# MODELING HABITAT CONNECTIVITY IN THE KANSAS CITY, MO REGION

*A review and demonstration of graph-theory-based approaches to animal habitat mapping and prioritization for the Mid-America Regional Council area*

A report prepared for

The Mid-America Regional Council

By

Martin Buchert

Senior Research Analyst

Metropolitan Research Center, University of Utah

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# Contents

# I: Introduction

## MARC's Challenge

In 2013, MARC took delivery of the Kansas City Natural Resource Inventory II (hereafter NRI), a high-resolution (2.5m) land cover map derived from remotely-sensed multi-spectral imagery and airborne LiDAR. This new data product represents a significant investment by MARC and has tremendous potential for expanding local planner's consideration of ecosystems and the services that they provide to the Greater Kansas City region. MARC now faces the exciting challenge and opportunity of realizing the promise embodied by the NRI; specifically, MARC now seeks to leverage its investment in the NRI land cover map to assist or facilitate other planning activities. One such planning application for this data set is as the input to models of ecosystem services provisioning, and among other ecosystem services, maintaining biodiversity by providing habitat connectivity.

## Nature of this research contract

As part of an omnibus contract involving other work relating to ecosystem services, MARC retained the University of Utah's Metropolitan Research Center to produce proof-of-concept analyses of habitat connectivity, including a habitat priority index (HPI) for patches in the study area. The author of this report, the Senior Research Analyst at the Metropolitan Research Center, has an academic research background in spatial conservation planning. The study should demonstrate to key MARC personnel the process involved in conducting habitat connectivity analyses. It should also produce results that could help educate stakeholders about how biodiversity is impacted by regional development, and show local and regional planners how they are uniquely situated to participate in biological conservation efforts. As was stressed during early discussions about this effort, this work should be understood as a demonstration of a vital new area of research in conservation planning but should not be interpreted as a conservation or management plan for any of the focal species; such efforts should be informed by a more thorough study; suggestions for such further work are offered in Section V.

## Structure of this report

Section II discusses some background issues relating to habitat connectivity, which is fundamentally a question of spatial and behavioral ecology. Like the rest of the report, this discussion is intended for an audience of urban and regional planners. Section III gives an overview of the methods used in this study to select focal species, model habitat, construct graph-theoretic (i.e. network-based) models of habitat connectivity, and finally to compute patch- and link-based metrics of connectivity. Expanded discussion of the scientific research findings used to parameterize our models of habitat and habitat connectivity are given in Appendix 1, along with a bibliography of literature researched for these model parameters. Section IV discusses the results of the habitat and connectivity modeling. Section V makes some concluding observations and recommendations, with a focus on MARC's interest in integrating explicit consideration of "soft green elements", that is, non-engineered landscape components, into its planning efforts.

## II: Habitat connectivity in ecology and planning

### Animal use of habitat

Animal populations perpetuate themselves through space and time as individuals find food and avoid predation, and as they mate and their offspring survive to maturity (Krebs and Davies 2009). All organisms are, to greater or lesser degree, adapted to particular environmental conditions; they may tolerate temperatures ranging between a minimum and a maximum temperature, or require vegetation cover that is at least a minimum density, or demand certain types of soil to burrow (or propagate seeds) into. In locations where conditions fall within these limits they find shelter, access to food resources, and opportunity to mate and raise offspring. The environmental limits to which an organism is adapted are known collectively as its *niche* (Hutchinson 1957).

Spaces where environmental conditions correspond to an organisms' niche comprise their *habitat*. An environment with conditions outside of the ranges that the organism is adapted for will not function as habitat for that organism. Where habitat declines in areal extent, is degraded due to environmental change, or becomes isolated from other appropriate habitat, a population relying on this habitat declines. Without demographic rescue from other populations of the same species, this organism may become locally, or eventually globally, extinct.

Different species' adaptations may both enable and require them to *use* a given landscape in different ways. For the same reason, different species may *perceive* the same landscape in different ways, and may even perceive or respond differentially to the same phenomena at different spatial scales. For example, a bird of prey may require dense forest with lots of old trees in neighborhoods where it will nest and raise chicks, but in a larger footprint demand a large fraction of open meadow in which to hunt for food.

### Habitat variability across space: patches and matrix

Landscapes vary across space and change over time, even without human intervention. Where environmental gradients are stark enough (or organismal requirements are narrow enough), it is useful to conceptualize landscapes as mosaics of habitat *patches*, embedded in a *matrix* of land that, while it may be highly variable itself (Ricketts 2001), is all unsuitable to greater or lesser degree as habitat per sé for a particular organism. This patch/matrix conception of landscapes imposes discrete boundaries on what may be a continuously varying landscape (Gustafson 1998).

Implicit in this conception is the notion that the definition of what constitutes a habitat patch must vary from organism to organism, depending on their adaptations and habitat requirements. Not only will organisms vary in their affinity for a particular piece of a landscape, but they may not share the perception of a given place as a "patch" at all—a boundary that is a meaningful distinction between habitat/non-habitat for one species may simply be a gradation of acceptability for another species.

Humans are no exception to this rule, even given our capacity to build tools that allow us to perceive beyond the capacity of our native senses and thrive in environments of every stripe. This point is worth emphasizing in the present context, because tools such as the NRI data product that MARC presently

seeks to use in habitat connectivity planning naturally reflects *human* perceptions of the landscape. It takes structured effort – research – to understand how other organisms perceive a landscape, and to be able to represent this perception for, say, planning purposes.

## Habitat variability over time: environmental change

Not only are environments spatially variable, they are always changing—even in the absence of human activities. Change that occurs on short time scales relative to a species' capacity to adapt is referred to as "disturbance", and most environments are characterized over moderate time scales (hundreds to thousands of years) by disturbance "regimes"–characteristic patterns of disturbance type that operate within typical ranges of intensity, spatial footprint and temporal frequency. While organisms have always dealt with habitat disturbances such as wild-fires, severe storms, earthquakes, floods, etc., and with other longer-term environmental changes, humans have become environmental engineers whose habitat-modifying impacts are increasingly felt at a global scale. Human-induced land-use/land-cover change (LULCC) has impacted habitats everywhere on Earth, and habitat loss and degradation is recognized as the most significant contributor to the current biodiversity crisis (Dirzo and Raven 2003).

## Landscape connectivity and fragmentation

From the perspective of many organisms, landscapes are patchy and demand movement from patch to patch in order to meet the needs of individuals, such as finding food and shelter, or the needs of larger groups, such as genetic mixing between sub-populations to prevent inbreeding. Although many organisms perceive their environments as patchy landscapes, human land use is characteristically interrupting the continuity of existing land cover all over the world, and the subsequent changes in land cover that result often act to perforate, dissect, fragment, and shrink (and finally eliminate) what was previously extensive contiguous habitat for other organisms (Forman 1995).

Patches that are accessible from one another by the organism are said to be *functionally* connected; that is, they are connected not simply in the conception of humans studying that landscape, but are actually experienced as connected by individuals of the species. Ecologists are in broad agreement that "connectivity is species-specific and should be measured from a functional perspective. That is, not only the spatial arrangement of the habitat (structural connectivity) but also the dispersal distances and/or the behavioral response of the focal species to the physical structure of the landscape (functional connectivity) should be taken into account" (Saura and Torné 2009).

## Network models of habitat connectivity

Given the importance of landscape structure to the persistence of biodiversity, ecologists have dedicated considerable interest in studying habitat connectivity in landscapes. There is now a rich history of ecological research and modeling that considers the movement of organisms through a patchy landscape, and conservation scientists and planners have created a diverse kit of tools and approaches for analyzing these systems. These approaches span a range in terms of complexity and their need for directly observed biological data (Calabrese and Fagan 2004), but one very fruitful approach that has seen explosive development over the past decade since the publication of a key early paper (Urban and Keitt 2001) is that of modeling landscapes of connected habitat patches as networks. Figure 1, reproduced from (Moilanen 2011), illustrates the growth in this field.
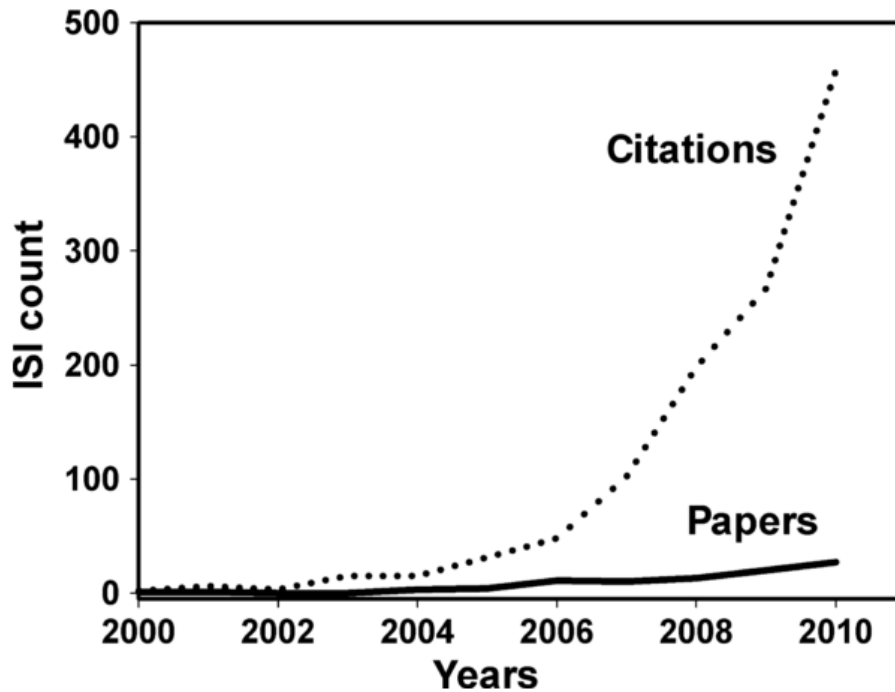
In the language of graph theory (a well-developed branch of applied mathematics), a network consists of some set of things (referred to as *nodes* or *vertices*) that are connected to one another via *edges* or *links* (Newman 2003). The networks we are concerned with here consist of nodes representing habitat patches embedded in a landscape matrix. Nodes are conceptually connected to one another when an organism can move between the patches to access habitat beyond any given single patch: that is, links represent functional connectivity between pairs of patches. Finally, the subset of a network consisting of all nodes that can be reached from one another is referred to as a *component* of the network. In other words, given some set of nodes, it is possible for some subset of the nodes (a component) to be interconnected via links but another subset (a second component) to be unreachable from the first because of a complete lack of connectivity between the components.

A network approach to analyzing habitat connectivity is appealing because networks have been intensively studied in many domains besides landscape modeling (Barthélemy 2011). In ecological applications, they require relatively little data compared with other approaches (Calabrese and Fagan 2004) and algorithms for analyzing them computationally are well developed and fast. In particular, conservation scientists working with network models have developed a rich understanding of ways to measure significant properties of networks. Recent work coalesces around metrics that measure habitat availability generally, recognizing that habitat within a given patch functions together with the habitat in other reachable patches to constitute the "available habitat" for an organism (Pascual-Hortal and Saura 2006). This acknowledges the ecological truth that what organisms need is not connectivity per se, but

7

rather, available habitat. If this available habitat is patchy, then functional connectivity between patches expands the realized amount of available habitat.

# III: Methods

## Selecting focal species in consultation with a local expert

We conducted a 1.5-hour telephone interview with Larry Rizzo, a Natural History Biologist with the Missouri Conservation Department on 05 December 2013, to discuss potential species of focus for this effort. The interview covered an overview of ecosystems in the nine-county MARC planning region, the recent (post-European-colonization) environmental history of the region, and particular species of present conservation concern. The overall purpose of the call was to collaboratively determine three focal species for this effort.

The selection criteria were that the three species should represent diverse cross-sections of vertebrate taxonomic diversity, habitat requirements, and dispersal behavior. During this conversation we further agreed that focal species should not include any species with legally protected status. In spite of the acute need these species have for state-of-the-art conservation planning, such species are typically the subject of heightened passions and pre-existing agendas that could distract potential audiences from MARC's effort to put habitat connectivity "on the table" for regional planning efforts. We did however actively target species with declining populations regionally, and species that are characteristic of the region and with which the general public might reasonably be expected to be familiar and even feel a sense of regional connection to.

Out of this call the decision was made to focus on the following species:



Figure 2 Left: Eastern meadowlark (*Sturnella magna*). Photo by AlastairRae. Center: Western painted turtle (*Chrysemys picta bellii*). Photo by Oregon Department of Fish & Wildlife. Right: White-tailed deer (*Odocoileus virginianus*). All photos licensed under Creative Commons Attribution-Share Alike 2.0 via Wikimedia Commons

*Sturnella magna* (Eastern Meadowlark). This small passerine (i.e. perching) bird with a distinctive song is iconic to the formerly extensive prairies of North America. *S. magna* (hereafter "meadowlark") nests and raises its chicks on the ground. Meadowlark habitat has been fragmented and shrunk to a small fraction of its historic area. As urban landscapes extensify and as industrial farming practices convert native

grassland to mechanically cultivated and chemically treated cropland, meadowlarks have an increasingly difficult time raising broods to maturity.

*Chrysemys picta bellii* (Western Painted Turtle). This small aquatic herptile is relatively common in the MARC region but requires wetlands, ponds, or other warm, slow-moving water for habitat. Along with many other herptiles and the rich biodiversity of wetlands generally, *C. picta* (hereafter "painted turtle") is impacted by massive and continuing conversion of wetlands to other types of land cover.

*Odocoileus virginianus* (White-tailed deer). This large herbivorous mammal is common throughout eastern North America. It is a habitat generalist that has adapted very well to human-engineered and dominated environments, to the extent that it is perceived as a nuisance in urban environments. In particular, *O. virginianus* is the source of rising public awareness and concern in the MARC region and elsewhere in the Midwest due to its frequent involvement in automobile collisions (Gonser, Jensen, and Wolf 2009).

## Reviewing primary literature for biological details on habitat and dispersal

We next conducted a review of the scientific literature for details on habitat requirements and movement behavior for each of the focal species. Graph-based models (and metrics) of habitat connectivity are theoretically grounded in the behavioral ecology of how organisms perceive and move about in their environments, and graph models must be parameterized with actual biological detail in order to generate biologically realistic outputs (Calabrese and Fagan 2004).

Detailed results from this literature review are given in Appendix 1, but one critical point requires mention here. Our literature review indicated clearly that the white-tailed deer is a habitat generalist and exhibits no sharp distinction between which landcovers it considers "habitat" and what it doesn't. Previous authors have shown that for such species, defining habitat patches operationally as discrete landscape elements is a complicated and data-intensive process (Boyce and McDonald 1999) which was deemed beyond the scope of this project. Accordingly, the deer was dropped from the list of focal species and no further habitat mapping or connectivity modeling work was conducted for it.

## Mapping habitat patches from NRI dataset

With relevant biological details from the literature in hand we proceeded to model painted turtle and Eastern meadowlark habitat from the NRI land cover data. All spatial data processing was performed using ESRI ArcGIS v 10.2 software.

### Painted turtle

We modeled painted turtle habitat by resampling the NRI to 10m pixels, which reduced the overall size of the dataset from ~50K x 50K pixels (nearly 5GB on disk) to ~12K x 12K pixels (~1/3 GB on disk) for analysis. This is critical when working with large landscapes, and is also justified given the NRI data producer's classification accuracy assessment and recommendations for appropriate scale of use (Applied Ecological Services 2013).

We reclassified the NRI into a water/non-water mask, and then dropped all patches smaller than 0.03 ha (i.e. patches consisting of 3 or fewer pixels) and all patches larger than 5.9 ha. The lower threshold was derived from visual inspection of the water mask, where patches in this class were clearly interpretable as scattered artifacts of classification and downsampling. Filtering out small patches in this way also helped to reduce an artifact of dissected linear river features. These are problematic from two perspectives: first, streams in the NRI data set typically show up as strings of water patches, cut up due to misclassification of interceding pixels as lowland deciduous forest. Second, it is impossible to determine from the NRI data how strong stream currents are. By filtering small patches of dissected stream features we minimized subsequent connectivity model's overstatement of connectivity from these strings of patches representing partially canopy-covered stretches of river. The upper threshold is the largest painted turtle habitat patch reported by (Cosentino, Schooley, and Phillips 2010). Painted turtles likely occupy optimal habitat when it occurs in patches larger than this, but our threshold also serves as a proxy distinguisher between shallow, low-energy water bodies of the sort preferred by this turtle and NRI water in the form of larger lakes and rivers.

11

The resulting habitat model included 32K+ patches which are too small to display effectively at the regional scale in this report. Because the number of potential links in a network scales approximately with the square of the number of nodes, this set of patches was computationally intractable to calculate graph-based metrics for[1]. Accordingly, we selected from the National Watershed Boundary Dataset two HUC 11 hydrologic units (roughly equivalent to watersheds) of similar size but contrasting in their intensity and pattern of human land-use/land-cover, as per Figures 3 through 6.
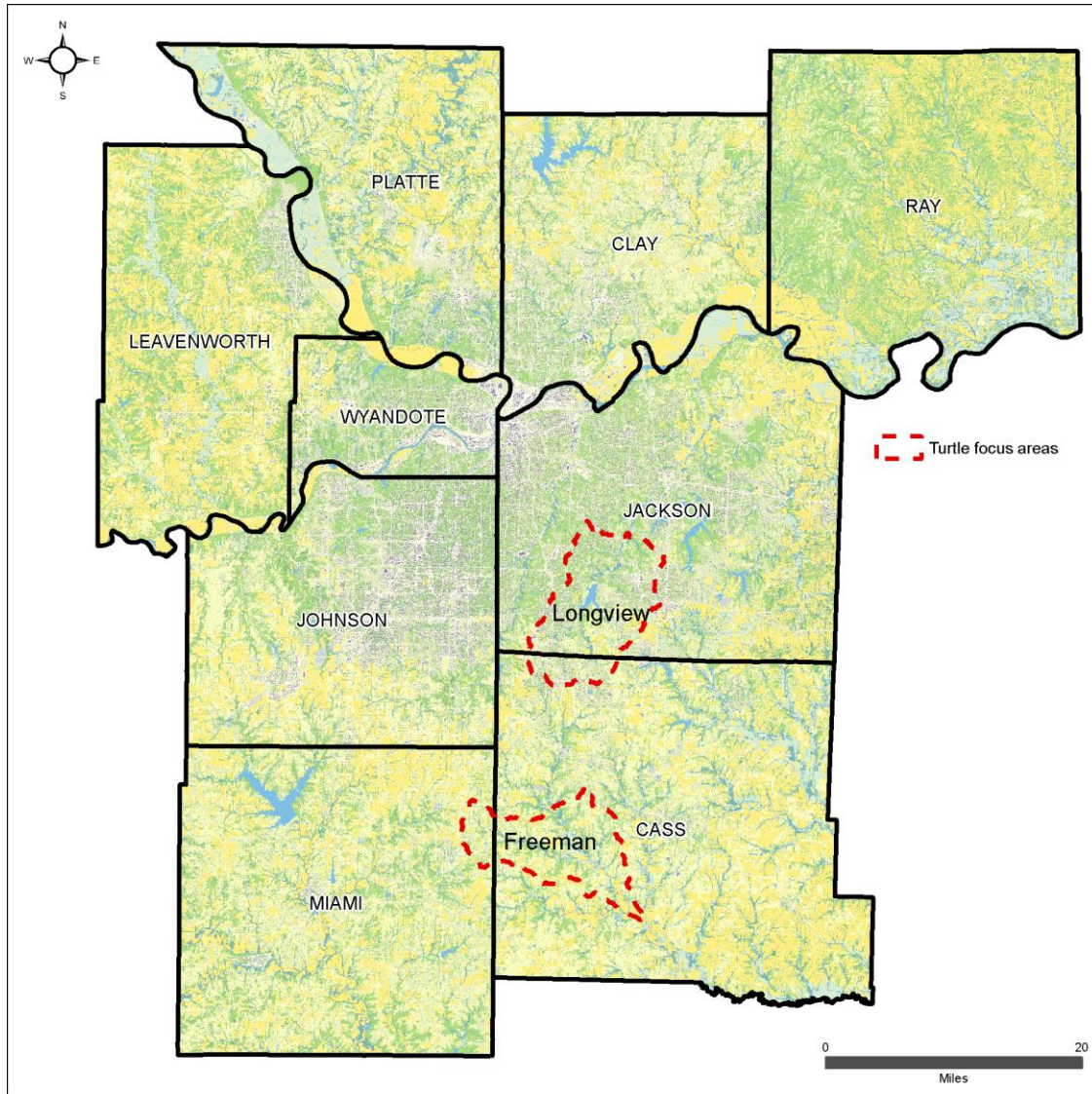


**Figure 3 Map of the MARC nine-county region, showing NRI landcover and the two HUC11 watersheds selected for painted turtle habitat connectivity analysis.**

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[1] Let L be the number of links and n the number of nodes in a fully connected graph; then $L = n(n-1)/2$. For large values of n, this means that L is proportionate with the square of n, and gets very large indeed - on the order of a billion links in a fully connected graph of these nodes. We experimented with running connectivity models on an engineering-grade GIS workstation (8-core Intel Core i7-2600 CPU; 16 GB RAM; Windows 7 64-bit OS) and on an Amazon Web Services virtual machine instance optimized for scientific computing with the processing equivalent of 100 cores. Neither system was able to complete processing the entire 32K+-patch turtle habitat model.

The Longview watershed (Fig. 4) lies on Kansas City's suburban fringe and covers 53,384 acres. It is clearly dissected by major highways and perforated by large lakes, most notably the Longview Reservoir. This landscape also displays large areas of suburban developments where agriculture has been displaced and historic hydrography and land cover have been altered in the course of urban development.
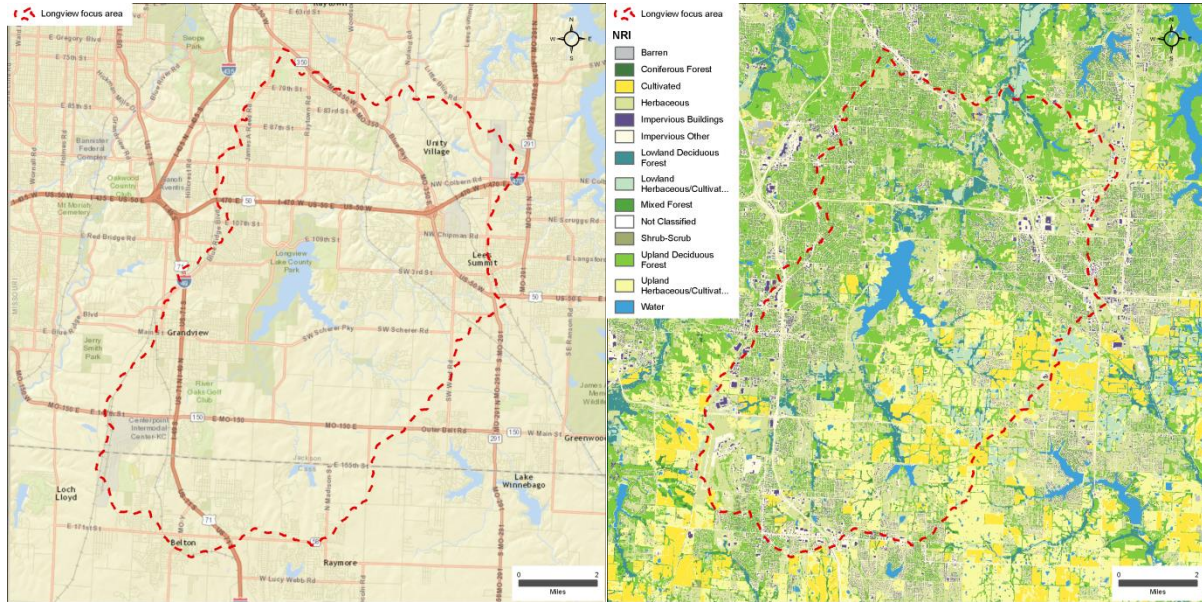


**Figure 4 "Longview" HUC11 watershed. Left: places, regional roadways, and topography. Right: landcover (from MARC NRI).**

In contrast, the 44,111 acre Freeman landscape (Fig. 5), which lies farther from the epicenter of the KC metroplex, remains dominated by agricultural land uses and remnant woodlot, and appears far less interrupted by major water or highway barriers. Freeman, MO (pop. ~500) is the major settlement.
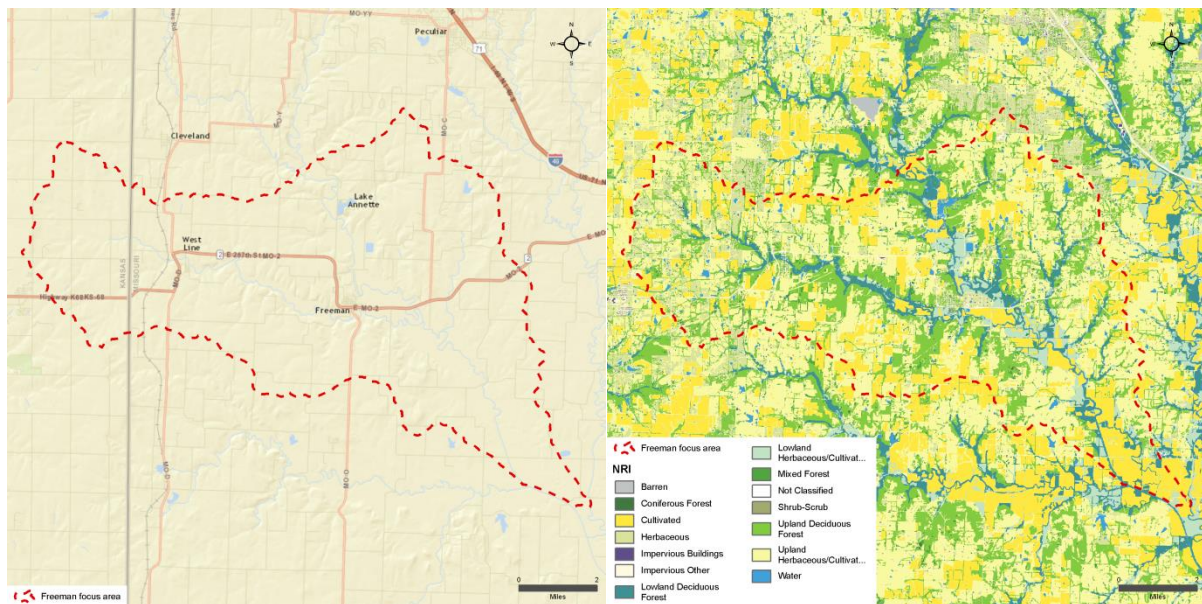


**Figure 5 "Freeman" HUC11 watershed. Left: places, regional roadways, and topography. Right: landcover (from MARC NRI).**

Considered in aggregate at the watershed scale, the landscape of the Longview watershed is less dominated by any single land cover and has substantially more surface water (measured by area) than the Freeman watershed. However, a much larger proportion of this water is concentrated into large water bodies and consequently the watershed has a smaller absolute quantity of painted turtle habitat, aside from questions of habitat distribution and connectivity.
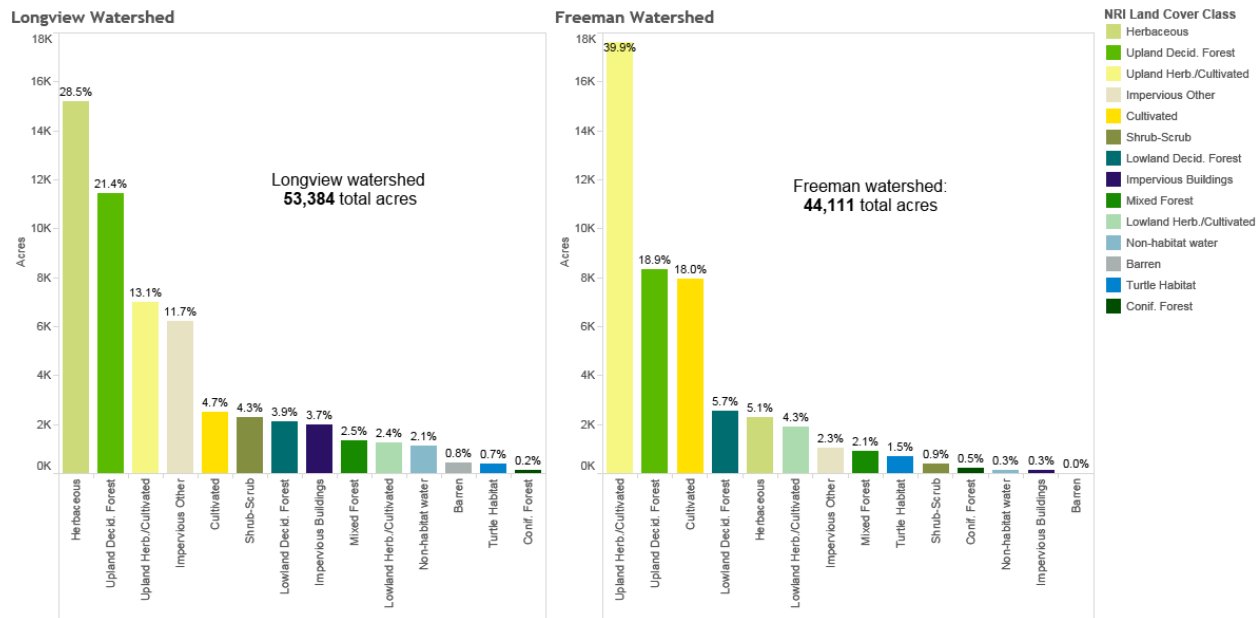


**Figure 6 Watershed-wide land cover area for the Longview (left) and Freeman (right) watersheds, by NRI land cover class. The water class has been broken into habitat and non-habitat sub-classes. In both graphs, land cover classes are sorted in descending order by total area. Disregarding patch structure, the Longview watershed is more diverse compositionally, a reflection of its urbanizing land use.**

Painted turtles have been observed to make inter-patch movements in straight lines ignoring drainage features (Bowne and White 2004), and so in the low-relief environment of the Kansas City region it is likely that painted turtles disperse between HUC11 watersheds. However, we believe that these watersheds are reasonable sub-units for this demonstration study: a) they are computationally tractable, b) they correspond with the reporting units for the structural descriptive landscape metrics task of this research contract and therefore allow for comparison of results between the two tasks, and c) watersheds have widespread utility as land units for environmental management. We judged that analysis at the scale of these two watersheds would be useful to MARC in demonstrating the potential and process of habitat connectivity modeling and highlighting the relationships between structural and functional landscape metrics. We extracted the habitat map for these watersheds from the MARC 9-county region for further processing.

Our literature review suggested that painted turtles are relatively insensitive to the specifics of landcover through which they move from habitat patch to habitat patch (Bowne, Bowers, and Hines 2006), with two significant exceptions. First, *C. picta* avoid deep water and strong currents (Rizkalla and Swihart 2006), and second, Bowne, Bowers, and Hines (2006) concluded that roads were the only matrix feature that significantly affected connectivity, where a 4-lane highway appeared to be a complete

barrier to movement. We mapped large and/or swift-flowing water bodies by filtering for large water patches as described above. We mapped large roadways by reclassifying the NRI data as a binary mask (non-building impervious vs. all else), then executing an "erode-then-dilate" strategy on this mask (Tomlin 2012) to identify all NRI non-building impervious features that are thicker than three 10m pixels (~33') wide. As vehicle lanes are typically 10'-12' wide, this gives a fair approximation of four- or higher lane roadways. Also captured by this process are large shopping- or office parking lots, which are likely also very hazardous for turtles to cross. We coded painted turtle habitat and large roadway pixels back into the NRI data as new landcover classes for use in habitat network generation and connectivity analysis.

Figure 7 shows modeled turtle habitat, large water bodies, and large roadways/parking lots for the Longview and Freeman watersheds. From the turtle's perspective, large water bodies *reduce* habitat availability, as they occupy area that might otherwise function as habitat. As barriers to direct movement they also reduce habitat by increasing the effective distance between patches they stand between, which decreases functional connectivity. Swift-flowing water features, also identified here as large contiguous patches of NRI water pixels, are also barriers to movement, as are large roadways. Barriers to movement can separate patches of habitat that otherwise might be functionally connected (Ricketts 2001). Figure 7 clearly shows that the Longview watershed has fewer painted turtle habitat patches, and that what habitat remains within the watershed is interrupted by low-patch-density areas, major highways and other paved development, and large water bodies. In contrast, the Freeman watershed is relatively un-dissected by major roads and displays a denser, more evenly distributed pattern of habitat patches.
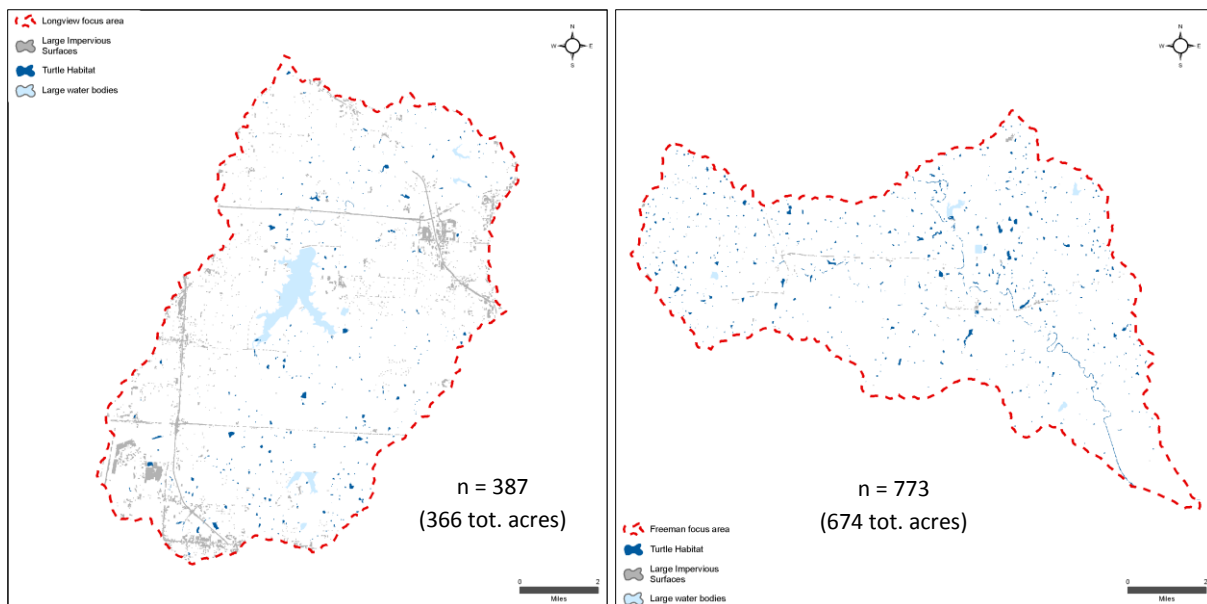


**Figure 7 Longview (left) and Freeman (right) watersheds. Three critical land cover types are shown: modeled turtle habitat (dark blue), large or swift-flowing water bodies (light blue), and large roads/parking lots (gray).**

## Meadowlark

For our model of meadowlark habitat, we resampled the NRI data to 20m pixels. We reclassified NRI as suitable (herbaceous and shrub-scrub) and unsuitable (all other classes), filtered out tiny "salt and pepper" patches using an "erode, then dilate" strategy and then simplified patch geometry with the ArcGIS "boundary simplify" tool. Finally, we eliminated all patches smaller than 50 acres, a threshold representing the liberal end (i.e. optimistic model of landscape connectivity) of the range for required patch size given by the local biologist consulted (50-100 acres; Rizzo 2013) and reasonably consistent with our literature review (mean home range of 80.9 ha; Jaster, Jensen, and Lanyon 2012). Figure 8 illustrates the processing steps involved in creating the meadowlark habitat model; Figure 9 gives a high-level view of how meadowlark habitat is distributed regionally.

At the regional scale, modeled meadowlark habitat forms a distinctive ring around the Kansas City conurbation. On the inside of this ring, intense commercial, residential, and industrial land development has by and large eliminated remnant habitat fragments as large as 50 acres. Exceptions tend to follow major drainages and frequently appear to be relictual traces of former agricultural landscapes, now surrounded by advancing suburban development. On the outside of the ring intense agricultural utilization of this fertile region has largely converted the historic prairie to croplands; substantial remnant patches are now found only along the zone where the respective urban and rural development pressures meet one another. The complete absence of modeled habitat from Ray County, at the north-east extent of the MARC nine-county region, is notable. This portion of the NRI footprint is differentiated in several raw input data dimensions (different satellite imagery acquisition date; lack of ancillary LiDAR data; uneven ground truth sampling during the accuracy assessment phase) from the rest of the MARC region and it could be that this void of modeled meadowlark habitat is simply an artifact of the NRI data product.

Once fully fledged and capable of flight, eastern meadowlarks disperse through – and over – the landscape with much greater ease than do painted turtles, suggesting that the character of the matrix may not be as important for the bird as for the turtle. A recent review of graph-based habitat connectivity studies (Galpern, Manseau, and Fall 2011a) found that several other authors have modeled bird (including songbird) movement using Euclidean distance (i.e. shortest, straight line distance as opposed to least-cost distance) between habitat patches and consequently, we followed this strategy as well in the functional connectivity we report on next.
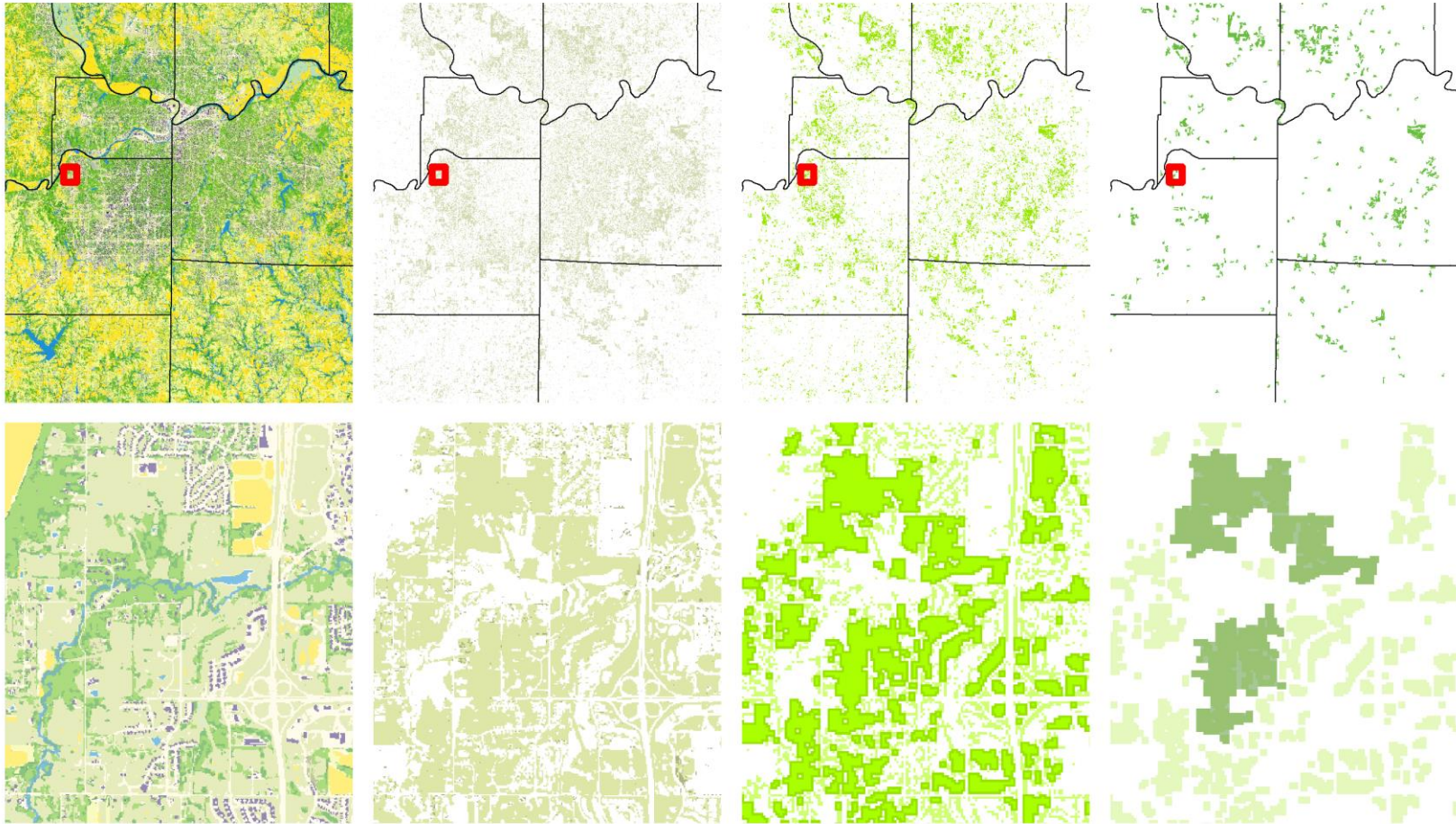
**Figure 8 Regional (top row) and local (bottom row) maps showing processing steps in modeling meadowlark habitat; columns (i.e. paired top and bottom figures) depict corresponding steps in the modeling process. The footprint of the bottom row figures is indicated in top row figures by a red rectangle. Column 1: Level 4 NRI data product. Column 2: NRI reclassified to retain only non-cultivated, non-forested, vegetative cover types. Column 3: raw candidate NRI classes from the previous step (pale green) were eroded by one 20m pixel in each direction to eliminate scattered small patches of ostensibly suitable habitat; the resulting patches (bright green) were dilated by one 20m pixel in each direction to resume a geometrically simplified approximation of their original extent (darker green perimeter). Column 4: remaining patches from the previous step were thresholded by patch area; patches smaller than 50 acres were discarded (pale green), while patches 50 acres and larger were retained and patch geometry simplified using a boundary-cleaning algorithm (dark green).**

**Figure 9 MARC-Region-wide distribution of modeled meadowlark habitat.**

## Producing functional connectivity graphs

Graph-based models of habitat connectivity require good parameterization from scientific research in order to be biologically meaningful and to be of conservation value. Galpern, Manseau, and Fall (2011) present a review of the rapidly-evolving area of practice and a detailed technical overview of the decisions and parameters involved. For both *C. picta* and *S. magna*, we used Graphab 1.2 software (Foltête, Clauzel,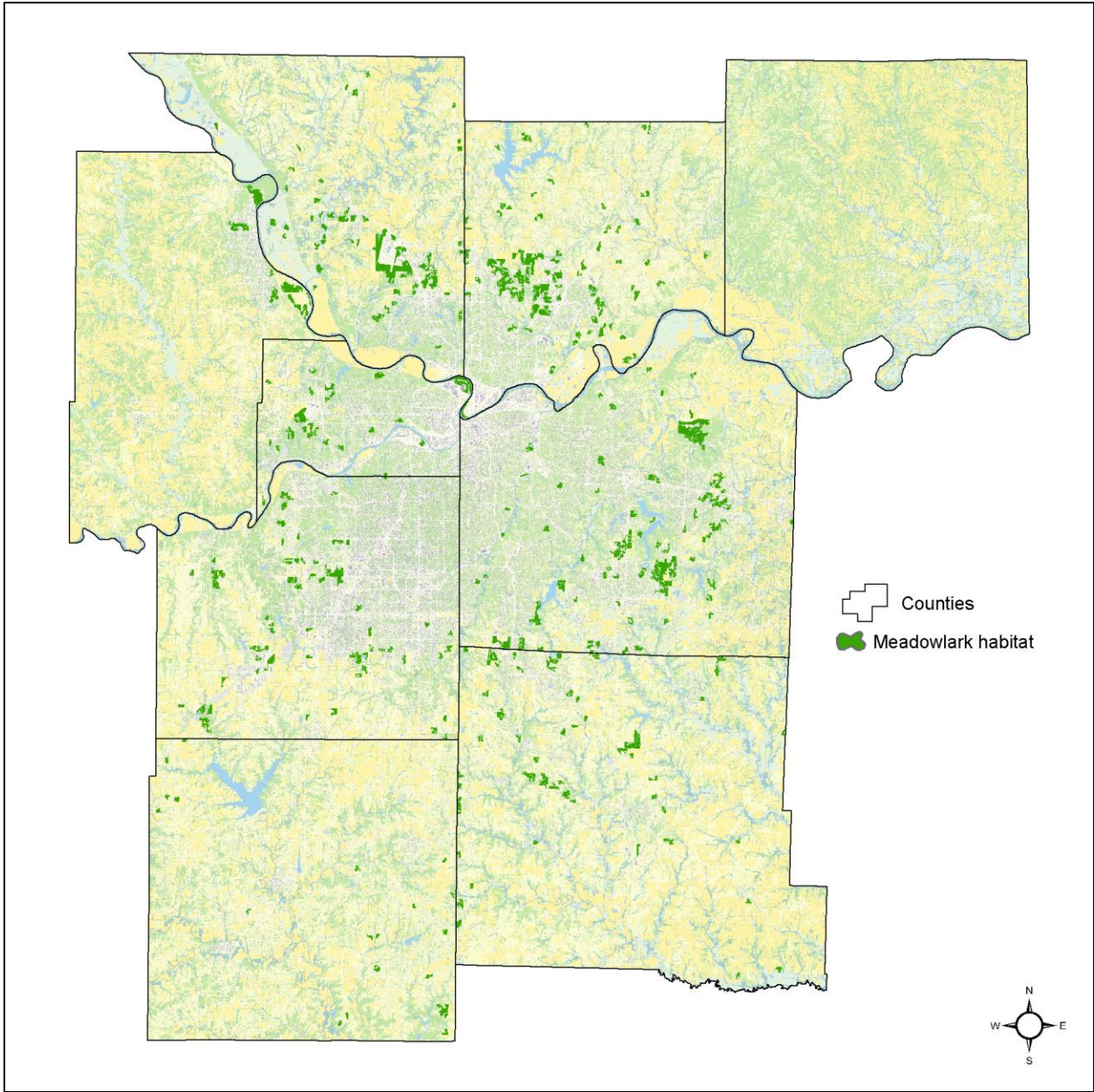 and Vuidel 2012a) to build functional habitat connectivity networks and compute per-patch metrics. Specific parameters used in graph creation (and subsequent computation of patch importance) were drawn from our review of the literatures for these two species; details are reported in Appendix 1 of this report.

## Computing connectivity metrics

MARC is interested in identifying which habitat patches (or which inter-patch connections) are of greatest importance in maintaining connectivity for the focal species. Graph theory has generated a rich literature on descriptive metrical properties of graphs, and conservation scientists experimenting with applications of graph theory have examined and used many of these. In the past few years a growing consensus has settled on a metric that is theoretically grounded in the ecology of animal movement, and that has been demonstrated to behave predictably and as desired in response to XXX. This metric is the Probability of Connectivity index (PC). PC measures "the probability that two animals randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of n habitat patches and the connections…among them" (Saura and Pascual-Hortal 2007). This index ranges from 0 (complete lack of connectivity) to 1 (complete connectivity, as when the entire landscape is comprised of a single patch of habitat). Patches that make more habitat available to a population occupying that landscape push this metric higher. This can be because a patch constitutes better habitat itself, whether because of its sheer size or some other quality, but could also be because by virtue of the patch's topological position in the graph it connects other far-flung patches that would otherwise be unreachable from one another.

By computing a graph metric and then removing each element (node or link) of a graph in sequence, recomputing the metric, and comparing the metric for the entire graph with and without that element, it is possible to evaluate the contribution of each element to a landscape's overall score (Urban and Keitt 2001). This approach is often referred to in the literature as a process of conducting "patch removal experiments" and the notation for this formulation of any metric $M$ is d$M$ ("d" for delta or difference). Applied to the PC metric, dPC is a measure of how much a given node or link in a network contributes to landscape- (i.e. network-) wide habitat availability. It can be thought of as an index of how irreplaceable the node or link is. We computed dPC for each node (patch) and each link in the graphs.

At the highest level then, our process was to model the spatial distribution of habitat for both species, then to model networks of functional connectivity between habitat patches (based on behavioral parameters drawn from the primary literature), and finally to compute metrics of habitat contribution for nodes and links in the modeled networks. In the following section we present the results of these latter two steps.

# IV: Results

## Painted turtle

Figure 10 shows overall PC for the Freeman and Longview networks. Nodes and links for both networks are rendered using the same classes and symbols to facilitate comparison between the two watersheds.
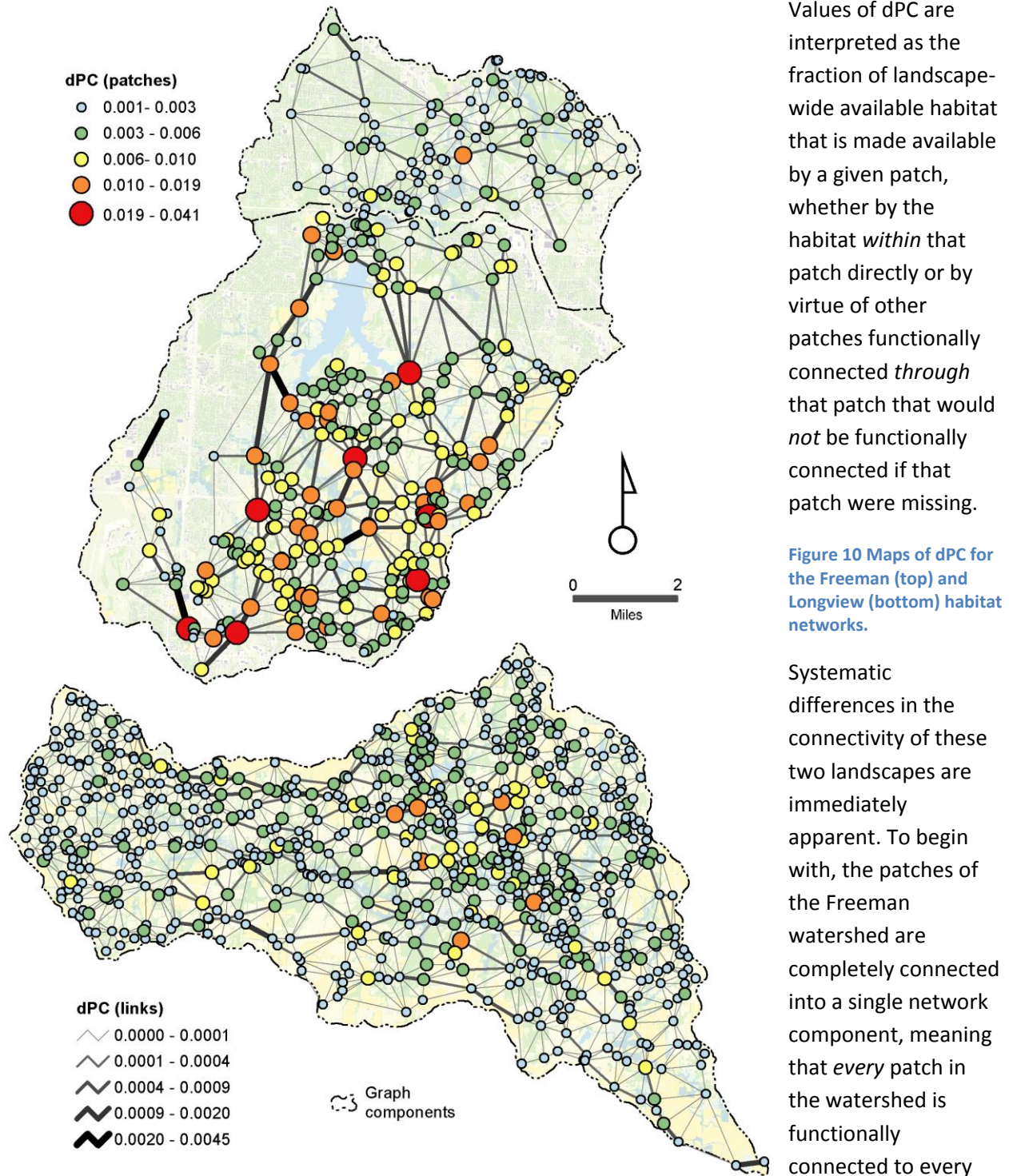


Values of dPC are interpreted as the fraction of landscape-wide available habitat that is made available by a given patch, whether by the habitat *within* that patch directly or by virtue of other patches functionally connected *through* that patch that would *not* be functionally connected if that patch were missing.

**Figure 10 Maps of dPC for the Freeman (top) and Longview (bottom) habitat networks.**

Systematic differences in the connectivity of these two landscapes are immediately apparent. To begin with, the patches of the Freeman watershed are completely connected into a single network component, meaning that *every* patch in the watershed is functionally connected to every

other patch. The Longview watershed, on the other hand, is bisected into two separate functional components by I-470 and US-50, which represent a complete barrier to north-south turtle movement through the landscape. A similar phenomenon is observable along the west edge of the watershed, where I-49 runs north-south and all but truncates this strip from the rest of the functional habitat in the Longview watershed[2]. For a turtle in the northern component, there is far less total habitat functionally available than for a turtle in the southern component: the removal of most of these northern-component patches results in a very low overall loss of watershed-wide habitat availability, as evidenced by their generally low dPC scores.

While results for the two networks are symbolized identically, keep in mind how the networks differ from one another and what the dPC metrics mean. The Freeman network represents a significantly larger amount of total available habitat (773 patches; 647 total acres of habitat) than does the Longview network (387 patches, 366 total acres of habitat). Low dPC is associated with small patches in habitat-rich landscapes, with small patches in well-connected landscapes, and with small patches in network components that represent a small fraction of landscape-wide total habitat, regardless of connectivity.
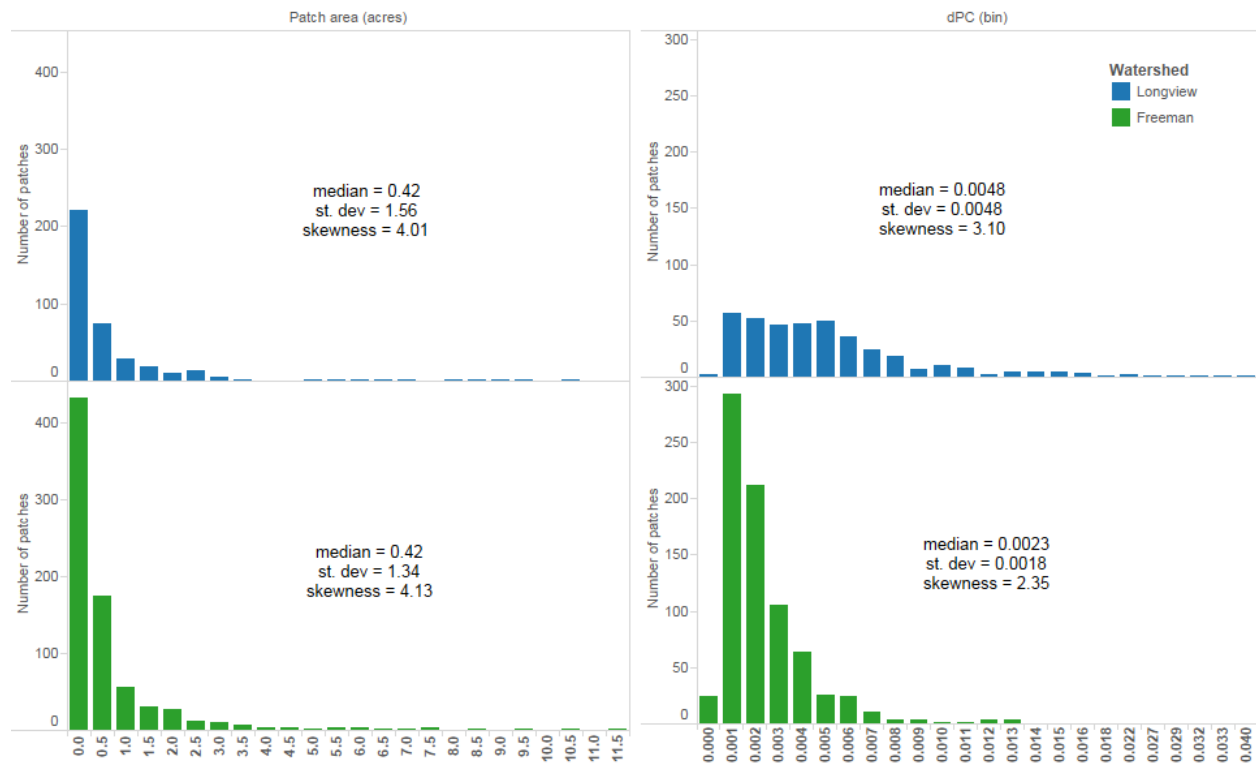


**Figure 11 Distributions of patch area (left) and dPC (right) for the Longview and Freeman watersheds.**

Figure 11, illustrating the distributions of patch area and $dPC_{patch}$, sheds light on further differences between the habitat networks of the two watersheds. In spite of the fact that the Freeman watershed contains twice as many patches and nearly twice the total area of habitat as the Longview watershed

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[2] This area to the west of I-49 remains connected in this model only because of gaps in the "large roadways" land cover class. This failure in the data could be remedied in future work by "burning in" to the NRI raster regional vector data on four-lane highways, as was done initially by the NRI data vendor.

(see Fig. 7), the distribution of patch sizes is nearly identical for the two landscapes. However, the watersheds' distributions of $dPC_{patch}$ are starkly different, reflecting strong differences in functional connectivity and subsequently in realized habitat availability. Higher median, standard deviation, and skewness of $dPC_{patch}$ in the Longview watershed indicate that a higher proportion of the patches in this network are more important in maintaining regional habitat availability. Lower median, standard deviation, and skewness of dPC in the Freeman watershed reflects the relatively robust network of connectivity between patches in this landscape, where connections are redundant enough (and total habitat plentiful enough) that few patches are individually critical to total habitat availability.

The upshot is that the Longview network is less evenly connected. Patches tend not to be as well connected to many other patches, and so there are more critical links whose removal would result in significant loss of total habitat availability. Conversely, the Freeman network is fundamentally better connected: there are more patches, and they tend to be interconnected more robustly and redundantly.

## Eastern meadowlark

The spatial pattern visible in our habitat model (namely, a ring of remnant patches around the KCMO metro area) is confirmed by the graph-based model of functional connectivity. On the outside of this ring intensive agricultural land uses (and therefore land cover) dominate the landscape, leaving very few 50+-acre relictual patches of herbaceous cover. Closer in, dense urbanization has resulted in a similar fate for *S. magna* habitat.
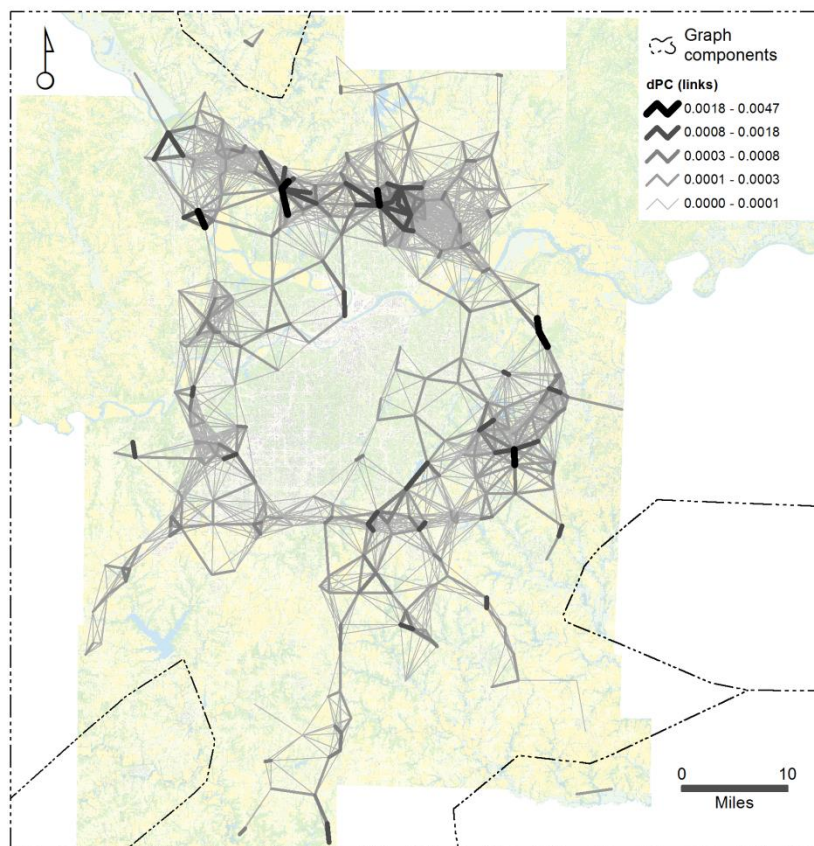


**Figure 12 Map of the MARC nine-county region, showing dPC for links in the meadowlark functional connectivity model.**

Several features of the functional connectivity model suggest that at the scale of the entire MARC nine-county region, habitat availability for the meadowlark is constrained simply by the total area of habitat rather than by the spatial arrangement of this habitat (i.e. by connectivity), and our literature review finds additional support for this conclusion. As shown in Figure 12, there are few patches (7 out of 325 in the entire landscape) from which the main component in the graph cannot be reached. Furthermore, $dPC_{link}$ values are generally very low, indicating

that the connectivity provided by any single link enables only very marginal overall gains in landscape-wide habitat availability. The dominance of a single component and the low overall dPC$_{link}$ scores are consistent with our impression of a redundantly connected network of patches, through which an individual in most cases has many alternative routes to choose from in order to reach other patches.
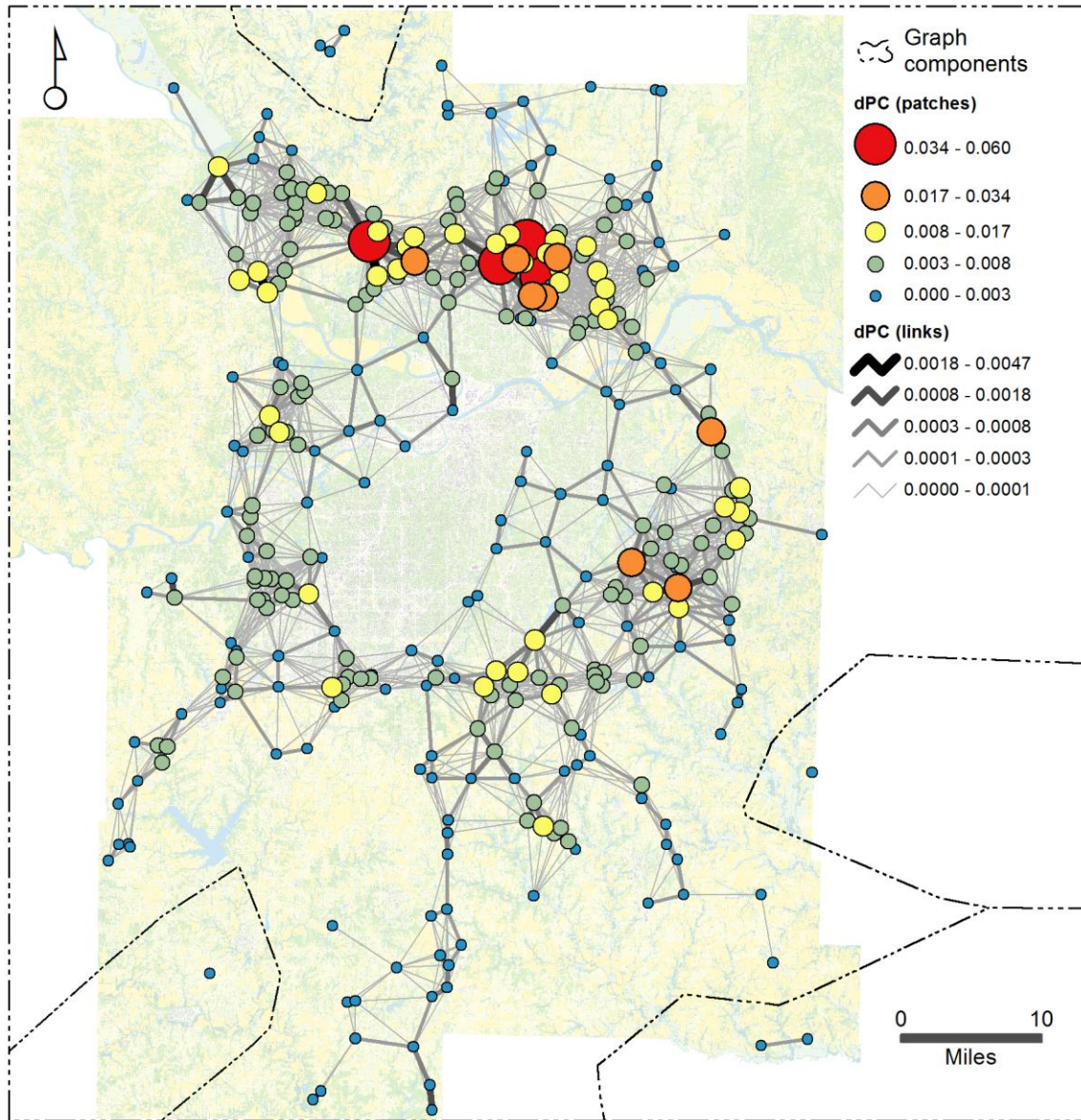


**Figure 13 Map of the MARC nine-county region, showing dPC for patches and links in the meadowlark model.**

As shown in Figure 13, the story is different when we consider the habitat patches themselves. From the perspective of an Eastern meadowlark, this landscape may be well-connected but is very habitat-sparse

and heterogeneous[3]. The four patches with highest $dPC_{patch}$ (large red circles in Figure 13) account for more than 10% of the total area of habitat in the landscape. Further, that the removal of any one of these four patches could result in such a dramatic change (between 3% and 6%) in landscape-wide total habitat availability, in spite of the denseness and redundancy of the network, is an indicator that within-patch habitat area is the limiting factor here. It could be said that there are many dots on the map in figure 13, but not much habitat; indeed, the largest 50 patches in the network (out of more than 300) account for more than *50%* of the total habitat acreage.



Network
- Longview (turtle)
- Freeman (turtle)
- MARC (meadowlark)

$\log(dPC) = 0.513101 * \log(\text{patch size}) - 2.19359$

$\log(dPC) = 0.496865 * \log(\text{patch size}) - 2.46355$

$\log(dPC) = 0.858776 * \log(\text{patch size}) - 4.16372$
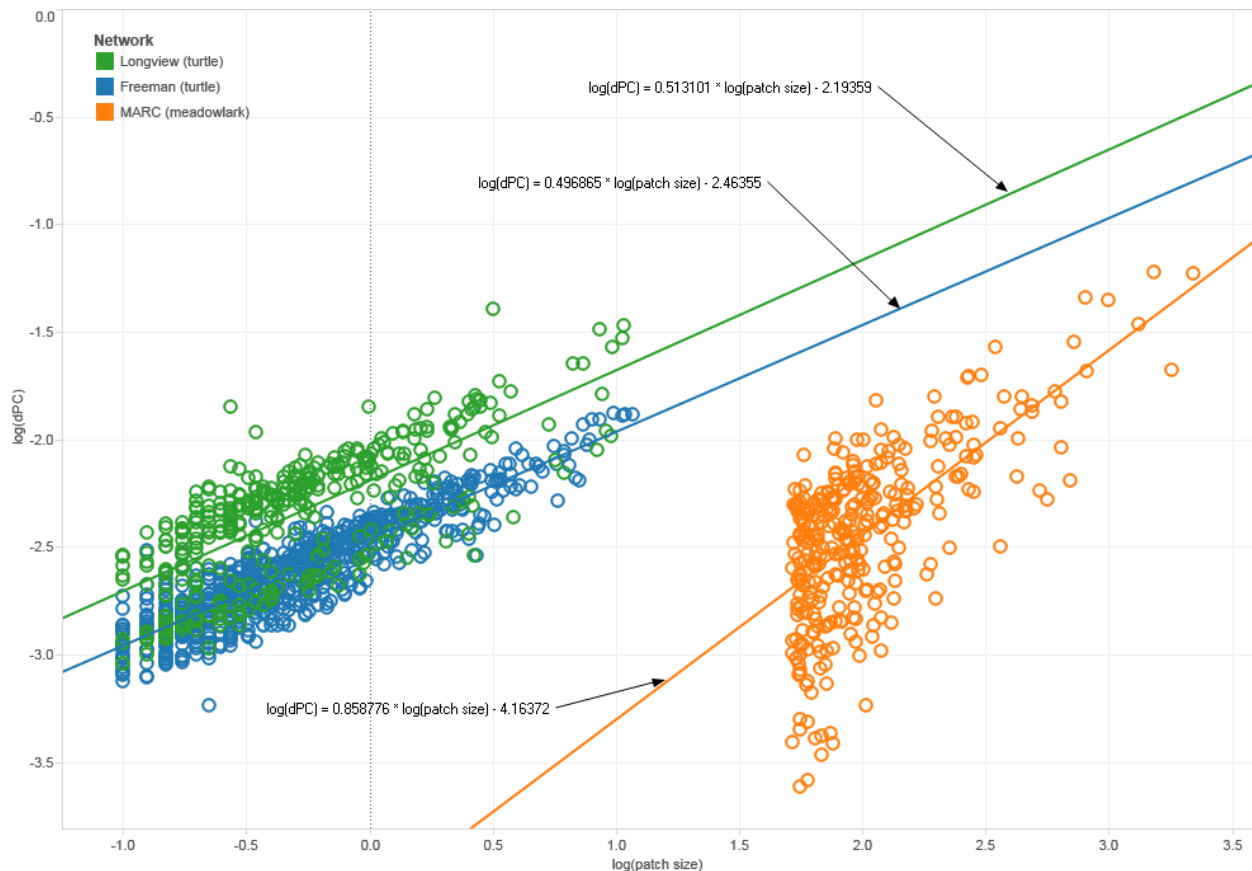
**Figure 14 Relationships between log of patch area (in acres) and log of patch dPC, for the Longview and Freeman graphs (turtle models) and the MARC-wide graph (meadowlark model).**

When we plot patch area vs. dPC for the Longview and Freeman turtle graph and the MARC-wide meadowlark graph as per Figure 14 (both variables are log-transformed because of their highly right-skewed distributions), this decreased meadowlark dependence on connectivity for overall habitat availability is apparent. Vertical banding at the low-area end of the turtle distributions is an artifact of the discrete, pixelized nature of the modeled habitat patches; similarly, the flat left-end to the distribution of meadowlark points reflects the minimum area threshold of 50 acres for habitat patches. There are four points to note.

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[3] The high level of connectivity manifest throughout this landscape is determined by the mobility capabilities of this songbird, which is a long-distance disperser relative to the typical inter-patch distances found in this landscape.

First, the relationship between area and dPC is log-linear for all three networks, indicating that large patches are disproportionately important in providing regional habitat availability for both species. In part this is because of the definition for habitat availability we are using, which explicitly includes intra-patch habitat, but it is possible that large patches are functioning in these landscapes as critical stepping-stones as well.

Second, while the slopes of all three are positive (as we'd expect) the bird model has a steeper slope than either of the turtle models. Larger patch area is directly associated with greater contribution to landscape-wide habitat availability, but in the turtle networks increased patch area doesn't yield as great an increase in dPC. This is because dPC is also a function of connectivity, which in these networks is a more significant contributor to overall dPC of the average given patch than is true in the meadowlark network. In essence, dPC at the low-area end of the turtle models is inflated by the (area-) disproportionate importance a patch can play by virtue of the connectivity it maintains in a poorly-connected landscape. The meadowlark habitat network is largely not constrained by connectivity and so smaller patches have no opportunity to make an outsized contribution to regional habitat availability on the basis of the irreplaceable connectivity they provide.

Third, while the log-transformed turtle models have nearly identical (lower) slopes, the richer and more robustly-connected Freeman network has a lower dPC-intercept than the sparser, more irregularly-connected Longview network. This reflects the higher "irreplaceability" of individual patches (essentially what dPC is measuring) in the Longview network relative to those in the Freeman network. Because the Freeman network contains more total habitat area, in more individual patches, in a smaller total landscape, it is less likely for any given patch to be as irreplaceable here than in the more highly impacted Longview landscape.

Fourth, patches from the Longview network (plotted in green over the blue points of the Freeman network) form two parallel elongate clouds in the log-log plot. The larger cloud is centered on and slightly above the regression line for the entire watershed, while the smaller cloud is largely co-extensive with the Freeman points. These two subsets of Longview points correspond with the nodes of the larger and smaller graph components respectively. Because the northern component's habitat patches have no functional connectivity with the majority of the landscape's habitat, they are less "irreplaceable". That is, their maximum contribution as stepping-stones is to the limited total sum of habitat contained in the northern graph component and therefore when experimentally removed in sequence by the dPC-calculating algorithm they can't make as large a difference to landscape-wide habitat availability. In consequence they score lower on dPC.

# V: Thoughts going forward for MARC

The previous sections of this report have detailed the theoretical basis for modeling habitat connectivity, as well as the modeling methods used in this study and the results of our modeling exercise. In this final section we take the opportunity to summarize a few key insights resulting from our literature review and from the joint demonstration of network-based measures of habitat connectivity and planning applications of MARC's NRI data asset. We address in turn: the theoretical question of how to model and prioritize habitat patches for multiple species with different habitat requirements; concrete suggestions for future work leveraging the NRI data product; and finally, general thoughts about incorporating habitat connectivity modeling into MARC's regional planning work.

## Prioritizing landscape units for multiple species

Our review of the literature on animal movement and habitat connectivity confirms our feedback to MARC at the beginning of this study: because organisms vary in their environmental needs and their abilities or behaviors to meet those needs, *every species potentially perceives the same landscape in a different way*. It is therefore difficult to create a "one-size-fits-all" mapping of habitat patches—say from contiguous regions of NRI pixels sharing the same land cover class—or of habitat connectivity. The process of modeling habitat connectivity for even a single species remains non-trivial, although experts are clear that a) when compared with other methods, graph theoretic approaches occupy an optimal midpoint on the opposing continua of data needs and biological realism, and b) biological realism is necessary for modeling results to be useful for planning purposes (Calabrese and Fagan 2004). Given the diversity of organismal needs and perception, there is a real challenge for conservation scientists and managers or planners of human systems to engage the critical question of habitat availability in a manageable, tractable way.

One suggested solution is to concentrate on species that are the object of special social focus, whether because of special legal protection, cultural significance, or scientific concern and hope that planning for the specific needs of this species provides benefit for other species simultaneously; this is the "umbrella species" approach (Lambeck 1997). Another is to abandon a species-centric approach and instead conduct conservation planning using species-agnostic "land facets" rather than species-specific units (Beier and Brost 2010; Beier et al. 2011; Brost and Beier 2012), although debate as to the utility of this approach is not new (Lambeck 1997). Alternatively, researchers have begun to develop methods for incorporating measures of connectivity into multi-species, landscape-scale conservation planning (e.g. Fuller et al. 2006) but it is fair to say that practices here are not as well supported by research as are methods for modeling habitat-patch-connectivity for single species.

The challenge of modeling multi-species habitat networks may be heightened by data inputs that discretize the natural variability of the earth's surface, thereby imposing (perhaps unspoken) anthropocentric assumptions about how the environment is perceived and structured. Regardless of the specific approach to reflecting perceptions and demands of different species, MARC planners should keep in mind the virtues and potential applicability of continuous field maps relative to discrete classifications (Hansen, DeFries, et al. 2002; Hansen et al. 2013).

Continuous field maps provide measurements at all locations (approximated operationally by sampling at a set raster resolution) for some continuously-varying phenomenon. Continuous fields of elevation, in the form of digital elevation models (DEM's) are familiar to many planners today, but many other phenomena vary continuously in space and can be represented in geodata structures this same way. An example is a map of percent woody vegetation canopy cover such as generated from MODIS satellite imagery as part of the Vegetation Continuous Fields family of data products. Here, the value for every pixel is the fraction of the pixel footprint that is covered by tree canopy. The value can vary continuously between 0 and 100%, and this representation of forest cover is inherently more information-rich in this one dimension than a discrete classification that categorically assigns each pixel to membership in a limited set of classes. From such a continuous field, maps of habitat (for example) could be generated for *multiple* species with differing habitat requirements vis a vis forest cover.

## Working with the NRI data product

Continuous fields of environmental variables are powerful tools for environmental modeling, but MARC's NRI data product is a unique asset because of its combination of regional (i.e. nine-county) extent with fine spatial grain (2.5 meter pixels). However, for many uses this will need to be down-sampled to coarser thematic or spatial resolutions, due to any or all of classification accuracy, the relevant spatial scale of the application at hand, or sheer computational tractability. Further, NRI represents a static snapshot of 2012 land cover conditions. While still representing an unprecedented resource for the KC region, as time passes the dynamic landscape will drift further and further from conditions represented by the NRI. MARC should consider a long-term strategy for refreshing this data product at reasonable intervals. MARC's planners should also take advantage of the growing library of publically available data products with national coverage that could be leveraged in conjunction with the NRI for habitat and connectivity modeling. These include but are not limited to:

- The National Land Cover Database, a 30 m resolution land cover classification derived from Landsat imagery and updated on a five-year cycle. Recent generations of this data set include continuous field estimates of impervious surface.
- The National Wetlands Inventory (NWI), a vector data product,
- Vegetation Continuous Fields (VCF) data products with 250 m resolution derived from space-borne MODIS sensors, with global coverage every 32 days. These include continuously varying surfaces of percent tree, shrub, and herbaceous vegetation, and bare land cover.
- USDA's Cropland Data Layer (CDL), a 30 m Landsat-derived raster data product that is updated annually and which shows specific crop species.
- The Protected Areas Database.
- The National Conservation Easement Database.

These national databases should be supplemented by MARC with relevant state or regional databases.

A note about some specific features of the NRI is merited, as they are likely to come up again in the context of habitat modeling for other species. Our literature review of *C. picta* habitat requirements indicates that the turtle prefers wetlands or other small, shallow, slow-moving water bodies. The NRI

product does not include an explicit wetlands class, and close visual inspection (born out by the NRI vendor's accuracy assessment) indicates that much of the wetland in the area is likely coded as Deciduous Lowland Forest. Relatedly, streams showed up as strings of small water patches that met our operational criteria for turtle habitat, strung along meandering corridors of lowland deciduous forest that were clearly stream corridors.

We judged that retrofitting the NRI with a wetlands class was clearly beyond the scope of this study, but for future applications we think it advisable that MARC reclassify wetlands, streams, and potentially other key land use/land cover classes into the data product, using ancillary data whose spatial accuracy is well-characterized and trustworthy. Aside from general modifications to the NRI product, it will likely be desirable to perform analogous but specific modifications when modeling habitat and connectivity for different species.

# Incorporating habitat connectivity into MARC's planning

Finally, we offer some thoughts on how MARC can realize its ambitions to extend regional habitat modeling efforts beyond this pilot demonstration and incorporate this kind of work into its regular regional planning work.

## Graph-based habitat connectivity models can help answer key planning questions

Authors have identified a broad range of questions answerable by graph-theoretic models of habitat connectivity. Not all of these questions will be of interest to MARC planners, but many may be.

- (Foltête, Clauzel, and Vuidel 2012b) identify three key questions that planners can answer using graph-based habitat network models:
    - What are the most important existing sites for *maintaining* habitat availability and connectivity?
    - What potential new or restored sites would be most beneficial for *expanding* habitat connectivity?
    - What are the *potential impacts* of a development project on a habitat network?
- In addition, (Galpern, Manseau, and Fall 2011b) add the following qustions:
    - What areas are connected?
    - How *strong* is the connection between areas?
    - How does the connectivity of one network compare with that of another?
    - Which corridors between patches are most important for maintaining connectivity?
    - Which *types* of patches are most important for maintaining connectivity?
    - Are there critical thresholds in connectivity, below which or above which landscape-wide connectivity changes dramatically?
    - What are the conservation or management implications of network topology[4]?
    - Which patches serve as sources or sinks for animal populations?

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[4] There are multiple metrics of network topology; one of interest is the number of links connecting a given node to other nodes is referred to as the "degree" of that node. (Minor and Urban 2008) among other authors have asked how the distribution of node degrees is related to transmission through a network; the traffic being transmitted might be an invasive species, a native being reintroduced, etc.

## Additional modeling strategies can improve habitat connectivity models

Our literature review and this modeling exercise emphasized several principles which subsequent habitat and connectivity models should continue to observe or ways in which they could be improved:

- Multiple authors emphasize the critical role of (and non-triviality of estimating) functional connectivity as opposed to the simpler, human-biased "structural" connectivity (e.g. Roe, Brinton, and Georges 2009).

- Modelers should try to get data on biological details directly from relevant species experts; this could save substantial time and effort on the part of the habitat modeler.

- For many species, matrix resistance is significant and should be explicitly included in functional habitat connectivity (i.e. trans-matrix movement) models (Zeller, Mcgarigal, and Whiteley 2012).

- For this demonstration study, patch quality was modeled as a simple function of patch area, but studies with a range of species have demonstrated that patch quality is often a function of landscape composition in the neighborhood surrounding the patch. Factors determining patch quality should be researched from the literature and accounted for in the habitat modeling process.

- Patch-neighborhood factors impacting patch quality can function at *multiple spatial scales*. Methods have been developed for evaluating the appropriate scales for analysis (Galpern, Manseau, and Fall 2011b; Foltête, Girardet, and Clauzel 2014a).

- Multiple authors (e.g. (Bowne and White 2004)Bowne, Bowers, and Hines 2006, Roe, Brinton, and Georges 2009, Harju et al. 2013) emphasize the importance of understanding the focal organism's movement behavior when planning in this realm, and caution that movement behavior and requirements can vary not only between species but within species depending on sex, age, and type of activity. MARC planners will need to carefully consider which organisms, in which life stages (infant? juvenile? adult?) or life conditions (dispersing from natal site? seeking a mate or a personal territory? foraging for food?) should be their modeling focus and then parameterize habitat and connectivity models to these specific demands.

- Some graph-theoretic habitat connectivity analysis tools have been optimized for parallel processing and should theoretically allow for rapid proceeding of very large data sets (Foltête, Clauzel, and Vuidel 2012b). Further experimentation is merited here to realize the NRI's potential for fine-grained, MARC-region-wide modeling.

## There are limits to the utility of graph-based models

This report has concentrated on the powers and potential of graph-based habitat connectivity models. However, all models are acknowlegedly imperfect representations of real-world phenomena and there has been some criticism focused on whether these network models are as biologically realistic as may be needed. Out of the flurry of graph-theoretic research papers in the past few years is the following critique from a key author in this field and a strong proponent of more complex, data-intensive methods:

Moilanen, A. (2011). On the limitations of graph-theoretic connectivity in spatial ecology and conservation. *Journal of Applied Ecology*, (2005), 1543–1547. doi:10.1111/j.1365-2664.2011.02062.x

### There is an increasing pool of experience and recommended best practice for planners to leverage

Finally, as we have discussed above, the obstacles to incorporating habitat into regional and urban planning remain significant. However, there is a growing body of literature that can help guide MARC in this critical effort. In particular we recommend the following three recent papers, which contain directly applicable methods and discussions of constructing habitat connectivity graphs (Galpern, Manseau, and Fall 2011b), applying them to various classes of planning problems (Foltête, Girardet, and Clauzel 2014b), and the challenges facing urban planners as they seek to apply these techniques (Bergsten and Zetterberg 2013):

Galpern, P., Manseau, M., & Fall, A. (2011). Patch-based graphs of landscape connectivity: A guide to construction, analysis and application for conservation. *Biological Conservation*, *144*(1), 44–55. doi:10.1016/j.biocon.2010.09.002

Foltête, J.-C., Girardet, X., & Clauzel, C. (2014). A methodological framework for the use of landscape graphs in land-use planning. *Landscape and Urban Planning*. doi:10.1016/j.landurbplan.2013.12.012

Bergsten, A., & Zetterberg, A. (2013). To model the landscape as a network: A practitioner's perspective. *Landscape and Urban Planning*, *119*, 35–43. doi:10.1016/j.landurbplan.2013.06.009

## Conclusion

In conclusion, it is our belief that MARC is well positioned to leverage a rich and historically unprecedented landscape of local and national data availability, the ongoing explosion of methods, metrics, and tools for characterizing landscape connectivity, and the growing body of species-specific knowledge that can translate these things into actionable knowledge.

MARC is pushing the regional planning envelope in its desire to explicitly include animal habitat availability and other ecosystem services into its planning work. What remains a largely unknown and untouched domain of practice to planners however is well understood by ecologists and conservation scientists as absolutely critical to the survival of the world's biodiversity and the continuity of ecosystem services mediated by this diversity. Implementing consideration of this knowledge into the ongoing evolution of cities and the other systems that embody the great human impacts on the Land is not something that ecologist can execute. Godspeed the Planners.

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# Appendix 1: Focal species literature review

## Synthesis of literature findings

### White-tailed deer

The literature on habitat requirements indicates clearly that *O. virginianus* is a habitat generalist and exhibits no sharp distinction between what landcover it considers "habitat" and what it doesn't. Previous authors have shown that for such species, defining habitat patches operationally as discrete landscape elements is a complicated and data-intensive process (Boyce & McDonald, 1999) which was deemed beyond the scope of this project. Accordingly, *O. virginianus* was dropped from the list of focal species and no further habitat mapping or connectivity modeling work was conducted for it.

### Painted turtle

#### *Land cover type*

The MO Department of Conservation summary page for C. picta (Anonymous, 2014) indicates that "in Missouri, the species may occur in slow-moving rivers, sloughs, oxbow lakes, ponds and drainage ditches" and that C. picta needs habitat with soft benthic substrates and aquatic vegetation for feeding and basking; the species cannot feed on land.

A study in Indiana found that C. picta "avoid deep water and strong currents"(Rizkalla & Swihart, 2006), in agreement with (Anderson, Gutierrez, & Romano, 2002) who noted that the turtle prefers habitats with "permanent water with low current velocities and abundant basking and refuge sites". Rizkalla and Swihart suggest that properties of the individual pond or wetland (e.g. prevalence of downed logs for basking sites) may be significant conditioners of patch quality.

#### *Patch surroundings*

What sort of land cover occurs in the vicinity of a pond or wetland may also affect how well it suits C. picta as a habitat patch. (Bowne, 2008) found that C. picta individuals spend significant amounts of time in upland habitat, suggesting that habitat protection efforts should consider uplands as well as lowlands.

(Semlitsch & Bodie, 2003), summarizing values from published studies from Idaho, Michigan, and Quebec indicate that C. picta regularly uses terrestrial habitat out to 600 m away from wetlands proper and that such regions should be considered "core habitat" for management and protection purposes. However, (Cosentino, Schooley, & Phillips, 2010) found that the area of the patch itself was a better predictor of patch occupancy than an alternative measure that also incorporated the amount of nesting habitat in a 300 m buffer outward.

(Rizkalla & Swihart, 2006) concluded that this turtle is more abundant in wetlands with a diversity of land uses in the immediate neighborhood but they are negatively affected by higher land-use diversity at the landscape (23 km$^2$) scale.

## Patch area

Observed patch size for C. picta is likely controlled more by the size of appropriate water bodies available to the turtle than by limiting patch size preferences of the turtle per se; larger water bodies are less likely to have the slow-currents, accessible muddy bottom, and/or warm water preferred by this organism. (Cosentino et al., 2010) report observing painted turtles in northern Illinois wetlands ranging between 0.1 and 5.29 ha in size.

## Disturbance regime

C. picta has been observed in highly urbanized environments where behaviors such as basking are subject to relatively intense human perturbation (Peterman & Ryan, 2009).

## Inter-patch distance

Researchers studying movements of C. picta between ponds in East-Central Kansas found that individuals usually moved to the nearest pond, and that individuals frequently moved to ponds almost 1 km away from where they started (House, Nall, & Thomas, 2010).

(Bowne, Bowers, & Hines, 2006) concluded that distance between C. picta habitat patches influences patch connectivity but that the composition of land cover between patches does not.

(Bowne & White, 2004) found that C. picta travels long distances between habitat patches in fairly straight paths.

## Matrix resistance

(House et al., 2010) found that small gravel roads with traffic limited to local vehicles and farm equipment did not generate significant mortality.

(Bowne & White, 2004) found that 2 of 13 turtles were killed during road crossings in a study of movement behavior.

(Bowne et al., 2006) concluded that roads were the only matrix feature that measurably affected connectivity, and that a 4-lane highway appears to be a complete barrier to movement.

## Eastern meadowlark

### Land cover

Eastern meadowlarks prefer native grasslands, where they feed, roost, and nest on the ground. In response to anthropogenic land cover change they are now also observed in other human-disturbed but open and vegetated habitats such as hay fields, orchards, golf courses, and the open spaces around airports (Jaster, Jensen, & Lanyon, 2012).

Ribic and Sample studied both grazed and ungrazed grassland fields and found eastern meadowlark density to be directly correlated with distance to woodlots, total length of hedgerows within 200 m of their transects, and total area of grasslands within 200 m.

Herkert et al note that non-native grasslands are more common than native grasslands in much of the mid-western and eastern US (Herkert et al., 2003), and that post-fledglings typically moved rather short distances from their nest sites and spend a great deal of time in agricultural habitats.

In their study of grassland birds in remnant prairie patches in Illinois, Kansas, Missouri, North Dakota, and Oklahoma, they detected fewer than five nests per year for more than half of all patches studied. They concluded that "bigger is better with respect to grassland-bird next success within prairie fragments, and that prairies 1000 ha or greater in size tend to support the most productive populations of grassland birds.

### Patch area

Studies approach patch area from several different directions, including sizes of territory or home range, and influence of patch size on breeding success, juvenile mortality, patch occupancy, and population density. We must distinguish between territory and home range. Loosely, territory is the area an organism will defend to exclude use by other individuals; home range is "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt, 1943). Home range is alternatively conceptualized as "the area that an animal knows and maintains in its memory because the area has some value. The individual then applies this memory or cognitive map across a landscape that contains habitat patches of varying utility with respect to its resource needs" (Kie et al., 2010). The area of an individual's home range will therefore always equal or exceed that of territory.

Rizzo indicates that Eastern meadowlarks need patches of 50 - 100 acres that remain unmown or - ploughed for 2 months to establish territory, nest, hatch, fledge (Rizzo, 2013). (Suedkamp Wells, Millspaugh, Ryan, & Hubbard, 2008) cite multiple studies concluding that 50 ha (~125 acres) is a reasonable minimum area for grassland birds, and found that "juvenile Eastern Meadowlarks in Missouri had a mean home range of 80.9 ha".

(Lanyon, 1956) reported mean territory size between 1.2 and 6.1 ha.

Herkert et all, in a large study of remnant prairie fragments, found that nest predation rates are significantly lower in larger prairie fragments, and that this effect is most pronounced at very large (i.e. > 1000 acre) fragments; they emphasized that the area bins used in their study design (<100 acres, 100 - 1000 acres, >1000 acres) do not allow them to determine whether 1000 acres is an actual threshold (Herkert et al., 2003). Nest predation is one control on recruitment of chicks into the next reproductive cohort.

(Ribic & Sample, 2001) studied both grazed and ungrazed grassland fields and found eastern meadowlark density to be directly correlated with distance to woodlots, total length of hedgerows within 200 m of their transects, and total area of grasslands within 200 m. This 200 m buffer around their sampling transects represents a 26 ha (64.25 acre) area, which accords well with the 50 acre patch size cited by Larry Rizzo. These authors found that patch area (field size) was not related to meadowlark *density*, but that landscape variables were. They also note that it is difficult to define patch size in grasslands.

### *Patch surroundings*

(Ribic & Sample, 2001) found that meadowlark densities were higher in grasslands further from woodlots but closer to hedgerows.

### *Disturbance regime*

Larry Rizzo says that mowing or ploughing during the 2 months it takes the bird to establish territory, nest, hatch a clutch of eggs, and for the chicks to fledge eliminates a patch as viable habit (Rizzo, 2013).

### *Inter-patch distance*

S. magna is non-migratory throughout most of its range, including in Kansas City region (Jaster et al., 2012), and adults return to the same territory year after year to mate (Lanyon, 1957), so dispersal is typically restricted to fledglings leaving the territory they were clutched in.

(Kershner, Walk, & Warner, 2004) studied the dispersal of young S. magna in the first weeks after fledging (when feathers are fully developed but parents are still providing care). They measured the distance dispersed from nest site at the point of their last radio-tracked location, and found that the bulk (more than 61%) of fledglings dispersed between 1 and 5 km from their birth site. Only 14.7% of observed fledglings dispersed *beyond* 5km from their natal site. However, these authors concluded that it is unlikely that post-fledgling dispersal movements are used to locate future breeding sites.

(Galpern, Manseau, & Fall, 2011) review the methods of 30 published graph-based connectivity models and note that Euclidean distance assumptions have been applied to studies of more than ten different songbirds, as well as other bird species.

(Suedkamp Wells et al., 2008) and (Kershner et al., 2004) report mean fledgling movements of similar distances at 2 weeks (100 – 150 m). The latter authors reported that 85% of tracked juveniles moved less than 5 km from their nest site by the time they had left their parents care.

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