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Habitat selection by critically endangered Florida panthers across the diel period: implications for land management and conservation

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Short Title: Habitat selection by Florida panthers

Abstract

Decisions regarding landscape management, restoration, and land acquisition typically depend on land managers' interpretation of how wildlife selects habitat. Such assessments are particularly important for umbrella species like the endangered Florida panther (*Puma concolor coryi*), whose survival requires vast wildlands. Some interpretations of habitat selection by panthers have been criticized for using only morning locations in defining habitat use. We assessed habitat selection using a Euclidean distance analysis (EDA) and location data collected throughout the diel period from GPS collars deployed on 20 independent Florida panthers. We corroborated aspects of earlier analyses by demonstrating selection of forested habitats by panthers. We also confirmed selection of open habitats (i.e., marsh–shrub–swamps, prairie–grasslands), a novel result. Habitat selection did not vary by sex or season but varied by time of day. Panthers were located closer to wetland forests in the daytime and used prairie–

grasslands more at night. Our assessment of the effect of patch size on selection of forest habitat revealed that panthers were not solely reliant on large patches (> 500 ha) but utilized patches of all sizes (≤ 1 ha, > 5–10 ha, > 1000 ha, etc.). Our results emphasize the importance of collecting panther location data throughout the diel period when assessing habitat selection. Conservation strategies for panthers should consider a mosaic of habitats, a methodology that will protect other sensitive flora and fauna in South Florida.

Key Words: conservation, endangered species, Euclidean distance analysis, Florida panther, GPS collars, habitat selection, *Puma concolor coryi*

Introduction

Loss of habitat remains the greatest threat to many wildlife species, especially those that are endangered and reliant upon large parcels of wildlands. Habitat loss results in population declines, and smaller populations are less likely to persevere (Mills, 2007). The fragmentation of wildlands that follows habitat loss can significantly affect species that are wide ranging and exhibit low densities and low fecundity (e.g., large carnivores). Therefore, the preservation of sufficient habitat to ensure the survival and promote the recovery of endangered carnivores, such as the Florida panther (*Puma concolor coryi*), requires that conservation planning be based on knowledge of habitat selection. Furthermore, decisions related to panther habitat selection will affect many other species across ecosystems, given the scale at which panthers range across the landscape.

Several studies have delineated habitat use by panthers (Belden *et al.*, 1988; Maehr & Cox, 1995; Comiskey *et al.*, 2002; Cox, Maehr & Larkin, 2006; Kautz *et al.*, 2006; Land *et al.*, 2008). Each of these studies highlighted the importance of forested habitats to panthers, but findings related to open habitats (e.g. marshes and prairies) could be construed as inconclusive and unclear, probably an artifact of the data used in these studies. All but Land *et al.* (2008) relied solely on VHF- telemetry data collected during aerial surveys by the Florida Fish and Wildlife Conservation Commission (FWC) and the National Park Service (NPS). These panther location data were typically collected during the same hours of the morning (0700–1100 hrs) and on the same days of the week. Data collected consistently during weekday mornings, although useful in answering some ongoing research objectives (e.g., survival, fecundity, cause-specific mortality, morning habitat use), cannot fully depict habitat selection across the diel period (Beier *et al.*, 2006). This limitation has been further substantiated in a habitat study of puma (*P. c.*) in the western U.S. (Dickson, Jenness & Beier, 2005). Using such data to decipher habitat preferences of panthers has brought criticism and controversy (Gross, 2005; Beier *et al.*, 2006).

Additional debate has stemmed from research that noted reliance of panthers on only large patches (> 500 hectares) of forested habitat in South Florida (Maehr & Cox, 1995; Maehr & Deason, 2002) and their infrequent use of nonforested habitat > 90m from forest patches (Maehr & Cox, 1995). These analyses used the same VHF-telemetry data collected only during morning hours, and therefore may be affected by biases previously noted for panther habitat selection. Panther locations collected across the diel period can provide a more complete depiction of how panthers use different forest patch sizes, as well as nonforested habitat, perhaps clarifying some of the controversy associated with previous analyses and permitting more appropriate habitat management initiatives.

Incorporating GPS into lightweight radiocollars has allowed evaluation of a range of wildlife research issues, including habitat selection (Moe *et al.*, 2007; Skarin *et al.*, 2008; Thurfjell *et al.*, 2009), movement patterns (Bruggeman *et al.*, 2007), road crossings (Waller & Servheen, 2005; Dodd *et al.*, 2007), and predation rates (Knopff *et al.*, 2009) at a finer spatial resolution than possible with VHF telemetry. The FWC began deploying GPS collars on panthers in 2002 and found no significant difference in habitat preferences of panthers between morning data gathered by VHF and data gathered by GPS (Land *et al.*, 2008). To allay criticism regarding biases associated with data gathered in the morning using VHF telemetry, Land *et al.* (2008) programmed GPS collars to collect a majority of locations at night (1900–0700hrs). In the present study, to address potential bias more thoroughly, we programmed GPS collars to collect data throughout the diel period.

We used a Euclidean distance-based analysis (EDA; Conner, Smith & Burger, 2003)to test hypotheses of habitat selection by Florida panthers . More specifically, we predicted that panthers would use habitat within or closer to forested patches more during the day than at night, given thermal cover afforded by forest for daytime rest sites (Kautz *et al.*, 2006). We also predicted that panthers would be found closer to or within open habitats more frequently at night than during the day, given the ease of travel under cover of darkness and the prey species often found in these habitat classes (Dickson *et al.*, 2005). Additionally, we expected that sex (Cox *et al.*, 2006) and season (wet vs. dry) would not affect habitat selection given the degree of overlap in panthers' home ranges and the animals' generalist nature. Finally, we predicted that panther locations would be within a heterogeneous matrix of forest-patch sizes that affords improved habitat for prey and hunting opportunities for predators (Kautz *et al.*, 2006).

Methods

Study Area

South Florida has a subtropical climate, is topographically flat, and is characterized by extensive permanent and ephemeral wetlands influenced by seasonal rains from May through October (Duever *et al.*, 1986). Wildland habitats include hardwood hammocks, cypress forests, pine flatwoods, freshwater marshes, prairies, and grasslands (Davis, 1943); lands used by humans include citrus, croplands, pastureland, rock mining, and areas of low- and high-density residential development. Our study area encompassed a large portion of the range of the breeding population of panthers in South Florida. This population exists within wildlands bordered by the urban areas of Miami–Fort Lauderdale to the east, Fort Myers–Naples to the west, the Caloosahatchee River to the north, and Florida Bay to the south (Fig. 1). One male panther (FP130) that had previously dispersed north of the Caloosahatchee River and established a definitive home range was fitted with a GPS collar for this study and monitored outside the breeding range until his collar failed.

Our capture efforts focused not only on the core population (panthers inhabiting large parcels of protected public lands important to the demographic stability of the population) in southwestern Florida (comprising portions of Big Cypress National Preserve north of I-75, Florida Panther National Wildlife Refuge, and Fakahatchee Strand Preserve State Park), but also on panthers residing in Everglades National Park and on public and private lands bordering the edges of the Florida panther primary zone (South

Florida lands essential to survival and long-term viability of Florida panthers; Kautz *et al.*, 2006) in the northern and western extent of its range (Fig. 1). These areas are vital to panther conservation for several reasons. First, panthers in Everglades National Park are somewhat isolated from the core population in southwestern Florida due to the semipermeable barrier posed by the Shark River Slough (Fig. 1). Second, habitat use in Everglades National Park is concentrated in upland areas, adjacent to the urban fringe of south Miami and Homestead. Third, habitat along the northern and western edges of the primary zone is being encroached upon by urban development. Finally, habitat in Okaloacoochee Slough State Forest (OK Slough SF; Fig. 1) is adjacent to the dispersal zone (lands that should be protected from development for a dispersal corridor; Kautz *et al.*, 2006), and monitoring patterns of habitat selection there may help in assessing whether south-central Florida north of the Caloosahatchee River could be naturally recolonized. Data from protected lands in Big Cypress National Preserve south of I-75 were not available (Fig. 1). Thus, we focused on the use of habitat by panthers in areas affected by habitat loss rather than unaffected areas.

Capture, GPS collaring, data compilation, and estimation of home range

We used trained hounds and houndsmen supplied by Livestock Protection Company (Alpine, Texas) to capture independent-age Florida panthers. We deployed five models of GPS collars produced by four manufacturers (Table 1), including Advanced Telemetry Systems G2110 (Isanti, Minnesota, USA), Lotek GPS3300s (New Market, Ontario, Canada), Followit Tellus and Tellus-GSM (Lindesberg, Sweden), and Telonics TGW-3401 (Mesa, Arizona, USA). Fix schedules programmed into collars varied (Table 1) but all were programmed to attempt fixes throughout the diel period via either a frequent or staggered fix schedule (see supplementary materials). A preliminary field trial for assessing location error associated with the GPS collar models used in this study revealed a mean error of 33.9 m (SE = 8.1, n = 3210 fixes; J. Benson and D. Onorato, FWC, unpublished report).

Data from all GPS collars were compiled and visually displayed in ArcGIS 9.3 (ESRI, Redlands, CA, USA).We qualified each fix as occurring during day (0700–1859 hrs) or night (1900–0659 hrs), and during the dry (15 October–14 May) or wet (15 May–14 October) season. We used GPS locations to estimate each panther's home range with 100% minimum convex polygons (MCP, see supplementary materials Fig. S1) in ArcGIS 9.3 using Hawth's Tools (Beyer, 2004).

Habitat analyses

We combined 43 land-cover classes categorized by the FWC (Kautz, Stys & Kawula, 2007) into six broader classes (see supplementary materials Table S1) after Land *et al.* (2008): upland forest, wetland forest, dry prairie–grassland, marsh–shrub–swamp, agriculture, and "other" (comprising all remaining types, including open water, mangrove swamp, exotic plants, and urban). Land-cover data were in raster format and correlated with ground conditions present in 2003 at a 30-m resolution, the most current and comprehensive available for our study area.

We chose the EDA of Conner *et al.* (2003) to assess third-order habitat selection (habitat selection within the home range; Johnson, 1980), because it uses individual panthers, not GPS locations, as the sampling unit and because of its use in recent studies (Cox *et al.*, 2006; Kautz *et al.*, 2006; Land *et al.*, 2008). The EDA compares the distance between animal locations and the nearest pixel of each land-cover class (i.e., habitat use) to the distance between random points plotted within the 100% MCP home range and the nearest pixel of each land-cover class (i.e., habitat availability). We generated 20,000 random points in a uniform distribution within each home range after testing a range of points (1000 to 30,000) to assess when the variance of the mean distance in each land-cover class began to stabilize (Moyer, McCown & Oli, 2008). Distances between points and land-cover classes were determined using the Euclidean distance tool in the Spatial Analyst extension in ArcGIS 9.3 and via the intersect points option in Hawth's Tools (Beyer, 2004).

A vector of six distance ratios was created for each panther by dividing the mean distance of its locations from each land-cover class by the mean distance of random points to each land-cover class (i.e., one distance ratio per land-cover class). A distance ratio > 1 indicates avoidance (i.e., the mean distance from a panther's location to a land-cover class is greater than the mean distance from random points within the home range to the same land-cover class), whereas a distance ratio < 1 indicates selection. The expected value for these ratios under the null hypothesis of no selection is 1, and we used MANOVA (PROC GLM) to test whether panthers were exhibiting habitat selection. A significant MANOVA test result indicates nonrandom use of land-cover classes as the mean distance vector differs from 1. We subsequently tested for selection or avoidance of individual habitats using univariate *t*-tests; paired *t*-tests were used to rank habitats by preference. We also tested the fixed effects of sex, season, and time of day. For seasonal and time-of-day analyses, the individual animal ID was included in the model as a random effect to account for data collected at both levels (wet or dry season; day or night) for each animal. A significant MANOVA test result for each fixed effect indicates a difference in land-cover use between the categories (female or male; wet or dry season; day or night). In the event of a significant fixed effect, we reviewed the GLM results to assess differences in selection between levels of fixed effects (e.g., night vs. day) within each land-cover class.

We assessed whether panthers were located closer to or farther from forest patches of different sizes using an EDA. We used ArcGIS 9.3 to create a forest-patch layer that combined upland and wetland forest layers with three additional land-cover classes (melaleuca [*Melaleuca quinquenervia*] and Australian pine [*Casuarina* sp.], invasive exotic trees established in South Florida; mangrove swamps, which are typically inundated) included in the "other" habitat category (see supplementary materials Table S1). Panthers have been documented within those habitats via field sign and VHF telemetry data, although they used them infrequently. To encompass a range of sizes, we qualified seven patch-size classes (0.1–1 ha, 1.1–5 ha, 5.1–10 ha, 10.1–100 ha, 100.1–500 ha, 500.1–1000 ha, and > 1000 ha). Statistical analyses were as described for the habitat analysis. We also determined the distance of panther locations in unforested habitat from the nearest forest patch to descriptively quantify the prevalence of those data. Finally, we used a Kolmogorov-Smirnov two-sample distribution test (PROC NPAR1WAY) to test whether the frequency distribution of locations within 11 distance-from-forest groups differed between daytime and night. All statistical tests were completed in SAS 9.1 (SAS Institute, Cary, NC, USA) and the EDA used code adapted from Conner and Plowman (2001).

Results

We collared 20 independent-aged (i.e., ≥ 1.5 years old) panthers (10 females, 10 males) between February 2005 and February 2009 (Table 1). Age at capture ranged from 1.5 to 13.3 years, and mean time collared was 306 days (range = 113–610 days). We collected 58,212 locations over 79,147 attempts (74% fix success rate). Successful fixes included a nearly even ratio of night:day fixes (53%:47%). The ratio of wet:dry season fixes was uneven (37%:63%) because all panthers were initially collared during the dry season when field conditions were favorable for capture. This uneven ratio may have affected our assessment of the impact of season on habitat selection.

Panthers exhibited habitat selection at the third-order level ($F_{6,13} = 25.31$, $P < 0.001$). Panthers selected upland forest, wetland forest, marsh–shrub–swamp, and prairie–grassland habitats (Table 2). Agricultural and the "other" land-cover classes were used in proportion to their availability; no class was avoided. Habitat selection did not vary by main effects of sex ($F_{6,13} = 2.30$, $P = 0.099$) or season ($F_{6,12} = 2.46$, $P = 0.087$), but it did vary by time of day ($F_{6,14} = 15.27$, $P < 0.001$). Panthers used wetland forests more during the day than night, but they used prairie grasslands more at night (Fig. 2). Use of the remaining selected land-cover classes (upland forests and marsh–shrub–swamp) did not differ significantly between night and day (Fig. 2). Even though the "other" land-cover class was used in proportion to its availability, panthers used areas near or in the "other" class significantly more at night than during the day (Fig. 2).

Panthers exhibited selection of the smallest (0.1–1.0 ha), intermediate (5.1–10.0 ha), and largest (> 1000 ha) classes of forest-patch size ($F_{7,12} = 8.49$, $P < 0.001$) within home ranges (Table 3). All other patch sizes were used in proportion to availability. Pairwise comparisons to rank forest-patch size revealed no significant differences, probably because all forest-to-patch-size ratios were < 1, demonstrating that panthers tend to be closer to forest patches than farther from them (ratio > 1). Nevertheless, 41.0% (23,850) of locations were outside of forest patches and 28.2% of those were > 90 m from a forest patch. The frequency of locations within 11 distance-from-forest categories was distributed differently between night and day (KSa = 4.30, P <0.0001; Fig. 3). Overall, 24.6% and 30.8% of fixes > 90 m from forests were made during the day and night, respectively.

Discussion

Findings related to habitat selection by Florida panthers have consistently caused controversy that has affected conservation and recovery of this endangered species (Beier *et al.*, 2006). Our results represent a rigorous assessment of panther habitat selection for several reasons. Our total sample of collared individuals comprised 17% of the recent (2007) minimum population count (McBride *et al.* 2008). Panthers that we collared used a large portion of the current breeding range in South Florida (see supplementary materials Fig. S1). By collecting panther location data across the diel period, we alleviated biases associated with studies relying on data collected from VHF-collared panthers in mornings (0700–1100hrs) only, which underestimated the use of more open habitats. A study using data collected solely at night would have similar biases (i.e., underestimation of the use of forested habitats).

Our results concur in some respects with analyses using VHF data collected in the morning (Belden *et al.*, 1988; Maehr & Cox, 1995; Cox *et al.*, 2006; Kautz *et al.*, 2006; Land *et al.*, 2008). Panthers have repeatedly been shown to select forested habitat either within their home range (third-order selection; Belden *et al.*, 1988; Cox *et al.*, 2006; Land *et al.*, 2008) or within a study area (second-order selection; Kautz *et al.*, 2006). In our study, panther locations were significantly closer than expected to upland and wetland forest classes, and these ranked highest in pairwise comparisons with other land-cover classes. Given consistent results from several studies using data collected in the morning or across the diel period and using different analytical methodologies (i.e., compositional analysis, [Aebischer, Robertson & Kenward, 1993]; EDA), we conclude that forested land-cover classes are of vital importance to Florida panthers in South Florida.

Forested habitats provide a variety of attributes critical to panther demography and conservation. Females choose den sites in forested habitats (Benson, Lotz & Jansen, 2008), especially woodlands with dense patches of saw palmetto (*Serenoa repens*). Forested habitats also provide rest sites, particularly important during South Florida's hot, humid summers. Research in western North America has noted that pumas must be able to approach prey to a certain minimal distance to improve their stalking success (Hornocker, 1970; Logan & Irwin, 1985; Beier, Choate & Barrett, 1995). Forests and the associated edge with adjacent open habitats may improve hunting success in pumas (Laundré & Loxterman, 2007). We often encountered panther kills in forests adjacent to more open habitats. Data collected from a GPS–GSM-collared male panther permitted us to locate six kill sites within a 20-day period in June 2008 (M. Criffield, FWC, unpubl. data). Three of these kill sites were on the edge between forested and open habitats; all were < 33 m from an edge (mean = 13.7 m, SE = 4.8 m). Although this sample size is small, the data highlight the importance of forested and open landscapes to panthers. Panthers may use the edge of forested habitat as stalking cover to ambush white-tailed deer (*Odocoileus virginianus*) or feral hogs (*Sus scrofa*) feeding in open areas, and then drag their kill into forested areas to feed. Feral hogs are habitat generalists, using a mix of open- and closed-canopy habitats (Ilse & Hellgren, 1995; Gabor, Hellgren & Silvy, 2001), for foraging and shade, respectively. Our findings thus emphasize not only the importance of forest to panther conservation, but also the benefits of heterogeneous habitat matrices and their higher proportion of edge.

Defining the use of forested habitats as a source of cover for panthers warrants additional discussion. If we define cover as "any physical or biological feature or arrangement of features that provides shelter from weather or concealment from or for predators" (Bolen & Robinson, 1999), then we note that panthers rely on more than just forested habitat for cover. Nonforest but densely vegetated habitats also provide sufficient cover. They could include thick patches of tall sawgrass (McBride, 2001) to expanses of mature saw palmetto adjacent to pine or oak forests. The use of varied habitats as cover by panthers is not unexpected given the persistence of other puma populations in deserts (Davis & Schmidly, 1994; Logan & Sweanor, 2001) characterized by minimal forest cover.

The most novel result of our study was the documentation of selection of prairie–grassland and marsh–shrub–swamp patches. Previous studies that assessed habitat selection using the EDA at the third-order level with VHF data (Cox *et al.*, 2006; Land *et al.*, 2008) did not show that panthers selected these open habitats. Cox *et al.* (2006) reported that panthers avoided open wetlands (which included freshwater, sawgrass, and cattail marshes and wet prairies), a category synonymous with our marsh–shrub–swamp (which included cover types compiled by Cox *et al.* [2006] as well as shrub swamps). Studies assessing habitat selection by pumas in western North America have demonstrated avoidance of open habitats such as grasslands (Logan & Irwin, 1985; Dickson & Beier, 2002). Both studies collected data with VHF collars and primarily during the day, constraints the researchers acknowledged may have biased their findings on a species known to be active during crepuscular periods. In fact, in a follow-up study by Dickson *et al.* (2005) that included nocturnal data, avoidance of grasslands was not apparent. This result substantiates the need to collect habitat-selection data during the daytime and at night to comprehensively delineate habitat requirements.

White-tailed deer and feral hogs would be expected to use open habitats such as grasslands because of the plentiful food sources there (Gabor *et al.*, 2001). Feral hogs in southern latitudes are typically nocturnal and forage primarily on grasses and underground plant parts (Ilse & Hellgren, 1995; Taylor & Hellgren, 1997). In addition, plants in marsh–shrub–swamps compose a major portion of deer diets (Labisky *et al.*, 2003). Open areas also permit prey to be more vigilant regarding predators.

The only other published study that has used GPS to assess panther habitat selection (Land *et al.*, 2008) did not reveal selection for open land-cover classes, although it did observe an increase in the percentage of panther locations in prairie-grasslands at night. We believe our results were different from those of Land *et al.* (2008) because 1) their sample size was smaller (12 vs. 20 independent panthers); 2) their study area was smaller; and 3) 82.6% of their GPS fixes were collected from 1900 to 0700 hrs. We collected a nearly even percentage of daytime vs. nighttime fixes. Although panthers are said to rest during much of the diurnal period, we documented movements throughout the diel period with sightings, motion-activated cameras, and via GPS data collected using frequent acquisition rates (e.g., hourly or every 15 minutes). Collecting data from individual panthers across the diel period provides the most complete characterization of habitat use by panthers and forgoes the need to qualify conclusions related to VHF data collected at morning locations or to model nighttime habitat selection based on daytime locations (Comiskey *et al.*, 2002).

As expected, panthers were located closer to forested habitats during the day than at night, although night and daytime use was significantly different only in wetland forests (Fig. 2). Forested habitats are likely to provide panthers with respite from the tropical South Florida climate, which can be extreme (> 35° C, 95% humidity) at some times of day. We predicted that panthers would use open habitats more frequently during the nocturnal period as opposed to during the day. Indeed, selection for prairie-grasslands was significantly greater during the nocturnal period than during the diurnal period. Marsh–shrub–swamps were not selected differently during the two time-of-day classes. We attribute the increased use of prairie–grasslands by panthers at night to optimization of predation opportunities and facilitation of movements across the landscape, activities that predators may carry out more covertly during darkness than in light. Dickson *et al.* (2005) allude to this idea in their findings on pumas in California, suggesting that open areas such as grasslands are used by pumas to traverse areas or to stalk and pursue prey.

Previous studies using VHF data in assessing the relationship of forest-patch size and distance from forest with the likelihood that an area supported panthers have been contentious (Maehr & Cox, 1995; Maehr & Deason, 2002) because of their potential impacts on panther recovery. These studies indicated that panther occupancy of forest patches declined significantly in patches of < 500 ha, and the resulting Panther Habitat Evaluation Model used this criterion when assessing the impact on panthers of development in available habitat (Maehr & Deason, 2002). In contrast, our findings indicate, as did those of Kautz *et al.* (2006), that panthers use a variety of forest-patch sizes, often within a matrix of open habitats. Our results have shown that panthers use habitat outside of forest patches (i.e., open land-cover classes) more frequently (in 41.0% of locations) than previously reported (Maehr & Cox, 1995). Maehr & Cox (1995), using VHF data collected during the morning hours, concluded that 96% of panther locations were located either in preferred land-cover classes or within 90 m of them. These classes included hardwood hammocks, hardwood swamps, and cypress swamps (synonymous with land-cover classes that comprised our forest-patch landscape class). In our study, 28.2% of panther locations were > 90 m from our forest patch land-cover class. The most likely explanations for the difference in the results between these studies are that (1) we collected data throughout the diel period and (2) distances measured relative to forest patches were more accurate than distances estimated by an observer in an aircraft making rapid spatial judgments from visual and auditory cues. Use by panthers of a heterogeneous matrix of forest-patch sizes, as well as open areas, is consistent with the adaptable nature of *Puma concolor* across its range (Logan & Sweanor, 2001). The historic distribution of puma from northwestern Canada through Patagonia in South America (Young & Goldman, 1946) attests to this. Franklin *et al.* (1999) descriptively noted the use by Patagonian pumas of forests and grasslands, depending on time of day. The other large felid in the western hemisphere, the jaguar (*Panthera onca*), is also wide-ranging and has adapted to a variety of landscapes, from evergreen woodlands to semidesert grasslands (Hatten, Averill-Murray & van Pelt, 2005). The Florida panther has adapted to a variety of ecosystems, as illustrated by its presence in 1) vast areas dominated by sawgrass (Everglades National Park); 2) cypress-dominated landscapes in portions of Big Cypress National Preserve; and 3) the more northern extents of its range, associated with forested uplands and prairie–grasslands. In summary, it appears that a mélange of small, medium, and large forest patches dispersed among open areas may increase the probability that panthers will occupy land-cover in South Florida. Such diverse landscapes may provide suitable prey (white-tailed deer and feral hogs) while providing more edge and therefore more opportunities to hunt successfully.

Conclusions

The selection by panthers of open habitats that include marsh–shrub–swamps and prairie–grasslands was a novel finding that may have ramifications on how resource-management agencies attempt to preserve, rehabilitate, and purchase habitat for panthers. For example, the U.S. Fish and Wildlife Service (USFWS) uses a compensation tool that generates the number of panther habitat units used to define impacts of development on panther habitat and subsequently recommend appropriate mitigation. The USFWS uses this tool in formulating biologically defensible opinions relating to federal actions that have an adverse impact on the Florida panther. The tool's current incarnation specifies that habitats selected by panthers should be ranked with higher scores than those used according to availability or that are avoided. Our findings, supported by data collected across the diel period, may merit review by the USFWS with regard to scores assigned to habitat containing marsh–shrub–swamps and prairie–grasslands, especially when interspersed with forested habitats.

Reclassifying panthers and delisting involves establishing three viable populations of 240 panthers (subadults and adults) for at least 12 years (USFWS, 2008). Pumas rely on extensive, interconnected landscapes even to maintain minimal populations (Logan & Sweanor, 2001). For the Florida panther, whose habitat is much more fragmented than that of western pumas, the area of a male's home range is still 435–650 km^2 (Onorato *et al.*, 2010). This scale underscores the challenges faced by researchers and managers in Florida, who need to pursue coordinated objectives with regional governments and private entities to propagate expansion of the population from the confines of South Florida. Although suitable relocation sites have been identified in other southeastern states (Thatcher, Van Manen & Clark, 2006) and in central Florida (Thatcher, van Manen & Clark, 2009), sociopolitical challenges must be overcome for a release program to be successful.

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Figure 1. Map depicting the breeding range of the Florida panther (lightly shaded green; Kautz *et al.* 2006) and major public land holdings (darker shading) in South Florida, USA. Key to abbreviations: BCNP, Big Cypress National Preserve; CREW, Corkscrew Regional Ecosystem Watershed; EVER, Everglades National Park; FSPSP, Fakahatchee Strand Preserve State Park; FPNWR, Florida Panther National Wildlife Refuge; OK Slough SF, Okaloacoochee Slough State Forest; PSSF, Picayune Strand State Forest. The Caloosahatchee River is the northern border of the present breeding range of the Florida panther. Panthers in Everglades National Park are partially isolated from the core population in Southwest Florida by the semi-permeable barrier of the Shark River Slough.

Figure 2. Comparison of habitat selection within land-cover classes during different times of day by Florida panthers, fitted with GPS collars, in South Florida. Land-cover classes selected for by panthers (ratios < 1, $P < 0.05$) included upland forests, wetland forests, prairie–grasslands and marsh–shrub–swamps. Dashed line represents the border between distance ratios that were < or > 1. Landcover classes used differently ($P < 0.05$) between night and day are denoted with *.

Figure 3. Distribution of the distances (m) of GPS locations of Florida panthers from forest patches in South Florida. A total of 23,850 of 58,212 locations were in nonforested patches. A total of 13,811 and 10,039 locations were in nonforested patches during the night and day, respectively.

Table 1. Data describing locations collected from Florida panthers fitted with GPS collars by the Florida Fish and Wildlife Conservation Commission, February 2005–February 2009 in South Florida, USA. The GPS collar models are described in the text; GPS days include the total number of days of GPS data collection. Daytime fixes were collected from 0700 hours to 1859 hours.

ID	Sex	Age	GPS Model	GPS Days	Fix Schedule	Fixes Acquired	Percent Fix Success	Percent Fix Night:Day
FP48	F	13.3	Tellus	610	hourly	10732	74.4	51:49
FP94	F	6.5	Tellus	427	hourly	8286	80.9	51:49
FP110	F	5.5	Lotek	504	7 hours	1156	66.6	51:49
FP113	F	4.5	Lotek	310	7 hours	743	69.7	53:47
FP121	F	4.5	ATS[a]	174	7 hours	366	58.7	55:45
FP128	F	6.5	ATS	230	7 hours	438	55.4	55:45
FP130	M	2	Tellus	429	hourly	8253	81.0	54:46
FP131	M	6.5	Tellus	394	hourly	7358	77.8	51:49
FP135	M	2.75	Telonics	253	7 hours	529	60.9	59:41
FP137	M	3.5	Tellus-GSM	236	2 hours	2038	72.1	52:48
FP142	F	2.5	Lotek	273	3 hours	1530	69.9	54:46
FP143	M	1.5	Lotek	341	7 hours	690	58.9	56:44
FP146[b]	M	3	Telonics	835	7 hours	1919	67.0	56:44
FP148	F	2.5	ATS	311	7 hours	583	54.6	58:42
FP149	F	2	ATS	114	7 hours	283	72.2	57:43
FP155	M	2.5	Tellus-GSM	285	15 min/hourly[c]	5689	73.5	54:46
FP156	M	2.5	Tellus-GSM	203	hourly/4 hours[c]	469	29.4	54:46
FP157	M	3	Tellus-GSM	113	30 min/hourly[c]	1966	67.4	51:49
FP160	F	5	Tellus-GSM	118	hourly/4 hours[c]	481	43.7	56:44
FP167	M	2.5	Tellus-GSM	261	hourly/4hours[c]	4705	5872	54:46

[a]Advanced Telemetry Systems.

[b]FP146 was initially collared on 27 February 2006 with a Telonics GPS collar and recollared on 29 January 2007 with another Telonics GPS collar allowing for a continuous data set of 835 days.

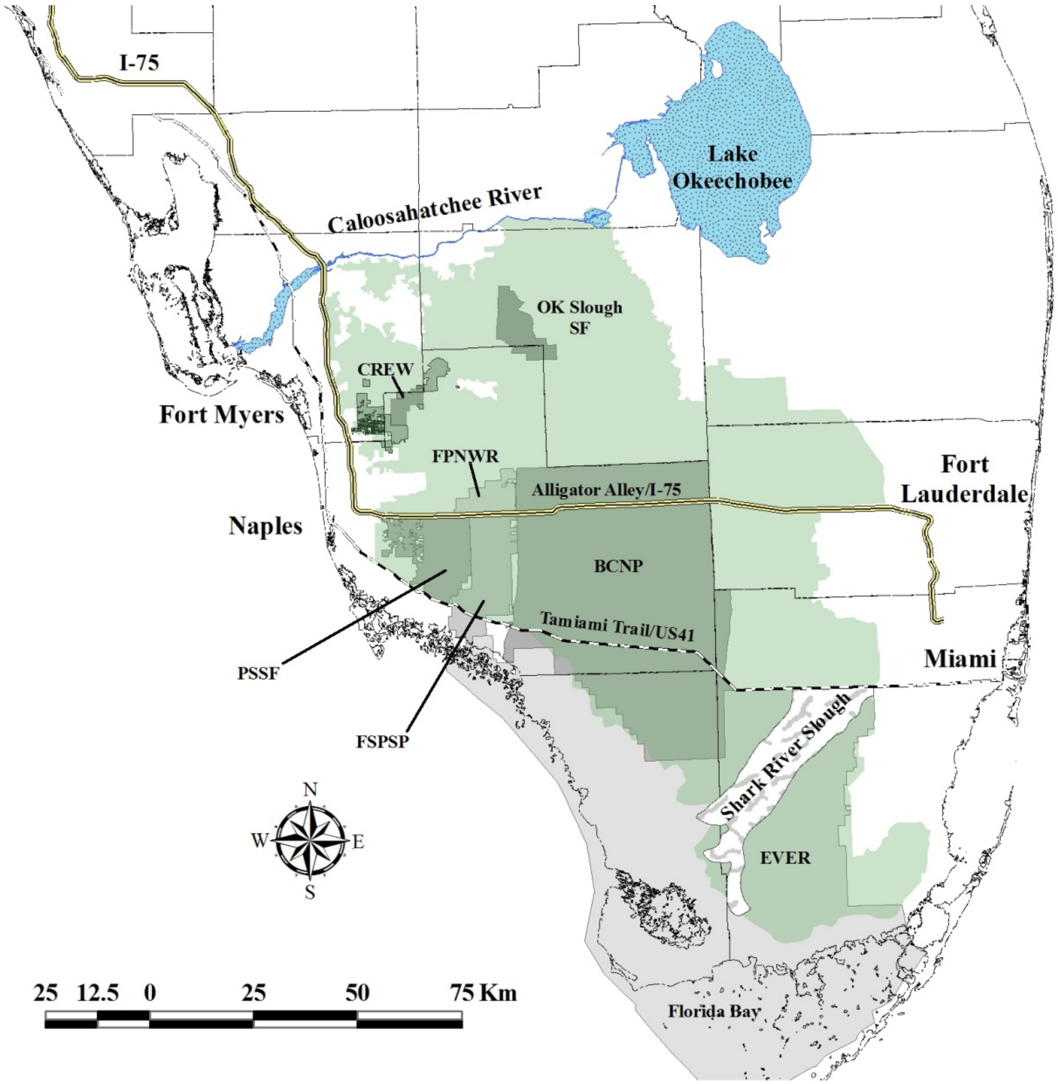
[c]These Tellus-GSM collars collected data across a range of fix schedules (min/max) for a concurrent project. A majority of the locations for these collars were collected using the longer fix attempt interval.

Table 2. Third-order habitat selection determined via Euclidean distance analysis using GPS location data from 20 independent Florida panthers monitored in South Florida. Ratios < 1.0 indicate habitat preference, whereas ratios > 1.0 indicate avoidance ($P < 0.05$). Habitats sharing any common letter rank were similarly preferred or avoided ($P > 0.05$, Bonferroni adjustment) or used in proportion to their availability.

Habitat	Ratio	*P*-value	Ranks
Upland forest	0.532	< 0.001	A
Wetland forest	0.620	< 0.001	AB
Prairie–grassland	0.785	0.001	B
Marsh–shrub–swamp	0.799	0.004	BC
Agricultural	1.039	0.618	C
Other	1.047	0.555	C

Table 3. Forest patch size selection determined via Euclidean distance analysis using GPS location data from 20 independent Florida panthers monitored in South Florida. Ratios < 1.0 indicate habitat preference and ratios > 1.0 indicate avoidance ($P < 0.05$).

Forest patch size (ha)	Number of patches	Mean patch size (ha)	Sum (ha)	Ratio	*P*-value
≤ 1.0	646353	0.2	119639	0.893	0.025
> 1-5	42937	2.2	92623	0.920	0.142
> 5-10	7774	7.0	54286	0.906	0.023
> 10-100	8187	27.1	221989	0.891	0.100
> 100-500	838	200.3	167838	0.947	0.309
> 500-1000	88	707.5	62259	0.979	0.586
> 1000	94	6431.0	604509	0.710	0.010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Caloosahatchee River
OK Slough SF
CREW
Fort Myers
FPNWR
Fort Lauderdale
Alligator Alley/I-75
Naples
BCNP
Tamiami Trail/US41
PSSF
Miami
FSPSP
Shark River Slough
N
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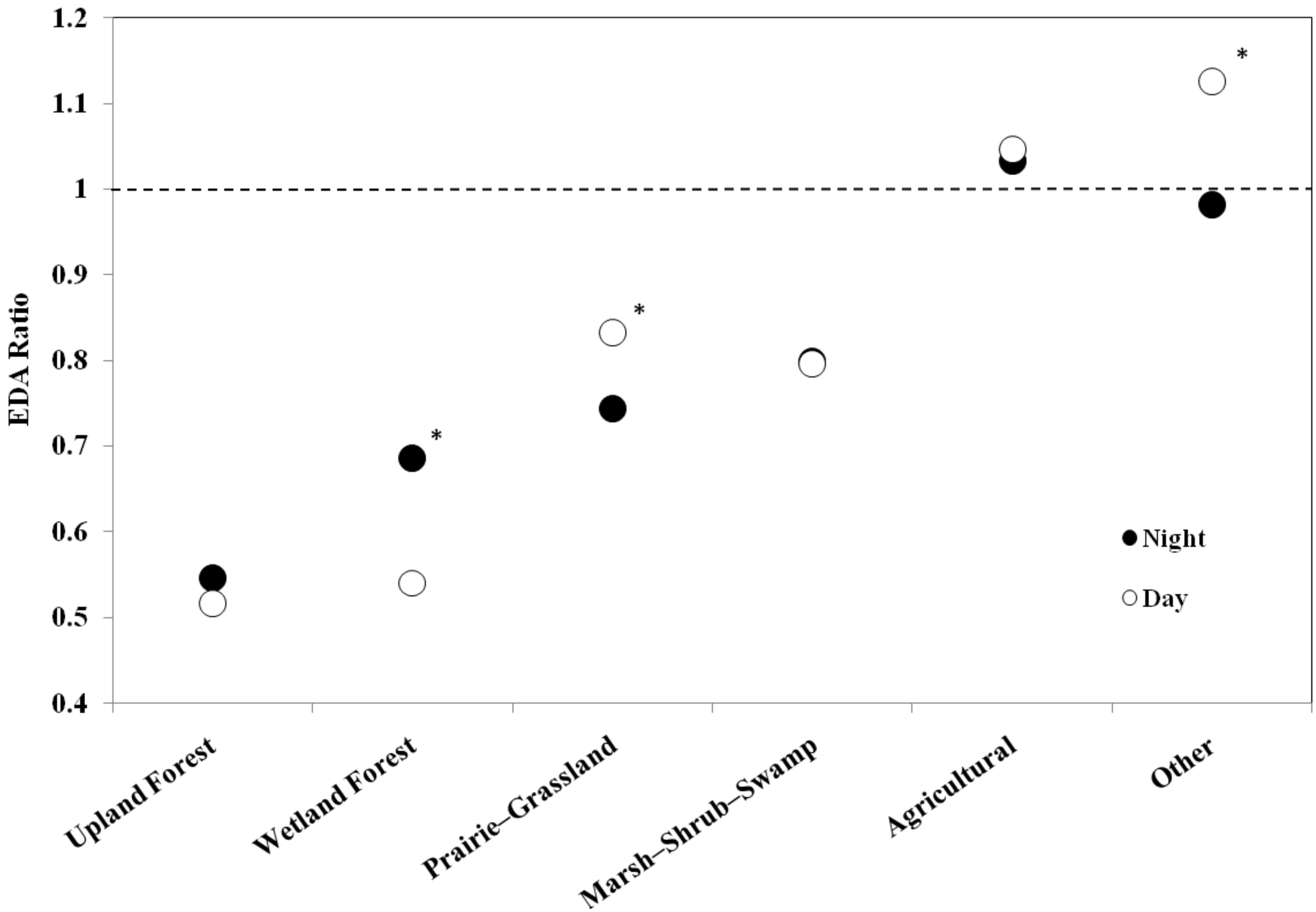
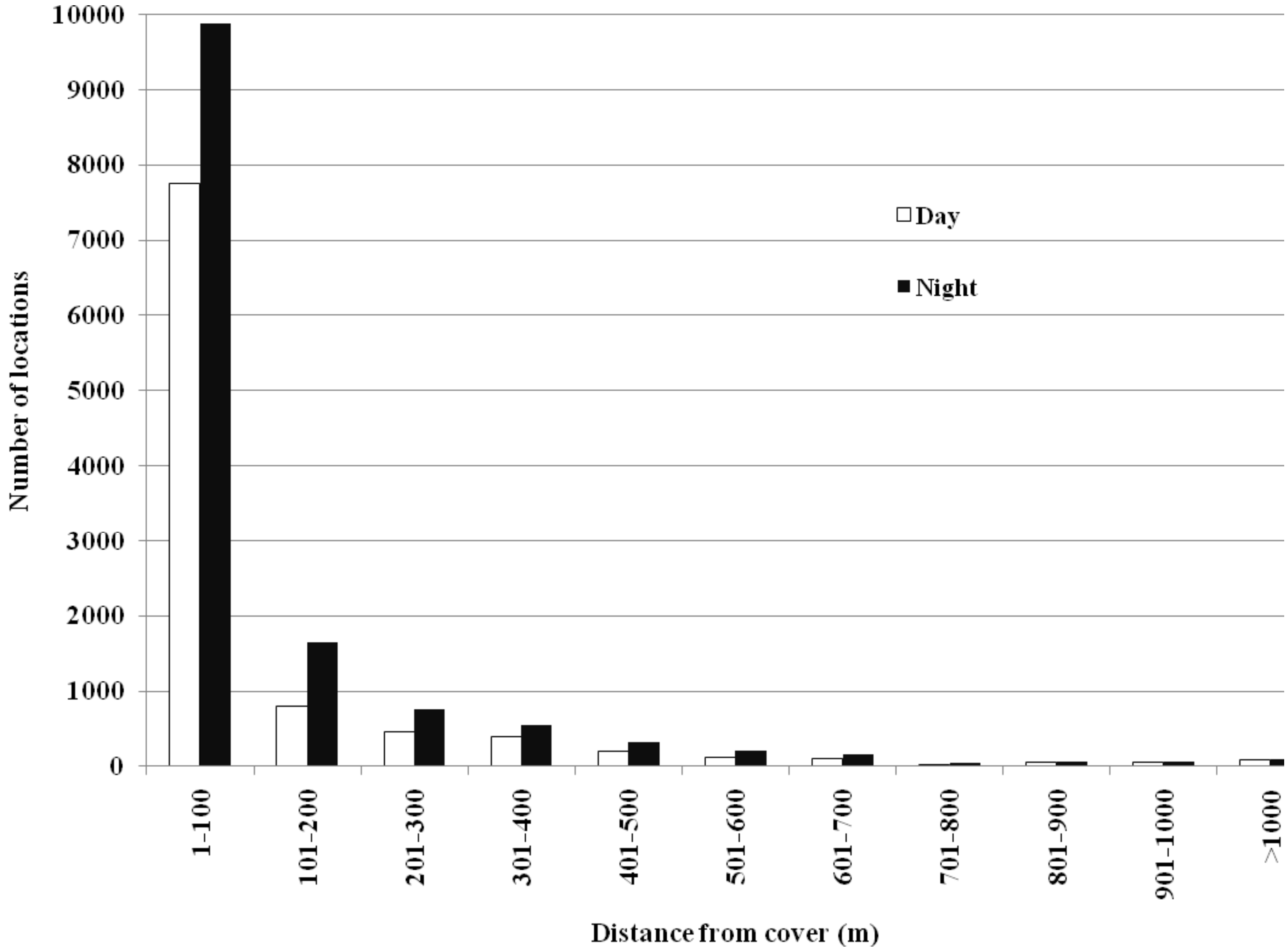
S
EVER
25 12.5 0 25 50 75 Km
Florida Bay

1


1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
EDA Ratio
*
*
*
*
Night
Day
Upland Forest
Wetland Forest
Prairie–Grassland
Marsh–Shrub–Swamp
Agricultural
Other

1



Number of locations
10000
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
Day
Night
1-100
101-200
201-300
301-400
401-500
501-600
601-700
701-800
801-900
901-1000
>1000
Distance from cover (m)

Onorato *et al.* Supplementary Material

Methods

GPS fix schedules

Fix schedules programmed into GPS collars varied, but all were programmed to attempt fixes throughout the diel period via either a frequent- or staggered-fix schedule. On a frequent-fix schedule, fixes were attempted, e.g., hourly or every 4 hours; on a staggered-fix schedule, attempts were made, e.g., every 7 hours, which, over 5 days, results in 1 fix attempt in every hour of a 24-hr diel period. Followit Tellus-GSM collars sent locations via e-mail when panthers were within range of a GSM (Global System for Mobile Communications) mobile telephone tower. Most data obtained with these GSM collars were collected either every two hours or hourly.

Habitat analyses

We used GPS locations to estimate each panther's home range with 100% minimum convex polygons (MCP, Fig. S1) in ArcGIS 9.3 using Hawth's Tools (Beyer, 2004). We used MCP estimates because they were deemed more reliable than kernel density estimators in assessing habitat availability for each panther. In a study of habitat use, as noted by Land *et al.* (2008), excluding areas used by panthers—as would have occurred had we implemented a fixed-kernel home-range estimator—is more problematic than including areas not used by panthers. Also, for the African lion (*Panthera leo*), Hemson et al. (2005) noted that estimates of home ranges using kernel-density estimators with least-squares cross validation could be unreliable when applied to large GPS data sets. We believe our GPS data for the Florida panther would have been similarly affected by these issues if we had implemented a fixed-kernel technique. Additionally, we used MCP home ranges because we wanted our analysis to be comparable to that of Land *et al.* (2008), the only other published study of habitat selection in panthers that used GPS data.

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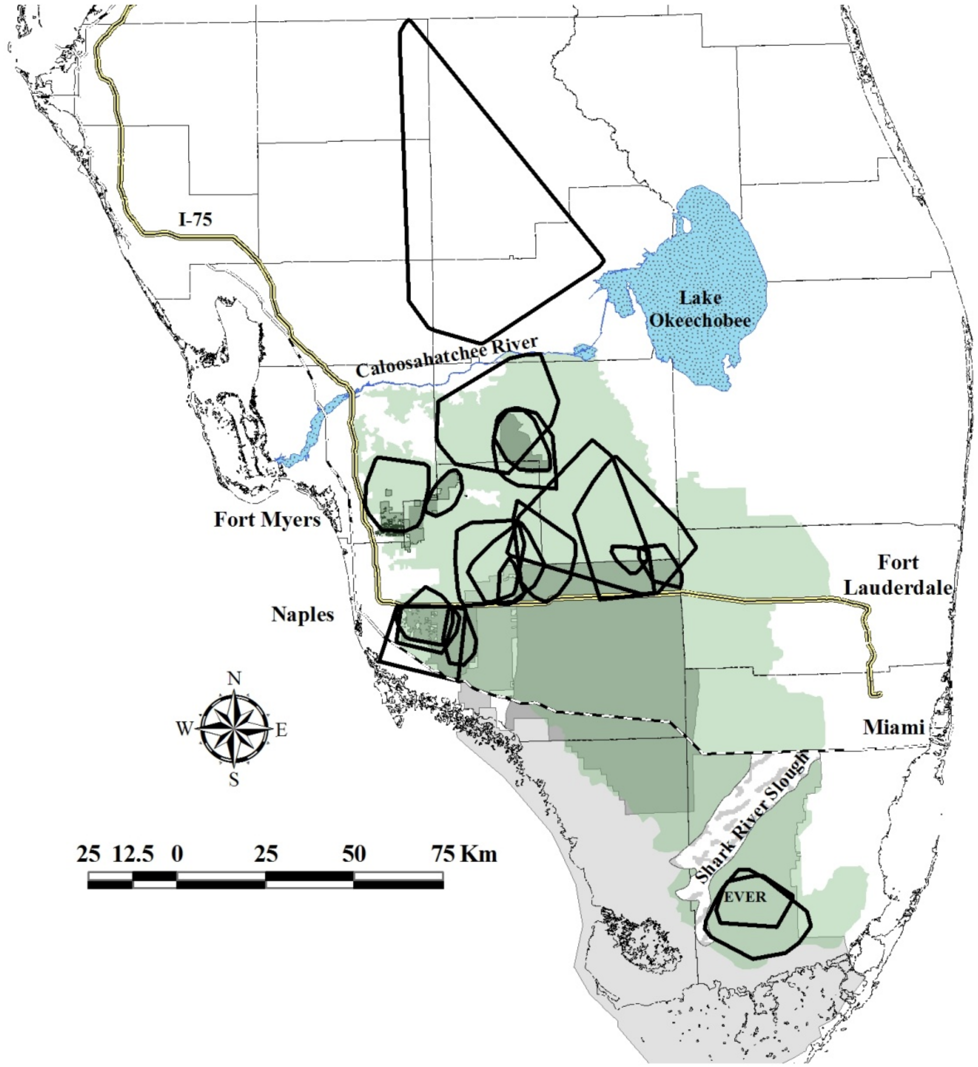
Figure S1. Map depicting the 100% minimum convex polygon (MCP) home ranges for 20 independent Florida panthers fitted with GPS collars in South Florida, February 2005–February 2009. These ranges were used to determine habitat available to panthers, which was then used in assessments of habitat selection by Euclidean distance analysis.

Table S1. Land cover classes from Kautz et al. (2007), reclassified for the analysis of habitat selection by Florida panthers. The forest patch category was used to define patches of habitat inclusive of forests (0 = nonforested; 1 = forested). Forest land cover classes not found within the study area (e.g., bottomland hardwood forest) were not included.

Original Land cover Class	Forest Patch Land cover Class	Reclassified Land cover Class
Coastal strand	0	Other
Sand/beach	0	Other
Xeric oak scrub	0	Other
Sand pine scrub	0	Other
Sandhill	0	Other
Dry prairie	0	Prairie –grassland
Mixed pine-hardwood forest	1	Upland forest
Hardwood hammocks and forest	1	Upland forest
Pinelands	1	Upland forest
Cabbage palm–live oak hammock	1	Upland forest
Tropical hardwood hammock	1	Upland forest
Freshwater marsh and wet prairie	0	Marsh–shrub–swamp
Sawgrass marsh	0	Marsh–shrub–swamp
Cattail marsh	0	Marsh–shrub–swamp
Shrub swamp	0	Marsh–shrub–swamp
Bay swamp	0	Other
Cypress swamp	1	Wetland forest
Cypress/pine/cabbage palm	1	Wetland forest
Mixed wetland forest	1	Wetland forest
Hardwood swamp	1	Wetland forest
Hydric hammock	0	Other
Bottomland hardwood forest	0	Other
Salt marsh	0	Other
Mangrove swamp	1	Other
Scrub mangrove	0	Other
Tidal flat	0	Other
Open water	0	Other
Shrub and brushland	0	Other
Grassland	0	Prairie–grassland
Bare soil/clearcut	0	Other
Improved pasture	0	Prairie–grassland
Unimproved/woodland pasture	0	Prairie–grassland
Sugar cane	0	Agriculture
Citrus	0	Agriculture
Row/field crops	0	Agriculture
Other agriculture	0	Agriculture
Exotic plants	0	Other
Australian pine	1	Other
Melaleuca	1	Other
Brazilian pepper	0	Other
High-impact urban	0	Other
Low-impact urban	0	Other
Extractive	0	Other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Lauderdale
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1