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The prairie sharp-tailed grouse *Tympanuchus phasianellus campestris* occurs throughout the north central region of North America. It is of management concern because it has decreased in the southeast portion of its range over the past three decades, including marked declines in Minnesota and the Great Lakes region, USA. Although there is general knowledge about the habitat requirements for this species, no quantitative lek site or landscape information has been documented. We quantified landscape composition around active and inactive sharp-tailed grouse lek sites and random points in brush landscapes in northeast Minnesota at multiple scales (200-3,000 m radii circles). Our objective was to compare landscape composition among these sites. We also developed a model to predict the probability of grouse lek site occurrence in the study area. Landscape composition around active and inactive lek sites differed from each other primarily at the 500 m and 1,000 m radii scales. Inactive sites had higher proportions of upland forest and brush cover types and active sites had a higher percentage of native grass than inactive sites. No differences were found in landscape composition between site types at the 200 m radius scale and only one landscape variable (number of cover types) was different at the 3,000 m radius scale. We found non-random distributions of this grouse species at four different scales. Random brush land sites differed from both active and inactive sites having higher percentages of forest and brush cover. In contrast, lek sites had more bare ground, emergent aquatic vegetation, bog brush and roads than the random points. A regression model for the grouse at the 3,000 m scale was used to predict the probability of grouse occurrence in the landscape. The model resulted in a spatial map with about 8% of the area having a probability of grouse occurrence of >80%. This information can be used to locate new lek sites and to guide management activities for this species.

Key words: GIS, habitat, landscape, Minnesota, model, prairie sharp-tailed grouse, USA

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The prairie sharp-tailed grouse *Tympanuchus phasianellus campestris* occurs throughout the north central region of North America. The historical range included almost all of Minnesota (Roberts 1932) and Wisconsin (Johnsgard & Wood 1968), whereas the current range covers a small portion of northern Wisconsin and a third of the area of northern Minnesota. The species' range initially decreased in the early 1900s following conversion of prairies to farmland, but the species colonized new areas in northern forests as fires and logging activities cleared the forest (Amman 1957). The species has decreased in most regions throughout its range over the past 30 years including a decline of about eight birds/route/year in Minnesota based on the Breeding Bird Survey data (Sauer, Hines, Gough, Thomas & Peterjohn 1997). The plains subspecies has also declined throughout Canada including about 12 birds/route/year decrease in Alberta and six birds/route/year decline in Saskatchewan. An increase in numbers has been documented for North and South Dakota (eight and nine birds/route/year; Sauer et al. 1997). In areas where the species is declining, the downward trend is likely due to advancing succession, conifer plantations, agricultural development (Berg 1987), predation and hunting pressure.

The general habitat requirements for the sharp-tailed grouse are known (Berger & Baydack 1992). For example, lek sites are characterized by low, sparse vegetation, and an excess of woody cover within 800 m of the lek site has a negative effect on male density (Gregg 1987, Prose 1987). Females require brushy or woody vegetation for nest cover within 3.2 km of the lek site (Prose 1987), and shrub habitat is also important for cover during the early brood stages (Johnsgard 1983). However, no one has quantified habitat requirements for this species at the lek site or landscape scale. We asked whether grouse selected lek sites in the landscape randomly and tested the hypothesis that landscape composition around active and inactive sites are not different from each other at multiple landscape scales. In addition, we developed a predictive model to calculate the probability of grouse lek site occurrence across the study area. The predictive model was developed to provide information to direct future management efforts for this species as well as other species that require an open grass/brush land ecosystem.

Study area and methods

We conducted our study in northeast and north central Minnesota (Fig. 1). This area includes the east central range of the sharp-tailed grouse in Minnesota and was selected because we had complete landscape information for the region, including remotely-sensed classified habitat information and historical records of grouse lek site locations.

We identified cover types within the study area with Landsat thematic mapper™ imagery (Wolter, Mladenoff, Host & Crow 1995). Because brush habitat is important to this species and is a type that is not easily classified with summer imagery, we acquired a winter image to distinguish brush habitat types as a distinct type. After brush was spectrally isolated, summer TM data were used to classify brush types as willow *Salix* spp., alder *Alnus* spp. and 'other'. Brush types were then divided into upland or lowland categories using National Wetlands Inventory (NWI) digital information.

We used survey information on the sharp-tailed grouse provided by the Minnesota Department of Natural Resources (DNR) to identify active and inactive lek sites. Wildlife biologists have surveyed grouse lek sites since 1974. Surveys were conducted during early morning hours in early spring and numbers of birds on each site were counted either from a vehicle or by counting birds that flushed when the lek was approached on foot. About 120 grounds were identified as poten-

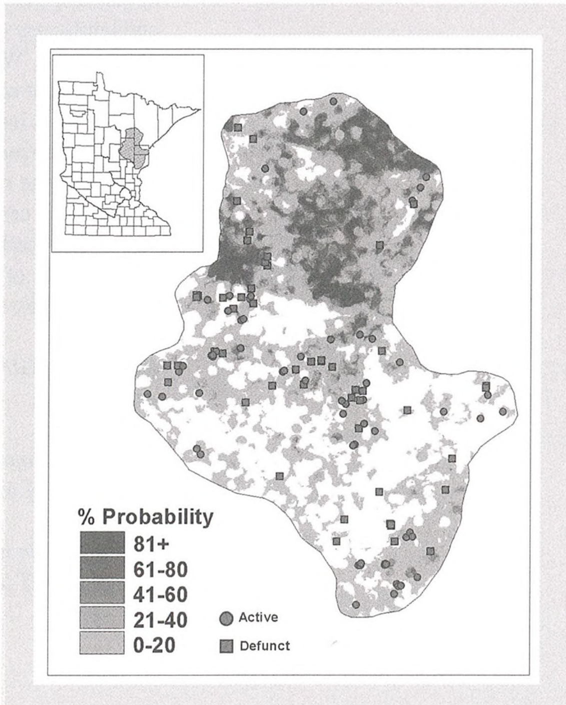

Figure 1. Location of study area in Minnesota (inset) and calculated probability of sharp-tailed grouse occurrence. The white portions indicate areas that had null values because none of the five landscape variables used to calculate probability existed there and, hence probability values could not be calculated. Active and inactive lek site locations are also displayed.

tial study sites. We used data collected during the 1996 survey and defined active sites as those having at least three individuals present in two subsequent years (e.g. 1996 and 1995) of surveys. Sites were classified as inactive if birds were not present for a period of at least two years prior to 1995.

Locations of lek sites were digitized into a geographic information system (GIS) from locations marked on maps provided by the DNR. GIS data layers that were available for Minnesota including lakes, streams and roads were displayed to aid in digitizing the precise locations of the lek sites. We digitized 53 inactive sites, 58 active sites, and 100 points that were randomly selected from areas where brush habitat occurred. Some lek sites moved from year to year and when this occurred we used the most recent location in the analysis.

After the lek sites were digitized, we created circular buffer zones of 200 m, 500 m, 1,000 m and 3,000 m radii around each point. We chose these scales because we felt that they were representative of the possible scales at which the grouse responded to the landscape. For example, at the smallest scale, the 200 m buffer zone represents habitat composition at or in close proximity to the lek site. In contrast, the 3,000 m buffer zone included an area that would encompass the entire home range of this species. It also corresponds to the average distance at which aspen *Populus tremuloides* trees were observed from active, large lek sites in our study (Christian & Hanowski 1997) and the maximum distance that nests have been found from the lek site (Prose 1987). The area included for the 200 m buffer zone was 13 ha, 79 ha for the 500 m, 314 ha for the 1,000 m, and 2,826 ha for the 3,000 m buffer zones, respectively. We characterized landscape components at each point for each buffer zone including: 1) area of each cover type separately, 2) area of combinations of similar cover types (e.g. upland forest, lowland forest), 3) Shannon-Wiener diversity index of cover types, and 4) number of cover types. We combined similar cover types because we did not know if grouse were sensitive to occurrence of specific habitat types (e.g. aspen) or to a group of similar habitat types (e.g. all upland forest types). We used the Shannon-Weiner index and number of cover types to determine whether habitat composition complexity was important in predicting grouse lek site occurrence in the landscape.

We normalized distribution of landscape variables (proportions of cover type in each area) with arcsine transformations before conducting statistical analyses. Analysis of variance (ANOVA) was used to determine differences and similarities among site types for each cover type and derived variable for each buffer width, and Tukey's multiple comparison test was used to determine whether individual means differed from each other. We used a multivariate analysis of variance (MANOVA) to test for overall differences among site types for each buffer width.

Logistic regression was used to determine landscape variables that discriminated active lek sites from randomly selected sites in brush habitat. Several logistic regression models were developed for each buffer width and outlier sites identified. Although it would have been possible to create one model that utilized habitat data at multiple scales, this approach was not used because it would have been difficult to predict the probability of grouse lek site occurrence in a GIS platform with this type of model.

All logistic regression models had P-values of <0.0001 and we selected the model for subsequent analyses based on five criteria: 1) approximate r^2-value, 2) goodness of fit, 3) percent concordance, 4) number of influential outliers and 5) coefficients for each predictor variable. No significant model could be developed for the 200 m buffer zone and no further analyses were conducted at the landscape scale. The best models for the other buffer widths had similar approximate r^2-values (range: from 0.7072 for the 500 m model to 0.6667 for the 3,000 m model), in percent concordance (94.0% for the 500 m model, 92.8% for the 1,000 m model, and 92.7% for the 3,000 m model), and in goodness-of-fit (0.9779 for the 500 m model, 0.8065 for the 1,000 m model, and 0.8266 for the 3,000 m model). The predictor variables and coefficients in each model were similar among the three buffer zones. We decided to use the 3,000 m model to predict the probability of grouse occurrence on the landscape in a GIS format because we found that sharp-tailed grouse in this region responded to habitat conditions at this scale from the lek site (Christian & Hanowski 1997) and most management for the species is done at this scale. As we used a sliding window that moved at 30 m intervals (versus a hopping window that would move at 500, 1,000, or 3,000 m intervals), the number of calculations would have been the same for each buffer width (8,674,377).

We used a logistic regression model in a GIS format to predict the probability of grouse occurrence at the landscape level. The first step in this process was to calculate percent area of each of the five cover types identified in the logistic regression model for each 3,000 m circular window. Each cover type was extracted separately from the original land cover and divided by the land cover total to get a percent land cover for each cell. Multiple calculations were then computed for each window to produce the final probability val-

Table 1. Mean and standard error (SE) of the percentage of cover that had significantly different means between active and inactive lek sites in northeast Minnesota at three buffer widths around the lek centre. P-values are from ANOVA with 53 inactive and 58 active sites. No differences were found for any variables in the 200 m buffer zone.

Variable	Buffer width (m)	Active		Inactive		P-value
		Mean	SE	Mean	SE	
Aspen *Populus tremuloides*	500	4.26	0.63	6.70	0.90	0.000
Native grass/sedge		16.65	1.89	11.86	1.39	0.004
Willow *Salix* spp.		1.30	0.27	1.95	0.29	0.000
Miscellaneous brush		1.44	0.30	1.93	0.23	0.000
Roads		1.06	0.17	2.14	0.24	0.003
Mixed conifer/deciduous forest		0.54	0.08	1.21	0.26	0.000
Upland brush		4.49	0.72	6.20	0.65	0.000
Number of cover types		18.14	0.71	21.09	0.67	0.000
Cedar *Thuja occidentalis*	1000	0.14	0.05	0.24	0.05	0.022
Tamarack *Larix laricina*		0.72	0.17	1.25	0.30	0.004
Aspen		7.37	0.75	10.59	0.84	0.000
Native grass/sedge		12.98	1.12	9.01	0.82	0.000
Lowland alder *Alnus* spp.		0.66	0.24	1.62	0.41	0.001
Roads		1.06	0.11	1.76	0.23	0.002
Mixed conifer/deciduous forest		1.13	0.22	1.69	0.20	0.000
Number of cover types		28.41	0.70	31.85	0.57	0.000
Number of cover types	3000	39.34	0.21	40.13	0.15	0.001

ue. We then displayed probability on a base map of the study area and overlaid active and inactive lek sites to determine the probability value for each active and inactive lek site.

Results

We found more differences in landscape composition between active and inactive sites at the 500 m and 1,000 m buffer widths than at the 3,000 m scale, but no differences at the 200 m scale (Table 1). Active lek sites had more native grass/sedge than inactive sites at the 500 m scale. However, inactive sites had more aspen/birch, willow brush, miscellaneous brush, roads, mixed forest, upland brush and a more diverse landscape composition (more cover types) than the active sites (see Table 1). Similar results were found for the 1,000 m buffer zone. At this scale, active sites had more native grass/sedge than inactive sites, but inactive sites had

Table 2. Mean and standard error (SE) of the percentage of cover within a 3,000 m buffer zone around active and inactive dancing grounds and random landscape points in northern Minnesota. P-values from ANOVA with 53 defunct sites, 58 active sites and 100 random sites are shown as well as letters to distinguish differences between groups for variables that had P-values of <0.05.

Parameter	Defunct		Active		Random		P-value
	Mean	SE	Mean	SE	Mean	SE	
Jack pine *Pinus banksiana*	0.11ab	0.03	0.06b	0.01	0.35a	0,11	0,017
Red pine *Pinus resinosa*	0.64ab	0.10	0.49b	0.14	0.78a	0.09	0.011
Black spruce *Picea mariana*	2.73a	0.41	2.05ab	0.32	1.69b	0.23	0.023
Acid bog conifer, stagnant	1.82a	0.35	1.33a	0.20	0.35b	0.06	0.000
Conifer, miscellaneous (low density)	0.09a	0.02	0.07ab	0.01	0.03b	0.01	0.003
Conifer, regen	0.26b	0.04	1.17b	0.02	0.49a	0.08	0.000
Hardwoods, miscellaneous (lowland)	0.78b	0.09	0.80b	0.08	1.31a	0.09	0.000
Aspen *Populus tremuloides*	17.14b	1.12	14.68b	0.92	20.12a	0.70	0.000
Hardwoods	6.10b	0.47	5.80b	0.58	9.30a	0.56	0.000
Oak *Quercus* spp.	1.44b	0.25	1.02b	0.19	2.75a	0.20	0.000
Hardwood, transitional	0.11b	0.02	0.26ab	0.08	0.25a	0.03	0.012
Bare ground	0.90a	0.27	0.40a	0.38	0.15b	0.01	0.002
Emergent	4.40a	0.71	4.72a	0.66	2.32b	0.22	0.001
Grass, native (lowland)	4.68a	0.50	5.68a	0.63	2.15b	0.10	0.000
Brush, alder (lowland) *Alnus* spp.	1.34a	0.23	1.00ab	0.18	0.62b	0.07	0.002
Brush, willow (lowland) *Salix* spp.	4.47a	0.41	4.51a	0.49	3.48a	0.20	0.042
Brush, miscellaneous	3.30b	0.28	3.26b	0.30	4.23a	0.13	0.000
Brush, bog species	0.89a	0.13	1.21a	0.23	0.29b	0.03	0.000
Roads	1.30a	0.15	1.09ab	0.16	0.92b	0.05	0.032
Conifers	0.74ab	0.13	0.49b	0.13	0.88a	0.17	0.038
Deciduous	22.62b	1.33	20.15b	1.29	31.13a	1.15	0.000
Lowland conifer	7.04a	0.80	5.50ab	0.66	4.38b	0.51	0.003
Lowland deciduous	5.04a	0.40	5.18a	0.42	6.29a	0.37	0.041
Upland brush	7.86ab	0.44	7.42b	0.48	8.67a	0.23	0.006
# cover types	40.13a	0.15	39.34b	0.21	40.09a	0.11	0.001

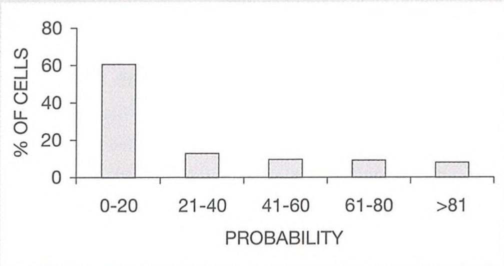

Figure 2. Percent of cells within five probability categories predicted by logistic regression model across the study area.

more cedar *Thuja occidentalis*, tamarack *Larix laricina*, aspen/birch, lowland alder brush, roads, mixed forest and more cover types (see Table 1). Of the 43 landscape variables 25 differed among active, inactive and random points at the 3,000 m buffer scale (Table 2). Landscape composition around active and inactive lek sites was more similar than landscape composition around random and active sites. Random sites which were centered around randomly selected brush habitat had more jack pine *Pinus banksiana*, red pine *Pinus resinosa*, regenerating conifer, lowland hardwoods, aspen/birch, hardwood forest, oak *Quercus* spp., miscellaneous brush, total conifer forest, total deciduous forest, total lowland deciduous forest, total upland brush, and number of cover types than the landscape surrounding active lek sites (see Table 2). In contrast, active lek sites had more bare ground, emergent aquatic vegetation, bog shrub species and roads than the random points (see Table 2).

The logistic regression model used for the GIS spatial model included five landscape variables; two had negative coefficients including conifer regeneration (-66.1) and upland hardwood forests (-9.6) and three variables, lowland conifer bog (22.2), lowland hardwood forest (16.3) and native grass (22.9) had positive coefficients. The approximate r^2 of this model was 0.667, the goodness-of-fit was 0.83 and the percent concordance was 92.7. Only one outlier was identified for this model. The model variables selected were the same variables that indicated significant differences in the MANOVA (see Table 2). Active sites were located in areas that had more native grass/sedge, lowland hardwood forests and conifer bog, and less conifer regeneration and upland forest.

A summary of probability values calculated for each of 8,674,377 cells within the study area with the logistic regression equation indicated that 60% of the study area had probabilities below 20% (Fig. 2). About 13% of the cells had probability values within the 21-40% range, 9.6% of the cells fell within the 41-60% range, 9.1% in the 61-80% range, and only 7.9% of the cells had probabilities larger than 81% (see Figs. 1 and 2). On average, the inactive dancing ground sites had higher probability values than the active sites (mean 11.4% vs 8.4%). This difference was not significant ($P = 0.32$). The distribution of probability values was not even across the study area. The northern area had a larger proportion of high values compared to the southern portion of the study area (see Fig. 1).

We found that points with the highest calculated probability values were in more hydric landscapes (Fig. 3). Points in higher probability categories had relatively more bog and lowland hardwood cover types than points in lower probability categories (see Fig. 3). Proportion of upland hardwood cover type was also negatively associated with probability value, but percentage of native grass/sedge cover type did not vary considerably across probability categories (see Fig. 3).

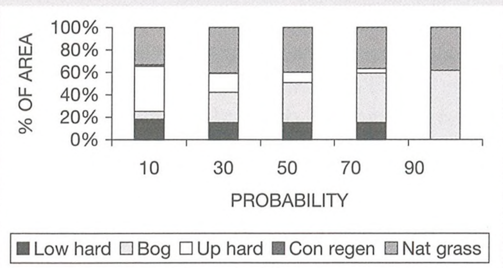

Figure 3. Percent of area of the five cover types used in the logistic regression model in five predicted probability categories.

Discussion

Sharp-tailed grouse population declines in the Great Lakes region have been linked to changing landscapes and types of habitat that the species prefers; however, only qualitative assessments of these changes exist. The cause of declining populations in Minnesota, from an annual harvest of 150,000 birds in 1949 to about 5,000 birds in 1997 has been attributed to advancing vegetation succession of open lands to brush and trees, increase in conifer plantations and intense agricultural development (Berg 1987). Our data support this observation. Active lek sites differed from inactive sites primarily in amounts of forest cover type, regenerating conifer, brush and native grass/sedge habitats. These differences were not evident within 200 m of the lek site but were apparent at distances up to 3,000 m of the lek site. The lack of difference between active and inactive sites at the 200 m scale suggests that changes in habitat at the lek site itself may be less important in explaining why grouse abandon lek sites than changes in habitat conditions in the surrounding landscape. This result is consistent with a study conducted in Alberta, Canada, that found that leks in that region were abandoned when aspen forest increased beyond 56% of the area in a 1,000 m circle surrounding the lek and when native grass/sedge decreased to below 15% (Berger & Baydack 1992). These results suggest that successful management for sharp-tailed grouse needs to be done at the landscape level.

Sharp-tailed grouse in this area of Minnesota appear to be sensitive to even small changes in amounts of grass/sedge, brush and forest cover types within their home range. Active sites will be abandoned when there are even small percentages of changes (1-2%) in upland forest cover type in their home range (Christian & Hanowski 1997). Based on this observation it was not surprising to find that grouse chose lek sites that are in a different landscape context than a random sample of brush habitat in this region. Sharp-tailed grouse are particularly sensitive to amounts of forest cover up to 3 km from the lek sites, particularly upland deciduous forests (Christian & Hanowski 1997). This result indicates that management for this species should not focus only on brush habitats, but also needs to consider other woody vegetation types.

The predictive model that we developed for the grouse included variables that we and other investigators (Berger & Baydack 1992, Gratson, Toepfer & Anderson 1990, Gregg 1987, Prose 1987) have found to be important in discriminating between active and inactive sites including amounts of native grass/sedge, regenerating conifer and upland forests. Random and active sites also differed primarily in that active sites were in areas that had more hydric forest types including lowland conifer and lowland hardwoods. Based on the predictive model, areas that had the highest probability values were in landscapes that were predominantly wet including the large expansive peatland in the northern part of the study area.

The average predicted probability value at inactive sites was higher than the mean probability at active lek sites because inactive and active sites had similar landscape composition at the scale at which the model was developed (3,000 m). Therefore we would expect that probability values calculated for this landscape scale would be similar for the two site types. It was surprising that several active and inactive lek sites were located in areas that had low calculated probability values and that there was a large area of high predicted values that had no active or inactive lek sites (see Fig. 1). This observation is likely due to several factors including: 1) a general difference in landscape context across the study area due to geomorphology, 2) population levels may be too low to occupy all suitable habitat on the landscape, 3) site level habitat differences between active and inactive sites were not accounted for in our landscape approach, 4) the juxtaposition, not just percentage of habitats that occur within active and inactive sites is also important in predicting grouse occurrence, or 5) a possibility that grouse occur in these areas of high predicted probabilities but these areas have not been adequately surveyed.

There are many geomorphological differences between the northern and southern regions of the study area which result in a gradient of habitat conditions across the region. The northern portion of the study area has more hydric soil conditions and is characterized by a large remote peatland with lowland conifer, lowland brush, and open grass/sedge habitat. This type of habitat exists in the southern portion of the study area, but in smaller patches. In addition, although the entire study area was forested before settlement, the southern region has undergone more extensive conversion of forests to agriculture and more recently some of this agricultural land has converted back to forests, pine plantations or brush habitat. Because two of the most highly weighted variables in the model (proportion of lowland conifer bog and lowland hardwood forest) are associated with hydric soil conditions and two of the most negative associated variables exist on dry soils (conifer regeneration and upland hardwood forest), it is not surprising that the model predicted that northern areas would be more suitable for sharp-tailed grouse.

Differences in site level conditions not captured by our landscape model could also explain the relatively low probability values calculated for active and inactive lek sites. For example, sharp-tailed grouse are sensitive to presence and height of vegetation within 3,000 m of the lek site (Christian & Hanowski 1997). Photographic studies on active and inactive lek sites indicated that vegetation height was lower above the horizon on active dancing ground sites and that these sites had less extensive areas of planted conifers. Although our landscape model explained 33% of the variation between active and random brush points, it did not account for the important explanatory variables that grouse respond to on a different scale. It is reasonable to assume that sites which had high predictive probabilities may not be suitable due to microhabitat conditions such as trees in the vicinity of open ground. Results of predictive models that are based on landscape should acknowledge this limitation in predicting occurrence of any species.

Our landscape model included metrics that quantified amounts of individual or groups of individual cover types within set distances from lek sites. Although several landscape metrics could have been developed (e.g. edge, patch size) in a GIS framework, we did not include them in our analysis because of the computation time and size of data output by these analyses. It is possible that sharp-tailed grouse are sensitive to patch size, patch shape or juxtaposition of suitable habitats in the landscape and not just to the percentage of habitat available (Miller 1963). The lack of this type of information in our landscape model could also explain some of the peculiarities of the predictive model.

It is also possible that more lek sites exist in remote areas of the northern region but have not been located because they are not easily accessible (B. Berg, pers. comm.). Many of the active and inactive lek sites in the northern region are located on the fringe of areas with the highest probability values. Some of these lek sites are in agricultural fields that have been created on the edge of this peatland complex. There are also lek sites on open bog sites in this region, but they are generally accessible by roads.

The landscape model that we developed for the sharp-tailed grouse for this area of Minnesota can be used as a coarse filter to identify key areas for management. Management for this species must be done at the landscape level and should consider both brush, open and upland forest cover types. In addition, successful management should include a site assessment to document heights of vegetation, especially planted conifers within the vicinity of the lek site.

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