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Insight

Shopping Centers as Panther Habitat: Inferring Animal Locations from Models

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ABSTRACT. A recent model of Florida panther (*Puma concolor coryi*) habitat erred in arbitrarily creating buffers around radio locations collected during daylight hours on the assumption that study animals were only at rest during these times. The buffers generated by this method likely cause an overestimation of the amounts and kinds of habitats that are used by the panther. This, and other errors, could lead to the impression that unfragmented forest cover is unimportant to panther conservation, and could encourage inaccurate characterizations of panther habitat. Previous 24-hour monitoring of activity and activity readings made during routine telemetry flights indicate that high levels of activity occur in the early morning hours. Literature on the behavior of the species does not support the creation of large buffers around telemetry locations to compensate for the lack of nighttime telemetry data. A thorough examination of ongoing studies that use global positioning systems may help calibrate future Florida panther habitat models.

INTRODUCTION

The main objective of resource selection studies is to determine where, how, and why animals make choices in the use of their environment. An important conservation issue is the determination of critical habitat for imperiled species. This is especially true for small populations, such as the Florida panther (*Puma concolor coryi*), that largely depend on private lands for current and future survival (Maehr 1990). Wide-ranging species and those that inhabit remote areas can be difficult to monitor. Aerial daytime telemetry data, despite their limitations (White and Garrott 1990, Land 1994, Maehr 1997), have been essential in determining panther spatial dynamics and in facilitating conservation planning (Hoctor et al. 2000, Maehr et al. 2002). Equipment limitations and safety issues related to working in darkness have precluded collection of location data at night. Comiskey et al. (2002) assumed that all daytime telemetry locations reflected resting sites and, through modeling, attempted to account for nocturnal habitat use and improve upon traditional methods of panther habitat analysis. The Comiskey et al. (2002) model is extremely simple: it draws lines between observations and creates buffers (up to 6.6 km in radius, 137 km^2) around each observation. Thus, the buffers include estuaries, vegetable farms, businesses, and highways as potential panther habitat without evidence of actual use or importance.

Although Comiskey et al. (2002) ultimately agree with the decades-old view of the Florida panther as a creature of the landscape (Maehr 1990, Land 1994, Maehr and Cox 1995, Maehr 1997), they make the novel claim that panthers use much more habitat at night than has been revealed by aerial telemetry data. We agree, as earlier works have demonstrated, that "the primary needs of panthers are an extensive area with a high degree of connectivity and minimal disturbance, the availability of large prey, and cover for denning and resting" (Comiskey et al. 2002). However, we do not agree that it is defensible to use such large buffers to capture habitats that are not otherwise identified by aerial telemetry or by any direct means, and that are likely of no value to panthers.

With the exception of the Everglades, Florida was almost entirely forested before European settlement (Brown 1909, Harlow 1965, Davis 1967). Clearly, other vegetation types than forest contribute to

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individual home ranges and support potential prey and movements, but some of these habitats (i.e., agricultural land, suburbs) have largely replaced much of the original forests in which the subspecies evolved. Only rarely have panthers been documented in these places (Maehr 1997). Urban areas, in particular, are unlikely to offer the "minimal disturbance" that Comiskey et al. (2002) claim is needed by the panther and should be excluded from consideration in resource selection studies.

The following analysis is the first examination of Florida panther activity readings that were collected during routine telemetry flights conducted more than a decade ago. We also examine selected peripheral locations with associated buffers that have been suggested as habitat by Comiskey et al. (2002) and that provide examples of how their model can be misleading. We hypothesize that the pattern of activity revealed by aerial telemetry should mirror the results of activity monitoring conducted on the ground (Maehr et al. 1990), with panthers remaining active well into daylight hours, and with most locations being associated with forest cover.

METHODS

We examined the aerial telemetry data collected by the Florida Game and Fresh Water Fish Commission during daylight hours between 1986 and 1993, primarily in southwest Florida, to gain insight into the relation between aerial location data and panther activity. These years and area were examined because activity readings are no longer recorded by panther researchers, because the radio collars used today no longer contain activity switches (D. Land, Florida Fish and Wildlife Conservation Commission, *personal communication*), and because researchers in southeastern Florida did not collect these data during their telemetry flights.

From 1986 through 1993, all radio collars deployed on panthers contained mercury tip switches that were sensitive to up-and-down head movements. The signal pulse rates changed as the transmitters passed through a horizontal plane (see Maehr et al. 1990 for a detailed description of the equipment and methods). A higher rate of pulse-rate change reflected more head movement of the panther. During each flight and during the process of pinpointing the location of each panther, researchers also noted whether or not the panther's radio signal was actively changing. For a location to be "active," the pulse-rate changes were required to be frequent and persistent during the few minutes that the researcher was circling about 150 m above the ground in a fixed-wing aircraft over a study animal. Otherwise, the location was recorded as "inactive" even if a few pulse-rate changes occurred. Specific behaviors were not attributed when an "active" designation was determined (Janis et al. 1999). At the same time, the researcher recorded the best estimate of the habitat type from which the radio signal emanated and plotted the location on a U.S. Geological Survey (USGS) 7.5-inch quadrangle topographic map (White and Garrott 1990). These locations were subsequently defined as Universal Transverse Mercator (UTM) coordinates and entered into a database.

We used the data from 35 radio-collared panthers that were studied between 1986 and 1993. For each panther, activity and habitat data were categorized by time of day (before 0600, 0601–0700, 0701–0800, 0801–0900, 0901–1000, 1001–1800, after 1800). The time periods represented by single hours are those that contained 85.2% of all aerial telemetry locations. More than 99% of all locations were collected between 0601 and 1800. These times allowed the researcher to clearly see the ground and estimate the habitat type associated with each radio location. Habitat associations were classified as "forest" or "non-forest" for these same time intervals. For each panther and time interval, we then determined the proportion of locations that were in forested habitat. We excluded panthers from the analysis if they wore known malfunctioning radio collars or if they were represented by fewer than 40 radio locations. Locations that did not have associated activity or habitat data were excluded from analyses of those respective variables. Activity rates for each time period are presented as means of activity rates (with standard error) calculated for all panthers that were represented in that time interval.

We also used ArcView 3.2™ and the Patch Analyst Extension™ (ESRI, Redland, CA) to examine the composition of three circular areas with 6.6-km radius circles (137 km^2) that correspond to male panther (Nos. 28, 64, 92) radio locations determined by aerial telemetry along the western edge of occupied range in southwestern Florida. These areas were suggested by Comiskey et al. (2002) as panther habitat and fall within the southwestern Florida urban/wildland interface where the issuing of development permits is contentious. Land cover data were taken from 1995 Thematic Mapper imagery with 30-m resolution that were updated with digital orthographic quarter quadrangle (DOQQ) aerial photography and enhanced with 2003 Landsat Thematic Mapper satellite imagery (Florida Fish and Wildlife Conservation Commission 2004). Habitats that we considered as native or potentially used by the panther included hardwood swamp, pinelands, cypress swamp, mixed wetland forest, dry prairie, unimproved pasture, improved pasture, hardwood hammock, freshwater marsh and wet prairie, shrub swamp, shrub and brushland, cypress–pine–palm forest, and mangrove swamp. Denatured habitats included high-impact urban, low-impact urban, bare soil/clearcut, open water, row crops, other agriculture, and extractive.

RESULTS

Activity

Panthers 24 and 53 were excluded, the former because its radio-collar had a malfunctioning tip switch, and the latter because there were too few data collected. The 33 other panthers in the analysis were represented by 14 551 radio locations that could be used in the analysis of activity. The proportion of active locations ranged from just over 0.20 to over 0.50, with the highest rates of activity recorded between 0600 and 0800 h and after 1800 h (Fig. 1). Small sample sizes for the two periods between 1800 h and 0600 h resulted in large standard errors for these periods. The remaining data mirror the crepuscular activity pattern revealed by Maehr et al. (1990), and forest was associated with 94–100% of all locations. These measurements may be slightly biased toward non-forested habitat, however, because we included “shrub marsh” as non-forest. This habitat is typified by herbaceous vegetation and scattered shrubs that can create a dense, woody canopy.

Habitat Composition

The three 137-km^2 circles were composed of 36–47% artificial habitat (Table 1). Semicircles of these areas revealed differing land cover patterns (Fig. 2). The mean proportion of denatured habitat was 0.52 (SE = 0.04) in western semicircles vs. 0.29 (SE = 0.02) in eastern semicircles. Forest cover averaged 0.37 (SE = 0.04) in western semicircles and 0.56 (SE = 0.04) in eastern semicircles. Increasing habitat fragmentation and urban uses characterize the landscape nearby and to the west of these points, whereas areas to the east exhibit increasing forest cover and less influence by humans. No other radio locations of panthers were documented to the west of the centers of the circles in Fig. 1.

DISCUSSION

The basic problems that Comiskey et al. (2002) have not solved are demonstrating what panthers do at night and where they do it. The Comiskey et al. (2002) buffer-based analysis is another way of examining the same temporally constrained data but it does not support their conclusion that panthers use non-forested areas at night, a period when telemetry or other means of observation have been unavailable. Although our analysis suggests some likelihood that daytime radio locations are not dissimilar to areas used by panthers at night, global positioning system (GPS) radio collars currently deployed as part of a feasibility study have not returned enough data to fully address this question. However, a cursory review of data collected to date suggests that nighttime locations are not dramatically different from those collected during the day (D. Land, Florida Fish and Wildlife Conservation Commission, *personal communication*, 29 June 2004). Furthermore, Maehr et al. (1990) found that panthers were very active around sunrise, a time of day that is well represented by aerial telemetry data but that Comiskey et al. (2002) claim is missing from previous analyses of panther habitat use. Although it is not known exactly what behavior each animal was engaged in at the time these data were collected, it likely included a variety of activities, e.g., walking, hunting, feeding, grooming, and resting. Clearly, daytime telemetry data include periods during which panthers are quite active.

There are other fundamental difficulties with Comiskey et al. (2002). The authors claim that “scats, tracks, urine markers, and kill sites” were used as dependable indicators of temporal habitat use and activity; however, the methods give no hint of the source of such data or how they were used in the model. In addition, they do not account for the dramatic variation in occupied panther range that follows a trend of declining forest from northwest to southeast (Maehr 1997), and no attempt was made to evaluate the effects of habitat aggregation on the sensitivity of the analysis with regard to study area boundaries (Erickson et al. 2001). Because Comiskey et al. (2002) arbitrarily used a 25 000-km^2 study area with tremendous landscape variation (virtually all of south Florida), their results likely produced spurious inferences (Johnson 1980, Porter and Church 1987). This geographic lumping creates a false impression of habitat use by generating an average panther. Furthermore, temporal and spatial differences in availability may affect individual animals' selection of habitat (White and Garrott 1990). Clearly, the habitat that is available to a panther in the mostly treeless Everglades is different from what is available 100 km away in the forests of Collier County. For these reasons alone, there is no reason to have any faith in the Comiskey et al. (2002) results.

Fig. 1. Activity rates of Florida panthers in southwest Florida as determined by 1986–1993 aerial telemetry monitoring, and compared to a 24-h activity profile developed by Maehr et al. (1990). Both graphs reveal activity peaks during times when telemetry flights are conducted.

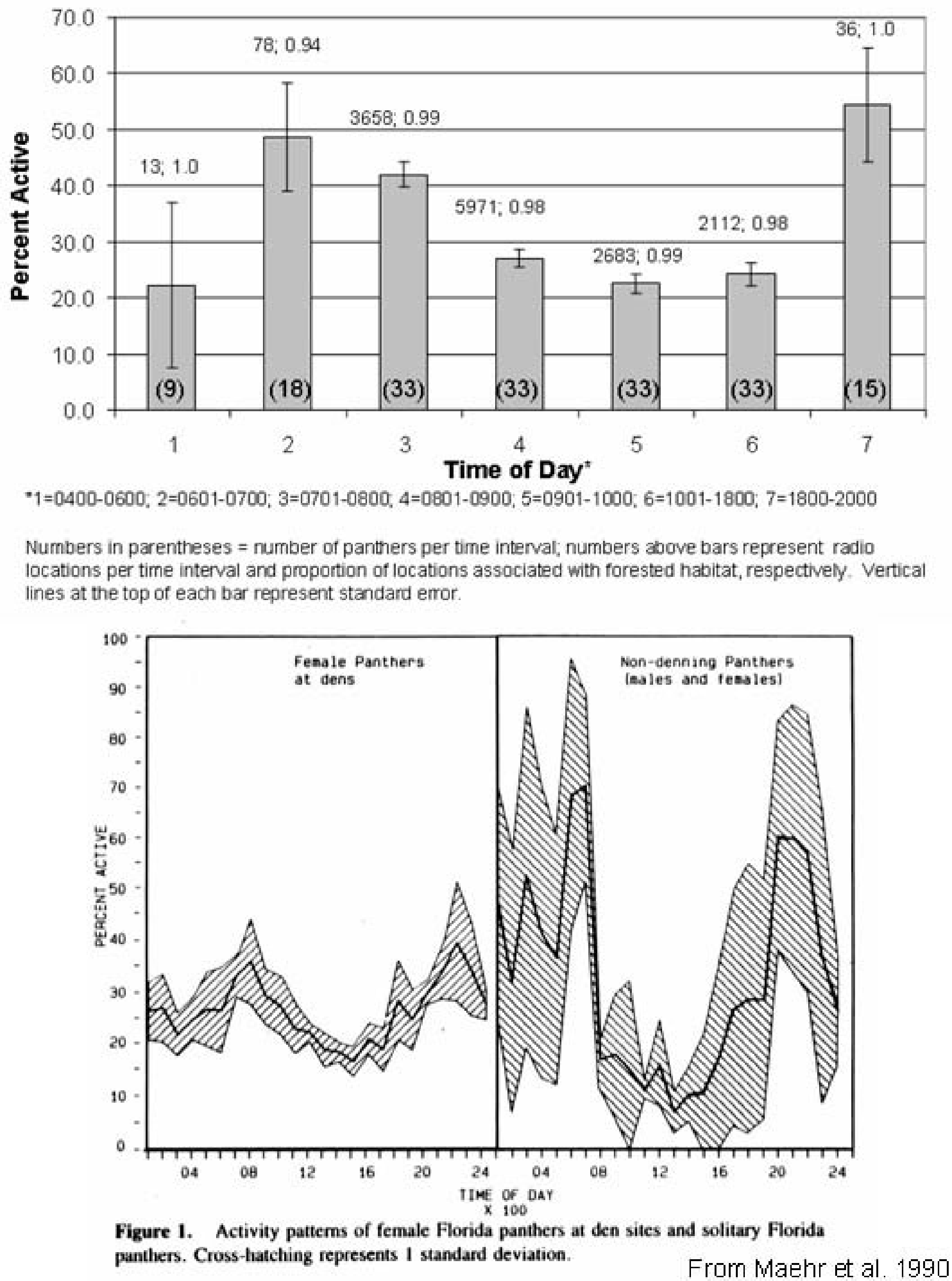

Fig. 2. Location and generalized composition of three circular areas (based on the 137-km^2 buffer area recommended by Comiskey et al. (2002) surrounding a male panther radio location (black dot) at the center. Green areas represent native cover and pasture. White areas include urban, bare soil, open water, row crops, and extractive industries.

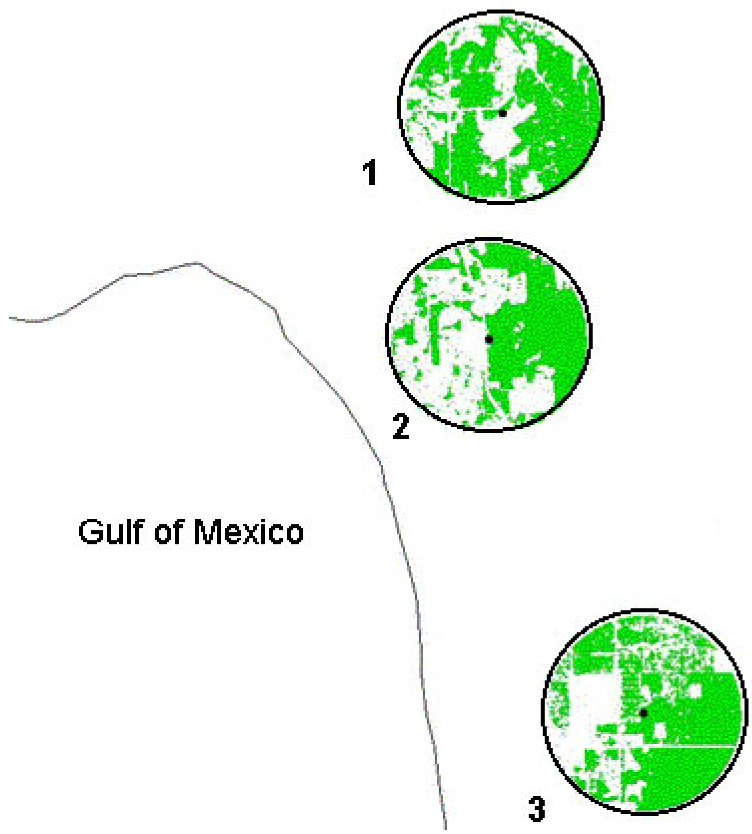

Table 1. Attributes of 137-km^{2}circles and semicircles associated with three peripheral male Florida panther locations in southwestern Florida. Numbers in parentheses are mean standard errors. Denatured habitats include urban, bare soil, open water, row crops, and extractive industries.

Area	Total circle denatured	Total circle forested	Semicircle west denatured	Semicircle west forested	Semicircle east denatured	Semicircle east forested
1	0.38	0.44	0.40	0.46	0.35	0.42
2	0.47	0.43	0.63	0.25	0.31	0.60
3	0.36	0.53	0.52	0.40	0.21	0.65
Mean std. error	0.40 (0.02)	0.47 (0.02)	0.52 (0.04)	0.37 (0.04)	0.29 (0.02)	0.56 (0.04)

Although Maehr et al. (1990) emphasized the importance of forests as daytime rest cover, they did not determine the habitats associated with the 24-h activity data collected through intensive ground telemetry. This was because logistical constraints related to tracking in darkness prevented the determination of habitat. In contrast, aerial telemetry offers the opportunity to consider the relation between activity rate and habitat during times of day that the crepuscular panther is most active (Maehr et al. 1990). Certainly, error rates of 200–300 m may be associated with aerial locations, but this is insufficient reason to conclude that a buffer of up to 6600 m (Comiskey et al. 2002) accounts for nighttime habitat use. Whereas anecdotes may refer to the ability of panthers to travel long distances at night (Young and Goldman 1946), the routes, habitats, and frequency of these bouts have not been measured or suggested. In other words, there is no behavioral foundation upon which to build the Comiskey et al. (2002) model. Had Comiskey et al. (2002) used “mean error of telemetry locations” (Rettie and McLoughlin 1999), the buffers selected would have been more than an order of magnitude smaller, and the results of habitat analyses would have been different, as would the conservation implications. Finally, that all other telemetry locations were to the east of peripheral coordinates (Fig. 2) suggests avoidance by panthers of landscapes dominated by denatured habitats. Although it is unknown to what extent a panther may wander from a daytime location, there is no evidence to suggest a pattern of use in the large circular areas suggested by Comiskey et al. (2002). Were this not the case, there would likely be many radio locations recorded to the west of the westernmost documented panther in southwest Florida.

When the time periods with fewer aerial locations and greater standard errors are excluded from consideration, the pattern of activity remains a remarkable match to that of panthers monitored using other methodologies (Maehr et al. 1990). These times capture the crepuscular hours during which panthers are most active and suggest that forest cover is the dominant habitat used. Furthermore, many of the daytime telemetry locations obtained from fixed-wing aircraft were collected during periods of peak activity (Maehr et al. 1990)—particularly those collected in the morning between 0600 and 0800 h. Thus, previous analyses based on these data reflect a wider range of behaviors than just resting. That nearly all locations were collected in forest areas during crepuscular and daytime hours simply suggests that there is no obvious distinction between the habitats used during peak activity periods and low activity periods in southwest Florida.

Other studies have shown that cougars tend to be crepuscular in their patterns of activity (van Dyke et al. 1986, Beier et al. 1995). Hopkins (1989) found that California cougars were most active during crepuscular hours and least active between 2200 and 0500 h. More recently, Sweanor et al. (submitted) noted that, although GPS-instrumented cougars in southern California tended to be active at night and during crepuscular hours, they selected woodlands and woodland edge habitats during these times. Interestingly, they speculated that the preference for wooded habitats, regardless of time of day, might have been even stronger if not for fix-rate biases related to GPS technology (fewer successful fixes under tree canopy). They also found that California cougars were selective in their use of habitat. Murphy et al. (1999) suggested that cougars in the Yellowstone ecosystem generally avoid grasslands and agricultural lands, despite the presence of abundant prey, because of insufficient hunting cover. When kills are made, cougars drag carcasses to the nearest cover, usually no more than 80 to 93 m (Beier et al. 1995, Robinette et al. 1959), and they spend up to 5 days with their kills (Beier et al. 1995) and are found no farther than 400 m from them. The longest recorded drags of kills were 335 m (Robinette et al. 1959) and 350 m (Beier et al. 1995). If similar patterns occur in Florida, then most radio locations collected during the day are likely identical to, or relatively close to, nocturnal and crepuscular locations. This body of literature is in agreement with the findings of Maehr and Cox (1995) and Maehr et al. (1991), and in disagreement with Comiskey et al. (2002), who suggested that panthers use habitat in a way that reflects the composition of the home range (i.e., no selection for habitat).

The conclusion by Comiskey et al. (2002) that panther telemetry data are useful in describing the distribution pattern of panthers in Florida is not new. However, the unsupported idea that panthers can “thrive” in non-forested landscapes should not be allowed to divert current conservation priorities that protect forests in south Florida. As has already been demonstrated in the Everglades, landscapes dominated by non-forested habitats cannot be relied upon to support sustained occupation (Bass and Maehr 1991). The release in 1995 of two female Texas cougars (*P. concolor* *stanleyana*) into the Everglades as a component of Florida panther genetic restoration is the only reason panthers exist in Everglades National Park today. Panther conservation needs will not be served by focusing on panthers in areas where periodic extinctions have occurred (Bass and Maehr 1991) and merging the results with those from other areas. Garton et al. (2001) stressed the need to use radiotelemetry findings to better understand source–sink population dynamics. In contrast, conservation strategies in the more forested northern fringes of occupied panther range are critical to ensuring the long-term survival of the panther (Maehr and Lacy 2002). The evidence suggests that the importance of forest is beyond any reasonable doubt. On the other hand, there is no evidence to support the idea that panthers abandon forested cover at night to become habitat generalists. In the contentious world of development permit issuing in south Florida, a view of the panther as, not only tolerant of, but "thriving" in landscapes with less than 15% forest (Comiskey et al. 2002) is an invitation for developers to push for more fragmentation of panther habitat, and could be used to cripple regulatory agencies from effectively opposing such unwarranted human sprawl. As Maehr et al. (2001) observed, fluctuating panther populations typify areas that offer <50% forest cover. Adherence to the Comiskey et al. (2002) model could also identify as important panther habitat extensive tracts of human-altered landscapes that have limited or no benefits for the panther population and that would serve only to complicate conservation initiatives by turning the panther into a greater liability for private landowners and land managers. As Erickson et al. (2001) observed, "In light of model selection limitations, professional judgment is important in establishing predictors of selection. The variables to consider should be limited to a reasonable set of possibilities, with decisions based on the knowledge of the animal under study."

Unfortunately, the view of panther habitat offered by Comiskey et al. (2002) is based on assumptions that are clearly false: that panther habitat is anything between two estimated telemetry locations or anything up to 6.6 km of an estimated telemetry location. Instead of adding to a body of knowledge that will become increasingly important for local, regional, and interstate planning, this paper creates an argument that is based on an indefensible view of panther ecology. It does not help us understand the over-arching patterns of panther abundance and distribution. However, it is possible that the model offered by Comiskey et al. (2002) will prove to be useful after it is calibrated with the best available data. Interestingly, the maximum distances that cougars drag kills is remarkably similar to the mean telemetry error of most aerial tracking studies. The use of this distance (80–350 m) might be a reasonable starting point as a telemetry location buffer. Perhaps, when the ongoing studies of the panther using GPS technology are concluded, an acceptable model of panther habitat use can be made.

Responses to this article can be read online at: http://www.ecologyandsociety.org/vol9/iss2/art9/responses/index.html

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