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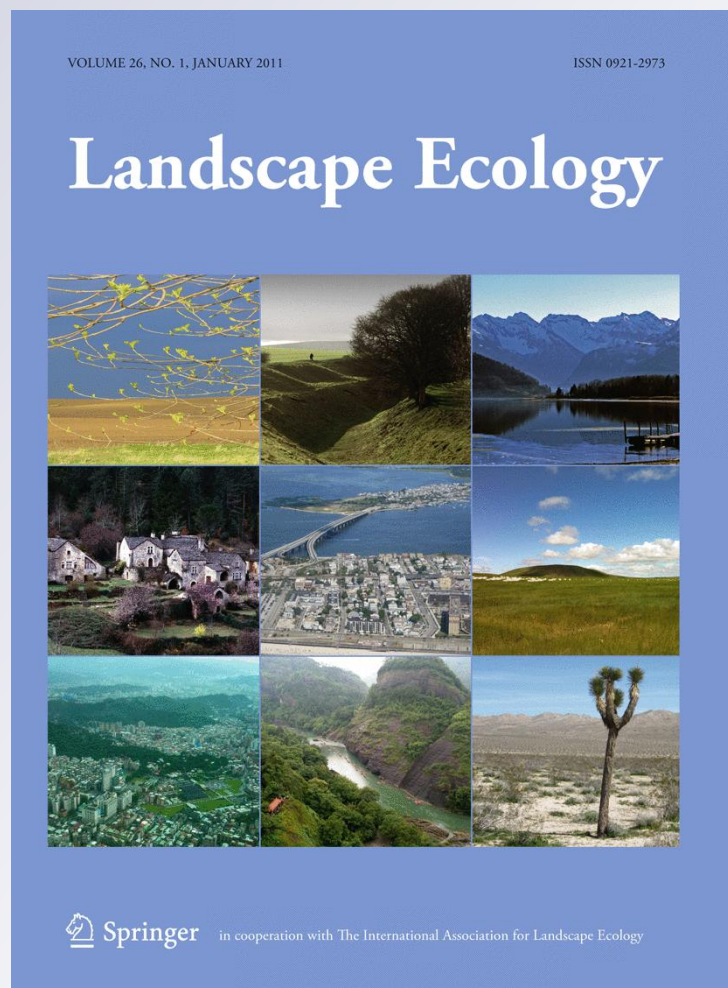
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An integration of habitat evaluation, individual based modeling, and graph theory for a potential black bear population recovery in southeastern Texas, USA

Anita T. Morzillo · Joseph R. Ferrari ·
Jianguo Liu

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Abstract Population recovery is difficult for species that require large contiguous areas of habitat, particularly within areas of heterogeneous land ownerships. Ecologically, potential for recovery success requires assessment of quantity, quality, and distribution of available habitat. Our objective was to evaluate habitat for a possible Louisiana black bear recovery in southeastern Texas. First, we categorized land cover and identified remote areas of highly suitable habitat. Next, we used the individual based simulation model J-walk to estimate ability of female black bears to move among remote habitat patches. Then, we applied graph theory to J-walk output to evaluate overall connectivity of remote habitat. An estimated 225,626 ha of remote habitat were identified in 901 patches, most of which was located within the eastern half of the study area. Network analysis showed specific areas where targeted conservation

efforts may help black bear population expansion throughout the study region. Ultimately, enough habitat area exists to sustain a black bear population and it is best connected among public and private lands largely within the eastern half of the study area. Habitat evaluation will need to be revisited if black bears establish themselves locally and actual habitat use data become available. Regardless, our analysis demonstrates an important first step that may be incorporated into a larger adaptive management framework, updated, and replicated as more-detailed habitat suitability and land use data are available.

Keywords Black bear · Connectivity · Conservation · Dispersal · Graph theory · Landscape ecology · Network analysis · Population recovery · *Ursus americanus*

A. T. Morzillo (✉) · J. Liu
Center for Systems Integration and Sustainability,
Michigan State University, East Lansing, MI 48824, USA
e-mail: anita.morzillo@oregonstate.edu

J. R. Ferrari
Appalachian Laboratory, University of Maryland Center
for Environmental Science, Frostburg, MD 21532, USA

Present Address:

A. T. Morzillo
Department of Forest Ecosystems and Society, Oregon
State University, 321 Richardson Hall, Corvallis, OR
97331, USA

Introduction

Management of both public and private land plays an important role for recovery of wildlife populations (Maehr et al. 2001; Woodroffe 2001). Public lands (e.g., reserves) often are not large enough to adequately protect species (Gurd et al. 2001; Liu et al. 2001). Likewise, private landowners may limit wildlife access to land (e.g., dislike of a species; Lindsey et al. 2005). As a result, recovery is difficult for species that require large contiguous areas of habitat that may no longer exist or are not easily

accessed because of human activity (Pelton 1986; Maehr et al. 2001). Ultimately, from an ecological standpoint, potential for a successful recovery requires assessment of the (1) quantity, (2) quality, and (3) distribution of available habitat (Reading and Clark 1996). Habitat distribution eludes to the spatial arrangement of resources for a particular species and whether these resources are directly or indirectly accessible, and is addressed by assessing connectivity. Overestimating habitat quantity, quality, and overall connectivity may hinder population growth; whereas underestimation may lead to overpopulation (Hamilton 1999).

Detailed habitat use data for a particular location typically is not available for species targeted for recovery, and evaluating available habitat is difficult because estimates can vary depending on evaluation tools, scale of analysis, and focal variables (e.g., Osborne et al. 2001; Miller et al. 2004). For example, habitat suitability indices (HSIs) provide basic comparisons between locations (USFWS 1981; e.g., van Manen 1991), but generalizing HSIs to spatial and temporal dynamics of landscapes is resource intensive (Schamberger et al. 1982). Thus, for species likely to seek various land covers for different activities (e.g., foraging vs. denning) across broad extents, suitability estimates often rely on habitat use data from other locations and professional judgment (e.g., Lookingbill et al. 2010).

We assessed the quantity, quality, and distribution (connectivity) of habitat for a Louisiana black bear (*Ursus americanus luteolus*) recovery in southeast Texas. Overharvest and habitat loss led to the demise of this subspecies (BBCC 1997), except for two small populations in eastern Louisiana, until two management plans spurred recovery (Bowker and Jacobson 1995; BBCC 1997). An increase in number of bear sightings in eastern Texas during the past decade (probably transients from neighboring states) prompted creation of an East Texas black bear management plan, the ultimate goal of which is to restore habitat for the purpose of reestablishing black bear as a viable ecosystem component (TPWD 2005).

Big Thicket National Preserve (BTNP) is one location of interest for recovery efforts. This 39,285-ha preserve consists of 12 disjunct administrative units, seven of which are river corridors that connect larger units. Individual units of BTNP contain suitable black bear habitat (Garner 1996), but habitat has not been

evaluated regionally. Therefore, our objectives were to (1) quantify black bear habitat, (2) assess potential habitat connectivity using an individual based simulation model and network theory, and (3) discuss implications of results from objectives (1) and (2) as related to a potential black bear population recovery. Our results will provide guidance to managers for prioritizing conservation efforts and a context for integrating socioeconomic processes affecting black bear habitat.

Methods

Study area and context

Our study area included 12 counties (approximately 2,737,700 ha) of southeast Texas (Latitude 30.52, Longitude -94.34; Fig. 1a). Much of the area is rural; more than 75% consists of private timberland, BTNP, and national forestland (Angelina, Davy Crockett, Sabine, Sam Houston). Numerous small towns and one larger community (Lufkin) are scattered throughout the region. The southern boundary contains dense suburban development from Houston and Beaumont.

Habitat analysis

Using Imagine 8.7 (Leica Geosystems GIS & Mapping, LLC, St. Gallen, Switzerland), we derived land cover classification from 2002 LandsatTM ETM+ multispectral imagery. We used images from November and March to maximize cloud-free availability and ground-truthed 255 training sites that were consistently identifiable throughout all seasons. We applied training site data to imagery classification and grouped land cover into eight categories: urban (including residential), water, sand, agriculture (including pastures), pine forest (plantation and natural), mixed (pine and hardwood) forest, clearcut (newly cleared and young regenerating forest), and bottomland forest (bottomland hardwoods that flood regularly) (Harcombe and Callaway 1997).

We assigned land cover data to one of four habitat classes (highly suitable, suitable, marginal, and unsuitable) based on black bear ecology (Pelton 2003) in the southern US (Weaver et al. 1990; Maehr et al. 2003; Larkin et al. 2004). Highly suitable habitat included mature mixed and bottomland forest

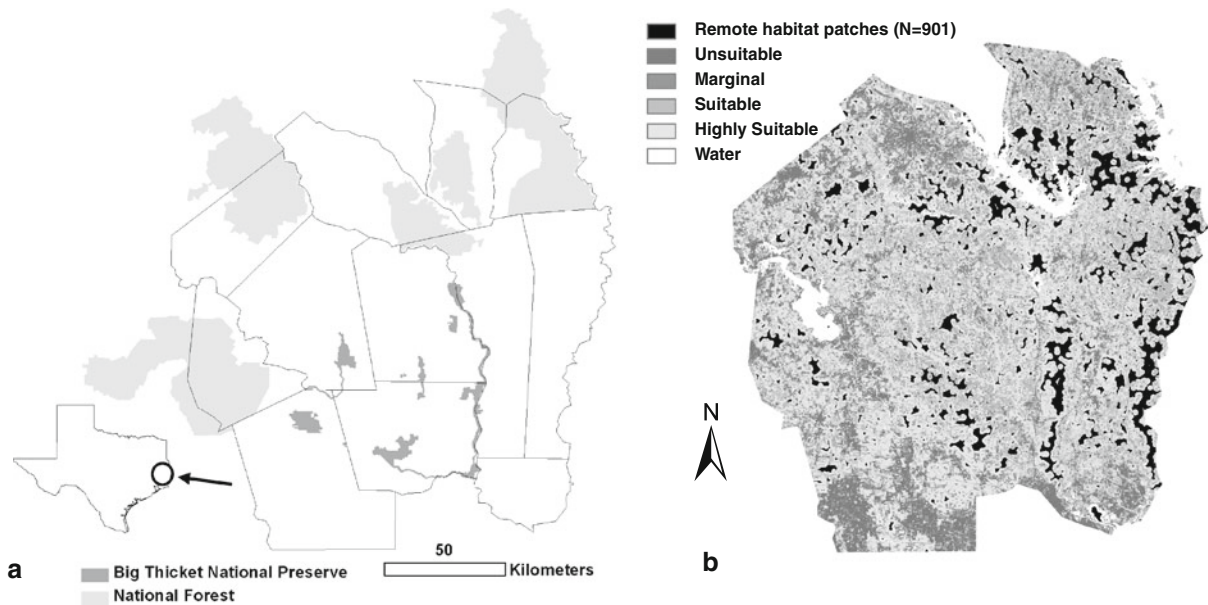


Fig. 1 **a** Study area in southeastern Texas, which includes Big Thicket National Preserve (*dark shaded*) and portions of four National Forests (*light shaded*). *Solid lines* illustrate county boundaries. **b** Habitat classification and remote habitat patches

that likely was the historic climax community (Harcombe and Marks 1977; Marks and Harcombe 1981; Peacock 1984), with mast and fruits important as food for black bears (e.g., oak, hickory) and large trees for denning (Larivière 2001; Pelton 2003). Suitable habitat included recent clearcuts and young regenerating forest containing early succession vegetation not present in mature forest which, if managed for growth of understory hardwoods, would have potential to become highly suitable. Regionally, bears use slash (woody debris remaining after timber harvest) for denning, and fruit-bearing vegetation is important foraging habitat (Wagner 1990; Weaver et al. 1990; Marchinton 1995; Nyland 1995; Anderson 1997; Larkin et al. 2004). Marginal habitat included locations that bears may traverse but were unlikely to reside in such as monotypic pine plantations and sun-exposed sandbars and arid environments (e.g., yucca, cacti; Peacock 1984). Unsuitable habitat consisted of agriculture (livestock and pasture) and urban, which included all human infrastructure because of difficulties differentiating among low- versus high-density urban at a 30-m scale. We did not include open water in habitat analysis.

We revised our initial scale of 30-m pixels to a scale more appropriate for estimating bear habitat use. Home ranges are seasonally dynamic and vary

greatly in area (e.g., Hellgren and Vaughan 1990; Wooding et al. 1994; Rudis and Tansey 1995; Anderson 1997; Beausoleil 1999; Larivière 2001; Maehr et al. 2003; Pelton 2003). In Louisiana, home ranges varied between 15 and 42 km² for females and 33 and 340 km² for males (Wagner 1990; Marchinton 1995). Because a scale of analysis based on home range area resulted in loss of image details (e.g., entire small towns), we redefined scale using black bear movement information (Pitt et al. 2009).

Bear movement may be estimated using average interlocation intervals varying between one and 24 h (Garshelis and Pelton 1981; Wagner 1990; Hellgren et al. 1991; Marchinton 1995; Nyland 1995). In the southern US, such intervals range from several hundred meters to >5 km (Reynolds and Beecham 1980; Wagner 1990; Marchinton 1995; Eastridge 2000). We assumed a conservative average interlocation distance of 2.5 km per 24 h period (Garshelis and Pelton 1981; Larivière 2001; Pelton 2003), which is equivalent to an hourly distance of 0.1 km (100 m), or the width of one square hectare. Thus, we resampled the classified habitat at a scale of one hectare, which accounted for bear movement and conserved key land cover features (e.g., human infrastructure). After resampling, we calculated total area of the four habitat classes and identified patches

of highly suitable habitat, defined as a contiguous area of similar classification (Turner et al. 2001). We considered any two pixels of similar cover touching in the four cardinal or four diagonal directions to be contiguous (“eight-neighbor rule”).

Female bears prefer denning in remote locations (BBCC 1997; Pelton 2003). Rudis (1986) defined “remoteness” as forest ≥ 0.8 km from human activity; Rudis and Tansy (1995) defined it as contiguous forest tracts $> 1,000$ ha. Linnell et al. (2000) suggested that grizzly bears, which may be more diet-specialist than black bears (Pelton 2003; Schwartz et al. 2003), tolerate human activity ≥ 1 km from dens. Therefore, from among highly suitable habitat, we further identified “remote” habitat as highly suitable habitat an Euclidean distance of ≥ 1 km away from unsuitable habitat (i.e., highly suitable habitat surrounded by ≥ 1 km of at least marginal habitat). These locations may provide bears the least disruption by and greatest distance from humans, and, hereafter, are referred to as “remote habitat.”

Estimating patch-level connectivity using individual-based simulation

Population expansion depends upon the ability of females to disperse, establish new home ranges, and breed. Therefore, similar to Clark et al. (1993), we restricted our analysis to adult females, and considered patches most likely to support denning and use by females with cubs (BBCC 1997; Pelton 2003) to be the remote habitat patches (see previous section), hereafter referred to as “patches.”

We used the individual-based simulation model J-walk (Gardner and Gustafson 2004) to estimate probability of successful female movement among patches. J-walk is a correlated, directionally biased random walk simulation model developed to estimate dispersal of vertebrate species within heterogeneous landscapes (Gardner and Gustafson 2004) and requires two datasets in raster format: (1) a habitat map and (2) a map of patches from which to estimate dispersal. We used the four-class habitat suitability for the habitat map, and the collection of remote patches for the patch map.

We parameterized J-walk using empirical data from the scientific literature supplemented with our professional judgment to collate information. Several parameters are required for J-walk simulations: the

maximum movement distance (T), the turn angle (C), and movement (p_m) and mortality (d_m) probabilities. First, we estimated $T = 150$ km after a review of black bear dispersal (e.g., Rogers 1987; Lee and Vaughan 2004) and movement data (e.g., White et al. 2000; Lee and Vaughan 2004; Larkin et al. 2004). Past research suggests that individuals may move as much as a 150 km gross distance, but most likely in a circuitous route. To account for meandering, we established a maximum net displacement of 30 km (e.g., Eastridge 2000; Wear et al. 2005). That is, a bear may walk 150 km but end up only 30 km from where it started. The J-walk parameter that controls the ratio of net (30 km) to gross (150 km) displacement is the turn angle parameter (C). This parameter introduces randomized turns in a homogeneous habitat, without any additional influences such as attraction towards more favorable habitats (Gardner and Gustafson 2004; Lookingbill et al. 2010). We calibrated C by releasing 10,000 simulated bears (“simbears”) from a common central point in a $300 \text{ km} \times 300 \text{ km}$ homogeneous landscape with a movement probability (p_m) of unity, a mortality rate (d_m) of zero, and $T = 150$ km. This parameter was adjusted until 99% of dispersers moved ≤ 30 km from the release point, resulting in $C = 0.52$.

For application to our heterogeneous landscape, we assumed that black bears prefer particular habitat classes during movement (p_m). This is an additional bias to any randomized turns introduced by calibrating C using homogeneous habitat, as observed movement data typically are collected from suitable habitat as assumed by organism presence and use of a particular location (e.g., Lookingbill et al. 2010). We also varied the probability of mortality in each land cover type as the animal traverses a pixel of that cover type (d_m). Because empirical movement data from our study area were absent, we referred to past research (see references in previous sections) and professional judgment to develop a rank order of and assign values of p_m and d_m to each habitat class from unacceptable (open water) to most preferred (highly suitable habitat; Table 1). The J-walk algorithm guides each step taken by an individual based on C (turn angle) and p_m values of the eight adjacent neighbor pixels, with preference given to neighboring pixels with relatively higher p_m values (Gardner and Gustafson 2004; Lookingbill et al. 2010).

Table 1 Movement (P_m) and mortality (D_m) parameters assigned to habitat classification for application of J-walk

P_m	D_m	Habitat type
0.01	0.05	Open water
0.25	0.01	Unsuitable
0.30	0.0005	Marginal
0.75	0.0001	Suitable
1.0	0.00001	Highly suitable

J-walk simulations were performed independently for each remote habitat patch, the objective of which was to estimate potential connectivity (Calabrese and Fagan 2004) among each possible pair of patches. Each simulation consisted of releasing 100,000 dispersers (simbeards) from randomly selected locations on the periphery of each patch; the large number of dispersers was used to ensure numerical accuracy. Simulation stopped for each disperser when the disperser reached the border of a different remote patch (i.e., successful dispersal), reached the maximum movement distance (T), or experienced a mortality event. We recorded the number of simbeards that reached any destination patch, and repeated this process for all remote habitat patches.

Network analysis

We transformed J-walk output to a network representation in order to evaluate connectivity among remote habitat patches. We did this by defining transport operator (ω_{ij}) as the number of successful dispersals from patch “ i ” to patch “ j ” divided by the number of dispersers modeled for each patch (100,000) and expressed either as a probability (0–1) or a percentage (0–100%). The value of ω_{ij} can be considered connection strength; a value of zero implies no connection exists, whereas a value of one (or 100%) implies that all dispersers leaving patch i will make it to patch j . The ensemble of ω_{ij} values was organized into an $N \times N$ matrix (Ω), where N was the total number of patches.

We performed several analyses using Ω , recognizing this matrix essentially as a weighted adjacency matrix, which is the foundation for network analysis (Gross and Yellen 2006). Rather than choose a specific ω_{ij} value to represent a potential network, we systematically evaluated potential connectivity across

a range of minimum acceptable ω_{ij} values, called the Minimum Connection Strength (MCS). MCS values ranged from 0 to 100%, with 1% increments used for $1\% < \omega_{ij} < 10\%$, and 2% increments for $\omega_{ij} > 10\%$. For each MCS value, a network was created and evaluated (e.g., MCS of 1% yielded a network where all connections $\omega_{ij} < 1\%$ were dropped). This type of evaluation has parallels with graph analyses across a range of distance-based dispersal abilities (e.g., Bunn et al. 2000; Urban and Keitt 2001). In the exercise presented here, rather than defining the graph (network) based on sequentially increasing distance-based gap crossing abilities, we sequentially increased the required minimum probability of successful inter-patch movement as estimated by J-walk. Essentially, the distance-based analysis asks “what is the minimum distance an organism must be able to cross in order for the collection of patches to be considered connected?” Instead, we asked “what is the minimum connection strength required for the landscape to be considered connected for black bear?”

An analysis was performed for each MCS value by setting to zero all $\omega_{ij} < \text{MCS}$. All remaining connections were given a value of 1 in an upper diagonal symmetric and binary adjacency matrix A (see Urban and Keitt 2001). An entry i, j in this matrix had value 1 if either ω_{ij} or $\omega_{ji} > \text{MCS}$, else the value was 0. For each MCS value we applied two metrics associated with the largest cluster (component) of inter-connected patches: (1) largest component area, A_{LC} , and (2) graph diameter, $d(G)$. Largest component refers to the larger of either the largest patch or the grouping of interconnected patches with the greatest aggregate area (Ferrari et al. 2007). Graph diameter is the longest path (chain of connected patches for a given MCS) between any two patches, where the path length between those patches is itself the shortest possible length (shortest total distance across all possible combinations of a path; Bunn et al. 2000), and was calculated using Euclidean inter-patch distances and Dijkstra’s algorithm (Dijkstra 1959). We assessed these metrics across all MCS values because a rapid increase in either metric can indicate formation of a “giant component” (GC) synonymous with a percolation threshold (Keitt et al. 1997; Ferrari et al. 2007). Existence of a GC implies a majority of habitat is directly or indirectly accessible from any

patch in the network, whereas lack of a GC suggests isolation of a majority of habitat patches. Because we defined our largest component as that with the largest area, a GC always contained a majority of habitat even if it did not contain a majority of patches. Both metrics were evaluated because thresholds in one metric may not correspond to changes in the other. For example, loss of connections to small patches on the periphery of the largest component may yield a dramatic change in $d(G)$ but not substantially influence A_{LC} (Ferrari 2005).

We also evaluated J-walk output across each MCS value using the full matrix Ω (a directed graph) and two additional metrics. First, area-weighted flux (AWF^* ; Eq. 1) is related to flux metrics (e.g., Bunn et al. 2000; Urban and Keitt 2001; Minor and Urban 2007), and is equivalent to equation four in Saura and Pascual-Hortal (2007) normalized to a 0–1 scale by A^* , the sum of all remote patch area:

$$AWF^* = \frac{\sum_{i=1}^N \sum_{j=1, i \neq j}^N a_i a_j \omega_{ij}}{A^*} \quad (1)$$

where a_i and a_j are the areas of patches i and j , respectively. This metric takes into account connection strength and patch size to estimate the flux of organisms across the network.

Second, we calculated a variant of the probability of connectivity index (PC ; Eq. 2), proposed by Saura and Pascual-Hortal (2007):

$$PC^* = \frac{\sum_{i=1}^{NP} \sum_{j=1}^{NP} a_i a_j p_{ij}^*}{A^*} \quad (2)$$

If two patches are in close proximity, p_{ij}^* equals ω_{ij} . If patches i and j are distant, the value of ω_{ij} approaches zero, yet a more direct path could exist across stepping stone-like paths between patches i and j , in which case p_{ij}^* is the maximum product of ω_{ij} values calculated across the paths (Saura and Pascual-Hortal 2007). Normalization of PC by A^* yields $PC^* = 1$ for a landscape where all patches are connected to every other patch with $p_{ij}^* = 1$.

We complemented the aforementioned network indices with two metrics calculated for each individual node. First, connection strength (S_i ; Yook et al. 2001; Eq. 3) combines information about a nodes out-degree, or number of outgoing connections (from the focal patch i to all others) and the strength of those connections:

$$S_i = \sum_{i=1}^N \omega_{ij} \quad (3)$$

Second, betweenness centrality (Freeman 1977; Eq. 4) is defined as:

$$BC_i = \sum_{l \neq k \neq i}^N \frac{\alpha_{lk}(i)}{\alpha_{lk}} \quad (4)$$

where α_{lk} is the number of shortest paths between any two nodes in the network, and $\alpha_{lk}(i)$ is the number of those shortest paths that pass through node i . Greater S_i values imply greater potential of a node to be a source node. Greater BC_i scores imply a greater potential for use during landscape traversal (Minor and Urban 2007). Nodes with greater values of either or both metrics were considered a greater importance for recovery efforts.

All network calculations were completed using a modified version of LANDGRAPHS software (Urban 2003; Ferrari et al. 2007; Ferrari and Lookingbill 2009; Lookingbill et al. 2010). Betweenness centralities were calculated using Pajek 1.26 (Batagelj and Mrvar 2010) using the inverse of ω_{ij} as distance for calculation of path lengths.

Results

More than half of the study area consisted of highly suitable habitat (1,430,500 ha; 55%), followed by suitable (471,400 ha; 18%), unsuitable (446,900 ha; 17%), and marginal (237,500 ha; 9%) habitat (Fig. 1b). Most unsuitable habitat was located along the southern and northwestern portions of the study area, which corresponded to the greatest density of humans and extensive row crop agriculture along the Gulf Coastal Plain. An estimated 225,626 ha of remote habitat were identified in 901 patches across the landscape (Fig. 1b), most within the eastern half of the area, along the Texas-Louisiana border, and among public lands.

Raw output (MCS = 0%) indicated 900 of 901 remote patches were connected as part of one giant component (hereafter GC). The GC had 30,102 connections of varying strength ranging from one successful transfer out of 100,000 attempts ($\omega_{ij} = 0.001\%$) to a maximum $\omega_{ij} = 90\%$. The number of connections decreased drastically with

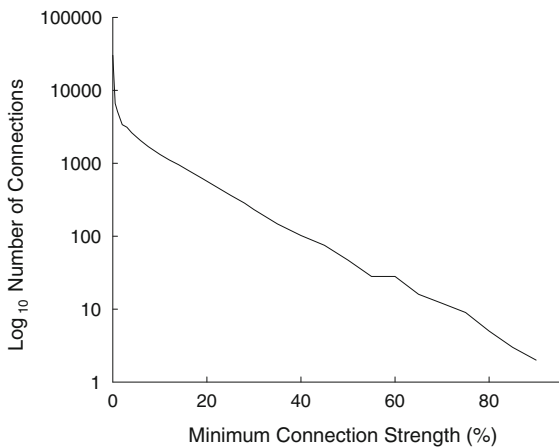


Fig. 2 Number of network connections (\log_{10}) versus minimum connection strength (MCS), or strength required to form network links, with maximum $Y = 30,103$

increasing MCS (Fig. 2), suggesting that many connections were relatively weak. For example, the network corresponding to $MCS = 0.5\%$ had 6,605 connections, or approximately 20% of the raw output connections. Thus, approximately 80% of the raw output connections had a success rate of less than one individual per 200 dispersal attempts. For $MCS > 4.0\%$, the relationship between number of connections and MCS appeared somewhat log-linear. Only two connections satisfied the largest $MCS = 90\%$.

The metrics A_{LC} , and $d(G)$ showed sharp changes across $MCS 5\text{--}6\%$ and $16\text{--}18\%$ (Fig. 3), which we considered thresholds. Across the first threshold (i.e., as connections of $\omega_{ij} \leq 5\%$ were removed leaving only connections of $\omega_{ij} \geq 6\%$), A_{LC} , and $d(G)$ decreased

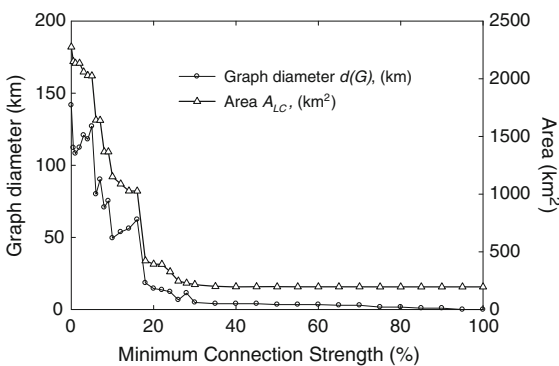


Fig. 3 Graph diameter ($d(G)$; km) and area of largest cluster (A_{LC} ; km^2), both versus minimum connection strength (MCS; %)

by 19 and 38%, respectively. These changes related to fragmentation of the GC, as described above. At $MCS = 5\%$, the network had 73 components; the largest with 643 patches and aggregate area of 202,540 ha. For $MCS = 6\%$, the network had 89 components; the largest with 455 patches and aggregate area of 164,200 ha. At the second threshold (i.e., as connections of $\omega_{ij} \leq 16\%$ were removed leaving only connections of $\omega_{ij} \geq 18\%$), A_{LC} and $d(G)$ decreased by 49 and 70%, respectively (Fig. 3). For $MCS = 16\%$ the network had 289 components; the largest with 206 patches and aggregate area of 102,700 ha. At $MCS = 18\%$ the network had 348 components; the largest with 64 patches and aggregate area of 42,200 ha.

The metrics AWF^* and PC^* showed a monotonic decrease with increasing MCS (Fig. 4). Differences in magnitude were because PC^* exploits shortest product probabilities and, unlike AWF^* , considers contributions from non-adjacent nodes. As MCS increased, the number of pathways was reduced, p_{ij}^* collapsed to ω_{ij} values, and the two metrics converged. Both metrics showed a distinct drop of approximately 10% across MCS values of 4–5%. More than 90% of the reduction in AWF^* and PC^* was a result of loss of connections from a large patch in the southeast part of the extent across $MCS 4\text{--}5\%$, and this loss was great enough to alter the flux-based metrics while still retaining undirected (symmetric/binary) connectivity, such that A_{LC} and $d(G)$ were unaffected. The loss of connections across the 5–6% threshold effectively removed a large amount of habitat from the largest component because of loss of

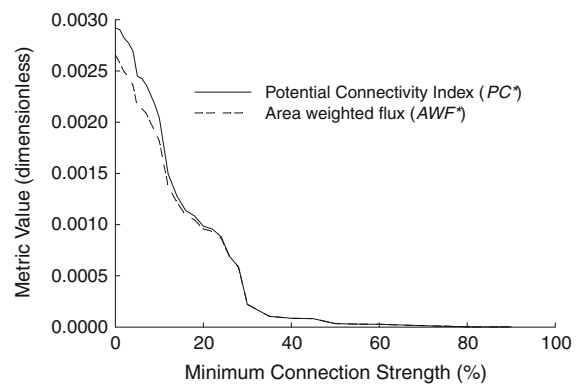
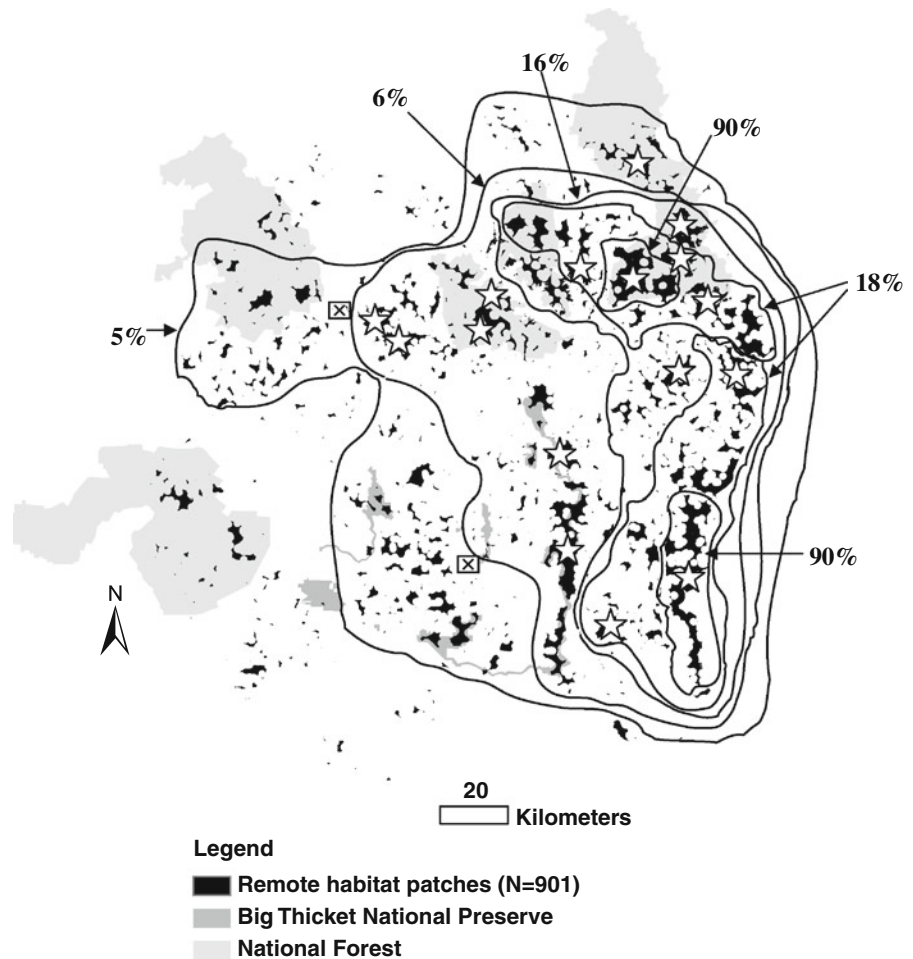


Fig. 4 Area weighted flux (AWF^*) and the probability of connectivity index (PC^*), both versus minimum connection strength (MCS; %)

Fig. 5 Remote habitat patches with *contour lines* indicating the largest component(s) at MCS values of 90, 18, 16, 6 and 5%. The two patches with MCS = 90% are the largest individual patches of remote habitat. *Shaded areas* indicate public lands (see Fig. 1). *Boxes with X's* (two) indicate connections lost across the MCS = 5–6% threshold. *Stars* (15) identify patches that have high scores of node strength multiplied by node area



connections between BTNP and National Forest lands to lands further north and east (boxes in Fig. 5), explaining the reduction in A_{LC} and $d(G)$.

S_i and BC_i varied across MCS values for each node. In lieu of describing metric behavior across 901 nodes, we assembled the information to prioritize patches as potential recovery sites. We calculated an importance weighting as the product of node area, S_i at MCS = 6% and S_i at MCS = 18%, under the presumption that node connectivity on the greater side of the observed threshold would be a better indicator of resiliency to loss of connections. Nodes with the highest weighting ($n = 15$; Fig. 5) included the largest patches of remote habitat, mainly located in the eastern half of the extent. This subset of 15 nodes had $BC_i = 0.0$ for MCS 18%, and BC_i values of similar magnitude for MCS 6%, with the exception of the largest patches, which had $BC_i = 0.0$, an

indication that these large patches are on the edge of the extent and act as points from which paths start or end.

Discussion

Black bear population recovery in eastern Texas may take place by either natural immigration of black bears from neighboring states (Louisiana, Oklahoma, and Arkansas) or physical reintroduction of black bears from other locations. Natural reestablishment of black bears in the Big Bend region of western Texas took approximately 50 years and relied heavily on a low-probability dispersal of a breeding female (Onorato and Hellgren 2001). In eastern Texas, impediments such as rivers (White et al. 2000) and human interferences (e.g., reservoirs, human activity)

may hinder natural recovery. Therefore, successful establishment of a breeding population might depend on translocated females. Regardless of mechanism, sufficient habitat is necessary for a newly established population to meet its resource needs.

Several management challenges exist related to black bear dispersal, movement, population expansion, and recovery (Clark et al. 2002). First, like many other large mammals, black bears exhibit a relatively low reproductive rate (Pelton 2003). Second, black bears often seek undisturbed locations for denning (Linnell et al. 2000; Pelton 2003). Third, male black bears are more likely to wander, whereas females are philopatric (Larivière 2001). Placing pregnant females or females with cubs into remote dens initially may minimize random and long-distance movement from release sites (Eastridge and Clark 2001; Wear et al. 2005). Regardless, an expanding population will require large areas of generally connected highly suitable habitat, particularly among areas suitable for denning and rearing cubs. Finally, black bears may exhibit shifts in home ranges following seasonal changes in food distribution, and may forage in less-suitable habitats (Rogers 1987; Hellgren and Vaughan 1990; Marchinton 1995). Any challenges likely will be compounded by conflicting interaction with humans (e.g., poaching, nuisance behavior, bear-automobile collisions). Acknowledging these challenges, sufficient habitat exists for a black bear population within our study area, and we sought to identify habitat furthest from intensive human activity. Though mostly on the eastern side, a large amount of highly suitable habitat exists throughout the area, including within (>90% highly suitable; Morzillo unpublished data) and in proximity to BTNP, and among National Forests.

Results of network analysis provide information about habitat connectivity and black bear population capacity. At our scale of analysis, connectivity of remote habitat was not dependent upon low strength ($\omega_{ij} < 4\%$) connections. Loss of connections with MCS increasing from 5 to 6%, and the resultant threshold-like decrease in metrics A_{LC} , and $d(G)$, indicate $\omega_{ij} = 5\%$ is the MCS required for formation of a GC. However, this assumes the GC connections are binary and bi-directional, whereas J-walk output indicates some connections may allow for only one-way movement of organisms. Flux based metrics (AWF^* and PC^*) account for bi-directional flows and

indicate a threshold at $MCS = 4\%$. Therefore, we conservatively recommend that the minimum successful probability of success for gap crossing among patches of remote habitat required to maintain high connectivity levels is $MCS = 4\%$. This value maintains relatively high flux values among patches and retains the structural integrity of the largest component. At $MCS = 4\%$, the largest component contains >202,000 ha of remote habitat. Past research suggests that an area of 7,580 ha is required to support a population of 50 black bears (Hellgren and Vaughan 1989; Rudis and Tansey 1995), and that criterion (7,580 ha) is met by each of the 15 patches of high node strength (Fig. 5). Therefore, each of the aforementioned 15 patches individually are potentially suitable targets for recovery efforts, and have connection potential to facilitate population expansion across the landscape.

Although other studies have used known estimates of MCS, such as to assess network properties for the Del Marva Fox Squirrel (Lookingbill et al. 2010), in our case we do not have a known estimate of MCS for black bear for our study area. Rather, our simulated results suggest that if future population viability analysis requires an $MCS > 4\text{--}5\%$ (to account for the thresholds of both MCS and flux-based metrics collectively), then patches and smaller components formed at MCS values $\leq 4\%$ would start to become disconnected from the GC. Specific disconnections at this threshold include (1) a large area in proximity to a National Forest in the northwest corner of the study area, and (2) western units of BTNP from eastern units of BTNP and private land along the Texas-Louisiana border (two locations noted in Fig. 5). Hypothetically, black bears relocated to western units of BTNP might have trouble dispersing eastward if land use change hinders the linkage with eastern units of BTNP and private lands. Conversely, black bears dispersing from Louisiana may have difficulty reaching western units of BTNP without the same linkage. Thus, we highlight the importance of habitat conservation on private lands between units of BTNP and between BTNP and Louisiana.

If population viability analysis for black bear requires MCS between 6 and 16%, the GC continues to shrink in size with increasing MCS . Although individual patches of remote habitat or smaller components may support populations, these will be

functionally disconnected from other areas also containing suitable habitat. Moreover, if black bear populations require connections with MCS 18% or larger, dispersal would be limited even further. Not only would all of BTNP become isolated from both the Texas–Louisiana border and National Forests, but BTNP units become more isolated from each other. Also, clusters near northern National Forest lands become disconnected from private lands further south. Therefore, if the expectation is for black bears to disperse either westward from Louisiana or originate within BTNP, connectivity would depend upon connections that would be lost across the 4–6% threshold along the southern portion of the study area. Ultimately, if black bear recovery relies on dispersal from other locations (i.e., neighboring states), and focuses on BTNP as a target recovery area, we recommend retaining all connections with $MCS \geq 4\%$. We suspect that engagement of and support from private landowners, including timber companies who own significant property in the area and particularly in locations mentioned as relevant to maintenance of the GC (Fig. 5), will be a critical step to achieve such an objective.

Two patches that are isolated only when $MCS > 90\%$ have a relatively large number of incident connections (Minor and Urban 2008) at $MCS = 6$ and 18% (Fig. 5). This suggests that both patches have a high potential for facilitating dispersal in multiple directions. The more-northern of the two patches is 13,500 ha and located mostly within a National Forest. The more-southern patch is approximately 19,600 ha and located on private land. Therefore, if a black bear population expands from the east, sufficient remote habitat in the eastern portion of our study area also is well connected. Further expansion to BTNP may occur, but will rely on lower strength connections.

To summarize our analysis of habitat distribution, even though BTNP contains patches that meet the 7,580 criterion, National Forest and private timber lands closer to the Louisiana border may be better suited, ecologically speaking, for initial black bear recovery efforts. Although the large privately-owned patches in the southeastern part of the study area are closer to BTNP, National Forests are protected currently. Therefore, National Forests may have potential as reservoirs for black bears, and black bears may move toward southeastern private lands

across $MCS = 16\%$ connections. Movement to BTNP may occur across connections of strength approximate to $\omega_{ij} = 5\%$, but these connections are less likely to occur than those with greater ω_{ij} values.

There are caveats to our analysis that will need to be revisited if black bears become established in the area. An unavoidable but major drawback is the current lack of locally observed black bear movement data, which results in our need to classify habitat using secondary information. Future observed data may affect habitat classification, organism-specific parameters, and resulting J-walk simulations, and ultimately assessment of connectivity. Furthermore, the MCS required to achieve population expansion is unknown; if determined to be $<4\text{--}5\%$, the region may be considered fairly resilient to disturbance of connectivity. Future sensitivity analysis (beyond the objectives of this paper) will address the responsiveness of our results to changes in each parameter. Therefore, it is important to consider our analysis as a first step in an adaptive management framework aligned with black bear habitat management guidelines (TPWD 2005), for which estimates of habitat suitability can be replicated, and network-related metrics revised, as empirical black bear habitat use and local land use data become available.

Another caveat is that condensing J-walk simulation output to transport operators for network analysis required the compression of large amounts of information. Although this resulted in a loss of information, we circumvented a pitfall associated with individual based simulators, such that output is voluminous and often difficult to communicate (Ovaskainen 2008). Because our objective was to evaluate connectivity (after identifying habitat), we leveraged attributes of network analysis to extract necessary information from J-walk output. Collapse of J-walk output to a single value (ω_{ij}) for estimating probability of inter-patch movement also eliminated our ability to evaluate whether movement occurred across one or multiple pathways. J-walk (and similar model) output can be analyzed using mathematical morphology to determine pathway redundancy (Vogt et al. 2008). Because evaluation of pathway redundancy across every potential connection may be cost-prohibitive, preliminary analyses such as ours are useful to identify specific connections for further study.

Ultimately, managers can examine results as relevant to particular land use and habitat

conservation goals. For example, constraints to conserving connectivity may exist if private landowners are not receptive to having their property classified as black bear habitat. This is plausible, as social survey results suggest that some residents may not be tolerant of black bears (Morzillo et al. 2007a). In fact, survey results also suggest that a natural recovery may receive more support from local residents than a reintroduction (Morzillo et al. 2010). In addition, broadly assessed spatial structure of opinions and attitudes regarding black bears suggests that residential proximity to BTNP and tolerance of bear presence may be inversely related, whereas more tolerance may exist near National Forests (Morzillo et al. 2007b). Someday, black bear populations may exceed estimates of carrying capacity of remote habitat. However, estimating carrying capacity of remote habitat serves as a more-conservative benchmark than the aggregate of highly suitable area for potential harvest limits. Local interest in future black bear harvest exists (Morzillo et al. 2009), and may become a helpful tool for future population management. With limited management resources, the value of our analysis is the ability to provide managers with a starting point for more detailed habitat and land use analysis.

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