Document cover Sheet—Studies in Avian Biology

Title: CONNECTING PATTERN AND PROCESS IN GREATER SAGE-GROUSE POPULATIONS AND SAGEBRUSH LANDSCAPES

File name: Knick and hanser.doc

RH: GREATER SAGE-GROUSE CONNECTIVITY—*Knick and Hanser*

Number of figures: 10

Number of tables: 6

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27 February 2009

CONNECTING PATTERN AND PROCESS IN GREATER SAGE-GROUSE POPULATIONS AND SAGEBRUSH LANDSCAPES

STEVEN T. KNICK AND STEVEN E. HANSER

Abstract. Spatial patterns influence the processes that maintain Greater Sage-Grouse (*Centrocercus urophasianus*) populations and sagebrush (*Artemisia* spp.) landscapes on which they depend. We used connectivity analyses to: (1) delineate the dominant pattern of sagebrush landscapes, (2) identify regions of the current range-wide distribution of Greater Sage-Grouse important for conservation, (3) estimate distance thresholds that potentially isolate populations, and (4) understand how landscape pattern, environmental disturbance, or location within the spatial network influenced lek persistence during a population decline. Long-term viability of sagebrush, assessed from its dominance in relatively unfragmented landscapes, likely is greatest in south central Oregon and northwest Nevada; the Owyhee region of southeast Oregon, southwest Idaho, and northern Nevada; southwest Wyoming; and south central Wyoming. The most important leks (breeding locations) for maintaining connectivity, characterized by higher counts of sage-grouse and connections with other leks, were within the core regions of the sage-grouse range. Sage-grouse populations presently have the highest levels of connectivity in the Wyoming Basin and lowest in the Columbian Basin management zones. Leks separated by distances >13–18 km could be isolated due to decreased probability of dispersals from neighboring leks. The range-wide distribution of sage-grouse was clustered into 209 separate components (units in which leks were interconnected within but not among) when dispersal was limited to distances <18 km. The most important components for maintaining connectivity were distributed across the central and eastern regions of the range-wide distribution. Connectivity among sage-grouse populations was lost during population declines from 1965–1979 to 1998-2007, most dramatically in the Columbia Basin management zone. Leks that persisted during this period were larger in size, more highly connected, and had lower levels of broad-scale fire and human disturbance. Protecting core regions and maintaining connectivity with more isolated sage-grouse populations may help reverse or stabilize the processes of range contraction and isolation that have resulted in long-term population declines.

Key Words: *Artemisia*, *Centrocercus urophasianus*, connectivity, graph analysis, Greater Sage-Grouse, landscape configuration, sagebrush

CONECTANDO PATRONES Y PROCESOS EN POBLACIONES DE GREATER SAGE-GROUSE Y EN PAISAJES DE ARTEMISA

Resumen. Los patrones espaciales influyen los procesos que mantienen a las poblaciones del Greater Sage-Grouse (*Centrocercus urophasianus*) y a los paisajes de Artemisa (*Artemisia* spp.) de los que dependen. Utilizamos análisis de conectividad para: (1) delinear el patrón dominante de paisajes de Artemisa, (2) identificar regiones actuales del rango de distribución del Greater Sage-Grouse que son importantes para la conservación, (3) estimar umbrales de distancia que potencialmente aíslan a las poblaciones, y (4) comprender cómo patrones de paisaje, disturbios ambientales, o la ubicación dentro de la red espacial influyó la persistencia del lek (asamblea de cortejo) durante un descenso de población. La viabilidad a largo plazo de Artemisa, evaluado a partir de su dominancia en paisajes relativamente no fragmentados, probablemente sea mayor en Oregon central del sur y Nevada del noroeste; la región de Owyhee del sudeste de Oregon, el sudoeste de Idaho, y del norte de Nevada; el sudoeste de Wyoming; y Wyoming central del sur. Los leks más importantes (sitios de reproducción) para mantener conectividad, caracterizados

por conteos más elevados de sage-grouse y conexiones con otro leks, se encontraron dentro de las regiones núcleo del territorio del sage-grouse. Actualmente las poblaciones de sage-grouse con los niveles más altos de conectividad se encuentran en el Wyoming Basin, y con los niveles más bajos en las zonas de manejo del Columbian Basin. Los leks separados por distancias de >13–18 km podrían aislarse debido a la disminuida probabilidad de dispersiones de leks vecinos. El rango de distribución del sage-grouse fue agrupado en 209 componentes separados (unidades en las que los leks se encontraban interconectados dentro pero no entre sí) cuando la dispersión estuvo limitada a distancias <18 km. Los componentes más importantes para mantener conectividad entre los leks se encontró distribuida a través de las regiones centrales y orientales de su rango de distribución. La conectividad entre poblaciones de sage-grouse fue perdida durante descensos de población entre 1965–1979 y 1998-2007, observándose la pérdida más dramática en las zonas de manejo del Columbian Basin. Los leks que persistieron durante este período eran de mayor tamaño, estaban altamente conectados, y tuvieron niveles más bajos de incendios y disturbios humanos de gran escala. Proteger las regiones del núcleo y mantener conectividad con poblaciones más aisladas de sage-grouse puede ayudar a revertir o estabilizar los procesos de contracción de territorio y aislamiento que han tenido como resultado descensos de población a largo plazo.

Greater Sage-Grouse (*Centrocercus urophasianus*) are wide-ranging, highly mobile birds that depend on sagebrush (*Artemisia* spp.) for most of their life requirements (Patterson 1952, Schroeder et al. 1999, Connelly et al. 2000a, Crawford et al. 2004). Extensive loss and alteration of sagebrush communities have resulted in regional and range-wide declines of Greater Sage-Grouse populations (Connelly and Braun 1997, Braun 1998, Connelly et al. 2004). The species currently occupies approximately half of its pre-EuroAmerican settlement range, and small populations at the edge are increasingly disjunct from larger populations at the core of the occupied range (Schroeder et al. 1999, 2004). The processes of range reduction, fragmentation, and isolation reduces connectivity among existing populations, which increases the probability of losses of genetic diversity (Benedict et al. 2003, Oyler-McCance et al. 2005) and extirpation from stochastic events (Reese and Connelly 1997, Aldridge et al. 2008).

Relationships between spatial pattern of Greater Sage-Grouse populations and sagebrush landscapes can provide insights into underlying processes critical for managing populations and maintaining viability of the species. Knowledge of sage-grouse response to structural features of sagebrush landscapes, such as quantity, composition, and configuration, can be used to identify conservation strategies that necessarily rely on maintaining or restoring sage-grouse habitat across broad regional extents (Wisdom et al. 2002, Meinke et al., in press).

Connectivity analysis provides a framework to understand the way in which spatial pattern of a species' habitat influences individuals and populations (Taylor et al. 1993). Patches of habitat within a regional mosaic vary in quality and permeability to animal movements. Analysis of the pattern of habitat, or resources, or structural connectivity within a landscape is relatively common (Collinge and Forman 1998, Tischendorf and Fahrig 2000). Landscape metrics describing physical attributes of habitats or resources of presumed importance to a species are readily integrated into spatial data layers using geographic information system (GIS) technology (Schumaker 1996, Calabrese and Fagan 2004, Taylor et al. 2006). A transferable measure of connectivity has been difficult to define because species differ in habitat use and mobility. Patterns of land cover that influence one species may be transparent to others (O'Neill et al. 1988, Keitt et al. 1997). Translating landscape structure into species response has proven elusive (Milne 1992, Wiens and Milne 1989, Wiens 2002, Calabrese and Fagan 2004), and relies on our ability to understand how a species perceives its environment (Wiens et al. 1993, With et al. 1997, Baguette and Van Dyck 2007). If animals are sensitive to arrangement of their habitat and if we can describe that relationship, we can understand how landscapes influence individuals or populations in daily and seasonal movements, how they disperse to new locations from natal ranges, and gene flow. Analysis of connectivity thus merges complementary evaluation of landscape pattern, resource selection, and population characteristics to identify core regions, key areas or locations that link core regions, and pathways important for conserving a species (Schultz 1998, Noss and Daly 2006, Crooks and Sanjayan 2006).

We described structural connectivity of sagebrush-dominated landscapes across the Sage-Grouse Conservation Area (SGCA), which is the maximum extent encompassing historical and currently occupied ranges of Greater Sage-Grouse (Connelly et al. 2004). Management actions for Greater Sage-Grouse are focused primarily on conserving and restoring its sagebrush habitat (Stiver et al. 2006). However, maintaining landscapes dominated by sagebrush is a major challenge because changes in fire regimes, widespread invasion by non-native plants, and increases in destructive land use are likely to accelerate the trajectory of fragmentation and loss (Knick et al. 2003, Wisdom et al. 2005a). Our objectives were to: (1) characterize the hierarchical pattern of sagebrush landscapes that results from natural and human disturbance, and (2) identify spatial scales perceived by Greater Sage-Grouse and other wildlife (Rotenberry and Wiens 1980, Wiens et al. 1987, Knick et al. 2008).

We used graph theory (Horary 1969, Cantwell and Forman 1993) to delineate spatial and temporal patterns in Greater Sage-Grouse populations. Graph theory, as applied to ecological phenomena, represents spatial configurations by a set of nodes that describes arrangement of habitat patches or population centers and a corresponding set of linkages among nodes (Cantwell and Forman 1993, Ricotta et al. 2000, Urban and Keitt 2001, Minor and Urban 2008). Relative importance of nodes is a combined function of their size and location within the spatial network. Linkages represent real or implied pathways that facilitate functional processes, such as dispersal or migration that maintain individual nodes and the population. The effect of loss or addition of nodes and linkages on a species' persistence can be assessed based on their contribution to overall connectivity (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007, Pascual-Hortal and Saura 2008). Greater Sage-Grouse are well-suited for graph analyses because populations are distributed around leks that represent spatial foci during the breeding season (Patterson 1952, Dalke et al. 1960). We analyzed nodes and linkages based on the spatial pattern of more than 5,000 leks surveyed across the SGCA from 2003–2007. Our objectives were (1) to identify lek locations and regions whose size and position within the sage-grouse range make them critical for maintaining connectivity, and (2) to determine thresholds in spatial distribution that limit dispersal and potentially isolate populations.

We also sought to determine if lek persistence during long-term population declines was related to their connectivity within the sage-grouse network, structure of sagebrush landscapes, or environmental and human disturbance. The process of range contraction of sage-grouse then might be understood in terms of interactions among a spatial network of populations (Hanski and Gilpin 1991, Hanski 1994) superimposed on spatial and temporal patterns of habitat patches.

Approaches such ours, that combine landscape ecology and metapopulation theory (Wiens 1996, 1997), might provide strongest insight into range-wide and regional dynamics of Greater Sage-Grouse populations.

STUDY AREA

The current range of Greater Sage-Grouse encompasses 670,000 km^2 and includes 11 states and two Canadian provinces (Schroeder et al. 2004). Seven individual sage-grouse management zones have been delineated for monitoring and conservation actions (Stiver et al. 2006).

Our analysis included all mapped sagebrush habitat and currently surveyed Greater Sage-Grouse leks within the SGCA (Connelly et al. 2004). The SGCA covers 2,063,000 km^2, of which sagebrush is the dominant land cover on approximately 530,000 km^2 (Knick et al., *this volume*). Patches of sagebrush within this region comprise 20 taxa in 11 major species and subspecies of *Artemisia* (McArthur and Plummer 1978, Miller and Eddleman 2001). Few areas dominated by sagebrush remain unchanged since pre-EuroAmerican settlement (Braun et al. 1976, West and Young 2000) although the total amount of habitat that has been lost or altered is difficult to determine (Miller et al., *this volume*).

METHODS

LANDSCAPE STRUCTURE OF SAGEBRUSH

We used the Landfire “Existing Vegetation Type” (Landfire 2006) as the base GIS layer of land cover types for describing spatial structure of sagebrush landscapes. Land cover was classified at 30-m spatial resolution from Landsat Thematic Mapper images taken between 2000 and 2004. The map contained 210 cover types, which we collapsed into two classes, sagebrush presence or absence. Sagebrush taxa have different environmental optima (West and Young 2000) and are not used equally by Greater Sage-Grouse (Crawford et al. 2004, Connelly et al., *this volume*). We grouped sagebrush into a single class because of map inaccuracies in delineating different *Artemisia* species and because range-wide similarities in spatial structure may offset site-specific preferences in taxa used by Greater Sage-Grouse.

We changed the resolution of the original land-cover data by resampling to 540-m grid-cells. We still were able to detect relatively fine-scale patterns at this resolution when considered at the spatial extent of the SGCA. Increasing minimum cell size to 540-m resolution would not influence detection of larger-scale disturbances, such as fire, and land cover changes of sufficient magnitude to influence ecological patterns and processes that affect sage-grouse and sagebrush distribution across a landscape. Our spatial resolution of 540-m precludes identification of understory species composition within the shrub community, or small openings within a shrub community. These characteristics can influence sagebrush and sage-grouse dynamics but are not readily and accurately detected by remote sensing across broad regions (Bradley and Mustard 2005, Peterson 2005).

Analysis of structural connectivity in landscapes is based on metrics describing physical availability and arrangement of resources (Li and Reynolds 1994, Turner et al. 2001). Landscape quantity and composition were estimated from percent area dominated by sagebrush or other land cover types. We measured configuration as the total amount of edge between patches of sagebrush and non-sagebrush land cover. We divided total edge (kilometers) by the area of sagebrush (kilometers^2) to standardize the metric relative to proportion of sagebrush because landscapes dominated by single cover types have little edge.

Leks are important for breeding although habitat characteristics at leks are less important than the surrounding landscape used for nesting and brood-rearing (Connelly et al. 1981, Connelly et al. 2000a). Conservation of sagebrush within 5 km of leks has been recommended to maintain the most locations used for nesting and early brood-rearing by nonmigratory populations, whereas 18-km radii have been recommended for migratory populations (Wakkinen et al. 1992, Connelly et al. 2000a, Holloran and Anderson 2005). Characteristics at 54-km radii may influence seasonal movements and also incorporate habitats used outside the breeding season (Swenson et al. 1987, Leonard et al. 2000). We modeled landscape patterns within 5-, 18-, and 54-km radii surrounding each grid cell in the habitat coverage using a moving window analysis (ArcMap 9.1, ESRI Redlands, CA). Thus, we changed spatial extent to examine how structure of environmental attributes changed in the hierarchical landscape within which the focal point was embedded without confounding our results due to changing variable and resolution across scales (Doak et al. 1992, O'Neill et al. 1992). We captured a range of spatial scales by varying spatial radii that might influence movement and resource use by Greater Sage-Grouse (Aldridge and Boyce 2007; Hanser and Knick, *this volume*).

SPATIAL STRUCTURE OF GREATER SAGE-GROUSE POPULATIONS

We graphed the spatial structure of Greater Sage-Grouse populations based on lek locations because populations are focused on these sites for breeding (Patterson 1952). We assumed the distribution of leks represented the spatial structure of sage-grouse populations and that our analysis of connectivity captured probability of exchange among leks. Adult sage-grouse exhibit strong fidelity to lek locations each year although subadults may disperse to neighboring leks (Gibson 1992). Broad-scale spatial arrangement of leks is relatively consistent and individual lek locations can be maintained >80 yr (Dalke et al. 1963, Smith et al. 2005).

We conducted separate graph analyses to: (1) assess connectivity of the current distribution of Greater Sage-Grouse, and (2) detect changes in connectivity from 1965–2007. The range-wide data base on location and size of Greater Sage-Grouse leks was developed in 2004 (Connelly et al. 2004) and updated by individual states and provinces for surveys conducted through 2007 (Garton et al., *this volume*). Lek locations may remain stable over long periods but leks may be relocated or new leks formed in response to population and environmental changes. We do not know what proportion of all leks was included in our range-wide sample.

Current Greater Sage-Grouse populations

We measured connectivity for the network of leks surveyed from 2003–2007 across the SGCA and within management zones. We assigned leks to management zones based on geographical location and assumed that primary movements among leks were intra-zone rather than inter-zone.

Landscape Probability of Connectivity (*PC*) (Saura and Pascual-Hortal 2007) is an index of connectivity negatively correlated with distance between nodes and isolation of populations. Higher values of connectivity indicate larger nodes or greater probabilities of exchanging individuals with other nodes. We adapted the index:

$$PC = \frac{\sum_{i=1}^{N} \sum_{j=1}^{N} a_i a_j p_{ij}^{*}}{A_L^2}$$

with sage-grouse leks (*N*) as the analysis unit in the range-wide or management zone network, *i* and *j* were individual leks, a_i and a_j were sizes of leks (measured as the average of the yearly maximum of males counted at leks), and A_L was total number of sage-grouse summed for all leks. The maximum product probability of moving between leks *i* and *j* (p_{ij}*), represents all direct and intermediate steps (p_{ij}) between a given pair of leks. The index was standardized by the range-wide $\mathrm{A_L}$ which permitted comparison among sage-grouse management zones. We used Conefor Sensinode 2.2 software to calculate connectivity indices (*PC*) (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007).

Sage-grouse populations can be connected directly by individuals moving between neighboring leks or indirectly through intermediary leks that serve as stepping stones. The probability that two leks can be connected is a function of dispersal distance. We modeled probability of dispersal between leks ($\mathrm{p_{ij}}$) as a exponential decay function (Bunn et al. 2000, Verheyen et al 2004):

$$p_{ij} = e^{-kd_{ij}}$$

where d_{ij} is the distance (km) between leks *i* and *j*, and *k* is a constant that is set so the function returns a probability of dispersing a given distance. We used a decay function, rather than a binary response, to incorporate an increasing cost associated with moving longer distances. Dispersal also includes potential costs due to crossing inhospitable terrain but a cost surface was not feasible in our study (Fall et al. 2007). Limited data on dispersal characteristics suggest that individuals were likely to move between leks *i* and *j* in equal proportions rather than as an asymmetrical flux from one density to another and that the proportion of dispersing males and females was similar (Dunn and Braun 1985). The probability of dispersal, and connectivity, between leks ranged from 0 for completely isolated leks to 1 for leks that can be reached with certainty.

Modeling dispersal in Greater Sage-Grouse is difficult because data are lacking. We defined dispersal as movements by yearlings to leks different than their maternal lek. Movement of some minimum number of animals must exceed the average distance between leks for potential genetic exchange to occur among leks and to effectively connect populations at different levels. Median dispersal distance for 12 yearling females in Colorado was 8.8 km and 7.4 km for 12 yearling males (Dunn and Braun 1985). Average distance traveled by Greater Sage-Grouse that visited more than one lek in Washington was 10.6 km for 5 males and 13.1 km for 14 females; the upper standard deviation ($P = 0.05$) of distances was 27.6 km (Schroeder and Robb 2003). We used a conservative approach to estimate an ~0.50 probability of dispersal beyond median distances reported for sage-grouse as well as to capture the upper standard deviation of distances in Washington. Setting $k = 0.1085$ yielded dispersal probabilities of 0.24 for 13.1 km, 0.38 for 8.8 km, and 0.58 for 5 km.

We calculated the importance of an individual lek for maintaining connectivity, *dPC*, as the difference in landscape connectivity (*PC*):

$$dPC(\%) = 100 \cdot \frac{PC - PC'}{PC}$$

when that lek was removed from the SGCA or management zone network (Pascual-Hortal and Saura 2006). Relative importance (higher *dPC*) of individual leks was a function of lek size (number of male sage-grouse) and position within the network (number and strength of connections to other high-ranking leks). Number of male sage-grouse counted at a lek is the primary factor in maintaining breeding populations when leks are far apart and probability is low of individuals dispersing from other leks. Location within the network becomes more important when leks are closely spaced (Keitt et al. 1997, Saura and Pascual-Horton 2007). We calculated *dPC* for each lek using range-wide connectivity (overall A_L held constant) to provide a comparable measure across the entire SGCA.

We estimated number of components in the current range-wide network of Greater Sage-Grouse leks relative to dispersal distance. A component is a spatial unit in which all leks are connected with no connections between separate components (Keitt et al. 1997, Pascual-Hortal and Saura 2006, Minor and Urban 2008). At one extreme, each individual lek represents a separate component when dispersal or exchange of individuals among leks is zero. Longer dispersal movements relative to inter-lek distances increase connectivity and decrease number of components. The network contains one component when all leks are connected. We assumed that distance between leks had behavioral or ecological significance relative to dispersal characteristics (Keitt et al. 1997). We varied dispersal distance as a binary response (rather than using a decay function) between 0 (no exchange) and 100 km. We also estimated the relative importance (*dPC*) for each component to rank their conservation significance within the sage-grouse distribution.

Temporal changes in connectivity in Greater Sage-Grouse populations

Connectivity in Greater Sage-Grouse populations (*PC*) should decrease with loss of larger leks, highly connected leks, or leks that serve as key stepping stones by connecting core regions. We used a subset of known lek locations that had been surveyed at least once within each interval from 1965–1974, 1980–1989, and 1998–2007 to avoid confounding analyses caused by increases in sampling effort that added new lek locations. Intervals were similar to periods used to estimate population trends (Connelly et al. 2004) and maximized the number of leks in the sample. Lek locations were surveyed in each interval even though sage-grouse were not uniformly observed and recorded. Therefore, connectivity could increase between intervals.

We expected that changes in connectivity (*PC*) would mirror changes in abundance of Greater Sage-Grouse across their range and within management zones (Connelly et al. 2004, Garton et al., *this volume*). Our results may be applicable to this cohort but we caution against their extrapolation to the entire Greater Sage-Grouse population because our sample was neither a random subset of surveyed leks nor stratified across the SGCA. We excluded the Colorado Plateau management zone from analyses because of low sample sizes.

We estimated average number of sage-grouse counted, number of linkages, and average distance of linkages for each lek within each temporal period and sage-grouse management zone. We also calculated the gamma (γ) index:

$$\gamma = \frac{L}{3(V-2)}$$

from the ratio of number of linkages (*L*) relative to maximum number of possible non-redundant pairwise linkages for a given number of nodes (*V*) (Forman 1995) to evaluate if linkages were lost at a higher rate than expected with leks that were abandoned.

Factors associated with lek abandonment

Analysis of the current network of leks could improve conservation strategies if fate of individual leks was related to connectivity within the network, landscape structure of sagebrush, or environmental factors related to disturbance. We assumed numbers of male sage-grouse counted and persistence of leks were directly related to landscape features surrounding the lek (Connelly et al. 2000a, Holloran and Anderson 2005). We assumed the surrounding landscape no longer supported sage-grouse if a lek was abandoned or that birds had moved to an alternate lek (Wallestad 1975, Emmons and Braun 1984). For this analysis, we followed the fate through subsequent survey intervals only for those leks where sage-grouse were known to be present in 1965-1974.

We used a discrete-time hazard model (Singer and Willett 2003) to evaluate why leks may have been abandoned or persisted through declines in Greater Sage-Grouse populations since 1965. Hazard models are based on rate or timing of an occurrence and can be used to identify the effect of predictor variables on probability of an event (Singer and Willett 2003). Hazard ratios provide a comparison of rate of change in probability relative to a unit change in predictor variables. We defined a hazard event as lek abandonment, which occurred if no sage-grouse were counted at a lek within an interval; lek persistence was based on sage-grouse presence at leks for one (1965–1974), two (1965–1974, 1980–1989), or three intervals (1965–1974, 1980–1989, 1998–2007). Leks were right-censored (an event had not occurred) if sage-grouse were present in the last period (1998–2007).

We used likelihood ratio tests to identify the combination of connectivity and environmental variables and most appropriate spatial scales that best fit the hazard function. Likelihood ratio tests are appropriate when alternate models are fit to identical data and reduced models are nested within the full model (Singer and Willett 2003). Competing models are evaluated based on comparison of deviance statistics (-2 log likelihood) to decide if additional predictor(s) improve the fit to the hazard function. Significant differences between deviance statistics are distributed as a χ^2 distribution with difference in number of estimated parameters as degrees of freedom.

We used a multi-step process for model building. We first tested the lag effect of lek connectivity (*dPC*) calculated for the previous interval on the intercept-only (no co-variate) hazard model as a time-varying predictor. We used this hazard function that included lek *dPC* as the base model to further identify environmental variables and spatial scales that influenced lek persistence.

Environmental variables characterizing habitat (landscape proportion of sagebrush), configuration (amount of habitat edge), and disturbance (proportion of burned area from 1965–2007; human footprint score [Leu et al. 2008]) were time-invariant predictors because estimates concurrent with each interval (other than area burned) were not available. Values of environmental variables were estimated for the 540-m grid cell in which the lek was located as well as at 5-, 18-, and 54-km radii. We identified the most appropriate spatial scale for sagebrush, habitat edge, burned area, and human footprint based on deviance statistics that indicated an improved model fit (χ^2, $P < 0.1$) and by excluding variables and spatial scales whose odds ratios included 1. Last, we used the single variable within each environmental class to identify the best combination fitting the hazard function by comparing deviance statistics of reduced models nested within the full environmental model.

RESULTS

STRUCTURAL PATTERN OF SAGEBRUSH LANDSCAPES

Different patterns of clustering within a landscape emerged with changes in the analysis radii (Fig. 1). Local patterns of sagebrush landcover, when mapped using a 5-km radius, were widely distributed and present across the Greater Sage-Grouse range. However, when using the larger 54-km radii, four primary regions with landscapes dominated by sagebrush land cover were evident: south central Oregon and northwest Nevada; the Owyhee region of southeast Oregon, southwest Idaho, and northern Nevada; southwest Wyoming; and south central Wyoming. Patterns of landscape fragmentation, delineated by calculating total distance of edge between sagebrush and other habitats, showed similar perspectives (Fig. 2).

CONNECTIVITY IN GREATER SAGE-GROUSE POPULATIONS

The current geographic range of Greater Sage-Grouse was represented by 5,232 active leks surveyed from 2003–2007. Eighty percent (N = 4,143) of the leks were surveyed in ≥2 yr and 50% (N = 2,596) in ≥4 yr. Number of leks surveyed within management zones ranged from 23 in the Columbia Basin to 1,495 in the Snake River Plain (Table 1). Average number of sage-grouse per lek was 20.3 ± 23.4 SD and ranged from 0.2–243.0 for the survey period. Average number of males counted per lek was highest in the Wyoming Basin and lowest in the Colorado Plateau management zone (Table 1).

The graph of Greater Sage-Grouse leks contained 37,989 potential linkages when dispersal distance was <18 km (based on results from the component analysis) (Fig. 3). Average length (km) of linkages range-wide was 16.6 ± 7.3 SD compared to average straight-line distance between nearest neighbor lek pairs of 5.9 ± 5.2 SD. Linkages were primarily within management zones; only 34 links (<0.1%) were between zones (Great Plains-Wyoming Basin 22; Snake River Plain-Southern Great Basin 3; Snake River Plain-Northern Great Basin 9).

The most important leks (*dPC*) were within core regions of the sage-grouse range (Fig. 4). The low probability of dispersal at long pair-wise distances resulted in isolation of leks and low relative importance, particularly in outlying regions of the range-wide distribution.

Relative measures of connectivity within sage-grouse management zones (standardized by total number of sage-grouse range-wide) were a function of number of leks, average number of male sage-grouse counted, and number of linkages. Average number of male sage-grouse counted accounted for a large portion of the lek's importance (Pearson's correlation r = 0.83). The Wyoming Basin had the most highly connected network of sage-grouse leks (landscape *PC*) followed by the Snake River Plain and Great Plains management zones (Table 1). Leks in the Colorado Plateau and Columbia Basin were the least connected of the management zones (Table 1).

The interaction of lek size and number of linkages in lek connectivity (*dPC*) was evident in comparisons among the Great Plains, Southern Great Basin, Snake River Plain, Northern Great Basin, and Columbia Basin. Average number of male sage-grouse counted per lek was similar among these zones and ranged from 15.3 (Columbia Basin) to 18.1 (Northern Great Basin) (Table 1). The small number of leks, longer average distance between leks, and few linkages in the Columbia Basin management zone resulted in low lek connectivity (average *dPC* = 0.005). Connectivity also was low in the Southern Great Basin (Table 1); even though average distance between leks was short, leks were arranged in widely-dispersed clusters separated by long-distances.

Number of separate components (units encompassing leks connected within components but unconnected with others) in the range-wide distribution decreased when potential dispersal distance was increased from 0 (no exchange) to 100 km (Fig. 5). Shorter dispersal distances limited linkages among leks by decreasing exchanges and resulted in larger numbers of separate components. An inflection point in the exponential relationship between a binary response in dispersal distance and number of components existed at distances between 13 and 18 km. Number of separate components increased rapidly when dispersal distances were <13 km because leks increasingly became more isolated. Most leks were connected when maximum dispersal distance was >18 km; further increases in dispersal distance resulted in proportionately less change in number of components. We used an 18-km dispersal distance in subsequent analyses for estimating connectivity among components.

Greater Sage-Grouse leks were clustered within 209 components when neighboring leks were connected by dispersal distances up to 18 km (Fig. 6). Relative importance of individual components (*dPC*), primarily reflected number of leks and total number of male sage-grouse counted within the component. Components with the highest relative importance within the sage-grouse range were distributed across the central and eastern parts of the SGCA (Fig. 6). Most components were small geographic units: 47% (N = 98) were <100 km^2 and 76% (N = 160) contained ≤10 leks (Fig. 7). Ten components were >5,000 km^2 (range 5,395–100,288 km^2) and 8 components contained >100 leks (range 143–1,139).

Temporal changes in connectivity in Greater Sage-Grouse populations

Our sample included 907 lek locations at which surveys were conducted at least once in each interval. Proportion of leks at which no sage-grouse were recorded increased from 13% in 1965–1974 to 22% in 1980–1989 and 36% in 1998–2007. Average number of sage-grouse counted at leks where sage-grouse were present was 25.0 (N = 789 leks) in 1965–1974, 19.5 (N

= 711) in 1980–1989, and 20.2 (N = 580) in 1998–2007. Relative landscape connectivity (*PC*) declined range-wide from 0.0054 in 1965–1974 to 0.0029 in 1980–1989 and 0.0025 in 1998–2007. Trends within individual sage-grouse management zones mirrored range-wide trends in this cohort (Table 2).

Landscape connectivity (*PC*) declined within sage-grouse management zones although at different rates among zones and between temporal intervals (Fig. 8). Greatest rate of declines were between 1965–1974 and 1980–1989. Relative stability in connectivity from 1980–1989 to 1998–2007 was reflected in landscape *PC* estimated for Snake River Plain, Southern Great Basin, and Wyoming Basin. Connectivity increased slightly in the Southern Great Basin and Wyoming Basin. Connectivity continued to decline between 1980–1989 and 1998–2007 in the Columbia Basin, Northern Great Basin, and Great Plains (Fig. 8). We did not evaluate changes in number of population components because most leks in our sample were widely dispersed.

Small leks with low connectivity were lost as abundance of sage-grouse declined (Fig. 9), which also changed the relative importance of persisting leks within the new network configuration (Fig. 10). Lek connectivity (*dPC*) was lower for 159 leks that were abandoned between 1965–1975 and 1980–1989 compared to 630 leks that persisted (Fig. 9). Similarly, 455 leks that persisted through all three sampling intervals had higher average abundance of sage-grouse and connectivity than 175 leks at which sage-grouse were present in 1965–1975 and 1980–1989 but were abandoned by 1998–2007 (Fig. 9). The slight decrease in average distance of links across intervals indicated that more-distant leks were abandoned. Decreased γ across intervals represented loss of a disproportionately higher number of linkages with leks that were abandoned.

Factors associated with lek abandonment

Proportion of the landscape dominated by sagebrush and amount of habitat edge were similar between leks at which sage-grouse were present in 1998–2007 compared to those that had been abandoned (Table 3). Amount of burned area and the human footprint was higher for leks that were abandoned by 1998–2007.

Lek connectivity (*dPC*) improved the fit ($\Delta_{-2LL} = 13.6$, χ^2_1, $P < 0.001$) to the hazard function without co-variates describing 271 leks that were abandoned between 1965–1975 and 1998–2007 and 546 leks that persisted (Table 4). This time-varying function was used as a base model for evaluating the subsequent contribution of environmental variables.

The most significant spatial scales for environmental predictors were proportion of sagebrush within 54 km of the lek ($P < 0.05$), proportion of burned area within 54 km of the lek ($P < 0.01$) and level of human footprint within 5 km ($P < 0.01$) (Table 4). Edge variables did not improve model fit ($P_{selection} = 0.1$) at any spatial scale and were not considered in subsequent model development.

The best model describing probability that a lek with sage-grouse present in 1965–1974 would be abandoned by 1998–2007 included proportion of area burned and level of human footprint (Table 5). The full environmental model including sagebrush did not further improve model fit ($\Delta_{-2LL} = 0.85$; $P > 0.1$). In the final hazard model (Table 6), probability of abandonment increased by 30% for each unit decrease in lek connectivity (*dPC*) during the previous interval [100 x (hazard ratio - 1)], by 30% for each unit increase in human footprint within 5 km of a lek, and by 800% for each unit increase in fire within 54 km of a lek (Table 5).

DISCUSSION

Connectivity analysis provides a conceptual framework for understanding dynamics of landscapes and wildlife (Schumaker 1996, Keitt et al. 1997, Ricotta et al. 2000, Crooks and Sanjayan 2006) but has not been applied previously to sagebrush systems. Spatial structure of sagebrush landscapes and Greater Sage-Grouse populations can reveal underlying processes that have led to long-term trajectories of habitat loss and population declines. These analyses also can provide a foundation for future conservation strategies by identifying critical locations necessary to maintain range-wide and regional networks of interacting populations of Greater Sage-Grouse.

STRUCTURAL PATTERN OF SAGEBRUSH LANDSCAPES

Primary structural characteristics of landscapes that interact with underlying processes can be measured by the quantity, composition, and configuration of land-cover types (Urban et al. 1987, Turner 1989, Turner et al. 2001). Sagebrush dominates >500,000 km^2 of the SGCA and landscapes are arranged in a diverse array of patterns that vary with spatial scale (Leu and Hanser, *this volume*). The primary challenge to modeling sagebrush landscapes was to reduce this variation to metrics that: (1) capture the primary characteristics of landscape structure, (2) identify similar or repetitive patterns, and (3) provide meaningful measures to relate to the dynamics of wildlife populations (Cantwell and Forman 1993). Percent sagebrush (quantity and composition) and amount of edge with other land-cover types (configuration) are related to disturbance and presence of the invasive annual cheatgrass (*Bromus tectorum*) (Knick and Rotenberry 1997), to distribution and population dynamics of passerine birds (Vander Haegen et al. 2000, Hamer et al. 2006, Vander Haegen 2007, Knick et al. 2008), and to presence and persistence of Greater Sage-Grouse (Aldrich and Boyce 2007; Doherty et al. 2008; Hanser and Knick, *this volume*). Numerous metrics have been developed (Gustafson 1998, Li and Wu 2004), but these basic attributes structuring sagebrush landscapes may be the primary characteristics that affect vegetation and disturbance dynamics, and wildlife responses.

Management and monitoring in sagebrush systems have focused on successional or state-and-transition dynamics that occur over time within a location but not across space (Bestelmeyer et al. 2003, West 2003a, Crawford et al. 2004). Spatial variation traditionally has been regarded as a consequence of different states of individual locations along similar vegetational trajectories with the assumption that locations function independently rather than interacting as a mosaic within a landscape (Allen-Diaz and Bartolome 1998, West 2003b, Briske et al. 2005). Yet, many processes, such as fire or invasion of non-native plant species, are inherently spatial, and they influence structure of current sagebrush landscapes as well as future dynamics of these systems (Peters et al. 2006, Davies and Sheley 2007).

Spatial attributes of land cover influence spatial and temporal stability and contribute to a system's resilience and resistance to change (Shugart 1998). Sagebrush systems in the western portion of the SGCA, including the Columbia Basin, Northern Great Basin, Southern Great Basin, and Snake River Plain management zones, have two primary endpoints that are resistant to further change (Hemstrom et al. 2002; Miller et al., *this volume*). A landscape dominated by sagebrush communities containing an understory of native grasses and forbs represents one stable endpoint because disturbance historically has been at small spatial scales and occurred at longer intervals than the period required for recovery (Laycock 1991; Baker, *this volume*). Cheatgrass-dominated grasslands without sagebrush represent an undesirable endpoint that remains stable because recurrent fires prevent recolonization by sagebrush and other native forbs and grasses (Young and Evans 1973, d'Antonio and Vitousek 1992, Chambers et al. 2007). A cheatgrass-dominated landscape persists because small islands of sagebrush are unlikely to remain as fire frequency increases (Brooks et al. 2004, Link et al. 2006). An intermediate mosaic of patches dominated by sagebrush and cheatgrass is inherently unstable. Small, dispersed patches of sagebrush within a larger landscape dominated by sagebrush can provide seed sources important for natural recolonization (Longland and Bateman 2002) or as building blocks for restoration (Wisdom et al. 2005b; Meinke et al., in press). Alternatively, increases in frequency, intensity, or spatial extent of disturbance can prevent extensive recovery and dominance of sagebrush. In many landscapes, cheatgrass becomes the dominant land-cover and return to sagebrush is unlikely (Billings 1990). Thus, basic structural attributes of composition, quantity, and arrangement expressed at multiple spatial scales are primary factors that affect future trajectories in sagebrush landscapes.

Landscape structure also influences the ability of an animal to move across a landscape. A single habitat patch can spread across an entire landscape when the proportion exceeds 60% in randomly-generated landscapes (O’Neill et al. 1988). The mapped distribution of sagebrush land cover >60% indicate how movements restricted by habitat configuration might be facilitated at one spatial scale but constrained at others by the hierarchical organization of sagebrush landscapes.

Critical thresholds where habitat amount becomes less important than habitat arrangement vary with dispersal, habitat requirement, mobility, and vagility characteristics of a species (Andrén 1994, With and Crist 1995, Flather and Bevers 2002). Configuration of land cover may be less important to mobile species, such as sage-grouse, because small amounts of clumped habitat distributed across a landscape can be exploited and serve as population sources

(With and King 2001). Agriculture is the primary factor influencing sagebrush landscapes in the Great Plains management zone (Connelly et al. 2004) and edge between land-cover types, rather than proportion of sagebrush in the landscape, is the dominant feature. Yet, landscape connectivity (*PC*) of current sage-grouse populations in this matrix of agriculture, grassland, and sagebrush in the Great Plains was similar to other management zones. In contrast, connectivity of sage-grouse populations was lower and populations have become increasingly isolated in the agricultural landscape of the Columbia Basin where quantity of sagebrush may be lower, available patches more widely dispersed, and the human footprint most intensive (Leu and Hanser, *this volume*).

CONNECTIVITY IN GREATER SAGE-GROUSE POPULATIONS

Modeling functional relationships of Greater Sage-Grouse to their sagebrush habitat is challenging because different characteristics are important at different spatial scales (Aldridge and Boyce 2007, Aldridge et al. 2008). Habitat availability also varies by season and across regions (Connelly et al. 2000a, Doherty et al. 2008). Fine-scale attributes of sagebrush habitats may influence within-season movements, such as choice of nesting or brood-rearing locations, and vital rates including survival and productivity (Connelly et al. 2000a, Crawford et al. 2004). Highly mobile individuals tend to collapse landscape heterogeneity (Kotliar and Wiens 1990, With 1994); sage-grouse moving between seasonal ranges may be more sensitive to the broader-scale matrix and traverse areas that do not contain suitable habitats (Connelly et al. 1988, Leonard et al. 2000). A broad diversity of habitat configurations and environmental stressors are encompassed within annual ranges of individual sage-grouse populations as well as within the full geographic range of the species (Schroeder et al. 1999, Leonard et al. 2000). Thus, sagebrush landscapes may have multiple structures that vary in importance from the perspective of sage-grouse.

Identification of appropriate spatial scale(s) is important to effectively model habitat associations or track species responses to changes in their habitat (Wiens 2002). Many shrubland birds are sensitive to landscape components at spatial scales much larger than individual home ranges (Vander Haegen et al. 2000, Knick and Rotenberry 2002). Large-scale characteristics within surrounding landscapes influenced locations selected by Greater Sage-Grouse in Alberta (1-km^2; Aldridge and Boyce 2007) and Wyoming (>4-km; Doherty et al. 2008). Probability of persistence of sage-grouse populations in a range-wide comparison of historical and current distributions was greatest in areas containing >30% sagebrush within a 30-km radius of a given point and with a human density <4/km^2 (Aldridge et al. 2008). In our study, fire within a 54-km radius and human activity within 5 km of a lek influenced the probability of persistence over 40 yr.

Connectivity in current populations of Greater Sage-Grouse

We delineated the spatial arrangement of Greater Sage-Grouse populations as a network of connected leks. We modeled connections between lek pairs as straightline distances although, in reality, movements are directed by patch characteristics and permeability of boundaries between patches (Wiens et al. 1993). We do not know how sage-grouse move through or over a landscape because radio-telemetry studies have emphasized daily or seasonal point locations of individuals rather than continuous movements during dispersal or seasonal migration. Our linkages estimated the minimum distance that individuals would have to traverse between leks or population components.

The range-wide distribution of Greater Sage-Grouse was dominated by a small set of core components each containing a large number of leks and encompassing >5,000 km^2. Numerous small components were interspersed in between core regions and at the edges of the range. Populations of sage-grouse may have a spatial structure similar to Capercaillie (*Tetrao urogallus*), a forest grouse that is broadly distributed throughout central Europe and associated with late successional coniferous forests. Population dynamics of Capercaillie in northern Europe are primarily affected by amount of nonforested area and differences in forest quality at large (100 km^2) spatial scales. In contrast, fragmented forest distributions throughout central Europe have resulted in a metapopulation structure in which connectivity is important to maintaining individual Capercaillie populations (Storch and Segelbacher 2000, Storch 2003). Population dynamics of sage-grouse within core components similarly may depend on amount and quality of sagebrush or level of disturbance. Sage-grouse populations distributed in more isolated components at the edge of the range-wide distribution may depend on dispersal from connecting leks.

Metapopulation theory (Gilpin and Hanski 1991, Hanski 1994) suggests that long-term persistence of sage-grouse could be maintained by equilibria between colonizations and extinctions among independently functioning components. Alternately, source-sink models predict that individuals dispersing from larger, more productive regions would maintain satellite populations that are not self-sustaining because of low recruitment (Pulliam 1988). Under either hypothetical population model, connectivity and ability for spatially structured populations to exchange individuals are important conservation concerns; little is known about either phenomenon in Greater Sage-Grouse. If distance separating leks resulted from ecological forces

(Keitt et al. 1997), the inflection of component number relative to dispersal distance suggests that dispersals up to 18 km occur with sufficient frequency to maintain exchanges of individuals within average constellations of leks within the network.

We do not know the extent to which gene flow is captured in the linkages (Oyler-McCance et al. 2005) and modeling distance or multi-generational dispersal derived from genetic analysis may delineate components differently. Genetic evidence indicates that exchange of individuals has not been inhibited through the core regions (Oyler-McCance and Quinn, *this volume*). However, increasing isolation of components at the fringes of the sage-grouse range decreases the probability of dispersal to these regions. Sage-grouse in the state of Washington and in the Mono Lake region, which straddles the Nevada-California border, have been genetically isolated from other populations (Benedict et al. 2003, Oyler-McCance et al. 2005). Our connectivity analysis suggests that isolation by distance, impermeable land cover, or topographical barriers could further increase the potential for loss of other population components.

Temporal changes in connectivity in Greater Sage-Grouse populations

Contraction of the geographic range occupied by Greater Sage-Grouse (Schroeder et al. 2004) reflected decreasing connectivity within the spatial network of leks, leading to their isolation and loss. Range-wide, Greater Sage-Grouse populations declined at an annual rate of 3.5% from 1965 to 1985 and 0.4% from 1986 to 2003 (Connelly et al. 2004). Connectivity among sage-grouse populations in our lek cohort declined across intervals (1965–1974, 1980–1989, and 1998–2007) primarily because a lower proportion of surveyed leks were active and fewer male sage-grouse were counted at remaining leks. Sage-grouse in some locations may have moved to alternate leks following disturbance (Wallestad 1975, Emmons and Braun 1984, Remington and Braun 1991) although this is unlikely for a large proportion of all leks abandoned within our cohort and in range-wide surveys (Connelly et al. 2004). Decreased indices of connectivity also reflected a greater loss of linkages between leks than expected on the basis of changes in maximum number of linkages possible in each interval.

Connectivity within sage-grouse management zones tracked population trends and changes in lek characteristics, which generally were similar to range-wide estimates although magnitude of change and temporal pattern varied (Connelly et al. 2004). However, decreases in connectivity despite more stable trend estimates (Connelly et al. 2004) indicate that isolation is continuing and is most severe within the Columbia Basin management zone.

Lek connectivity (*dPC*) was a strong predictor of persistence to the next survey interval. Small decreases in lek connectivity resulted in large increases in probability of lek abandonment. Abandoned leks had fewer male sage-grouse than leks that persisted and had lower importance reflecting position within the network in the interval(s) prior to abandonment. However, connectivity among persisting leks declined because abandoned leks also tended to have more linkages with other leks.

Lek persistence was not strongly related to land cover of sagebrush or configuration. All active leks from 1965–1974 were in areas currently dominated by sagebrush. Sagebrush land cover dominated 70% of the surrounding landscape within 5 km of the lek and almost 50% within 54 km. Area burned and human-footprint score, which may estimate landscape quality from the perspective of sage-grouse, were the primary factors influencing fate of leks. Sage-grouse avoid burned areas in sagebrush landscapes because habitat characteristics important for nesting, brood concealment, and food are destroyed by fire and have slow recovery rates (Connelly et al. 2000b; Beck et al., in press). Fire also facilitates invasion by cheatgrass and other non-native plant species (Brooks et al. 2004). Fires, prescribed and natural, have long-term effects (>10 yr) and sage-grouse may continue to avoid burned areas even after sagebrush has recovered (Nelle et al. 2000). Frequent, large fires that resulted in loss of sagebrush were more likely to lead to extinction of simulated sage-grouse populations than small fires occurring at low frequencies across the landscape (Pedersen et al. 2003). In our analysis, small increases in the amount of area burned, particularly in the 54-km region surrounding a lek, had a large influence on the probability of lek abandonment.

Extensive conversion of sagebrush to agriculture within a landscape has decreased abundance of sage-grouse in many portions of their range (Swenson et al. 1987, Leonard et al. 2000, Smith et al. 2005, Aldridge and Boyce 2007, Aldridge et al. 2008). Negative influences of other human disturbances, such as energy development, on sage-grouse populations also have been documented (Doherty et al. 2008; Naugle et al., *this volume*). The human-footprint score in our study assessed the physical and ecological effect of urbanization, infrastructure development (roads and powerlines), agriculture, and energy development (Leu et al. 2008). We were unable to identify a specific source of human disturbance because the score represented a summed influence of all anthropogenic features. The cumulative effect of human activities may have a greater influence on persistence of sage-grouse populations than single land uses.

CONSERVATION IMPLICATIONS

Connectivity analysis provided a framework for quantifying the range-wide pattern of sage-grouse populations that integrated landscape arrangement of habitat and populations, population dynamics within components, and exchange of individuals among leks and components. Our analysis of spatial patterns in sage-grouse populations reflects processes such as dispersal and response to changes in their environment that can be incorporated into range-wide and regional conservation strategies.

The environmental matrix on which the network of sage-grouse leks were superimposed also was undergoing fragmentation, loss, and altered disturbance regimes (Knick et al. 2003, Wisdom et al. 2005a). Environmental factors, rather than stochastic events within the population, likely are the influences on population trend for Greater Sage-Grouse. Extinction currently is more probable than colonization for many sage-grouse components because of their low abundance and isolation coupled with fire (Pedersen et al. 2003; Baker, *this volume*; Miller et al., *this volume*) and human influence (Leu and Hanser, *this volume*). Population declines will track habitat loss or environmental changes, and extinctions occur when a species is unable to find suitable habitat within its dispersal distance (Thomas 1994). Thus, conservation strategies for species like sage-grouse should focus on conserving existing habitats, preserving large areas or connected networks of populations or habitat patches, and creating or restoring habitat within the species dispersal capabilities (Thomas 1994). Conserving smaller, more isolated components might depend on identifying or creating suitable habitat or connecting leks within 18 km that could function as intermediary islands or stepping stones for migrating individuals.

Conservation of declining or endangered populations with limited resources involves assessing which populations or regions are critical to range-wide persistence. A primary concern in reviewing whether listing Greater Sage-Grouse under the US Endangered Species Act was warranted involved evaluating whether the species could persist 100–200 yr into the future

(United States Department of the Interior 2005). Thus, it may be important to identify regions where Greater Sage-Grouse are likely to persist and whether we can focus conservation actions on specific regions or components to avoid global extinction. Our hierarchical analytic structure delineated leks nested within components, and components within the range-wide distribution. We then ranked each lek or component by a connectivity index (*dPC*) to prioritize its importance based on abundance of sage-grouse and location within the network. These rankings can suggest allocation of resources based on a relative measure of importance for maintaining a lek or component within the network. A strategy of no net loss (Stiver et al. 2006) may not be possible because altered fire regimes, spread of non-native plants, climate change, and human land use present challenges to maintaining and restoring sagebrush habitats (Miller et al., *this volume*; Pyke, *this volume*).

The highest-ranked sage-grouse components for maintaining connectivity generally aligned with dominant patterns of sagebrush distribution. However, the variables that we used to represent sagebrush cover and fragmentation in the landscape did not influence lek persistence. Rather, landscape disturbance, measured by amount of fire since 1965 and level of human activity, was the primary factor affecting lek persistence. Of the major components delineated by connectivity, human land use in the form of energy development is high for the Powder River, south central, and southwestern Wyoming. Fire and conversion of sagebrush to cheatgrass-dominated landscapes is a concern for important sage-grouse components in the western part of their range. Our results suggest that restoration of sagebrush will not be as successful in increasing the viability of sage-grouse populations long-term if those areas also are heavily influenced by human activities or fire.

We do not fully understand whether results from this cohort of leks are transferable to all leks within the sage-grouse range. We recommend that connectivity be monitored not only by counting sage-grouse on currently identified leks, but by conducting spatially extensive surveys to detect newly established leks, re-use of traditional locations, or those relocated to new sites (Connelly et al. 2003).

Over 5,000 leks currently are surveyed each year across the range of Greater Sage-Grouse. Tracking changes in connectivity of these leks can complement trend estimates and provide valuable information for conserving sage-grouse. The number of populations and active leks may further decrease in many of the management zones because fire continues to be a dominant disturbance across much of the sage-grouse range (Baker, *this volume*). Human land use also is pervasive and broad-scale creation of infrastructure (highways, transmission corridors, etc.) coupled with local-scale energy development (Leu et al. 2008, Knick et al., *this volume*) are likely to have strong influence at multiple scales on sagebrush landscapes that will be reflected by changes in sage-grouse populations and their connectivity.

ACKNOWLEDGMENTS

The Wilburforce Foundation and the project *Analysis and conservation prioritization of landscape connectivity in Nevada* provided the impetus for our application of connectivity concepts to Greater Sage-Grouse populations. We appreciate insights by C. W. Carroll, D. S. Dobkin, E. Fleishman, M. Leu, B. H. McRae, and N. H. Schumaker in developing this study. We consulted with B. S. Cade and L. Bond for statistical assistance. We thank the Western Association of Fish and Wildlife Agencies and members of the Greater Sage- and Sharp-tailed Grouse Technical Committee for sharing data on lek counts and location. J. W. Connelly critiqued our presentation of sage-grouse ecology. J. A. Bissonette, D. S. Dobkin, E. Fleishman, M. Leu, N. H. Schumaker; students and faculty in the College of Natural Resources, University of Idaho; and the Colorado Division of Wildlife reviewed the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

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TABLE 1. Average number of male sage-grouse counted at leks (based on surveys from 2003–2007) and connectivity indices (*dPC*) for Greater Sage-Grouse range-wide and within management zones. Lek *dPC* measures the change in landscape connectivity when individual leks were removed from the network.

Sage-grouse management zone		Sage-grouse leks			Links among leks		
		N	Average male count [a]	Average lek *dPC* [a]	N	Average distance (kilometer) [a]	Average minimum distance (kilometer) [a]
I	Great Plains	1,252	17.3B	0.021B	7,759	11.1B	5.8B
II	Wyoming Basin	1,397	29.5A	0.062A	9,046	11.2B	5.7B
III	Southern Great Basin	448	16.2B	0.011B	1,358	9.2C	5.9B
IV	Snake River Plain	1,495	16.9B	0.029A	14,430	10.4B	4.3C
V	Northern Great Basin	565	18.1B	0.031B	4,814	10.5B	4.5C
VI	Columbia Basin	23	15.3B	0.005C	56	12.5A	9.5A
VII	Colorado Plateau	52	5.7C	0.002D	492	8.6C	2.9C
	Range-wide	5,232	20.3	0.034	37,955	10.7	5.2

[a] Management zones having different letters have significantly different ($P < 0.05$) values in a univariate analysis of variance: average number of individuals counted ($F_{6,5225} = 54.1$, $P < 0.001$), average lek *dPC* ($F_{6,5216} = 109.0$, $P < 0.001$), and average pair-wise distance between leks ($F_{6, 37,948} = 81.0$, $P < 0.001$)

TABLE 2. Change in average number of male Greater Sage-Grouse counted at leks and connectivity (*dPC*) among leks during surveys conducted in 1965–1974, 1980–1989, and 1998–2007. The gamma (γ) function is the ratio of number of linkages relative to maximum number of possible non-redundant pairwise linkages for a given number of leks.

			Greater Sage-Grouse				
Sage-grouse management zone		Year	Leks N	Average male count	Average lek *dPC*	Links among leks N	Links among leks γ
I	Great Plains	1965–1974	118	24.3	1.27	484	1.39
		1980–1989	109	18.4	1.26	414	1.29
		1998–2007	69	9.6	1.20	196	0.98
II	Wyoming Basin	1965–1974	213	23.7	0.59	1,122	1.77
		1980–1989	194	14.1	0.59	828	1.44
		1998–2007	182	15.5	0.58	734	1.36
III	Southern Great Basin	1965–1974	139	18.8	0.94	500	1.22
		1980–1989	129	15.2	0.89	420	1.10
		1998–2007	107	14.0	0.88	258	0.82

IV	Snake River Plain	1965–1974	259	20.5	0.55	1,488	1.93
		1980–1989	234	15.0	0.53	1,434	2.08
		1998–2007	182	11.5	0.50	838	1.55
V	Northern Great Basin	1965–1974	41	22.2	2.96	100	0.85
		1980–1989	29	16.7	3.13	56	0.69
		1998–2007	30	13.8	2.79	62	0.74
VI	Columbia Basin	1965–1974	18	24.8	8.68	60	1.25
		1980–1989	16	16.0	8.44	56	1.33
		1998–2007	10	10.4	7.87	22	0.92

TABLE 3. Univariate comparisons (two-sample t-test) of environmental variables at known leks where Greater Sage-Grouse were present (N = 580) compared to leks at which male sage-grouse were present in either 1965–1974 or 1980–1989 but absent by 1998–2007 (N = 326). Values of environmental variables were estimated for the grid cell in which leks were located, and for 5-, 18-, and 54-km buffer zones surrounding the lek.

		Greater Sage-Grouse leks			
	Buffer (kilometer)	Present 0 ± SE	Abandoned 0 ± SE	t =	P =
Sagebrush (%) [a]	Lek	74.3 ± 0.02	73.0 ± 0.02	0.43	0.67
	5	69.4 ± 0.01	66.7 ± 0.02	1.19	0.23
	18	57.0 ± 0.01	57.9 ± 0.01	0.83	0.41
	54	46.7 ± 0.01	48.8 ± 0.01	1.60	0.11
Burned (%) [a]	Lek	10.0 ± 0.01	16.3 ± 0.02	2.77	0.006
	5	10.1 ± 0.01	14.4 ± 0.02	2.70	0.007
	18	9.3 ± 0.01	12.3 ± 0.01	2.52	0.01
	54	8.9 ± 0.01	11.3 ± 0.01	2.66	0.008
Edge [b]	5	1.9 ± 0.08	2.0 ± 0.12	0.93	0.35

	18	2.1 ± 0.06	2.1 ± 0.09	0.12	0.90
	54	2.2 ± 0.05	2.2 ± 0.08	0.49	0.62
Human footprint [c]	Lek	4.3 ± 0.06	4.4 ± 0.08	1.10	0.27
	5	4.1 ± 0.04	4.3 ± 0.06	2.70	0.007
	18	4.0 ± 0.04	4.2 ± 0.06	2.31	0.02
	54	4.0 ± 0.03	4.1 ± 0.04	2.72	0.007

[a] Data were arcsine-transformed.

[b] Amount of edge was transformed relative to % sagebrush in the landscape.

[c] The human footprint was a cumulative score ranging from 0 (no effect) to 10 (maximum) derived from multiple submodels quantifying anthropogenic effects (Leu et al. 2008).

TABLE 4. Candidate predictor variables, spatial scale, and likelihood ratio tests to calculate fit to hazard models predicting lek abandonment. Lek connectivity was first tested against the model without covariates. The model including lek connectivity was then used to test subsequent models to identify most significant spatial scale within environment categories. Likelihood ratios were the difference in deviance statistics (-2LL) between competing models. Hazard ratios (presented with 95% CI) estimate the relative change in an event (lek persistence) for each unit change in value of a predictor.

	Buffer [a]	-2LL	Likelihood ratio [b]	Hazard ratio	95% CI
Model without co-variates		1,387.90			
Lek connectivity *dPC*		1,374.30	0.00	0.35	0.19–0.66
Sagebrush (%)	Lek	1,374.25	-0.05	0.97	0.71–1.31
	5	1,374.29	-0.06	0.98	0.59–1.63
	18	1,371.94	-2.36	1.55	0.88–2.71
	54	1,370.21	-4.089*	1.94	1.02–3.71
Fire (%)	Lek	1,366.40	-7.90**	1.71	1.19–2.46
	5	1,366.61	-7.68**	2.06	1.26–3.38
	18	1,366.90	-7.40**	2.61	1.34–5.11
	54	1,364.43	-9.87**	4.82	1.84–12.60
Edge [c]	5	1,374.24	-0.06	0.99	0.93–1.06
	18	1,373.89	-0.41	0.97	0.89–1.06
	54	1,373.02	-1.28	0.94	0.84–1.05
Human footprint	Lek	1,371.85	-2.49	1.08	0.98–1.19
	5	1,365.84	-8.46**	1.21	1.06–1.37
	18	1,368.47	-5.83*	1.18	1.03–1.35

	54	1,368.69	-5.61*	1.23	1.04–1.47

[a] Values of environmental variables were estimated for the grid cell in which leks were located, and for 5-, 18-, and 54-km buffer zones surrounding the lek.

[b] * = P <0.05, ** = P <0.01; significance level of likelihood ratio test for $H_o:\beta_{dPC}=\beta_{dPC}+\beta w_1=0$.

[c] Edge was not calculated for the cell in which leks were located.

TABLE 5. Evaluation of competing models combining environmental variables that best fit the hazard function describing probability of lek abandonment from 1965–1974 to 1998–2007. Likelihood ratios were the difference in deviance statistics (-2 LL) between candidate models and the base hazard function including the time-varying predictor for lek connectivity (*dPC*). Environmental variables (Table 4) used in candidate models were % sagebrush and % burned area within a 54-km buffer of a lek and human footprint score within 5 km.

Candidate model	-2LL	Likelihood ratio
Lek *dPC* + sagebrush$_{54km}$ + fire$_{54km}$	1,364.18	-10.12
Lek *dPC* + sagebrush$_{54km}$ + human footprint$_{5km}$	1,358.11	-17.24
Lek *dPC* + fire$_{54km}$ + human footprint$_{5km}$	1,348.74	-25.56
Lek *dPC* + fire$_{54km}$ + human footprint$_{5km}$ + sagebrush$_{54km}$	1,347.88	-26.42

TABLE 6. Final hazard function identified from candidate models (Table 5) describing the probability of lek abandonment by 1980–1988 or 1998–2007. Lek connectivity (*dPC*) was a time-varying predictor included in the base model (Table 4). Environmental variables were % fire within 54-km of a lek and human footprint score within 5 km. Hazard ratios (presented with 95% CI) estimate the relative change in an event (lek persistence) for each unit change in value of a predictor.

Variable	Coefficient	SE	Hazard ratio	95% CI
Lek connectivity *dPC*	-1.18	0.43	0.31	0.16–0.58
$\text{Fire}_{54\text{km}}$	2.12	0.52	9.00	3.25–24.95
$\text{Human footprint}_{5\text{km}}$	0.27	0.07	1.31	1.15–1.50

FIGURE LEGENDS

FIGURE 1. Percent of the landscape dominated by sagebrush within a 5-km (top) and 54-km (bottom) radius of each 0.5 km grid cell.

FIGURE 2. Small- and large-scale fragmentation of sagebrush habitats represented by the total distance of edge between sagebrush and other land-cover types within a 5-km (top) and 54-km (bottom) radius of each 0.5 km grid cell.

FIGURE 3. Distribution of current (2003–2007) Greater Sage-Grouse leks. Populations at leks were connected if the straightline distance to neighbors was <18 km. (Sage-grouse management zones are in Table 1).

FIGURE 4. Importance of individual leks in maintaining connectivity in the range-wide distribution of Greater Sage-Grouse. Lek *dPC* measures change in landscape connectivity that results when a lek is removed from the network. Higher *dPC* values reflect larger numbers of sage-grouse at a lek and greater connectivity within the network.

FIGURE 5. Number of components within the Greater Sage-Grouse range relative to dispersal distances. Components are spatially separated units in which leks are connected within but not among components. Distances between 13 and 18 km represent a threshold at which decreasing potential dispersal distance decreases the connections among leks and increases the number of components.

FIGURE 6. Location of 209 components and their importance (*dPC*) in maintaining connectivity across the range-wide distribution of Greater Sage-Grouse. Number and spatial arrangement of components was evaluated for a dispersal distance of 18 km.

FIGURE 7. Size distribution of components (spatially separated units in which leks are connected within but not among components) relative to number of leks (a) and component area (b). Eight components contained >100 leks and 10 were >5,000 km^2.

FIGURE 8. Change in landscape connectivity (*PC*) within sage-grouse management zones between 1965–1974, 1980–1989, and 1998–2007. Landscape *PC* is a relative index. Relative pattern but not absolute relationships are comparable among management zones.

FIGURE 9. Connectivity dynamics within a cohort of 789 leks surveyed in 1965–1974, 1980–89, and 1998–2007. Sage-grouse were present at all leks in 1965–1974.

FIGURE 10. Change in connectivity (*dPC*) of individual leks and connections within a network of leks in central Washington over survey intervals from 1965–1974, 1980–1989, to 1998–2007. Ellipses enclose leks that will be abandoned by 1998–2007.

Figure 1.

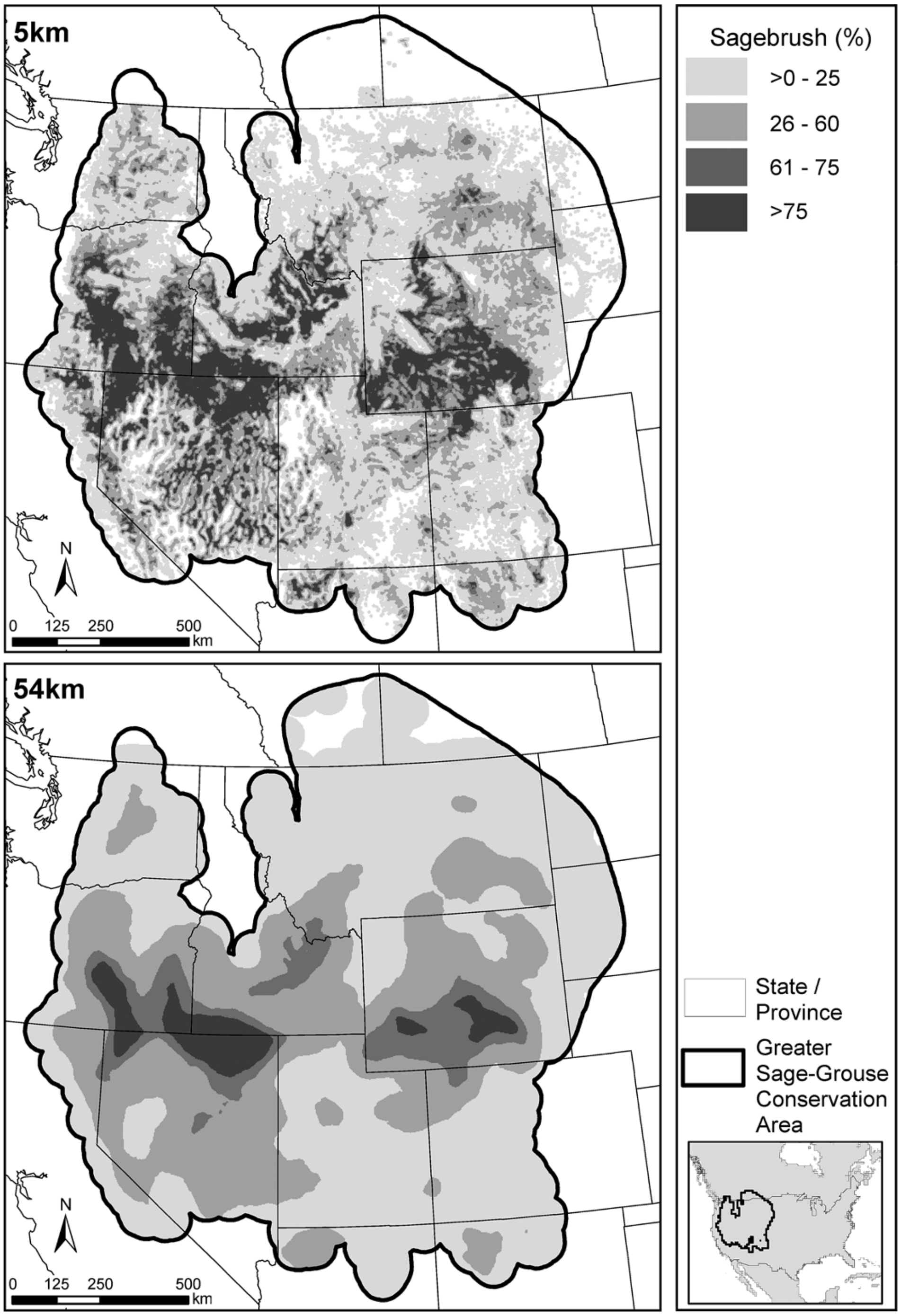

5km
54km
N
0 125 250 500
km
Sagebrush (%)
>0 - 25
26 - 60
61 - 75
>75
State / Province
Greater Sage-Grouse Conservation Area

Figure 2.

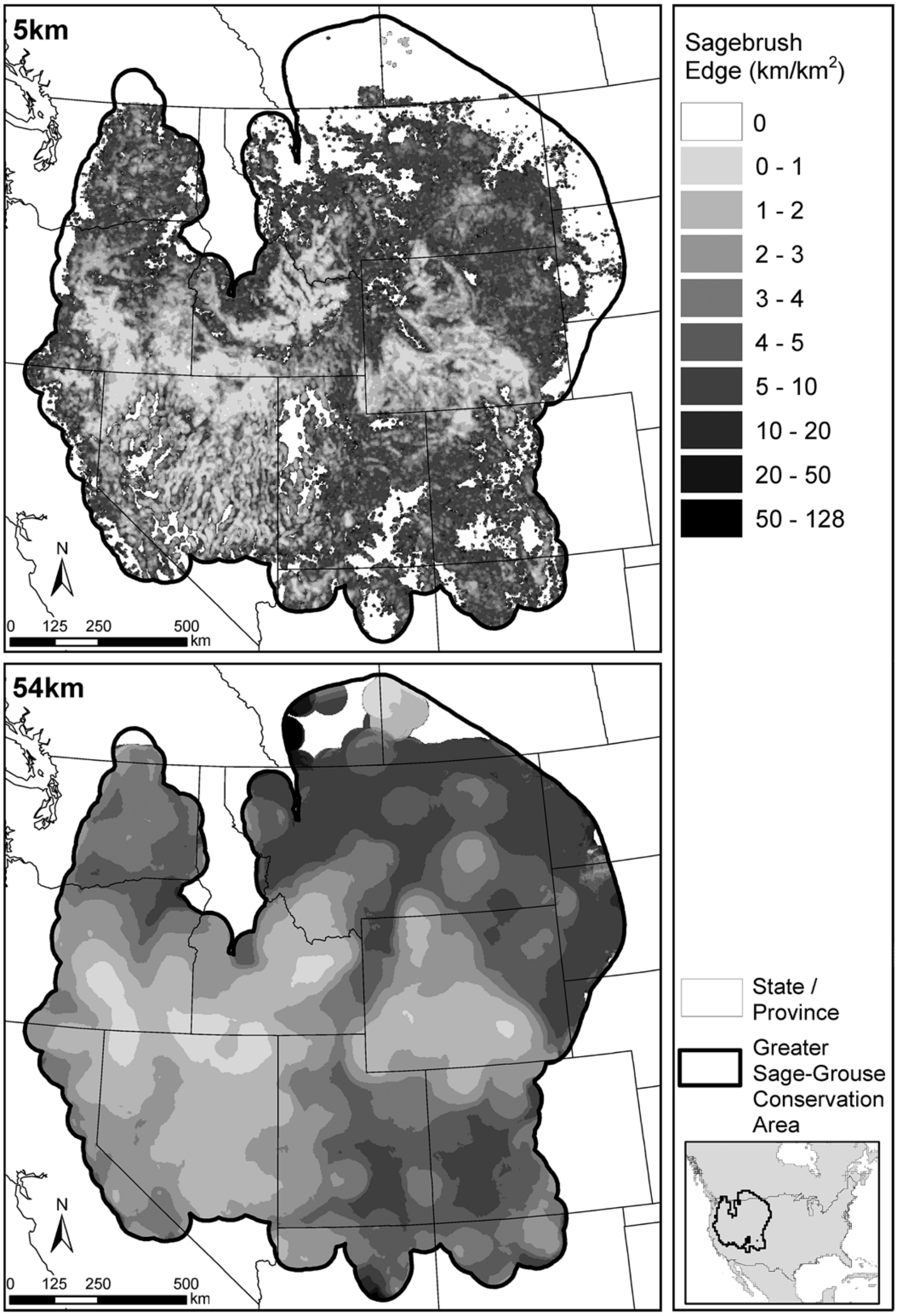
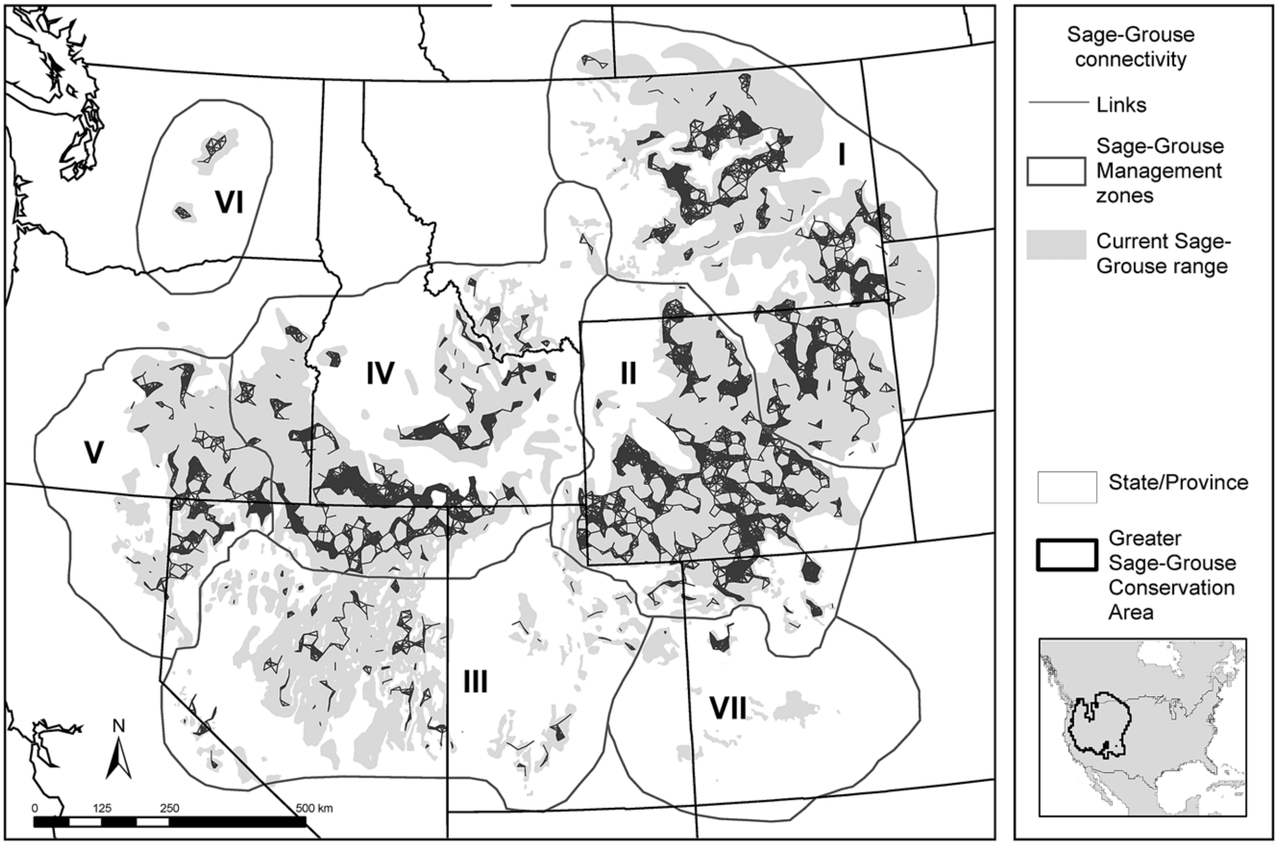

5km
54km
Sagebrush Edge (km/km²)
0
0 - 1
1 - 2
2 - 3
3 - 4
4 - 5
5 - 10
10 - 20
20 - 50
50 - 128
State / Province
Greater Sage-Grouse Conservation Area
N
0 125 250 500 km

Figure 3.



Sage-Grouse connectivity
Links
Sage-Grouse Management zones
Current Sage-Grouse range
State/Province
Greater Sage-Grouse Conservation Area
I
II
III
IV
V
VI
VII
N
0
125
250
500 km

Figure 4.

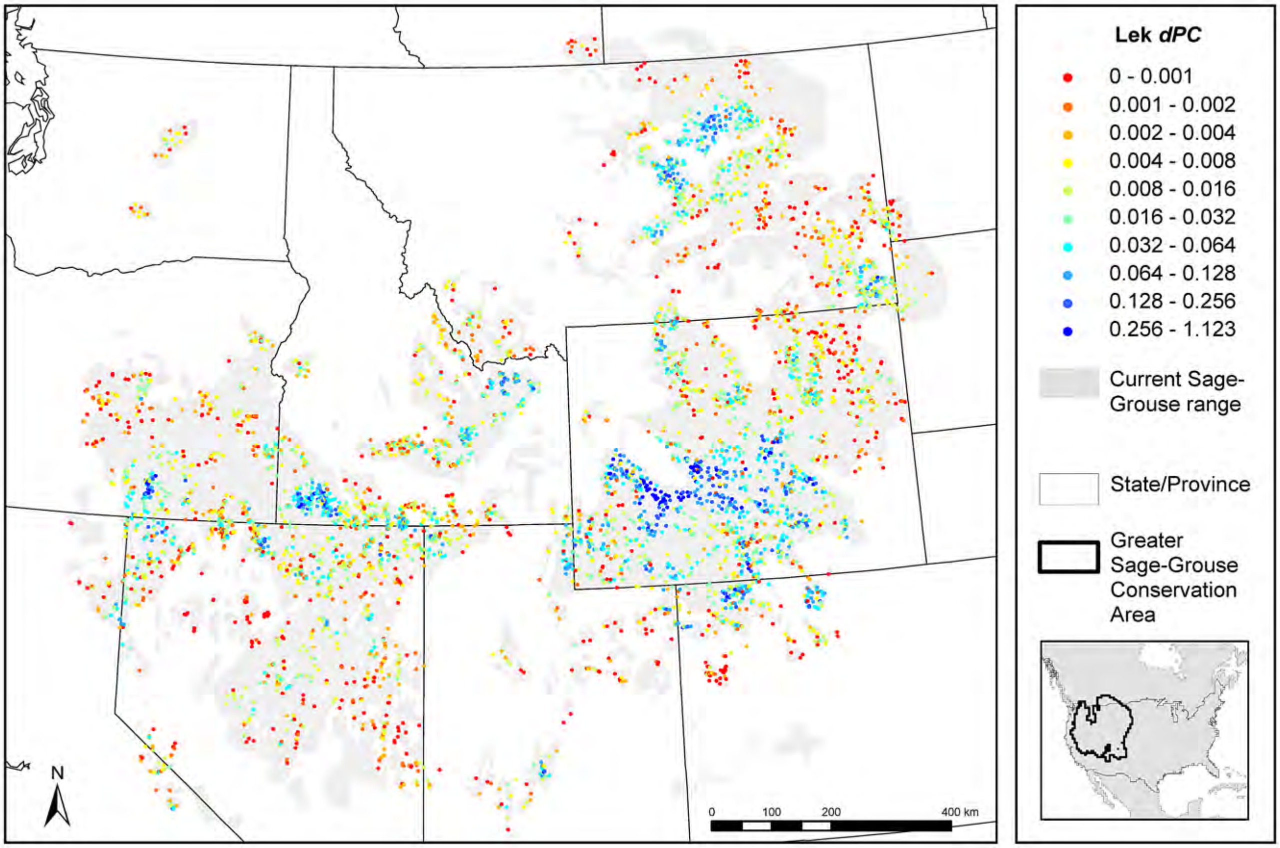

Lek dPC
0 - 0.001
0.001 - 0.002
0.002 - 0.004
0.004 - 0.008
0.008 - 0.016
0.016 - 0.032
0.032 - 0.064
0.064 - 0.128
0.128 - 0.256
0.256 - 1.123
Current Sage-Grouse range
State/Province
Greater Sage-Grouse Conservation Area
N
0
100
200
400 km

Figure 5.

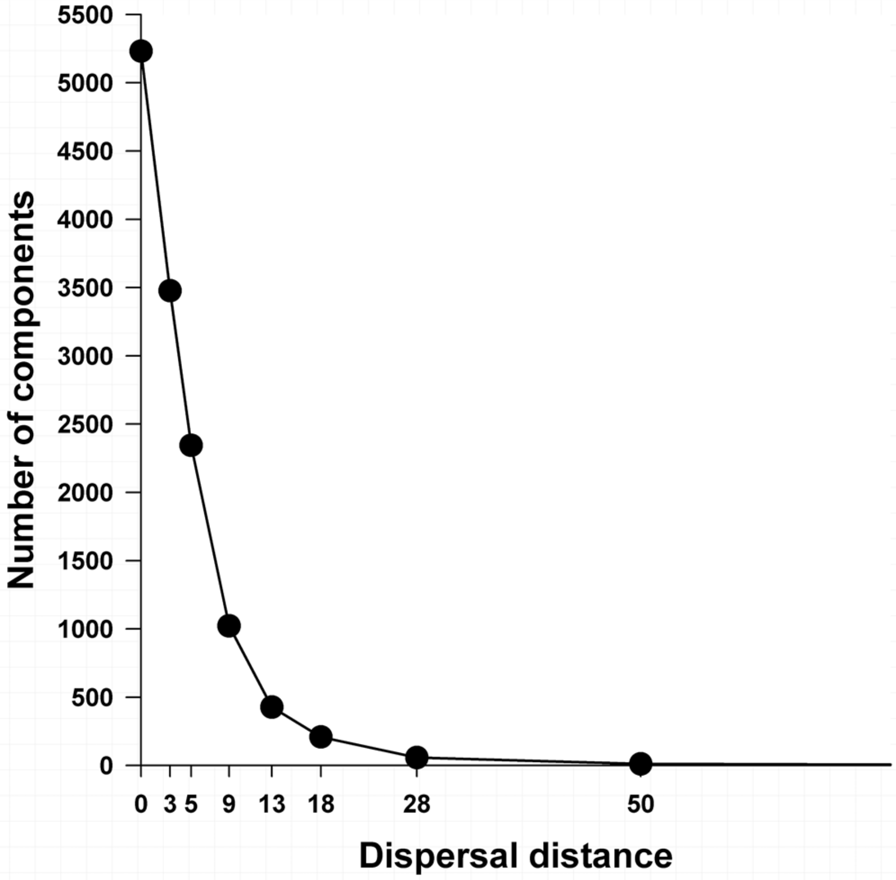

Number of components
5500
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
0
3
5
9
13
18
28
50
Dispersal distance

Figure 6.

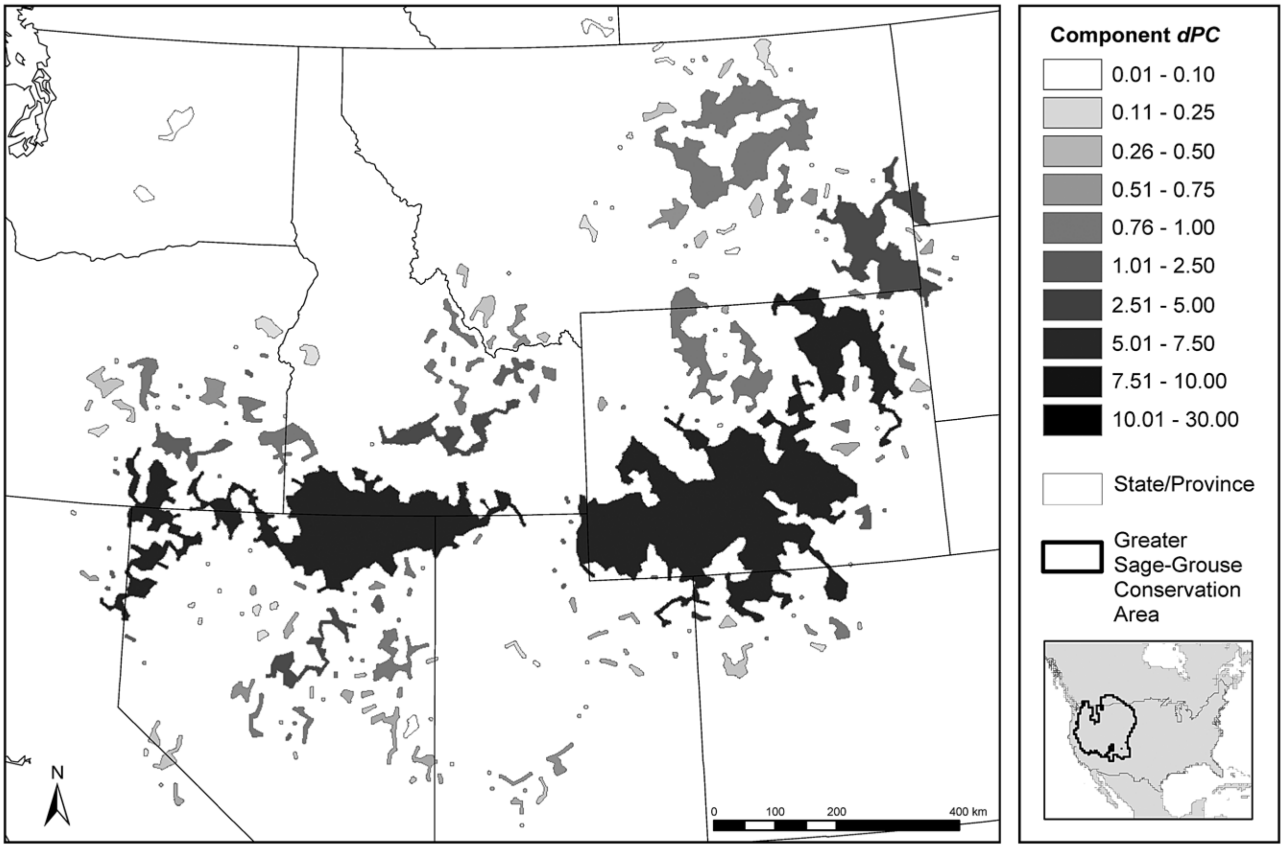
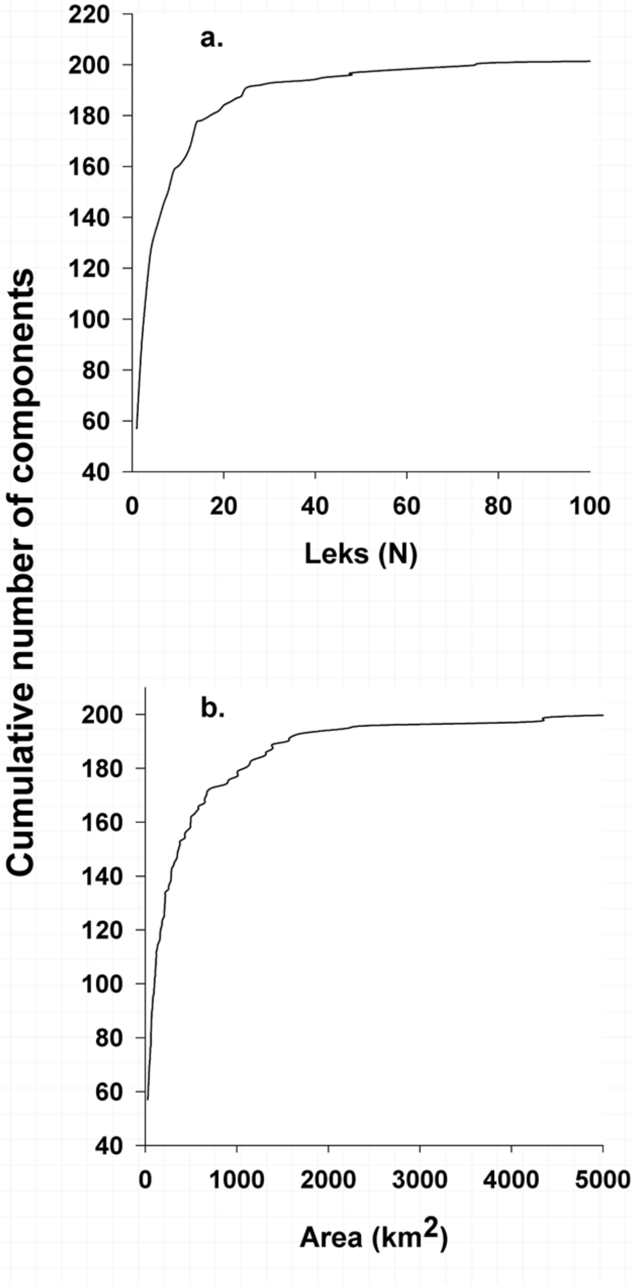
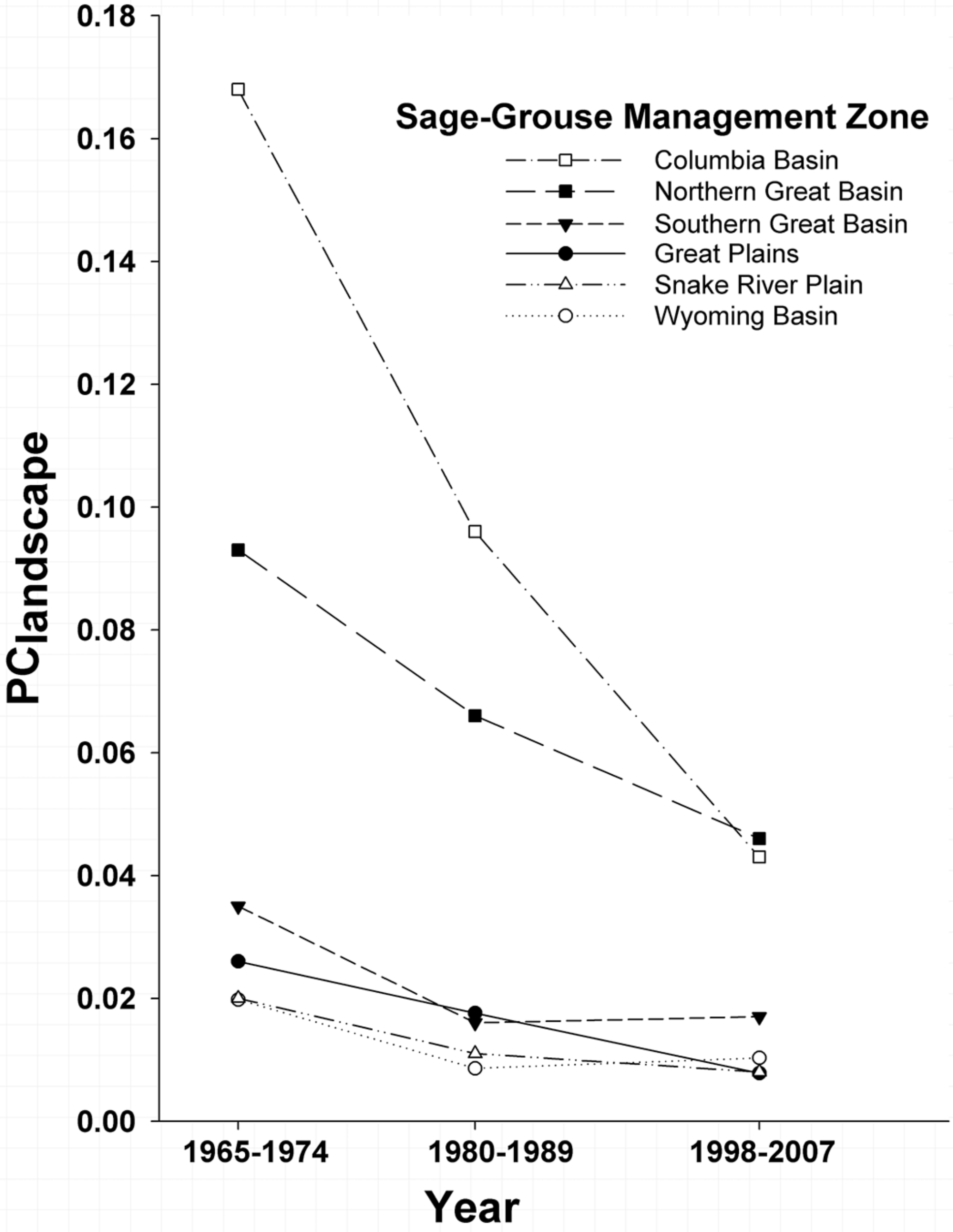

Component *dPC*
0.01 - 0.10
0.11 - 0.25
0.26 - 0.50
0.51 - 0.75
0.76 - 1.00
1.01 - 2.50
2.51 - 5.00
5.01 - 7.50
7.51 - 10.00
10.01 - 30.00
State/Province
Greater Sage-Grouse Conservation Area
N
0
100
200
400 km

Figure 7.



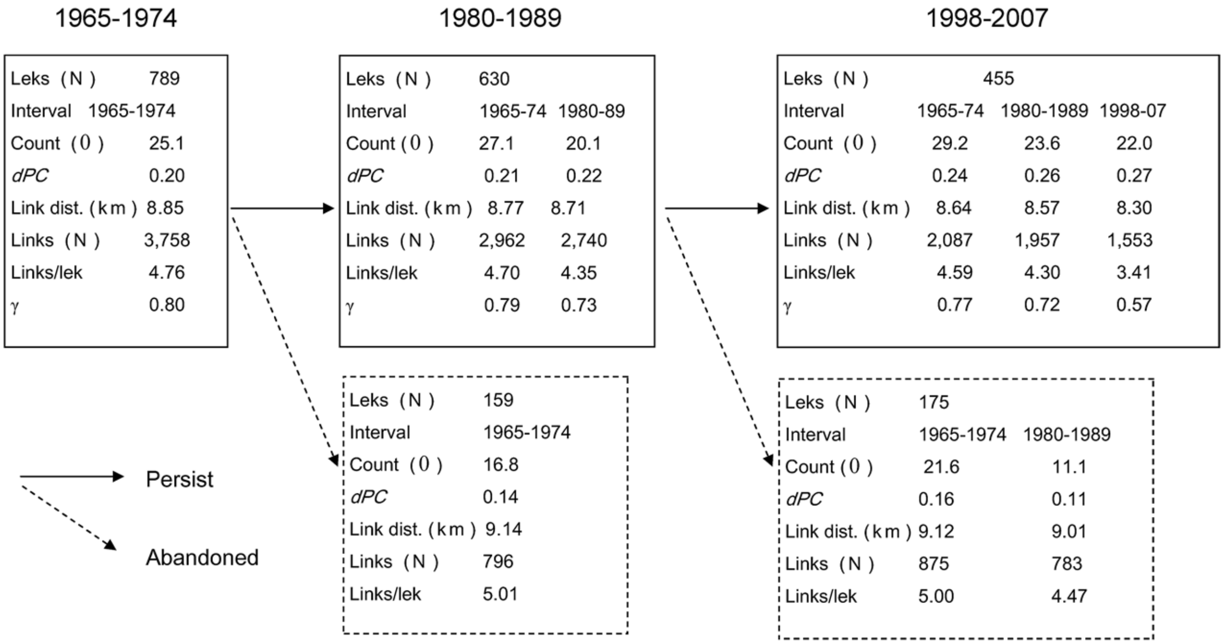
a.
220
200
180
160
140
120
100
80
60
40
0
20
40
60
80
100
Leks (N)
Cumulative number of components
b.
200
180
160
140
120
100
80
60
40
0
1000
2000
3000
4000
5000
Area (km2)

Figure 8.



0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
PClandscape
Sage-Grouse Management Zone
Columbia Basin
Northern Great Basin
Southern Great Basin
Great Plains
Snake River Plain
Wyoming Basin
1965-1974
1980-1989
1998-2007
Year

Figure 9.



Leks (N)	789	
Interval	1965-1974	
Count (0)	25.1	
dPC	0.20	
Link dist. (km)	8.85	
Links (N)	3,758	
Links/lek	4.76	
γ	0.80	

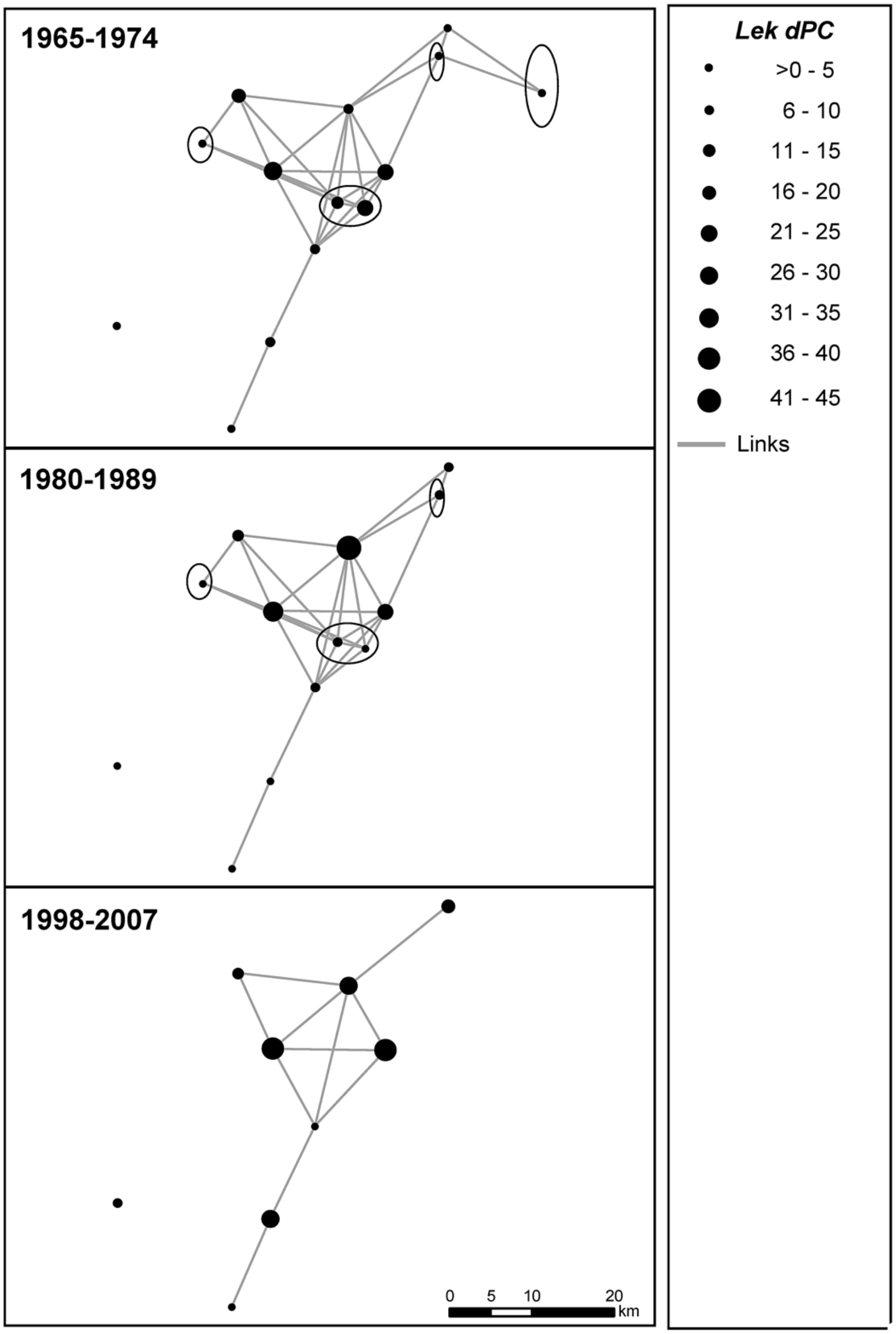
Leks (N)	630	
Interval	1965-74	1980-89
Count (0)	27.1	20.1
dPC	0.21	0.22
Link dist. (km)	8.77	8.71
Links (N)	2,962	2,740
Links/lek	4.70	4.35
γ	0.79	0.73

Leks (N)		455	
Interval	1965-74	1980-1989	1998-07
Count (0)	29.2	23.6	22.0
dPC	0.24	0.26	0.27
Link dist. (km)	8.64	8.57	8.30
Links (N)	2,087	1,957	1,553
Links/lek	4.59	4.30	3.41
γ	0.77	0.72	0.57

Leks (N)	159
Interval	1965-1974
Count (0)	16.8
dPC	0.14
Link dist. (km)	9.14
Links (N)	796
Links/lek	5.01

Leks (N)	175	
Interval	1965-1974	1980-1989
Count (0)	21.6	11.1
dPC	0.16	0.11
Link dist. (km)	9.12	9.01
Links (N)	875	783
Links/lek	5.00	4.47

Figure 10.


1965-1974
1980-1989
1998-2007
Lek dPC
>0 - 5
6 - 10
11 - 15
16 - 20
21 - 25
26 - 30
31 - 35
36 - 40
41 - 45
Links
0
5
10
20
km