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Energy development and conservation of sympatric wildlife : new approaches to meet growing challenges

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ENERGY DEVELOPMENT AND CONSERVATION OF SYMPATRIC WILDLIFE:
NEW APPROACHES TO MEET GROWING CHALLENGES

by

William C. Dunn

B.S., Wildlife Biology, University of Montana, 1978
M.S., Biology, University of Nevada, Las Vegas, 1984

DISSERTATION

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ABSTRACT

Conflicts between energy development and conservation of sympatric wildlife are becoming more acute as demand for energy increases. Resolving these conflicts is complex; solutions must address the role of location, scale, and connectivity in persistence of populations.   In Chapter 1, I use the MaxEnt species distribution model and pertinent climate variables to predict the natural distribution of the Lesser Prairie Chicken (LPC) (*Tympanuchus pallidicinctus*), a prairie grouse adversely affected by habitat loss from energy development. Within the geographic range of LPC, precipitation was strongly associated with its distribution in the north, whereas temperature was strongly associated with its distribution in the south. Most of the geographic range did not possess optimal characteristics for population persistence. Climate characteristics were marginal in the southwestern part of the geographic range which has been subject to oil and gas extraction for 80 years.

In Chapter 2, I introduce a spatially-explicit patch model and used LPC population counts and oil and gas data from southeastern New Mexico to investigate the effects of energy development on persistence of sympatric wildlife populations. Without protection, LPC went extinct within 100 years, although more conservative rates of energy development resulted in longer persistence times. Designating patches initially occupied by LPC as refugia resulted in population persistence for the entire 100 year period. However, several patches occupied initially became empty number because connectivity for colonization was destroyed by energy development.

In Chapter 3, I develop and demonstrate a new security index based on majority rule renormalization. It provides a measure of security for patches of habitat as well as for the matrix between patches. This provides a foundation for determining the best corridors between habitat patches.

In Chapter 4, I examine scaling relations within a riverine system in eastern Kansas. Hierarchical, self-organizing networks, as found in riverine systems, are increasingly recognized as a common topological framework of natural systems. This provides a new perspective through which to analyze and conserve habitat patches and corridors upon which metapopulations depend. Scaling relations may be particularly useful in addressing energy-wildlife conflicts through prediction of the effect of perturbations from energy development on metapopulation patch and corridor networks.

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ENERGY DEVELOPMENT AND CONSERVATION OF SYMPATRIC WILDLIFE:

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INTRODUCTION

Worldwide competition for energy, particularly fossil fuels, promises to become increasingly acute as more countries develop modern economies (Brown et al. 2011). The United States and China stand out above all other countries in their potential for energy consumption. Between now and 2020, consumption of oil by the United States is expected to increase by over one-third (20.7 to 28.3 million barrels/day) and China's consumption may triple (6.5 to 20.7 million barrels/day); combined these two countries will account for 42% of the worldwide demand (www.nationmaster.com). The United States has responded to its growing energy needs with a sharp increase in development of alternative energy resources and a 3-fold increase in active drill rigs during the past decade to develop domestic oil and natural gas sources (www.eia.doe.gov).

This increased activity presents a formidable challenge for wildlife conservation. Most energy developments whether fossil fuel or alternative sources are characterized by dense networks of roads and structures. Wildlife habitat is destroyed or abandoned; the configuration of what is left often changes from a fractal mosaic of natural components (vegetation, soils, topography) to either a simplified configuration characterized by large homogeneous patches or a fragmented mixture of anthropogenic and natural patches (Mader 1984, Krummel 1987).

In the face of these habitat alterations, wildlife populations decline or are extirpated. The Lesser Prairie-Chicken (LPC) (*Tympanuchus pallidicinctus*) is a prime example of this. In southeastern New Mexico, oil and gas extraction (n = 59,000 wells) has been implicated in the decline of active LPC mating grounds (leks) from 33 to 1 (Hunt and Best 2004). Across the geographic range, habitat loss from both energy development and agriculture has reduced distribution of LPC to <20% of what it was historically (Hagen and Giesson 2005). It is now a candidate for listing as Threatened under the federal Endangered Species Act.

Commonly used approaches to mitigate the impacts of energy on sympatric wildlife include limiting energy-related activities in areas and during times critical to population persistence, restoring habitat, reestablishing extirpated populations through translocations and if needed, captive breeding. All of these options are costly and may be ineffective if implemented at the wrong scales or locations. For example, turning off oil pumps during early mornings in spring near mating grounds is a common practice to reduce disturbance of prairie grouse mating rituals (Doherty et al. 2008). This action may prevent energy extraction from causing a reduction in breeding rates, but the number of days when and area where cessation of early morning pumping is applied generally does little to reduce disturbance during nesting and brood rearing. Thus, recruitment, and in turn persistence, of the targeted population is still adversely affected by energy extraction.

Location is a particularly important consideration for restoration of habitat and populations. Despite improved techniques and higher success rates, a substantial proportion of populations continue to be established where resources provided by the natural environment are inadequate for self-sustenance (Seddon 2007). Management is then required to sustain these populations; this in turn diverts resources away from restoration efforts that might be more beneficial to species recovery. In particular, the limited distribution, small populations, and few locations for restoration associated with imperiled species magnify the need to employ all available tools and information to identify locations where population persistence can be maximized.

In this dissertation, I use existing tools and develop new techniques to demonstrate how scale and location can be incorporated into addressing energy-wildlife conflicts. In **Chapter 1**, I employ MaxEnt, a top performing species distribution model (Elith et al. 2006), to identify niche characteristics most associated with presence of LPC and identify where those characteristics are found across its geographic range. Mitigation almost always is the primary focus where anthropogenic disturbance is involved in a species' decline. However, the effort will do little for recovery if underlying environmental characteristics where mitigation occurs are inadequate for long-term persistence. Thus, the first step should be to find where environmental characteristics provide a high probability of persistence, then initiate mitigation.

In **Chapter 2**, I develop and use a cellular automaton model to describe and predict how energy development affects persistence of sympatric wildlife populations. The underlying foundation is a spatially-explicit derivation of the Levins (1969) metapopulation patch model that includes the effect of patch destruction (Bascompte and Sole 1996).

The association between habitat loss and energy disturbance has been well documented (Sawyer et al. 2006,Walker et al. 2006, Aldridge and Boyce 2007, Doherty et al. 2008, Carpenter et al. 2010, Holloran et al. 2010, Naugle 2011). However, successful mitigation requires focus on what habitat remains and the degree to which it can support persistent populations.

Energy-wildlife conflicts are analogous to competition between two species in which the superior competitor, energy development, usurps enough of the shared landscape to cause substantial reduction and possible extirpation of the inferior competitor, wildlife (Nee and May 1992). An alternative to extirpation is finding a non-trivial stable equilibrium in which both competitors are able to persist via spatial or temporal separation at critical scales (Dill and Bromberg 2002). In the context of energy and wildlife, this would equate to energy extraction managed so that quality, abundance, and connectivity of undisturbed habitat is adequate for sympatric wildlife to persist. I use data from eastern New Mexico, specifically colonization and extinction rates of LPC leks and initiation and completion dates of extraction of O&G wells, to model the dynamics of patch occupancy where LPC have historically occurred but have been subjected to long-term energy development.

In **Chapter 3**, I describe and demonstrate a new method to measure security (the ability of landscapes to provide refugia for organisms from disturbance and predation) at multiple scales across a landscape. Loss of security is at the crux of why energy-related habitat fragmentation is so deleterious to persistence of sympatric wildlife populations.

The sheer complexity of landscapes and idiosyncrasies of organisms makes measuring security a difficult task. Importantly, the effect of anthropogenic disturbances on landscape configuration may affect organisms differently depending on the scale at which each operates (e.g., m^2 for rodents, ha for ungulates). To address this, I developed a security index in which spatial renormalization (Milne and Johnson 1993) of simulated landscapes (lattices of equal-sized cells) is used to measure fine-scale patterns at a cellular level, then translate them to broader, more coarse-scale representations through aggregation of cells. The result is a continuum of values across the lattice that reflects proximity to and density of habitat at multiple scales.

In **Chapter 4**, I examine scaling relations among streams within a riverine system in eastern Kansas. Networks of pipelines that transport oil from wells or transmission lines that carry electricity from wind turbines share similar structural characteristics as stream systems. In stream networks, structure size, flow volume, and energy that drive the system all increase at predictable rates as the number of contributing tributaries increase. Techniques in this chapter show how those rates can be determined and then used to describe and predict the impact of energy transport systems as development expands across landscapes.

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Chapter 1

Climatic Heterogeneity and the Implications for Conservation of the Imperiled Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*)

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Abstract

A geographic range is a heterogeneous matrix in which the natural capability to support the resident species at any given location may vary from detrimental to optimal. Given this, the first step in recovery of imperiled species should be determining where optimal environments exist. We used MaxEnt species distribution modeling to distinguish climatic characteristics associated with persistent leks from those at random locations as a means of characterizing the niche and predicting the potential distribution of the imperiled Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). Annual, brood period, and winter precipitation were most important in characterizing the niche across the geographic range, but maximum temperature during nesting was a key characteristic in the southern part of the range. Only 26% of LPC habitat across the geographic range had climate similar to locations of persistent leks; the largest proportions were in Texas and western Kansas and Oklahoma. Lesser Prairie-Chickens appear constrained on the western edge of their range by abiotic factors, namely aridity, unfavorable temperatures, and a lack of sandy soil. Conversely, they appear constrained on the eastern edge by biotic factors, namely hybridization and competition. Maintaining populations in western Kansas and Oklahoma as well as east-central New Mexico will be key to conserving this species. Aridity, unfavorable temperatures, and a paucity of habitat make eastern Colorado and southeastern New Mexico challenging areas for LPC persistence.

Introduction

Environmental conditions that contribute to persistence of organisms generally have been considered best in the center of geographic ranges with decreasing quality and quantity towards the periphery (Haldane 1956, Brown 1984, Hall et al. 1992, Guo 2005). An analysis of breeding bird surveys by Brown et al. (1995) empirically demonstrated this pattern, but also found extensive multimodality; a few locales supported high population densities, but most did not. The contrast between the center and periphery, however, does not discount the value of the range periphery; it might contain the best remaining populations or habitat in the wake of anthropogenic disturbance (Lomolino and Channell 1998) and may provide populations or stepping stones key to metapopulation persistence (Gilpin 1980, Kiett et al. 1997). Thus, a geographic range is a heterogeneous matrix in which the suitability at any given location may vary from detrimental to optimal; areas important to the persistence of populations potentially can occur anywhere (Senft et al. 1987, Brown et al. 1995, Lomolino and Channell 1998).

Recognizing the heterogeneity of geographic ranges is especially important when considering locations to pursue recovery and conservation of imperiled species. A hierarchy of three criteria can be used to focus the selection process: geographic range, habitat, and climate. Solely using presence within the geographic range has several shortcomings. Often historic surveys from which range boundaries were derived were not systematic and were limited both spatially and temporally. Thus, not all occupied parts of the geographic range may have been identified. Conversely, characteristics of surveyed areas may have been used as a basis for designating unsurveyed areas as occupied; in reality that may not have been the case. Further, information generally was insufficient to assess persistence of documented populations.

A second criterion, distribution and abundance of habitat within the historic range, can reduce ambiguity about persistence. Organisms generally persist longest where habitat occurs in large patches that are close to one another (Prugh 2009). However, the ability of habitat to contribute to persistence is dependent on a third criterion, optimal environmental characteristics that provide needed resources at times optimal for organismal fitness (Pulliam 1988).

Habitat and environmental characteristics are especially important considerations when anthropogenic disturbance is a consideration in planning recovery and conservation efforts. Mitigation of the disturbance often becomes the priority for improving conditions for the species of interest. However, results may fall short of expectations; little benefit might be gained if the natural environment is incapable of supporting persistent populations.

Consideration of all three criteria is particularly pertinent in the case of the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) (LPC), a candidate for listing as threatened under the federal Endangered Species Act. Development of fossil fuel and renewable energy resources and conversion of native prairie to agriculture have reduced the distribution of this species to <20% of its historic range (Hagan and Giesson 2005) and undoubtedly will continue to affect persistence of LPC for the foreseeable future.

Increasing numbers and expanding distribution of LPC by restoring habitat or reintroducing populations will be a challenge, particularly finding sites where (1) habitat is adequate or can be increased enough in areas where optimal climatic conditions exist to support persistent populations, (2) anthropogenic disturbance is minimal or can be cost-effectively mitigated, and (3) landowners are willing to cooperate in conservation efforts. Reintroductions are particularly problematic because less than one-third of reported prairie grouse reintroductions have resulted in populations that persist for more than a few generations (Reese and Connelly 1997, Snyder et al. 1999) and establishment of a reintroduced LPC population has yet to be documented (H. Whitlaw, U. S. Fish and Wildlife Service, personal communication). Thus, it is crucial to select sites where LPC have the best opportunity for long-term persistence.

Species distribution modeling can identify where conservation might be most profitable (Guisan and Thuiller 2005, Elith and Leathwick 2009). These models characterize the niche, environmental conditions that allow recruitment to be greater than or equal to mortality (Chase and Leibold 2003), and predict the potential distribution, the geographic region where those conditions occur (James et al. 1984). A primary benefit is a systematic, consistent means to characterize environmental heterogeneity across the geographic range.

Here we employ MaxEnt (Phillips et al. 2006), one of the best performing species distribution models (Elith et al. 2006), to determine how climatic characteristics associated with LPC persistence differ between locations of persistent leks (mating grounds) and all locations where leks possibly could occur. Specifically, we (1) identify which climate variables best characterize the niche of this species across its geographic range and within 5 different climate zones, (2) quantify, by location, the climatic potential to support LPC, and (3) use those results to identify habitat with climate similar to locations of persistent leks (hereafter “climatically-similar habitat”). We then examine the amount and configuration of total and climatically-similar habitat to identify where LPC might best persist.

Methods

Modeling Approach

MaxEnt is based on the principle of maximum entropy in which the best approximation of an unknown probability distribution is defined as the one closest to uniform but subject to constraints (Jaynes 1957). With MaxEnt, that translates to a distribution that encompasses all locations where the expected values of predictor variables are equivalent to the average value of those variables at locations where the species of interest has been documented to have occurred (Phillips et al. 2006). A Bayesian approach is used to achieve this: the probability of a value of an environmental variable, x, based on where the species of interest, y, occurs, $p(x \mid y = 1)$, is used to predict where the species might occur based on where similar values of the environmental variable are found, $p(y = 1 \mid x)$ (Elith et al. 2011). To do this, characteristics of occurrences (in this study, persistent leks) are compared against the same characteristics at randomly selected locations (hereafter “background“) that represent the full range of environments (in this study, climate) available within the geographic range.

MaxEnt offers a myriad of options for modeling (www.cs.princeton.edu/~schapire/maxent/). We chose the following: (1) the entire sample of occurrences was modeled first, followed by subsets of occurrences found within each climatic zone; (2) regularization, an algorithm to smooth distributions and increase generalization of results, was varied from 0.1 (closer to training data) to 5 (more generalized); (3) model iterations ceased at 500 or when log loss of deviance per iteration was $< 10^{-5}$; (4) variables in linear (continuous values), quadratic (squared values), and product (multiplied with other variables) formats were used to determine constraints via the mean, variance and covariance, respectively; (5) the importance of predictor variables was measured by permuting training data to increase gain and also by jackknife sampling, in which each predictor variable was used alone in, and then excluded from, models; (6) all predictor variables were included in initial model runs, but those whose permutation importance was <10% and jackknife values were not among the top 50% of variables were eliminated during subsequent runs; (7) response curves created by modeling each predictor variable in isolation of others were used to determine the range of values where the probability of LPC being present was ≥ 0.5 (hereafter "presence probability values"); (8) model fits were tested via 10-fold cross-validation using clamped data (test data values limited to the range of training data); and (9) predicted distribution of LPC was projected across the entire geographic range. Logistic values of habitat cells produced by the best MaxEnt model (based on the area under receiver operating curves (AUC) and gain) were categorized into two groups using a threshold where sensitivity and specificity values were equal (Liu et al. 2005). A map was created of those habitat cells with values above the threshold to show habitat that is climatically-similar to locations of persistent leks.

Occurrence and Background Locations

We obtained locations, survey dates, and counts at leks in 4 of 5 states where LPC were historically found: Oklahoma, Kansas, Colorado, and New Mexico (Table 1; Fig.

1). Data on individual leks were not available from Texas because of confidentiality agreements between Texas Department of Parks and Wildlife and private landowners.

Three methods were used by resource agencies to survey LPC: (1) listening at designated points along transects, then counting LPC at identified leks (if locations were accessible), (2) completely searching defined geographic areas, then counting LPC at identified leks, and (3) annually revisiting and counting LPC at known leks. Use of these methods varied among states but sampling units (leks), weather conditions (calm, clear), observation periods (one-half hour before to 2 hours after dawn during the breeding season- late March-early May), and number of annual visits (usually 1, never more than 3) were consistent; thus counts were comparable. The low number of annual visits could have inflated the error of omission; LPC may have been using the lek, but were not present when the observer arrived. To compensate for this, we considered LPC as being present if ≤2 years separated previous and subsequent observations from the survey in which they were not observed.

Occurrence data need to meet three criteria to ensure model accuracy. First, they should represent populations in equilibrium with their environment (Elith and Leathwick 2009). To achieve this, we used leks in which LPC were documented to be present for ≥5 consecutive years, the maximum lifespan of LPC (Campbell 1972). Second, occurrences should not be autocorrelated. We tested for spatial autocorrelation among these persistent leks by comparing counts from each pair of leks made during the same years via linear correlation. If significantly correlated, one randomly chosen lek of the pair was removed from the sample.

Lastly, occurrence data need to be collected randomly or systematically to avoid models that reflect heavily sampled more than preferred locations. Our data did not meet this criterion, so we adapted one option of Phillips et al. (2009), selecting background locations in the same proportion as occurrences within study area subdivisions. We subdivided the geographic range into 5 zones based on differences in mean annual precipitation or temperature; zone boundaries were defined by the edge of the geographic range and counties in which population surveys occurred (Fig. 1). Proportions of leks and background locations for each zone were based on population densities, instead of numbers of leks, because most leks were used by > 1 LPC. Some surveys in each zone were conducted systematically which allowed calculation of lek densities. These values were then multiplied by the mean LPC counted per lek. The proportion of persistent leks and background locations for each zone was the population density of that zone divided by the sum of population densities for all zones.

Predictor Variables

Nine measures of climate related to LPC demographics were used to differentiate conditions at persistent leks from background locations (Appendix A; Table 2). Precipitation and temperature data were derived from GIS raster layers (800 m cells) available from the PRISM Climate Group (http://www.prism.oregonstate.edu). Precipitation variables derived from these raster layers included 30 year means (1971-2000) for amounts produced annually as well as during winter (November-March), nesting (April-May), and brood rearing (June-August). Additionally, a coefficient of variation was calculated for annual precipitation. Temperature variables included 30 year means for daily maximum and minimum temperatures during the nesting period, and mean daily maximum temperature during the brood rearing period. A raster of mean potential annual evapotranspiration (PET) was obtained from MODIS imagery (http://modis.gsfc.nasa.gov/).

Habitat Data

We limited our analyses to LPC habitat because including non-habitat inflates AUC values (Lobo et al. 2008). A habitat layer was created in ArcMap 9.3.1© (Environmental Science Research Institute, Redlands, CA) by extracting grass-shrub landcover types known to be used by LPC from GAP Analysis raster databases (http://gapanalysis.usgs.gov/). These raster databases were based on satellite imagery from the mid- to late 1990's. Accuracy was 55-60% which is considered adequate for modeling at a regional scale (e.g., our climate zones) (Lowry et al. 2005).

We measured amount of total and climatically-similar habitat within each climate zone and Texas. MaxEnt logistic values for cells of climatically-similar habitat were divided into 5 quantiles; a Chi-square test was used to determine differences ($P \leq 0.05$) in number of habitat cells among quantiles and climate zones. We also measured amount of total and climatically-similar habitat within 3.2 km of leks (i.e., lek ranges) and background locations in the 5 climate zones. Differences in amount of habitat among habitat-zone categories were determined with a two-way analysis of variance and post-hoc Tukey tests.

Results

We obtained data for 694 leks; LPC were present for $\geq$5 consecutive years at 352 of them (Table 1). Occurrence data consisted of 183 persistent leks which included all recorded in southeastern New Mexico and western Kansas/Oklahoma, and random subsets of leks in east-central New Mexico (n = 60 of 214), eastern Colorado (n = 35 of 42), and eastern Kansas/Oklahoma (n = 35 of 54).

Overall, climate at persistent leks across the geographic range was characterized by increasing precipitation and decreasing temperature from southwest to northeast (Fig. 2). Nest period and winter precipitation in New Mexico was half the amount that falls in eastern Kansas/Oklahoma. Conversely, annual precipitation was twice as variable in southeastern New Mexico as in eastern Colorado, Kansas and Oklahoma. Temperatures generally were highest in New Mexico but exceptions were minimum nest and maximum brood period temperatures, which were higher in eastern Kansas/Oklahoma than in east-central New Mexico. Temperatures were consistently lowest in eastern Colorado.

Climate variables that differentiated persistent leks from background were consistent for all values of regularization. Here, we present results from the most generalized models we created, those in which regularization was set at 5. Across the geographic range, the niche of LPC was characterized by annual, brood period, and winter precipitation (Table 3). Brood period precipitation had the highest permutation importance, but winter precipitation produced the strongest jackknife values (i.e., highest when included alone, lowest when excluded). The range of presence probability values for annual, brood, and winter precipitation were 38-44, 17-21, and 6-10 cm, respectively.

Within individual climate zones, temperature in the south and precipitation in the north differentiated persistent leks from background locations (Table 3). Maximum temperature during nesting had the highest permutation importance in southeastern and east central New Mexico and the strongest jackknife values in southeastern New Mexico. Winter precipitation produced the strongest jackknife values for all climate zones other than southeastern New Mexico. Other variables that made substantial contributions included annual precipitation (eastern Colorado, Kansas, Oklahoma), brood period precipitation (eastern Colorado, eastern Kansas/Oklahoma), and maximum temperature during the brood period (east-central New Mexico).

Presence probability values of climate variables differed between the geographic range and individual climate zones in several cases (Fig. 3). Precipitation generally was higher in Kansas/Oklahoma and lower in southeastern New Mexico than across the geographic range. Conversely, maximum temperatures during nesting were lower in Kansas, Oklahoma, and eastern Colorado and higher in southeastern New Mexico.

The geographic range contained 6.6 million ha of LPC habitat (Fig. 4a). Over half was in Texas and almost one-third was in eastern Kansas/Oklahoma (Table 4). Only 26% was climatically-similar habitat. The largest proportions were in east-central New Mexico and western Kansas/Oklahoma. For the most part, climatically-similar habitat extended northeast from east-central New Mexico and west Texas to northeastern Kansas (Fig. 4).

Climatically-similar habitat also was less than total habitat within 3.2 km of leks and random locations ($F_{9,10195} = 188$, $P < 0.001$; Fig. 5). Lek ranges contained more total and climatically-similar habitat than background locations except for total habitat in eastern Colorado. Lek ranges in western Kansas/Oklahoma contained the most habitat and also differed most from random locations.

The number of cells of climatically-similar habitat differed among MaxEnt quantile-zone groups ($\chi^2_{6,5} = 2861$, $P < 0.0001$) (Fig. 6). Based on contributions to the Chi-square value, the number of cells for New Mexico and eastern Colorado were higher than expected for low MaxEnt values and lower than expected for high MaxEnt values. The opposite was true for Kansas and Texas. .

Discussion

Our choice of data and approach to modeling addressed many potential pitfalls that can plague species distribution modeling. We used a large sample of occurrences from persistent (and therefore likely to be in equilibrium with their environment) populations. Occurrences encompassed the breadth of environmental conditions that characterize the historic range of LPC. We focused our efforts on identifying the climate envelope (Duncan et al. 2009) in which the LPC can exist. Our purpose in segregating habitat from climate and concentrating on a limited number of ecologically relevant variables (Appendix A) was to obtain clear results that could be easily applied to conservation. Importantly, our choices were based on empirical data from an abundance of studies and surveys conducted throughout the geographic range during a variety of climatic regimes. Thus, it is improbable that factors such as dispersal barriers or unknown biotic interactions masked knowledge of critical components that characterize the niche of LPC (Jimenez-Valverde et al. 2008).

Several variables, particularly measures of precipitation, were highly ($r > 0.75$) correlated, but were included to determine if climate effects were annual or seasonal. MaxEnt addresses confounding effects of correlated variables by modeling the contribution of each variable both with, and in isolation of, the others (Phillips et al. 2006).

We chose GAP landcover raster layers to map LPC habitat because they were the only data in which mapping methods were comparable across the entire geographic range. We found patterns of habitat consistent with other reports (Ligon 1927 Sullivan 2000, Hagan and Giesson 2005), field observations, and more intensive mapping efforts. For example, LPC habitat in the Texas panhandle is shown by GAP as scattered in the southwest and more connected in the northeast, consistent with field observations (S. Kyle, Texas Parks and Wildlife Department, personal communication). Additionally, accuracy of GAP was 55% with no error of commission when compared with a map created via remote imagery, verified by extensive field sampling, and focused solely on identifying LPC habitat in southeastern New Mexico (Neville et al. 2005).

It was not unexpected that precipitation, particularly during winter, would be the main determinant differentiating persistent leks from background locations given the association between precipitation (particularly two winters prior to surveys of gallinaceous birds) and population size (Bailey 1999). Grasses on which LPC depend require consistent, interannual precipitation to replenish and maintain densities. In turn, this provides LPC with forage to fuel natality and cover to reduce mortality.

The transition of dominant climate drivers from temperature in the south to precipitation in the north underscores the importance of intrarange analyses to reveal species-environment relationships. The extent of the niche of LPC can be defined by the range of presence probability values derived from leks in all climate zones. These values provide a benchmark for how well each climate zone meets niche requirements. Three zones fell short (Fig. 3). In southeastern New Mexico, low population densities were undoubtedly associated with high maximum temperatures during nesting and brood rearing and low precipitation combined with the high potential evapotranspiration and variable patterns of precipitation.

Cool maximum temperatures can benefit LPC during nesting by reducing the potential for hyperthermia and desiccation (Appendix A; Table 2). However, in eastern Colorado the low maximum and minimum temperatures (Fig. 2) might be detrimental, causing LPC to divert energy to thermoregulation that would otherwise be invested in reproduction. Additionally, cool conditions might delay germination of plants and hatching of insects, thereby limiting food resources during critical reproductive periods.

In eastern Kansas/Oklahoma, high precipitation should enhance reproduction and survival of LPC. However, it also contributes to the transition of habitat from grass-dominated to a patchwork of woody vegetation and grass. The latter type is more associated with the Greater Prairie-Chicken (*Tympanichus cupido*) than LPC (Schroeder and Robb 2005).

Thus, mechanisms defining distributional limits of LPC are consistent with patterns found elsewhere in the natural world (Brown et al. 1996). Specifically, constraints that define one edge (western) of the geographic range are abiotic, namely aridity, unfavorable temperatures, and a lack of sandy soil to support preferred vegetation. Conversely, constraints that define the opposite edge (eastern) are predominantly biotic, namely hybridization and competition with Greater Prairie-Chickens (Hagen and Giesson 2005).

Distribution of climatically-similar habitat also was consistent with a center-periphery pattern (Haldane 1956, Brown 1984, Hall et al. 1992, Guo 2005). The highest proportion of climatically-similar habitat was in more centrally-located western Kansas/Oklahoma. Conversely, low MaxEnt values were concentrated along the edge of the geographic range in southeastern New Mexico, eastern Colorado and northern Kansas as well as the southeastern part of the range in Texas (Fig. 4). Jackson and DeArment (1963) speculated this part of Texas was a wintering area for LPC. Our results suggest this assumption may have been largely without merit.

Several of our findings provide direction for conservation. First, the abundance of climatically-similar habitat underscores the importance of maintaining viable populations in Kansas and Oklahoma (Fig. 4). Maintaining populations in east-central New Mexico will be equally important. Because of different anthropogenic influences and a more arid climate, LPC in New Mexico possess genetic structure and reproductive strategies markedly different than more northerly populations in Oklahoma (Van Den Bussche et al. 2003, Patten et al. 2005).

Next, reestablishing populations in should be considered in the northern panhandle of Texas based on abundant climatically-similar habitat and west Texas based on the high quality of climatically-similar habitat. In particular, populations established in west Texas would enhance persistence of LPC in the southern part of the geographic range. However, results for Texas should be interpreted with some caution because they were based on projecting results well away from occurrence and background locations (Elith and Leathwick 2009).

Lastly, unfavorable climate characteristics and a paucity of habitat make eastern Colorado and southeastern New Mexico challenging areas for LPC persistence. Based on proximity, populations in the southern part of eastern Colorado likely benefit from demographic support of populations in western Kansas. However, populations in southeastern New Mexico likely would gain little demographic support from either east-central New Mexico or west Texas because of extensive oil and gas development.

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Appendix A. Niche characteristics of Lesser Prairie-Chickens

Historically, LPC have been found throughout the southern great plains from central Kansas to southeastern New Mexico, occupying grass-shrub habitats dominated by shinnery oak (*Quercus havardii*), sand sage (*Artemisia filifolia*), and big, little, and sand bluestem (*Andropogon gerardii, Schizachyrium scoparium A. hallii*., respectively) (Hagen and Gieson 2005). Most of their activity is ≤3.2 km from their mating grounds (leks); nesting often is ≤1.8 km from a lek (Campbell 1972 Giesen 1994, Hagen et al. 2005, Pitman 2006a). Nesting and brood rearing (late March-August) is most successful where vegetation affords a high degree of vertical and horizontal cover that protects LPC from predation, extreme temperatures, and desiccating winds (Riley et al. 1992, Giesen 1994, Johnson et al. 2004, Hagen et al. 2005, Patten et al. 2005b, Pitman et al. 2005).

Fat reserves average <5% of the body weight of grouse, so daily foraging is critical to meeting energy needs (Thomas and Popko 1981, Thomas 1982, Dehaley and Moss 1996). Important dietary components include seeds, acorns, and cultivated grains during fall and winter (Davis et al.1981, Riley, et al. 1993), forbs during spring (Davis et al. 1981), and invertebrates during summer (Jamison et al. 2002, Hagen et al. 2005). Invertebrate abundance is positively related to forb cover (Jamison et al. 2002) which in turn responds to grazing (McNaughton et al. 1985) and to precipitation particularly that which occurs during the winter preceding, and the spring of, the nesting season (Muldavin et al. 2008, Xia et al. 2010).

Wide population fluctuations are common among LPC (Johnsgard 1983) and demographics are considered to be largely influenced by a strong relationship between precipitation and recruitment. Precipitation affects vegetative growth, and in turn, food and cover (Campbell 1972, Riley et al. 1992, Pitman et al. 2005, Giesen 2000, Patten et al. 2005).

Jackson and DeArment (1963) speculated LPC from the panhandle historically wintered in central Texas (>100 km distance); however, most documented movements have been ≤10 km (Campbell 1972, Riley et al. 1994, Hagen 2003, Pitman et al. 2006b). Range expansion occurs incrementally during fall through natal dispersal (Pitman et al. 2006b) and during spring through establishment of new leks by subordinate males when populations are high (Dunn and Braun 1985, Haukos and Smith 1999). Conversely, ranges contract when leks become inactive because of declining populations.

Table 1. Surveys of Lesser Prairie-Chickens in 5 climate zones found in four of five states historically occupied by Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) (LPC). Data from Texas were unavailable for analyses. Persistent leks were defined as active leks in which LPC were present for $\geq$5 consecutive years.

Zone	Persistent leks (leks used as occurrences)	Surveys/Persistent Lek (SD)	LPC/Persistent Lek (SD)	LPC/km^2
Southeastern New Mexico	14 (14)	13.3 (3.5)	6.1 (0.74)	0.05
East-central New Mexico	213 (60)	8.1 (7.3)	9.7 (0.32)	0.53
Eastern Colorado	42 (42)	13.7 (7.5)	8.7 (0.55)	0.24
Western Kansas/Oklahoma	40 (40)	28.1 (7.4)	14.0 (0.83)	0.52
Eastern Kansas/Oklahoma	54 (35)	21.3 (14.1)	12.1 (0.56)	0.3

Table 2. Climate variables used as predictors for modeling the niche and potential distribution of Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*). See Appendix A. *Niche Characteristics of Lesser Prairie-Chickens* for an explanation of how each variable may affect LPC population persistence.

	Climate variable	**Potential effect on population persistence**
Precipitation	Annual	Positive: Cover and forage
		Negative: Hypothermia, less favorable habitat
	Coefficient of Variation in Annual Precipitation	Negative: Variable recruitment that might adversely affect persistence.
	Winter [1]	Positive: Cover and forage during nesting and brood rearing.
		Negative: Depletion of energy reserves for thermoregulation.
	Nesting[2]	Positive: Cover and forage
		Negative: Hypothermia
	Brood Rearing[2]	Positive: Invertebrate abundance
Temperature	Mean Daily Maximum- Nesting	Negative: Hyperthermia, egg desiccation.
	Mean Daily Minimum-Nesting	Negative: Hypothermia
	Mean Daily Maximum-Brood Rearing	Negative: Hyperthermia
Evaporation	Potential Evapotranspiration	Negative: Organismal/egg/forage desiccation.

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[1] Winter: November-March. Nesting: April-May. Brood Rearing: June-August

Table 3. Contribution of climate variables in differentiating persistent leks from background locations across the geographic range of lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) and within 5 climate zones of that range. Shown are variables that contributed most to the differentiation: annual precipitation (ppt-annual), brood period precipitation (ppt-brood), winter precipitation (ppt-winter), maximum temperature during nesting (max temp-nest), maximum temperature during brooding (max temp-brood). Regularization value was 5 for the models that produced these results. Permutation importance was the contribution of each variable when it was randomly permuted. Training and Test Gain and AUC values were derived from jackknife sampling when each climate variable was used alone (included), and then excluded from models. Higher values when variables were included and lower values when they were excluded from models signify increasing contribution to discriminating persistent leks from background.

Climate Zone	AUC	Variable	Permutation Importance (%)	Training Gain		Test Gain		AUC	
				Included	Excluded	Included	Excluded	Included	Excluded
Entire Geographic Range	0.91	ppt-annual (cm)	31.3	0.8	1.1	0.18	1.41	0.67	0.91
		ppt-brood	39.3	0.36	0.98	0.41	1.25	0.72	0.88
		ppt-winter	24.1	0.76	0.65	0.86	0.78	0.84	0.83
Southeastern New Mexico	0.98	max temp-nest	72.3	2.32	1.9	2.5	2.34	0.98	0.98
		ppt-winter	21	0.59	2.42	0.63	2.86	0.73	0.99

Table 3, continued.

East-central New Mexico	0.98	max temp-brood	12.6	0.07	2.09	0.13	2.54	0.6	0.96
		max temp-nest	31.7	0.98	1.98	1.12	2.35	0.87	0.95
		ppt-winter	15.9	1.21	1.38	1.44	1.51	0.91	0.92
Eastern Colorado	0.98	ppt-annual	32.9	0.27	3.3	0.64	3.26	00.88	0.98
		ppt-brood	31.6	0.59	3.18	1.16	3.6	0.96	0.98
		ppt-winter	19.3	2	2.54	3.03	2.64	0.98	0.97
Western Kansas/Oklahoma	0.98	ppt-annual	14.6	0.14	3.04	0.54	4.73	0.89	0.99
		ppt-winter	76.4	2.52	2.48	4.05	4.54	0.99	0.99
Eastern Kansas/Oklahoma	0.99	ppt-annual	7.5	1.15	1.67	1.54	2.02	0.96	0.92
		ppt-brood	46.7	1.09	1.35	1.2	1.99	0.96	0.92
		ppt-winter	44	1.18	1.49	1.67	1.76	0.94	0.94

Table 4. Total and climatically-similar habitat found in the geographic range of LPC and in 5 climate zones and the part of Texas within the range. Total habitat is comprised of GAP Analysis landcover types (http://gapanalysis.usgs.gov/) known to be used by LPC. Climatically-similar habitat included the subset of habitat cells that had climatic characteristics similar to characteristics where LPC leks persisted for $\geq$5 years.

Climate Zone	Total Habitat (ha)	Climatically-similar habitat (ha)	% of total habitat that is climatically-similar to locations of persistent leks
Entire Geographic Range	6,593,634	1,726,762	26.2
Southeastern New Mexico	171,218	35,347	20.6
East-central New Mexico	222,759	93,085	41.7
Eastern Colorado	153,585	22,515	14.5
Western Kansas/Oklahoma	361,141	239,488	66.0
Eastern Kansas/Oklahoma	2,227,286	512,816	23.0
Texas	3,457,645	823,511	23.8

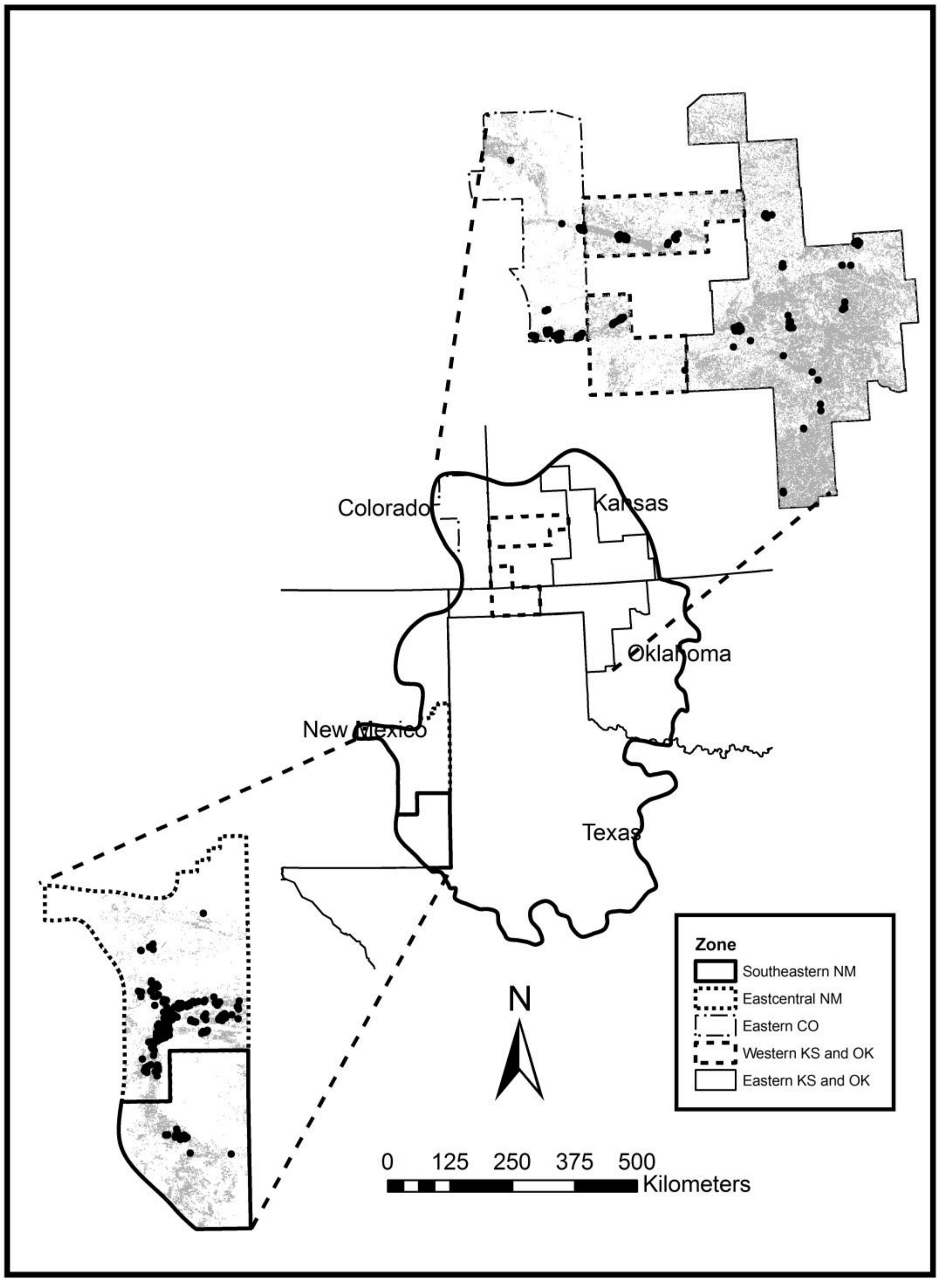
Figures

1. The geographic range and five climate zones used to model the niche and potential distribution of the lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). Gray shading is LPC habitat derived from Gap Analysis landcover types known to be used by this species. Black dots are persistent leks (LPC present $\geq$ 5 continuous years). The boundary of the geographic range was adapted from Davis et al. (2005).
2. Mean values (*) and 95% confidence intervals (|) of 9 climate variables at persistent leks in 5 climate zones within the geographic range of the Lesser Prairie-Chicken: 1=Southeastern New Mexico; 2= East-central New Mexico; 3 = Eastern Colorado; 4 = Western Kansas/Oklahoma; 5 = Eastern Kansas/Oklahoma. Differences among zones were determined by non-overlapping 95% confidence intervals. Climate variables with differences among zones: annual precipitation (ppt-annual)- 5>4>3>2>1; variation in annual precipitation (ppt-annual CV) – 1>2>3=4=5; potential evapotranspiration (PET)- 1=2>3>4>5; precipitation during nesting (ppt-nest)- 5>4>3>2=1; precipitation during brooding (ppt-brood)-5>4>3>2>1; precipitation during winter (ppt-winter)-5>4>3>2=1; maximum temperature during nesting (max temp-nest)- 1>2>5>3=4; minimum temperature during nesting (min temp-nest)- 1>5>2>4>3; maximum temperature during brooding (max temp-brood)- 1>5>2=4>3.
3. Range of values of 4 climate variables within the geographic range and 5 climate zones in which a probability of presence > 0.5 was predicted by MaxEnt: 1=Southeastern New Mexico; 2= East-central New Mexico; 3 = Eastern

Colorado; 4 = Western Kansas/Oklahoma; 5 = Eastern Kansas/Oklahoma. 6= entire geographic range (dark bars).

4. Total and climatically-similar Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) habitat. Total habitat included cells containing GAP landcover types known to be used by LPC. Climatically-similar habitat included the subset of habitat cells that had climate similar to locations where LPC leks persisted for ≥5 years. Climatically-similar habitat is displayed in 5 categories of MaxEnt logistic values. The boundary of the geographic range was adapted from Davis et al. (2005).
5. Total and climatically-similar (C-S) Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) habitat within 3.2 km of persistent leks and background locations. Values for all habitat-climate zone groups were different based on analysis of variance and post-hoc Tukey test.
6. Proportion of cells within 5 quantiles of MaxEnt logistic values of climatically-similar habitat. Based on contributions to the Chi-square value, quantiles where observed numbers of cells were greater than expected are designated by > whereas quantiles where observed numbers of cells were less than expected are designated by <.

Figure 1.


Colorado
Kansas
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Zone
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Eastcentral NM
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Western KS and OK
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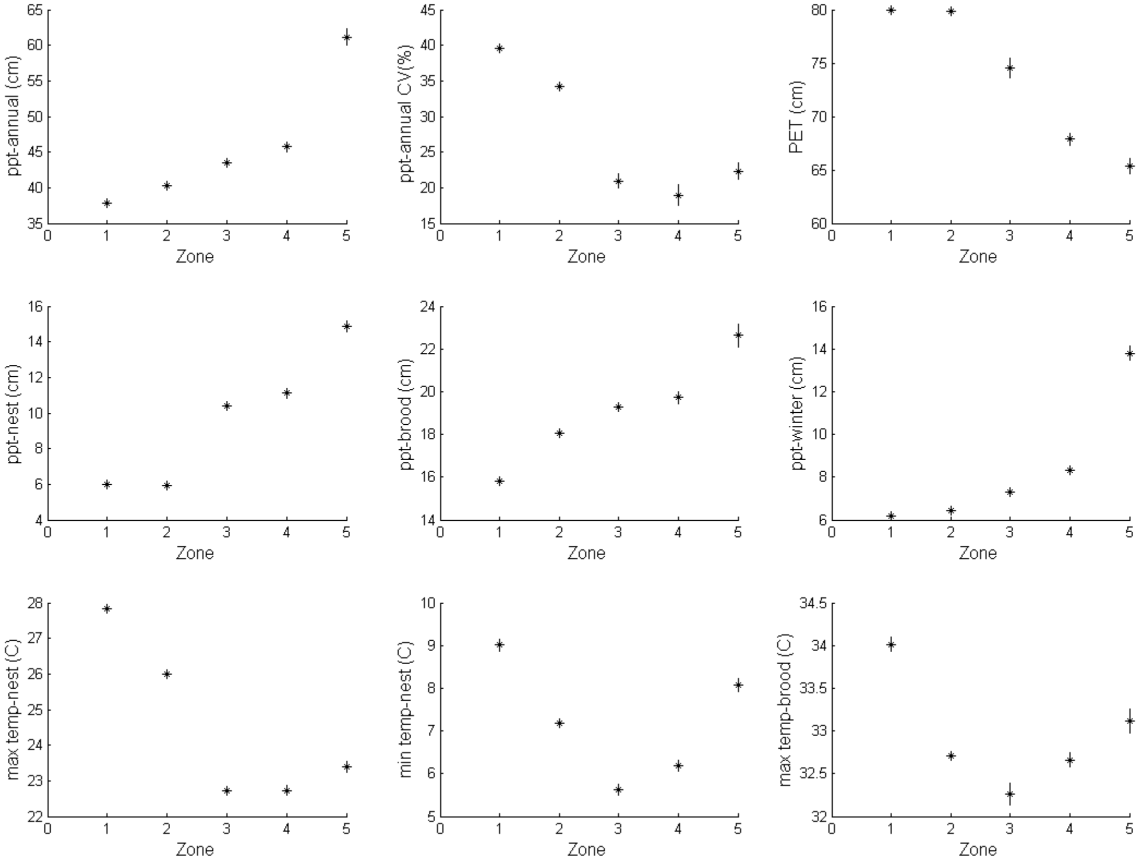
ppt-annual (cm)
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ppt-annual CV(%)
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ppt-nest (cm)
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ppt-brood (cm)
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ppt-winter (cm)
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max temp-nest (C)
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min temp-nest (C)
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7
6
5
max temp-brood (C)
34.5
34
33.5
33
32.5
32
0
1
2
3
4
5
Zone

Figure 3.

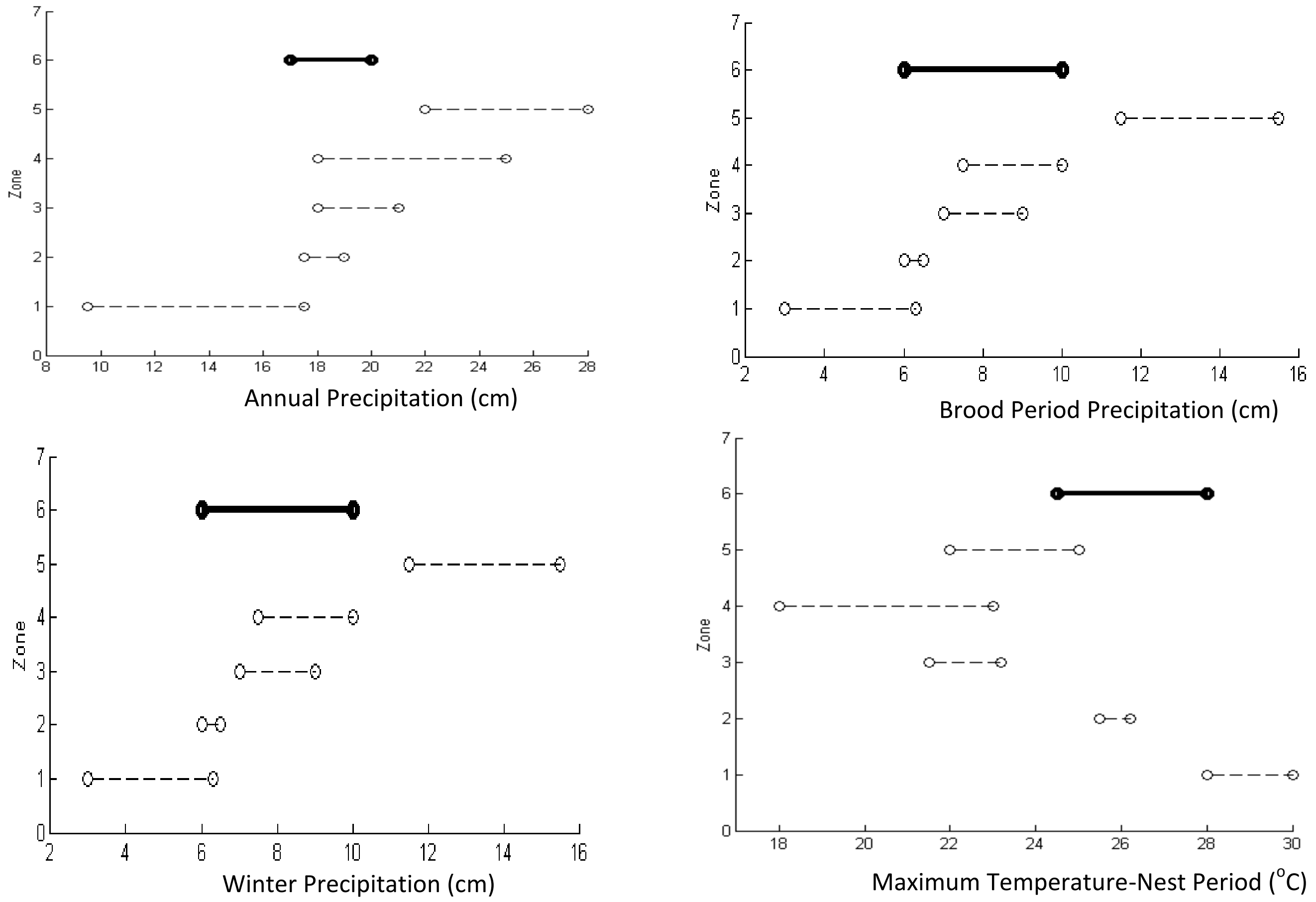

Zone
0
1
2
3
4
5
6
7
8
10
12
14
16
18
20
22
24
26
28
Annual Precipitation (cm)
Zone
2
4
6
8
10
12
14
16
Brood Period Precipitation (cm)
Zone
Winter Precipitation (cm)
Zone
18
20
22
24
26
28
30
Maximum Temperature-Nest Period (°C)

Figure 4.

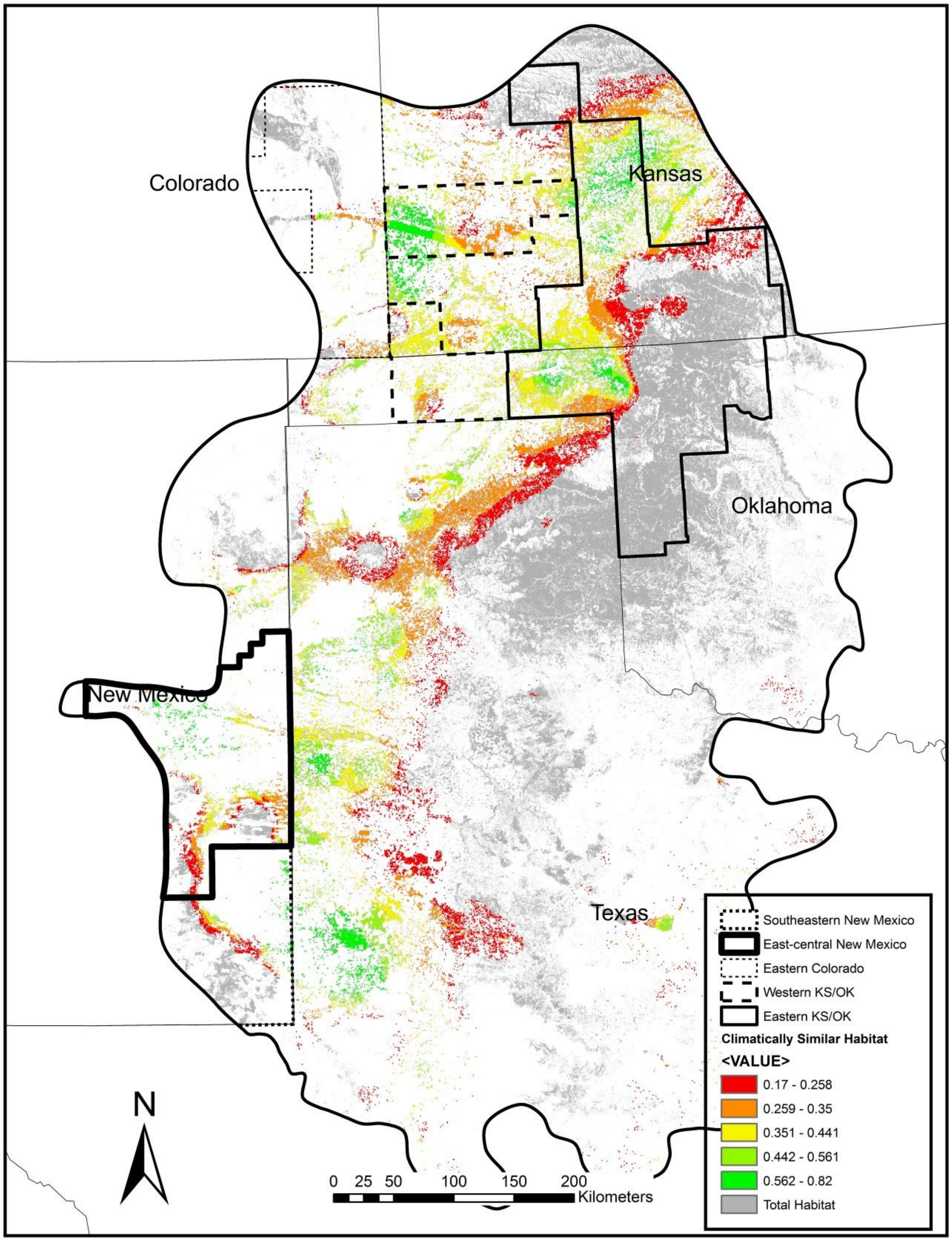
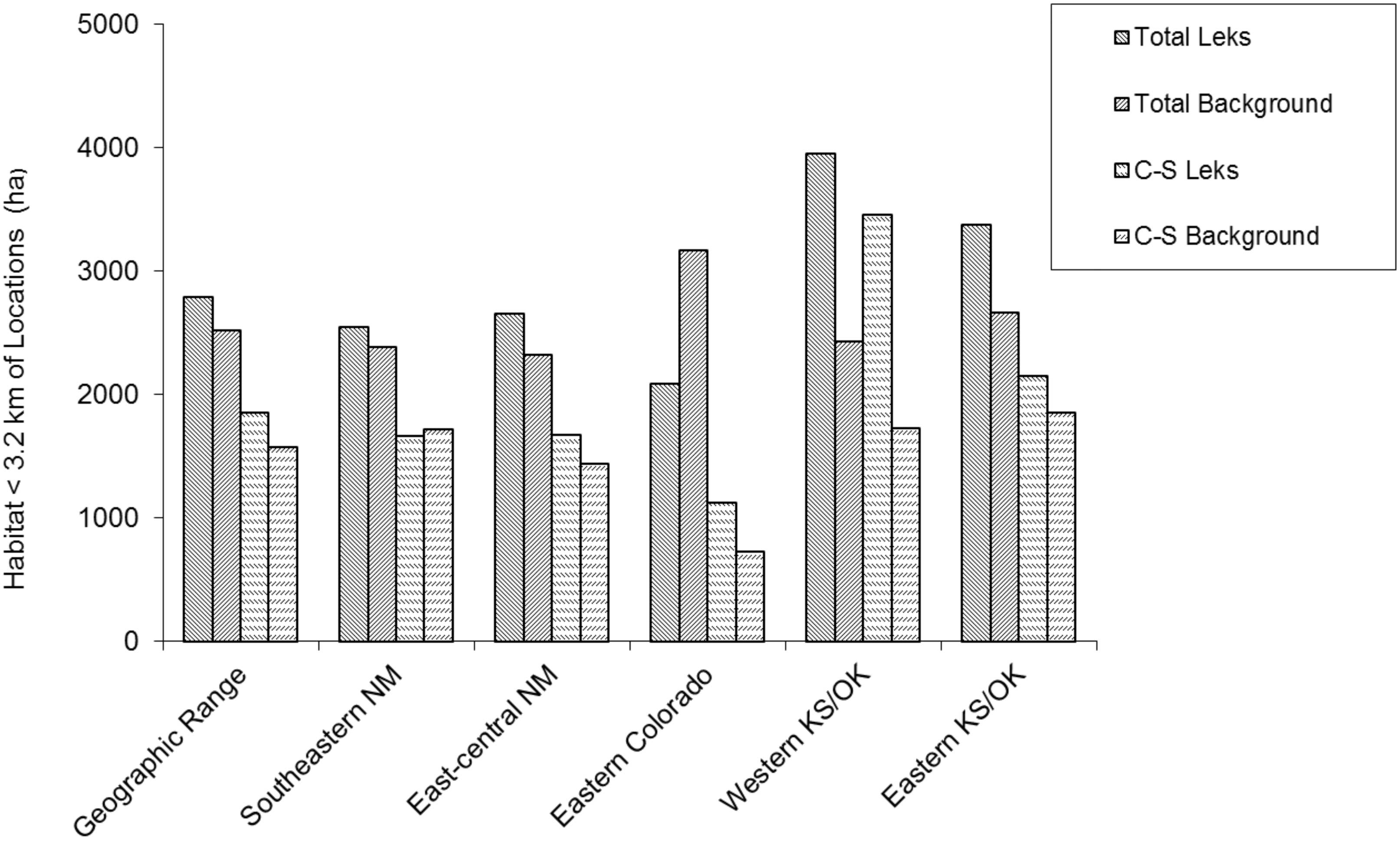
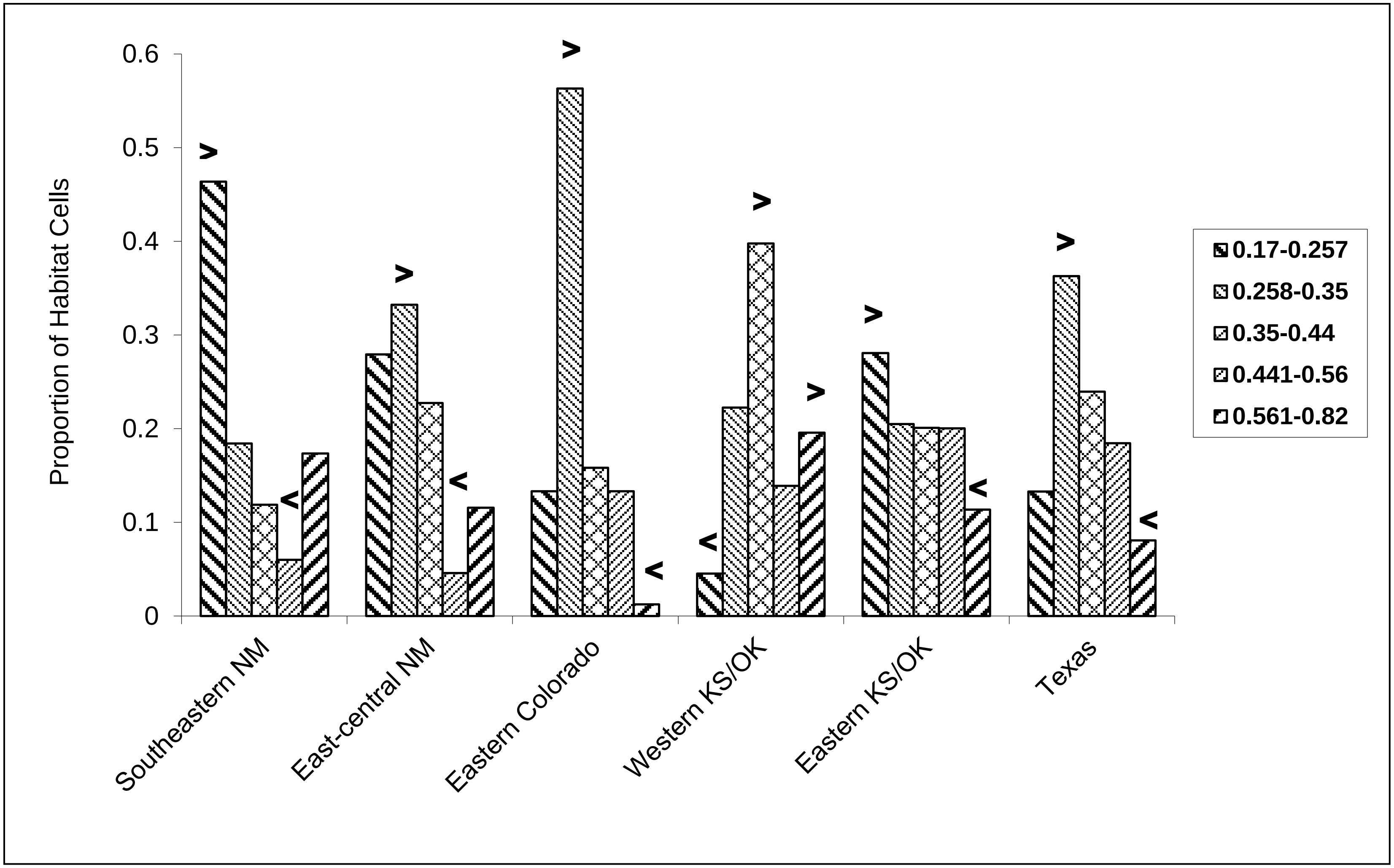

Colorado
Kansas
Oklahoma
New Mexico
Texas
Southeastern New Mexico
East-central New Mexico
Eastern Colorado
Western KS/OK
Eastern KS/OK
Climatically Similar Habitat
<VALUE>
0.17 - 0.258
0.259 - 0.35
0.351 - 0.441
0.442 - 0.561
0.562 - 0.82
Total Habitat
N
0 25 50 100 150 200
Kilometers

Figure 5.



5000
4000
3000
2000
1000
0
Habitat < 3.2 km of Locations (ha)
Geographic Range
Southeastern NM
East-central NM
Eastern Colorado
Western KS/OK
Eastern KS/OK
▧ Total Leks
▨ Total Background
▧ C-S Leks
▨ C-S Background

Figure 6.


Proportion of Habitat Cells
0.6
0.5
0.4
0.3
0.2
0.1
0
Southeastern NM
East-central NM
Eastern Colorado
Western KS/OK
Eastern KS/OK
Texas
>
<
0.17-0.257
0.258-0.35
0.35-0.44
0.441-0.56
0.561-0.82

Chapter 2

Modeling the Dynamics of Landscapes Occupied By Energy Development and Wildlife

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Abstract

Worldwide energy demand is increasing at an unprecedented rate. One result is significant loss of wildlife habitat. We developed a spatially-explicit patch model to determine the effect energy development on patch occupancy by sympatric wildlife. We used data from 80 years of oil and gas (O&G) extraction in southeastern New Mexico and counts of sympatric Lesser Prairie Chickens (LPC) (*Tympanuchus pallidicinctus*) to explore the dynamics of energy-wildlife relationships. If unprotected from energy development, all patches occupied by LPC went extinct, but time of persistence was inversely related to rate of O&G development. If patches initially occupied by LPC were protected from development, LPC persisted beyond the 100 year modeling period. However, the effectiveness this measure does have limitations. As rates of development increased, the number of years in which patches occupied by LPC were connected across the landscape decreased. The increased isolation was reflected in lower proportions of occupied patches at the end (0.22) of the modeling period than at the beginning (0.27). The reason is that there are fewer avenues for recolonization, so protected cells become increasingly isolated and, in turn, remain empty.

Introduction

Worldwide competition for energy, particularly fossil fuels, is becoming increasingly acute as more countries develop modern economies (Brown et al. 2011). The United States and China stand out above all other countries in their potential for energy consumption. Between now and 2020, consumption of oil by the United States is expected to increase by over one-third (20.7 to 28.3 million barrels/day) and China's consumption may triple (6.5 to 20.7 million barrels/day); combined they will account for 42% of the worldwide demand (www.nationmaster.com). The United States has responded to its growing energy needs with a sharp increase in development of alternative energy resources and a 3-fold increase in active drill rigs during the past decade to develop domestic oil and natural gas (O&G) sources (www.eia.doe.gov).

This presents a formidable challenge for wildlife conservation. Most energy developments whether fossil fuel or alternative sources are characterized by dense networks of roads and structures. Wildlife habitat is destroyed or abandoned; the configuration of what is left is changed from a fractal mosaic of natural components (vegetation, soils, topography) to either a simplified configuration characterized by large homogeneous patches or a fragmented mixture of anthropogenic and natural patches (Mader 1984, Krummel 1987).

Adverse impacts to wildlife may include (1) facilitated predation because roads provide easy access for ground-based predators and power poles provide perches from which raptors can search areas where prey previously had been secure; (2) additive mortality to avifauna caused by power line collisions; (3) greater difficulty in detecting mates and predators because of anthropogenic sources of noise, (4) increased energy expenditure for vigilance and flight to avoid predation or anthropogenic disturbance (Freddy et al. 1986, Bevanger 1995, 1998, Bowles 1995, Forman 2003, Taylor and Knight 2003).

The growing challenge of energy-wildlife conflicts has generated extensive research particularly in western North America. Decreased use of habitat has been associated with (1) proximity to wells for Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) (Robel et al. 2004) and Sage Grouse (*Centrocercus urophasianus*) (Walker et al. 2006, Aldridge and Boyce 2007, Carpenter et al. 2010, Halloran 2010), (2) density of wells for songbirds (Gilbert and Chalfoun 2011) and Sage Grouse (Doherty et al. 2008, Naugle 2011), and (3) time since beginning of energy extraction for mule deer (*Odocoileus hemionus*) (Sawyer et al. 2006). These studies provide critically important data, but their findings emphasize habitat that has been lost. For mitigation and conservation, the focus needs to be on the habitat that remains and the extent to which it can support persistent populations.

The conflict between energy development and sympatric wildlife is analogous to competition between two species in which the superior competitor, energy development, usurps a resource (habitat), thereby contributing to reduction, and possibly extirpation, of the inferior competitor wildlife in the area of sympatry (Nee and May 1992).

One alternative to extirpation is a non-trivial stable equilibrium in which both species are able to persist via spatial or temporal separation at critical scales (Dill and

Bromberg 2002). For energy-wildlife conflicts, this would equate to energy extraction managed so that enough undisturbed habitat remains for continued persistence of sympatric wildlife. The difficulty in determining and maintaining this level of management is that conditions governing size and location of energy development and wildlife populations are in constant flux (Fig. 1). For oil and gas, the period of extraction and density of wells at any given location varies with amount of resource, ease of extraction, and market demand. For wildlife, occupancy varies with resource availability and biotic interactions. These factors result in a landscape in which the composition and configuration of patches occupied by each competitor vary over time.

The metapopulation patch model pioneered by Levins (1969) provided a format for investigating changing patch occupancy and importantly provided a means to determine colonization and extinction rates that maintain patch occupancy at a non-trivial equilibrium. Karreva and Wennergren (1995) incorporated the effect of patch destruction into the Levins model and Bascompte and Sole (1996) examined how this revised model behaved in a spatially-explicit environment

In this paper, we adapt the methods of Bascompte and Sole (1996) to explore the effect of oil and gas development (O&G) on patch occupancy by Lesser Prairie Chickens (*Tympanuchus pallidicinctus*) (LPC) in eastern New Mexico. We develop and use a cellular automaton model (Keymer et al. 2000) to test how variation in growth rates of O&G development, opportunity to colonize, and degree of protection affects persistence of LPC.

Methods

Our model was adapted from Karreva and Wennergren (1995), who developed a derivation of the Levins (1969) spatially-implicit metapopulation patch model:

$$\frac{\partial V_{WL}}{\partial t} = cV_{WL}(1 - V_{WL} - D_{EN}) - eV_{WL} \qquad [1]$$

where $\frac{\partial V_{WL}}{\partial t}$ is the change in proportion of patches occupied by wildlife over time, c is the rate of colonization, V_{WL} is the proportion of patches occupied by wildlife and $1\text{-}V_{WL}$ is the proportion of empty patches available to be colonized, D_{EN} is the proportion of patches occupied by energy development, e is the rate of extinction if wildlife patches. The proportion of patches that need to be occupied by wildlife for the population to remain at equilibrium when both energy and wildlife occupy the landscape is calculated by.

$$V^*_{WL} = 1 - D_{EN} - \left(\frac{e_{WL}}{c_{WL}}\right) \qquad [2]$$

where V^*_{WL} is the proportion of patches occupied by wildlife at equilibrium, D_{EN} is proportion of patches occupied by energy development, e_{WL} is the rate of extinction of wildlife patches and c_{WL} is the rate at which patches are occupied by wildlife.

Following Keymer et al. (2000), energy-wildlife interactions were modeled on simulated landscapes, lattices comprised of equal-sized cells. Predetermined proportions of cells were randomly assigned to one of three categories: occupied by energy development, occupied by wildlife, or empty. Each cell represented the area occupied by a tractable demographic group of the species being modeled, i.e., an individual, sub-population, or population. Values were then assigned to model parameters: (1) number of iterations (time-steps), (2) colonization and extinction rates of wildlife and energy , (3) distances from wildlife cells over which colonization would occur and from energy cells over which development would expand , (4) the probability that energy would be developed at locations beyond the development distance (NewDevProb), (5), the number of new developments that would be initiated beyond the development distance, and (6) the degree of protection afforded to wildlife cells.

During each time-step, a number (based on assigned extinction rates) of wildlife and energy cells were randomly selected and reclassified to empty. Next, cells within the colonizing distance of remaining wildlife cells or development distance of remaining energy cells were identified. A subset (based on assigned colonization rates) of empty colonizable cells were randomly selected and classified as wildlife. Likewise, a subset of cells available for expansion of energy development (not currently developed and not protected for wildlife) were randomly selected and classified as energy cells. Lastly, a random number was selected and, if larger than NewDevProb, the predetermined number of additional undeveloped patches were randomly selected and classified as energy patches.

Wildlife cells, orthogonally or diagonally adjacent to one another, were combined into patches. Wildlife patch sizes and proportion of wildlife and energy cells on the landscape were recorded. The effect of energy development on connectivity of wildlife habitat was measured by comparing changes in the order parameter, a well-known metric for identifying critical phenomena:

$$\Omega = \frac{S_{\max}}{\sum_{ij} \Theta_{ij}} \qquad [3]$$

where S_{max} is the number of wildlife cells in the largest patch and Θ_{ij} is the sum of all wildlife cells. When wildlife cells are well connected across the landscape, the value of Ω remains close to one. When connectivity is lost, the value decreases rapidly towards zero (Bascompte and Sole 1996).

We focused our analysis of energy-wildlife relationships on LPC and O&G development in eastern New Mexico (Fig. 2). Oil and gas has been extracted from this area for 80 years; intensity of development varied from high in southeastern to low in the east-central New Mexico. During the early 1990's, a decline in active LPC mating grounds ("leks") from 33 to 1 (Hunt and Best 2004) in southeastern New Mexico coincided with acceleration in O&G development (Fig. 3). East-central New Mexico supports some of the higher densities of leks of the entire geographic range of LPC (W. C. Dunn, unpublished data). Oil extraction in this part of the study area peaked in the mid-1960's at levels markedly lower than southeastern New Mexico.

For modeling, we used values for LPC from a variety of empirical studies and population surveys to represent realistic scenarios for eastern New Mexico. Values for O&G were derived from a database of all wells drilled in New Mexico (New Mexico Bureau of Geology, Socorro, NM). Density of patches occupied by LPC at the beginning of each model simulation (0.27) was based on occupancy equilibrium derived from equation 2 in which $c_{WL} = 0.15$, $e_{WL}=0.11$ and $D_{EN} = 0$ (i.e., state of the LPC population before initiation of energy development).

Changes in cell occupancy were modeled during 100 time-steps (years) across a 25 x 25 cell lattice. Each cell represented a lek range, the 3.2 km radius around leks within which LPC spend most of their lives (Hagen and Giesson 2005). Colonization for LPC and extinction rates for LPC and O&G were held constant for all model runs at 0.15, 0.11, and 0.02, respectively. Colonization and extinction were year-to-year transitions in the state of leks between active and inactive (no LPC present for >2 continuous years). The low extinction rate for O&G patches reflected the long period of extraction common for wells in southeastern New Mexico. Colonization rates were derived from documented increases in drilling that occurred in the study area (Fig. 2).

LPC colonization and O&G development distances were 1 (i.e., adjacent cells) reflecting localized movement patterns of LPC (generally $\leq$5 km) and a tendency of oil and gas producers to fully develop energy leases before initiating development elsewhere. The probability of a new O&G development being initiated beyond development distances during a given time-step was 0.1. Six different scenarios were modeled using combinations of 3 rates of O&G colonization and 2 levels of protection for LPC. The colonization rates were (1) low- 0.05 for the first 50 years, then 0.1 for the final 50 years, (2) moderate- 0.1 for 100 years; (3) high- 0.1

for the first 50 years, then 0.2 for the final 50 years. The low rate represents peak development in east-central New Mexico during the mid-1960's to the early 1970's whereas the high rates represent the rate of development in southeastern New Mexico during 80 years of extraction. The levels of protection for LPC were (1) none-development could expand to any non-O&G patch or (2) patches occupied by LPC at initiation of modeling were protected from O&G development throughout the modeling period.

We examined how development of O&G affected landscape connectivity for LPC during each time-step by subtracting proportions of LPC and O&G cells from the well known threshold of percolation (P_{crit} = 0.4072). When cells encompass a proportion of the landscape above P_{crit}, they form a "spanning cluster" resulting in connectivity across the landscape. Below P_{crit}, the landscape is increasingly fragmented. For each simulation, we graphed the values derived by subtracting proportions of LPC and O&G cells from P_{crit} on a 4 quadrant phase plane (Fig. 4). Data in the lower right quadrant represented time-steps when proportions of LPC cells were above P_{crit}. Data in the upper left quadrant represented time-steps when proportions of O&G cells were above P_{crit} .

Results

All populations in which all LPC cells were subject to usurpation by O&G went extinct, but time of persistence was inversely related to rate of O&G development (Table 1; Fig. 5). Conversely, all populations in which initial LPC cells were protected from O&G development persisted beyond the modeling period.

However, the predicted year of extinction decreased as the rate of development increased.

Order parameters dropped below 0.5 sooner when all LPC patches were subject to O&G development than when initial LPC patches were protected. This finding also is reflected in patterns shown by the phase planes. More values are in the lower right quadrant for models in which the initial LPC patches are protected from development and rates of O&G development are low.

Discussion

The colonization and extinction rates we used for LPC leks were from periods when LPC were thriving in east-central New Mexico; however, they do not account for the long-term variability characteristic of this species. Populations vary with precipitation which governs availability of forage and cover needed for reproduction and recruitment. Favorable recruitment following wet years results in increased colonization, namely natal dispersal during fall and establishment of new leks by subordinate males during spring. Given their short life span (3 years), extinction of local populations can occur in a few years when dry conditions result in little or no recruitment. Eastern New Mexico experiences high interannual variation in precipitation which is reflected in dramatic fluctuations documented for LPC populations (Fig. 1). Despite this variability, we chose to maintain these rates throughout all modeling periods to determine the effect of O&G development on LPC under optimal conditions.

The results were consistent and clear: without limits on development, LPC populations subjected to energy development go extinct. Lower rates of development prolong, but do not guarantee, persistence. Conversely, designating areas occupied by LPC at initiation of development as refugia appears to be a successful mitigation to attain the desired non-trivial equilibrium needed for long-term persistence. However, the effectiveness this measure does have limitations. As rates of development increased, the number of years in which LPC cells were connected across the landscape decreased (Fig. 6). When high rates of O&G development were used, the increased isolation was reflected in lower proportions of LPC cells at the end (0.22) of the modeling period than at the beginning (0.27). Natural extinction occurs independent of anthropogenic disturbance. However, as more of the landscape is developed, there are fewer opportunities for recolonization, so protected cells remain empty. Ramifications of increased isolation include not only a decrease in total size of LPC populations but likely reduced genetic diversity. Combined, these two factors would serve to accelerate extinction throughout the landscape.

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Table 1. Predicted persistence of metapopulations of Lesser Prairie Chickens (*Tympanuchus pallidicinctus*) (LPC) and connectivity of their landscapes (1) when subjected to 3 levels of development of oil and gas and (2) when lek ranges present at initiation of modeling are either protected from or are subject to development. Results are based on 100 year simulations using a spatially-explicit metapopulation patch model adapted from Bascompte and Sole (1996). Values are means from 5 simulations with each combination of development and protection. Rates of Development: Low=0.5 for the first 50 years, 0.1 for the second 50 years; Moderate=0.1; High = 0.1 for the first 50 years, 0.2 for the second 50 years. The predicted year of extinction is when V* = 0. A decrease in the order parameter (Ω) to 0.5 signals loss of connectivity across the landscape for LPC. See methods concerning V* and Ω.

Rate of Development of Oil and Gas	Lek Ranges Protected?	Predicted Year of Extinction	Actual Year of Extinction	Year Order Parameter ≤ 0.5	Proportion of LPC Patches when Order Parameter ≤ 0.5
Low	No	50	97	59	0.46
Low	Yes	60	Population Persists	93	0.34
Moderate	No	32	87	42	0.35
Moderate	Yes	44	Population Persists	>100	NA
High	No	32	81	52	0.32
High	Yes	42	Population Persists	76	0.28

List of Figures

1. (a) Lesser Prairie Chickens (*Tympanuchus pallidicinctus*) counted at leks and (b) oil and gas wells drilled in eastern New Mexico.
2. Lek ranges and all oil wells drilled within them in (a) east-central New Mexico (n=214 lek ranges) and (b) southeastern New Mexico (n= 14 lek ranges); (c) oil and gas wells (n=27,000) drilled in eastern New Mexico from 1927-2007.
3. Growth in (a) active and (b) total wells in east-central and southeastern New Mexico, 1927-2007. Mean growth rates used in simulations: $r = 0.07$ (East-central New Mexico, 1960-1975); $r = 0.12$ (Southeastern New Mexico, 1930-1980); $r = 0.22$ (Southeastern New Mexico, 1980-2005).
4. Simulated trajectory of patch occupancy for Lesser Prairie Chickens (*Tympanuchus pallidicinctus*) (LPC) and oil and gas development over a 100 year period. Lines labeled "Equilibrium for Prairie Chickens" represent the predicted trajectories of patch occupancy for LPC based on the spatially-implicit model $V^* = 1 - D - e/c$. Model scenarios are (a) and (b): low oil and gas development rates (c) and (d) moderate oil and gas development rates; (e) and (f) high oil and gas development rates. Graphs on the left side show model results when LPC cells present at the initiation of modeling were subject to development; those on the right side show model results when those cells were protected from development.
5. Phase plane used to illustrate change in connectivity of LPC and O&G patches. Values are calculated by subtracting the proportion of cells of each

type from the critical value of percolation ($p_{crit} = 0.4072$). Positive values indicate that cells are abundant enough to provide connectivity across the landscape. Values in the lower right quadrant represent the period during modeling when LPC cells are connected. Values in the upper left quadrant represent the period during modeling when O&G cells are connected and LPC cells are not.

6. Phase planes showing connectivity when the landscape is colonized by oil and gas wells at (a) low, (b) moderate, and (c) high rates. Arrows represent the chronological order of data points during the 100 year modeling period. In all scenarios, both proportions of O&G or LPC cells are below p_{crit} at the beginning of the modeling period, but proportions of O&G cells are above p_{crit} at the end.

Figure 1.

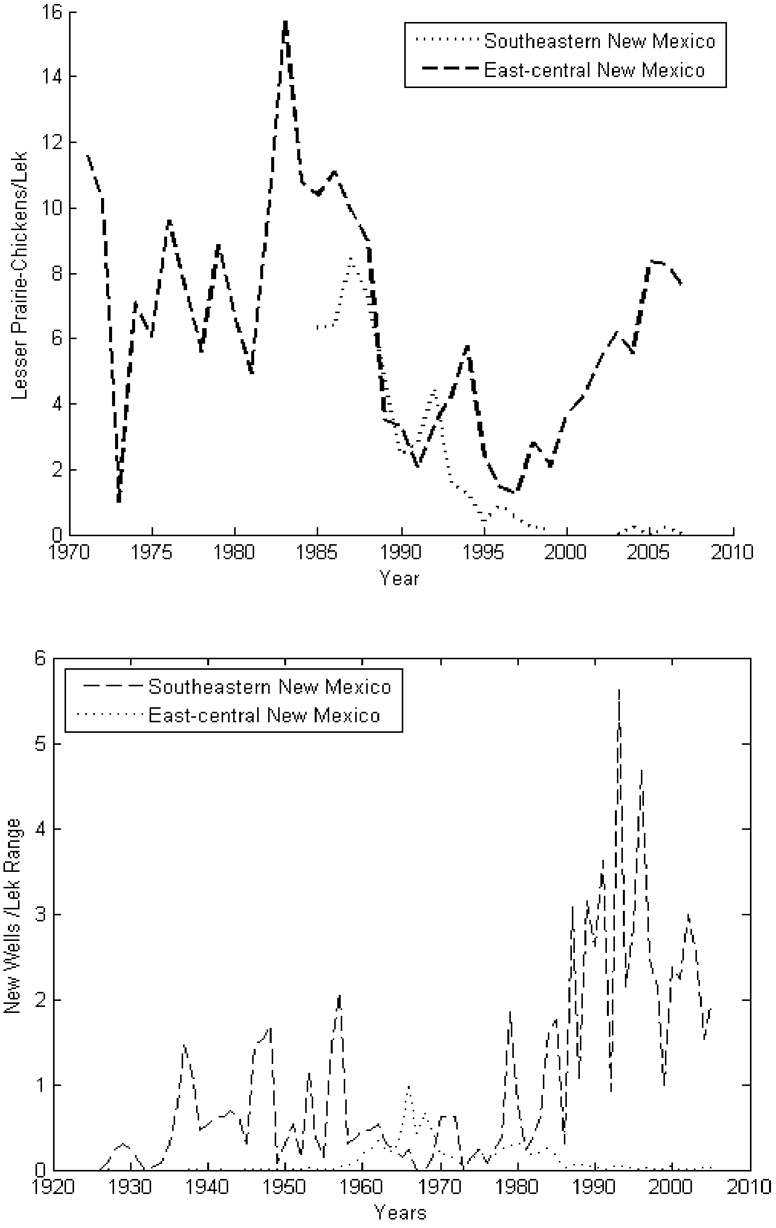

Lesser Prairie-Chickens/Lek
0
2
4
6
8
10
12
14
16
1970
1975
1980
1985
1990
1995
2000
2005
2010
Year
Southeastern New Mexico
East-central New Mexico
New Wells /Lek Range
0
1
2
3
4
5
6
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010
Years
Southeastern New Mexico
East-central New Mexico

Figure 2.

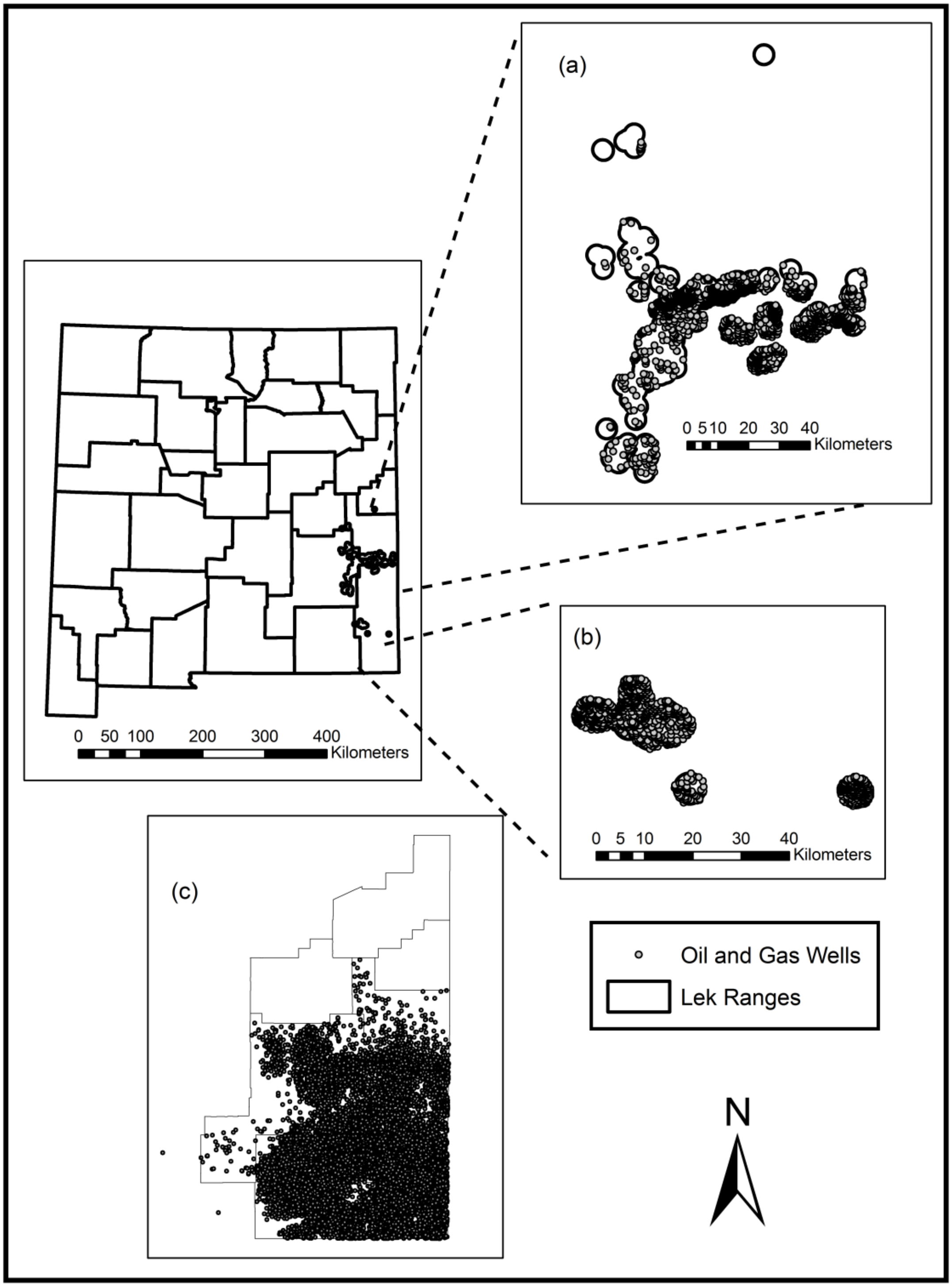
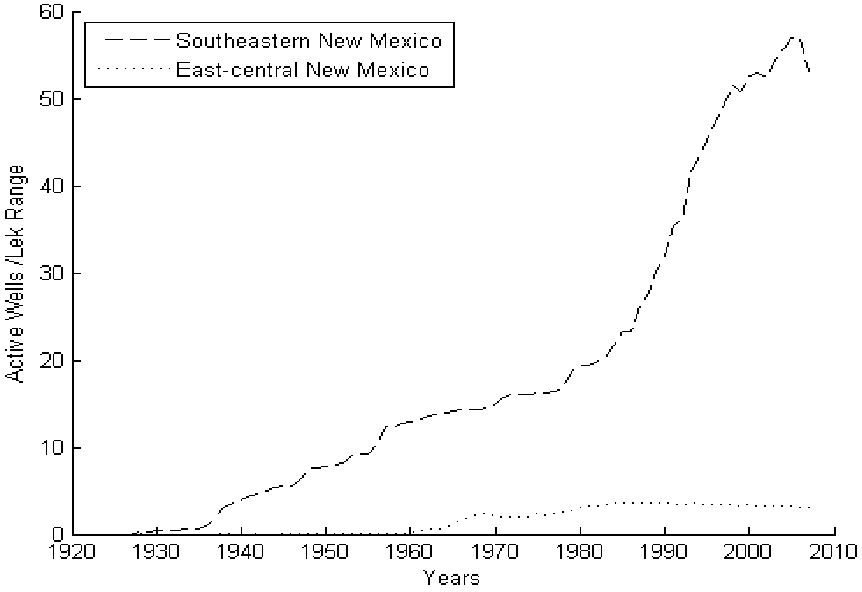

(a)
0 5 10 20 30 40
Kilometers
(b)
0 5 10 20 30 40
Kilometers
0 50 100 200 300 400
Kilometers
(c)
Oil and Gas Wells
Lek Ranges
N

Figure 3.


Southeastern New Mexico
East-central New Mexico
Active Wells /Lek Range
Years
60
50
40
30
20
10
0
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010

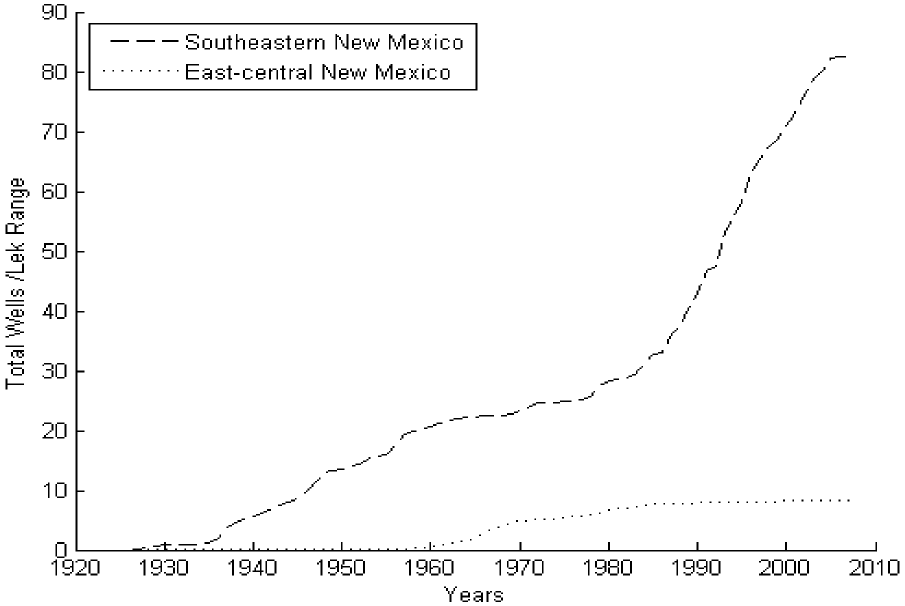

Southeastern New Mexico
East-central New Mexico
Total Wells /Lek Range
Years
90
80
70
60
50
40
30
20
10
0
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010

Figure 4.

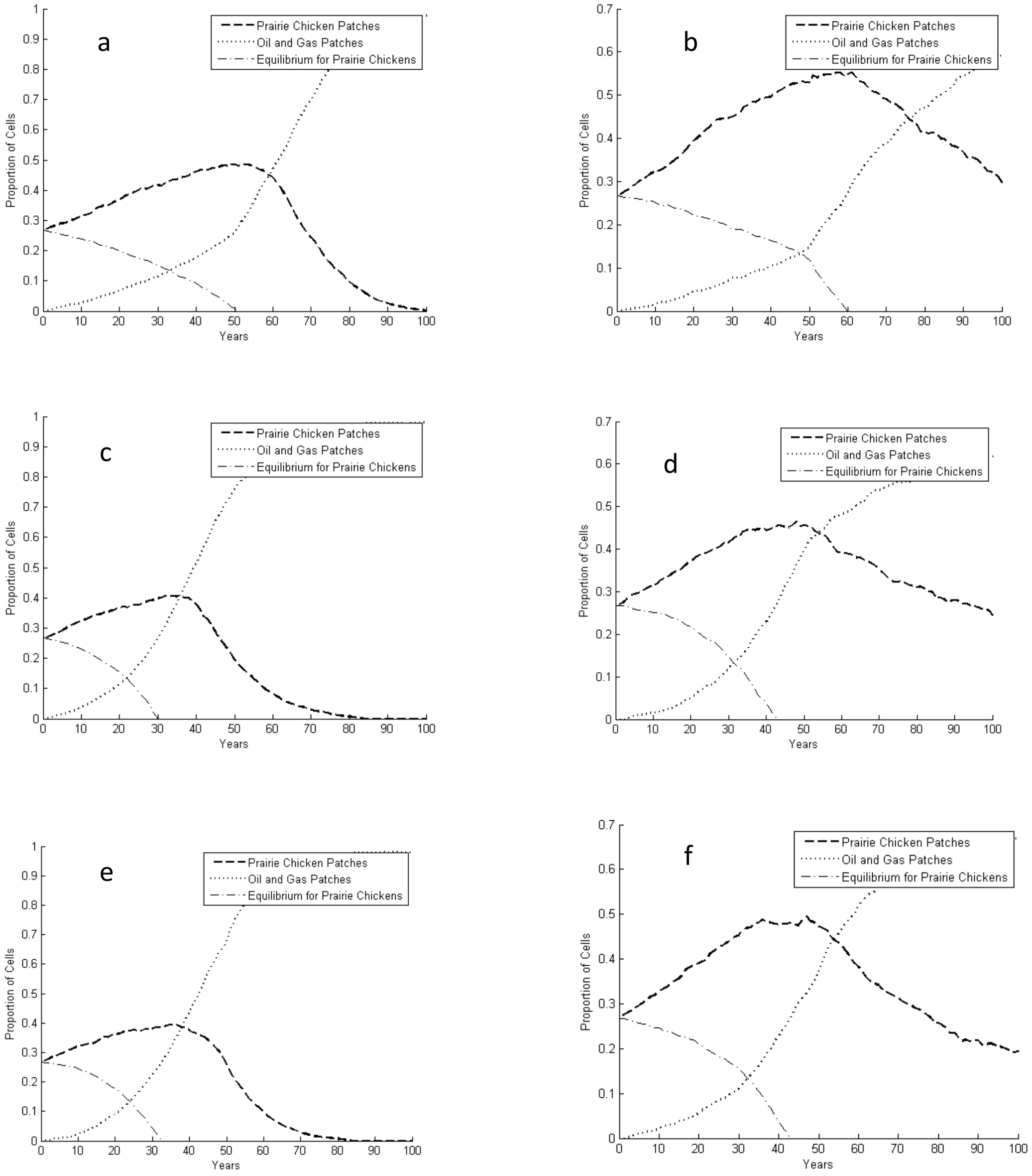

a
b
c
d
e
f
Prairie Chicken Patches
Oil and Gas Patches
Equilibrium for Prairie Chickens
Proportion of Cells
Years
0
10
20
30
40
50
60
70
80
90
100
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

Figure 5.

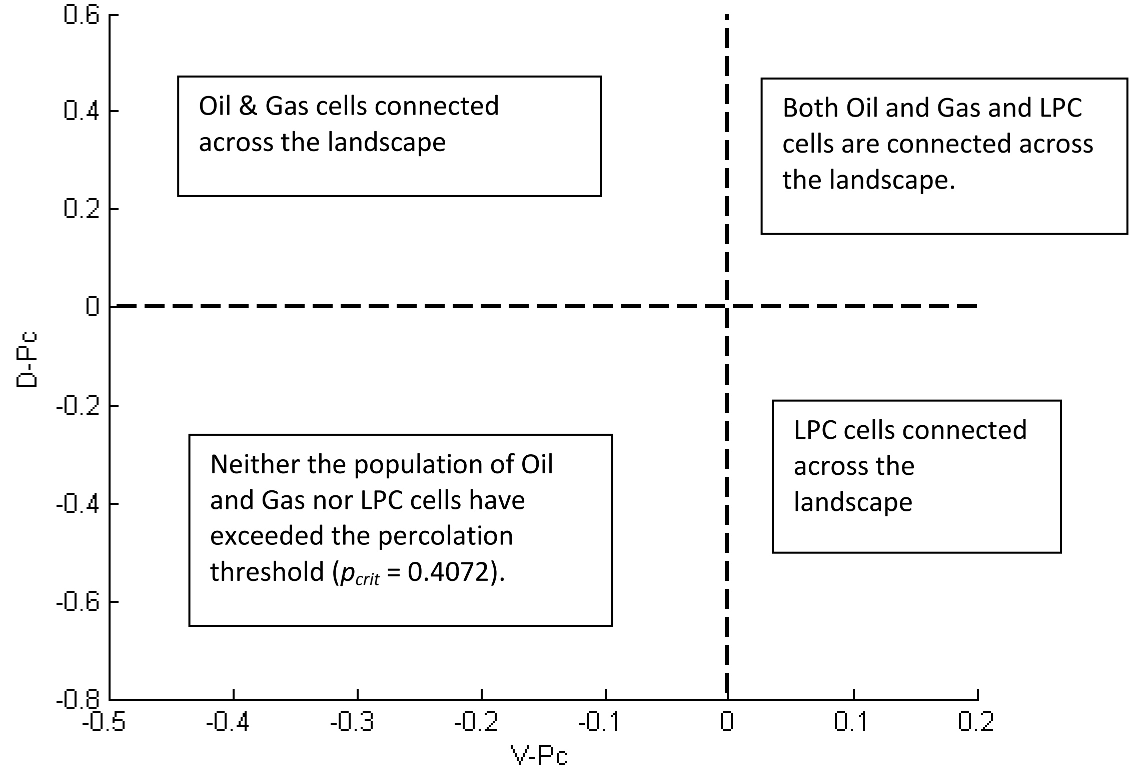
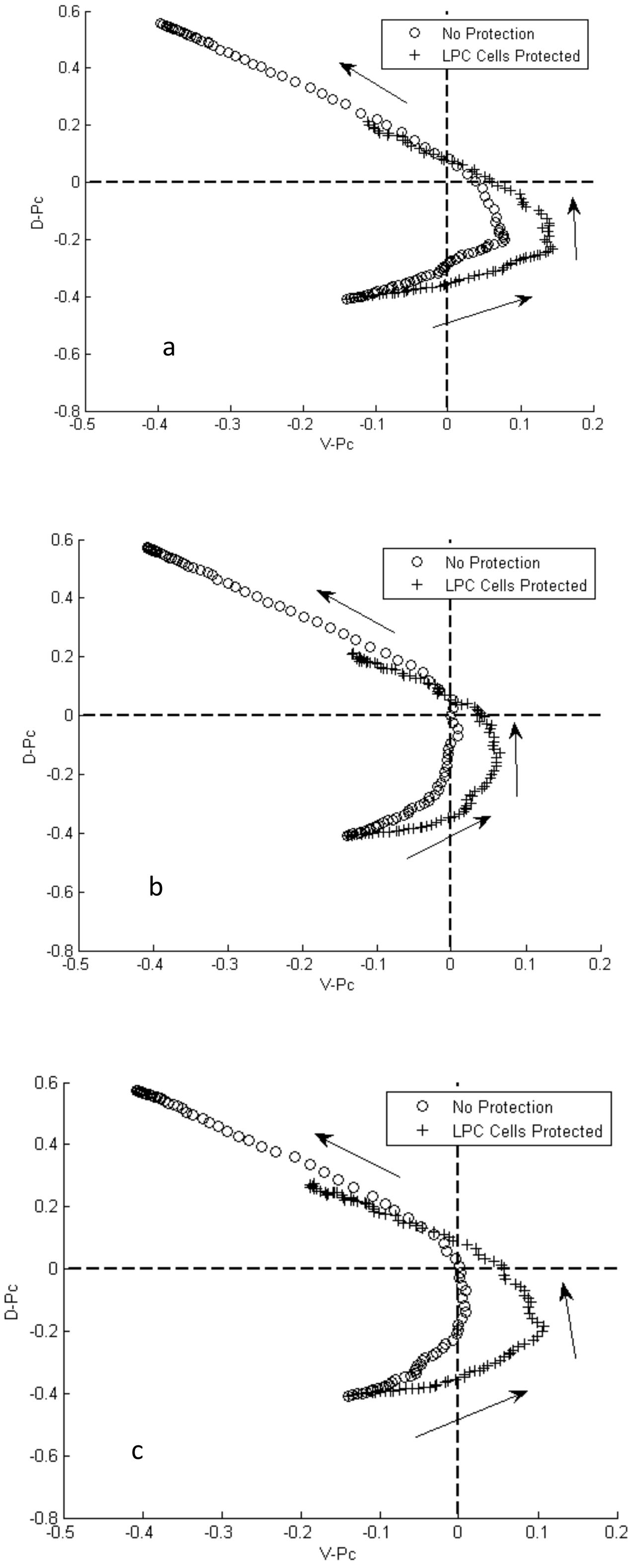

0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
D-Pc
-0.5
-0.4
-0.3
-0.2
-0.1
0
0.1
0.2
V-Pc
Oil & Gas cells connected across the landscape
Both Oil and Gas and LPC cells are connected across the landscape.
Neither the population of Oil and Gas nor LPC cells have exceeded the percolation threshold (p_{crit} = 0.4072).
LPC cells connected across the landscape

Figure 6.


No Protection
LPC Cells Protected
a
b
c
D-Pc
V-Pc
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-0.5
-0.4
-0.3
-0.2
-0.1
0
0.1
0.2

Chapter 3

Spatial Renormalization as a Multiscale Approach to Determining the Security of Landscapes

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Abstract

A landscape is a heterogeneous mosaic in which the contribution of each location to organismal fitness, particularly security, varies along a continuum from detrimental to optimal. Yet, currently available connectivity indices provide a discrete categorization of landscapes: patches have value, but the matrix does not. We used majority rule renormalization to measure security of individual cells across entire landscapes. Simulated landscapes, lattices of equal-sized cells that were classified as habitat (value = 1) or non-habitat (value = 0), were sampled with non-overlapping 2 x2 cell windows. All cells within the window were reclassified to the same numerical value as the majority of cells. The sum of values derived from all renormalizations was the Security Index (*SI*) for each cell.

Using simulated landscapes, we randomly classified cells as habitat in densities of $p = 0.1$ to 0.9 and calculated *SI*. We also introduced different-sized disturbances and measured changes in *SI*. Values of *SI* increased nonlinearly with habitat density at all scales. As scale increased, a spatial phase transition in *SI* became evident at $p = 0.5$. In disturbed landscapes, mean ΔSI increased with size of disturbance, scale, and habitat density. Small disturbances did not affect *SI* beyond 20 cells from disturbances. Medium and large disturbances affected *SI* more than 25 cells from all disturbances. Our results are consistent with empirical observations concerning the value of landscapes in providing security. This technique can contribute to more accurate evaluations of landscapes for corridor conservation, habitat restoration, and translocations of wildlife.

Key Words: connectivity, disturbance, landscape, renormalization, scale, security

Introduction

Organisms persist in nature by maintaining a positive energy balance. More energy must be gained through intake of nutrients than lost through metabolism, reproduction, and behavior and movements to obtain resources or to avoid mortality (Fahrig 2002; Brown et al. 2004)

No landscape provides this positive balance at all locations (Senft et al. 1987). Rather, a landscape is a heterogeneous mosaic in which the contribution of each location to fitness of an organism varies from detrimental to optimal. Determining the relationship between landscape pattern and organismal fitness requires measuring composition and configuration of landscapes at scales that are pertinent to the species of interest.   This is especially important when considering the effect of anthropogenic disturbances which can change natural patterns to which organisms are adapted either through fragmentation or simplification of landscapes (Mader 1984, Krummel et al. 1987).

One critical aspect of the relationship between landscape pattern and organismal fitness is how heterogeneity affects security. Specifically, security is characterized by landscape traits that provide protection from disturbance and mortality and contribute to a positive energy balance by reducing the frequency of vigilance and flight (Freddy et al. 1986, Hobbs 1989, Berger 1991, Taylor and Knight 2003). Security of a landscape is the degree to which those traits are available to organisms. Traits that drive security include vegetation and topography that reduce the probability of organisms being seen or heard, and distance that diminishes the intensity of sounds and movements that disrupt normal activities (Bowles 1995).

The sheer complexity of landscapes and idiosyncrasies of organisms makes measuring security a difficult task. This difficulty often is overcome by representing landscapes as lattices of equal-sized cells with each cell classified as habitat (i.e., essential life requisites, including security, are provided) or non-habitat for the species of interest. Adjacent cells of habitat are then grouped into patches. Numerous indices have been developed to measure connectivity among the resulting patches; all generally use patch size and/or distance among patches as foundational metrics (Turner et al. 1989; Li and Reynolds 1995; Keitt et al. 1997; Gustafson 1998; Moilanen and Nieminen 2002; Winfree et al. 2005; Magle et al. 2009; Prugh 2009). Increasing patch size and decreasing distance among patches result in higher values, presumably indicating better security.

Connectivity indices have proven valuable but they do not provide all essential measures for characterizing landscape quality. First, the single value given each patch ignores within-patch heterogeneity. In the context of security, the difference between the interior and edge of a patch, for instance, has been recognized for over 70 years (Leopold 1933) and this difference may be critically important in the population dynamics of certain species. A prime example is the disproportionately high frequency of parasitism by cowbirds on nests of other bird species located within 300 m of forest patch edges (Brittingham and Temple 1983; Sedgwick and Knopf 1988).

Connectivity indices also reduce landscapes to binary entities: patches have value, but the matrix does not. This segregation is a holdover of island biogeography theory (MacArthur and Wilson 1967) in which the ocean between source and target islands is of no value to colonizing organisms. However, terrestrial matrices contain a mix of features that offer varying levels of security. Stepping stones (fragments of preferred habitats too small for long-term residency) are particularly valuable components; indeed, Gilpin (1980) posited size and placement of stepping stones within a matrix contribute more to colonization than size of the destination patch. By affecting rate, direction, and distance of movements among patches, and in turn, energy expenditure, matrix heterogeneity and the variation in security it offers has a major effect on organismal fitness and population persistence (Forman 1997; Sakai and Noon 1997; Tischendorf and Fahrig 2001; Ricketts 2001; Baum et al. 2004).

Lastly, connectivity indices do not facilitate examination of a landscape at multiple scales relevant to the suite of species that occupy it. The proportion of a landscape and size of patches used by organisms is positively related to body size and attendant energy needs (Charnov 1976; Peters 1983; Milne et al. 1991; Peterson et al. 1998). Thus, security provided by an isolated cluster of patches may be adequate for a population of small organisms with highly localized distributions. The same cluster may provide little security for large, wide-ranging organisms because the small search area and long distance to other clusters might cost too much in vigilance and flight to maintain a positive energy balance.

One solution to these shortcomings lies in spatial renormalization where fine-scale patterns of landscapes are measured at a cellular level and translated to broader, more coarse-scale representations through aggregation of cells (Creswick et al. 1992; Milne and Johnson 1993). Spatial renormalization has been used to model wildfire behavior (Loreto et al. 1995), red-cockaded woodpecker habitat, (Milne 1997) and woodland ecotones (Milne et al. 1996). We employed spatial renormalization to model security of landscapes at multiple scales. In this paper, we provide an overview of the origin and properties of our Security Index (*SI*), followed by an analysis of how *SI* values (1) differ from those of a representative connectivity index, (2) differ between the perimeter and interior of patches and between patches and the matrix, and (3) differ with size of, and distance from, disturbance.

Methods

Origin and Properties of the Security Index

All analyses were conducted using MatLab 7.4© programming language (The MathWorks, Inc., Natick, MA). We used majority rule renormalization (Turner et al. 1989) to measure security. For this technique, maps of equal-sized cells, in which each cell was classified as habitat (value = 1) or non-habitat (value = 0), were sampled with non-overlapping windows of length $L = 2$ (i.e., 2 x 2 cells) (Fig. 1). Windows were assigned the same numeric value as the majority of the cells within them or randomly assigned 0 or 1 if there were equal numbers of cells of each value. Values of each window were translated to the cells of the original map that comprised that window. This process was repeated with windows of the previous renormalization becoming cells (i.e., cells increased in size by 2^k, where k = the number of renormalizations) until the size of windows encompassed the area of interest, such as a species' home range. The Security Index (*SI*) for each cell was the sum of values derived from all renormalizations.

Majority rule renormalization possesses a well-known critical probability (p_{crit}) of 0.5 (Creswick et al. 1992; Milne and Johnson 1993). Above p_{crit}, the density of cells reclassified to 1 increases with each change in scale; below this value, the density decreases. We examined *SI* to see if it exhibited a similar pattern around p_{crit}. First, we derived an equation to model this relationship by subtracting the original probability of a cell being assigned a value of 1 (p) from an expression for the sum of probabilities that could produce cells with a value of 1 at the next scale (p'). Thus,

$$\Delta p/\Delta L = p' - p = 3p^2 (1 - p)^2 + 4 p^3 (1 - p) + p^4 - p \qquad [1]$$

where $3p^2 (1 - p)^2$ represents the half of the 6 possible combinations of 2 cells with values of 1 (p) and 2 cells with values of 0 ($1-p$) (since these combinations have an equal probability of resulting in 0 being assigned to the next scale), $4p^3 (1-p)$ represents the four possible combinations of 3 cells with values of 1 and 1 cell with a value of 0, and p^4 represents the one combination of 4 cells with values of 1. Expanding the equation and collecting terms resulted in the cubic function,

$$\Delta p/\Delta L = -p + 3 p^2 - 2 p^3 \qquad [2]$$

Next, we created a 256 x 256 cell gradient map in which the probability of a cell being classified as habitat increased linearly along the x-axis and renormalized the map once (Fig. 2). The rate of change in probability of cells being assigned a value of 1 with change in scale ($\Delta p/\Delta L$) was graphed against *SI* for all values of *SI* =

2p by inputting values of p into Eq. 2 to create an analytical curve and by graphing the renormalized values of the gradient map (Fig. 3).

Is SI different from Connectivity Indices?

The method for calculating *SI* may differ from that of connectivity indices, but if the resulting values are the same, it would offer little improvement in measuring security across landscapes. To compare values, we created neutral landscapes (With et al. 1997), 256 x256 cell maps in which a pre-determined density of cells were randomly selected and classified as habitat. We renormalized the maps as described above 1 and 7 times (the smallest and largest scales for 256 x 256 cell maps).

Connectivity was calculated using the Incidence Function Model (*IFM*) (Prugh 2009)

$$IFM = A_i^c \sum_{j \neq i}^{n} A_j^b \exp\left(-\alpha d_{ij}\right) \qquad [3]$$

where A_i^c is the area of focal patch i of which a cell is a part, scaled by the rate of emigration (c), A_i^b is the area of neighboring patch j, scaled by the rate of immigration (b), d_{ij} is the minimum edge-to-edge distance between patches i and j, α is the inverse value of the average dispersal distance for the organism of interest. We chose this distance-weighted, area-based model for comparison because it has outperformed buffer and nearest neighbor models (Moilenan and Nieminen 2002, Bender et al. 2003, Prugh 2009). Patches were groups of habitat cells that were orthogonally and diagonally adjacent to one another. Patches <1000 cells in which $\geq$1 cell was part of the border of the map were deleted because patch statistics might be biased by truncation. The 300 largest patches were selected for further analysis. Area was the number of cells encompassed by a patch. Edge-to-edge Euclidean distances were calculated from each patch to all other patches. Five values of α (0.01, 0.1, 1, 10, and 100) were used in this analysis, but immigration (b) and emigration (c) were set to 1 because *IFM* has been found to be insensitive to changes in those parameters (Prugh 2009).

Both *SI* and *IFM* are affected by values of neighboring cells or patches, so patches may not be independent of their neighbors. To address this, we divided each map into 32 x 32 cell blocks and randomly selected one patch from each block for a maximum of 64 patches. Using a new map each time, we conducted 25 simulations for each combination of habitat density ($p = 0.1$ to 0.9, i.e., 10 to 90% of the map classified as habitat), α, and scale (2^k, $k = 1, 7$). Correlation coefficients (ρ) were then calculated between *IFM* and mean *SI* values of the selected patches.

Do SI values vary by Landscape Component?

The basis of security is availability of habitat and this should be reflected in the order of *SI* values for the 3 major landscape components, namely patch interiors (surrounded by habitat) > patch perimeters ($\geq$ 1 side bounded by habitat) > matrix (not bounded by habitat except if part of a fragment). Additionally, values of all components should increase with a uniform increase in habitat density since habitat will be more available at all locations. To test these expectations, we created maps and combined cells into patches as described above. We calculated *SI* and classified cells as matrix if they were not part of a patch $\geq$ 9 cells (the smallest patch containing interior cells), perimeter if they were located at the maximum or minimum addresses in rows and columns of a patch, and interior if otherwise. For each of the 3 classifications, we randomly selected 1000 cells and calculated the mean *SI* of the sample. These steps were repeated 100 times for each combination of habitat density (p = 0.1 to 0.9) and scale (2^k, k = 1, 7) and a grand mean and 95% confidence intervals were calculated from the resulting values. Values of components within and among habitat densities were considered the same if their confidence intervals overlapped.

How is SI affected by disturbance?

Organisms respond to anthropogenic activities by reducing their use of, or altering their behavior in, areas where those activities adversely affect them. The result is a reduction in availability or use of habitat, and in turn, reduced security. Based on this, aspects of disturbance that might affect security at a given location include disturbance size, amount of habitat disturbed, proximity to the disturbance, and proximity to undisturbed habitat. We tested the behavior of *SI* when landscapes are disturbed by first measuring *SI* in 256 x 256 cell maps as described above. Then a disturbance was simulated by making all cells equal to 0 within a specified area that was randomly located $\geq$50 cells from the map border. We re-measured *SI* and calculated the change in values of each cell in the map. Mean change in *SI* (ΔSI) per cell was recorded where the disturbance occurred and within 5 distance categories: 1-5, 6-10, 11-15, 16-20, and 21-25 cells away from the orthogonal edges of the disturbance.

We repeated these steps 100 times for each combination of 3 factors: disturbance size (L = 5, 25, 50), scale (2^k, k = 1, 7), and habitat density (p = 0.3, 0.5, and 0.7). Analysis of variance (ANOVA) was used to determine differences in response of *SI* to the 3 factors and to distance from the disturbance (Zar 1974). Post-hoc comparisons of Δ*SI* for individual factors were conducted using Tukey's test. Confidence intervals (95%) were calculated around the grand mean of Δ*SI* for the 100 simulations of each combination of factors.

Results

With values from the gradient map, the rate of change in the probability of a cell being assigned a value of 1 with a change in scale, $\Delta\square p/\Delta\square L$, decreased below and increased above SI_{crit} (p_{crit} after one renormalization: $SI_{crit} = 2p_{crit} = 1$) (Fig. 3). The pattern matched the analytical curve derived from the cubic function except for deviations when cells with value = 1 were extremely sparse or extremely abundant.

Across all habitat densities, *SI* and *IFM* were correlated in only 29 of 386 simulations (7.5%) when k =1 and 31 of 386 simulations (8.0%) when $k = 7$ (Fig. 4). The highest number of correlations was at $p = 0.4$ (9/25 and 10/25 for $k = 1$ and $k = 7$, respectively).

Values of *SI* were highest in patch interiors and lowest in the matrix for all habitat densities. Differences in *SI* among cell types remained relatively constant (i.e., Δ*SI* between perimeter and matrix cells ~1.5) across habitat densities and at small and large scales (Fig. 5). Security increased nonlinearly with habitat density for all cell types at both small and large scales. Increases in *SI* were relatively continuous for $k = 1$. For $k = 7$, a phase transition was evident at p_{crit}.

All factors and all interactions among factors affected *SI* when landscapes were disturbed (Table 1). Distance from disturbance had the largest effect, followed by scale. Mean Δ*SI* increased with size of disturbance, scale, and habitat density. It decreased markedly from the disturbance to distance category 1 (1-5 cells), but much less so for subsequent distance categories (Fig. 6). Small disturbances (L=5) had no effect on *SI* values beyond 10 cells (category 2) for p = 0.3 and 0.5 when k = 7, and beyond 20 cells (category 4) for all habitat densities when k = 1 and p = 0.7 or when k = 7. Medium and large disturbances (L=25, 50, respectively) affected *SI* values more than 25 cells from the disturbance for all habitat densities and scales.

Discussion

For over a century, ecologists have recognized that landscape heterogeneity affects ecological processes at all scales (Cowles 1899; Elton 1927; MacArthur 1972; Forman and Godron 1986; Li and Reynolds 1995; Gustafson 1998). Yet, determining just how landscape heterogeneity influences organismal fitness continues to be an evolving process (Gustafson and Gardner 1996). Our technique contributes to this process with an ecologically relevant means of modeling security, a key contributor to fitness.

The matching patterns between the analytical curve and values from the gradient map (Fig. 3) provide a proof of the *SI* concept and show how security will change with any two-fold change in scale. Deviations between the analytical curve and gradient map data when cells with values of 1 were extremely sparse or abundant illustrate the effect of neighborhood composition on security. As p approached 0, there was an increasing chance of a habitat cell receiving a value of 0 during renormalization because that was the value of most surrounding cells. The opposite was true with high habitat densities; within a local domain, non-habitat cells received higher security values than expected due to proximity to habitat cells (i.e. a form of "rescue effect" (Brown and Kodric-Brown 1977)).

Both *SI* and connectivity indices, such as *IFM*, are based on amount of, and distance to, habitat. Additionally, the basic grain of both types of techniques is the cell when connectivity indices are calculated from a lattice. Given this, one might expect *SI* and *IFM* values would be correlated. The reason we found few correlations likely is a consequence of *SI* being a cell-level and *IFM* a patch-level measure. The fine scale of the single cells yields a continuum of values across a landscape (Fig. 7). With *IFM*, cells are combined into patches with each cell within a patch having the same value; the result is a markedly coarser grain. Including the matrix (valued at 0) yields a disjunct distribution in contrast to the more continuous distribution of values produced by *SI*.

The positive relationship between security and habitat density (Fig. 5) is consistent with well-known empirical findings that patch size increases and distance decreases as the amount of habitat increases (Forman 1997). The order of security among landscape components (patch interior>patch perimeter>matrix) emphasizes the importance of composition of the immediate neighborhood to security at any given location.

The relatively continuous increase in security with habitat density at $k = 1$ suggests organisms operating at small scales would be sensitive to changes in their immediate neighborhood (Fig. 5a). Conversely, the disjunct relationship between security and habitat density at large scales (Fig. 5b) reflects a relative insensitivity to fine-scale changes in habitat geometry (Milne and Johnson 1993; Milne 1998; Peterson 2002). Based on this pattern, large, wide-ranging organisms might be expected to have a much more discrete perception of their landscape: either it is secure or it is not. Small increases in *SI* from $p = 0.1$ to 0.4 or $p = 0.6$ to 0.9 provide some improvement in structural connectivity (Tischendorf and Fahrig 2001), but functional connectivity (that which contributes to change in organismal behavior, such flight or vigilance) likely only changes when habitat densities change between minority and majority status on the landscape.

Analyses of disturbance generally are focused on three aspects: (1) site-specific physical destruction of habitat, (2) behavioral changes of organisms which result in avoidance of habitat near disturbances (Pitman et al. 2005), and (3) increased energy expenditure for vigilance and flight (Hobbs 1989). Our results revealed other factors warrant consideration. First, disturbance size is not necessarily equivalent to impact. A large disturbance may be inconsequential if little habitat is in its path (Figs. 6e 8a, 8c). Conversely, destruction of a small patch of high density habitat could reverberate well beyond the area directly disturbed through its effect on landscape connectivity (Fig. 6d). Kiett et al. (1997) provides an excellent example of this concept: one of the smallest islands of habitat for Mexican spotted owls (*Strix occidentalis lucida*) in the southwestern United States was found to be one of the most important because of its strategic role as a stepping stone between two much larger islands.

Next, scale plays an essential role in defining impact. Although seemingly counterintuitive, disturbances may impact species that operate at small scales less than those that operate at large scales. Species with localized distributions might be decimated in the vicinity of a disturbance, but may continue to persist if populations occur elsewhere on the landscape. Conversely, the same disturbance might directly impact only a few individuals of a wide-ranging species, but population persistence could be greatly reduced because access to critical resources is reduced or destroyed.

Lastly, total destruction of habitat may not mean total loss of security at a particular location. A disturbed location in the landscape may still be used if it is adjacent to large accessible patches of undisturbed, secure habitat (Fig. 7d).

Applications for Conservation

Determining how to best conserve natural resources requires field studies to obtain empirical data. However, spatial modeling is equally important, providing a venue for discovering how landscape composition, configuration and scale define relationships between organisms and the landscapes they occupy (Brooker et al. 1999). In this context, *SI* can contribute to conservation in three important roles: selecting corridors, evaluating the benefits of habitat restoration, and determining the natural potential of translocation sites. For each application, *SI* provides a means of determining how site-specific impacts affect any location on the landscape simply by changing the state of a single or group of cells and calculating ΔSI at pertinent scales.

Least cost path analysis is a popular analytical technique to identify the matrix corridor between two patches most beneficial to organismal fitness. However, the resulting single path does not account for connections across the landscape and their effect on security along the path. Preserving the route might prove futile if habitat elsewhere on the landscape that provides connectivity along the path is destroyed. Using *SI* in new cost path techniques, such as multiple shortest paths (Pinto and Kiett 2009), can provide a dataset to compare multiple routes, evaluate how species that operate at different scales may benefit from each potential route, and evaluate how a specific disturbance may affect security of each route.

Habitat restoration is playing an increasingly important role in countering the adverse impacts of anthropogenic disturbances. However, recognition of benefits often is limited to the restoration site. We demonstrated that *SI* can identify how disturbance may reverberate across the landscape. In the same way, *SI* also can identify how restoration might enhance connectivity and provide indirect benefits to other parts of the landscape. Restoration is a costly endeavor; employing a wider perspective can help determine the true value of investment.

Many translocated populations of birds and mammals go extinct or need long-term management to persist (Wolf et al. 1996). Predation sometimes plays a significant role because translocated individuals are naïve about resident predators, sympatric domestic livestock may attract predators thereby increasing predation rates on translocated individuals, and the small size of the founding population may make individuals particularly conspicuous (Rominger et al. 2004; Rominger and Weisenberger 2002). The *SI* technique can help identify areas of vulnerability for translocated individuals and provide a tool to analyze mitigative measures that might reduce vulnerability.

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Table 1. Analysis of variance of changes in the Security Index (Δ*SI*) due to disturbance. Factors and their values included in the analysis included habitat density (0.3, 0.5 or 0.7), distance (categories: 1-5, 6-10, 11-15, 16-20, 21-25 cells away from the edge of the disturbance), number of renormalizations (k = 1, 7), and size of disturbance (L=5, 25, 50 cells). Mean values of Δ*SI* were derived from 100 simulations for each combination of factors.

Source	Degrees of Freedom	Mean Square	F value	P value
Habitat Density (HabDens)	2	216.61	1362.11	0.0072
Distance from Disturbance (Dist)	5	704.66	4431.10	0
Number of Renormalizations (*k*)	1	374.13	2352.63	0
Size of Disturbance (Size)	2	77.64	488.19	0.003
HabDens *Dist	10	86.88	546.32	0.016
HabDens **k*	2	78.46	493.4	0.003
HabDens *Size	4	17.19	108.1	0.0013
Dist* *k*	5	114.85	722.23	0.0112
Dist*Size	10	7.75	48.71	0.0013
k *Size	2	50.01	314.51	0.0018
HabDens *Dist* *k*	10	26.49	166.59	0.0052
Dist* *k* *Size	10	7.58	47.7	0.0013
HabDens *Dist*Size	20	3.52	22.17	0.0013
HabDens * *k* *Size	4	12.6	79.2	0.0006
HabDens *Dist* *k* *Size	20	2.86	18.03	0.0007
Residual	10692	0.16		
TOTAL	10799			

Figures

1. Aggregation and reclassification of cells using majority rule renormalization. All cells within a 2x2 cell window at the original resolution (*L*, dotted line) are grouped as a single cell at the next level, *L*'. A second renormalization transforms a block of larger cells (dashed line) to a single cell at the third scale, *L*''. The security index (*SI*) of each cell is its original state (habitat = 1, non-habitat = 0) plus the values derived from subsequent renormalizations.

2. A gradient map showing security values for each cell following one renormalization. In the original map, the probability, *p*, of a cell being classified as habitat (value = 1) increased linearly along the x-axis.

3. Change in probability of a cell being assigned a value of 1 with a change in scale, $\Delta p / \Delta L$. Shown is the probability of a cell being assigned a value of 1 for any two-fold change in scale based on an analytically derived cubic function (line) and based values derived from a gradient map where the probability of habitat increased uniformly along the x-axis. The probability of cells receiving a value of 1 after renormalization of the gradient map is noticeably different from when habitat is extremely sparse (“impoverished”) or extremely abundant (“enriched”).

4. Correlations between Security Index (*SI*) and Incident Function Model (*IFM)* values for habitat densities ranging from $p = 0.1$ to 0.9 at (a) small ($k = 1$) and (b) large ($k = 7$) scales. Values of $\rho > 0.246$ (horizontal dashed lines) indicate positive correlations.

5. Mean *SI* for interior, perimeter, and matrix cells at habitat densities ranging from $p = 0.1$ to 0.9 at (a) small ($k = 1$) and (b) large ($k = 7$) scales. Vertical lines represent 95% confidence intervals around mean *SI* values. Values of *SI* differed among all cell types for all habitat densities.

6. Mean change in *SI* (ΔSI) with increasing distance from disturbance for three densities of habitat ($p = 0.3$, 0.5, 0.7). Vertical lines represent 95% confidence intervals around each mean. Distances categories along the x axis (0 , 1, 2, 3, 4 , and 5) represent the disturbance, and 1-5, 6-10, 11-15, 16-20, 21-25 cells from the orthogonal edges of the disturbance, respectively. Results are from 100 simulations for each combination of disturbance size (*L*) and number of renormalizations (*k*).

7. Lattice displaying values derived from the (a) Security Index and (b) Incidence Function Model.

8. Change in security (ΔSI) at small ($k = 1$) and large ($k = 7$) scales and low ($p = 0.3$) and high ($p = 0.7$) densities of habitat.

Figure 1.

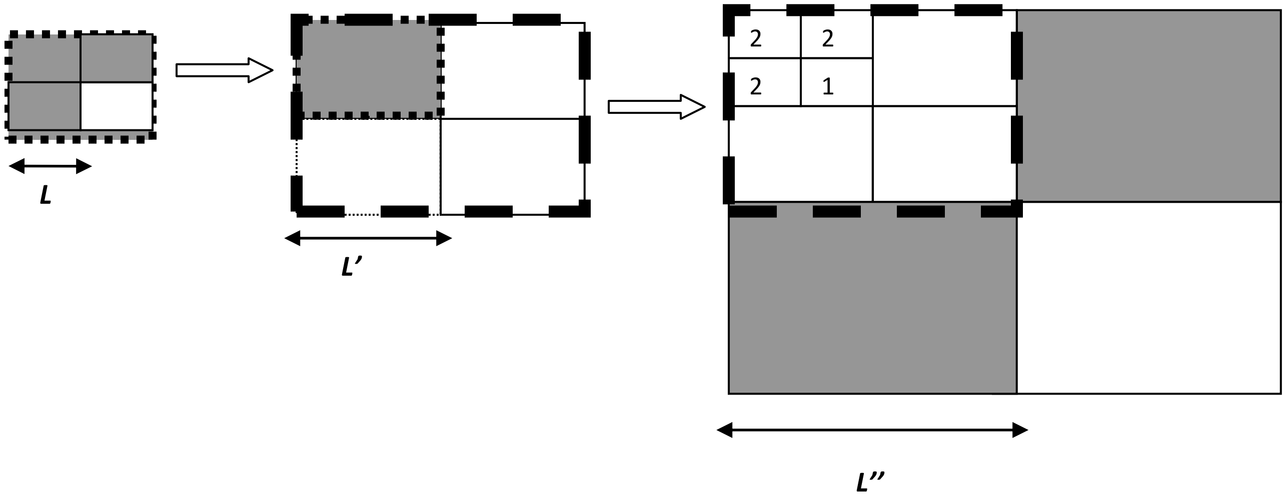
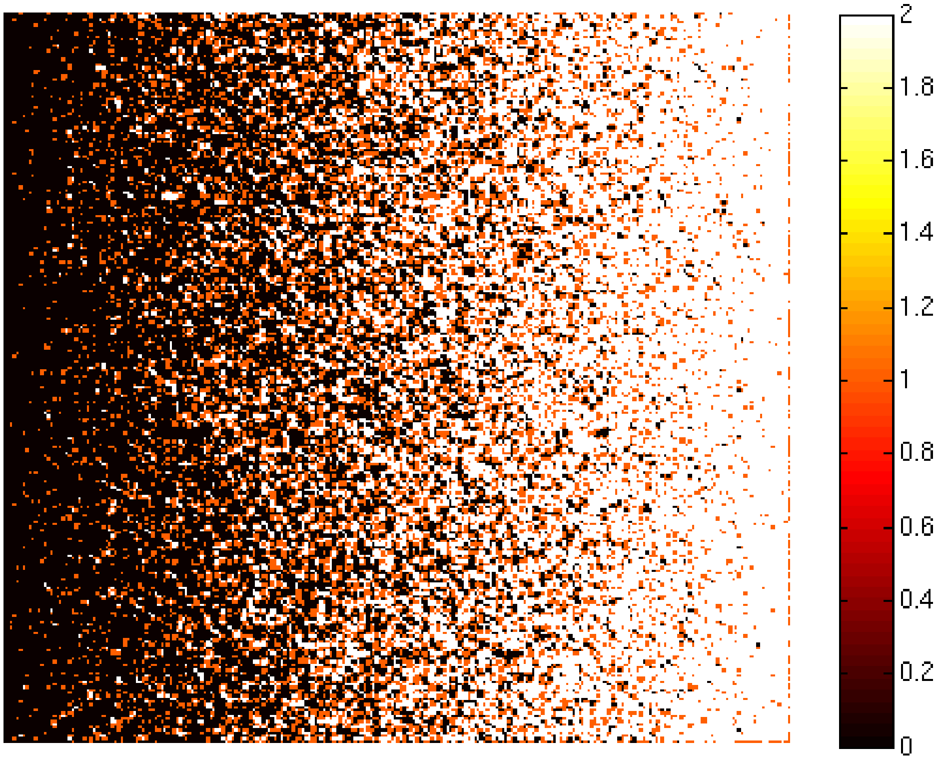
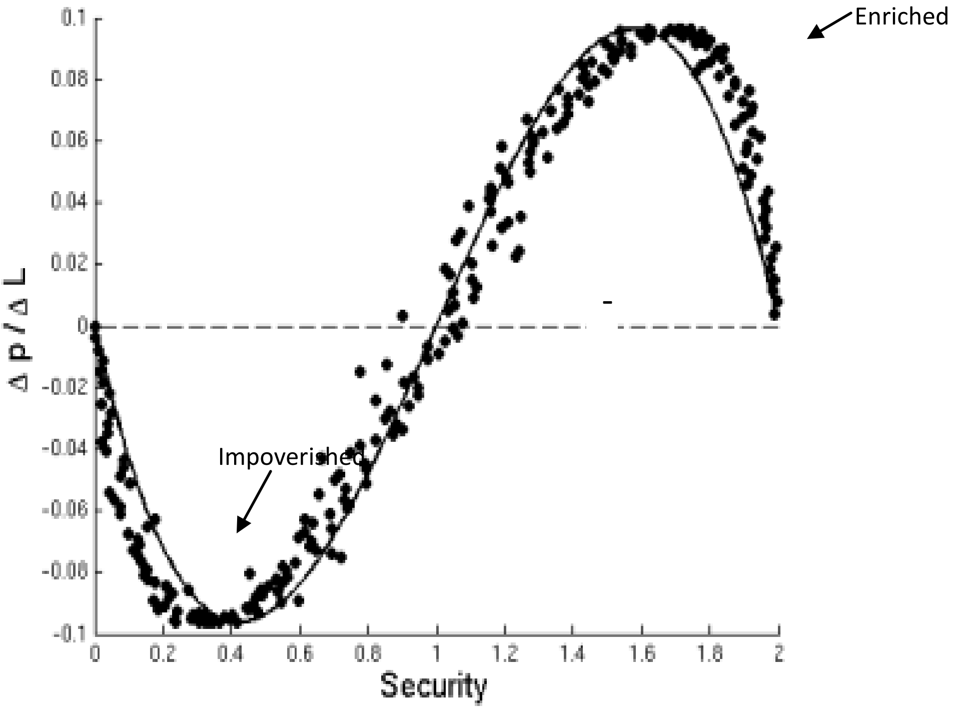


Figure 2.



.Figure 3.



Enriched
Impoverished
0.1
0.08
0.06
0.04
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
Δ p / Δ L
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
Security

Figure 4.

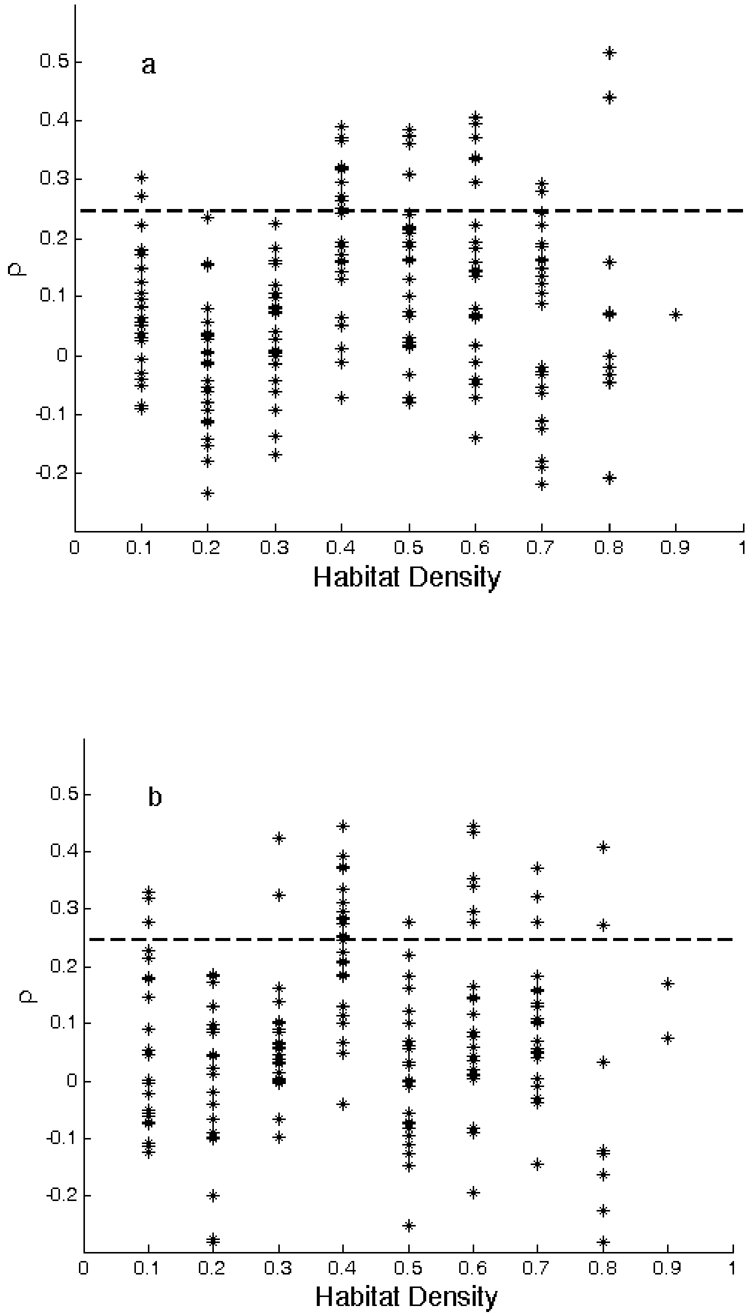

a
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
P
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Habitat Density
b
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
P
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Habitat Density

Figure 5.

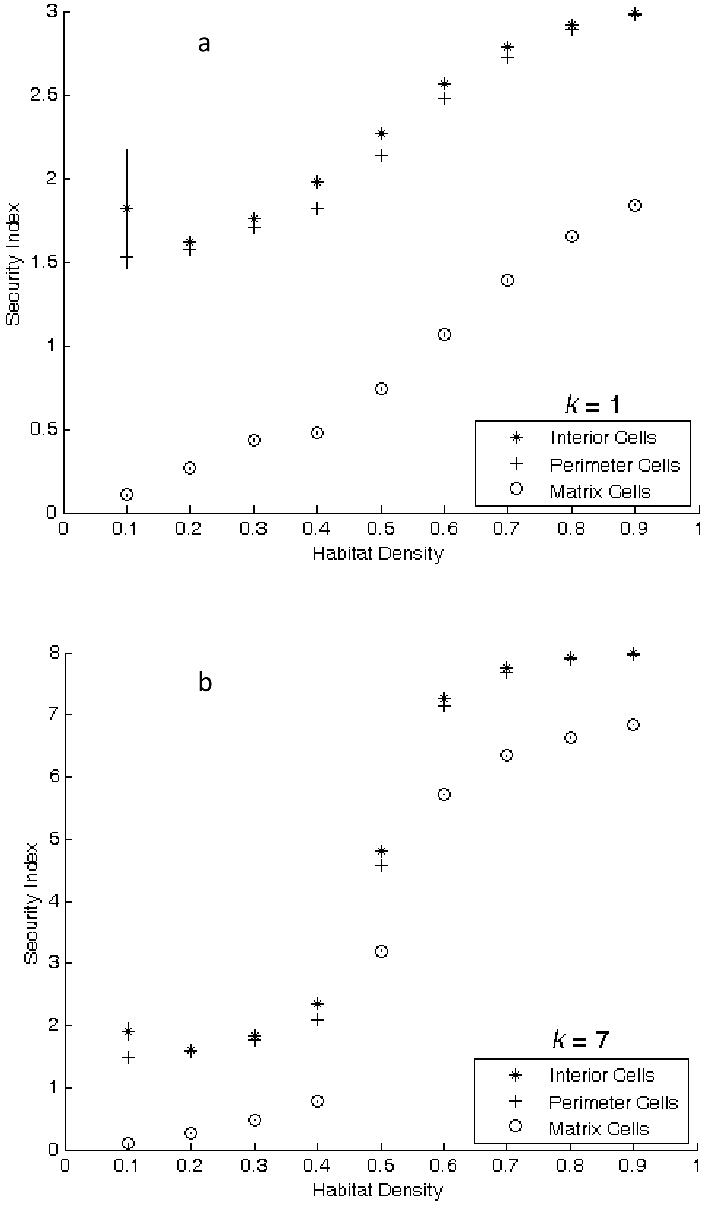

a
Security Index
Habitat Density
0
0.5
1
1.5
2
2.5
3
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
k = 1
Interior Cells
Perimeter Cells
Matrix Cells
b
Security Index
Habitat Density
0
1
2
3
4
5
6
7
8
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
k = 7
Interior Cells
Perimeter Cells
Matrix Cells

Figure 6.

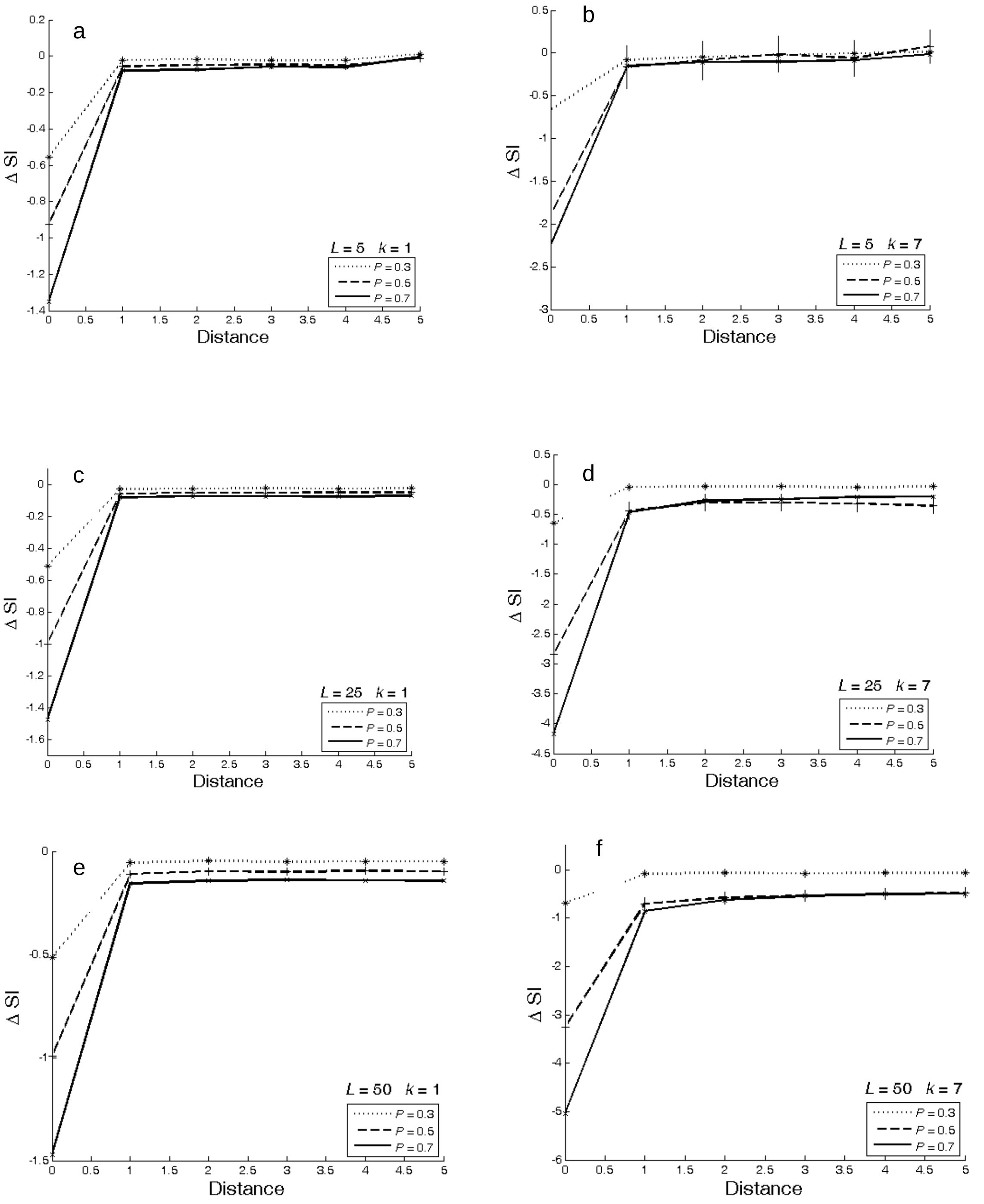

a
Δ SI
Distance
L = 5 k = 1
P = 0.3
P = 0.5
P = 0.7
b
Δ SI
Distance
L = 5 k = 7
P = 0.3
P = 0.5
P = 0.7
c
Δ SI
Distance
L = 25 k = 1
P = 0.3
P = 0.5
P = 0.7
d
Δ SI
Distance
L = 25 k = 7
P = 0.3
P = 0.5
P = 0.7
e
Δ SI
Distance
L = 50 k = 1
P = 0.3
P = 0.5
P = 0.7
f
Δ SI
Distance
L = 50 k = 7
P = 0.3
P = 0.5
P = 0.7

Figure 7.

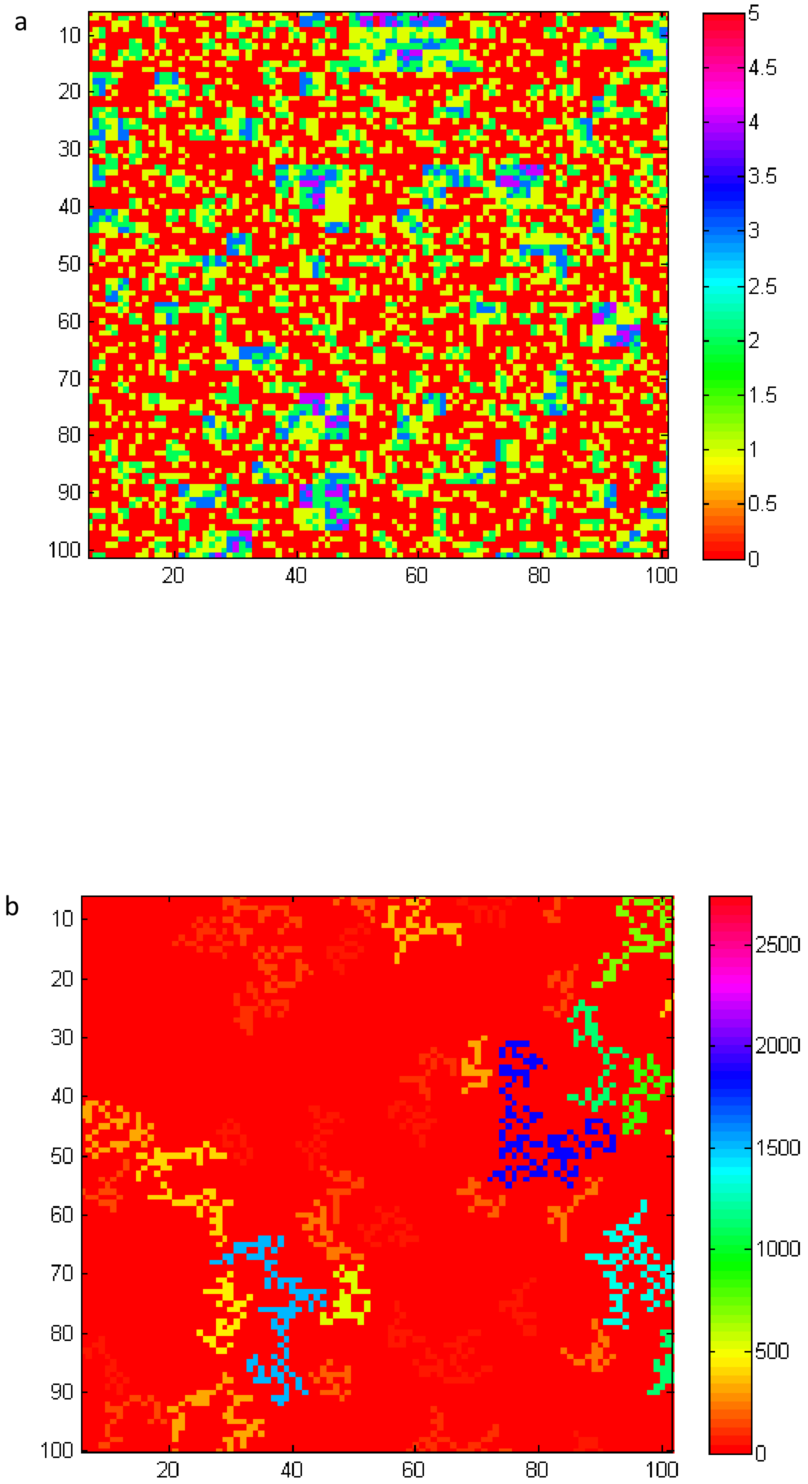
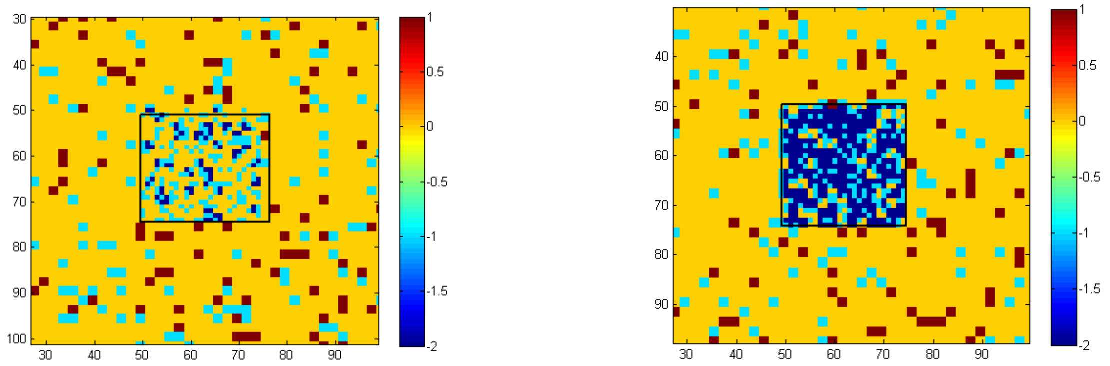
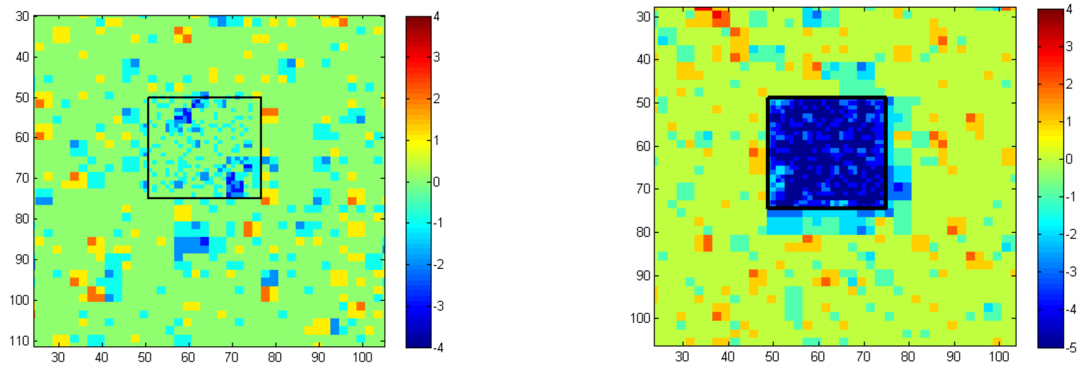

a
10
20
30
40
50
60
70
80
90
100
20
40
60
80
100
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
b
10
20
30
40
50
60
70
80
90
100
20
40
60
80
100
2500
2000
1500
1000
500
0

Figure 8.

a. *k* = 1 *p* = 0.3 b. *k* = 1 *p* = 0.7



c. *k* = 7 *p* = 0.3 d. *k* = 7 *p* = 0.7



Chapter 4

Scaling Relations between Riparian Vegetation and Stream Order in the Whitewater River network, Kansas, USA

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Abstract

Riparian communities have been well-studied along individual streams, but not within the context of networks of which streams are a part. To study networks, hydrologists use Horton-Strahler ordering to assign streams to discrete categories in which increasing numerical value (ω) reflects increasing size of the stream and complexity of the network. A key use of this classification method has been to demonstrate scaling relations between hydrogeomorphic variables and order. These relations now provide a foundation to determine how ecological processes are associated with the geometry and topology of river networks. We used geographic information systems (GIS) to map and measure the stream network and riparian vegetation of the Whitewater River basin of eastern Kansas, USA. With the resulting data, we tested if (1) riparian vegetation scaled with order, and (2) riparian vegetation at confluences of two streams differed from that found along constituent streams. Most characteristics of riparian vegetation scaled with order. In confluence zones, density and diversity of riparian vegetation generally were equivalent to that of the largest constituent stream. Scaling relations between riparian vegetation and order provide a framework to quantify the role of riparian vegetation in the water balance of stream networks and a tool to predict area and distribution of riparian vegetation from network topology.

Key Words: basins, Horton laws, Horton-Strahler, network, order, riparian, scaling, self-similarity, streams.

Introduction

In their River Continuum Concept, Vannote et al. (1980) characterize riverine systems as gradients in a state of equilibrium in which biotic and abiotic properties vary continuously from headwaters to the mouths of rivers. Subsequently, rivers were recognized more as treelike networks with the gradient of change punctuated by added flow from tributaries (Ward and Stanford 1995, Fisher 1997, Poole 2002).

To study stream networks, hydrologists and geomorphologists have long used Horton-Strahler ordering to assign streams to discrete groups (orders, ω) in which increasing numerical values reflect increasing size of the link and complexity of the network (Horton 1945; Strahler 1952; Melton 1959). This classification system has been used to determine scaling relations, also known as Horton laws (Horton 1945; Strahler 1952). These laws exist if mean values of variables plotted against order produce log-linear fits reflecting constant ratios across orders. Generalization of these laws to higher order statistics is indicated when cumulative distribution functions of variables rescaled by their means share a common distribution among orders (Peckham and Gupta 1999). Horton laws are asymptotic and hold as the limit of network order approaches infinity (Troutman 2005; McConnell and Gupta 2008).

Scaling relations are diagnostic of self-similar, fractal-like networks (i.e., subsets are topologically similar to the entire network) and have been found for a wide variety of hydrogeomorphic variables including basin area and slope, channel length, width and depth, number of links per stream, and flow (Leopold and Miller 1956; Rodriguez-Iturbe and Rinaldo 1997; Tokunaga 2003; Mantilla and Gupta 2005; Troutman 2005; Rinaldo et al. 2006). These findings provide a framework to determine how ecological and physical processes are connected with, and organized through, interactions with the geometry and topology of river networks.

Legitimate inclusion of ecological processes within this framework requires determining the extent to which Horton laws apply to riparian vegetation. Riparian vegetation is integral within both hydrologic and biotic cycles and affects fluvial dynamics by capturing water and nutrients, trapping sediments, slowing flow of water, and modulating nutrient concentrations in streams (Martin and Johnson 1987; Gregory et al. 1991; National Research Council 2002). In turn, fluvial dynamics affect distribution of riparian vegetation, sediments and nutrients (Malard et al. 2002; Poole 2002). Given this reciprocal coupling, riparian vegetation can be expected to scale with order similar to hydrogeomorphic variables. However, studies of riparian communities to date have not addressed scaling across networks, but instead have focused mainly on different segments of single streams (e.g., Martin and Johnson 1987; Johnson 1994; van Coller *et al.* 2000; Turner et al. 2004; VanLooy and Martin 2005)

In this paper, we examine scaling properties of riparian communities of the Whitewater River network in eastern Kansas, a system where hydrogeomorphology has been intensively studied (Mantilla and Gupta 2005; Mantilla 2007; Clayton and Kean 2010). We hypothesized that amount and composition of riparian vegetation in the Whitewater River network scales with order. We also hypothesized that, because confluence zones receive the totality of energy, water, and matter from 2 streams, diversity and density of riparian vegetation would be greater than that which is found along either constituent stream.

Methods

Study Area

The Whitewater River network is located within a 1087 km^2 basin of rolling prairie in eastern Kansas (37.9° N, -97.08°W) (Fig. 1). It is at the western edge and driest part of the eastern deciduous woodlands (Abrams and Knapp 1986), a favorable environment for examining the role of woody riparian vegetation in hydrologic systems. In this region, soil moisture generally is adequate to support trees and shrubs (necessary water potential $\geq$ -3 MPa (Abrams and Knapp 1986; Ni and Pallardy 1990)) only where it is enhanced by subsurface flow from streams. Thus, boundaries between riparian and adjacent upland communities tend to be discrete. Additionally, the study area is characterized by gentle terrain (elevation range = 400 -480 m) so the role of topography in driving flow rates is minor compared to river networks in the montane west or Appalachian Mountains of the eastern United States.

Land use is predominately agriculture (61% cropland, 25.5% grazed prairie) and road densities are low (1 km/km^2). Annual precipitation averages 85 cm, occurring mostly as summer thundershowers. Precipitation records from weather stations at the north and south ends of the study area over the past 50 years were highly correlated (B. Milne, unpublished data), suggesting that precipitation across the study area is spatially uniform.

Network Delineation

The stream network was delineated from 7.5 minute (30 x 30 m cells) National Elevation Datasets (NED; United States Geological Survey, http//ned.usgs.gov). Channels were identified by first creating a flow direction matrix in *CUENCUS*, a Geographic

Information System (GIS) specifically developed for hydrogeomorphic scaling analysis (Mantilla and Gupta 2005). Flow direction for each cell was the path of maximum descent found by comparing the elevation of that cell to those of its eight neighboring cells (O'Callaghan and Mark 1984; Fern et al. 1998). Each cell within the study area was either a part of a channel or hillslope. Channel cells received flow from ≥ 2 cells, were lower than all but one neighbor, and were connected to at least one other cell that met the same criteria. Hillslopes were all cells with flow directions towards a specific channel; combined, they comprised the drainage basin of that channel. Connected channel cells formed links (continuous, uninterrupted parts of a channel) connected at nodes (confluence of 2 links) to form a network (Fig. 2). Streams were connected links of the same order. Links were assigned to Horton-Strahler orders based on 3 rules: (1) terminal links with no upstream tributaries were assigned order $\omega = 1$; (2) downstream links resulting from confluence of 2 links of equal order were assigned an order one more than the tributaries ($\omega + 1$) and, (3) downstream links resulting from confluence of 2 links of unequal order (ω_1 and ω_2) were assigned the maximum order of the respective tributaries ($\max(\omega_1, \omega_2)$) (Horton 1945; Strahler 1952; Melton 1959) (Fig. 2). The resulting network was converted to a layer in ArcGIS© 9.1 (Environmental Research Systems Institute, Inc. Redlands, CA), the GIS platform used for all analyses in this paper.

Preparation of the Riparian Vegetation Layer

A GIS layer of riparian vegetation was created from the Kansas Gap Analysis Project (GAP) land cover map (Egbert 2001). We classified 6 of 40 land cover alliances (hereafter "riparian vegetation types") as riparian habitat because they contained a high proportion of obligate riparian or wetland species (http://plants.usda.gov/) or were located in floodplains (Table 1).

We used photoverification to determine accuracy of the land cover map. Five hundred points with 50 m radius buffers were randomly located along streams and classified by order. Occurrence of riparian vegetation within the buffer on the land cover map and on a 1:24,000 digital color infrared aerial photograph (www.kansasgis.org) was recorded for each point. Riparian vegetation could not be identified to specific type on the aerial photograph, but its morphology was classified as tree or shrub/herbaceous. Error of commission (“false positives”) was the ratio of points with riparian vegetation on the land cover map but not on the photograph to the total points on the photograph that did not contain riparian vegetation. Error of omission (“false negatives”) was the ratio of points with riparian vegetation on the photograph but not on the land cover map to the total points on the photograph that contained riparian vegetation.

Cells of the same riparian vegetation type which were orthogonally or diagonally adjacent were grouped into patches. Layers were converted from raster to polygon to facilitate spatial analyses. For each order, 100-m buffers were created around individual streams and intersected with the 6 riparian vegetation types.

Riparian vegetation was further classified as being in one of two zones: exclusive (within 100 m of one and only one stream) or confluence (where buffers of 2 streams overlapped). Confluence zones were labeled by the orders of the constituent streams (e.g., “3 x 4” for confluence zones where order 3 and order 4 stream buffers overlapped).

Overlapping buffers at confluences made assignment of riparian vegetation to constituent streams problematic since a given patch could be assigned to either stream. To rectify this problem, we defined total riparian area, $A_r(\omega)$, along a stream as the sum of riparian area within its exclusive zone, $A_{ex}(\omega)$, plus a portion of the riparian vegetation within the confluence zone to which it contributed. This portion (by vegetation type) was assigned to each constituent stream based on how much streams of that order contributed to the total riparian vegetation in the entire network. Thus, $A_r(\omega) = A_{ex}(\omega) + p(\omega)A_{\cap}(\omega, \omega + k))$ where $A_{\cap}(\omega, \omega + k)$ is the area of riparian vegetation within the confluence zone. The fraction, $p(\omega)$, assigned to constituent stream ω was the proportion of the exclusive zone vegetation area expected for combinations of orders ω and $\omega + k$: $p(\omega) = \overline{A}_{ex}(\omega) / (\overline{A}_{ex}(\omega) + \overline{A}_{ex}(\omega + k))$. For example, if order 3 streams contained a mean of 2.2 ha and order 4 streams contained an average of 4.6 ha of Cottonwood Floodplain Forest per stream, respectively, 32.4% percent ($p(3) = 2.2/(2.2 + 4.6)$) of the riparian vegetation area within 3x4 confluence zones would be added to the order 3 stream total, $A_r(\omega)$, and 67.6% would be added to the order 4 stream total, $A_r(\omega + k)$.

Analysis of Riparian Vegetation

We measured variables associated with amount and composition of riparian vegetation: area and density of riparian vegetation, diversity of riparian vegetation types, stream sinuosity, and number and shape (perimeter:area ratio) of patches (Table 2). Some variables were measured at multiple levels. For example, measures of area of riparian vegetation included total area per order, total area per stream (grouped by order), and total area per patch (grouped by order). Density of riparian vegetation (area of riparian vegetation divided by the area of the stream zone in which it was found) and diversity of riparian vegetation types were measured for both exclusive and confluence zones.

We used the Shannon index (Whittaker 1975) to measure mean diversity of vegetation types (data were not available by species) for each order:

$$\overline{H}(\omega) = -\frac{1}{n(\omega)} \sum_{j=1}^{n(\omega)} \sum_{i=1}^{S(j)} p_{i,j} \ln p_{i,j} \qquad [1]$$

where $\overline{H}(\omega)$ is the mean diversity for order ω, $S(j)$ is the number of vegetation types, *i*, present on stream *j* of order ω, $p_{i,j}$ is the area of vegetation type *i* along the exclusive zone of stream *j* divided by the total area of riparian vegetation in all exclusive zones, and $n(\omega)$ is the number of streams of order ω. Shannon diversity is a measure of how vegetation is distributed across its potential range. We divided the area of each riparian vegetation type along each stream by total area of riparian vegetation found along all streams under the null hypothesis of no difference in diversity of riparian vegetation types among orders.

Flow direction (sinuosity) affects, and is affected by distribution of riparian vegetation (Martin and Johnson 1987; Gregory *et al.* 1991; Tabacchi et al. 1998). We measured sinuosity of each stream by dividing the Euclidean distance between the starting and ending points into the total stream length:

$$\zeta = \frac{l}{\sqrt{(x_o - x_e)^2 + (y_o - y_e)^2}} \qquad [2]$$

where sinuosity, ζ, varies with stream length, l, measured along the channel between nodes, divided by the Euclidean distance from the Cartesian coordinates of the origin, (x_o, y_o), to the end node (x_e, y_e).

For confluence zones, we used only density and diversity of riparian vegetation types in our investigations. We did not measure patch characteristics because confluence zones were markedly smaller than exclusive zones and boundaries truncated many patches within them. This introduced changes in patch area and shape not associated with natural processes. Density and diversity of riparian vegetation types in confluence zones were compared to those found in the exclusive zones of constituent streams using Kruskal-Wallace nonparametric analysis of variance and a modified Newman-Keuls test (rank sum values were substituted for means) for post-hoc pairwise comparisons (Zar 1974). Non-parametric tests were employed because many of the distributions were heavily-skewed even after log-transformation.

We employed classic Hortonian analyses to determine and describe scaling relations (Peckham and Gupta 1999; Mantilla and Gupta 2005). First, we regressed the natural logarithm of variable means against orders. We began with basin area, stream length and number of streams, 3 benchmark measures of river network structure that have been widely studied (Rodriguez-Iturbe and Rinaldo 1997), followed by riparian vegetation variables listed above. We tested for differences ($\alpha = 0.05$) among orders with analysis of variance and post-hoc Tukey tests for pairwise comparison of log-transformed data for all streams in each order (Zar 1974). We used *F*-tests (Zar 1974) to determine differences in slopes between area of riparian vegetation per stream and basin area per stream as well as stream length.

Next, we constructed cumulative distribution functions by order for basin area, stream length, and total area of riparian vegetation. We used Kolmogorov-Smirnov tests (Zar 1974) to determine similarity in distributions for each pair of orders, first for raw values and then for values rescaled, or divided, by their means. Finding similar distributions between orders when using raw values implicates small sample size as a factor contributing to similar distributions of rescaled values.

Lastly, we calculated Horton ratios for variables that scaled with order based on log-linear regression fits. For a given dependent variable, X, the Horton ratio, R_x, between k orders is

$$R_x = \left(\frac{E[X_{\omega+k}]}{E[X_{\omega}]} \right)^{1/k} \qquad [3]$$

the k^{th} root of the expected value of X for streams of order $\omega + k$ divided by that for order ω. By definition, the slopes of log-linear regressions equal ln R_x.

For scaling analysis, we grouped confluence zones by differences in orders (labeled k) of the constituent streams. Thus, group $k = 0$ contained confluences of streams of the same order, group $k = 1$ contained confluences of streams whose orders differed by one, and so on**.** We plotted the natural log of mean values of density and diversity of riparian vegetation in confluence zones against lowest order of constituent streams to determine if riparian vegetation in confluence zones scaled with order and if density and diversity increased as differences in k increased. We tested for differences in density and diversity among groupings (k) with analysis of variance (Zar 1974).

Results

The Whitewater River network contained 13,063 individual streams in 7 orders (Table 3). We omitted the single order 7 stream from our analyses because it was not completely within the study area. Over 75% of streams in the network were classified as order 1. Lower order streams (orders 1-3) were ubiquitous throughout the network and flowed directly into streams of all higher orders (Fig. 1).

The land cover map possessed miniscule (<1%) errors of commission for all orders and decreasing errors of omission as orders increased (59, 66, 40, 25, 10, and 0% for orders 1 through 6, respectively). Vegetative morphology on the land cover map agreed with appearance on the aerial photograph for 71.4% of the points. This suggests the land cover map provided a reasonable representation of the distribution of vegetation types.

Riparian vegetation shown on the land cover map encompassed 6% of the study area and included 6 types (Table 1). Ash-Hackberry-Elm Floodplain Forest comprised over 70% of all riparian vegetation along streams and contained the largest patches.

Characteristics of order 1 streams were measured but not included in any scaling analyses in this paper. These streams normally are not used in determining scaling relations; their fluvial properties differ from higher order streams because order 1 streams receive flow directly from hillslopes (Peckham and Gupta 1999, Mantilla and Gupta 2005). Characteristics of order 2 streams were measured but not used in scaling analyses of riparian vegetation because of a high error of omission.

Log-linear regression fits were found for basin area, stream length, and number of streams demonstrating that the Whitewater River network possesses a Hortonian structure (Fig. 3). Additionally, cumulative distributions for rescaled basin area and stream length were the same among orders (Fig. 4, Table 4).

Cumulative distributions of rescaled total area of riparian vegetation per stream were the same for all pairwise comparisons of orders 4-6 and for orders 3 and 6, but not for orders 3 and 4 or 3 and 5. Low statistical power was evident for orders 5 and 6; pairwise comparisons were not different using raw values for stream length and area of riparian vegetation.

Total area of riparian vegetation within orders was independent of order ($y = -0.07x + 5.7$, $r^2 = 0.42$; $F_{1,3} = 2.21$, $P = 0.23$) as was total number of patches ($y = -0.17x + 7.3$, $r^2 = 0.65$; $F_{1,3} = 6.2$, $P = 0.09$). At the stream level, total area of riparian vegetation, number of patches, and diversity of vegetation types all scaled positively with order (Fig. 5). From orders 3 through 6, total area of riparian vegetation per stream increased from 1.1 (*SD* 1.56) to 91 (*SD* 76.0) ha ($F_{3,570} = 87.2$, $P < 0.02$), number of patches increased from 2.94 (*SD* 3.2) to 87.2 (*SD* 54.1) ($F_{3,570} = 134.9$, $P = 0.0002$) and diversity increased from 0.0018 (*SD* 0.003) to 0.1003 (*SD* 0.07) ($F_{3,570} = 1328.28$, $P < 0.001$). Regression slopes for basin areas and stream length differed ($F_{1,6} = 41.38$, $P < 0.0001$), but slopes for basin areas and total area of riparian vegetation per stream did not ($F_{1,6} = 1.5$, $P = 0.75$).

Sinuosity increased but did not scale log-linearly with order; a quadratic expression was required to avoid systematic residuals (Fig. 6). Mean sinuosity differed among orders ($F_{3,\ 570}$ = 2097, P <0.001) and was three times higher for order 6 than for order 3 streams.

At the patch level, both area and shape (Perimeter:Area Ratio) scaled with order (Fig. 7). Mean patch area increased from 2.98 (*SD* 3.26) to 215 (*SD* 174) ha ($F_{3,\ 3212}$ = 17.8, P = 0.014). Perimeter:Area ratios decreased from 1.12 (*SD* 0.05) to 1.10 (*SD* 0.06) ($F_{3,\ 3212}$ = 62.6; P = 0.004); however, high variance resulted in similar values across several orders.

Within confluence zones, density and diversity of riparian vegetation mostly were equal to values within exclusive zones of the higher order and greater than or equal to those of the lower order constituent streams (Tables 5 and 6). Both variables scaled positively with order **(**Density**:** $F_{3,\ 1602}$ **=** 376.1, P < 0.0001; Diversity: $F_{3,\ 1602}$ = 20.3, P = 0.0004; Fig. 8). Density and diversity increased as differences in order increased except for $k \leq 1$ (Density: $F_{3,17}$ = 329.01, P < 0.0001; Diversity: $F_{3,17}$ = 16.2, P = 0.01).

Discussion

We found Hortonian scaling for 3 key geomorphologic characteristics of the Whitewater River network and for most riparian vegetation characteristics. One exception was the cumulative distribution for area of riparian vegetation in order 3 differed from distributions of orders 4 and 5. This suggests asymptotic behavior common in lower orders (McConnell and Gupta 2008) may break down for riparian vegetation below order 4, although high errors of omission may have been a contributing factor in this study.

Another exception was the quadratic relation between sinuosity and order, a consequence of multiple interacting factors. Besides riparian vegetation, one contributing factor probably was soil type. Less permeable Permian substrates were dominant in uplands where mostly low (1-3) order streams occurred whereas more permeable Holocene and Pleistocene alluviums were dominant in valley bottoms where most high (4-6) order streams occurred (Penner et al. 1975; Aber 1991). Increased permeability provides more channels for both surface and sub-surface flow (Shumm 1963, Smith 1998), which in turn increases the areas that have water potential adequate to support riparian vegetation.

Hortonian scaling was pervasive for all components of the Whitewater River network and similar slopes of basin area and area of riparian vegetation suggest a connection between geomorphological and ecological characteristics. The link is subsurface flow which is dependent on volume of water provided to streams by the basin in which it is located and the permeability of sediment in the adjacent terrestrial system (Fisher 1997; Malard et al. 2002). The pattern of increasing width and continuity of riparian vegetation indicates this connection becomes stronger as stream order increases.

Like any river network, Whitewater River is a dynamic system and its riparian community may be subject to major perturbations, particularly flood events. Yet our findings of predictable, systematic change across orders support the proposition of Vannote et al. (1980) that river networks are maintained in a stable equilibrium (Dill and Bromburg 2002). Feedback mechanisms between the lotic and terrestrial components work to maintain the consistency we found within orders. Low order streams draw from small basin areas (Mantilla and Gupta 2005) resulting in low base flow rates. In fact, during field investigations we found many order 1 streams in the Whitewater basin were ephemeral. Flood events from heavy downpours occur periodically during summer months. The total precipitation from these events might be enough for riparian vegetation to grow along these streams, but the water likely does not remain long enough for adequate seepage to occur. With a paucity of woody species, there is inadequate structure to capture and hold sediments and nutrients (Gregory et al. 1991). Thus, inconsistent water flow and evacuation of sediments and nutrients inhibit riparian community development and dampen biotic diversity (Table 3; Figs. 5 and 7).

In contrast, higher order streams collect water from larger basin areas via lower order tributaries. This results in greater and more consistent base flows and subsurface seepage, thereby encouraging development of riparian vegetation (Malard et al. 2002). Root and branch structure are developed enough to capture sediments and nutrients evacuated from contributing low order streams during floods (Tabacchi et al. 1998; Turner et al. 2004). The sediments and nutrients in turn contribute to maintenance and enhancement of riparian patches. In short, low order streams displayed all the classic maladies of a highly fragmented landscape that inhibit persistence of a diverse, well-connected community whereas high order streams displayed opposite patterns (Harris 1984; Forman and Godron 1986).

The increase in sinuosity with order is consistent with mechanisms described above. Whereas water flow from basins to streams connects the terrestrial to lotic system, sinuosity represents the feedback from lotic to terrestrial systems, particularly through its contribution to riparian diversity. Sinuosity can be considered analogous to pulsatile pumping in cardiovascular networks, i.e., flow reduction which encourages diffusion (West et al. 1997). For stream networks, enhanced diffusion means more areas and potentially more types of soils and topography receiving adequate water to support riparian vegetation. Greater size and diversity of niches would be expected to result in a greater amount and diversity of organisms (in this case, riparian vegetation) that occupy those niches (Ritchie and Olff 1999). This pattern was apparent in the Whitewater River network. Although diversity could not be measured for riparian species, given the well-known relationship between species and area (Preston 1962) and the strong scaling relations between area of riparian vegetation per stream and order, it is a reasonable assumption that species diversity would increase and scale with order assuming equal probability of colonization and establishment for all riparian species.

Our findings did not support the hypothesis that diversity and density of riparian vegetation in confluence zones were greater than that of constituent streams. The contribution of constituent streams apparently is not additive. Instead, our finding that properties of riparian vegetation in confluence zones most often equaled that of the highest order constituent stream validates the Horton-Strahler rule that the link following the confluence of unequally ordered streams is the higher value of the two orders (see Methods- Network Delineation).

We assumed that scaling of riparian vegetation in the Whitewater River network was driven mainly by amount and persistence of stream flow. An alternative explanation is that scaling patterns were a consequence of riparian vegetation removal to create or expand crop fields. Given the diversity of ownership and land use practices, it is highly doubtful that such clear patterns between riparian vegetation and order could have been caused primarily by agricultural activity. If vegetation removal was a factor, riparian vegetation along low order streams would have been most vulnerable because it occurs in small, dispersed patches. Strong scaling relationships in orders 4-6 where riparian vegetation is not as susceptible to removal suggests stream flow more than vegetation removal shaped the scaling patterns. Conversion of uplands to crop fields could also affect scaling by modifying runoff thereby affecting stream flow. Variation in peak flows among rainfall-runoff events has been observed to affect slopes and intercepts of regressions, but not the existence of scaling relations themselves (Gupta et al. 2010).

Implications for Research and Conservation

What is the nature of diversity and how is diversity maintained are central questions in ecology (MacArthur 1972; Shmida and Wilson 1985). This study contributes to answering these questions for riparian communities of stream networks. We hypothesize scaling of riparian vegetation is rooted in random self-similarity, a property found by Mantilla et al. (2010) in 26 of 30 stream networks from widely different hydro-climatic zones. Given this, our findings should apply to other stream networks and therefore offer contributions to theory, land management and conservation.

For theory, scaling in riparian vegetation adds to the growing body of knowledge that hierarchical, self-organizing networks are prevalent in nature (Brown et al. 2002, 2004). As such, riparian communities could be used in further development of theory concerning how scaling from individuals to ecosystems affects structure and dynamics of forests and woodlands that are in a demographic and resource steady-state (Enquist et al. 2003; 2009). Additionally, Horton scaling of diversity (Fig. 5) from probabilities normalized of the entire network supports application of maximum entropy theory in studies of diversity (Harte et al. 2008).

For land management and conservation, riparian communities are a challenge but also a high priority. These communities are inherently susceptible to disturbance and destruction due to naturally limited spatial extent, quasi-linear geometry, and a high edge to interior ratio (Poff et al. 1997). Yet, riparian communities are valuable because they support an inordinate amount of biodiversity compared to most communities, a consequence of their position adjacent to channels that serve as repositories of water, nutrients and energy for the entire watershed (Harris 1984, Knopf 1986; Wooster and DeBano 2006; Eckness and Randhir 2007).

This study represents a step forward in understanding interrelations between biotic and hydrologic/geomorphologic components within stream networks. Scaling relations can be used to determine the water balance of stream networks, especially the role of riparian vegetation in subsurface uptake and evapotranspiration back into the atmosphere. Given the key role of water availability in distribution of riparian vegetation, these data will be valuable to making informed decisions for conservation and management of riparian communities.

The ability to make site-specific predictions using scaling relations is limited by variation within orders, but they nevertheless can afford initial insights into the properties of stream networks. First, Horton ratios can provide estimates of mean values of riparian vegetation in stream networks that are not completely sampled. Data from two orders, say 4 and 6, could provide the Horton ratio to interpolate a mean value for order 5 streams. Additionally, Horton-Strahler ordering can provide insights into the effects of perturbing stream flow. For example, loss of low order streams to agricultural conversion is analogous to pruning a tree. Order 2 streams that received flow from streams that were destroyed would be reclassified as terminal branches (order 1) with appropriate reclassification cascading through all connected streams. With this, the full impact can now be recognized of what was traditionally viewed as a localized disturbance.

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Table 1. Riparian vegetation types in the Whitewater River network, Kansas, USA (from Egbert et al. 2001).

Vegetation Type	Exclusive zones			Area in confluence zones (ha)	Total area (ha)	Dominant Species
	No. of Patches	Mean Patch Size (ha ± SD)	Area (ha)			
Pecan Floodplain Forest	152	0.35±0.84	53.6	54.6	108.2	*Carya illinoiensis, Celtis occidentalis, Acer negundo*
Ash-Elm-Hackberry Floodplain Forest	3471	0.52± 4.7	1793.3	2161.5	3954.8	*Fraxinus pennsylvanicus, Ulmus sp., C. occidentalis, Juglan nigrans*
Cottonwood Floodplain Forest	1463	0.39± 1.3	567.2	526.2	1096.4	*Populus deltoides, Plantus occidentalis, A. negundo*
Cottonwood Floodplain Woodland	784	0.46± 1.18	322.2	260.8	583.0	*P. deltoides, Salix nigra, A. negundo*
Willow Shrubland	35	0.35±0.47	10.3	1.2	11.2	*Salix exigua, Andropogon gerardii*
Low or Wet Prairie	385	0.32± 0.83	121.5	117.9	239.4	*Spartina pectinata, Eleocharis sp.*
Cattail Marsh	939	0.31± 1.07	287.9	248.9	536.8	*Typha sp., Eleocharis sp.*
Total	**7229**	**-**	**3156.0**	**3371.0**	**6527.0**	

Table 2. Variables used to determine scaling relationships between riparian vegetation and Horton-Strahler orders in the Whitewater River network, Kansas, USA. Also listed are the levels and stream zones where variables were measured.

Variable	**Level**	**Stream Zone**
Area of Riparian Vegetation (ha)	Order	All[2]
	Stream	All
	Patch	Exclusive
Number of Patches	Order	Exclusive
	Stream	Exclusive
Density of Riparian Vegetation (m^2/m^2)	Stream	Exclusive, Confluence
Diversity of Riparian Vegetation Types (n/m^2)	Stream	Exclusive, Confluence
Sinuosity (m/m)	Stream	Exclusive
Perimeter:Area ratio (m/m^2)	Patch	Exclusive

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[2] Exclusive + Portion of Confluence Zone; see Methods

Table 3. Stream characteristics of Horton-Strahler orders in the Whitewater River network, Kansas, USA.

Order	Number of streams	Range of lengths (km)	Mean length (± SD) (km)	Total length of all streams (km)	Riparian vegetation in exclusive zones	
					Number of Patches	Area (ha)
1	10333	0.015-2.03	0.28 (0.19)	2850.0	2889	893
2	2155	0.02-3.05	0.5 (0.43)	1086.5	1018	358
3	450	0.03-6.28	1.2 (0.96)	539.6	873	370
4	95	0.11-8.12	2.46 (1.7)	223.4	1036	333
5	24	0.28-16.7	7.8 (5.6)	195.2	875	517
6	5	1.46-40.1	18.95 (15.0)	94.8	431	439
7	1	24.3	24.3	24.3	-	-
Totals	**13063**	**0.015-40.1**		**5013.8**	**7122**	**2910**

Table 4. Comparisons of cumulative distributions between pairs of Horton-Strahler orders for rescaled basin area, stream length, and total area of riparian vegetation per stream. Values are K statistics of Kolomogrov-Smirnov tests; p-values are in parentheses. Bold values indicate different distributions. Underlined values indicate where small sample sizes may have contributed similar distributions.

Pairs of Orders	Basin Area	Stream Length	Total Riparian Vegetation
3 - 4	0.108 (0.30)	0.097 (0.44)	**0.263 (0)**
3 - 5	0.112 (0.92)	0.185 (0.38)	**0.299 (0.03)**
3 - 6	0.340 (0.52)	0.238 (0.90)	0.382 (0.37)
4 - 5	0.130 (0.88)	0.175(0.56)	0.111 (0.96)
4 - 6	0.326 (0.6)	0.253 (0.87)	0.158 (0.99)
5 - 6	0.308 (0.74)	0.167 (0.99)	0.133 (1.0)

Table 5. Density of riparian vegetation in confluence zones and in exclusive zones of constituent streams for Horton-Strahler orders 3-6 in the Whitewater River network, Kansas, USA.

Difference between orders	Comparison among groups	Confluence mean density (±SD)	High order mean density (±SD)[3]	Low order mean density (±SD)	Values for Kruskal-Wallis tests	Pr>F
0	3x3 = 3a = 3b[1]	0.06 (0.09)	0.08 (0.13)	0.18 (0.26)	$F_{2,318} = 1.39$	$P = 0.25$
0	4x4 = 4a = 4b	0.25 (0.25)	0.17 (0.18)	0.2 (0.23)	$F_{2,71} = 0.2$	$P = 0.42$
0	5x5 = 5a = 5b	0.47 (0.34)	0.25 (0.18)	0.34 (0.04)	$F_{2,12} = 0.61$	$P = 0.56$
0	6x6 > 6a = 6b[4]	0.98	0.336	0.334	-	
1	3x4 =4 > 3	0.15 (0.2)	0.15 (0.21)	0.07 (0.11)	$F_{2,460} = 13.06$	$P < 0.0001$
1	4x5 = 5 > 4	0.34 (0.25)	0.30 (0.13)	0.18 (0.23)	$F_{2,121} = 8.83$	$P = 0.0005$
1	5x6 = 6 > 5	0.46 (0.21)	0.46 (0.13)	0.30 (0.13)	$F_{2,30} = 3.29$	$P = 0.051$
2	3x5 > 5 > 3	0.37 (0.16)	0.31 (0.1)	0.09 (0.13)	$F_{2,518} = 42.06$	$P < 0.0001$
2	4x6 = 6 > 4	0.52 (0.17)	0.42 (0.1)	0.09 (0.11)	$F_{2,23} = 16.4$	$P < 0.0001$
3	3x6 = 6 > 3	0.50 (0.1)	0.42 (0.1)	0.14 (0.18)	$F_{2,63} = 10.02$	$P = 0.0002$

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[3] For *k*=0, High Order refers to group a and low order to group b.

[4] Only 1 6x6 confluence zone occurred in the study area.

Table 6. Diversity of riparian vegetation in confluence zones and in stream zones of constituent streams for orders 3-6 in the Whitewater River network, Kansas, USA.

Difference between orders	Comparison among groups	Confluence mean diversity (±SD)	High order mean diversity (±SD)[5]	Low order mean diversity (±SD)	Values for Kruskal-Wallis tests	Pr>F
0	3x3=3a=3b	0.024 (0.1)	0.08 (0.22)	0.12 (0.27)	$F_{2, 318} = 3.55$	$P = 0.067$
0	4x4<4a=4b	0.06 (0.19)	0.44 (0.41)	0.12 (0.27)	$F_{2, 72} = 16.0$	$P < 0.001$
0	5x5=5a=5b	0.26 (0.26)	0.84 (0.52)	0.64 (0.42)	$F_{2, 12} = 3.33$	$P = 0.065$
0	6x6<6a<6b	0	0.24	0.62	-[6]	
1	3x4 = 4 > 3	0.4 (0.42)	0.44 (0.41)	0.11 (0.24)	$F_{2, 460} = 68.5$	$P < 0.0001$
1	4x5 = 4 < 5	0.30 (0.37)	0.75 (0.45)	0.49 (0.42)	$F_{2, 121} = 6.3$	$P = 0.002$
1	5x6 = 6 = 5	0.4 (0.23)	0.37 (0.18)	0.37 (0.4)	$F_{2, 30} = 3.6$	$P = 0.06$
2	3x5 = 5 > 3	0.5 (0.38)	0.48 (0.38)	0.074 (0.22)	$F_{2, 153} = 95.6$,	$P < 0.0001$
2	4x6 = 6 = 4	0.34 (0.4)	0.4 (0.19)	0.27 (0.36)	$F_{2, 23} = 0.56$	$P = 0.7$
3	3x6 = 6 > 3	0.55 (0.36)	0.41 (0.18)	0.1 (0.25)	$F_{2, 63} = 19.1$	$P < 0.0001$

---

[5] For k=0, High Order refers to group a and low order to group b .

[6] Only 1 6x6 confluence zone occurred in the study area

Figures

1. The Whitewater River network, Kansas, USA. Also shown are representative streams and associated riparian vegetation (shaded patches) for Horton-Strahler orders 3 and 6.
2. Stream network components used in analysis of the Whitewater River basin, Kansas, USA.
3. Scaling relations between 3 key geomorphic characteristics of stream networks and Horton-Strahler orders. Symbols represent the natural log of the means for each order. Lines represent regression fits.
4. Cumulative distribution functions of basin area per stream, stream length, and total riparian vegetation per stream for orders 3 through 6 using untransformed values (left) and values transformed by dividing them by the mean value of the order.
5. Scaling relations between characteristics riparian vegetation along streams and Horton-Strahler orders in the Whitewater River network, Kansas, USA: (a) total area of riparian vegetation per stream (b) number of patches per stream and (b) Shannon diversity of riparian vegetation types per stream. Open circles represent the natural log of the means for each order. The thick dashed line represents the regression fit against orders 3 through 6. Solid and dotted vertical lines represent 95% confidence intervals and standard deviations, respectively. Different letters denote differences in means among orders. The regression equation, coefficient of determination (r^2), and Horton Ratio (R_) are shown in the upper left of each graph.

6. Scaling relations between stream sinuosity and Horton-Strahler orders in the Whitewater River network, Kansas, USA. Open circles represent the natural log of the means for each order. The thick dashed line represents the regression fit for Horton-Strahler orders 3 through 6. Solid and dotted vertical lines represent 95% confidence intervals and standard deviations, respectively. Different letters denote differences in means among orders. The regression equation and coefficient of determination (r^2) are shown in the upper left of the graph
7. Scaling relations between characteristics of riparian vegetation patches and Horton-Strahler orders in the Whitewater River network, Kansas, USA: (a) area, and (b) perimeter:area ratio. Open circles represent the natural log of mean values for each order. The thick dashed line represents the regression fit against Horton-Strahler orders 3 through 6. Solid and dotted vertical lines represent 95% confidence intervals and standard deviations, respectively. Different letters denote differences in means among orders. The regression equation, coefficient of determination (r^2), and Horton Ratio (R_) are shown in the upper left of each graph.
8. Density of riparian vegetation and diversity of riparian vegetation types within confluence zones grouped by differences in Horton-Strahler orders (*k*) of constituent streams. Symbols represent the natural logs of the means for each combination of orders. Dashed lines represent regression fits between characteristics of riparian vegetation and lowest Horton-Strahler order of the constituent streams. The regression equation, coefficient of determination (r^2), and Horton Ratio (R_) are shown in the legend box of each graph.

Figure 1.

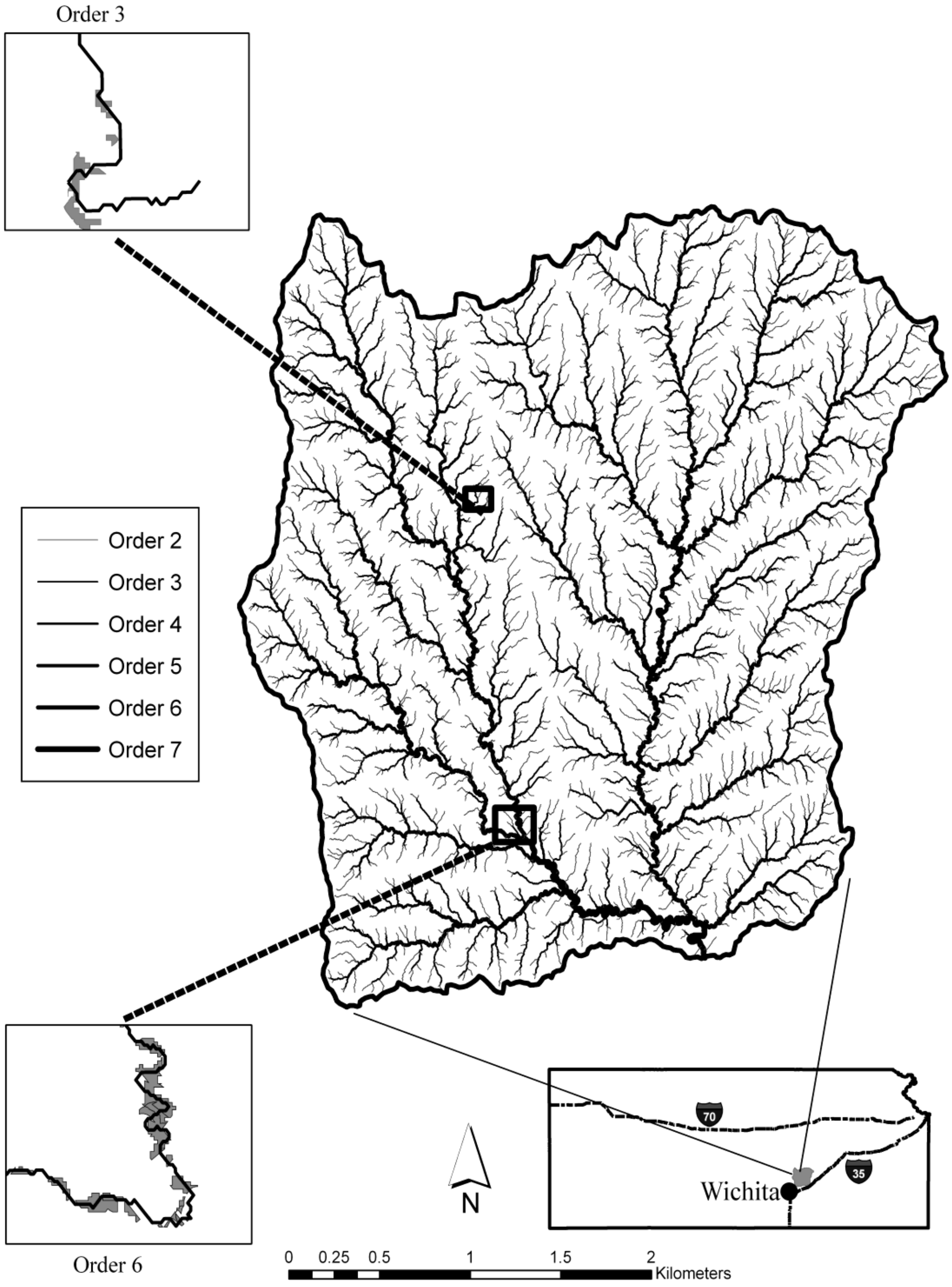

Order 3
Order 2
Order 3
Order 4
Order 5
Order 6
Order 7
70
35
Wichita
N
Order 6
0
0.25
0.5
1
1.5
2
Kilometers

Figure 2.

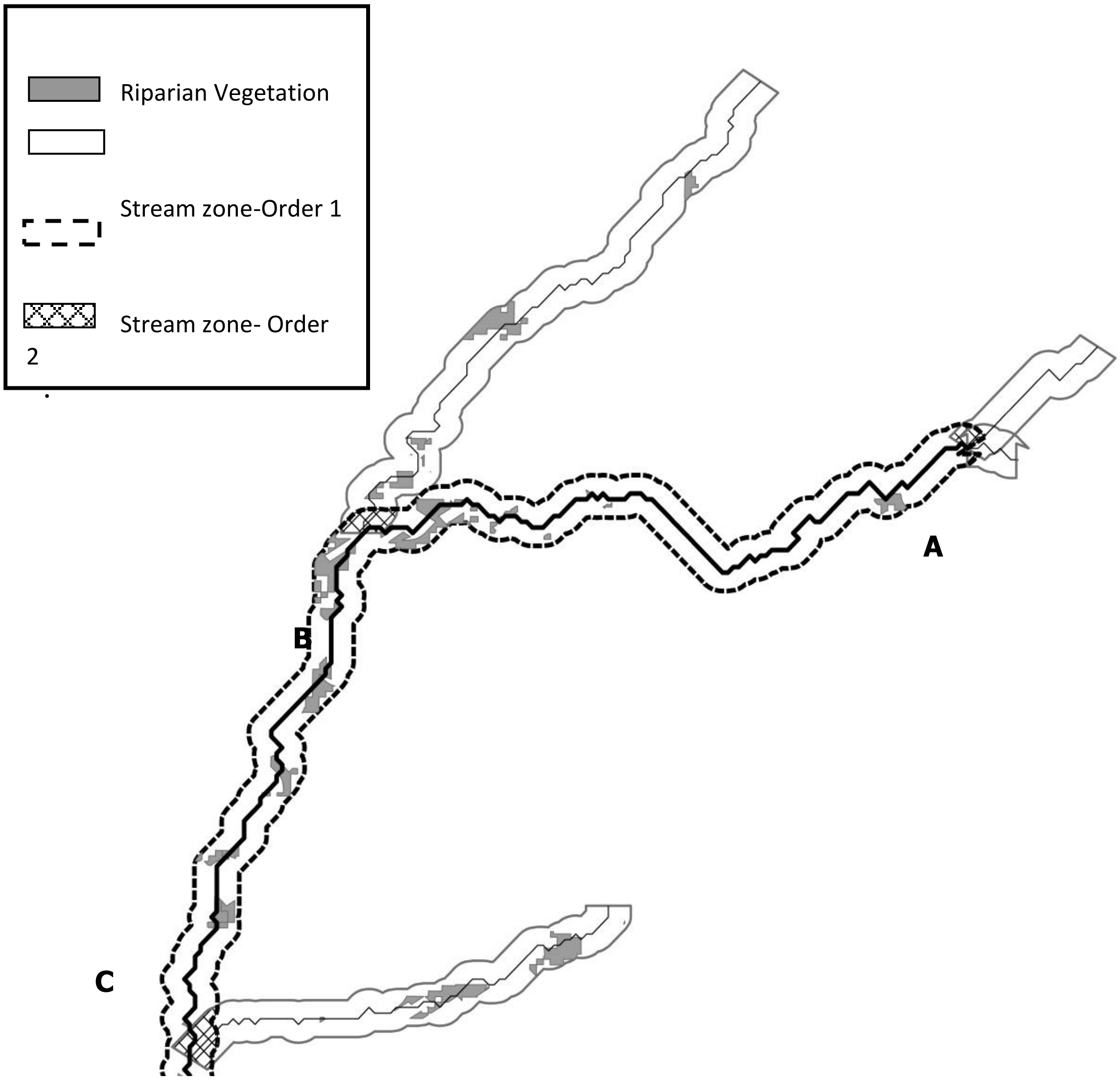
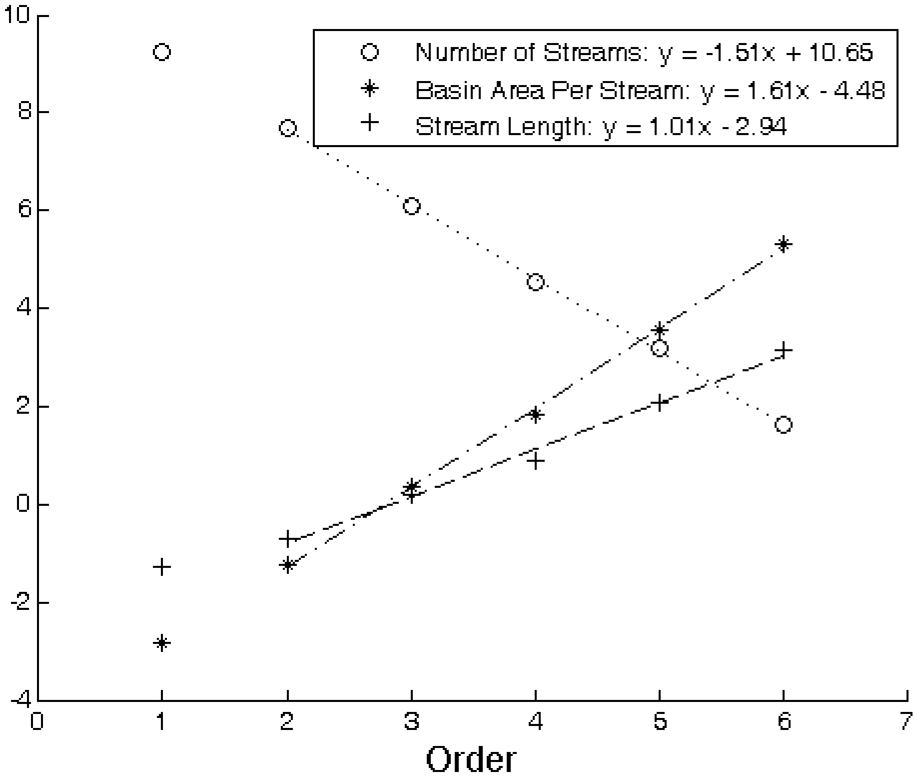

Riparian Vegetation
Stream zone-Order 1
Stream zone- Order 2
A
B
C

Figure 3.



10
8
6
4
2
0
-2
-4
0
1
2
3
4
5
6
7
Order
○ Number of Streams: y = -1.51x + 10.65
✱ Basin Area Per Stream: y = 1.61x - 4.48
+ Stream Length: y = 1.01x - 2.94

Figure 4.

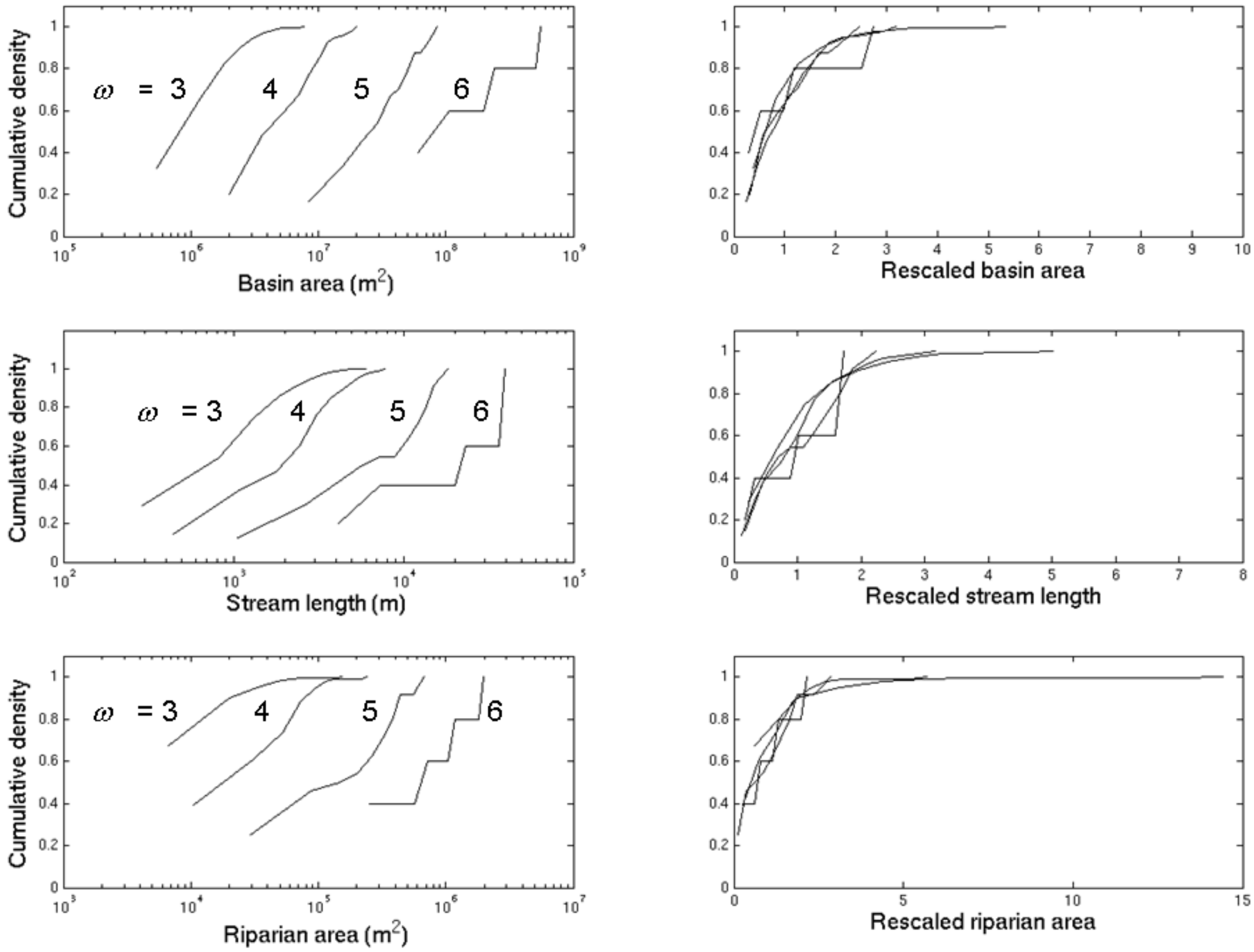
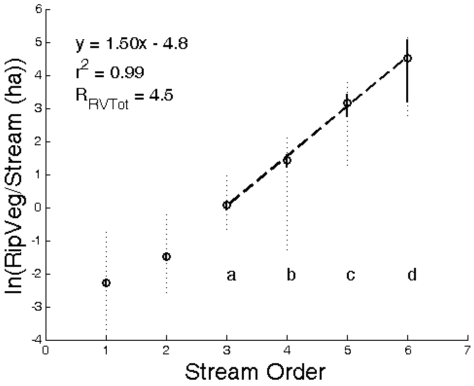
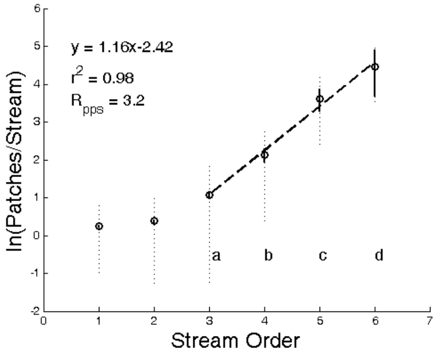

Cumulative density
ω = 3
4
5
6
Basin area (m^2)
Rescaled basin area
Cumulative density
ω = 3
4
5
6
Stream length (m)
Rescaled stream length
Cumulative density
ω = 3
4
5
6
Riparian area (m^2)
Rescaled riparian area
0
0.2
0.4
0.6
0.8
1
10^5
10^6
10^7
10^8
10^9
0 1 2 3 4 5 6 7 8 9 10
10^2
10^3
10^4
10^5
0 1 2 3 4 5 6 7 8
10^3
10^4
10^5
10^6
10^7
0 5 10 15

Figure 5

a.


y = 1.50x - 4.8
r^2 = 0.99
R_{RVTot} = 4.5
ln(RipVeg/Stream (ha))
Stream Order
a
b
c
d
6
5
4
3
2
1
0
-1
-2
-3
-4
0
1
2
3
4
5
6
7

b.


y = 1.16x-2.42
r^2 = 0.98
R_{pps} = 3.2
ln(Patches/Stream)
Stream Order
a
b
c
d
6
5
4
3
2
1
0
-1
-2
0
1
2
3
4
5
6
7

c.

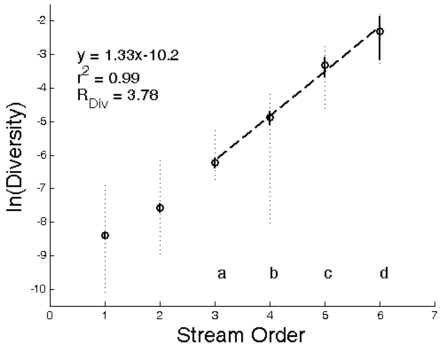

y = 1.33x-10.2
r^2 = 0.99
R_{Div} = 3.78
ln(Diversity)
Stream Order
a
b
c
d
-2
-3
-4
-5
-6
-7
-8
-9
-10
0
1
2
3
4
5
6
7

Figure 6.

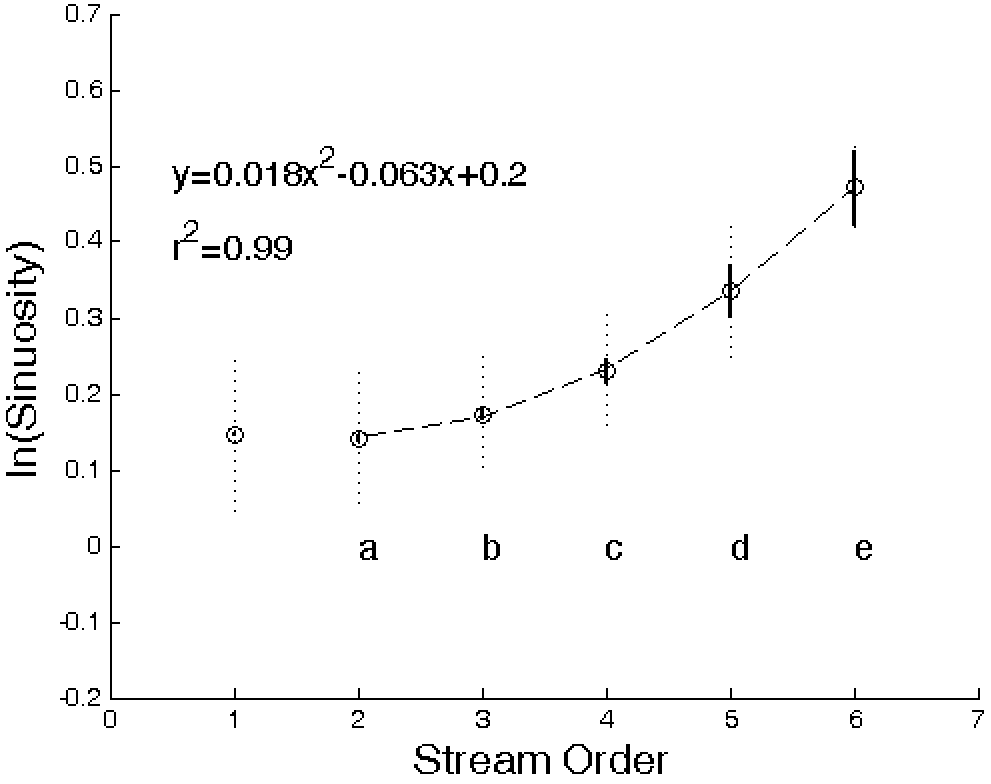
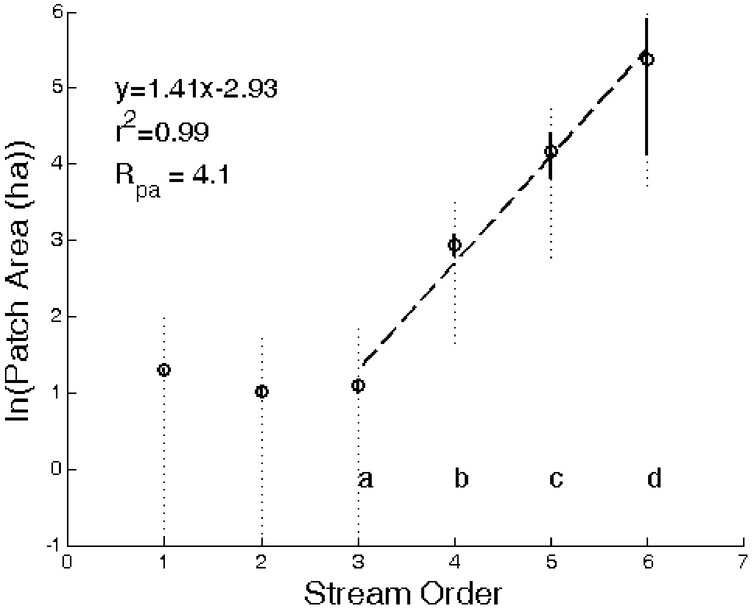

y=0.018x^2-0.063x+0.2
r^2=0.99
ln(Sinuosity)
Stream Order
a
b
c
d
e
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
0
1
2
3
4
5
6
7

Figure 7

a.


y=1.41x-2.93
r^2=0.99
R_{pa} = 4.1
ln(Patch Area (ha))
Stream Order
a
b
c
d
6
5
4
3
2
1
0
-1
0
1
2
3
4
5
6
7

b.

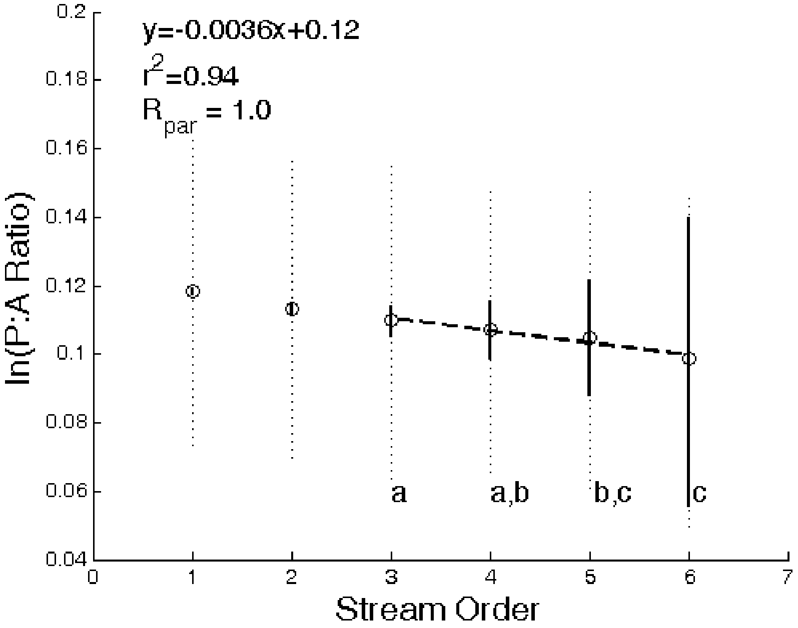
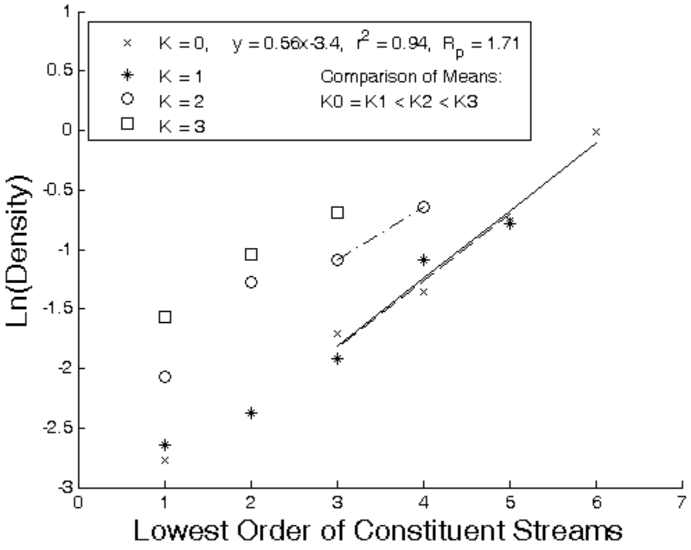

y=-0.0036x+0.12
r^2=0.94
R_{par} = 1.0
ln(P:A Ratio)
Stream Order
a
a,b
b,c
c
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0
1
2
3
4
5
6
7

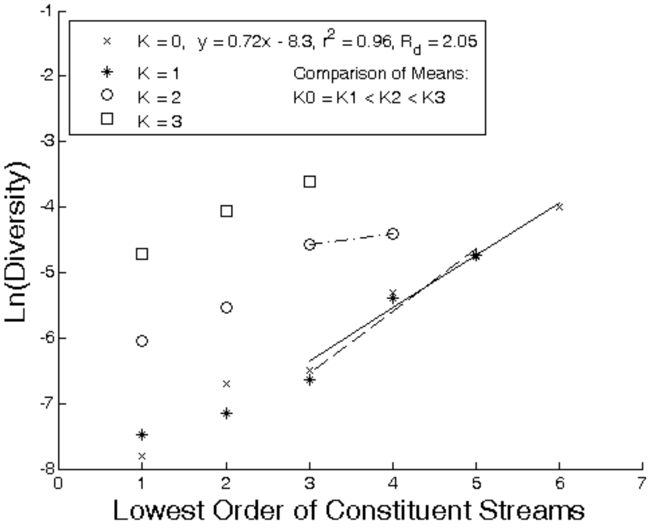
Figure 8.

a.



K = 0, y = 0.56x-3.4, r^2 = 0.94, R_p = 1.71
K = 1
K = 2
K = 3
Comparison of Means:
K0 = K1 < K2 < K3
Ln(Density)
Lowest Order of Constituent Streams
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
0
1
2
3
4
5
6
7

b.



K = 0, y = 0.72x - 8.3, r^2 = 0.96, R_d = 2.05
K = 1
K = 2
K = 3
Comparison of Means:
K0 = K1 < K2 < K3
Ln(Diversity)
Lowest Order of Constituent Streams
-1
-2
-3
-4
-5
-6
-7
-8
0
1
2
3
4
5
6
7

ENERGY DEVELOPMENT AND CONSERVATION OF
SYMPATRIC WILDLIFE:
NEW APPROACHES TO MEET GROWING CHALLENGES

BY

William C. Dunn

CONCLUDING REMARKS

The unprecedented rate at which energy development is affecting wildlife habitat has become one of the biggest challenges for conservation and will continue to be so into the foreseeable future. Given the scale at which wildlife populations are being affected and the limited resources available to address those impacts, conservation interests must carefully choose how and where to best concentrate efforts. Providing new and innovative approaches to accomplish this was the purpose of the research in this dissertation. The Lesser Prairie Chicken (*Tympanuchus pallidicinctus*) (LPC) was a fitting subject; oil and gas development is a major reason for its imperilment. Woven throughout this dissertation was the concept that location, scale, and connectivity were keys to providing innovative solutions and comprehensive information for decision makers. In Chapter 1, species distribution modeling was used to narrow the choice of locales where conservation of LPC should be focused and the result was a very small proportion of the historic geographic range. Specifically, most of the geographic range did not contain LPC habitat and most habitat was not where environmental characteristics (i.e., climate) promoted persistence of this species. Further, many locales with suitable characteristics were considered too small and isolated to ensure persistence. Undoubtedly, knowing where a species can persist is essential for its conservation, but of equal value is knowing where it cannot persist. Unsuitable sites may contain valuable energy resources; offering them for development provides a powerful bargaining tool to protect more viable sites needed for species conservation.

However, bargaining with sites that are seemingly unsuitable should be undertaken with care. A key finding from the spatially-explicit patch model in Chapter 2 is that reliance on refugia (i.e., sites with highly suitable habitat) as the primary conservation strategy is not a panacea for energy-wildlife conflicts. The true suitability of a site is based not only on characteristics within it but also on the landscape around it. This is because few refuges are large enough to ensure populations are immune from natural extinction processes. Thus, management needs to occur at the metapopulation scale, specifically focusing on maintaining the dynamics of colonization and extinction by allowing vacant habitat to exist. Energy development negatively affects both: it accelerates extinction by usurping habitat where populations reside and decreases colonization by reducing connectivity with other populations. In short, the important take-home lesson from the analysis in this chapter is that conserving connectivity between refuges is as important as conserving the refuges themselves.

One contribution that the security index presented in Chapter 3 offers is a means to identify those key corridors. Implicit within standard connectivity indices is that the shortest route between patches is the most secure route. Yet, the configuration of, and distance between, habitat fragments scattered throughout the matrix may be such that a more circuitous route offers better security. The security index provides the means to objectively compare, at multiple scales, all options for corridors.

The analysis of stream networks in eastern Kansas in Chapter 4 did not directly address energy-wildlife conflicts, but structurally, wildlife metapopulations share similar network characteristics. Hierarchical, self-organizing networks, such as riverine systems, are increasingly recognized as a common topological framework of natural systems. This provides a new perspective through which to analyze and conserve metapopulations. One contribution to energy-wildlife conflicts is using scaling relations to predict the effect of perturbations on network structure. Focusing on scaling relations could significantly increase the scope and accuracy in predicting the effect of expanding energy development on persistence of affected metapopulations.

Techniques to find and extract energy are evolving at a rapid rate. Some increase, whereas others decrease, the footprint of energy developments. The methods and findings in this dissertation will contribute to solving energy-wildlife conflicts. But a more significant contribution will occur if they stimulate new thinking and innovation as society works to meet its needs for energy as well as its obligation to conserve the natural world.