



Research Article

# Connectivity Among Subpopulations of Louisiana Black Bears as Estimated by a Step Selection Function

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**ABSTRACT** Habitat fragmentation is a fundamental cause of population decline and increased risk of extinction for many wildlife species; animals with large home ranges and small population sizes are particularly sensitive. The Louisiana black bear (*Ursus americanus luteolus*) exists only in small, isolated subpopulations as a result of land clearing for agriculture, but the relative potential for inter-subpopulation movement by Louisiana black bears has not been quantified, nor have characteristics of effective travel routes between habitat fragments been identified. We placed and monitored global positioning system (GPS) radio collars on 8 female and 23 male bears located in 4 subpopulations in Louisiana, which included a reintroduced subpopulation located between 2 of the remnant subpopulations. We compared characteristics of sequential radiolocations of bears (i.e., steps) with steps that were possible but not chosen by the bears to develop step selection function models based on conditional logistic regression. The probability of a step being selected by a bear increased as the distance to natural land cover and agriculture at the end of the step decreased and as distance from roads at the end of a step increased. To characterize connectivity among subpopulations, we used the step selection models to create 4,000 hypothetical correlated random walks for each subpopulation representing potential dispersal events to estimate the proportion that intersected adjacent subpopulations (hereafter referred to as successful dispersals). Based on the models, movement paths for males intersected all adjacent subpopulations but paths for females intersected only the most proximate subpopulations. Cross-validation and genetic and independent observation data supported our findings. Our models also revealed that successful dispersals were facilitated by a reintroduced population located between 2 distant subpopulations. Successful dispersals for males were dependent on natural land cover in private ownership. The addition of hypothetical 1,000-m- or 3,000-m-wide corridors between the 4 study areas had minimal effects on connectivity among subpopulations. For females, our model suggested that habitat between subpopulations would probably have to be permanently occupied for demographic rescue to occur. Thus, the establishment of stepping-stone populations, such as the reintroduced population that we studied, may be a more effective conservation measure than long corridors without a population presence in between. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

**KEY WORDS** corridor, dispersal, GPS, interchange, model, movement, pathway, population recovery, *Ursus americanus luteolus*.

Human-caused loss and fragmentation of wildlife habitat are fundamental causes of population decline and increased risk of extinction for many wildlife and plant species worldwide. Subdivision of contiguous populations into small, isolated

subpopulations can have serious demographic and genetic consequences that increase the likelihood of local extirpations and the eventual collapse of entire population systems. For example, small populations are subject to increased probabilities of extinction compared with larger populations simply because of stochastic demographic processes (MacArthur and Wilson 1967, Shaffer 1987, Lande 1993). Also, small populations are more prone to chance fixation of deleterious alleles caused by stochastic processes such as

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genetic drift, founder effects, and inbreeding depression (Tewksbury et al. 2002, Boulet et al. 2007, Spear et al. 2010, Mills 2012).

Populations composed of spatially discrete subpopulations often depend on dispersal to facilitate demographic rescue or recolonization and maintain genetic variability essential to long-term persistence (Hanski 1996, McCullough 1996, Anderson and Danielson 1997, Duke et al. 2001). Consequently, landscape connectivity plays an important role in the conservation and management of fragmented populations by facilitating long-range movement for migratory species, promoting genetic interchange and demographic rescue among small populations, and enabling range shifts of species in response to permanent or ephemeral degradation of local habitat (Beier and Loe 1992). Movement corridors are effective conservation tools used in conservation planning for a variety of species with the goal of restoring or maintaining landscape connectivity in fragmented landscapes (Nelson et al. 2003, Noss 2003, Dixon et al. 2006, Gilbert-Norton et al. 2010). To be effective, corridor design should be based on clearly defined ecological and socio-political objectives. For example, Noss et al. (1996) presented a conceptual model for a reserve network that included corridors designed to facilitate dispersal among subpopulations with the objective of supporting recolonization processes capable of rescuing local patches from extinction. Once corridor objectives are defined, a landscape assessment is necessary to evaluate whether functional corridors exist on the landscape that need protection or additional conservation actions are required to establish new corridors. Such an assessment should be based on information about life-history traits, habitat requirements, and movement ecology of the focal species.

Habitat assessments and corridor designs used in conservation planning are often based on expert opinion (Beier et al. 2009, Eycott et al. 2011). However, such approaches can perform poorly compared with approaches that use empirical data based on analytical methods (Clevenger et al. 2002, Pullinger and Johnson 2010). High-resolution time series of animal location data produced by global positioning system (GPS)-based radio tracking combined with sophisticated statistical methods of data analysis such as resource selection functions, now make it possible to rigorously model animal movement behavior and accurately quantify relationships between landscape characteristics and those behaviors (Chetkiewicz et al. 2006). Such methods can be used within a geographic information system (GIS) framework to evaluate existing or identify new linkages between fragmented populations (Tischendorf and Fahrig 2000).

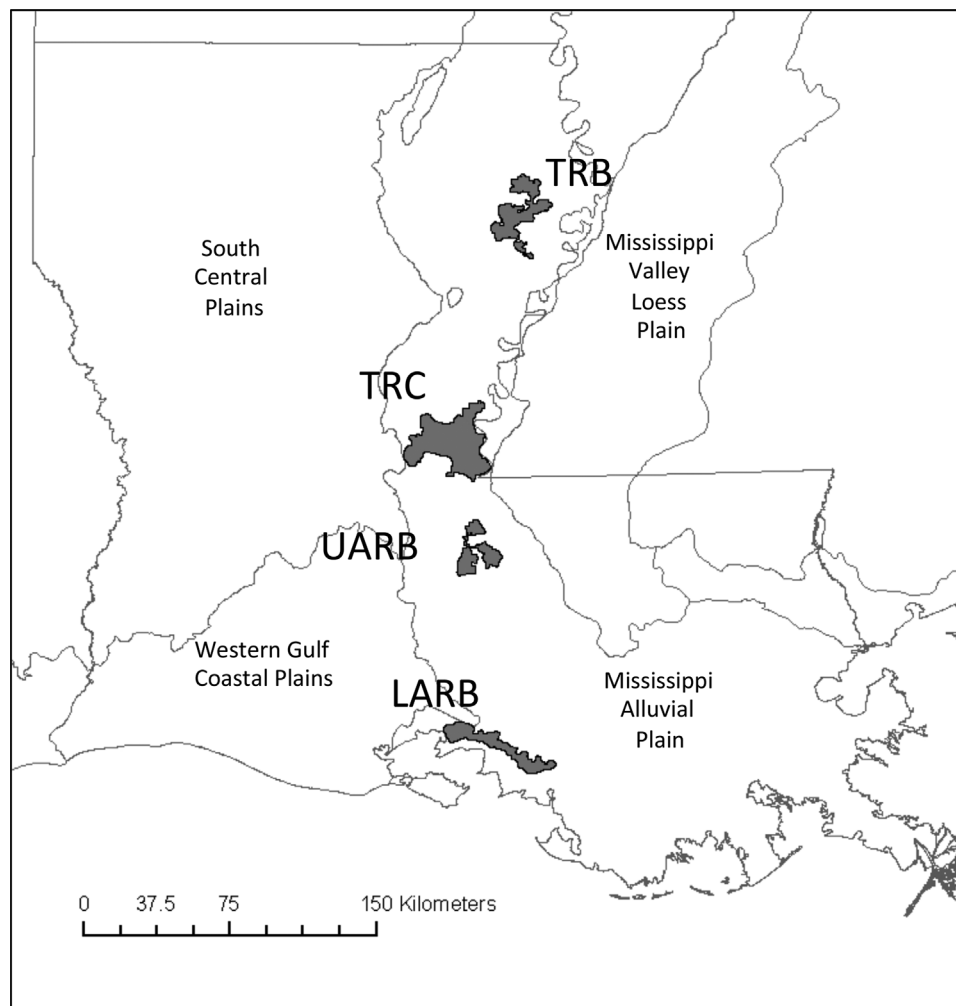
The Louisiana black bear (*Ursus americanus luteolus*), a subspecies of the American black bear, once occurred in the forests throughout Louisiana, in southern Mississippi, in southern Arkansas, and in eastern Texas (Hall 1981). Today, forest cover in the Mississippi Alluvial Plain (MAP) is highly fragmented because of land clearing for agriculture, with >80% of the bottomland hardwood habitat being lost (USFWS 1995, Stanturf et al. 2000). As a consequence, Louisiana black bear numbers are greatly reduced and the

remaining bear populations in the region are small and fragmented. In 1992, the USFWS granted the Louisiana black bear threatened status under the United States Endangered Species Act of 1973, listing loss of habitat as a primary threat (USFWS 1992) and a Recovery Plan was drafted soon thereafter (USFWS 1995). Goals of the Recovery Plan are 1) two viable subpopulations, 1 each in the Tensas River Basin and Atchafalaya River Basin; 2) the establishment of immigration and emigration corridors between the subpopulations deemed viable; and 3) protection of the habitat and interconnecting corridors that support each of the 2 viable subpopulations (USFWS 1995). Today, researchers and managers generally consider there to be 4 distinct black bear subpopulations in Louisiana consisting of the Tensas River (TRB), Upper Atchafalaya (UARB), Lower Atchafalaya (LARB) river basins, and the reintroduced Three Rivers Complex (TRC) subpopulation (Fig. 1; Csiki et al. 2003, Triant et al. 2004). Although some movement of radio-collared, live-captured, or DNA-sampled bears between Louisiana subpopulations has been documented, the potential for inter-subpopulation movement has not been quantified, nor have effective travel routes between habitat fragments been identified.

Quantifying animal movement processes based on highly accurate GPS locations can help identify landscape characteristics conducive to Louisiana black bear movement and to project potential movement pathways based on those processes (Chetkiewicz et al. 2006, McRae et al. 2008, Forester et al. 2009, Cagnacci et al. 2010, McClintock et al. 2012, Thurfjell et al. 2014). We used GPS locations of collared bears throughout the 24-hour period to quantify bear movement based on a step selection function (Fortin et al. 2005). Step selection functions are similar to resource selection functions (Manly et al. 2002) in that an observed movement is compared with a random set of potential movements that were possible but not chosen. Instead of using individual points on the landscape as the sample units, which is commonly done for resource selection functions, step selection function models use movement steps as the sample units, which are defined as the length and turning angle between 2 sequential radiolocations. Based on such models, movement pathways can be simulated on the landscape to determine where animals are likely to travel and the relative frequency that particular routes are chosen. We used the step selection approach to address criteria 2 and 3 of the Recovery Plan. Specifically, our objectives were to 1) characterize black bear movements on the landscape, 2) identify fine-scale characteristics important for such movements, 3) predict pathways for dispersal based on habitat selection, 4) estimate the relative rate at which projected pathways intersected adjacent subpopulations (hereafter referred to as successful dispersals, Tischendorf and Fahrig 2000), and 5) assess whether land cover essential for such movement is currently protected from development or alteration.

## STUDY AREA

Our analysis area included the entire state of Louisiana and western Mississippi and small portions of southern Arkansas



**Figure 1.** Map of the study area showing each of the 4 subpopulations of Louisiana black bear (gray polygons) within the Mississippi Alluvial Plain in Louisiana, USA. Subpopulations are Tensas River Basin (TRB), Three Rivers Complex (TRC), Upper Atchafalaya River Basin (UARB), and Lower Atchafalaya River Basin (LARB).

and eastern Texas. From a practical standpoint, field data collection was restricted to the 3 original subpopulations in the Tensas and Atchafalaya river basins and the reintroduced subpopulation at TRC. Those populations were in the MAP in areas of bottomland deciduous forest consisting of ash (*Fraxinus* spp.), elm (*Ulmus* spp.), cottonwood (*Populus deltoides*), sugarberry (*Celtis laevigata*), sweetgum (*Liquidambar styraciflua*), water tupelo (*Nyssa aquatica*), oak (*Quercus* spp.), and bald cypress (*Taxodium distichum*). Upland areas outside the MAP consisted of South Central Plains, West Gulf Coastal Plains, and Mississippi Valley Loess Plain where loblolly (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) were dominant. Louisiana had 18,795 km<sup>2</sup> in evergreen forest, 18,370 km<sup>2</sup> in emergent-herbaceous wetlands, 17,288 km<sup>2</sup> in row crops, 11,724 km<sup>2</sup> in mixed forest, and 10,530 km<sup>2</sup> in deciduous forest (<http://www.ldaf.state.la.us/portal/Offices/Forestry/ForestManagement/ForestLegacyProgram/tabid/234/Default.aspx>). Row crops primarily consisted of corn, soybeans, and wheat (Neal 1990). None of the subpopulations were hunted and survival rates were high (Laufenberg 2014). Occasional conflicts with

humans occurred, particularly in the LARB, but human-mediated translocations of nuisance bears among subpopulations were rare.

## METHODS

### Telemetry Data

We focused our radio-tagging activities on young males that were more likely to exhibit long-range movements, but we also radio-collared a smaller sample of females. We captured bears in culvert traps, immobilized them, and equipped them with store-on-board GPS radio collars (Telonics, Mesa, AZ; North Star Science and Technology, King George, VA) programmed to obtain 1 radiolocation/2–4 hr; collar batteries were expected to last about 1.5 years. Collars were equipped with remote detachment mechanisms that were programmed to release prior to the end of their anticipated battery life or the end of the study period. In addition to the store-on-board data, data from the North Star collars were capable of being uploaded via satellite. Because of intermittent satellite availability, we used the potentially reduced

satellite data sets only when the collars were not retrievable for obtaining data stored on board. Animals were handled according to University of Tennessee Institutional Animal Care and Use Committee protocol number 1716.

### Data Analysis

We deleted GPS locations with dilution of precision (PDOP) >7 (Lewis et al. 2007) and those collected during the denning season, which we defined as 15 November–15 April for females and 15 December–1 April for males, loosely based on the work by Waller et al. (2012). We also deleted sequential locations <100 m apart because we were interested in characterizing bears that were actively moving (Latham et al. 2011). Because collars were programmed to collect location data at different intervals (2, 3, or 4 hr), we included all steps consisting of location pairings <4.1 hr apart; we added 0.1 hr to include locations that were on the margin. Our assumption was that step selection would not be affected by the differences in fix rates given the spatial and temporal scales of our analysis (Thurfjell et al. 2014). To determine if step length was correlated with turning angles, we calculated an angular-linear correlation coefficient (Fisher 1995).

We used Geospatial Modeling Environment (GME) software (Beyer 2012) to separately calculate step lengths and turning angles for males and females. To characterize step lengths, we binned the observed step lengths ranging from 100 to 10,000 m into 24 arbitrary categories. We grouped observed turning angles into 18 20-degree bins. Potential step length and turning angle distributions for each bear were based on the empirical data from all the other radio-tagged bears of the same sex. Based on these empirical distributions, we created 10 random steps for every observed step for each bear, which was reasonable given the scale and objectives of our study (Thurfjell et al. 2014).

We used a variety of spatial data to characterize landscape attributes that we thought might be associated with

movement. For land cover, we used the National Land Cover Database (NCLD) 2006 (Fry et al. 2011) which is a 16-class land cover classification scheme (Table 1). We simplified the land cover data by creating a mast-producing forest category comprised of deciduous forest, mixed forest, and woody wetland cover types using ArcMap<sup>®</sup> 10.1 (Environmental Systems Research Institute, Redlands, CA). Those cover types have been shown to be important to Louisiana black bears (Nyland 1995, Benson and Chamberlain 2007, Murrow and Clark 2012). The non-forest category represented all other land cover types including urban, agricultural, and barren areas. We created a data layer consisting of the Euclidian distance to nearest forest based on the hypothesis that bears would be more likely to select steps ending in or near forest. We also calculated forest density based on a neighborhood analysis within a 150- × 150-m focal area of the mast-producing forest category. Because other natural cover types could be used by bears, we created a distance to natural land cover variable, which consisted of deciduous forest, evergreen forest, mixed forest, shrub-scrub, grassland-herbaceous, and woody wetlands. The natural data layer also included Conservation Reserve Program and Wetland Reserve Program lands (A. Dolan, USFWS, unpublished data). We then calculated natural land cover density based on a larger focal area (1,500- × 1,500-m) to characterize land cover at a coarser scale. The 150- × 150-m scale represented use of microhabitats (e.g., a berry patch), whereas the 1,500- × 1,500-m scale represented the use of larger patches (e.g., a forest woodlot) on the landscape. Because the forest and natural variables were correlated, we did not simultaneously use both in any model. Using the NLCD 2006 data, we created 2 agriculture variables: percent agriculture and Euclidean distance to the edge of the nearest polygon in agriculture based on the expectation that bears would choose pathways near agricultural areas.

**Table 1.** Variables used to develop step selection functions for black bears in 2010–2012, Louisiana, USA. All variables were based on 30-m cell sizes.

Variable (units)	Source	Procedure
Distance to forest (m)	2006 National Land Cover Database, combined deciduous forest, mixed forest, woody wetland	Calculated minimum Euclidian distance to nearest forest
Forest (%)	2006 National Land Cover Database, combined deciduous forest, mixed forest, woody wetland	Neighborhood analysis in 150-m focal area
Distance to natural (m)	2006 National Land Cover Database, combined deciduous forest, mixed forest, woody wetland, shrub-scrub, grassland-herbaceous	Calculated minimum Euclidian distance to nearest natural area
Natural (%)	2006 National Land Cover Database, combined deciduous forest, mixed forest, woody wetland, shrub-scrub, grassland-herbaceous	Neighborhood analysis in 1,500-m focal area
Distance to agriculture (m)	2006 National Land Cover Database	Calculated minimum Euclidian distance to nearest cultivated crops
Agriculture (%)	2006 National Land Cover Database	Neighborhood analysis in 150-m focal area
Distance to water (m)	2006 National Land Cover Database	Calculated minimum Euclidian distance to nearest open water
Contagion	2006 National Land Cover Database	Fragstats software
Splitting index	2006 National Land Cover Database	Fragstats software
Landscape shape index	2006 National Land Cover Database	Fragstats software
Distance to roads (m)	2012 TIGER/line data	Calculated minimum Euclidian distance to nearest open water

The land cover maps did not accurately show forests available to bears in some areas because much of the woody wetlands cover type identified by Landsat was permanently flooded and not used. Therefore, we downloaded flood model data (<http://abp.cr.usgs.gov/Library/Default.aspx?folder=268>) and the map showing the mean gage level at Butte La Rose Louisiana ([http://waterdata.usgs.gov/nwis/inventory/?site\\_no=07381515&agency\\_cd=USGS](http://waterdata.usgs.gov/nwis/inventory/?site_no=07381515&agency_cd=USGS)), which we determined to best coincide with the 14.6-ft (4.45-m) flood map. We then reclassified the forest and natural cover maps so that only non-flooded areas remained. We classified open water as a single cover type from the land cover map and calculated the Euclidean distance to the nearest water. Our expectation was that bears would select areas near streams and rivers for travel. We obtained road information from 2012 TIGER/Line® data that were based on the redistricting 2010 census (U.S. Bureau of the Census 2010). We calculated the Euclidean distance to primary roads from that same dataset, presuming that bears would avoid roads for movement.

We used Fragstats software (McGarigal and Marks 1995, Haines-Young and Chopping 1996, Turner et al. 2001) to calculate 3 variables (i.e., contagion, splitting index, and landscape shape index) to quantify broad-scale patterns of forest-wetland edge and patch configuration. Contagion is a measure of both the spatial distribution and intermixing of patch types and is inversely related to edge density (McGarigal and Marks 1995). Splitting index is a measure of the patchiness of the landscape; the index increases as the landscape is subdivided into smaller patches. Landscape shape index is a measure of landscape shape, including land cover aggregation. Our supposition was that areas that had more contiguous forest cover would be selected over more patchy and fragmented areas. Following the creation of the spatial variables, we used the GME tool Isectlinerst to combine the observed and potential steps with the landscape data. Although 5 summary attributes could be assigned to each landscape variable and step (i.e., the value at the beginning of a step, the end of a step, the maximum value, the minimum value, and the linear weighted mean), the GME tool does not allow attributes to be mixed for evaluating interaction effects, so we used only the attributes at the end of each step.

To estimate a step selection function for each sex, we used conditional logistic regression in Program R 2.15.3 (R Core Team 2013) based on a Cox proportional hazards model in the Survival package (Therneau 2013). First, we performed a correlation analysis and excluded 1 variable of any pair of correlated variables (i.e., Pearson's  $r > 0.6$ ). We then tested all possible models of the remaining variables and their interactions using the MuMIn package (Bartoń 2014) based on the lowest Akaike's Information Criterion scores (AIC; Burnham and Anderson 1998). We tested quadratic effects (i.e., non-linear effects) for distance variables and retained them if AIC scores were reduced by  $>2$ .

We wanted to evaluate whether agriculture would be used differently by bears during the growing season when crops provided some food and hiding cover. Therefore, we

modeled the growing season (Jun–Nov) and the non-growing season as an interaction term with distance to agriculture in a separate model. Finally, we fit models that incorporated random (mixed) effects, which allow for inference beyond the individuals radio monitored. We did so by modeling deviations of individual bears ( $b_i$ ) from the mean response ( $\beta$ ) as  $\beta + b_i$ , where  $b_i \sim \text{Normal}(0, \sigma^2)$  and  $\sigma^2$  was the variance term describing the dispersion across individuals (Duchesne et al. 2010). Autocorrelation among sequential location data can produce biased estimates of variance (Nielson et al. 2002), which can lead to model selection errors. Therefore, we estimated robust standard errors for fitted parameters from fixed-effects models based on a sandwich estimator (Fortin et al. 2005, Forester et al. 2009). We used methods described by Forester et al. (2009) whereby we first fit the model with the full data set and calculated the deviance residuals for each stratum (i.e., used vs. random pairings). We then fit an intercept-only mixed effects model and plotted the autocorrelation function of that model to graphically determine the lag of correlation (the number of consecutive locations after which autocorrelation was minimal [ $\alpha < 0.05$ ]). We then recoded the data by grouping the sequential observations based on the lag into clusters and re-fit the model using the Cluster option in the R-package clogit. We reported uncorrected standard errors for mixed-effects models because sandwich estimators were not available.

To evaluate the fit of our models, we used  $k$ -fold cross-validation procedures, which involved calculating the correlation between the step selection function ranks and area-adjusted frequencies for a withheld subset of data. More specifically, we randomly subset the GPS data for each bear into 5 equally sized bins, 4 for refitting the model (i.e., training) and 1 for testing (Boyce et al. 2002, Wiens et al. 2008, Thurfjell et al. 2014). We then refit our top model based on the training data, used that model to predict values for the test data, and sorted those values into 10 equally sized bins. We calculated the index score as the proportion of observed/expected observations in each bin. We repeated that process for each of the 5 subsets of withheld data. Finally, we averaged those index scores and estimated a Spearman correlation coefficient. Following Wiens et al. (2008), if 95% confidence intervals of the correlation coefficient of the index did not include 0, we classified the model as acceptable and if the confidence intervals included 1 we classified the model as good. We performed this procedure for both the entire study area and for the MAP only.

We used the GME simulation tool Movement.ssfsim1 to simulate paths of hypothetical bears in each of the subpopulations based on the fixed-effects step selection function for each sex. The simulation tool functioned by beginning at 1 of 100 random starting points within a polygon circumscribing each subpopulation (Fig. 1) and then choosing a random bearing associated with that point. Next, the tool generated a number of available steps ( $n = 10$ ) based on our empirical distributions of step lengths and turning angles after which it calculated the likelihood of each step

based on the landscape covariates and our linear step selection function. Finally, the simulation tool selected a step based on its likelihood and the process continued for a pre-defined number of steps and replications; the probability of a particular step being selected was proportional to its likelihood resulting from the step selection function and the landscape variables. These series of steps were essentially empirical correlated random walks (Bovet and Benhamou 1988, Turchin 1998) because we used turning angles instead of random bearings, resulting in serial correlation. The paths were representative of our telemetered bears in the sense that turning angles and step lengths were chosen randomly from the empirical distributions we estimated based on the GPS fixes. We projected 1,895 and 2,236 steps for females and males, respectively, which represented the number of expected GPS fix intervals during the non-denning season per year (i.e., hours during the non-denning season divided by the mean fix interval). We used 100 random locations within each subpopulation as starting points and created 40 replicate projections of each (i.e., 4,000 paths). We then calculated the proportion of paths that intersected adjacent subpopulations (i.e., successful dispersals); we used this proportion as a measure of connectivity among the subpopulations.

To evaluate the effects of corridors on connectivity among the subpopulations, we created hypothetical 1,000-m- and 3,000-m-wide corridors consisting of natural cover types between each of the closest pairings of the 4 subpopulations. These were simplistic, straight-line corridors depicting the minimum distance between the 4 areas and were simply intended to determine if a direct linkage increased successful dispersals. We then re-ran the path simulation routine to evaluate whether addition of these potential corridors affected the number of dispersals.

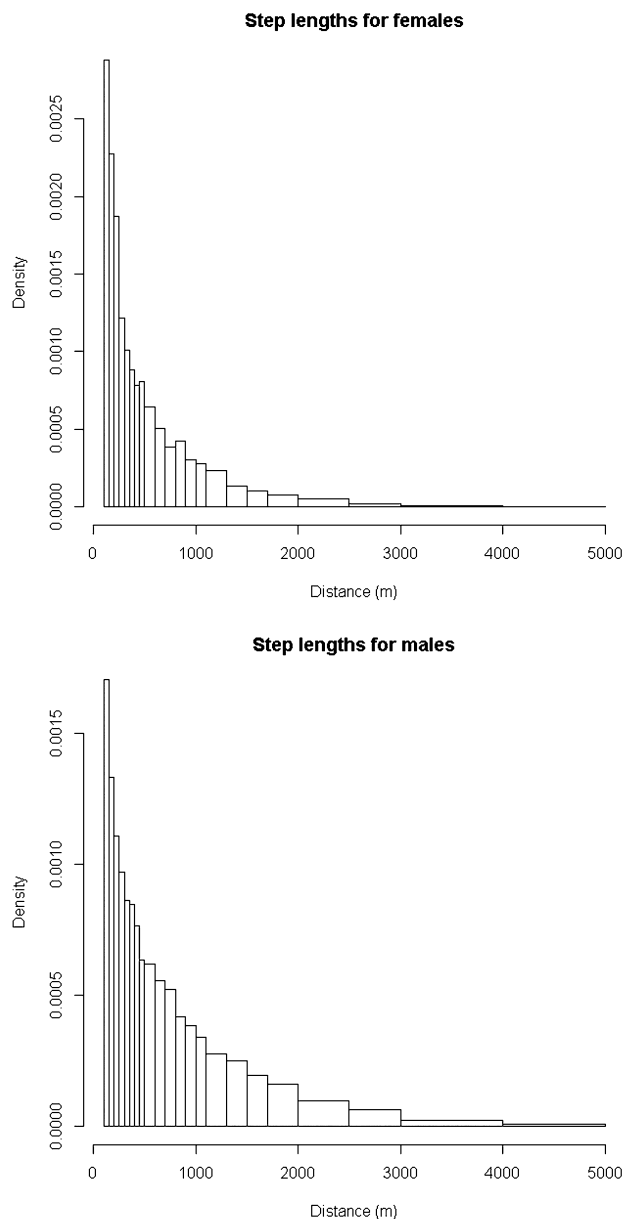
To evaluate the loss of natural cover types in areas without permanent protection, we re-ran the path simulation routine after excluding all natural areas from the analysis except those occurring on state and federal lands. Federal lands consisted of USFWS National Wildlife Refuges and Partners for Fish and Wildlife Lands, National Forest Land, Wetland Resources Protection Land, United States Army Corps of Engineers Lands, Tribal Lands, Nature Conservancy Lands, National Park Lands, Mitigation Bank Lands, Louisiana State Wildlife Management Areas, Farmers Home Administration lands, Ducks Unlimited Conservation Easement Lands, and Bureau of Land Management lands. This analysis essentially excluded all natural land cover in private ownership and resulted in a recalculation of the distance to natural data layer. We applied the models to the modified landscape in ArcMap based on logistic transformations of step selection functions for each sex to graphically depict the probability of selection. We then calculated the inverse of those values, which we defined as relative costs for traveling through a given 30-m pixel (Chetkiewicz and Boyce 2009). Finally, we wanted to identify areas where the frequencies of successful dispersals were highest. To do so, we used the Line Density tool in ArcMap<sup>®</sup> 10.1 to sum the number of successful simulated paths intersecting each cell to identify

dispersal pathways between the 4 areas for male and female bears.

## RESULTS

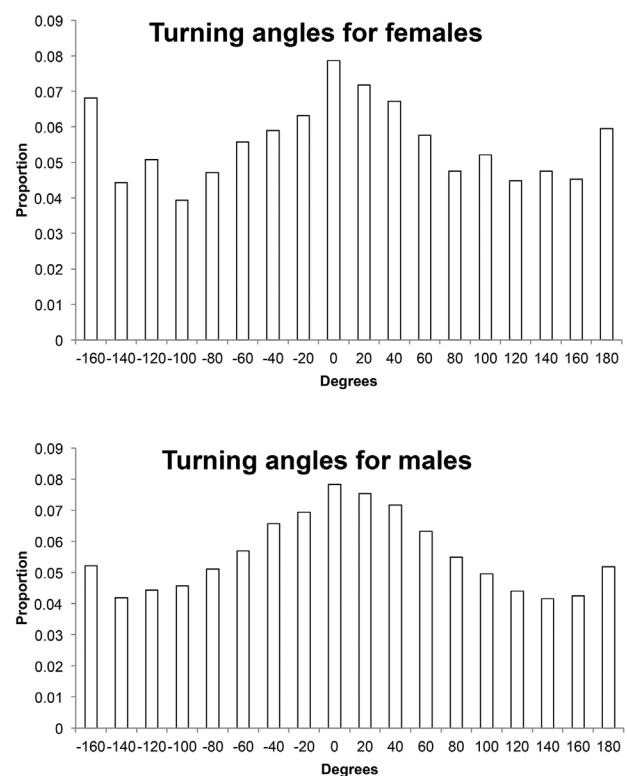
From April 2010 to 2012, we radio collared 8 female and 23 male bears ranging from 1 to 11 years of age. Most bears were young, with 4 of the females and 18 of the males being  $\leq 3$  years of age. We obtained 5,400 fixes for females and 30,832 for males from April 2010 to October 2012. After generating steps from sequential pairings of locations and eliminating those that did not meet our inclusion criteria, we retained 2,104 (range [among individuals] = 30–579) and 15,233 (range = 78–2,706) steps with median lengths of 391.6 (range = 100.0–1,527.3) and 649.5 m (range = 100.0–8,090.8) for females and males, respectively. Mean interval between GPS fixes was 2.71 hr (SD = 0.73) for females and 2.78 hr (SD = 0.74) for males. Step lengths for both sexes were skewed toward shorter distances but extreme step lengths were more common for males (Fig. 2). Turning angles were most frequent around 0 degrees, meaning that movements of both sexes exhibited directional persistence (Fig. 3). There was a secondary tendency for steps to return in the direction from which they came. Turning angles and step lengths were independent for both sexes ( $R^2 < 0.001$ ). Path lengths during the period of monitoring (i.e., 25.2–804.8 days,  $\bar{x}$  = 241.4) ranged from 32.9 to 419.1 km ( $\bar{x}$  = 185.5, SD = 53.9) for females and from 73.5 to 2,670.2 km ( $\bar{x}$  = 623.7, SD = 134.5) for males. The Euclidean distances moved from the beginning to end point of a path (displacement) ranged from 0.6 to 6.5 km ( $\bar{x}$  = 3.6, SD = 1.9) for females and from 0.5 to 88.5 km ( $\bar{x}$  = 11.2, SD = 17.9) for males. The maximum distance from the point of origin ranged from 3.1 to 10.8 km ( $\bar{x}$  = 7.3) for females and 4.0 to 88.5 km ( $\bar{x}$  = 18.2) for males.

After removing correlated variables, the top fixed-effects model (i.e., no individual random effects) for females from the all-possible model selection procedure included distances to natural land cover, agriculture, roads, and water for which the probability of a step being selected increased as the distance to natural land cover and distance to agriculture at the end of the step decreased and as the distance to roads at the end of a step increased. The sign of the coefficient for distance to water indicated avoidance of water, which was probably the result of the presence of large bodies of water on the landscape (e.g., lakes, ocean) that were avoided by bears but portrayed a presumed false relationship between bear movement and linear water features. Therefore, we did not include that variable in our final models to avoid confounding effects in our movement path simulations. The probability of a step was also influenced by an interaction between distance to natural and distance to roads and an interaction between distance to natural and distance to agriculture (Table 2). If near natural cover, the selection coefficient slightly increased as the distance to roads increased but decreased if far from natural cover (Fig. 4a). Selection decreased as the distance to agriculture increased only if near natural cover types and increased otherwise (Fig. 4b). The deviance reduction associated with the removal of



**Figure 2.** Step lengths for female and male Louisiana black bears based on global positioning system (GPS) radio collar data collected in Louisiana, USA from 2010–2012.

each variable from the model suggested that distance to natural land cover ( $-626.7$ ) had the greatest effect on step selection followed by distance to roads ( $-71.5$ ) and distance to agriculture ( $-13.4$ ). We identified a cutoff of 10 autocorrelated steps for females so we based our robust standard error estimates on that cluster size. Although we did not attempt to incorporate temporal covariates into our path projections, we found an interaction between distance to agriculture and season for females ( $\beta = -3.15\text{E-}04$ ,  $\text{SE}_{\text{robust}} = 2.83\text{E-}05$ ), with selection declining during the growing season as distance to agriculture became greater but increasing during the non-growing season. Based on the mixed-effects models, we found that the relationship between the probability of a selected step and the distance



**Figure 3.** Turning angles for female and male Louisiana black bears based on global positioning system (GPS) radio collar data collected in Louisiana, USA from 2010–2012.

to the nearest natural cover type varied by individual ( $\sigma^2 = 3.70\text{E-}05$ ,  $P < 0.001$ ). Regardless, most (93.1%) would be expected to exhibit a negative relationship with distance to natural cover based on a cumulative normal distribution function with mean  $-9.01\text{E-}03$  and standard deviation  $6.09\text{E-}03$  (Duchesne et al. 2010, Table 2). Within the context of the entire study area consisting of all of Louisiana and much of Mississippi, the adjusted  $r^2$  of the fixed-effect model for females was 0.85 ( $P < 0.001$ ), and the slope for natural land cover was 1.20 (95% CI = 0.87–1.53), which indicated a good model because the 95% CI of the slope included 1 but did not include 0. Within the MAP only, the fixed-effects model for females was good as well (adjusted  $r^2 = 0.85$ ,  $P < 0.001$ ;  $\beta = 0.92$ , 95% CI = 0.67–1.17).

For males, the top fixed-effects model included distances to natural land cover, agriculture, and roads. The probability of a step increased as the distance to natural land cover and its square at the end of a step decreased and as the distance to agriculture at the end of a step decreased (Table 2). Additionally, we found a quadratic relationship with roads; step selection was more likely as distance to roads and its square increased. Although the 95% confidence intervals of an interaction effect between distance to natural and agricultural cover types included 0 ( $-2.51\text{E-}06$  to  $3.36\text{E-}07$ ; Table 2), the model was improved reflected in the reduction of 34.4 units in AIC, so we kept the interaction term. The deviance reduction associated with the removal of each variable from the model suggested that distance to

**Table 2.** Cox proportional hazards models to create step selection functions for black bears in 2010–2012, Louisiana, USA. All distance variables are measured at the end of a step.

Variable	$\beta$	SE	95% CI	Standardized $\beta$
Female model (fixed effects)				
Distance to natural (end)	−4.74E-03	1.26E-03 <sup>a</sup>	−7.21E-03 to −2.36E-03	−0.719
Distance to agriculture (end)	−2.19E-04	3.45E-05 <sup>a</sup>	−2.86E-04 to −1.51E-04	−0.194
Distance to roads (end)	1.97E-05	1.97E-05 <sup>a</sup>	−1.89E-05 to 5.82E-05	0.038
Distance to natural × distance to roads	−1.87E-06	1.55E-07 <sup>a</sup>	−2.17E-06 to −1.56E-06	−1.325
Distance to natural × distance to agriculture	1.95E-06	4.62E-07 <sup>a</sup>	1.04E-06 to 2.85E-06	0.605
Wald test $\chi^2_5 = 14.1$ , $P = 0.015$				
Female model (mixed effects)				
Fixed				
Distance to agriculture (end)	−2.06E-04	8.62E-05	−3.75E-04 to −3.72E-05	
Distance to roads (end)	2.33E-06	5.64E-05	−1.08E-04 to 1.13E-04	
Distance to natural × distance to roads	−1.07E-06	5.18E-07	−2.09E-06 to −5.91E-08	
Distance to natural × distance to agriculture	1.75E-06	8.72E-07	3.84E-08 to 3.46E-06	
Random				
Distance to natural   bear ID	−9.01E-03	2.71E-03	−1.43E-02 to −3.70E-03	
SD of coefficient	6.09E-03			
Maximum log likelihood −4,649.8				
Likelihood ratio test $P < 0.001$				
Male model (fixed effects)				
Distance to natural (end)	−6.61E-03	3.18E-04 <sup>a</sup>	−7.23E-03 to −5.99E-03	−1.083
Distance to agriculture (end)	−1.67E-04	2.49E-05 <sup>a</sup>	−2.16E-04 to −1.18E-04	−0.123
Distance to roads (end)	2.50E-04	5.77E-06 <sup>a</sup>	2.38E-04 to −2.61E-04	0.400
Distance to natural <sup>2</sup>	3.05E-06	1.34E-06 <sup>a</sup>	4.26E-07 to 5.68E-06	0.601
Distance to roads <sup>2</sup>	−3.58E-08	4.97E-09 <sup>a</sup>	−4.55E-08 to −2.60E-08	−0.359
Distance to natural × distance to agriculture	−1.09E-06	7.26E-07 <sup>a</sup>	−2.51E-06 to 3.36E-07	−0.425
Wald test $\chi^2_6 = 432.2$ , $P < 0.001$				
Male model (mixed effects)				
Fixed				
Distance to agriculture (end)	−1.75E-04	2.75E-05	−2.29E-04 to −1.21E-04	
Distance to roads (end)	2.48E-04	2.91E-05	1.91E-04 to 3.05E-04	
Distance to natural <sup>2</sup>	2.89E-06	3.28E-07	2.25E-06 to 3.54E-06	
Distance to roads <sup>2</sup>	−3.72E-08	4.87E-09	−4.68E-08 to −2.77E-08	
Distance to natural × distance to agriculture	−1.16E-06	1.99E-07	−1.56E-06 to −7.73E-07	
Random				
Distance to natural   bear ID	−6.63E-03	5.52E-04	−7.71E-03 to −5.54E-03	
SD of coefficient	2.36E-03			
Maximum log likelihood −34,797.0				
Likelihood ratio test, $P < 0.001$				

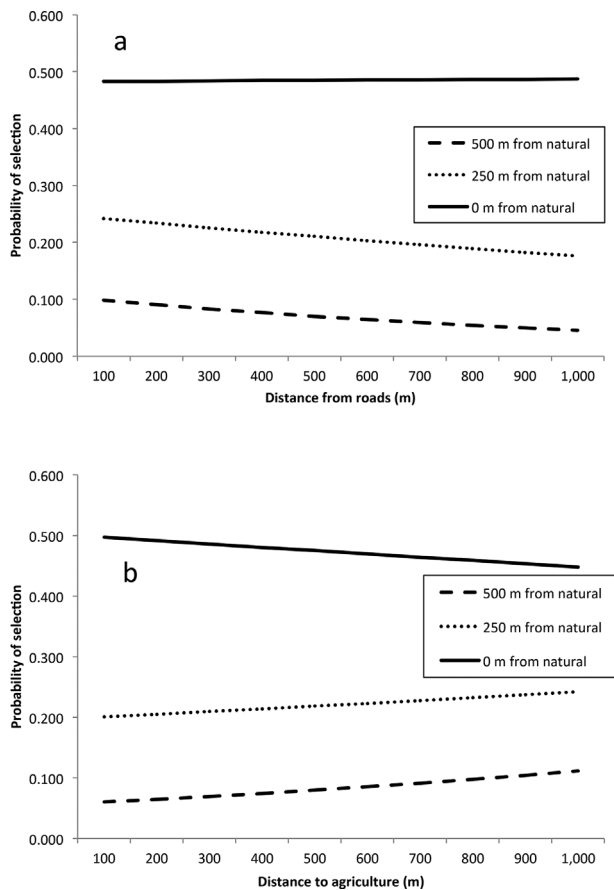
<sup>a</sup> Robust estimates accounting for autocorrelation using sandwich estimators.

natural (−2,779.2) had the greatest effect on step selection followed by distance to roads (−76.5) and distance to agriculture (−4.0). We identified a cutoff of 24 for autocorrelated steps. As with females, we found an interaction between distance to agriculture and season ( $\beta = -1.48E-04$ ,  $SE_{\text{robust}} = 3.96E-05$ ). Based on the mixed-effects models, we found that the distance to natural cover varied by individual bear ( $\sigma^2 = 5.59E-03$ ,  $P < 0.001$ ), but the relationship was expected to be negative for essentially all male bears (>99%) based on a cumulative normal distribution function with mean −6.63E-03 and standard deviation 2.36E-03 (Table 2). For the entire analysis area (adjusted  $r^2 = 0.74$ ,  $P < 0.001$ ;  $\beta = 1.12$ , 95% CI = 0.69–1.54) and for the MAP only (adjusted  $r^2 = 0.75$ ,  $P < 0.001$ ;  $\beta = 1.12$ , 95% CI = 0.71–1.53), model fit was good.

Based on the fixed-effects step selection function models, we generated 4,000 correlated random walks of 1,895 and 2,236 steps for females and males, respectively, from each of the 4 subpopulations. The least potential for interchange

among subpopulations was between TRB and TRC and between UARB and LARB as a result of only 2 successful dispersals for females and 164 for males in 16,000 simulated paths (4,000 paths from each of the 4 subpopulations; Table 3). As expected, the highest proportion of successful dispersals was from UARB to TRC (937/4,000 [23.4%] and 316/4,000 [7.9%] for males and females, respectively), followed by paths in the reverse direction (617/4,000 [15.4%] and 199/4,000 [5.0%] for males and females, respectively). The cost surface maps revealed patchy resistance values in the Mississippi Alluvial Valley, which is reflective of the fragmented nature of that landscape (Fig. 5). The line density map of simulated successful dispersals revealed more convoluted paths for females (Fig. 6a) than males (Fig. 6b), though long net displacements for females were infrequent and some pathways were described by only 1 successful dispersal. The addition of 1,000-m- and 3,000-m-wide corridors between the 4 subpopulations had negligible to slightly negative effects for most subpopulation pairings, the exception being an increase from the LARB to the UARB





**Figure 4.** Relationships between distance to natural cover and distance to roads (a) and distance to agriculture (b) and selection probabilities of steps for female Louisiana black bears from 2010–2012.

for males (Table 3). Finally, when we considered only permanently protected natural land cover, the incidence of successful dispersals dramatically decreased (Table 3).

## DISCUSSION

Although we detected relationships between distance to natural land cover, agriculture, and roads, the factor having greatest influence on successful dispersal probably was Euclidean distance. The distance between the TRB and TRC (91.3 km) and between the LARB and UARB (87.1 km) was so great that females likely would not move enough within a year and male movements of that length would be too infrequent for meaningful interchange to take place. The reintroduced population at TRC, however, essentially reduced the distance between occupied fragments and resulted in increased successful dispersals. Without that stepping-stone population, our model predicted no dispersals of either sex from UARB to TRB and vice versa. Ancillary data corroborated our modeling results. For example, genetic assignment tests conducted as part of a mark-recapture study revealed some mixing from the UARB subpopulation to TRC (27%; Laufenberg 2014), thereby supporting our high predicted interchange between those subpopulations. Conversely, mixing among the LARB and UARB subpopulations was low (<0.2%), which is also consistent with our step

selection function models. Observation data supported our findings as well. Three male bears born and genotyped to known females at TRC were captured 1–4 years later at DNA hair sampling sites at TRB (Laufenberg 2014). Two of these bears had ancestries that were mixed with UARB, suggesting that a male(s) from UARB dispersed and bred with the reintroduced females at TRC. Also, a male bear born at UARB in 2012 was captured and radio-collared at TRC in 2014 and subsequently radio located at TRB in 2015 (S. Murphy, Louisiana Department of Wildlife and Fisheries, unpublished data). No evidence of natural female dispersal between subpopulations has been documented thus far, which is also consistent with model predictions. The higher number of simulated movements from the UARB to TRC compared with movements in the opposite direction may have been partially because of the larger relative size of the TRC, thus making intersections more likely.

The hypothetical corridors were only effective for males dispersing from the LARB to UARB. When viewing the projected pathways relative to the natural cover type, it is evident that our model projected male and female bears occasionally crossing gaps, even some large ones, if the step ended in or near natural cover. We speculate that the hypothetical corridors were not more effective than the broken habitat matrix that surrounded many of the subpopulations. Furthermore, the hypothetical corridors may have led bears into areas where the surrounding matrix of natural cover was sparse, which effectively reduced interchange. This is not to say that corridors are not important. The increase in movements from the LARB to the UARB suggests that corridors through a depauperate habitat matrix can be beneficial. Although the cost surface maps suggested greater ease of movement in upland areas compared with the MAP, upland forests were mostly mixed or evergreen and differed from the bottomland hardwoods common in the MAP where the bulk of the GPS data were collected. Consequently, application of the model beyond the MAP may not be reliable even though the  $k$ -fold analyses suggested an adequate fit.

Selection was relatively weak for most variables based on standardized  $\beta$  values, suggesting that there was much variation in step selection that we could not explain. Distance to water was a weak predictor of female steps but the slope suggested avoidance which may have been because of large water bodies that bears did not use. An analysis of only river and streams may have been more revealing. The interaction effect between distance to agriculture and season reflected greater use during the growing season. Much of the agriculture surrounding our study areas was in corn, which provided some cover later in the year.

We acknowledge that our exclusive use of landscape attributes associated with the end of each step may have reduced our ability to evaluate cover used by bears along that step. The true path taken by bears between individual radiolocations was not known and probably is not well represented by a straight line. However, a post-hoc analysis revealed that models based on the linear weighted mean of

**Table 3.** Number of simulated black bear paths out of 4,000 that originated from a population and intersected adjacent subpopulations (i.e., successful dispersals) in Louisiana, USA, 2010–2012, with and without the addition of hypothetical corridors and non-permanently protected natural cover. Proportions are in parentheses. Subpopulations are Tensas River Basin (TRB), Three Rivers Complex (TRC), Upper Atchafalaya River Basin (UARB), and Lower Atchafalaya River Basin (LARB).

Dispersal route and distance	No. successful dispersals with no additional corridor	No. successful dispersals of 4,000 with addition of a 1,000-m-wide corridor	No. successful dispersals of 4,000 with addition of a 3,000-m-wide corridor	No. successful dispersals when only permanently protected natural cover available
<b>Females</b>				
TRB to TRC (91.3 km)	0	0	1 (<0.001)	0
TRC to TRB (91.3 km)	1 (<0.001)	0	0	0
TRC to UARB (22.8 km)	199 (0.050)	141 (0.035)	189 (0.047)	0
UARB to TRC (22.8 km)	316 (0.079)	253 (0.063)	266 (0.067)	1 (<0.001)
UARB to LARB (87.1 km)	0	0	1 (<0.001)	0
LARB to UARB (87.1 km)	1 (<0.001)	0	0	0
<b>Males</b>				
TRB to TRC (91.3 km)	40 (0.010)	32 (0.008)	30 (0.008)	0
TRC to TRB (91.3 km)	24 (0.006)	24 (0.006)	30 (0.008)	0
TRC to UARB (22.8 km)	617 (0.154)	541 (0.135)	602 (0.151)	0
UARB to TRC (22.8 km)	937 (0.234)	879 (0.220)	931 (0.233)	55 (0.014)
UARB to LARB (87.1 km)	44 (0.011)	32 (0.008)	40 (0.010)	0
LARB to UARB (87.1 km)	56 (0.014)	66 (0.017)	74 (0.019)	0

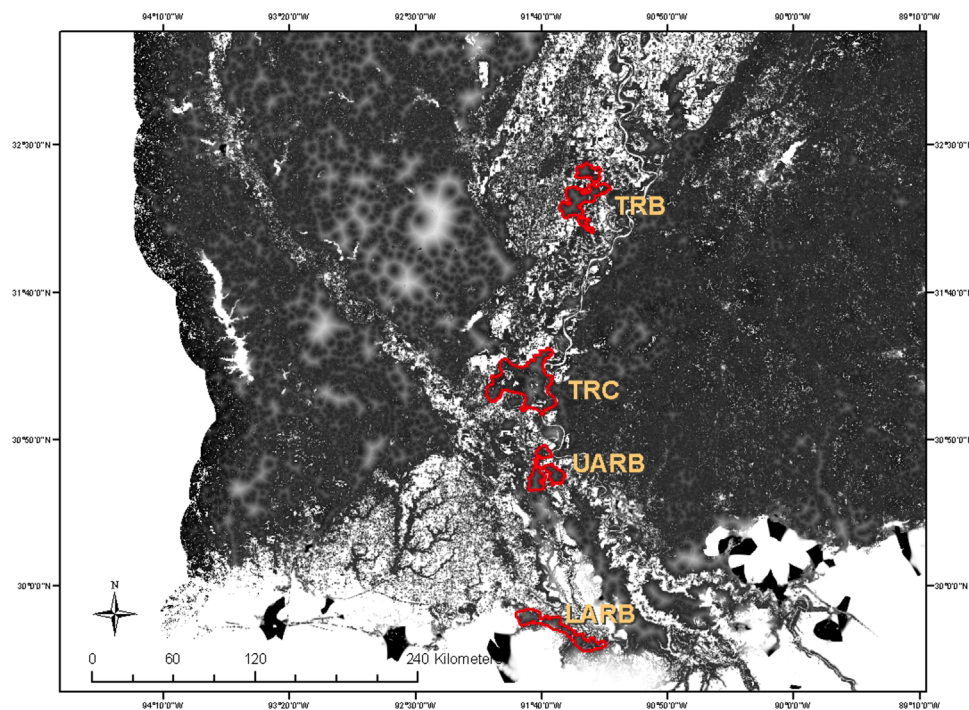
land cover characteristics along the steps were less parsimonious than models based on the ending points of the steps ( $\Delta\text{AIC} = 1,288.2$  for males and 252.1 for females). Therefore, we conclude that the end points were adequate, which was substantiated by our  $k$ -fold cross-validations indicating good model fit. The mean distance moved from 1 to 4 hr differed by only 135 m compared with distances moved from 1 to 2 hr, which we suggest is minor from a biological standpoint. Nevertheless, the potential exists for the effects of linear features on bear movements to be underestimated. Decreasing the time interval between radiolocations may reveal more about the fine-scale movement behavior of bears in patchy landscapes.

Only 1 radio-collared animal (Nstar13, displacement = 88.5 km) exhibited the type of long-range, directed dispersal behavior that has been documented in other black bears studies (80–145 km; Rogers 1987, Lee and Vaughan 2003); most other males did not ( $\bar{x} = 7.7$  km, max. = 19.2 km). We recorded no dispersal events for females, which tend to disperse only as a result of extreme environmental events (Hellgren et al. 2005). We chose not to model home range fidelity (Rhodes et al. 2005) because we wanted to characterize movement activity that might be associated with an animal in unfamiliar surroundings in search of habitat. Regardless, our model predictions of limited female dispersal and greater successful dispersals for males in more proximate

subpopulations generally agreed with our observations described above and the cross-validations.

We did not add step length as a model covariate as suggested by Forester et al. (2009) because turning angle and step lengths were not correlated (Thurjfell et al. 2014). We also did not model step selection based on time of day or month because our goal was to project movement pathways over the course of 1 active season, which would encompass all times of day and most months. Furthermore, we did not investigate whether presence of conspecifics affected movement paths or dispersal behavior and did not incorporate individual random effects into our path projections because of the complexity of implementation. Regardless, the signs of the effects were similar for most individuals (93.1% and >99% of females and males, respectively) based on random effects. We also assumed there were no bears between subpopulations and note that the number of pathways projected for each subpopulation (4,000) greatly exceeds the number of likely dispersal events. Thus, our estimates of the movement paths are only approximations of the relative probabilities of successful dispersals between subpopulations over a 1-year activity season.

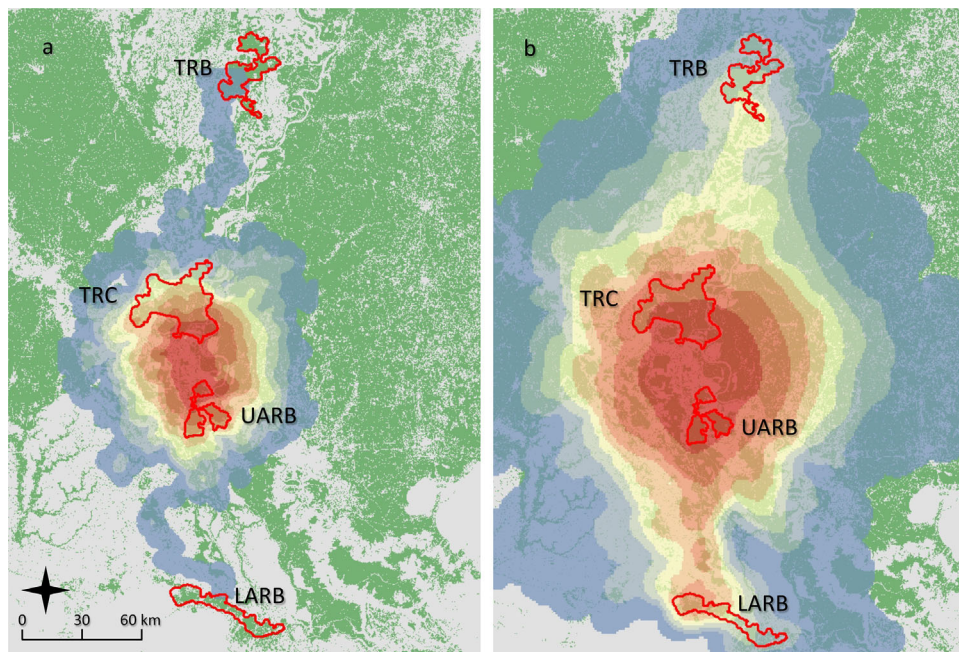
Landscape ecologists have used genetics data to develop maps that show resistance to migration or gene flow based on environmental barriers (Proctor et al. 2005, Cushman et al.



**Figure 5.** Cost surface for female bears, Louisiana, USA, 2011–2012. Areas with lower costs of travel are in darker colors. Red polygons are bear subpopulations in the Tensas River Basin (TRB), Three Rivers Complex (TRC), Upper Atchafalaya River Basin (UARB), and Lower Atchafalaya River Basin (LARB).

2006, Storfer et al. 2010). However, the biggest challenge is assigning resistance values to individual landscape features because the actual effects on movement, survival, and abundance are usually not known (Spear et al. 2010). Least-cost pathways often are used to characterize resistance, but such models do not incorporate the stepwise process by which most animals explore new environments. Instead, connectivity should be measured from a functional perspec-

tive rather than judged based solely on the spatial arrangement of habitat (Tischendorf and Fahrig 2000). The movement characteristics of the focal species such as its dispersal capabilities and behavioral responses to the physical structure of the landscape should also be taken into account. We used step selection functions to mimic the step-by-step decision making process that bears use to move across the landscape to empirically link behavior with landscape



**Figure 6.** Relative densities of simulated successful dispersals (movement from 1 subpopulation to another) for female (a) and male (b) black bears in Louisiana based on data collected 2010–2012. Highest line densities are in red and lowest are in blue.

configuration. Based on our ancillary data and  $k$ -fold analyses, we conclude that our projected paths were adequately representative of bear movement across the landscape and that our models are useful tools for evaluating relative rates of successful dispersals between subpopulations and the potential effects of conservation planning on bear movement.

## MANAGEMENT IMPLICATIONS

The 1995 Louisiana black bear recovery plan requires the establishment of immigration and emigration corridors between the 2 viable subpopulations in the Tensas and Atchafalaya river basins that are considered sustainable (USFWS 1995). Effective interchange between isolated populations undoubtedly was the intent when the Louisiana black bear recovery criteria were developed. Our data indicate that habitat exists through which contemporary interchange of bears between the Tensas and Atchafalaya river basins can occur, though perhaps not as a result of a continuous corridor of natural land cover. Our results suggest that the patchwork of natural cover among subpopulations may be sufficient to allow exchange if the distance between focal areas is short. The addition of contiguous corridors was only marginally effective at increasing successful dispersals. More important to interchange between the Tensas and Atchafalaya river basins was the establishment of a reintroduced population at TRC. Without the TRC subpopulation, our model predicted no male interchange between UARB and TRB. Female dispersals are rare and projected dispersals appeared to be most affected by the distance between subpopulations. For female dispersal and demographic rescue to occur, some habitat between subpopulations would probably have to be permanently occupied in order to decrease that distance. Thus, the establishment of satellite populations of resident breeding bears between the subpopulations to be linked, as illustrated by the TRC population, may be a more effective measure than the establishment of long corridors without a population presence in between. The Recovery Plan also requires long-term protection of the habitat and inter-connecting corridors that support each of the 2 viable subpopulations used as justification for delisting. Land occupied by the LARB and TRC subpopulations and most of the habitat matrix that connects all the subpopulations is not in state or federal ownership. Furthermore, the loss of private lands would result in nearly complete isolation of the 4 subpopulations. Thus, private landowners will play an important role in the future of the Louisiana black bear. Conservation easements and other incentives to landowners to keep land in natural cover will be essential and our step selection model could be used for conservation planning to identify such areas that could be critical for Louisiana black bear conservation.

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