ^2 = 6.86, P < 0.05). Survival times were likewise positively associated with increased vegetative density at the 0-point of our vegetation transects (χ^2 = 43.91, P < 0.0001).

FIGURE 6. Adult survivorship of the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) in relation to shrub cover (entire 52,000-ha study area and Oklahoma data, October 2000–June 2003). Survivorship increases as shrub cover increases ($\chi^2 = 6.86$, $P < 0.05$). Reproduced from Patten et al. (2005b).



REPRODUCTION

Throughout our 52,000-ha study area, the number of Lesser Prairie-Chicken nests varied among years across the 5 breeding seasons (2001–2005) of the focused study, with a high of 35 nests in 2002 and a low of 10 nests in 2004 ($\bar{x}$ = 20.3 ± 4.4SD nests / year). In the smaller core study area (Fig. 1), numbers were, predictably, smaller ($\bar{x}$ = 9.4 ± 6.5SD nests / year). The number of nests was correlated positively and highly with the number of hens being tracked (r = 0.93; Table 4); for example, the lowest number of nests (10) corresponded with the same season (2004) that had the fewest number of females being tracked (21), which in turn was apparently the result of very low overwinter survival of females: only 7 birds tagged in previous years were alive and being tracked in the spring of 2004 (Table 4). That said, the low nesting effort that season (47.6%) could have been real or could have been the result of an inability to find nesting birds (or both).

TABLE 4. Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) hen availability and reproductive output across the 5 breeding seasons of the focused study (2001–2005), from throughout the 52,000-ha study area.

year	tracked hens			tracked hens found . . .			percentages	
	from prior year	new	total	on nests	with broods	total	nests only	all effort
2001	4	20	24	18	0	18	75.0	75.0
2002	15	31	46	32	1	33	69.6	71.7
2003	23	14	37	25	2	27	67.6	73.0
2004	7	14	21	10	0	10	47.6	47.6
2005	12	11	23	20	0	20	87.0	87.0
total			151	105	3	108	69.5	71.5

Most females nested only once per season; <10% (8 of 108) of females re-nested after their first nest failed. By contrast, nearly half (29 of 67) of females nested in multiple years (this figure necessarily excludes females nesting for the first time in 2005 but does included females which had nested in 2000). Two females nested in 3 different years.

In the core study area (Fig. 1), nests (n = 45) were on average 7.8 cm deep with lateral dimensions of 20.7 × 18. 1 cm. Nests were placed on flat terrain (slope $\bar{x}$ = 1.7%), with only two nests at sites with ≥10% slope (one at 10%, one at 25%). We measured nest concealment on a 5-point scale (4 = ~100%, 3 = ~75%, 2 = ~50%, 1 = ~25%, and 0 = ~0%) above the nest and at each of the four cardinal directions. Because a low score in a given direction is disproportionately worse, we calculated lateral concealment as the harmonic mean (i.e., rather than the arithmetic mean) of the four directional measures. On average, nests were concealed a little under half from above ($\bar{x}$ = 1.87 ± 1.16SD) and a little over half laterally ($\bar{x}$ = 2.38 ± 0.91SD).

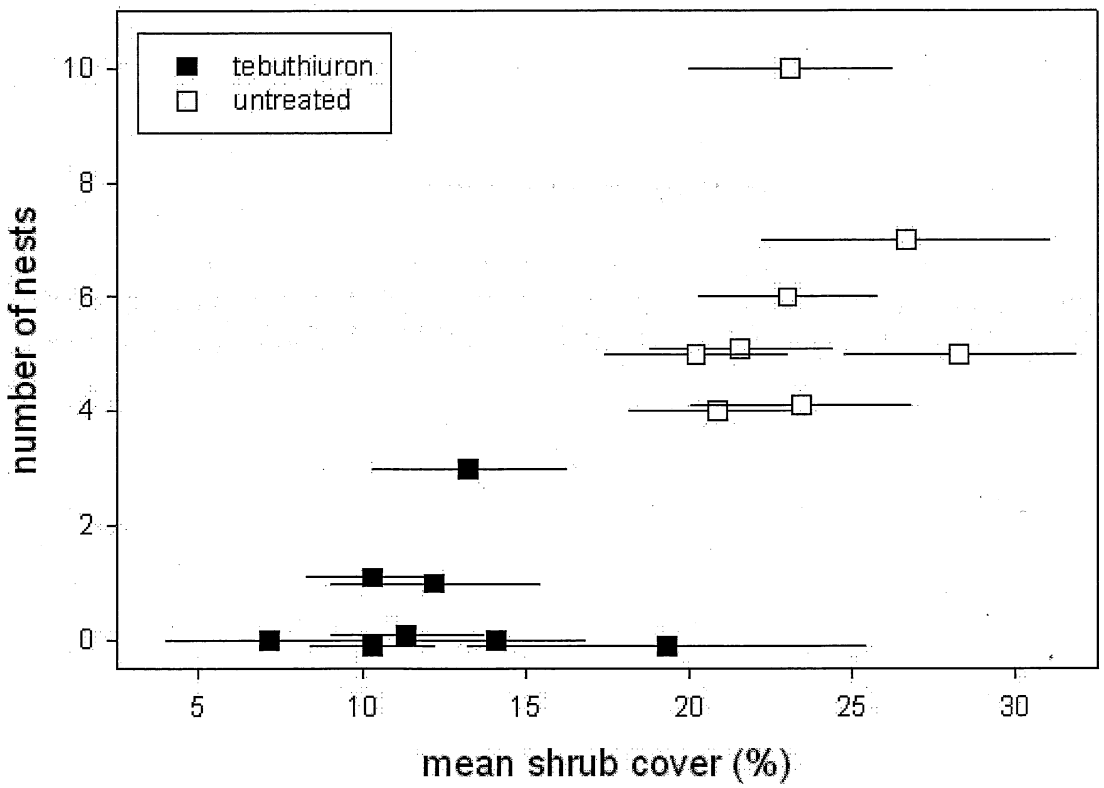
Nests typically were placed in a mix of tallgrass and shinnery oak (56%); indeed, 80% (36 of 45) of nests had grass and 75% (34 of 45) had oak as a component of the overstory cover. The only other common overstory shrubs were sand sagebrush (22% [10 of 45] of nests) and yucca (16% [7 of 45]). (Note that because the overstory may include multiple species, percentages will not sum to 100.) On average nests were close to woody vegetation ($\bar{x}$ = 17.1 ± 22.4SD cm; median = 7 cm) of low stature (<1 m).

TABLE 5. Vegetation at Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) nest sites (n = 45) relative to availability (n = 414 random vegetation surveys) in the core study area (Fig. 1) from 2001–2005. *Shrub* and *grass* values were transformed to percentages *post hoc*. Density was estimated as the number of contacts on a vertical rod. *Post hoc* significance tests (Tukey's HSD) control for experimentwise α at 0.05; significantly larger means are boldfaced. Separate analysis by each year does not materially change these results.

category	measure	nest site mean	random mean	effect size
	shrubs (%)	**53.82**	29.47	0.98
cover	grasses (%)	**47.31**	34.67	0.55
	shinnery oak (%)	**41.01**	20.22	0.95
	canopy height (cm)	**63.82**	24.21	1.44
	<10 cm	**1.18**	0.71	0.36
density	10–50 cm	**6.57**	1.75	1.52
	>50 cm	**0.66**	0.26	0.47

Relative to random samples, females selected nest sites with higher cover, greater canopy height, and higher vegetation density (Table 5). In particular note that shrub cover (especially of shinnery oak), canopy height, and mid-height (10–50 cm above ground) density are markedly higher at nest sites (Table 5; $P < 0.0001$ for each univariate ANOVA, plus generally large effect sizes). Given their strong preference for sites with high shrub cover, it follows that birds may avoid nesting in blocks treated with tebuthiuron, which they did (Wilcoxon two-sample: $C = 99.0$, $P = 0.005$), and avoidance can be linked directly to the expected reduction in shrub cover resulting from treatment (Fig. 7). Power was low, but 2003–2005 nests ($n = 18$) were not associated with grazing ($C = 75.0$, $P > 0.40$), although the effect of tebuthiuron on nest placement remained apparent even with this reduced sample size ($C = 94.0$, $P < 0.02$).

FIGURE 7. Number of Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) nests as a function of shrub cover (mean ± SE) per block (Fig. 1), estimated from 414 random vegetation surveys. Mean shrub cover accounts for ~67% of variation in nest number (least squares regression weighted by 1/SD: $y = 3.40x - 3.39$).

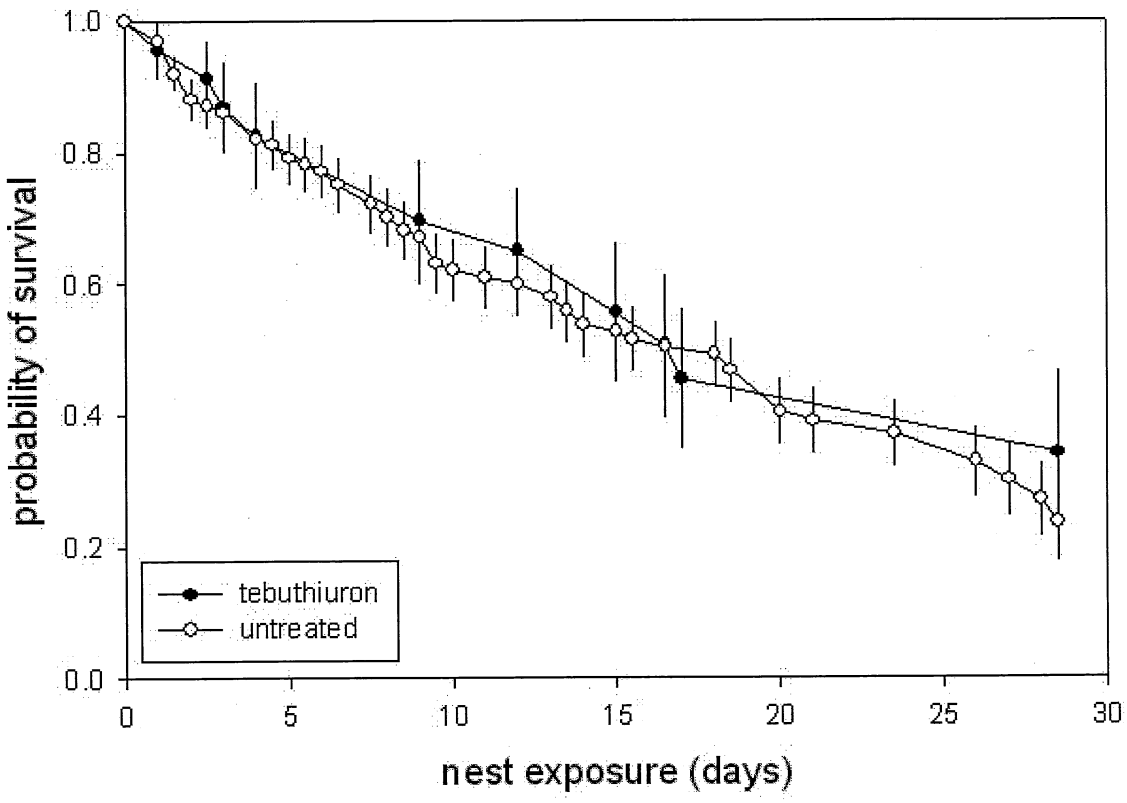


Clutch size did not vary among years (ANOVA: $F_{4,76} = 0.68$, $P > 0.60$; grand $\bar{x} = 8.67 \pm 1.94$SD eggs, $n = 81$ nests). By contrast, fledgling production did vary among years, both for all nests ($F_{4,107} = 3.67$, $P < 0.01$; $n = 112$ nests) and for successful nests only ($F_{4,33} =$

4.16, $P < 0.01$; $n = 38$ nests). Regarding the last group, per Tukey's HSD the difference arose entirely from 2002 being a poor year ($\bar{x} = 4.13 \pm 2.03$SD chicks; $n = 8$ nests) relative to the other years (grand $\bar{x} = 7.57 \pm 3.06$SD chicks; $n = 30$ nests). This difference in fledgling output was a reflection of nest success, which reached a low of 22.9% in 2002 (across other years, $\bar{x} = 41.0\%$ and weighted $\bar{x} = 42.0\%$; range = 30.0% [2004] to 55.6% [2001]). In the study area, fledgling production ($n = 44$ nests) was not affected by cattle grazing ($F_{1,42} = 0.76$, $P > 0.35$) or by tebuthiuron application ($F_{1,42} = 1.04$, $P > 0.30$).

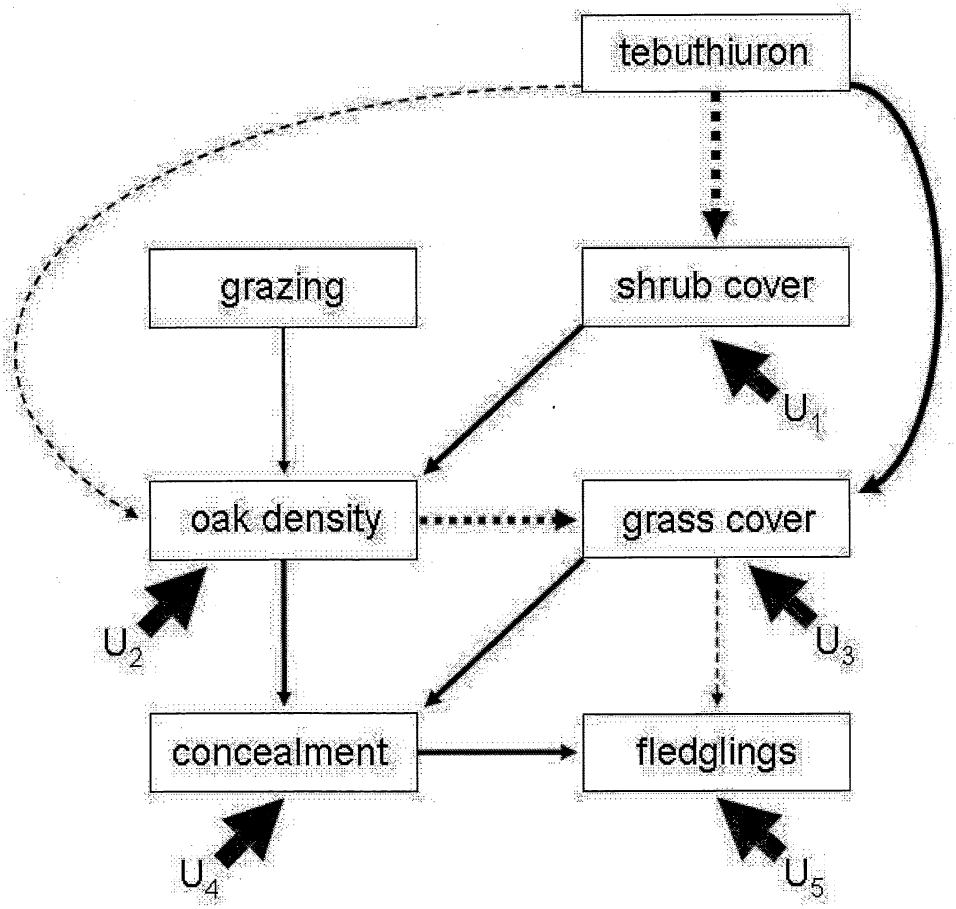
There were too few nests in the treated half of our core study area, but using data from all nests ($n = 126$) from our 52,000-ha study area, we further saw that tebuthiuron did not affect rates of nest survival (Fig. 8)—nests were as likely to succeed and lasted roughly the same amount of time before failure regardless of whether herbicide was applied. Also, although tebuthiuron had the expected effect of greatly reducing shrub cover and the density of shinnery oak and in turn greatly increasing grass cover (Fig. 8), nest survival was not associated with the extent of shrub cover (Cox regression: $\chi^2 = 1.43$, df = 1, $P > 0.20$) or grass cover ($\chi^2 = 2.14$, df = 1, $P > 0.10$) or with oak density ($\chi^2 = 0.37$, df = 1, $P > 0.50$).

FIGURE 8. Survival of Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) nests by tebuthiuron application (bars are standard errors). The survival curves do not differ (log-rank test: $\chi^2 = 0.56$, df = 1, $P > 0.40$).



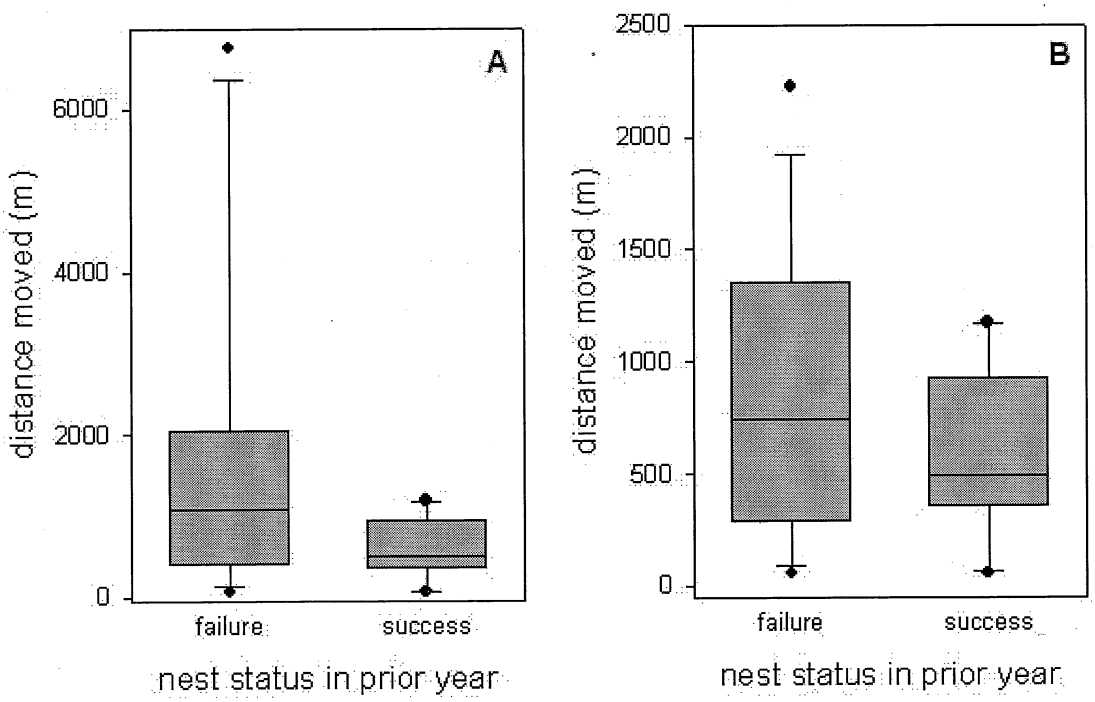
Nest survival—which did not vary with female age (log-rank $\chi^2 = 2.29$, df = 1, $P > 0.10$)—was, however, associated with how well the nest was concealed ($\chi^2 = 3.84$, df = 1, $P = 0.05$), which itself was associated with both oak density and grass cover (Fig. 9). The path analysis suggests a reason fledgling production differed little between treated and untreated areas. The resultant model shows that the herbicide has a complex relationship with fledgling production, such that tebuthiuron traces both positive and negative paths to this endpoint. For example, tebuthiuron reduces shrub cover and oak density, even though the latter is an important component of nest concealment. Tebuthiuron also increases grass cover, both directly and mediated through the reduction of oak density. Grass cover is an important component of nest cover, but grass cover *per se* has an additional negative effect on fledgling production (Fig. 9). The end result is that tebuthiuron has an insignificantly negative effect on fledgling production ($r_{pb} = -0.03$) because its effects were dampened or counterattacked through a complex string of causes and effects.

FIGURE 9. Path analysis of the effects of tebuthiuron on fledgling production in the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). The model provided a good fit for the data ($\chi^2 = 6.00$, df = 10, $P > 0.80$). Paths are postulated to be direct cause–effect relationships. The width of a path corresponds to the strength of the relationship, with negative relationships shown by dashed lines. The U_i refer to sources of unknown variation (i.e., not explained by the model).



Site fidelity in successive years was plastic, but distance between subsequent nests tended to be lower if a previous nest had succeeded (Fig. 10). Even so, variation was high, so distance did not differ significantly (median two-sample test: $P > 0.40$). Three outliers from hens that failed (4487, 6197, and 6762 m) drive the pattern (Fig. 10A); other hens that failed (range = 59–2228 m) generally moved the same as those that succeeded (range = 59–1176 m), as is apparent with the outliers removed (Fig. 10B).

FIGURE 10. Site fidelity of individual nesting Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) in years following a failed (n = 16) or successful (n = 12) nest. Boxes represent the 25th–75th percentiles, with the 10th–90th percentile shown as lines and outliers shown as dots. The line crossing each box is the median. Note that the median distance moved by hens with successful nests lies within the bulk of data for those with failed nests, regardless of whether outliers are included (A) or excluded (B).



We conducted brood counts only in 2005, during which there were seven successful nests. We flushed broods at ~14 days after hatching, and again at ~30 and ~60 days after hatching. Data from our flush counts (Table 6) highlight the problems with the technique: when small, chicks do not flush readily and are missed easily. Another complication was that some counts at ~60 days were the result of mixed broods for different hens. In particular, hens 1230 and 1240 appeared to be interacting and their broods mixing during July 2005 counts. Without marked chicks it impossible to determine which hen's brood had survived, meaning we cannot say even what percentage of broods survived after hatching, although at least one brood was lost and at least four had at least one surviving poult.

TABLE 6. Brood counts for the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) for all successful nests (n = 7) in 2005.

female	initial brood	14 days	30 days	60 days
1035	10	2	1	8
1042	?	0	0	1
1061	7	1	6	6
1068	9	2–3	8	7
1230	?	3	1	2
1237	9	0	0	0
1240	11	8	2	4

Likewise, we have too few data on brood survival to conduct a meaningful analysis, but a cursory glance at the data suggests that roughly half (25 of 46) of chicks survived 2 months after hatching. Additional data, partly reported by Luke (2005), were not available to us for pooling and analysis.

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