Vehicle-related mortality and road crossing behavior of the Florida panther

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GIS
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Road crossings
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ABSTRACT

The Florida panther (Puma concolor coryi) is a relatively well studied species and it is well established that the most important threat to panthers include limited habitat area and continued habitat loss and fragmentation. Despite the recognition that roads result in panther mortality and may limit panther movement there has been very limited research on the importance of roads. In the current study panther telemetry data from 1981 until 2004, detailed road networks and vegetation maps were used to determine vehicle-related mortality and road crossing behavior of the Florida panther. Differences by age and gender were determined, as well as the effect of road size. Results indicate that vehicle collisions are a major threat to the Florida panther population, especially adult males. Major roads present a stronger barrier to movement than minor roads, and the movement of females is more affected than that of males. Road networks in south Florida have essentially segregated the movement of the sexes and have fragmented the limited remaining habitat of the Florida panther.

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Introduction

One of over 20 subspecies of cougar (Puma concolor), the Florida panther’s (Puma concolor coryi) range once extended throughout most of the southeastern United States, including Louisiana, north to Tennessee, and east to the Atlantic as well as the entire state of Florida (FFWCC, 1999). Currently the Florida panther is considered one of the most publicized endangered animals in the United States, and there are an estimated 70 to 100 adult Florida panthers in their last remaining population in southwest Florida (Kautz et al., 2006).

The Florida panther is a relatively well studied species, but despite over 25 years of research some aspects of its habitat requirements remain poorly understood. Although inferences on panther dependence on forest cover have been made (Maehr & Cox, 1995; Kerkhoff, Milne, & Maehr, 2000), those conclusions have been criticized by those involved in panther research and recovery (Comiskey et al., 2002; Beier, Vaughan, Conroy, & Quigley, 2003). Despite this controversy it is well established that the most important threat to panthers include limited habitat area and continued habitat loss and fragmentation. In addition, roads have been recognized as an important factor to consider, but major assumptions have been made about the variability of the influence of roads by type with limited empirical evidence (Jordan, 1994; Maehr & Cox, 1995; Cramer, 1999; Cramer & Portier, 2001; Thatcher et al, 2006; Kautz et al., 2006).

A review of the past 25 years of Florida panther research and scientific literature (Beier et al., 2003) identified several major weaknesses in current research: (1) the findings that panthers prefer large forest patches and are reluctant to travel from forests are unreliable due to questionable analysis techniques, and (2) research on panther reintroduction in other areas has been severely lacking and little has been done on this area since Belden and Hagedorn (1993) and Jordan (1994). The review also identified issues of concern in panther research methodologies, some of which include the use of diurnal telemetry data to establish 24-h habitat attributes and patterns, the selective use of the telemetry dataset, the use of individual locations as the sampling unit, the currency of landcover data used in habitat analyses, and the calculation of home range size and its relationship to amount and fragmentation of forest cover. Some of these criticism presented by the review have been addressed by several recent studies based on new data (Land et al., 2008) as well as re-analysis of existing data (Cox, Maehr, & Larkin, 2006).

A lack of consistent habitat knowledge can lead to continued fragmentation and destruction of the Florida panther’s last occupied available habitat, and the importance of roads in this context has not been determined. A solid understanding of the influence of

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roads is necessary to determine the viability of the current population in south Florida, to add to the existing knowledge base on panther–habitat relationships, and to identify possible reintroduction areas necessary to reestablish a successful population. The research goal of the current study is to develop a better understanding of the influence of roads on the Florida panther. This is addressed by the following research objectives: (1) Determine the importance of vehicle-related mortality relative to other causes of mortality for the Florida panther population including any spatial, temporal, age, or gender patterns in vehicle-related mortality, and; (2) Determine patterns in road crossing behavior as demonstrated by telemetry observations, by gender and by road type and class. The hypothesis is that vehicle-related mortality plays a prominent role in overall Florida panther mortality and that Florida panther crossing behavior and movement patterns are influenced strongest by major roads relative to minor roads.

Background

Despite the controversy surrounding current Florida panther habitat research, several general conclusions can be drawn from 25 years of Florida panther research (Beier et al., 2003): (1) forests are important daytime rest sites; (2) white-tailed deer and feral hogs are the most significant prey for the panther; (3) the most prominent threats to panther survival as a species are habitat loss and fragmentation in the increasingly limited habitat area in south Florida; and (4) recovery of the panther depends critically on establishing additional populations outside of south Florida.

Vegetation preferences

Vegetation preferences of the Florida panther are a widely contested issue, particularly the amount of forest cover the panther requires for suitable habitat. Maehr and Cox (1995), cited as one of the most influential papers on panther habitat requirements by Beier et al. (2003, p6), identified the importance of forests as part of the panther habitat, including a dependence on large forest patches of 500 ha or larger. Maehr and Cox (1995) also concluded that most panther locations occurred within 90 m of preferred forest types, which has later been interpreted (Maehr, Horst, & Harris, 2001; Maehr & Deason, 2002) to indicate that panthers are reluctant to cross non-forested areas between habitats. These conclusions, however, have been heavily criticized because they ignore the effects of telemetry error, use a biased sample of the telemetry dataset, and are limited to diurnal telemetry data to make conclusions about 24-h panther habitat characteristics (Comiskey et al., 2002; Beier et al., 2003). According to Beier et al. (2003) the Maehr and Cox (1995) work has been cited, and mis-cited, on numerous occasions, compounding the error, and their conclusions have been applied to land management decisions that involve the remaining Florida panther habitat.

The proportion of forest cover within an individual panther’s home range necessary for livelihood is also a point of contention. Both Maehr and Cox (1995) and Kerkhoff et al. (2000) concluded that there is an inverse relationship between panther home range size and percent forest in the home range. Kerkhoff et al. (2000) also deduced that habitat cover is most likely to contain at least 25% forest cover. Using the same analysis techniques, Comiskey et al. (2002) concluded that the aforementioned inverse relationship was weak and that some panthers regularly used habitats with less than 25% forest cover, opposing the conclusions of Kerkhoff et al. (2000), Beier et al. (2003) state, despite the oversights of the above analyses, that there is reasonable evidence to support the conclusion that “forests are the most important habitat for diurnal locations of panthers (p12).” Although this connection has been established, there has been no reliable comparison of available forest patch distribution to those patches used by Florida panthers as indicated by diurnal telemetry observations. In a more recent re-analysis of the historic panther diurnal telemetry data Cox et al. (2006) have reaffirmed the importance of forests for Florida panthers when establishing a home range and selecting habitats within them. Starting in 2002 the Florida Fish and Wildlife Conservation Commission (FFWCC) has supplemented its radio-telemetry program with GPS telemetry during diurnal and nocturnal period. Based on a sample of 12 panthers for the period 2002–2005 both types of telemetry data yielded similar results as panthers selected upland and wetland forested habitat types (Land et al., 2008). Habitat composition of nocturnal and diurnal GPS locations appeared similar, confirming the validity of using historic diurnal radio-telemetry locations for the analysis habitat selection (Land et al., 2008).

Home range

In terms of home range size, Belden, Frankenberger, McBride, and Schwikert (1988), Maehr, Land, and Roof (1991) and Comiskey et al. (2002) report that both male and female panthers require comparatively large patches of suitable habitat, 435–650 km² and 193–396 km², respectively. The review by Beier et al. (2003) suggests that these estimates are defendable, since the statistical algorithms used in the analyses (Minimum Convex Polygon and kernel density techniques) are not very sensitive to telemetry location error or the use of diurnal locations.

Panther road ecology

The general types of impacts of roads on wildlife have been well documented and include: vehicle-related mortality, reduced access to habitat due to road avoidance, fragmentation of wildlife populations, restriction of wildlife movements and the disruption of gene flow and meta-population dynamics (e.g. Jackson, 2000). However, these impacts have received very little attention in the research on the Florida panther. Annual reports by the FFWCC make reference to the importance of vehicle-related mortality, but no empirical evidence has been presented in the literature on other effects of roads on the Florida panther. Several studies have assumed some degree of road avoidance (Jordan, 1994; Maehr & Cox, 1995; Cramer 1999; Cramer & Portier, 2001; Thatcher, Van Manen, & Clark, 2006, 2009; Kautz et al., 2006) but limited empirical evidence is present, highlighting the need for a better understanding of panther road relationships. Jordan (1994) incorporated a variable to estimate the influence of roads on the Florida panther in his evaluation of potential panther population reestablishment sites, but did not differentiate between road types, treating six lane highways the same as public dirt roads. Cramer and Portier (2001) cite the use of “perceived Florida panther preferences based on empirical evidence (p65)” and make distinctions for road influence between male and female panthers, but these values are based on the telemetry observations of only a few panthers with established home ranges adjacent to both I-75 and SR29 (Maehr, 1990; Maehr et al., 1991). Using the same model, Cramer (1999) applied weights to several classes of roads to simulate the influence of roads in panther movement and also estimated mortality probability rates based on “personal assumptions (p78)”. Kautz et al. (2006) identified least cost paths as important landscape linkages that considered major roads a “greater impediment to panther movement” than minor roads, but do not provide empirical evidence for such a ranking. Recent studies on panther reintroduction assessment (Thatcher et al., 2006, 2009) have distinguished between the densities of minor
roads and major roads for the purpose of modeling habitat suitability but without a specific justification other than a mailing survey of experts. The lack of empirical research in these studies provides the impetus for the current study.

The use of wildlife highway underpasses by the Florida panther has been explored to some degree (Foster & Humphrey, 1995; Lotz, Land, & Johnson, 1996; and Lotz, Land, & Johnson, 1997), suggesting that a necessary natural adaptation to the structures is the cause of a slow increase in use over time. Foster and Humphrey (1995) also assert that the use of wildlife underpasses not only mitigates vehicle-related mortality, but also reduces habitat fragmentation, although certain underpasses were more favorable for panther use (surrounding forested habitat, drier conditions, etc.) and therefore more frequently used than others. This may permit movement between fragmented habitats at specific underpass locations. However, the inherent territoriality of Florida panthers can prevent the use of an underpass by more than one individual, essentially isolating adults whose reproductive success is critical to species propagation.

Cougar (Puma concolor) road-ecology research includes studies of road crossing behavior, roads as barriers, and wildlife underpass use. Cougars have been found to generally avoid 2-lane roads or larger, but dirt roads may have facilitated movement, particularly during travel and hunting (Dickson, Jenness, & Beier, 2005). Dickson and Beier (2002) found that cougars tend to avoid human-dominated habitats and establish home ranges at a distance from major roads, except where preferred habitat dominated the area. Clevenger and Waltho (2005) surveyed highway crossing structures in Banff National Park to determine attributes of the structures most desirable for several species of large mammals, including cougars. Cougars preferred structures that were more constricted than other designs and where distance to forest cover was minimal. Gloyne and Clevenger (2001) also monitored cougar movements through crossing structures in Banff National Park and found cougars to use the underpasses more frequently in winter than summer. They also found that cougars preferred underpass structures more than overpass structures, and those underpasses located in high-quality cougar habitat.

Techniques in wildlife road ecology

The influence of roads on other species of wildlife is relatively well researched, particularly for those species under threat of anthropogenic habitat loss and population fragmentation. A wide range of methodologies is employed and the following provides illustrative examples of these approaches for large mammals.

A first approach is to examine patterns in animal–vehicle collisions and vehicle-related mortality. Several approaches exist to this, including characterizing collision hotspots, determining relationships between collisions and habitat-related parameters, and analyzing road network related parameters such as road network density, traffic volume and traffic speed (Litvaitis & Tash, 2008). For example, Gonser, Jensen, and Wolf (2009) determined the spatial relationships in deer–vehicle collisions in Indiana using nearest neighbor analysis and landscape metrics. Result showed non-random patterns and the importance of habitat type and structure in the location of collisions. A similar analysis of deer–vehicle collisions in Edmonton, Alberta by Ng, Nielsen, and St.Clair (2008) identified areas of high speed limits and areas of non-forested vegetation in close proximity to roads as hotspots for collisions. A study of deer–vehicle collisions in Illinois by Finder, Roseberry, and Wolf (1999) determined the importance of forest cover and topographic features in explaining collision patterns.

A second approach can be characterized as determining avoidance behavior. For example, road avoidance by grizzly bears based on distance was determined by Gibeau, Clevenger, Hererro, and Wierczowsi (2002). Distances were measured from telemetry points of radio-collared grizzly bears to the nearest human use feature, including roads. These distances were then compared to random points placed in the study area. Results indicated a gender difference between male and female grizzly bears, with females more influenced by human development (including roads). Another way to determine road avoidance behavior is to use short-term detailed movement patterns. For example, in a study of the influence of roads on bobcats and coyotes, Tigan, Van Vuren, and Sauvajot (2002) estimated activity patterns based on rates of movement between telemetry recordings in association with nearby human activity and road networks. Results indicate behavioral adaptation to anthropogenic disturbances through temporal and spatial avoidance. A more general road avoidance model is presented by Jeager et al. (2005) and includes road surface avoidance, car avoidance and noise avoidance.

A third approach is comparing survivorship in the absence and presence of roads. For example, the influence of roads and vehicle-related mortality on Amur Tigers was investigated through the use of survivorship estimates of radio-collared tigers and their cubs (Kerley et al., 2002). Survivorship values were based on road types found bisecting the tigers’ home ranges. Over nine years of study, adult female survivorship was greatest in home ranges that did not include any major roads, while all adult females in the study with home ranges bisected by major roads either died or disappeared prematurely (Kerley et al., 2002).

A fourth approach is to compare actual movement paths to simulations. For example, Dickson et al. (2005) simulated movement paths of cougars in southern California, calculated crossings with a local road network, and compared them to the crossings of an actual movement path. These simulated movement paths were limited to the calculated home range for each individual panther under study. The results indicated that cougars tend to avoid human-dominated habitats and establish home ranges at a distance from major roads, except where preferred habitat dominated the area. Another example of this approach is presented by the study of the effects of industrial development on caribou by Dyer, O’Neill, Wasel, and Boutin (2002) using simulated random sets of roads within an individual caribou’s home range. Calculated crossings between the caribou travel path derived from telemetry locations and the actual and simulated road networks were then compared. Results indicated significant habitat loss through avoidance patterns.

A fifth and final approach is to examine patterns in observed crossings. For example, a road impact study on Florida black bears in the Ocala National Forest (McCown, Kublis, Eason, & Scheick, 2004) used radio-telemetry to track 138 adult Florida black bears and estimated crossings and seasonal home ranges using telemetry records taken by fixed-wing aircraft. Results indicate males cross more than females, and bears with higher crossing frequencies are more likely to be involved in a vehicle-related collision.

For the current study, based on the nature of the telemetry record and the possible confounding factors (such as the influence of forest cover), an examination of observed vehicle-related mortalities and road crossing behavior presented the most reliable analysis methodology.

Methodology

Study area

The study area for this analysis is defined by the telemetry dataset of radio-collared Florida panthers. This area of southwest Florida includes the counties of Lee, Hendry, Collier, Broward, Monroe, and Miami-Dade as well as Everglades National Park and
Big Cypress National Preserve. The general area occupied by the Florida Panther has been described in several other studies (e.g., Kautz et al., 2006). This region also includes the intersection of State Road 29 and Interstate 75 which both have several wildlife underpasses. A total of 24 underpasses were constructed when the 2-lane State Road 84 known as Alligator Alley was updated to a 4-lane highway (I–75) between 1986 and 1992. Right-of-way fencing was placed along the I–75 corridor to prevent animals from entering the roadway and the underpasses were constructed to allow animal movement. Underpasses were placed at approximately 1.5 km intervals with each underpass consisting of 2 concrete bridges under a 4-lane divided highway. Shortly following the completion of the underpasses field research determined that the underpasses were used by panthers, bobcats, deer, raccoons, alligators and black bears (Foster & Humphrey, 1995).

Data sources and processing

A Florida panther radio-telemetry dataset from February 1981 to December 2004 was provided by the Florida Fish and Wildlife Conservation Commission (FFWCC). This dataset includes 71,220 records for 145 individual cats, including eight Texas pumas integrated into the population for the 1995 genetic restoration project. This dataset was collected through the use of radio-collar telemetry techniques. Collared animals were monitored approximately every other day (Monday, Wednesday, Friday) from fixed-wing aircraft and locations were plotted on 7.5-min USGS topographic maps and recorded as Universal Transverse Mercator points (Land, Cunningham, Lotz, & Shindle, 2004). This sampling design limits analysis, primarily because individuals cannot be tracked during their exact movement pattern, and because these recordings are all diurnal when panthers are most likely at rest. Positional accuracy, based on the differences between aerial measurements and GPS locations of 36 panther dens or carcasses, is approximately 115 m (±29.7 m) (Land et al., 2004). Other estimates of the error associated with this particular panther telemetry dataset were derived by Belden et al. (1988), Janis and Clark (2002) and Dees, Clark, and Manen (2001), whose estimates ranged from 77 to 230 m with varying degrees of confidence.

A subset of the telemetry data was extracted based on several criteria. First, only those telemetry observations were utilized which were recorded when the individual panther was an adult, or at least two years of age (FFWCC, 1999). The reported birth month and year (Land et al., 2004) was used to calculate age of each individual through their telemetry record. Generally, adult panthers exhibit more stable home ranges than juveniles, which demonstrate more erratic movement patterns and potentially travel far distances as they search for a suitable area to establish their adult home range (Maehr, Land, Shindle, Bass, & Hoctor, 2002). This study therefore does not use juvenile telemetry points and only describes adult habitat characteristics and movement patterns. Secondly, potential bias in home range estimation and movement path delineation was reduced by choosing individuals with frequent observations and long telemetry records, i.e. the number of telemetry observations for an individual panther over the span of a year had to consist of a minimum of 100 observations and the complete telemetry record had to be a minimum of 3 years. Thirdly, the telemetry records for the eight female Texas pumas were excluded since their behavior may not be representative. The final telemetry subset used for analysis included 21 males and 35 females, representing a group of individual panthers with the most reliable movement patterns obtainable from the existing telemetry record.

Organizing the analysis at the level of individual panthers is supported by both logic and literature. Grouping the data for multiple individuals as a set of locations as opposed to analyzing individual panthers can create serious bias. For example, some of the panthers have substantial telemetry records (10 + years) while others have a very short record of two years or even less. Frequency of telemetry observations also varies within a given time period. The FFWC scientific review team concluded that performing analysis on individual panthers and then drawing conclusions across those individuals is preferred to using the entire dataset as a pooled sample (Beier et al., 2003), an opinion supported by Dickson et al. (2005). Analysis of the data by individual panther highlights the variability within the population and minimizes error associated with sampling bias.

A dataset of collared and uncollared Florida panther mortalities and injuries with georeferenced locations from 1972 to 2004 was provided by FFWC. The dataset included 170 records, 11 of which are injuries while the remainder are mortalities. Mortalities and injuries of uncollared panthers typically consisted of carcasses encountered by private landowners who then contacted authorities or panther–vehicle collisions reported by drivers. Georeferencing of mortalities and injuries was carried out by FFWC staff based on descriptions in reports and/or field inspections.

A 1:24,000 USGS road network (1998) was obtained from the Florida Geographic Data Library (FGDL). This road network contains road type descriptions, varying from class 1 (primary routes) to class 5 (trails). Table 1 describes how the original road segment descriptions were used to established road classes (1 through 5) and road types (major and minor). Both road type and class were used to discriminate patterns of influence on individual panthers that may not be identified using just one road classification system. Duplicate segments in the road network were removed that represented divided highways, roads, and streets, and those segments with a class of zero (cul-de-sacs, highway on-ramps, etc.) in order not to bias estimates for road lengths and crossings. The locations of wildlife underpasses and fencing were obtained from the July 2004 version of the Florida Department of Transportation (FDOT) Roads Characteristics Inventory (RCI).

A landcover grid derived from 30-m Landsat imagery for 1997 was provided by FFWC and used mostly as visual reference. The grid was reclassified into forest and non-forest, according to preferred panther forest types (Kerkhoff et al., 2000): cypress swamp, hardwood hammocks and forests, hardwood swamp, mixed hardwood-pine forests, and pinelands. All other vegetation types (including non-preferred forest) were classified as non-forest, in addition to categories for wetlands and water.

Analysis

To characterize an individual Florida panther’s established diurnal territory annual and lifetime home ranges were determined using a 100% Minimum Convex Polygon (MCP). Annual home range considers all telemetry points within a calendar year.
year, while lifetime home range considers all telemetry points in the record for a particular panther, i.e. a minimum of three adult years for the sample of panthers used in this analysis. Annual and lifetime home ranges were mapped and visually inspected for any patterns relative to forest cover and roads. Statistical differences in lifetime home range size between male and female were determined using an independent samples t-test.

Florida panther vehicle-related mortality was investigated through the use of the panther mortalities dataset. Composition of radio-collared and uncollared panther deaths over time, by gender, age, road type and class, and location relative to wildlife underpasses was examined. Vehicle-related mortality by road class was determined by assigning the attributes of the nearest road to the recorded location of vehicle-related mortality or injury. These deaths and injuries are very likely to have occurred on the road class assigned unless an individual panther traveled a substantial distance after a collision. For comparison total road length was determined within a single 100% MCP of all locations in the telemetry subset.

To determine road crossings behavior by collared Florida panthers, individual lifetime movement paths were delineated from the telemetry locations. These movement paths were intersected with the road network to determine points of crossing. This method does not determine the exact location of a crossing, but provides a reasonable estimate of the number of crossings per road type and class by connecting daytime resting sites, typically 2 or 3 days apart. In order to remove the bias of observation length, the number of crossings was divided by the total length of observation, calculated as the difference in years between the first and last observation date used in the telemetry subset for each individual panther. Crossing densities were calculated as the ratio between the number of crossings for each road type and class, and the total length of each road type and class. Road lengths were based on those road segments that fall within an individual's lifetime home range. This resulted in estimates of road crossing density (in # crossings/km/year) for each individual panther by road type and class.

Statistical comparisons of road crossing densities were performed using paired t-tests. The comparisons were carried out

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**Fig. 1.** Adult Florida panther lifetime home ranges for individuals included in telemetry subset employed in this study.
Fig. 2. Adult lifetime home range and telemetry record for female panther 78.

Fig. 3. Lifetime home range sizes of adult Florida panther by gender (outliers are labeled by panther ID number).
separately for each gender in order to minimize any error associated with aggregation by gender, since the movement patterns and habitat size requirements for males and females differ substantially. Adult males have larger home ranges, are more territorial, and disperse farther than females which frequently share established home ranges with their mother and tolerate home range overlaps (FFWCC, 1999). ANOVA was considered as an alternative to performing multiple paired \( t \)-tests but not employed due to substantial differences in the variance of data in certain groups.

### Results

#### Home range characteristics

Fig. 1 shows the extent of all lifetime home ranges for the 56 individual panthers. Most home ranges of both genders are located in areas of high forest density, specifically around the I-75 corridor. Some panthers, mostly female, have established themselves in the extreme south of the peninsula, creating a sort of subpopulation, as there are expansive wetlands and little forest cover between the two established habitats. This region is part of the Everglades National Park and is under the Comprehensive Everglades Restoration Plan which would increase water flow through this area over the next 30 years (US Army Corps of Engineers 2006), essentially cutting off the smaller subpopulation at the southern tip of Florida. There are also several individuals, particularly one male, that have extended their home range north and west, beyond the more panther-friendly forested areas.

The diversity in size and shape among the home ranges points to several trends. Many of the female lifetime home ranges overlap in both time and space, further confirming that females generally tolerate overlapping territories, particularly with their own offspring (FFWCC, 1999). Males, alternatively, have much larger home ranges, disperse farther than females, are more territorial, and tolerate overlaps much less than females do (FFWCC, 1999).

Home ranges for several individuals are shaped according to the surrounding major road network. The telemetry records for several of these individuals also reveal a clustering of locations against the road, much as a captive animal paces the length of its cage. Interestingly, the most striking examples of this “cage effect” are all females, indicative of a trend in gender differences in the influence of roads on panther movement. All of these examples occur along the same section of SR29 and I-75, both of which provide numerous wildlife underpasses for safe crossings. An illustrative example of this is shown in Fig. 2. This suggests that roads, even with safe crossings present, act as a barrier to movement for some panthers since there is available forest cover directly on the other side of these roads. Alternatively, there are several examples of males which regularly cross this section of highway by using the underpasses.

Some of the differences between the male and female Florida panther habitat requirements were statistically confirmed using home range characteristics. While both genders show variability among individuals, average male annual home range size \((540.7 \text{ km}^2, n = 21)\) is much higher than for females \((211.3 \text{ km}^2, n = 35)\). Lifetime home range characteristics differ between the genders as well. Fig. 3 shows a box-plot of the distribution of

![Box-plot of home range characteristics](image-url)

**Table 2**

<table>
<thead>
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<th>Cause</th>
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</tr>
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<tr>
<td>Infection</td>
<td>4</td>
</tr>
<tr>
<td>Shooting</td>
<td>2</td>
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</table>

**Fig. 4.** Causes of Florida panther mortality or injury (1972–2004).
lifetime home range sizes for males \( (n = 21) \) and females \( (n = 35) \). An independent samples t-test (Levene’s test did not reject the null hypothesis of equality of variances) between the lifetime home range sizes of males and females demonstrates a significant difference \( (t = 2.780, p = 0.010) \). This result only further justifies the subsequent split of the analyses based on gender in order to minimize any error associated with aggregation by gender since the movement patterns and habitat size requirements for males and females differ substantially.

**Vehicle-related mortality**

The examination of the mortality dataset highlights the importance of vehicle-related deaths as a major cause of mortality among the population. Table 2 summarizes the major causes of mortality and injury among radio-collared Florida panthers, both natural and anthropogenic. Although intraspecies aggression is the most prominent cause of death, one out of five deaths or major injuries of radio-collared Florida panthers occurs as a result of vehicle collision.

Fig. 4 describes causes of mortality or injury among Florida Panthers for the period 1972 to 2004. Collaring of panthers only started in 1981 and the first recorded mortality of a collared panther occurred in 1982. There is a general increase in the amount of recorded deaths which can in part be attributed to a modest increase in the population over the time period considered. The FFWCC reported a population of about “70 adult panthers [remaining] in national and state parks and nearby private lands in southwest Florida” in 1999 (FFWCC, 1999) and a little less than 100 adults in 2001 (FFWCC, 2001). This affirms that the 1995 genetic restoration project substantially increased the population of the Florida panther, resulting in an increased number of recorded deaths. Additionally, the large percentage of intraspecies aggression mortalities reflects considerable aggression between panthers as the population of the notoriously territorial species grows in an increasingly fragmented habitat.

There is a strong increase in the number and relative importance of vehicle-related deaths in recent years, but this is confounded by a bias in the recording of the incidents. The FFWCC Florida panther mortality dataset only records those incidents which are associated with radio-collared panthers and those uncollared panthers whose death was easily found (i.e. vehicle collisions or deaths located on private lands). Non-vehicle-related mortality of uncollared panthers is therefore under-reported. Despite this bias, six or more vehicle-related deaths or injuries annually since 2000 is substantial considering an estimated population of around 100 individuals. For collared panthers, the number of vehicle-related mortalities has remained fairly consistent and is two or less per year for the

<table>
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<th>Road Class</th>
<th>Deaths</th>
<th>Injuries</th>
<th>Total study area road length (km)</th>
<th>Deaths/km</th>
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</tbody>
</table>

Fig. 5. Florida panther vehicle-related mortalities and injuries by gender (1972–2004).
reporting period and the majority of vehicle-related mortalities in recent years has resulted from uncollared panthers.

Fig. 5 shows the locations of Florida panther vehicle-related mortalities and injuries from 1972 to 2004 of both radio-collared and uncollared panthers, and depicts high numbers of vehicle-related mortalities on major roads, such as SR29. Female vehicle-related deaths occurred mostly on SR29 and CR846, and are more clustered than for males. Male vehicle-related deaths are generally more dispersed, with the exception of SR29, and the broader distribution corresponds to their larger home ranges. SR29, however, is a considerable “hotspot” for vehicle-related deaths of both genders over the last twenty-five years and is a major contributor to the overall vehicle-related death composition. The spatial distribution of non-vehicle-related deaths and injuries (not shown) revealed no major gender difference, other than the fact that some male mortalities are found further north than the female mortalities.

Table 3 presents a summary of total deaths and injuries by road class and deaths per kilometer of road in each road class. Road classes 1 and 2 (major roads) have the lowest total length within the study area but have by far the highest number of deaths per kilometer compared to the remaining minor classes. These major roads are a primary cause in the total vehicle-related mortality rates of the remaining Florida panther population.

Vehicle-related mortalities and injuries were summarized by gender and age. Results are shown in Table 4. Males tend to have higher numbers of vehicle-related deaths and injuries than females, and adults are killed more often than juveniles. There is little difference between the genders at the juvenile level, suggesting an equal risk of vehicle-related death at this age when movement between habitats is high for both males and females as they search for their own adult home range. Once a home range has been established, females are at a lower risk, as indicated by the lower number of vehicle-related deaths compared to male adults. These estimates are not controlled for population composition, however, and do not take into account the true ratio of males to females and adults to juveniles in the entire Florida panther population.

The examination of the mortality dataset indicates much higher vehicle-related mortalities on road classes 1 and 2, compared to...
the other road classes. Adult males are more at risk in terms of vehicle-related mortality than adult females, but there is no gender difference for juveniles. Since the installation of wildlife underpasses and high fencing on I-75 which was completed in 1992, there have been no reported deaths on that stretch of I-75. However, there are still frequent vehicle-related deaths on SR29, containing two underpasses just north of I-75 but little fencing.

Crossing behavior

Figs. 6 and 7 show the distributions of the average annual road crossing densities for males and females by road type and road class, respectively. Both Figures reveal an increase in annual crossing density as the road size diminishes (increase in road class number). However, females have higher crossing densities for the minor class roads (3, 4, and 5) on average than males.

Crossing densities by road type and class were tested for significant differences within each gender using paired-sample t-tests. Table 5 shows the results of these tests. A negative $t$-value indicates an increase in crossing densities as the road size decreases. For example, $t$-test results for major versus minor roads for both genders indicate a negative $t$-value, because crossing densities for major roads are lower than for minor roads. In fact, almost all of the $t$-test values are negative, indicating a general trend of increasing crossing densities as road size decreases. The differences between the crossing densities of major and minor roads are significant at the 0.01 level for both genders. When the crossing densities are split into classes, however, significance is lost using the pair-wise $t$-tests; the difference between adjacent classes in general is not large enough to produce significant results. The $t$-test between class 3 and 4 roads for males was significant, because a substantial number of males in the subset have home ranges that are located closer to residential areas (north of the I-75/

![Diagram showing road crossing densities](image)

**Fig. 7.** Annual road crossing densities for adult Florida panthers by road class (outliers are labeled by panther ID number).

<table>
<thead>
<tr>
<th>Class 5</th>
<th>Class 4</th>
<th>Class 3</th>
<th>Class 2</th>
<th>Class 1</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>0</td>
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</table>

<table>
<thead>
<tr>
<th>Sample size</th>
<th>$t$-value</th>
<th>$p$-value</th>
<th>Degrees of freedom</th>
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</thead>
<tbody>
<tr>
<td>Female</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Major - Minor</td>
<td>21</td>
<td>$-3.350$</td>
<td>0.001**</td>
</tr>
<tr>
<td>Class 1 - Class 2</td>
<td>8</td>
<td>$-2.038$</td>
<td>0.081</td>
</tr>
<tr>
<td>Class 2 - Class 3</td>
<td>15</td>
<td>$-1.379$</td>
<td>0.189</td>
</tr>
<tr>
<td>Class 3 - Class 4</td>
<td>30</td>
<td>$-2.121$</td>
<td>0.235</td>
</tr>
<tr>
<td>Class 4 - Class 5</td>
<td>34</td>
<td>$-0.745$</td>
<td>0.462</td>
</tr>
<tr>
<td>Male</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Major - Minor</td>
<td>21</td>
<td>$-3.412$</td>
<td>0.003**</td>
</tr>
<tr>
<td>Class 1 - Class 2</td>
<td>14</td>
<td>$-0.741$</td>
<td>0.472</td>
</tr>
<tr>
<td>Class 2 - Class 3</td>
<td>21</td>
<td>$-0.846$</td>
<td>0.407</td>
</tr>
<tr>
<td>Class 3 - Class 4</td>
<td>21</td>
<td>$-6.943$</td>
<td>0.000**</td>
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<tr>
<td>Class 4 - Class 5</td>
<td>21</td>
<td>$0.304$</td>
<td>0.764</td>
</tr>
</tbody>
</table>

**---** significant at 0.01.
This strongly suggests roads act as barriers to movement, even with home range, essentially shaped to adjacent to the major road network show an elongation of their females, both annual and lifetime. Several individuals located panther population in south Florida.

Discussion and conclusions

While it is well established that the most important threat to panthers include limited habitat area and continued habitat loss and fragmentation, the importance of roads in this context had not been determined prior to this study. Vehicle-related mortality and road crossing behavior were analyzed to characterize the influence of roads on the movement patterns of the remaining Florida panther population in south Florida.

Males have significantly larger average home ranges than females, both annual and lifetime. Several individuals located adjacent to the major road network show an elongation of their home range, essentially shaped to fit the surrounding road network. This “cage effect” is most striking in the cases of females, specifically along I-75 which contains many wildlife underpasses. This strongly suggests roads act as barriers to movement, even with the availability of constructed safe crossings.

The influence of vehicle-related mortalities on a population already struggling for survival is substantial. Vehicle-related mortalities over the past 25 years constitute a considerable twenty percent to the overall mortality of radio-collared panthers. With an estimated total population of around 100 adults, 40 vehicle-related mortalities (collared and uncollared combined) in the time period 2000 to 2004 are also very considerable.

A gender difference was found in the spatial distribution of vehicle-related mortalities. Male mortalities are much less clustered than those of females, most likely due to greater dispersal behavior of males. For both genders, however, SR29 is a major “hotspot” for vehicle-related mortalities. Additionally, major roads (classes 1 and 2) contain the highest number of deaths per kilometer of road within the study area, and are a major contributor to vehicle-related mortalities. Minor roads result in very few mortalities. Demographically, adult males seem to be most at risk in terms of vehicle-related mortality, while females and juveniles of both genders total fewer deaths and injuries.

Road crossing density was determined as the number of crossings by an individual panther per year per kilometer of road in each individual panther’s home range, separated by road type and class. For both genders, crossing densities increase with decreasing road size, although females in general had higher crossing densities than males, in part because road densities in female home ranges are higher overall. A series of paired-sample t-tests between crossing densities by road type and class revealed significant differences between major and minor roads for both genders. Major roads were found to be a greater barrier to movement of the Florida panther than minor roads, particularly for females. This significant difference was lost when the analysis was carried out by road class.

The results point to substantial gender differences in several aspects. Female adult panthers have smaller home ranges, avoid crossing major roads more often and suffer less from vehicle-related mortalities. Adult males have larger home ranges, cross major roads more often than females and suffer higher vehicle-related mortalities. Overall this suggests that adult males are the “risk takers” of the population.

Although the investigation covers several aspects of the influence of roads on the movement of the Florida panther, there are still several gaps to be filled with further research. For example, the current study did not incorporate any data for juvenile panthers and their movement patterns and home ranges are expected to differ from those of adults. Secondly, more intensive tracking could be used to determine the influence of roads in more detail, for example using the newer telemetry data that employs a Global Positioning System (GPS) device. This type of tracking would facilitate the use of hourly locations to determine a much more accurate movement path, indicating the exact frequencies, times and locations of road crossings. This would also allow for determining nocturnal locations and movement patterns, which would be very significant for Florida panther research, since they are most active during night hours and most existing telemetry is diurnal only. GPS telemetry data for the Florida panther has been collected since 2002 (Land et al., 2008) but consists of a modest sample of panthers and the data itself has not been released for research purposes. The effectiveness of the wildlife underpasses and right-of-way fencing could also be investigated in more depth since specific underpass use is impossible to determine with the current telemetry record. Other methods of underpass data collection, such as digital event recorders and cameras (Foster & Humphrey, 1995), should be explored and applied to panther movement research, particularly as a resource for tracking underpass use by uncollared panthers. Alternatives to the underpass/fencing combination that ensures mortality mitigation but promotes more free movement between habitats should also be considered.

Pressures on the Florida panther’s remaining habitat have continued to grow over the past two decades, including pressures from agriculture, surface mining, and urban expansion. Both Collier County and Lee County have been among the fastest growing counties in Florida, resulting in numerous development proposals that infringe upon the panther’s habitat. This also includes new road segments. For example, in the late 1990s construction of the Daniels Parkway Extension in Lee County, FL was approved despite controversy over the habitat model employed at the time to evaluate the impacts of the roadway on the Florida panther (Gross, 2005). A recent review article in Science concluded that while genetic restoration efforts have seen encouraging results, continued habitat loss, persistent inbreeding, infectious agents, and possible habitat saturation pose new dilemmas for the management of the Florida panther population (Johnson et al., 2010).

Finally, the application of the findings of this investigation to reintroduction efforts is critical. If any such effort is to be successful, the influence of roads, both major and minor, should be considered in the placement of subpopulations and establishment of ecological corridors for movement between subpopulations. Recent studies on panther reintroduction (Thatcher et al., 2006, 2009), have only incorporated the potential impacts of road networks to a very limited extent. As the Florida panther’s current habitat range is barely sufficient to sustain the current population, reintroduction efforts are critical for the survival of the species. Any reintroduction effort needs to carefully consider vehicle-related mortality and the barriers formed by major roads. Potential mitigation efforts need to be considered, such as additional protected lands, road closings, traffic control measures, fencing, and appropriate wildlife underpasses.

References


