Research Article

Identifying Suitable Sites for Florida Panther Reintroduction

CINDY A. THATCHER, *University of Tennessee, Department of Forestry, Wildlife and Fisheries, Knoxville, TN 37996, USA*

FRANK T. VAN MANEN,[1] *United States Geological Survey, Southern Appalachian Research Branch, University of Tennessee, Department of Forestry, Wildlife and Fisheries, Knoxville, TN 37996, USA*

JOSEPH D. CLARK, *Untied States Geological Survey, Southern Appalachian Research Branch, University of Tennessee, Department of Forestry, Wildlife and Fisheries, Knoxville, TN 37996, USA*

Abstract

*A major objective of the 1995 Florida Panther (*Puma concolor coryi*) Recovery Plan is the establishment of 2 additional panther populations within the historic range. Our goal was to identify prospective sites for Florida panther reintroduction within the historic range based on quantitative landscape assessments. First, we delineated 86 panther home ranges using telemetry data collected from 1981 to 2001 in south Florida to develop a Mahalanobis distance (*D^2*) habitat model, using 4 anthropogenic variables and 3 landscape variables mapped at a 500-m resolution. From that analysis, we identified 9 potential reintroduction sites of sufficient size to support a panther population. We then developed a similar* D^2 *model at a higher spatial resolution to quantify the area of favorable panther habitat at each site. To address potential for the population to expand, we calculated the amount of favorable habitat adjacent to each prospective reintroduction site within a range of dispersal distances of female panthers. We then added those totals to the contiguous patches to estimate the total amount of effective panther habitat at each site. Finally, we developed an expert-assisted model to rank and incorporate potentially important habitat variables that were not appropriate for our empirical analysis (e.g., area of public lands, livestock density). Anthropogenic factors heavily influenced both the landscape and the expert-assisted models. Of the 9 areas we identified, the Okefenokee National Wildlife Refuge, Ozark National Forest, and Felsenthal National Wildlife Refuge regions had the highest combination of effective habitat area and expert opinion scores. Sensitivity analyses indicated that variability among key model parameters did not affect the high ranking of those sites. Those sites should be considered as starting points for the field evaluation of potential reintroduction sites.* (JOURNAL OF WILDLIFE MANAGEMENT 70(3):752–763; 2006)

Key words

Florida panther, habitat models, Puma concolor, *radiotelemetry, reintroduction, south Florida, southeastern United States.*

The Florida panther (*Puma concolor coryi*) is one of the most imperiled mammals in the United States, having been federally listed as endangered since 1967 (Endangered Species Preservation Act of 1967 and Endangered Species Act of 1973). Habitat loss and fragmentation are severe threats to the panther in Florida (Kautz 1994), resulting in limited potential for natural population expansion. Movement impediments, such as the Caloosahatchee River and urban areas, inhibit natural dispersal north to other portions of the historic range, particularly for females (Maehr et al. 2002). The Florida Panther Recovery Plan lists the reestablishment of 2 additional panther populations within other portions of the historic range as a major objective (U.S. Fish and Wildlife Service 1995). That recovery goal can only be accomplished by reintroducing panthers to currently unoccupied areas.

Habitat conditions in the southeastern United States have dramatically changed since the Florida panther was first listed as an endangered species. A number of factors have substantially improved prospects for panther reintroduction, including the purchase and protection of large tracts of public land, the large-scale recovery of forest habitats after extensive logging at the turn of the previous century, the increase in populations of prey species such as white-tailed deer (*Odocoileus virginianus*), changes in human attitudes towards wildlife conservation, and the legal protection afforded by the Endangered Species Act. The Florida Panther Recovery Team has recognized habitat assessment to identify potential reintroduction sites as an important step toward panther recovery (U.S. Fish and Wildlife Service, unpublished report). Such an assessment, however, should be objective, biologically driven, data-based, and defensible.

Reintroduction of large carnivores has been the subject of much renewed interest (Clark et al. 2002). Reintroduction is a costly and time-consuming endeavor; however, only about 11% of all species reintroductions result in viable populations (Earnhardt 1999). In general, reintroduction success is enhanced if a large number of founders are used, there is low environmental variation, and the released animals have access to refugia. Success is also greater for species with high genetic variability, a high and steady rate of population increase, and low intraspecific competition (Griffith et al. 1989). Panthers rate low for almost all those criteria. Also, because the sociopolitical issues regarding the reestablishment of an extirpated, large carnivore may be more daunting than the biological issues (Clark et al. 2002), panther reintroduction presents many challenges.

Because of the biological and sociological complexities of panther reintroduction, it is critical that the best possible sites and release methods are used. Beginning in 1988, the feasibility of panther reintroduction was evaluated by Belden and Hagedorn (1993) and Belden and McCown (1996) by releasing mountain lions (*P. concolor stanleyana*) from western Texas into northern Florida. Those experiments suggested that the successful restoration of Florida panther populations will largely depend on the selection of appropriate reintroduction sites. Jordan (1994) evaluated 14 potential reintroduction sites in the southeastern United States based on biological and anthropogenic criteria but

[1] *E-mail: vanmanen@utk.edu*

indicated that additional analyses would be needed once more definitive data became available. In recent years, the availability of Geographic Information System (GIS) tools and detailed digital map layers have dramatically increased, as have advances in landscape characterizations and habitat-use analyses (Scott et al. 2002). Those developments, combined with an extensive database of panther locations from south Florida (1981–2001), formed the basis for our quantitative analysis of the landscape and habitat characteristics needed to support viable panther populations in the southeastern United States. Our overall research hypothesis was that some sites within the historic range of the Florida panther provide more suitable habitat conditions for panther reintroduction than others and that those differences could be discerned from generalized landscape and habitat characteristics associated with panther radiolocations from south Florida. To test that hypothesis, we identified and compared prospective reintroduction sites within the historic range by integrating 1) a multiscale, quantitative analysis of the landscape characteristics of home ranges of radio-collared panthers in southern Florida; 2) an assessment of colonization potential of areas adjacent to prospective panther reintroduction sites; and 3) an expert-assisted analysis of habitat factors that could affect reintroduction success. Finally, we tested the hypothesis that our choice of parameter estimates, and error in those estimates, would not alter our overall findings. To accomplish that, we performed a sensitivity analysis of critical input parameters.

Study Area

Our 1,128,000-km^2 study area was the entire historic range of the Florida panther, which included most of the southeastern United States, from Arkansas and Louisiana east to North Carolina and south to the tip of the Florida peninsula (Hall 1981). The historic range was within the humid temperate and humid tropical domains, and it included the following physiographic provinces: Central Appalachian Forest, Eastern Broadleaf Forest, Everglades, Lower Mississippi Riverine Forest, Ouachita Mountains, Ozark Mountains, Outer Coastal Plain Mixed Forest, and Southeastern Mixed Forest provinces (Bailey 1980). Approximately 24% of the study area was composed of agricultural land-cover types, 3% was urban, 8% was open water, and the remaining 65% of the study area consisted of natural land-cover types, including forest, shrublands, grasslands, and woody and herbaceous wetlands. Public lands comprised 9.7% of the study area. Based on U.S. Census 2000 data, 56.4 million people lived within the study area, with substantial spatial variation in human population density.

The current distribution of panthers in south Florida served as the reference area for our habitat analyses. South Florida is made up of a variety of natural, agricultural, and urban land-cover types and is characterized by flat topography and poorly drained soils, resulting in extensive wetlands. The climate of southern Florida is tropical, with a summer wet season and a winter dry season (Davis 1943). Large tracts of publicly owned land were located within the Florida panther's current distribution, including Big Cypress National Preserve, Everglades National Park, Florida Panther National Wildlife Refuge, and Fakahatchee Strand State Park (Fig. 1). Agriculture comprised approximately 9% of land-cover types within the current distribution of the Florida panther, 2% was urban, 2% was open water, and the remaining 87% consisted of natural land-cover types. In 2000, approximately 294,000 people lived within the Florida panther's current range, with 68% of the land in federal and state ownership.

Methods

Landscape-Scale Statistical Model

Telemetry data.—We obtained panther radiotelemetry locations collected by the Florida Fish and Wildlife Conservation Commission, the National Park Service, and the University of Tennessee. That database contained >60,000 locations of 113 panthers that were monitored approximately 3 times per week throughout the year from 1981 to June 2001 (Fig. 1). The database included 8 female Texas mountain lions introduced to south Florida in 1995 and their subsequent progeny. Although these animals originated from areas with different ecological conditions and were released into a population with an existing social structure, they established home ranges and survived, so we included those cats in our analysis. We excluded panthers that were <1.5 years of age because of probable movement and activity biases (Janis and Clark 2002). Sampling intensity varied among the 3 agencies, so we randomly selected 3 locations/panther/week. To reduce autocorrelation, we included no more than 1 location/panther/day (Janis and Clark 2002). Mean telemetry error was estimated to be 176 m, and 95% of the radiolocations were estimated to be within 489 m of the true location (Janis and Clark 2002).

Home-range analysis.—We used the fixed-kernel method to calculate a 95% probability contour for each panther (Worton 1989) using the Animal Movement extension (Hooge and Eichenlaub 1997) in ArcView® GIS (ESRI, Redlands, California). We chose this method because recent studies have demonstrated its relative lack of bias (Seaman et al. 1999). We selected the 95% home-range contour to adequately measure the overall area requirements of panthers for our analysis. Seaman et al. (1999) suggested ≥50 locations per animal to reduce bias in home-range estimates using the fixed-kernel method. Because our data set was large, we further limited our sample to panthers with ≥100 radiolocations to exclude individuals that were tracked for short periods (<6 months). Eighty-six panthers (39 M, 47 F) met our age and sample size requirements, with tracking periods ranging from 6.5 months to 12.5 years. For animals with multiple years of telemetry data, we calculated home ranges by pooling locations.

GIS data layers.—We generated GIS map layers, with a pixel size (resolution) of 500 × 500 m, to examine habitat conditions throughout the historic range of the Florida panther (Table 1). Because habitat and landscape conditions in south Florida differed markedly from those in the remainder of the historic range, we chose landscape variables for the habitat model that were applicable rangewide. For example, south Florida contains large tracts of emergent herbaceous vegetation that are not as common in other portions of the southeastern United States. Had we developed a habitat model with that cover-type classification as the frame of reference, we likely would have classified almost all of the remainder of the historic panther range as unfavorable panther habitat because of the relative scarcity of wetlands outside south

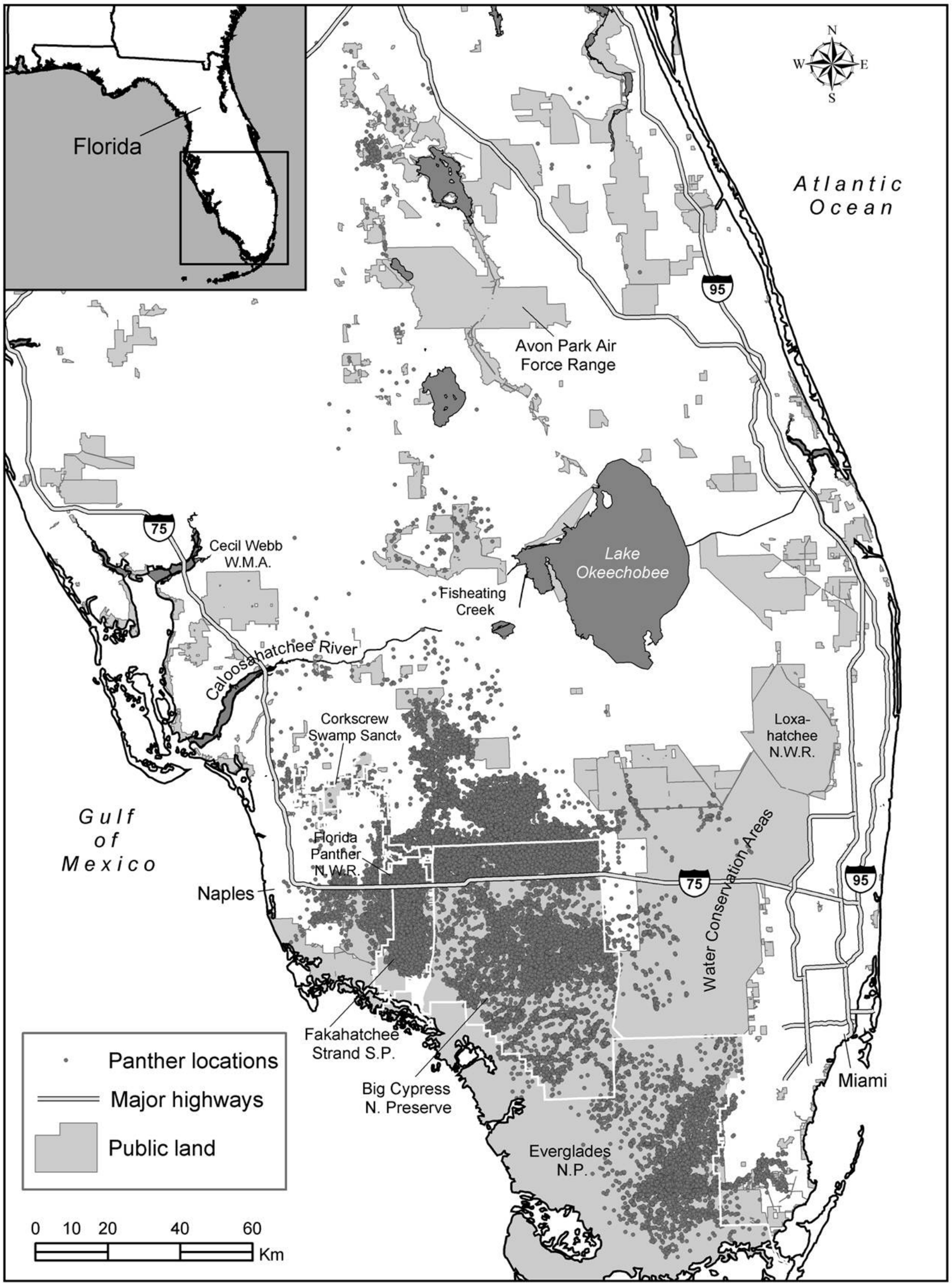

Figure 1. Distribution of Florida panther telemetry locations, south Fla., USA, 1981–2001.

Florida. To avoid that bias, we aggregated land-cover classes from 1992 National Land Cover Data (Vogelmann et al. 2001) into a binary map of natural land cover versus all remaining land-cover types. For that binary classification, natural land cover included deciduous forest, mixed forest, evergreen forest, woody wetlands, emergent (roots below water) herbaceous wetlands, shrublands, and grasslands. Urban areas, agricultural areas, and water constituted the other binary class. We note that the various land-cover types included in the natural land-cover class likely are not equally important to panthers but simply represent the broad spectrum of land-cover types associated with panther use.

We selected 7 variables for our final habitat model based on their biological importance, uniqueness, and spatial compatibility between south Florida and the historic range. We calculated 3 landscape metrics with Program FRAGSTATS 3.1 (McGarigal and Marks 1995) based on our classification of natural land cover: 1) percentage of natural land cover, calculated as the proportion of natural land-cover patches within an area; 2) contagion, which quantified the spatial aggregation of natural land-cover patches; and 3) patch density, whereby higher patch density indicated an increase in fragmentation of natural land cover (McGarigal and Marks 1995, Riitters et al. 2000). We measured anthropogenic influences on the landscape with the other 4 variables: 4) human population density, 5) minor road density, 6) major road density, and 7) percentage of urban land cover. We calculated human population density from block group-level census data by dividing the population within each block group by its area (U.S. Census Bureau 2002). Roads sometimes serve as barriers to panther movements, result in panther mortalities from vehicular collisions (Maehr and Cox 1995), and reflect human influence on the landscape. However, panthers may respond differently to different road types. Therefore, we separated major and minor roads as different variables. We calculated road density as the total length of roads within a specified area. Major roads were restricted to interstate highways, U.S. highways, and state highways (U.S. Geological Survey 1999), whereas minor roads represented all other roads, including unimproved roads (U.S. Census Bureau 2002). The final anthropogenic variable was percentage of urban land cover, meant to characterize the importance of minimizing panther–human interactions (Belden and Hagedorn 1993).

Habitat selection of large carnivores likely is influenced by landscape features at the home-range scale or greater (Carroll et al. 1999). Therefore, we examined multiple measurement scales by calculating habitat variables using circular moving windows equal in area to the average home-range sizes of female and male panthers, respectively (Kerkhoff et al. 2000). To determine which measurement scale was most appropriate for our analysis, we calculated the coefficient of variation for the 7 variables at both scales by sampling pixels in the 86 panther home ranges. For each variable, we chose the measurement scale with the lowest coefficient of variation because it represented a more precise relationship between panther home-range placement and habitat attributes (Pereira and Itami 1991).

Mahalanobis distance (D^2) analysis.—We used the Mahalanobis distance (D^2) statistic for our analysis because only presence data are used, and available habitat need not be estimated (Clark et al. 1993, Alldredge et al. 1998, Farber and Kadmon 2003). Additionally, variables can be correlated and the assumption of multivariate normality does not have to be met (Knick and Rotenberry 1998). We calculated the D^2 statistic in ArcGIS™ 8.2 (ESRI) on a pixel-by-pixel basis for the entire historic range of the subspecies (Clark et al. 1993). We estimated means, variances, and covariances of the 7 habitat variables within home ranges of panthers instead of using individual radiolocations as our sampling unit, which could be biased by time of day and telemetry error. We then used those target values to calculate D^2 for all pixels within the historic range. In the resulting D^2 map, pixels with low D^2 scores were similar in the measured characteristics associated with panther home ranges in south Florida, whereas pixels with larger values represented dissimilar conditions. We use the terms favorable and unfavorable to describe the similarity or dissimilarity with panther habitat in south Florida.

Although the D^2 map represented a continuum of site conditions, we used a threshold value to delineate and compare potential reintroduction sites. We identified an appropriate threshold D^2 score by optimizing the trade-off between correctly classifying the habitat of panther home ranges on the landscape while also providing the most specific geographic delineation of favorable habitat in the study area. For the range of D^2 scores, we first graphed the percent cumulative frequency of panthers for which the average D^2 score of the home range was less than the examined score (Pereira and Itami 1991). For the same range of D^2 scores, we also graphed the cumulative frequency of 86 random home ranges (47 F, 39 M) within the study area (null model). We then identified the D^2 score within which the greatest difference between the 2 cumulative frequency distributions occurred. We chose this threshold score to depict areas in the Southeast with habitat features that were similar to those used by panthers in south Florida.

We used 10-fold cross-validation to quantitatively test the reliability of the model and to identify those panther home ranges that did not fit the model well. We defined reliability as the fraction of model predictions that correctly classified an area as favorable for a panther home range. In this resampling procedure, we partitioned the panther home-range data set into 10 random subsamples. We calculated the D^2 model with 9 subsamples and tested them with the excluded subsample. We repeated that process until each subset had been excluded once. We then determined model reliability by calculating the proportion of correctly classified panther home ranges (mean D^2 of pixels in home range below the D^2-threshold score) for all 10 D^2 models (Verbyla and Litvaitis 1989).

Finally, we delineated contiguous areas of favorable habitat in the study area. We only considered pixels with D^2 scores below the threshold value that shared $\geq$1 entire edge with a pixel of similar value. Belden and Hagedorn (1993) suggested that 2,590 km^2 was the minimum area requirement for panther reintroduction sites. For further analysis, we only considered favorable habitat patches that met those criteria.

Local-Scale Statistical Model

A single spatial scale may be inadequate to examine the associations of landscape structure and Florida panther habitat use because important local-scale conditions may not be detected at a 500-m resolution. Therefore, we also calculated D^2 at 90-m resolution within potential reintroduction sites to characterize local-scale conditions. We also reduced the radius of the moving windows to 3,000 m (28.3-km^2 area), which approximately corresponded to the mean daily movement rate of male and female panthers (Janis and Clark 2002). Panther home ranges were again used as the sampling unit for estimating means, variances, and covariances of the 7 habitat variables. For each of the prospective reintroduction sites, we then recalculated the area composed of favorable habitat. We hypothesized that the local-scale analysis examined resource use at approximately a daily-movement scale, whereas the landscape model reflected resource use at the home-range scale.

Potential for Population Expansion

It is important to verify areas of favorable panther habitat adjacent to prospective reintroduction sites that may be colonized after reintroduction. Therefore, for each prospective reintroduction site, we calculated the area of favorable habitat (500-m resolution) within a range of dispersal distances of female panthers. We only considered dispersal distances for females because colonization of adjacent habitat areas requires female residency and reproduction. Maehr et al. (2002) reported dispersal distances of female panthers ranging from 6.2 to 32.3 km, with a mean of 20.3 km ($n = 9$). With increasing distance, the probability of successful dispersal declines. Therefore, we weighted the area calculations for each distance by estimating the relative dispersal probability based on the reported minimum, maximum, and mean dispersal distances. Favorable habitat within the minimum dispersal distance received a weight of 1.0 (all panthers dispersed $\geq$ this distance), areas beyond that distance but within the mean dispersal distance received a weight of 0.5, and all other areas within the maximum dispersal distance received a weight of 0.11 (1 of 9 panthers dispersed $>$ this distance; Maehr et al. 2002). The area of adjacent habitats was then multiplied by those weights and summed for each prospective reintroduction site.

Expert-Assisted Landscape Model

Analytic Hierarchy Process

We developed an expert-assisted model to evaluate variables for which south Florida was not a good reference site and, thus, were not appropriate for the empirical D^2 model. We developed variables for the expert-assisted model by consulting a small group of Florida panther experts, and the variables reflected the practical concerns of identifying reintroduction sites with a low likelihood of panther–human conflicts and low levels of human disturbance. We used a pairwise comparison technique (Analytic Hierarchy Process) developed by Saaty (1980), whereby experts rank the relative importance of each variable in a pair using a continuous scale.

We obtained or developed quantitative data for each variable and represented each as a spatial map layer, using the same resolution as the statistical landscape-scale model (500 m). We based variables on county-level data, or we averaged them using a moving-window analysis representing an area of 2,590 km^2 (minimum size for a panther reintroduction site; Belden and Hagedorn 1993).

Based on results of a pilot study, our survey incorporated questions related to 3 variables. The availability of public lands (variable 1) may affect the number of human–panther conflicts and, thus, may influence the success of panther reintroduction. That variable was not appropriate for our statistical analysis because large tracts of public lands are more prevalent in the area where panthers occur compared with other portions of the Southeast. The basis for this variable was a map of public lands (including national forests, national parks, national wildlife refuges, state parks, wildlife management areas, military bases, and other public lands).

We developed a livestock-depredation variable (variable 2) to address the extent that livestock depredation may influence the success of panther reintroduction. We could not use this variable for the statistical analysis because it is unlikely that panther distribution in south Florida is influenced by livestock-depredation conflicts. We obtained information on the density of cattle by county (1997 data) from the National Agricultural Statistics Service (U.S. Department of Agriculture 2003) to represent livestock density. No information was available on goat or sheep densities in the southeastern United States.

Finally, we measured human population growth (variable 3) from 1990 to 2000 (U.S. Census Bureau 2002) as an indicator of where future population growth (or decline) is likely to occur, which may impact panther restoration efforts. That measure was different from the human population density variable used in the statistical model. Because human growth rate and livestock density may have a negative association with the suitability of panther reintroduction sites, we calculated the inverse of these variables so that greater values indicated more favorable areas (Eastman et al. 1995). We standardized all variables using linear scaling ([$\text{Value}_{max} - \text{Value}_{min}/\text{Value}_{max}$] $\times$ 100; Eastman et al. 1995).

Expert Survey

In May 2003, we sent a survey to 50 experts, including the Florida Panther Recovery Team and additional *P. concolor* experts from the western United States. We averaged survey responses from individuals because it was logistically more feasible, it weighted the opinion of each expert equally, and it tended to reduce the influence of extreme values, thus improving the consistency of the pairwise comparisons (Schmoldt and Peterson 2000). We requested that each participant select the variable (as previously defined) deemed to be more important in each of 3 pairwise comparisons and rank how important the selected variable was, compared with the other, on a scale of 1 (equally important) to 9 (extremely more important). We used a Web-based program (Web-HIPRE; Mustajoki and Hämäläinen 1999) to transform the pairwise comparisons into a matrix of ranks based on the Analytic Hierarchy Process model (Saaty 1980). We calculated those ranks by averaging the survey scores of all respondents for each pairwise comparison, and we represented the relative importance of each variable against another variable. For example, if variable 1 was ranked 5 times more important than variable 2, the respective entries in the matrix would be 5 and its reciprocal 1/5. To determine the degree of consistency among the experts in rating the pairwise comparisons, we calculated a consistency ratio based on Saaty (1980). A consistency ratio $\leq$0.1 is preferred. When relatively high consistency ratios are obtained, the pairwise comparisons should be reevaluated. From the matrix of pairwise ranks, we calculated the weight of each variable (0–1 scale) based on the principal eigenvector of the pairwise comparison matrix (Saaty 1980, Mustajoki and Hämäläinen 1999). Next, we used GIS to multiply each habitat variable by its weight as calculated from the pairwise comparisons. We then summed the weighted map layers, providing a single score (0–100 scale) for each pixel in the study area. Areas with greater values indicated greater expert-judged potential to support a panther population. Finally, we calculated the mean score and ranked each potential reintroduction site.

Model Integration and Sensitivity Analysis

To integrate our different analyses into a more interpretable form, we used the landscape-scale D^2 model to calculate the area of available, favorable habitat and added the weighted area of favorable habitat from the colonization-potential analysis. We then multiplied that total area by the percentage of pixels defined as favorable habitat based on the local-scale statistical-habitat model. The result was a calculation of the area of favorable

Table 1. Mean values of the habitat variables used in the Mahalanobis distance (D^2) model to evaluate potential sites for reintroduction of the Florida panther in the southeastern United States, 2003–2005. South Florida data are provided for reference purposes. Size of the analysis window was 765 km^2, except for natural land cover (245 km^2).

Site label	Site name	% natural land cover	Human density (no./km^2)	Major road density (km/km^2)	Minor road density (km/km^2)	Patch density	% urban land cover	Contagion
A	Ozark National Forest region	86.4	5.4	0.069	1.025	0.027	0.11	44.1
B	Ouachita National Forest region	86.9	4.5	0.073	1.048	0.031	0.20	47.0
C	Southwest Arkansas	90.8	6.6	0.075	1.160	0.013	0.59	55.5
D	Felsenthal National Wildlife Refuge region	88.8	9.6	0.072	1.159	0.018	0.64	50.7
E	Kisatchie National Forest region	89.8	7.2	0.080	1.196	0.017	0.50	52.3
F	Homochitto National Forest region	77.4	8.7	0.062	1.019	0.046	0.47	27.3
G	Southwest Alabama	88.7	7.0	0.061	1.023	0.011	0.23	50.2
H	Apalachicola National Forest region	92.4	4.7	0.068	1.037	0.012	0.37	59.2
I	Okefenokee National Wildlife Refuge region	93.3	4.0	0.058	0.895	0.009	0.32	63.6
	South Florida (current range)	90.2	3.1	0.038	0.333	0.022	0.59	62.1

panther habitat at each site, including adjacent habitat patches that potentially could be colonized by dispersing panthers (effective habitat area). Finally, we multiplied the effective habitat area by our expert-assisted model scores to assess the relative reintroduction potential of each site. Our assumption was that larger areas of suitable habitat combined with high expert model scores would correspond to greater success of panther reintroductions.

Biological systems are inherently variable. There are different methods for estimating the same parameter (e.g., home-range size). Choice of scale (e.g., resolution) can affect model performance, and we had to use judgments on certain criteria (e.g., minimum area for reintroduction site). Therefore, we considered whether changes in model parameters would result in different outcomes in our study. We performed a sensitivity analysis by recalculating the ranking scores of potential reintroduction sites after increasing or decreasing 4 key parameters by 20% and comparing the scores with those of the original model (Stoms et al. 1992). In so doing, we could determine whether our conclusions would be altered and which parameters were most sensitive, which is particularly important when management decisions could be controversial (Stoms et al. 1992).

First, we examined the change in the Mahalanobis distance model using measurement scales that were 20% smaller or larger than those based on the original model. This evaluated the effect that errors in estimating male or female home ranges would have on our model outcomes. For example, a variable measured with a 15.6-km-radius window was also measured using radii of 12.5 (20% smaller) and 18.7 km (20% larger). We repeated the same approach for the local-scale statistical model by using window sizes of 18.1 km^2 (–20%) and 40.7 km^2 (+20%) to calculate the habitat variables in addition to the original window size of 28.3 km^2.

Our next sensitivity analysis addressed the minimum area criterion based on the Belden and Hagedorn (1993) study. Clearly, their suggestion for a minimum area of 2,590 km^2 ($\approx$640,000 acres) necessary to support a viable population of panthers was not intended as a strict criterion. Therefore, we examined whether decreasing or increasing this criterion by 20% would result in a different delineation of potential reintroduction sites.

Lastly, we examined sensitivity of the colonization potential analysis. Although female dispersal >32.3 km has not been documented, Maehr et al. (2002) suggested that females occasionally may disperse farther, as has been documented for mountain lions in the western United States. Therefore, we examined dispersal distances that differed by ±20% from our 3 original estimates of dispersal distances based on Maehr et al. (2002).

Results

Landscape-Scale Statistical Model

Mean home-range size was 243.6 km^2 ($n = 47$, SD = 175.0, range = 5.4–806.0) for female panthers and 767.3 km^2 ($n = 39$, SD = 820.0, range = 28.4–4,682.3) for males. Based on those home-range sizes, we calculated habitat variables for the D^2 model using circular moving windows with radii of 8,800 m and 15,600 m, representing mean female and male home-range areas, respectively. Because of lower coefficients of variation, we measured all habitat variables using moving windows the size of male home ranges, except percentage of natural land cover, which was measured at the female home-range scale (Table 1).

We calculated D^2 for the study area based on multivariate similarities to the 86 panther home ranges in south Florida (Fig. 2). The cumulative frequency graph indicated that D^2 values $\leq$26 correctly classified the greatest percentage of panther home ranges (81.4% of home ranges) while being most specific for delineating favorable habitat in the southeastern United States (Fig. 3). Only 5.8% of randomly placed home ranges (null model) were located within favorable habitat (Fig. 3).

The 10 iterations of the cross-validation indicated the high accuracy of model predictions: on average, 79.8% of panther home ranges were correctly classified. That accuracy was consistent among the 10 iterations, ranging from 76.7% to 81.4%. The influence of outliers was small. The mean difference in D^2 values for individual panthers between the final and 10-fold validation models was 3.8. The greatest difference in D^2 (79.8) occurred for panther 85, a male whose home range extended near urban areas in southeastern Florida.

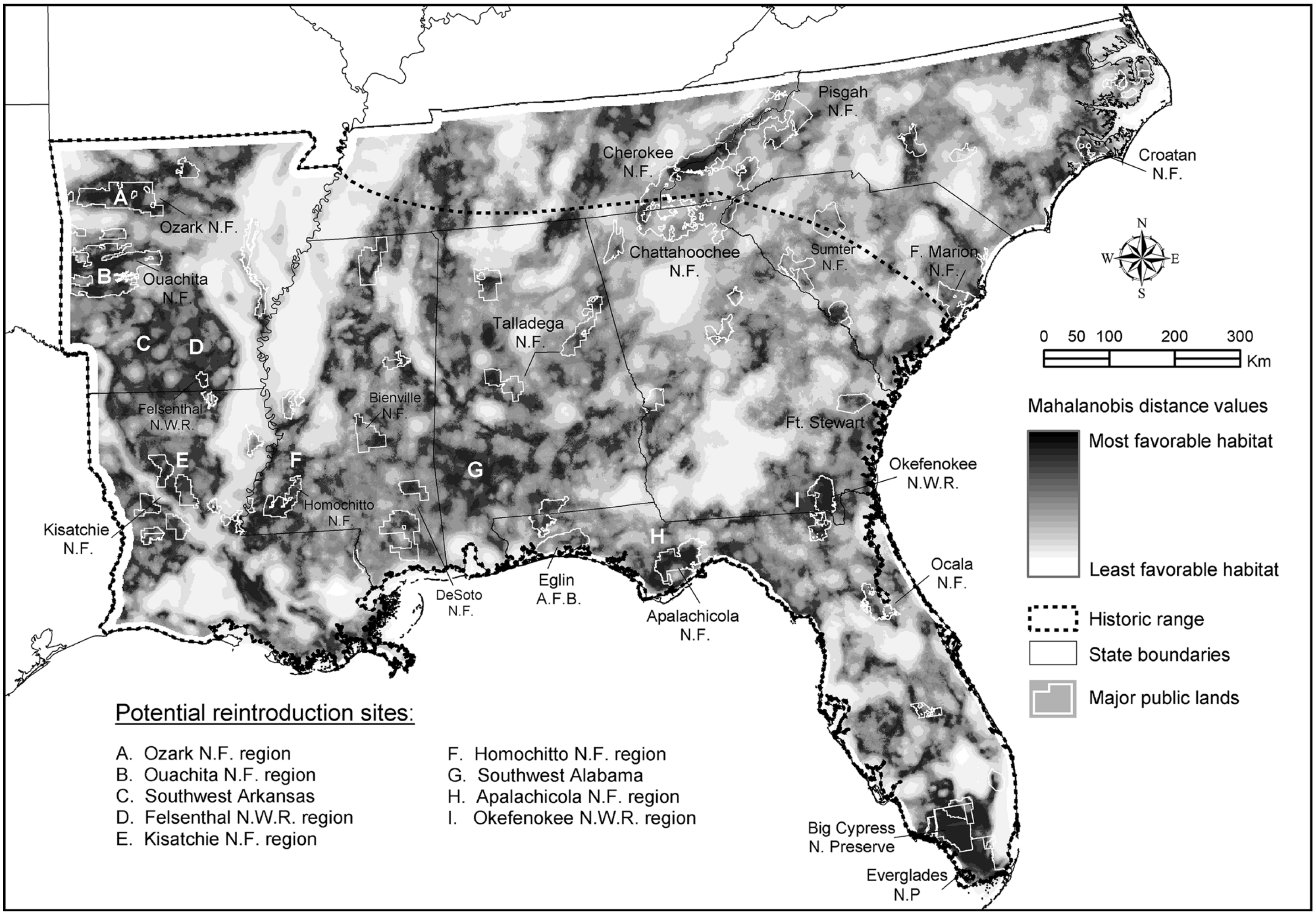

Figure 2. Mahalanobis distance (D^2) values used to identify potential sites for reintroduction of the Florida panther in the southeastern United States, 2003–2005.

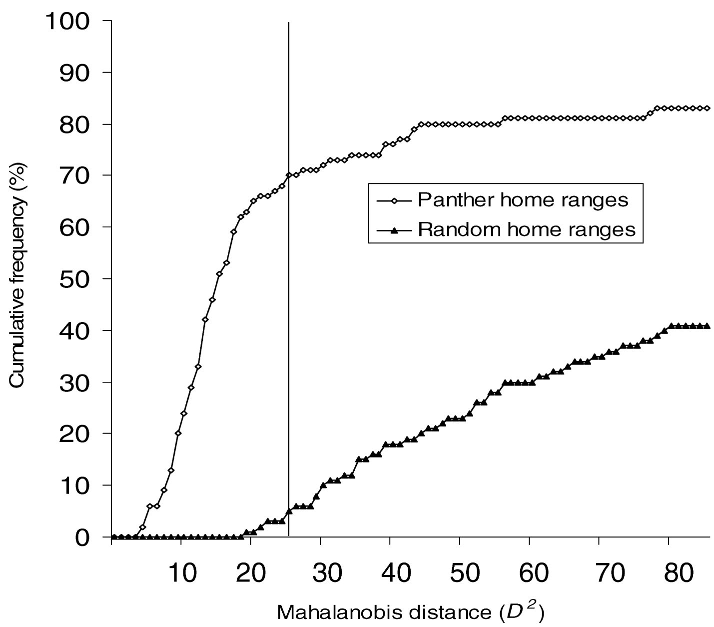

Figure 3. Percent cumulative frequency of Mahalanobis distance (D^2) values used to identify potential sites for reintroduction of the Florida panther in the southeastern United States, 2003–2005. The null model represents data from 86 random home ranges (47 F, 39 M) within the study area. Vertical line indicates threshold value of D^2 to define favorable habitat areas ($D^2 \leq 26$).

We identified 9 contiguous areas of favorable habitat ($D^2 \leq 26$; $>2,590$ km^2 in size) within the historic range: Ozark National Forest region, Ouachita National Forest region, southwest Arkansas, Felsenthal National Wildlife Refuge region, Kisatchie National Forest region, Homochitto National Forest region, southwest Alabama, Apalachicola National Forest region, and Okefenokee National Wildlife Refuge region (Table 2; Fig. 2).

Local-Scale Statistical Model

Among the 9 potential panther reintroduction sites we identified, substantial variation of D^2 values at the 90-m resolution was apparent in some areas (Table 2). The Homochitto National Forest region had the lowest percentages of favorable habitat at the local scale compared with the landscape scale (Table 2). Conversely, the Okefenokee and the Apalachicola National Forest regions had greater proportions of favorable habitat at the local scale.

Potential for Population Expansion

The total area of habitat within female dispersal range of potential panther-reintroduction sites, based on our weighting system, ranged from 84 km^2 for the Apalachicola National Forest region to 1,181 km^2 in southwest Arkansas (Table 2). The percent

Table 2. Summary statistics to evaluate potential sites for reintroduction of the Florida panther in the southeastern United States, 2003–2005. Data from south Fla., USA, are provided for reference purposes.

Site label	Site name	Size of site (km^2)[a]	Proportion of local-scale habitat[b]	Area of potentially colonized patches (km^2)[c]
A	Ozark National Forest region	7,556	0.6719	287.7
B	Ouachita National Forest region	4,066	0.7068	358.7
C	Southwest Arkansas	3,124	0.7255	1,180.6
D	Felsenthal National Wildlife Refuge region	10,599	0.6995	1,068.0
E	Kisatchie National Forest region	2,918	0.7849	825.2
F	Homochitto National Forest region	6,882	0.5553	410.8
G	Southwest Alabama	7,728	0.7474	745.0
H	Apalachicola National Forest region	2,993	0.8167	84.4
I	Okefenokee National Wildlife Refuge region	4,585	0.8416	301.3
	South Florida (current range)	8,560	0.7185	180.6

[a] Area of contiguous pixels with $D^2 \leq 26$.
[b] Percentage of pixels, based on 90-m resolution, within potential reintroduction sites with $D^2 \leq 26$ (favorable habitat).
[c] Area of favorable habitat available within dispersal distances of 6.2 km, 20.3 km, and 32.3 km of potential reintroduction site; area calculations were weighted by factors of 1.0, 0.5, and 0.11, respectively.

increase in area size ranged from 2.1% for the current range in south Florida to 37.7% in southwest Arkansas.

Expert-Assisted Landscape Model

Sixteen of 50 (32%) *P. concolor* experts evaluated the relative importance of the 3 variables to characterize potential suitability of reintroduction sites in the southeastern United States. The consistency ratio (0.032) for the comparison matrix indicated high consistency among survey responses. The experts considered human population growth to be the most important variable (relative weight = 0.503), followed by the amount of public land (relative weight = 0.408) and livestock density (relative weight = 0.089; Table 3). We multiplied the 3 GIS map layers by their respective weights and then summed them to create a score (0–100 scale; Fig. 4).

Model Integration and Sensitivity Analysis

The effective habitat area for the 9 sites ranged from 2,513 km^2 (Apalachicola National Forest region) to 8,161 km^2 (Felsenthal National Wildlife Refuge region; Table 4). We divided those area values by 1,000 and then multiplied them by the scores of the expert model. The regions associated with the Okefenokee National Wildlife Refuge, Ozark National Forest, and Felsenthal National Wildlife Refuge had the highest ranks (Table 4).

The sensitivity analysis indicated that the site rankings did not change drastically when key parameters were changed (Table 5). In all 8 iterations of the sensitivity analysis, we found the same potential reintroduction sites in the top tier of the rankings, although the order varied slightly. Similarly, the bottom tier of the rankings also changed little. The additional sites identified by reducing the measurement scale of the landscape-scale habitat model or by reducing the minimum area requirement for a reintroduction site all received low-ranking scores (Table 5). Modeling outcomes were most sensitive to deviations in the measurement scale of the landscape-scale statistical model.

Discussion

Anthropogenic factors heavily influenced our landscape model. The D^2 model identified habitat conditions in the southeastern United States where human populations and road densities were low and where natural land-cover types were dominant, with high mean patch densities. Those results were similar when we changed the measurement scale (±20%). Of the 9 prospective reintroduction sites that we identified, some sites had much-reduced favorable habitat at the local scale (Table 2). That lack of favorable habitat could be indicative of fine-grained habitat fragmentation, primarily because of urban or agricultural land use interspersed with natural (forest) areas. Our analysis of colonization potential was simplistic in that any favorable habitat within the dispersal

Table 3. Mean values of habitat variables used in the expert-assisted model to evaluate potential sites for reintroduction of the Florida panther in the southeastern United States, 2003–2005. Data for south Fla., USA, are provided for reference purposes.

Site label	Site name	Area of public land (km^2)	Livestock density (no./km^2)	Human population growth rate (%)
A	Ozark National Forest region	3,269	20.1	16.0
B	Ouachita National Forest region	2,693	14.1	12.3
C	Southwest Arkansas	81	6.7	–2.4
D	Felsenthal National Wildlife Refuge region	527	7.1	5.7
E	Kisatchie National Forest region	840	5.2	9.2
F	Homochitto National Forest region	1,013	9.2	5.3
G	Southwest Alabama	5	4.3	4.9
H	Apalachicola National Forest region	2,058	0.7	26.9
I	Okefenokee National Wildlife Refuge region	2,144	2.7	16.7
	South Florida (current range)	6,998	5.4	24.8

Table 4. Effective habitat area, expert-assisted model scores, and site ranking scores of 11 potential sites for reintroduction of the Florida panther in the southeastern United States, 2003–2005. Data for south Fla., USA, are provided for reference purposes.

Site label	Site name	Effective habitat area (km^2)[a]	Mean expert model score	Ranking score[b]
I	Okefenokee National Wildlife Refuge region	4,112	46.9	193
A	Ozark National Forest region	5,270	30.4	160
D	Felsenthal National Wildlife Refuge region	8,161	19.2	157
B	Ouachita National Forest region	3,127	47.1	147
G	Southwest Alabama	6,333	17.5	111
H	Apalachicola National Forest region	2,513	44.0	111
E	Kisatchie National Forest region	2,938	29.8	88
F	Homochitto National Forest region	4,050	21.4	87
C	Southwest Arkansas	3,123	22.9	72
	South Florida (current range)	6,280	63.8	401

[a] Area of the potential reintroduction site plus weighted area of favorable habitat within dispersal distances of 6.2 km, 20.3 km, and 32.3 km (from the colonization potential analysis); that total area was then multiplied by the percentage of pixels defined as favorable habitat ($D^2 \leq 26$) in the local-scale statistical-habitat model.

[b] Effective habitat area (÷ 1,000) × mean expert model score.

distance could be colonized, regardless of potential barriers (e.g., roads, water bodies). Although the relative increase in habitat area because of colonization potential was not dramatic, our analysis provided a conservative indication of the isolation of prospective reintroduction sites. Increasing and decreasing these dispersal values in our sensitivity analysis did not alter our general conclusions. The site representing current panther range in Florida had the second-lowest potential for range expansion of the sites we evaluated, thus strengthening our premise that reintroduction will be necessary to establish additional populations.

Although the level of expertise and familiarity with panther ecology varied, the 16 responses to our survey for the expert-assisted model were from established researchers and managers intimately familiar with panther ecology ($n = 11$) or resource managers highly knowledgeable regarding south Florida habitats ($n = 5$). We also included 1 response from a Florida panther interest group. The results of our expert-assisted analysis seemed to reflect concerns that human influence on the landscape and conflicts may be an important limiting factor for the success of panther reintroduction efforts. Indeed, earlier reintroduction assessments revealed human-panther conflicts to be a significant factor (Belden and Hagedorn 1993, Belden and McCown 1996). Based on those results, the current panther range in south Florida provides the best landscape conditions, primarily because of the low human and road densities and large tracts of public land (Fig. 4; Table 3). That result supports the notion that the remoteness and inaccessibility of habitats in south Florida were important contributing factors to the survival of that population.

There are limitations inherent in our range-wide evaluation of habitat. For example, our model identified several inundated

Table 5. Site rankings based on sensitivity analyses of 4 key parameters used in models to identify potential sites for reintroduction of the Florida panther in the southeastern United States, 2003–2005.

			Measurement scale of landscape-scale D^2 model		Minimum area requirement for site		Measurement scale of local-scale D^2 model		Dispersal distance	
Site label	Site name	Original rank	−20%	+20%	−20%	+20%	−20%	+20%	−20%	+20%
I	Okefenokee National Wildlife Refuge region	1	3	1	1	1	1	1	1	1
A	Ozark National Forest region	2	5	2	2	2	2	2	2	3
D	Felsenthal National Wildlife Refuge region	3	1	3	3	3	3	3	3	2
B	Ouachita National Forest region	4			4	4	4	4	4	4
G	Southwest Alabama	5	2	5	5	5	5	6	6	6
H	Apalachicola National Forest region	6	4		6		6	5	5	7
E	Kisatchie National Forest region	7	7		7		8	7	8	8
F	Homochitto National Forest region	8	6	4	8	6	7	8	7	9
C	Southwest Arkansas	9			9	7	9	9	9	5
	South Tennessee/Northern Alabama		14							
	Holly Springs National Forest region		17							
	Eastern Talladega National Forest region		15							
	Western Talladega National Forest region		10							
	Tombigbee National Forest region		13							
	Northwest Florida		11							
	Western Kisatchie National Forest region		8		10					
	Atchafalaya National Wildlife Refuge region		12		11					
	Florida Gulf Coast		9							
	Southeastern Alabama		16							

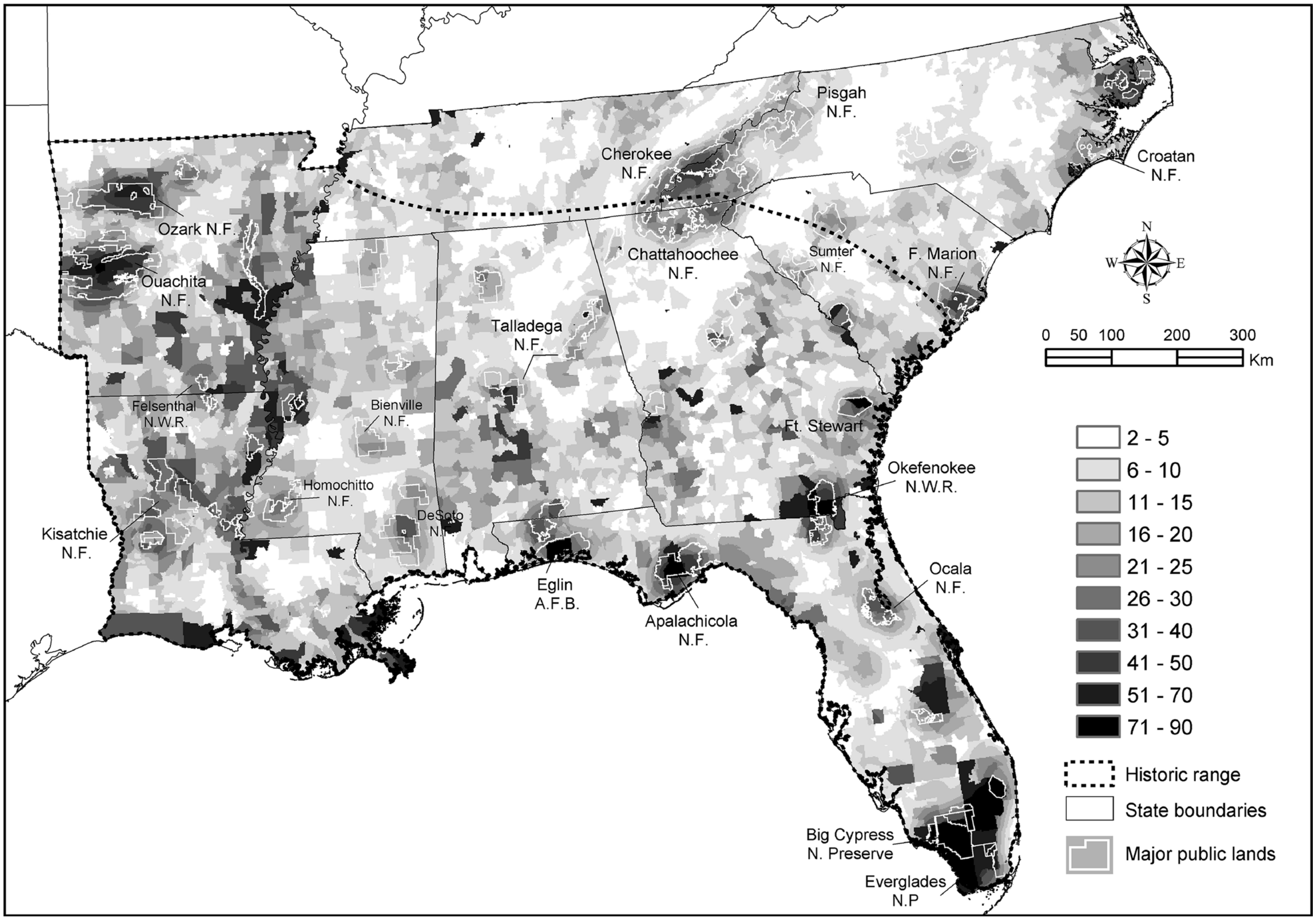

Figure 4. Expert-assisted model scores (0–100 scale) to identify potential sites for reintroduction of the Florida panther in the southeastern United States, 2003–2005.

Water Conservation Areas in south Florida as favorable habitat, although panthers rarely used those areas. We suspect the model could not adequately discern subtle differences with areas that were used by panthers because of our generalization of the land-cover data. We chose GIS data sources and resolutions consistent with the broad scale at which panther habitat use occurred, the large extent of our study area, and the limitations of the radiotelemetry and expert-opinion data. The GIS-based habitat models often cannot incorporate fine-scale habitat characteristics, such as vegetation structure and detailed information on prey availability (e.g., small mammal density, stalking cover). Nevertheless, the models provided an objective and quantitative evaluation of the overall landscape conditions that enabled us to identify prospective sites for further analysis.

Jordan (1994) identified and ranked potential reintroduction sites for the Florida panther based on expert opinion. Our empirical model identified large tracts of favorable habitat at 9 of 14 sites identified by Jordan (1994). Jordan (1994) identified several areas as potential reintroduction sites (e.g., coastal South Carolina, Georgia/South Carolina Piedmont region, western Kisatchie National Forest region, and the Big Bend region of Florida), whereas our statistical-landscape model did not. Although favorable habitat was found in these regions, the areas of contiguous habitat did not meet our size criterion to qualify as potential reintroduction sites. When we decreased our area size criterion by 20%, one of those sites was included. Generally, our sensitivity analysis of the size criterion resulted in the identification of fewer or more reintroduction sites, but the top-ranked sites did not change.

Managers should determine which additional site characteristics should be given consideration and which panthers (e.g., age, sex, origin) are the best candidates for release. Also, because of the inherent limitations of a broad-scale habitat analysis, we recommend that field surveys of the chosen reintroduction sites be undertaken. Such surveys of local habitat conditions should involve an assessment of localized prey densities and the availability of understory vegetation or varied topography for stalking and denning cover. Other potential concerns include the extent of seasonal inundation in certain areas and the presence of highly disturbed landscapes that appear to be natural land cover in the GIS data, local hunting regulations and traditions, and human accessibility of the site. Decisions ultimately will also be made using less-quantitative and biologically based criteria than those we have presented. For example, sociological information, such as public attitudes towards carnivore reintroduction, will need to be evaluated and addressed at the top-ranked reintroduction sites.

Management Implications

The Okefenokee National Wildlife Refuge, Ozark National Forest, and Felsenthal National Wildlife Refuge regions ranked as the best prospective reintroduction sites based on the numerical combination of effective habitat area and expert model scores (Table 4). The lowest scores were for those sites most limited in effective habitat area, such as the Homochitto National Forest and Southwest Arkansas sites (Table 4). The Okefenokee National Wildlife Refuge region ranked highest in our assessment because of its high expert model score and high habitat quality at the local scale. It is similar to the landscape within the current range of the Florida panther in that the interior of the refuge is virtually roadless and extremely inaccessible to humans. This site was used as a test site for 2 pilot reintroduction studies (Belden and Hagedorn 1993, Belden and McCown 1996). The reintroduced mountain lions made only limited use of the refuge interior, possibly because the extensive freshwater wetlands in the interior of the refuge (Loftin et al. 2000) had low densities of white-tailed deer, although this was not readily apparent from our modeling process. The lack of an existing social population structure and the origins of the mountain lions may also have influenced the success of those translocations. We considered potential for successful panther reintroduction for Ozark National Forest to be high because it contains the greatest amount of public land, with the exception of the current panther range. The Ozark National Forest region also has low human densities and low habitat fragmentation. Another advantage of this site is that its large size (7,556 km^2; Table 2) and rugged topography limit human access. Although the site's proximity to rapidly growing population centers in northwest Arkansas could result in future human encroachment, this may be of little consequence because of the large size of the site. We identified the Felsenthal National Wildlife Refuge region as the largest site with an effective habitat area of 8,161 km^2. That site also has the advantage of close proximity to other large habitat patches, which may facilitate colonization beyond the reintroduction site. There are no large urban centers nearby, and the site contains large tracts of privately owned timber and extensive bottomland forests associated with the Saline River, Ouachita River, and Bayou Bartholomew. The drawbacks of this area are the relatively high road and human densities and the lack of large areas of public land.

Acknowledgments

Our study was funded by the U.S. Fish and Wildlife Service; we thank J. Kasbohm, D. Jennings, and P. Halupa for all their support throughout the study. We thank the Florida Fish and Wildlife Conservation Commission and the National Park Service for providing Florida panther telemetry data. Special thanks to C. Belden of the U.S. Fish and Wildlife Service, who assisted us with many aspects of this study and provided helpful comments regarding the statistical landscape model. We are grateful to B. Nunley of the National Wildlife Federation for providing public lands data. We thank R. Kautz of the Florida Fish and Wildlife Conservation Commission and T. Hoctor for helpful suggestions regarding the addition of a local-scale habitat model to our analyses, and we thank R. Telesco at the University of Tennessee for help with the design of the expert-assisted model. We also express our appreciation to the Florida panther experts who participated in our expert-assisted model survey. Finally, we express our gratitude to J. Kasbohm, C. Belden, K. Logan, M. Boyce, D. Maehr, and an anonymous reviewer for their constructive criticism of earlier drafts of the manuscript.

Literature Cited

Alldredge, J. R., D. L. Thomas, and L. L. McDonald. 1998. Survey and comparison of methods for study of resource selection. Journal of Agricultural, Biological, and Environmental Statistics 3:237–253.

Bailey, R. G. 1980. Description of the ecoregions of the United States. U.S. Department of Agriculture Miscellaneous Publication 1391, Fort Collins, Colorado, USA.

Belden, R. C., and B. W. Hagedorn. 1993. Feasibility of translocating panthers into northern Florida. Journal of Wildlife Management 57:388–397.

Belden, R. C., and J. W. McCown. 1996. Florida panther reintroduction feasibility study. Florida Game and Fresh Water Fish Commission, Bureau of Wildlife Research, Tallahassee, Florida, USA.

Carroll, C., W. J. Zielinski, and R. F. Noss. 1999. Using presence–absence data to build and test spatial habitat models for the fisher in the Klamath region, USA. Conservation Biology 13:1344–1359.

Clark, J. D. 2001. Florida panther. Pages 234–239 *in* J. G. Dickson, editor. Wildlife of southern forests: habitat and management. Hancock House, Blaine, Washington, USA.

Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management 57:519–526.

Clark, J. D., D. Huber, and C. Servheen. 2002. Bear reintroductions: lessons and challenges. Ursus 13:335–345.

Davis, J. H., Jr. 1943. The natural features of southern Florida, especially the vegetation and the Everglades. Florida Geological Survey Bulletin 25. Tallahassee, USA.

Earnhardt, J. M. 1999. Reintroduction programmes: genetic trade-offs for populations. Animal Conservation 2:279–286.

Eastman, J. R., J. Weigen, P. A. Kyem, and J. Toledano. 1995. Raster procedures for multi-criteria/multi-objective decisions. Photogrammetric Engineering and Remote Sensing 61:539–547.

Farber, O., and R. Kadmon. 2003. Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. Ecological Modelling 160:115–130.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477–480.

Hall, E. R. 1981. The mammals of North America. John Wiley and Sons, New York, New York, USA.

Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to ArcView. Version 2.04 beta. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, USA.

Janis, M. W., and J. D. Clark. 2002. Responses of Florida panthers to recreational deer and hog hunting. Journal of Wildlife Management 66:839–848.

Jordan, D. B. 1994. Final preliminary analysis of some potential Florida panther population reestablishment sites. Final Report, U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

Kautz, R. S. 1994. Historical trends within the range of the Florida panther. Pages 285–296 *in* D. B. Jordan, editor. Proceedings of the Florida Panther Conference, U.S. Fish and Wildlife Service, Gainesville, USA.

Kerkhoff, A. J., B. T. Milne, and D. S. Maehr. 2000. Toward a panther-centered view of the forests of South Florida. Conservation Ecology 4:1. <http://www.consecol.org/vol4/iss1/art1>. Accessed 2002 Jul 01.

Knick, S. T., and J. T. Rotenberry. 1998. Limitations to mapping habitat use areas in changing landscapes using the Mahalanobis distance statistic. Journal of Agricultural, Biological and Environmental Statistics 3:311–322.

Loftin, C. S., W. Rasberry, and W. M. Kitchens. 2000. Development of a grid-cell topographic surface for Okefenokee Swamp, Georgia. Wetlands 20: 487–499.

Maehr, D. S., and J. A. Cox. 1995. Landscape features and panthers in Florida. Conservation Biology 9:1008–1019.

Maehr, D. S., E. D. Land, D. B. Shindle, O. L. Bass, and T. S. Hoctor. 2002. Florida panther dispersal and conservation. Biological Conservation 106: 187–197.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA Forest Service General Technical Report PNW-351, Portland, Oregon, USA.

Mustajoki, J., and R. P. Hämäläinen. 1999. Web-HIPRE—a Java applet for AHP and value tree analysis. Fifth International Symposium on the Analytic Hierarchy Process, 12–14 August 1999, Kobe, Japan.

Pereira, J. M. C., and R. M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression: a study of the Mt. Graham red squirrel. Photogrammetric Engineering and Remote Sensing 57:1475–1486.

Riitters, K. H., J. D. Wickham, J. E. Vogelmann, and K. B. Jones. 2000. National land-cover pattern data. Ecology 81:604.

Saaty, T. L. 1980. The Analytic Hierarchy Process: planning, setting priorities, resource allocation. McGraw-Hill, New York, New York, USA.

Schmoldt, D. L., and D. L. Peterson. 2000. Analytical group decision making in natural resources: methodology and application. Forest Science 46:62–75.

Scott, J. M., P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson. 2002. Predicting species occurrences: issues of accuracy and scale. Island, Covelo, California, USA.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Stoms, D. M., F. W. Davis, and C. B. Cogan. 1992. Sensitivity of wildlife habitat models to uncertainties in GIS data. Photogrammetric Engineering and Remote Sensing 58:843–850.

U.S. Census Bureau. 2002. United States Census 2000. U.S. Census Bureau, Washington, D.C., USA. <http://www.census.gov/main/www/cen2000.html>. Accessed 27 Aug 2002.

U.S. Department of Agriculture. 2003. National agricultural statistics. National Agricultural Statistics Service, Washington, D.C., USA. <http://www.usda.gov/ nass>. Accessed 25 Jun 2002.

U.S. Geological Survey. 1999. National Atlas of the United States of America: major roads of the United States. U.S. Geological Survey, Reston, Virginia, USA. <http://nationalatlas.gov/atlasftp.html>. Accessed 13 Feb 2004.

U.S. Fish and Wildlife Service. 1995. Second revision: Florida panther (*Felis concolor coryi*) recovery plan. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

Verbyla, D. L., and J. A. Litvaitis. 1989. Resampling methods for evaluating classification accuracy of wildlife habitat models. Environmental Management 13:783–787.

Vogelmann, J. E., S. M. Howard, L. Yang, C. R. Larson, B. K. Wylie, and N. Van Driel. 2001. Completion of the 1990s national land cover data set for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. Photogrammetric Engineering and Remote Sensing 67:650–662.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Associate Editor: Strickland.