AN ASSESSMENT OF HABITAT NORTH OF THE CALOOSAHATCHEE RIVER FOR FLORIDA PANTHERS

Final Report

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INTRODUCTION

The Florida panther (*Puma concolor coryi*) has been federally listed as "Endangered" since the inception of the Endangered Species Preservation Act of 1967 and the subsequent Endangered Species Act of 1973. As the only surviving subspecies of *Puma* in the eastern United States, the Florida panther is limited to a single breeding population of <100 animals (U.S. Fish and Wildlife Service [USFWS] 2006). Although the historic range of the Florida panther once encompassed the southeastern United States, the population is currently limited to the southern portion of the Florida peninsula. Based on radiotelemetry data, the population extends as far north as Okaloacoochee Slough in Hendry County, approximately 15 km south of the Caloosahatchee River.

Being small and geographically isolated, the Florida panther population is vulnerable to stochastic events such as extreme weather, disease, or a sudden loss of its prey base (Clark 2001). In addition, suitable but unoccupied panther habitat in south Florida continues to be converted to agricultural and urban land uses. Consequently, establishment of panther populations outside south Florida should be a high priority to improve the likelihood of survival of the subspecies (Maehr et al. 2002, Clark 2001). Indeed, one of the objectives of the Florida panther recovery plan is to expand the panther range north of the Caloosahatchee River (USFWS 2006) in an effort to increase the probability of long-term persistence of the species.

Although several male panthers have been documented north of the Caloosahatchee River via radiotelemetry data, vehicular mortalities, and other confirmed panther sign, no females have been documented there since 1973 (McBride 2002). Juvenile males can disperse long distances but females typically remain within or near their mother's home range (Maehr et al. 2002). Additionally, natural population expansion has been inhibited because of habitat fragmentation and barriers to dispersal (USFWS 2006). The Caloosahatchee River and surrounding agricultural lands and highways may also act as impediments to panther movement. Such barriers, coupled with the relatively short dispersal distances of females, reduce the likelihood that the breeding range of the Florida panther will naturally expand north of the Caloosahatchee River. The poor ability to colonize unoccupied habitats has been documented for other large carnivores and translocation efforts to mitigate for poor natural dispersal have often been successful (Clark et al. 2002). Therefore, translocation of female Florida panthers has been suggested as a means to facilitate the establishment of a breeding subpopulation north of the Caloosahatchee River (Maehr et al. 2002, USFWS 2006).

The documentation of male panthers in good condition north of the Caloosahatchee River suggests that there is sufficient prey and cover to support the species (Maehr et al. 2002). Likewise, Thatcher et al. (2003) estimated that the habitat north of the Caloosahatchee River is suitable for Florida panthers. However, no fine-scaled, quantitative assessment of the ability of the landscape in central Florida to support Florida panthers has been undertaken. Therefore, the objective of this project is to estimate the quantity and quality of Florida panther habitat north of the Caloosahatchee River.

STUDY AREA

The study area contained 31 counties in southern and central Florida, encompassing an area of 78,427 km^2 (Fig. 1). Publicly owned land accounted for 29.5% of the study area (Florida Geographic Data Library 2005). The largest public land parcels were Everglades National Park, Big Cypress National Preserve, and several Water Conservation Areas, all located at the southern portion of the Florida peninsula.

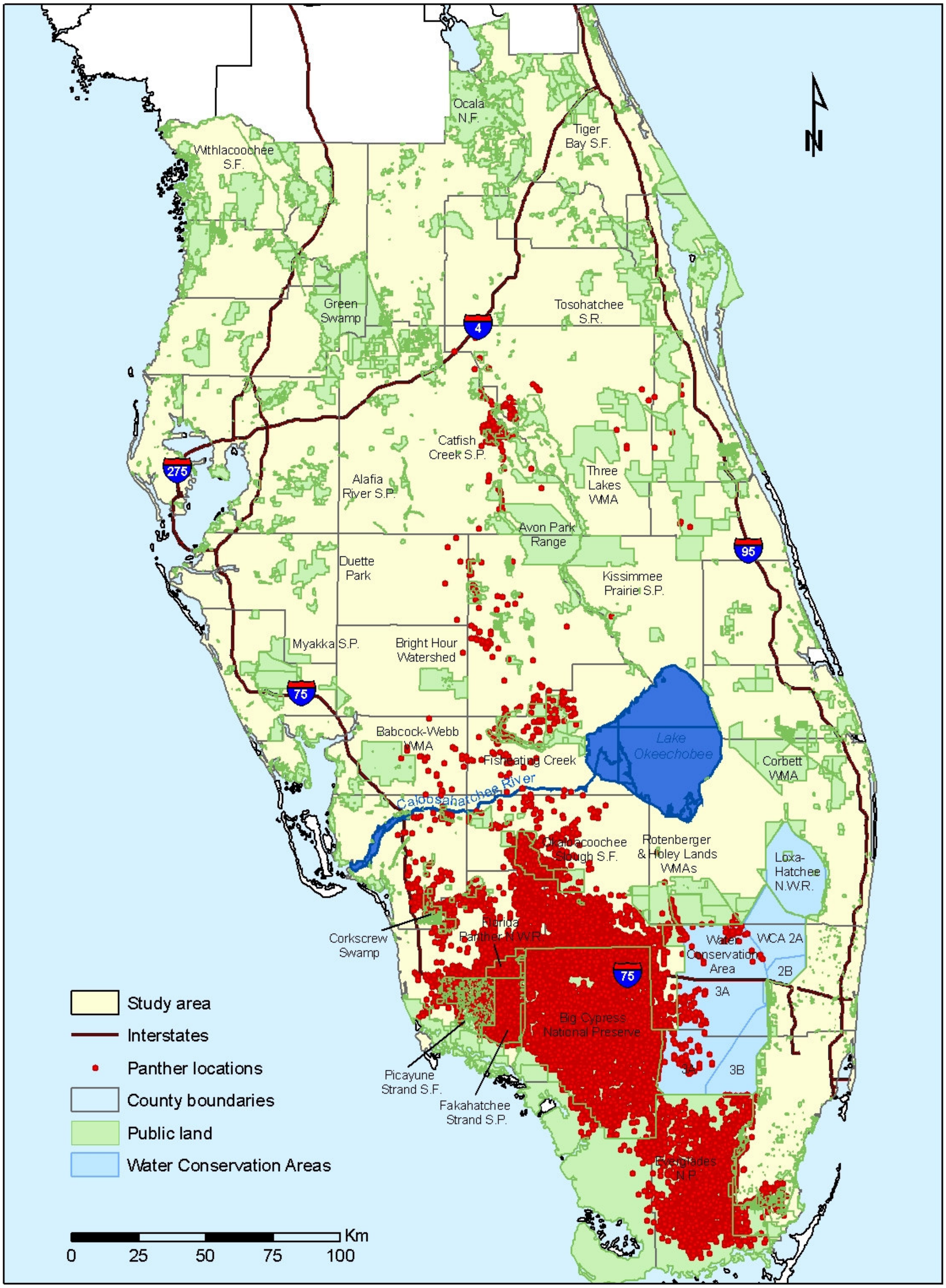

Figure 1. Study area and distribution of Florida panther telemetry locations, 1981–2005.

Southern Florida is characterized by relatively flat topography and poorly drained soils, resulting in extensive wetlands (Davis 1943). Elevations range from sea level to 95 m. The climate of southern Florida was tropical, with a summer wet season and a winter dry season (Davis 1943). Major vegetation types included pine forests, cypress (*Taxodium* spp.) and mixed hardwood swamps, hardwood hammocks, cabbage palm (*Sabal palmetto*) forests, mangroves (*Avicennia germinans*, *Rhizophora mangle*), saw palmetto (*Serenoa repens*) prairies, and herbaceous wetlands such as sawgrass prairies (*Cladium mariscus var. jamaicense*; Florida Fish and Wildlife Conservation Commission 2003). Mean annual rainfall ranged from 114 to 157 cm (U.S. Department of Agriculture Natural Resources Conservation Service [USDA NRCS] 1997). Approximately 14% of the study area was used for agriculture, including pasture, sugarcane fields, citrus orchards, and row crops (Florida Fish and Wildlife Conservation Commission 2003). About 10% of the study area was characterized by urban land use, particularly along the Atlantic and Gulf coasts and inland along the Interstate-4 corridor.

The Caloosahatchee River was located in Lee, Glades, and Hendry counties. The river was approximately 110 km long and connects Lake Okeechobee to the Caloosahatchee Estuary and ultimately to the Gulf of Mexico near Fort Meyers. The Caloosahatchee River has been dredged and channelized, and its route artificially altered to connect with Lake Okeechobee (South Florida Water Management District 2006). The channel had steep banks and is 50–130 m wide in the upstream freshwater portions of the canal. Agriculture and urban areas were the most common land uses along both sides of the river.

METHODS

General Approach

We delineated Florida panther habitat based on a statistical model in combination with a geographic information system (GIS; Thatcher et al. 2006). Our approach was to identify landscape conditions north of the Caloosahatchee River that were similar to those associated with the current panther population in south Florida. We define landscape conditions as any combination of variables such as land-cover type, roads, and other human development activities, and indices that we developed in GIS to quantify fragmentation, patch configuration, road density, and other similar metrics. Habitat has been defined as the physical space, including its biotic and abiotic properties, in which animals live (Morrison and Hall 2002). Patches are discrete units of contiguous habitat. We developed a habitat model based on the Mahalanobis distance (D^2) statistic, using Florida panther home ranges from 1988 to 1998 as the reference. We tested the habitat model using a 10-fold crossvalidation technique (Verbyla and Litvaitis 1989) and by using independent data (panther home ranges based on 2002–2005 telemetry data).

Patch size and the degree of connectivity with other patches could be important for the persistence of Florida panther populations. To quantify those factors, we first determined a threshold value for the D^2 model to classify Florida panther habitat. Using that binary map, we next delineated potential habitat patches. We examined connectivity among these patches by using a least-cost-path modeling algorithm (Kindall and van Manen 2006).

Telemetry Data

Panther telemetry data were collected by the Florida Fish and Wildlife Conservation Commission, the National Park Service, and the University of Tennessee during 1981–present, and included >76,000 locations. Mean telemetry error for locations collected by all agencies was estimated to be 176 m, with 95% of locations within 489 m (Janis and Clark 2002). Panthers were monitored year-round, with an average of 3 relocations per week.

We excluded data for panthers <18 months of age because these animals were usually dependent on their mothers and likely exhibited probable movement and activity biases (Janis and Clark 2002). Our telemetry data subset included locations from 8 female Texas mountain lions (*Puma concolor stanleyana*) and their offspring introduced to south Florida in 1995. Sampling intensity varied among the 3 agencies that collected telemetry data, so the data were standardized to $\leq$3 locations per week for each animal. We excluded panthers with <50 locations because of possible bias in home-range estimation when using the fixed kernel method (Seaman et al. 1999). Sixty-two panthers (32 F, 30 M) with a total of 36,066 telemetry locations met the age and sample size requirements.

Telemetry locations were primarily obtained during morning hours, a time when Florida panthers are typically resting (Comiskey et al. 2002). Although daytime telemetry locations should not be used to describe 24-hour habitat use, the telemetry data are suitable for determining panther home ranges (Beier et al. 2003). Because of the low potential for such spatiotemporal biases and because our estimated telemetry error should have little influence on home-range calculations, we used panther home ranges as the sampling unit in the habitat analysis rather than individual telemetry locations. Finally, the use of home ranges also allows the use of individual panthers as the sampling unit, rather than individual telemetry locations, thus avoiding pseudoreplication biases.

We delineated a home range for each panther by calculating a 95% probability contour using the fixed kernel method (Worton 1989) available in the Animal Movement extension (Hooge and Eichenlaub 1997) to ArcView® GIS (ESRI, Redlands, California, USA). Although the telemetry data spanned up to 10 years for some animals and some animals exhibited home-range shifts, we calculated a single home range for each animal.

Landscape Data

Ideally, habitat models should be based on current land-cover data so that relevant management decisions can be made. However, we wanted to identify habitat characteristics associated with Florida panther home ranges so we used landscape data from approximately the same time period as the telemetry data (Beier et al. 2003). Although the most recent land-cover data were from 2003, we instead used 1993 GAP land-cover data (Florida Cooperative Fish and Wildlife Research Unit 2000) to better coincide with the dates of telemetry data collection. We similarly selected other GIS data (Table 1). Moreover, we used a subset of telemetry data collected within 5 years of the 1993 Florida GAP land-cover data (1988–1998) to develop the habitat model. Once the model was developed, we then applied it with more recent land-cover data. Florida GAP land-cover data were derived from 1993 Landsat satellite imagery, and were classified to the species alliance or association level. We grouped the data from 71 detailed vegetation and land-cover types into 10 general vegetation, agricultural, and urban land-cover associations (Fig. 2). GAP land-cover data were in grid format and had a resolution of 30 m.

Table 1. Data sources for habitat models to identify potential Florida panther habitat north of the Caloosahatchee River in Florida.

Data source	Year	Agency
TIGER/line roads	2005	U.S. Census Bureau
TIGER/line roads	1992	U.S. Census Bureau
Block-group level human population data	2000	U.S. Census Bureau
Block-group level human population data	1990	U.S. Census Bureau
National Wetlands Inventory	1977–present	U.S. Fish and Wildlife Service
GAP land cover	1993	USGS/ Florida Cooperative Fish and Wildlife Research Unit
Florida habitat and land cover	2003	Florida Fish and Wildlife Conservation Commission

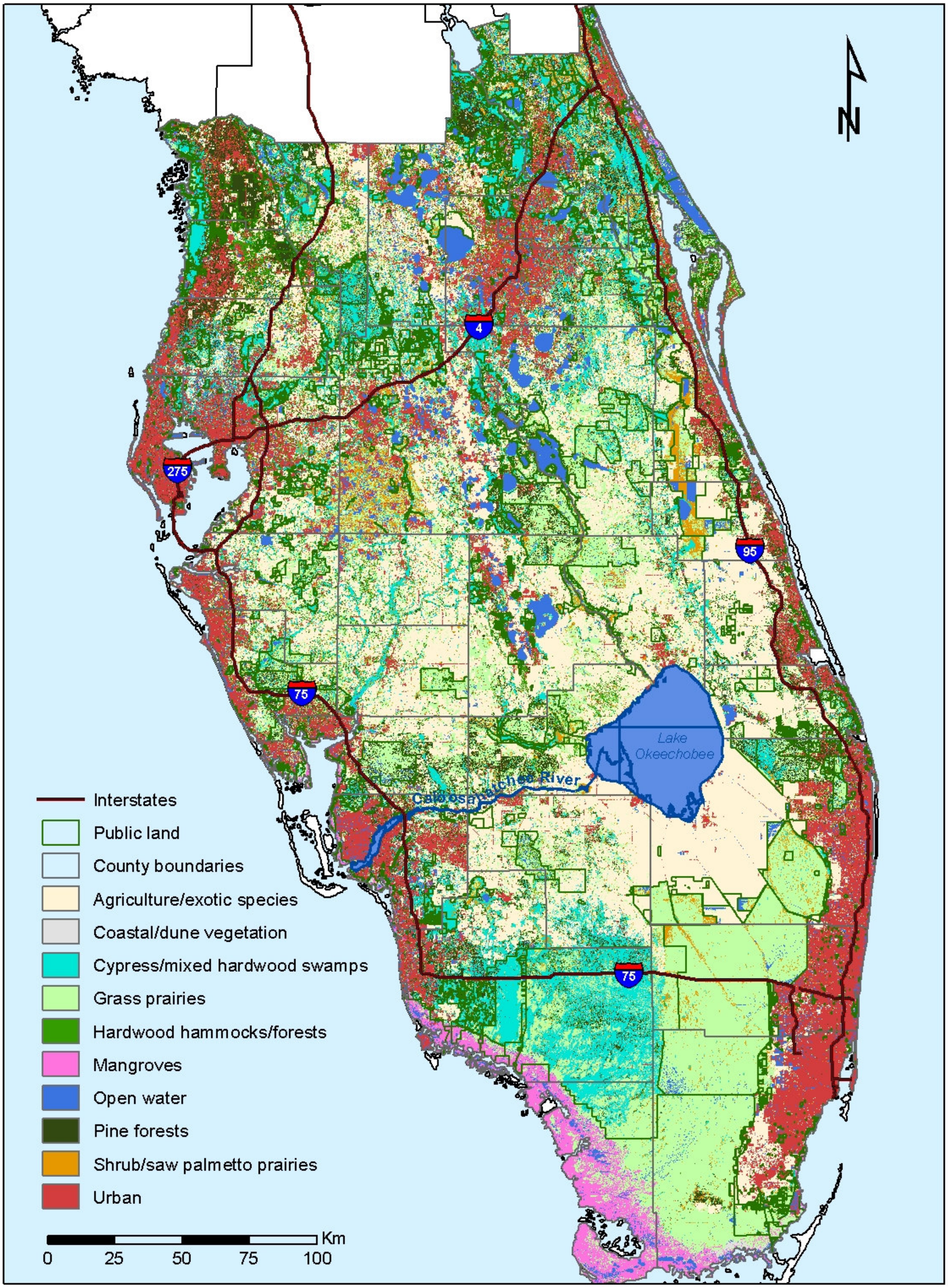

Figure 2. Florida land-cover data (2003) for the study area in south Florida.

We used ArcGIS™ to develop fine-scale (30-m resolution) landscape variables for the habitat model (Table 2). Those variables were used to quantify spatial patterns of landscape heterogeneity and fragmentation, and to represent different configurations of land-cover type. Each variable was calculated using moving windows with a 3,280-m radius, a scale equivalent to the mean daily movement rate of male and female panthers (Janis and Clark 2002). Thus, each pixel in the resulting GIS grid represented the average landscape characteristics within a circle with a radius equal to a panther's average daily movement distance. We selected several variables for the initial habitat models based on a reclassification of the Florida GAP land-cover data: percent agriculture and exotic species, calculated as the proportion of agricultural and exotic species land-cover within a 3,280-m radius; percent grass prairies, shrublands, and saw palmetto prairies; percent pine; percent cypress swamps and hardwood hammocks; percent coastal vegetation and mangroves; and percent urban land cover. Urban land-cover types included commercial and residential areas, paved or open areas, and roads. We also calculated landscape variables based on more general land-cover characteristics, such as percent forest and percent natural habitat (natural habitat was defined as forest, grassland, shrub, and wetland land-cover types). Finally, we calculated the density of forest and natural land-cover patches with Program FRAGSTATS 3.1 (McGarigal and Marks 1995), with higher patch densities indicating greater habitat fragmentation.

Spatial data on roads and human population density were included in the habitat model as a measure of anthropogenic influences on the landscape. Human disturbance may increase habitat fragmentation, create impediments to panther movement, and increase the risks to panthers from vehicular mortality and poaching (Comiskey et al. 2002). Human population density was developed from 1990 blockgroup-level U.S. Census Bureau data (Florida Geographic Data Library 2002*a*). A block group is a polygon representing an area of varying size generally containing between 600 and 3,000 people, with a typical population of 1,500 (U.S. Census Bureau 2002). Road density, developed from 1992 U.S. Census Bureau TIGER/Line data (Florida Geographic Data Library 2002*b*), was calculated as the total length of roads within a moving window with an area equal to a 3,280-m radius circle. The road data included all roads except unpaved roads and roads accessible only by 4-wheel-drive vehicles. We excluded those roads

Variable	Range for home ranges	Range for study area	Mean for home ranges	Mean for study area	Variable definition
Human impact on landscape					
Paved road density	1–19	0–164	7	19	Total length of paved roads divided by window area * 10,000
Major road density	0–91	0–1186	22	61	Total length of major roads divided by window area * 10,000
Distance to major roads	3,038–31,174	0–71,761	12,625	9,450	Euclidean distance (m) to major roads
Major roads (categorical)	0-1	0-1	0.002	0.005	Presence (1) or absence (0) of major roads
Human population density	0.12–50.61	0–8,370	3.78	123.0	Human density per km^2 averaged within window
Percent urban land cover	0–83.6	0–100	1.2	12.1	Proportional abundance of urban land cover
Water regime (NWI data)					
Percent upland	2.2–80.2	0–100	33.7	60.8	Proportional abundance of well-drained or irregularly flooded land
Percent seasonally flooded	16.0–96.9	0–100	61.2	19.1	Proportional abundance of seasonally flooded land
Percent permanently flooded	0.2–45.9	0–100	6.0	19.4	Proportional abundance of semi-permanently to permanently flooded land
Vegetation type					
Percent coastal vegetation/mangroves	0–2.5	0–11.3	0	0	Proportional abundance of coastal vegetation or mangroves
Percent pine forest	1.9–24.7	0–80.2	9.3	11.1	Proportional abundance of pine forest
Percent cypress and hardwood swamps	2.6–71.4	0–94.9	37.9	11.8	Proportional abundance of cypress and hardwood swamps
Percent shrubland/saw palmetto	0–65.6	0–67.7	7.3	7.7	Proportional abundance of shrubland and saw palmetto
Percent grasslands, shrub, and saw palmetto	13.3–88.4	0–100	35.4	24.4	Proportional abundance of grass, shrub, and saw palmetto
Percent forest	6.0–80.6	0–98.5	47.2	22.8	Proportional abundance of forest vegetation types
Percent natural land cover	42.7–99.8	0–100	82.6	47.1	Proportional abundance of natural land-cover types
Percent agriculture	0–54.8	0–100	15.2	31.6	Proportional abundance of agriculture
Distance to forest/shrubland	0–1.3	0–57.6	74	391	Euclidean distance (m) to forest or shrubland
Pattern of vegetation cover					
Forest patch density	0.03–25.07	0.03–27.38	4.36	5.17	Number of forest patches divided by window area
Natural land-cover patch density	0.43–10.32	0.03–66.75	3.71	9.84	Number of natural land-cover patches divided by window area

Table 2. Mean and range of values of landscape variables within Florida panther home ranges (n = 62) in south Florida.

because they usually have very little traffic. We developed a second road variable that consisted of interstate and U.S. highways only. These wide, heavily-trafficked roads can act as barriers to panther movement (Foster and Humphrey 1995, Dickson et al. 2005). We converted interstate and U.S. highways from vector to grid data, using a distance of 90 m to represent the highways and adjacent areas of open shoulder.

The Water Conservation Areas east of the current panther range are intensively managed by a system of canals and levees to provide flood control and water storage. Areas that were perennially inundated were less able to support white-tailed deer (*Odocoileus virginianus*), an important source of prey for Florida panthers (Fleming 1994, Comiskey et al. 2002). Therefore, we included variables related to water regime in our models based on National Wetlands Inventory (NWI) data (Cowardin et al. 1979). NWI data were developed nationwide by the U.S. Fish and Wildlife Service from aerial photographs to map the extent and characteristics of wetland habitats. We used the water regime classification in the NWI attribute tables to group the wetlands data into 3 categories: permanently flooded or open water; seasonally flooded; and uplands or intermittently flooded. We added areas that were classified as diked or impounded in the NWI attribute tables (primarily the water conservation areas in Broward and Palm Beach counties) to the permanently flooded and open water category. As with the previous variables, we used moving windows analyses to calculate percent flooded or open water, percent seasonally flooded, and percent upland.

Mahalanobis Distance Analysis

We calculated the mean value of each landscape variable within each panther home range. The mean landscape conditions within panther home ranges formed the target to which the remainder of the study area was compared. We also used the mean values of each landscape variable within panther home ranges to calculate a correlation matrix to identify any redundancies among variables.

We used Mahalanobis distance (D^2) as the primary habitat modeling technique (Clark et al. 1993). D^2 is a multivariate statistic that represents a measure of dissimilarity (Rao 1952). This technique provides an effective approach to predict species occurrence based on location data and GIS data layers using the following equation:

$$D^2 = (\underline{x} - \underline{\hat{u}})' \sum^{-1} (\underline{x} - \underline{\hat{u}}),$$

where $\underline{x}$ is a vector of landscape characteristics in the GIS grid, $\underline{\hat{u}}$ is the mean vector of landscape characteristics estimated from the set of panther home ranges, and $\sum^{-1}$ is the inverse of the variance-covariance matrix calculated from the home ranges (Rao 1952). The D^2 statistic provides a dimensionless index of similarity to the multivariate landscape conditions associated with the target species (Knick and Rotenberry 1998). Small values of D^2 represent landscape conditions similar to those within panther home ranges, whereas larger distance values represent increasingly different conditions. The Mahalanobis distance technique is well-suited for modeling a secretive, wide-ranging animal such as the Florida panther because it requires only presence data for input, rather than both presence and absence data. This statistical technique avoids the potential difficulties involved in classifying available habitats as unused as is required for other techniques (e.g., logistic regression).

We calculated the D^2 statistic in ArcMap™ 9.2 (ESRI, Redlands, California, USA) for each pixel in the study area. The values represent a quantitative index of panther habitat use, using panther home ranges in south Florida as a reference of landscape conditions that support panthers. Because D^2 scores can range from 0 to infinity, it can be difficult to interpret and evaluate these scores. However, assuming multivariate normality, D^2 scores can be recoded to *P*-values based on the Chi-square distribution with $n - 1$ degrees of freedom, whereby n equals the number of landscape variables in the model (Clark et al. 1993). The *P*-value represents the probability of observing a D^2 value $\geq$ than the actual D^2 value, assuming that the predictor values were sampled from a population whose mean is the ideal combination of predictor values estimated from the radio-collared panthers. However, if there is no multivariate normality, the *P*-values simply represent a rescaling of D^2 values from 0 to 1 (Jenness 2003). *P*-values closer to 1 indicate a greater similarity to the landscape conditions defined by the panther home ranges (Jenness 2003); thus, greater *P*-values correspond to more favorable landscape conditions.

Model Selection and Testing

One limitation of the D^2 modeling technique is that there is no formal model selection procedure. We developed several habitat models before choosing a final model. Some models were developed to evaluate the effect of an individual variable in the multivariate model. Other models were created during the process of selecting the best method to calculate certain variables. For example, to incorporate the effect of major roads on panther habitat, we calculated density of major roads, distance to major roads, and major roads as a categorical variable. Other variables were included then omitted because of apparent biases when comparing landscape conditions in the current panther range to landscape conditions north of the Caloosahatchee River. For example, patterns of natural land cover were much different in south Florida, where large expanses of unbroken natural land-cover types exist, resulting in low patch density. In contrast, areas of low patch density north of the Caloosahatchee River often consisted of large expanses of agricultural fields interspersed with a few small patches of natural land cover, which generally is poor panther habitat (Kautz et al. 2006). Because these very different landscapes both had low patch density, the habitat model poorly distinguished between the two areas. Our initial assessment of the various models was performed by comparing the resultant D^2 maps with the known panther distribution in south Florida. Large areas identified as favorable landscape conditions that were not occupied by panthers or vice versa would be indicative of a poor model. Florida panther experts from the U.S. Fish and Wildlife Service and the Florida Fish and Wildlife Conservation Commission assisted us in these evaluations.

Once the initial model was developed, we tested model predictions by calculating the mean *P*-value within each panther home range and comparing those with home ranges randomly placed throughout the study area. Those random home ranges were equal in size and number to the average male and female home ranges of our sample. We repeated this process to produce 10 sets of randomly-placed home ranges for comparison with actual panther home ranges. We calculated the mean *P*-values within panther home ranges and within the random home ranges.

We used a cumulative frequency distribution graph to help determine the optimal *P*-value cutoff. The *P*-value that showed the greatest separation between the panther home ranges and random home ranges is usually chosen as a threshold value. This process is useful to seek a balance between specificity (the probability that the predicted absence of a home range was correct) and sensitivity (the probability that the predicted presence of a home range was correct) of the model.

We used 10-fold crossvalidation to test model performance and identify panther home ranges that were outliers. In this resampling procedure, the panther home-range dataset was partitioned into 10 subsamples. Each subsample contained 6 or 7 home ranges (10% of the sample size). The habitat model was calculated with n - 1 subsamples and tested with the excluded subsample. Once all subsamples were excluded, we calculated the mean sensitivity of all 10 models (Verbyla and Litvaitis 1989).

Finally, we used telemetry data that were not available at the beginning of the project to test the model developed from recent landscape data. We obtained telemetry data from 2002 to 2005 collected by the Florida Fish and Wildlife Conservation Commission and the National Park Service. Individual panthers that were also monitored in previous years and whose home ranges were used to develop the habitat model were excluded. Using the 95% fixed kernel home ranges from the remaining 25 panthers that met our age and sample size requirements, we calculated the mean P-value within each home range and determined the proportion of home ranges correctly classified as occurring within favorable landscape conditions based on circa 2003 landscape data.

Model Application

Once the model was developed, we applied it using more recent landscape data. Data sources included 2003 land cover (Florida Fish and Wildlife Conservation Commission 2003), 2000 block-group level human population data (U.S. Census Bureau 2002), and 2005 roads (U.S. Census Bureau 2005; Table 1). Using the P-value cutoff identified during model testing, we created a map layer of panther habitat based on the same technique we used to delineate habitat patches from the 1993 habitat model. To estimate the minimum patch area capable of supporting a panther subpopulation, we overlaid panther home ranges onto the 1993 model. The smallest patch that had substantial overlap with at least one female panther home range was used as a minimum threshold for consideration as a potential translocation site.

Habitat Connectivity

We conducted a least-cost-path analysis to identify potential linkages and to provide a relative measure of connectivity between habitat patches. Least-cost-path models have been used to identify dispersal pathways for Florida panthers (Kautz et al. 2006) and habitat connectivity for other large carnivores such as black bears (*Ursus americanus*; Kindall and van Manen 2006). Our purpose was to identify those patches north of the Caloosahatchee River that, if occupied by panthers, had the greatest potential for connectivity to other habitat patches. We delineated habitat connectivity with a cost-surface grid, which represented relative value (or "cost") of habitat based on the panther habitat model. Areas with greater D^2 values were less likely to be used by panthers, providing poor habitat connectivity (high cost). Using D^2 as the cost surface, we calculated the cost-weighted distances from each habitat patch that met our minimum size requirements to all pixels in the study area using the COSTDISTANCE function in ArcGIS™. We used the resulting cost-weighted distance grids to map habitat connectivity (CORRIDOR function in ArcGIS™) between pairs of nearby patches.

RESULTS

Home Ranges

Sixty-two panthers (30 males, 32 females) met our minimum age and sample size requirements ($\geq$18 months of age, with $\geq$50 locations per animal). Mean male home range-size was 977.9 km^2 and mean female home-range size was 304.1 km^2. We defined panther habitat based on the mean vector of landscape conditions within panther home ranges and used that as the point of reference to develop the habitat model.

Habitat Model

We developed several fine-scale (30-m resolution) landscape variables based on Florida GAP land-cover data. Initial models indicated that our variables based on land cover were too specific. For example, grasslands were common in the southern part of the study area but were rare in the north, whereas the opposite was true for shrub/saw palmetto prairies. We initially calculated percent grasslands and percent shrubland/saw palmetto prairies as separate variables. Consequently, some large areas of natural land-cover types in the northern portion of the study area were classified as unsuitable by the model. We used the results of the initial habitat models to help guide the process of grouping land-cover types into fewer, more general variables. We experimented with different groupings of land-cover types, but eventually developed a binary class by separately grouping all natural land-cover types (forests, grasslands, shrublands, and cypress swamps) and non-natural types (urban, open water, agriculture, and mangrove).

The final model included paved road density, major highways (U.S. and interstate highways; categorical variable), human population density, percent permanently or semi-permanently flooded, and percent natural land cover. The resulting map based on circa 1993 landscape data consisted of D^2 values ranging from 0.62 to 1,920,439.75 (Fig. 3). When the same multipliers from the D^2 model were applied to circa 2003 landscape data, the D^2 values ranged from 0.62 to 1,304,802.75 (Fig. 4). The greatest D^2 values, indicating landscape conditions that were most dissimilar to current panther habitat, corresponded with highly urbanized areas such as Miami and areas occupied by major highways. Because the D^2 values exhibited an extremely large range, we rescaled the D^2 values to P-values to facilitate model interpretation and assessment (Figs. 5 and 6).

Model Assessment

The cumulative frequency graph of P-values for the 1993 habitat model indicated that a P-value = 0.12 maximized the difference between specificity and sensitivity (Fig. 7). A P-value cutoff of 0.12 corresponded with a D^2 cutoff value of about 8 (Figs. 3 and 4). At this P-value cutoff, the habitat model correctly classified 100% of the panther home ranges while restricting predictions of panther habitat to 22.6% of the random home ranges and 15.6% of the study area in general.

We applied the P-value cutoff of 0.12 to the 2003 habitat model. The model predicted that 16.3% of the study area was panther habitat, an increase of 0.7% compared with the 1993 model. The model correctly predicted 100% of the 25 panther home ranges from the 2002–2005 telemetry data when we applied the 2003 habitat model.

The crossvalidation results also indicated that 100% of the panther home ranges had mean P-values above the cutoff value. However, we also calculated the percent of panther habitat within the home ranges in each subsample as a more sensitive measure of error. In this case, error represented the difference in the percentage of habitat in a home range between the final habitat model and the habitat model developed from the subset with that home range left out. The mean error based on the 10-fold crossvalidation was 1.35% (range = 0.02–15.85%). The largest error occurred for panther #64, a male who inhabited the northern portion of the Corkscrew Swamp area, a narrow strip of cypress and hardwood swamps

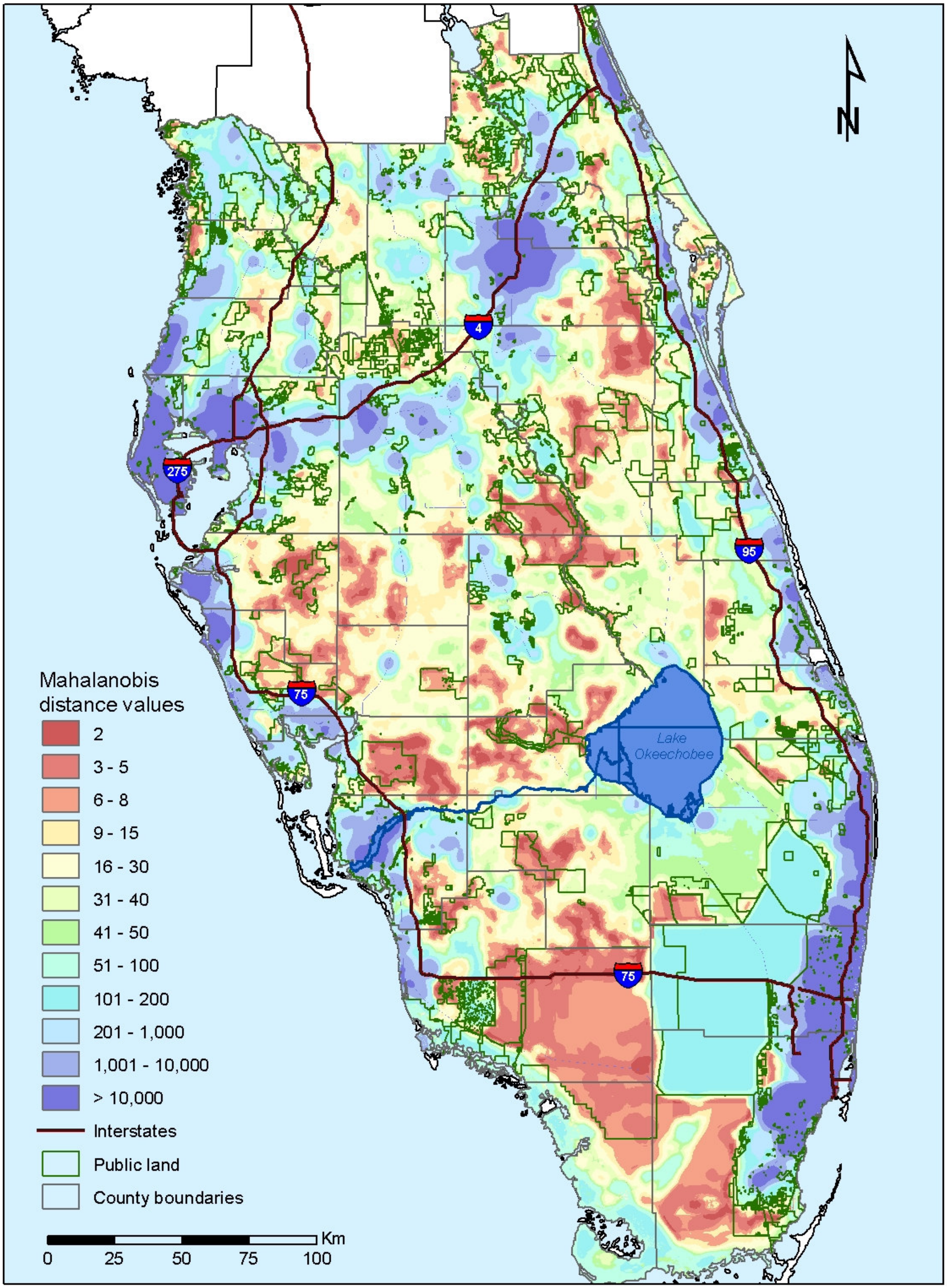

Figure 3. Mahalanobis distance values used to identify potential Florida panther habitat north of the Caloosahatchee River in Florida based on circa 1993 landscape conditions.

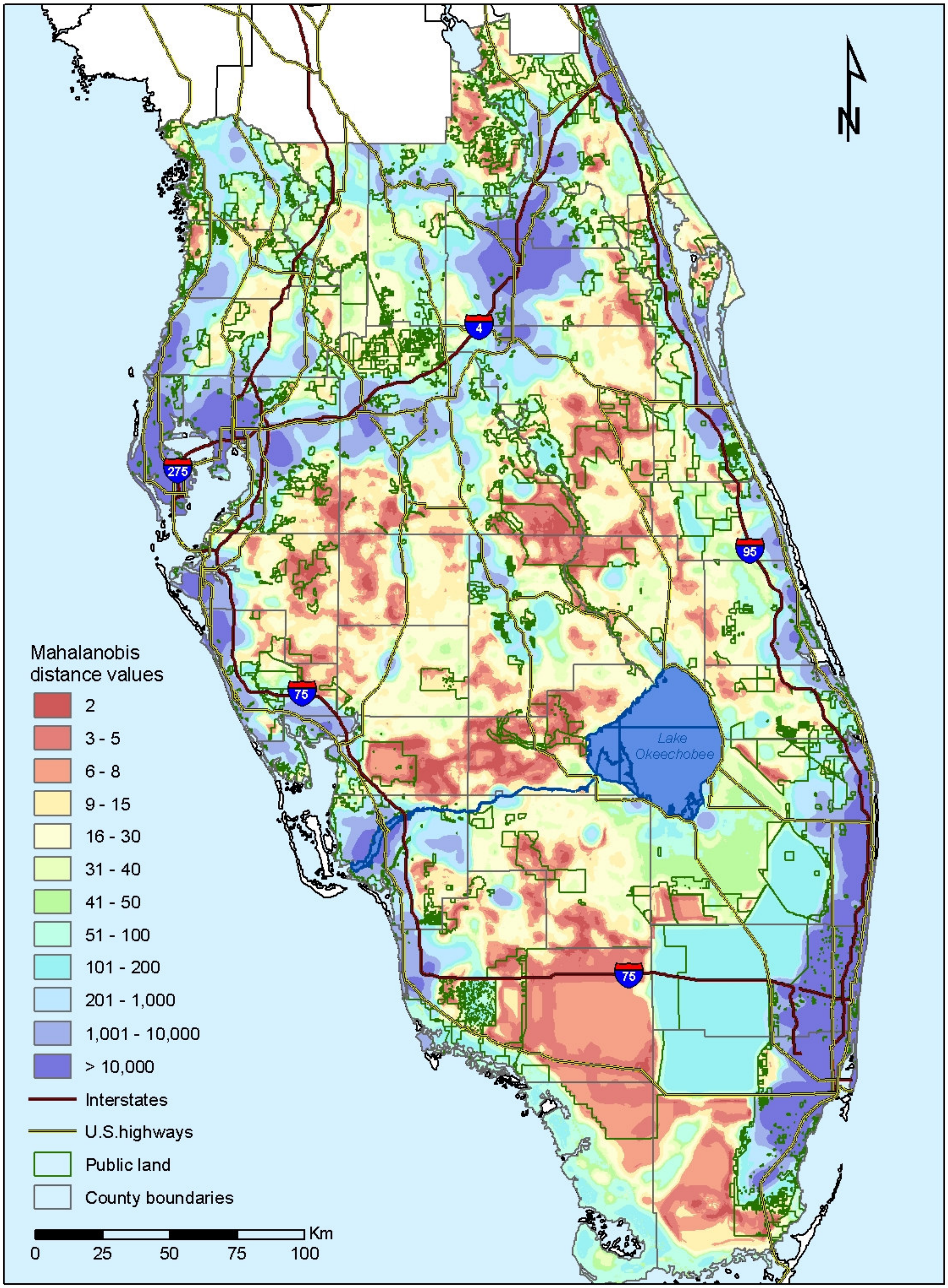

Figure 4. Mahalanobis distance values used to identify potential Florida panther habitat north of the Caloosahatchee River in Florida based on circa 2003 landscape conditions.

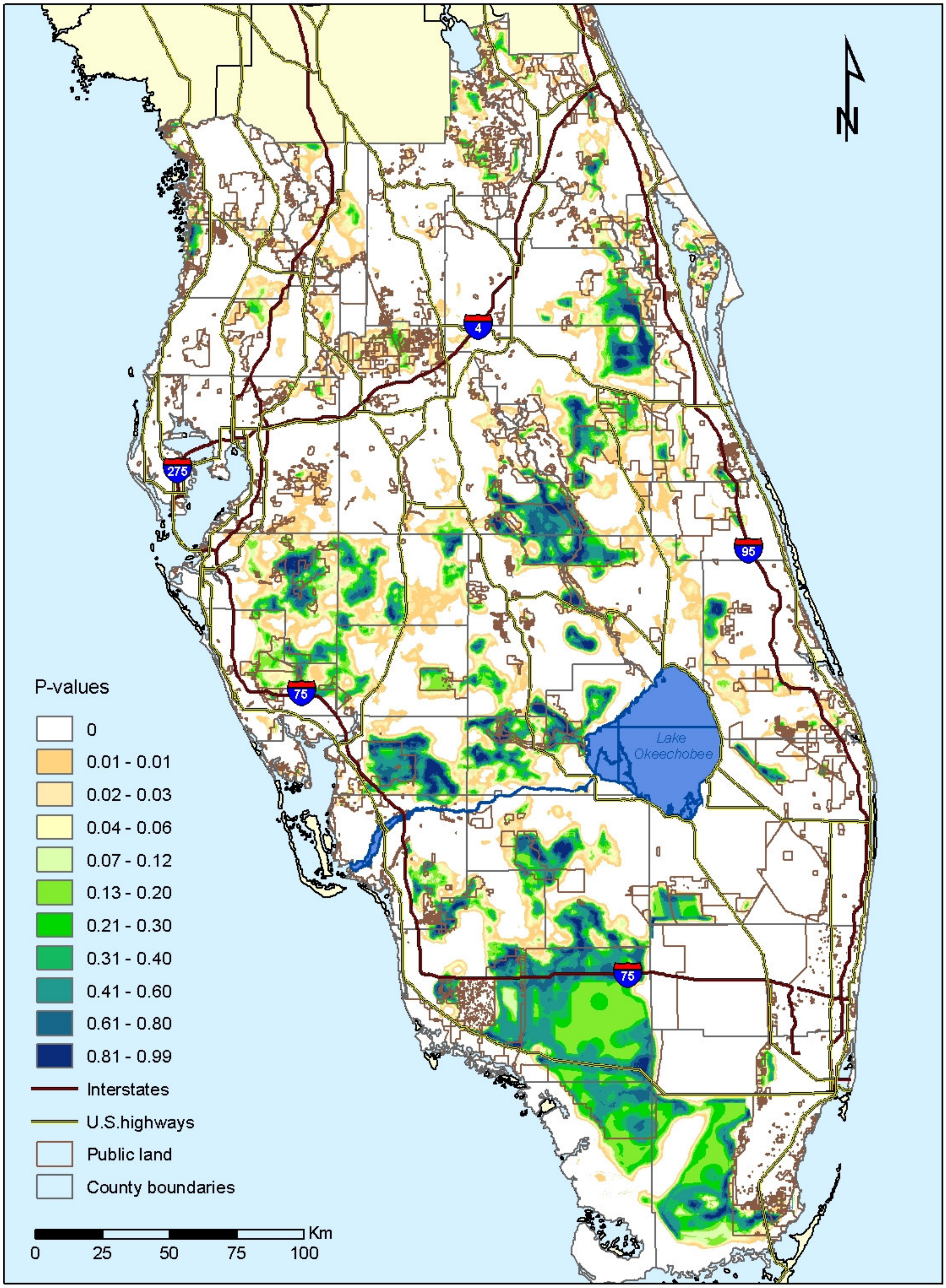

Figure 5. *P*-values used to identify potential Florida panther habitat north of the Caloosahatchee River in Florida based on circa 1993 landscape conditions.

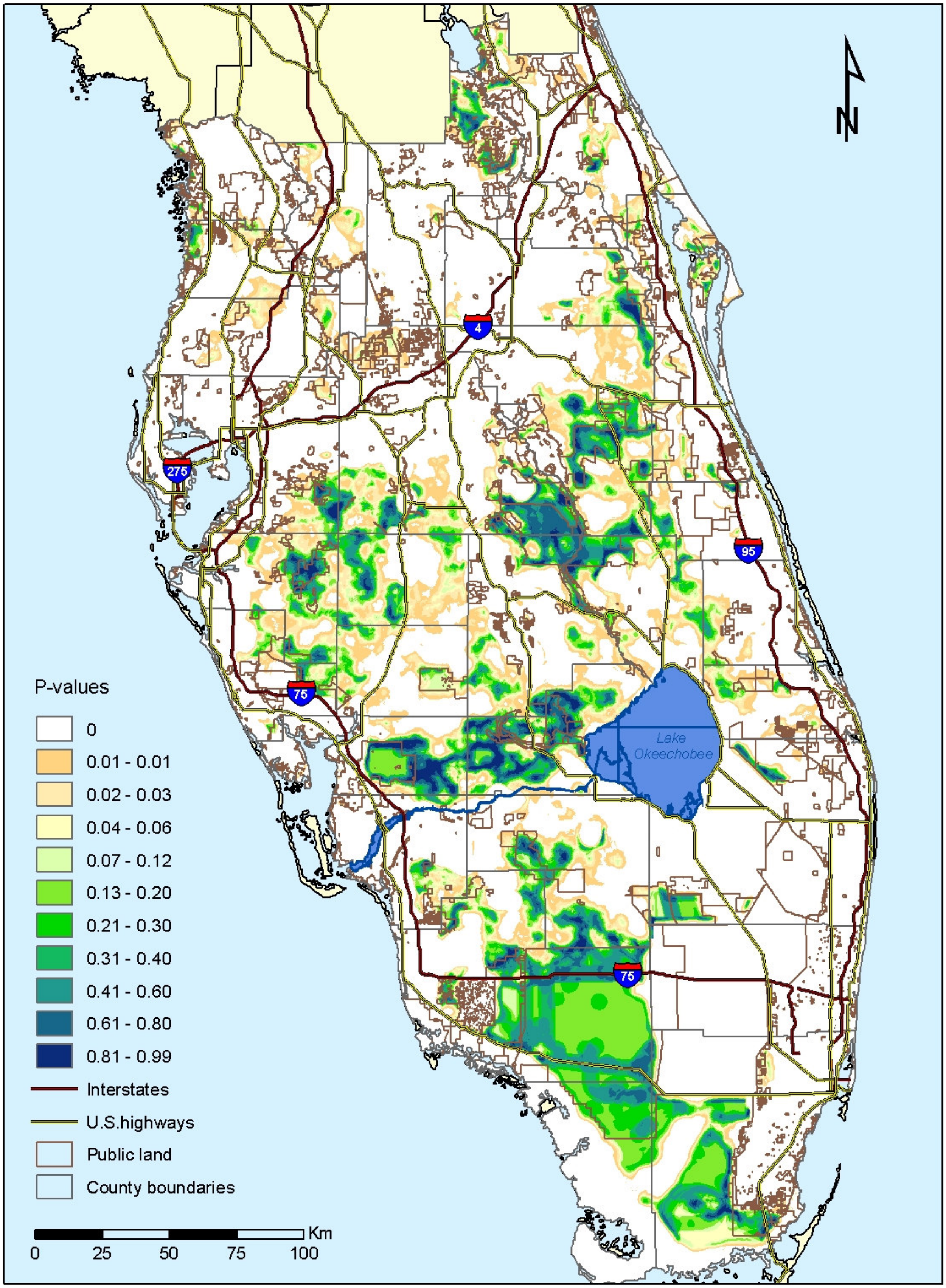

Figure 6. *P*-values used to identify potential Florida panther habitat north of the Caloosahatchee River in Florida based on circa 2003 landscape conditions.

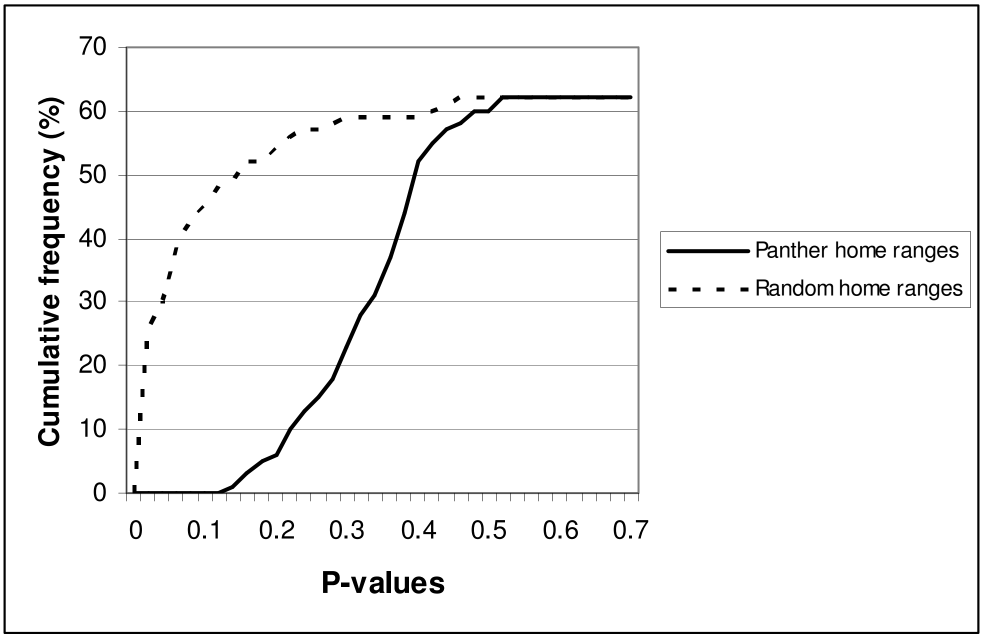

Figure 7. Cumulative frequency distribution of mean *P*-values within Florida panther home ranges compared with mean *P*-values within randomly generated home ranges in south Florida.

in a matrix of agriculture and urban land use. We found that, on average, 66.6% of the land area within each home range was panther habitat.

Habitat Patch Delineation

Contiguous areas of panther habitat with *P*-values $\geq$0.12 (1993 habitat model) ranged in size from <1 km^2 to 2,141 km^2 (Fig. 8). Otherwise contiguous areas of habitat often were divided into separate patches by the presence of major highways. The Everglades area was the largest patch (2,141 km^2) and was also the largest patch that supported female panthers (Table 3). The smallest patch that supported a female panther was a 427-km^2 parcel in the Okaloacoochee Slough area. The average patch size that supported female panthers was 1,296 km^2. We provide the area of smaller, unoccupied patches in 1993 in Table 3 for comparison with the larger, occupied patches.

Based on the 2003 habitat model, habitat patch size ranged from <1 km^2 to 1,759 km^2 (Fig. 9). The Big Cypress National Preserve area south of Interstate 75 was the largest patch supporting panthers (1,759 km^2), whereas the smallest patch supporting female panthers was in the southern Everglades, with an area of 807 km^2 (Table 4). The average size of all patches that supported panthers in 2003 was 1,255 km^2.

The smallest patch that had substantial overlap with at least 1 panther home range in 1993 was 427 km^2, so this size was used as a minimum threshold for consideration as a potential translocation site. In 2003, there were 4 currently unoccupied habitat patches that met that minimum size criterion: Avon Park Bombing Range, Babcock-Webb Wildlife Management Area/western Fisheating Creek, Duette Park/Manatee County, and eastern Fisheating Creek.

Habitat Connectivity

We identified habitat connections among the 4 habitat patches we delineated (Fig. 10). We also delineated a habitat connection between the northernmost portion of the current range (Okaloacoochee Slough) and the nearest potential panther habitat patch north of the Caloosahatchee River (Babcock-Webb Wildlife Management Area/western Fisheating Creek). Regarding the latter, the strongest habitat connection was located in a matrix of

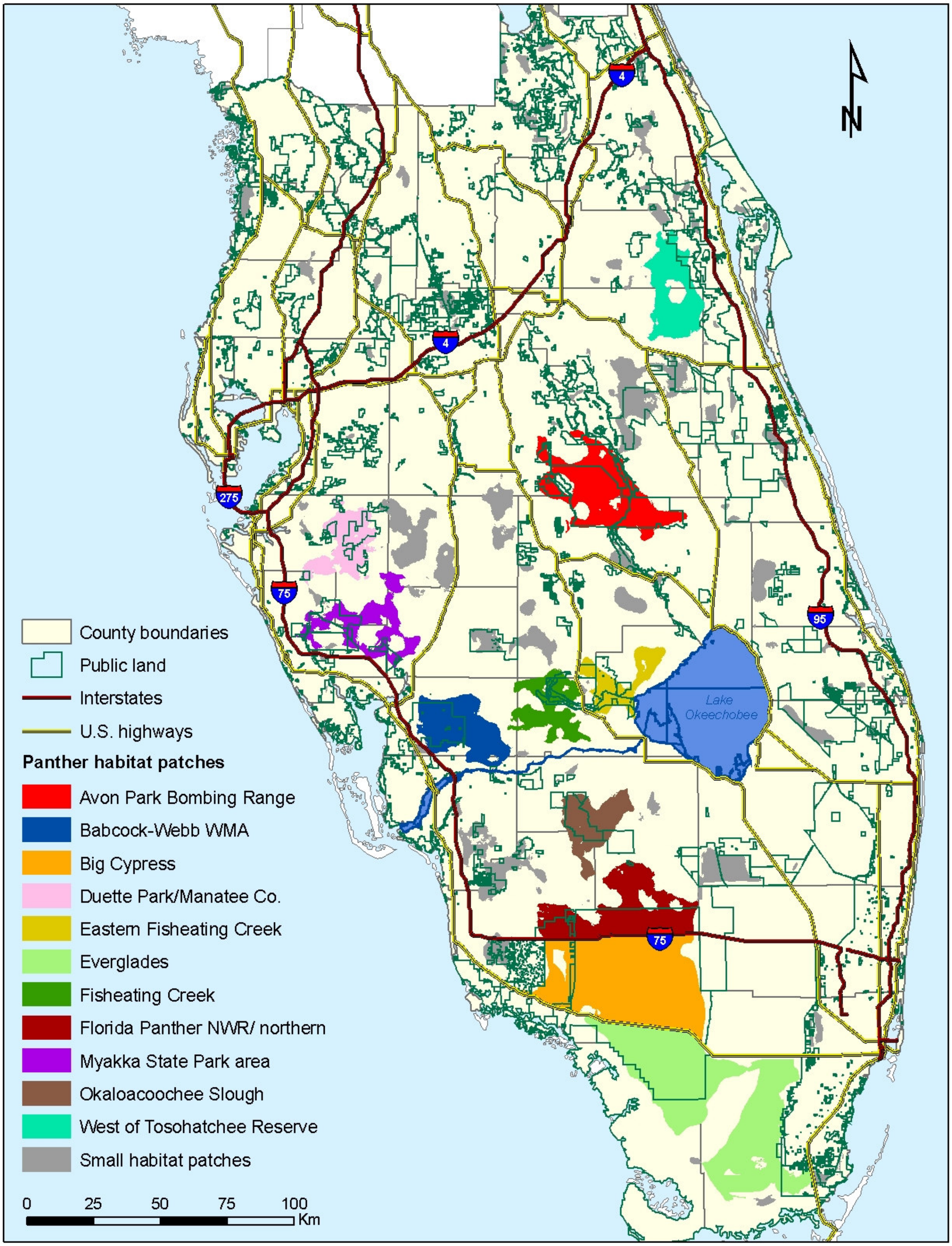

Figure 8. Potential translocation sites for the Florida panther in south Florida based on 1993 landscape data, with a minimum size of 427 km^2.

Table 3. Patches of Florida panther habitat with an area >300 km^2 based on the 1993 habitat model results.

Patch label	Patch name	Area of patch (km^2)	Within current range?
L	Everglades National Park	2,141	Yes
K	Big Cypress National Preserve and Fakahatchee Strand State Preserve	1,775	Yes
C	Avon Park Bombing Range	932	No
J	Florida Panther National Wildlife Refuge / northern Big Cypress National Preserve	840	Yes
H	Babcock-Webb Wildlife Management Area	592	No
A	West of Tosohatchee State Reserve	522	No
E	Myakka State Park	485	No
I	Okaloacoochee Slough	427	Yes
D	Duette Park / Manatee County	426	No
G	Fisheating Creek	424	No
B	Three Lakes Wildlife Management Area	320	No
F	Eastern Fisheating Creek	326	No

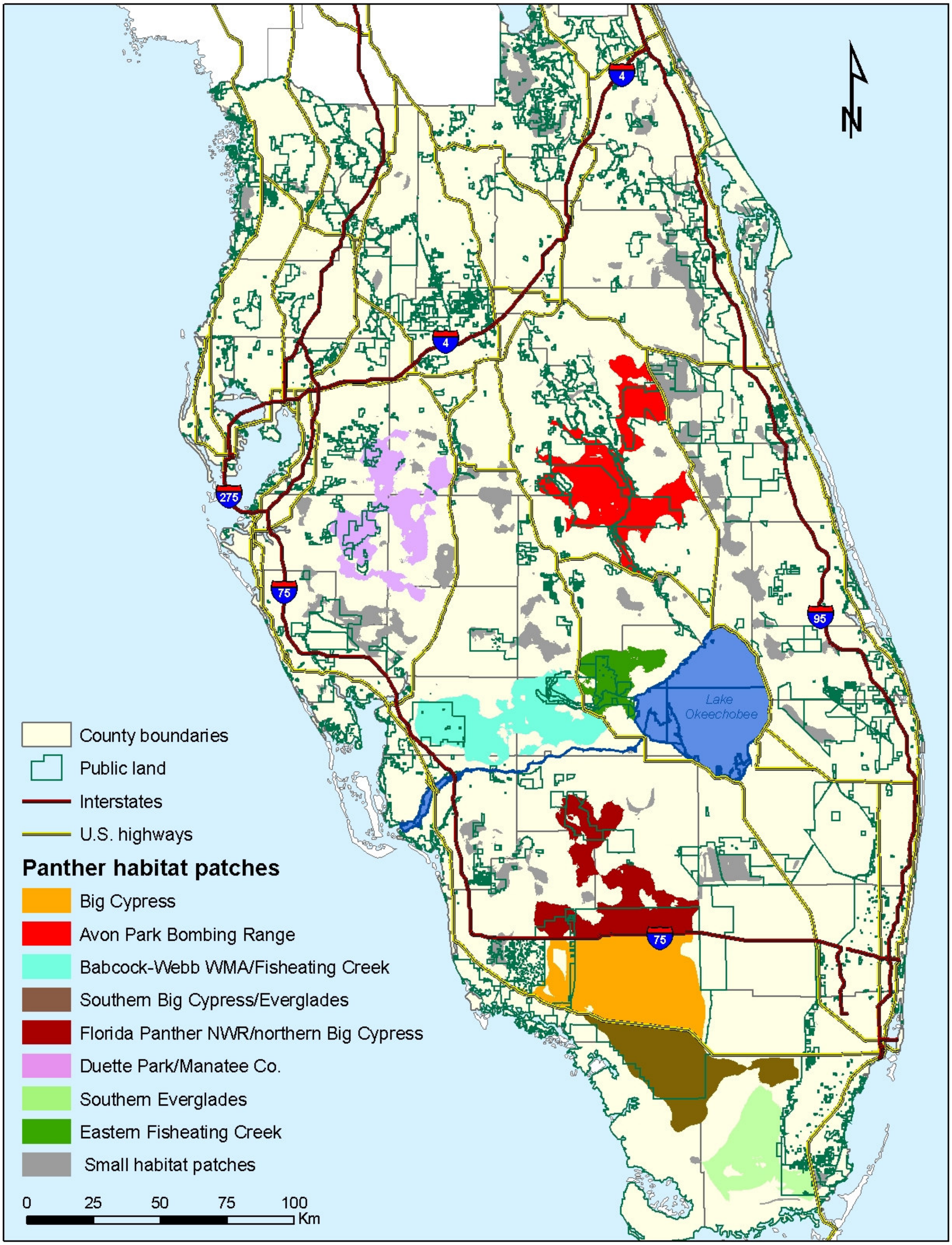

Figure 9. Potential translocation sites for the Florida panther in south Florida based on 2003 landscape data, with a minimum size of 427 km^2.

Table 4. Patches of Florida panther habitat with an area >427 km^2 based on the 2003 habitat model results.

Patch label	Patch name	Area of patch (km^2)	Within current range?
F	Big Cypress National Preserve	1,759	Yes
A	Avon Park Bombing Range	1,558	No
D	Babcock-Webb Wildlife Management Area / western Fisheating Creek	1,289	No
G	Southern Big Cypress National Preserve	1,228	Yes
E	Okaloacoochee Slough / Florida Panther National Wildlife Refuge / northern Big Cypress National Preserve	1,226	Yes
B	Duette Park / Manatee County	1,062	No
H	Southern Everglades	807	Yes
C	Eastern Fisheating Creek	478	No

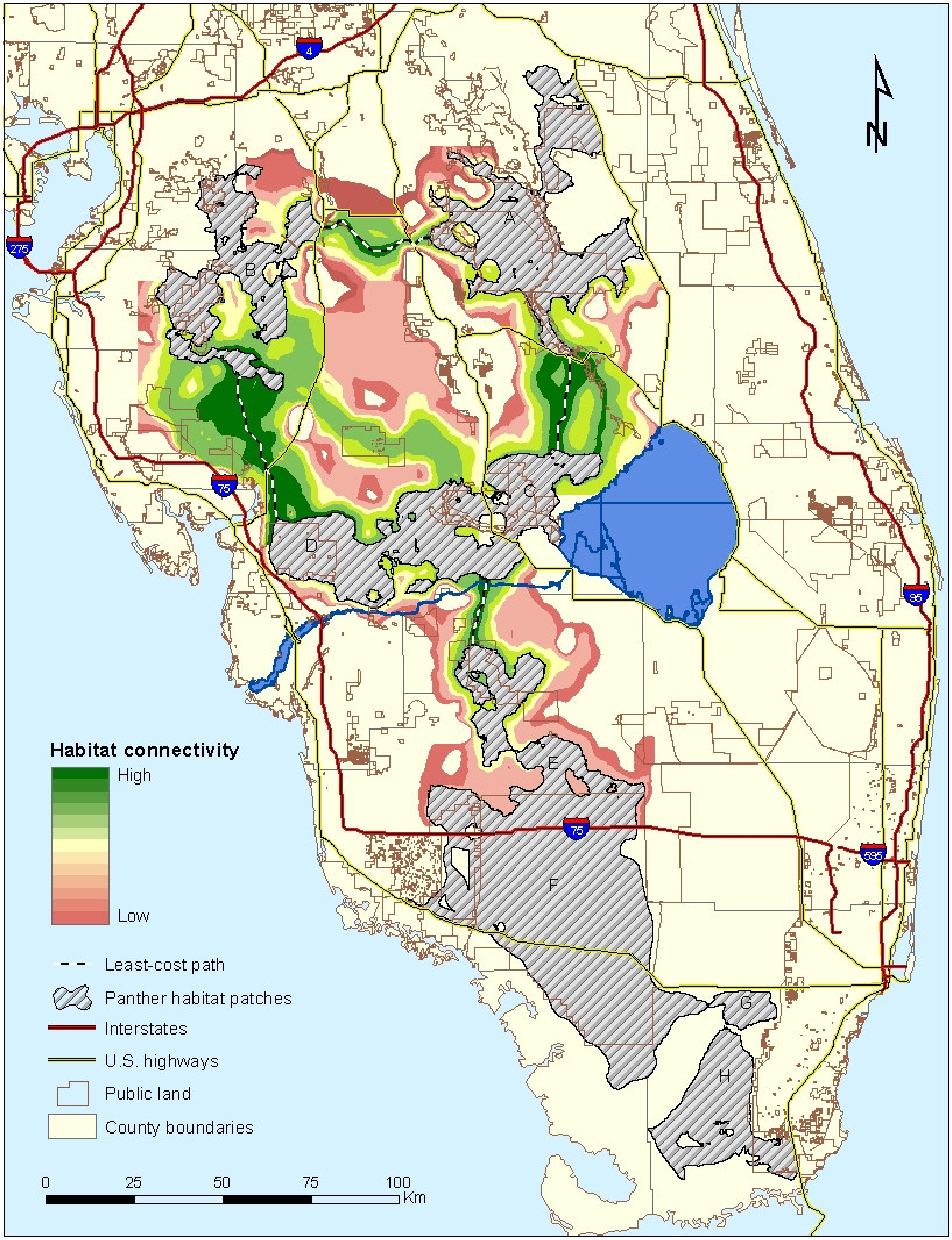

Figure 10. Habitat connectivity based on a least-cost-path analysis among potential Florida panther translocation areas in south Florida, 2003. Labels A–H are described in Table 4.

agriculture and forest to the east of the town of Goodno and to the west of Port La Belle. This corridor was also identified by other researchers (Meegan and Maehr 2002, Kautz et al. 2006) and was used by at least some of the radiocollared male panthers who crossed the Caloosahatchee River.

The relative cost distance for a panther to travel between Okaloacoochee Slough and Fisheating Creek was much lower than the relative cost to travel between other habitat patches north of the Caloosahatchee because this was the only habitat connection we examined that did not require crossing a major highway. Traversing major highways to move between habitat patches incurred a very large "cost" because of the strong negative impact that the major roads variable had on the results of the habitat model.

The shortest habitat connection between Okaloacoochee Slough and Fisheating Creek was 19.8 km in length and crossed through small patches of pine and hardwood forests interspersed between large areas of citrus groves and pasture. The habitat linkage between the Avon Park Bombing Range region and the Duette Park/Manatee County region was 39.3 km and required traversing patches of hardwood swamp, wet prairie, and citrus groves and crossing U.S. Highways 17 and 27. The 28.3-km long habitat connection between the Avon Park Bombing Range and eastern Fisheating Creek traversed citrus groves, pastures, and wet prairies. The linkage between the Duette Park/Manatee County region and the Babcock-Webb WMA/Fisheating Creek area was 44.9 km in length. That route traversed a variety of land-cover types, including pastures, prairies, hardwood swamps, and bottomland hardwood forests associated with Horse Creek and Peace River in DeSoto County.

DISCUSSION

Major highways had a strong effect on the model results, suggesting that they may act as substantial impediments to panther movement. The *P*-value from the cumulative frequency plot (Fig. 7) that maximized the separation of the 2 curves had a Type I error (predicting lack of panther habitat when habitat actually exists) rate of zero and a low (12.9%) Type II error rate (falsely predicting existence of panther habitat). Consequently, all panther home ranges had a mean *P*-value above the cutoff (i.e., all home ranges were correctly classified as panther habitat). Overall, the model clearly distinguished between habitat typical of panther home ranges and areas not used by panthers.

We produced models for 2 time periods only because we needed to maintain concurrency with the time period of the telemetry data and, at the same time, produce a model that represented current conditions in the study area. Our goal was not to document detailed habitat changes over time because of differences in data collection methods between the 2 time periods. Based on comparisons with 1-m aerial photos, the 2003 land-cover data probably were more accurate, perhaps because of advances in remote sensing techniques. A qualitative comparison between the 2 time periods, however, confirms the comments of Kautz et al. (2006) that some panther habitat loss has occurred because of urbanization, particularly in the western portion of the range.

Because of their strong influence on the model, major highways were the primary reason for fragmentation of otherwise large and contiguous habitat patches. This seems to be an accurate reflection of the way Florida panthers respond to their environment. Radiotelemetry data indicate that females were reluctant to cross major highways. Only 7 out of 32 females in our sample (1988–1998) ever crossed a major highway. In fact, major highways often formed the boundaries of both male and female home ranges.

In addition to the antrhopogenic influence from road variables, the influence of the human population density variable was especially apparent on both coasts and along the Interstate 4 corridor. The percent flooded/semi-permanently flooded variable enabled the habitat model to distinguish between the inundated Water Conservation Areas and other parts of the current panther range that have similar vegetation cover but are less often flooded and are thus more suitable for panthers. Finally, the percent natural land cover variable indicated that the contiguity of natural land cover is much lower north of the Caloosahatchee River compared to south Florida. This difference is reflected in the habitat model results, in which there are few habitat patches north of the Caloosahatchee that are sufficiently large enough to support Florida panthers.

North of the Caloosahatchee River, road densities generally are greater and major highways more common than in south Florida. The presence of major highways impedes panther movements among patches, particularly for females, and exposes dispersing panthers to increased risk of mortality due to vehicle collisions. Habitat patches north of the Caloosahatchee River are smaller and more isolated compared with the current Florida panther range. The amount of public land north of the Caloosahatchee River is much less compared with the current breeding range, although most of the largest habitat patches remain centered on public lands.

To estimate minimum patch size, it was necessary to use a cutoff value to discriminate between habitat and non-habitat. However, the D^2 values in our model represent a continuum and absolute cutoff values are an oversimplification of the method. Cutoff values higher or lower than the value we chose may be more appropriate depending on the management objectives and associated risks. With that in mind, the Okaloacoochee Slough area was the smallest patch occupied by a female panther (427 km^2), so we used it as the minimum criterion for consideration as a potential translocation site. However, this is an absolute minimum and larger areas likely would be needed for potential translocation sites. We identified 4 potential translocation sites using the habitat model results: the Avon Park Bombing Range area, Fisheating Creek/Babcock-Webb Wildlife Management Area, eastern Fisheating Creek, and the Duette Park/Manatee County area. Other sites may have been identified had other cutoff criteria been used. We discuss positive and negative aspects of each potential translocation site.

With an area of 1,558 km^2, the Avon Park Bombing Range region is the largest potential translocation site. It incorporates a large amount of public land (approximately 1,000 km^2) including Avon Park Bombing Range, Kissimmee Prairie Preserve State Park, Three Lakes Wildlife Management Area, and Lake Wales Ridge State Forest. The potential translocation site is separated only by U.S. Highway 441 from other relatively large habitat patches that are mainly on public land (i.e., Bull Creek Wildlife Management Area and Triple N Ranch Wildlife Management Area). The Avon Park Bombing Range region is characterized by large contiguous areas of natural land cover, mainly consisting of pine and oak forests, gallberry (*Ilex* spp.) and saw palmetto shrublands, and dry prairies. The drawback of this site is that it is far from the current Florida panther range, reducing the probability that panthers would disperse between the two areas. The presence of major highways to the east (US 441), west (US 27), and south (US 98) also increases the isolation of this site from other habitat patches in the region.

The Duette Park/Manatee County region is 1,062 km^2 in size and extends into Hardee, Polk, and Hillsborough Counties. In addition to the 82-km^2 Duette Park, the potential translocation site includes Alafia River State Forest and several other small public land parcels. A variety of land-cover types are represented, including oak hammocks, pine forests and plantations, bottomland hardwood forests along the Alafia and Manatee rivers, freshwater marshes, and some areas of pasture and citrus groves. Disadvantages of this site are its distance from the current range of the Florida panther and its isolation caused by large areas of agriculture that surround the site, U.S. Highway 17, and rapidly growing metropolitan areas such as Lakeland, Tampa, and Sarasota. The least-cost-path analysis indicated that the habitat connections to other patches were much longer (39.3 km and 44.9 km) than those required to travel between the other potential translocation sites. In addition, the Duette Park/Manatee County region has the highest road and human densities of the 4 potential translocation sites.

The Fisheating Creek/Babcock-Webb Wildlife Management Area region is relatively large with an area of 1,289 km^2. It is separated from the eastern Fisheating Creek site (478 km^2) only by U.S. Highway 27 so we discuss the two together. Several collared and uncollared male Florida panthers have been documented in the Fisheating Creek area in recent years, and the last female seen north of the Caloosahatchee River was found there as well (McBride 2002). Currently, Florida panther #130 incorporates portions of the Fisheating Creek area into his home range, suggesting that the area can support Florida panthers. Dominant land-cover types in the 2 potential translocation sites include pine forests, cypress swamps, freshwater marshes, gallberry and saw palmetto marshes, and pasture. According to the least-cost-path analysis, the shortest habitat connection between Fisheating Creek and Okaloacoochee Slough (at the northern portion of the current range) is 19.8 km, a dispersal distance that has been documented for both male and female panthers (Maehr et al. 2002). However, the extensive agricultural lands (citrus, sugarcane, and pasture) and urban areas near Port La Belle and LeHigh Acres could act as impediments to movement. An additional drawback to these 2 sites is that they mainly consist of private lands; only 272 km^2 of the Babcock-Webb Wildlife Management Area and 291 km^2 of Fisheating Creek are protected by conservation easements.

Connectivity between patches is an important consideration because most of the patches north of the Caloosahatchee are relatively small. Habitat connectivity provides outlets for dispersing animals and promotes genetic diversity among panthers, thereby increasing panther population viability (Kautz et al. 2006, Maehr et al. 2002). The least-cost-path analyses identified potential habitat linkages that could play an important role in maintaining a metapopulation (Hanski 1999) if Florida panthers were translocated north of the Caloosahatchee River. The analysis also highlighted the extreme isolation of panther habitat in portions of the study area, particularly those north of Interstate 4. That isolation is caused by the combined effects of Interstate highways and highly urbanized areas such as Orlando and Tampa.

MANAGEMENT IMPLICATIONS

An important consideration is whether there is sufficient panther habitat north of the Caloosahatchee River to support a viable Florida panther population in the long term. The landscape matrix within which the largest habitat patches exist provides relatively poor habitat connectivity among the patches. However, as habitat generalists, other *Puma* subspecies (i.e., mountain lions in southern California) have shown that they can thrive even in highly anthropogenic landscapes as long as sufficient prey are available. Our habitat model identified 4 regions in the study area north of the Caloosahatchee River that provide favorable habitat conditions for Florida panthers. Using a recent density estimate for panthers in south Florida as a reference (Kautz et al. 2006; 1 panther/129 km^2), we estimate that the Avon Park Bombing Range region and the Babcock-Webb Wildlife Management Area/western Fisheating Creek region may support the most panthers (approximately 10–12 each). The Duette Park/Manatee County region may support 8 panthers and the Eastern Fisheating Creek area may support 4 panthers. Of course, panther densities in the potential translocation sites may be higher or lower than those in south Florida depending on local variation among important habitat factors such as prey density and understory cover.

Telemetry data suggest that most panthers, particularly females, do not explore areas north of Okaloacoochee Slough far enough to reach the Caloosahatchee River. It is unlikely that the river itself impedes northward movements, but rather the lack of natural land cover in the landscape south of the river due to agricultural and urban land use (Maehr et al. 2002, McBride 2002). Future exchange between any translocated populations and the current range of the Florida panther would be facilitated by improved habitat connectivity across the Caloosahatchee River between Okaloacoochee Slough and Fisheating Creek. Because such restoration would require substantial time and effort, the primary goal of improving habitat connectivity would not be to facilitate dispersal and colonization of areas north of the

Caloosahatchee River in the short term but to enhance population exchange once female panthers have been reestablished there. Given the limited dispersal rates of female panthers, it is likely that human intervention will be required to establish females north of the Caloosahatchee.

Our analysis highlighted the negative impact of major highways on Florida panther habitat. The current breeding range in south Florida contains the largest roadless areas within the historic range of the species (Thatcher et al. 2003). Yet, vehicular collisions continue to be one of the leading causes of Florida panther mortality (USFWS 2006). Road densities generally are greater north of the Caloosahatchee River and several of the potential translocation sites we identified were separated from other habitat areas by major highways. Thus, the potential demographic impacts of mortalities due to vehicle collisions would need to be considered. Mitigation of those impacts (e.g., reduced speed limits, wildlife underpasses) likely would enhance survival of translocated panthers.

The Mahalanobis distance model formed the basis of our statistical assessment of landscape conditions for Florida panthers in south Florida. However, some important variables, such as vegetation structure and prey density, could not be included because spatial data were not available. For example, understory vegetation such as saw palmetto could not be measured but provides an important habitat component (i.e., stalking cover, den sites). Availability of deer and feral hogs (*Sus scrofa*) as prey is an important consideration but local densities can vary substantially. Therefore, we recommend that the results of our study are augmented with information from field surveys of the potential translocation sites. Finally, the success of any Florida panther translocations also would be influenced by public attitudes (Belden and Hagedorn 1993) and should be considered in combination with the biological factors we examined.

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