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# Assessing impacts of intrinsic and extrinsic factors on Florida panther movements

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Movement patterns can influence an animal's ability to secure food, find mates, and avoid enemies, potentially affecting individual fitness. We studied movement patterns of 10 male and 3 female endangered Florida panthers (*Puma concolor coryi*) using location data collected from a long-term (2005–2012) GPS collar study. Males traveled faster and covered longer daily distances than females during both the wet and dry seasons (wet:dry—males 289:372 m/h and 4,616:6,701 m; females 186:280 m/h and 2,629:5,239 m). Panthers occupying higher-selected habitat traveled faster, but with shorter daily movement distances in comparison to habitats that were less frequently selected. An index of risk (derived using traffic volume and road density) that was linked to habitat predicted to be avoided by panthers was associated with reduced daily movement distances. Our results suggest that Florida panthers alter their movement patterns in response to environmental change and anthropogenic disturbances.

Key words: Florida panther, GPS collars, hydroperiod, large carnivore, movement patterns, *Puma concolor coryi*

How animals travel across landscapes affects their ability to secure food, find mates, minimize predation risk, and evade intraspecific conflict. Because movement patterns can influence an animal's ability to survive and reproduce, they can directly influence individual fitness and population dynamics. This recognition, as well as advances in GPS collar technology for deployment on wildlife, has spurred substantial interest in movement ecology over the past decade (e.g., Fryxell et al. 2008; Nathan et al. 2008; van de Kerk et al. 2015). An important goal of movement ecology is to elucidate factors and processes that influence animal movement patterns and variation in those patterns. Studies often focus on understanding how intrinsic states (e.g., sex, age, reproductive or dispersal status) and extrinsic environmental factors (e.g., habitat quality, mortality risk, distribution and abundance of prey) affect movement (Fryxell et al. 2008; Nathan et al. 2008).

In many terrestrial mammals, movement patterns generally differ between sexes and age classes (e.g., dispersing subadults, breeding adults—Fryxell et al. 2008; Avgar et al. 2013; van de Kerk et al. 2015; Karelus et al. 2017). However, substantial variation in movement patterns exists even among individuals of a particular sex and age class, especially in relation to environmental factors. For example, Avgar et al. (2013) showed that spatial and temporal variation in caribou (*Rangifer tarandus caribou*) movement patterns were explained by local environmental conditions related to forage availability, predation risk, and habitat permeability. They also provided a rigorous framework for discerning environmental factors that influence animal movement patterns. Their approach was to quantify movements in terms of simple metrics (e.g., step length, directional persistence, directional bias, and mean squared displacement) and to analyze them using generalized linear mixed models to test for the effect on movement of spatial and temporal covariates. Step length is the distance between subsequent locations; directional persistence measures the meander of a path and directional bias looks at this path over time. The mean squared displacement is an important metric that is proportional to the spread of a population and can be used to assess migration and dispersal (Avgar et al. 2013).

Studying movement patterns of large carnivores such as pumas (*Puma concolor*) is challenging because they typically roam over extensive wildlands (Hemker et al. 1984; Maehr 1990; Beier et al. 1995; Schmidt et al. 2003; Dickson et al. 2005; Laundré 2005; Sweanor et al. 2008) making it difficult to monitor them continuously using traditional VHF radiocollar technology. These difficulties have been partially overcome with the advent of GPS collars. GPS collars have been deployed on endangered Florida panthers (*P. c. coryi*; hereafter, panthers) by the Florida Fish and Wildlife Conservation Commission (FWC) since 2002 (Land et al. 2008; Onorato et al. 2011). Collars have been programmed to attempt to collect location data on panthers hourly (but sometimes more or less frequently—Onorato et al. 2011). The high-resolution location data that result make it possible to study movement and fine-scale habitat-use patterns of this cryptic carnivore (Land et al. 2008; Onorato et al. 2011; van de Kerk et al. 2015).

Using the analytical framework developed by Avgar et al. (2013) and locational data collected using GPS collars, we sought to discern intrinsic and extrinsic factors that influence movement patterns of panthers. Specifically, we tested 4 predictions relating to movement patterns of panthers: 1) Because male panthers are more territorial than females, we predict movement patterns to differ between sexes with male panthers moving faster than females and covering more of their home ranges over time because they will adopt strategies to protect resources. 2) Because movement across dry terrain should require less energy compared to movements across a flooded landscape, we predict panthers should move with a greater directional persistence and cover longer distances per unit time during the dry season than during the wet season. 3) We predict panthers should minimize time spent in risky areas and so, movement speed and displacement distance of panthers should be positively related to areas with higher road densities and increased vehicle traffic. 4) We predict that habitats selected by panthers should be associated with lower movement rate and displacement distance as panthers reduce travel speeds to search for prey due to better hunting opportunities in higher-quality habitat. Knowledge garnered from analysis of panther movement patterns can play a key role in management initiatives such as corridor establishment, assessment of habitat patch accessibility within the current and potential range, developing spatially explicit models of gene flow, and other landscape-level strategies that should prove useful in enhancing the conservation of panthers.

## MATERIALS AND METHODS

*Study area.*—South Florida is characterized by a tropical climate and comprises extensive permanent and ephemeral wetlands that are affected by seasonal summer rains between May and October (Cox et al. 2006; Kautz et al. 2006). We defined 2 seasons based on this rainfall pattern: wet (15 May–14 October) and dry (15 October–14 May). Natural habitats include hardwood hammocks, cypress forests, pine flatwoods, freshwater marshes, prairies, and grasslands (Davis 1943), whereas human land use includes citrus, croplands, pastureland, rock mining, and areas of low- and high-density residential development (Onorato et al. 2011).

Panthers were captured and fitted with GPS collars within their current breeding range (Frakes et al. 2015; Fig. 1). This area includes private land but is predominately public. The majority of captures occurred on public land (Fig. 1) within the Picayune Strand State Forest, Fakahatchee Strand Preserve State Park, Big Cypress National Preserve, Florida Panther National Wildlife Refuge, Big Cypress Seminole Indian Reservation, Okaloacoochee Slough State Forest, and Everglades National Park.

*Panther capture and data collection.*—Independent panthers (> 1 year old) were captured using trained hounds and houndsmen provided by Livestock Protection Company (Alpine, Texas). FWC staff fitted male and female panthers with GPS collars from February 2005 through January 2012. Capture protocols, biomedical procedures, and morphometric data recorded during capture events have been described elsewhere (Cunningham et al. 2008; Onorato et al. 2011; FWC 2016) and followed guidelines of the American Society of Mammalogists (Sikes et al. 2016). Sex was determined for all captured panthers, and they were assigned to an age class (subadult or adult; males become adults at 3 years of age, females at

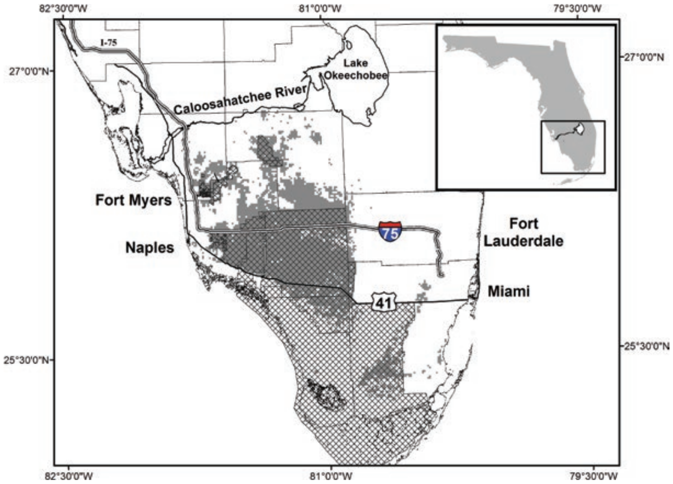

**Fig. 1.**—Map of the study area depicting suitable breeding habitat of the Florida panther (*Puma concolor coryi*; shaded gray—Frakes et al. 2015) and major public land holdings (crosshatch) in southern Florida. The Caloosahatchee River is the northern limit of the current (2017) major breeding range of the Florida panther. Interstate 75, U.S. Route 41, and major urban areas are shown for reference.

2 years) based on tooth wear and pelage characteristics (Shaw et al. 2007). We deployed Tellus and Tellus-GSM (global system for mobile communications) GPS collars produced by Followit (Lindesberg, Sweden). The Followit Tellus-GSM collars sent locations via e-mail when panthers were within range of an appropriate GSM mobile-phone tower. Fix schedules programmed into GPS collars varied, but all were programmed to collect hourly fixes for a period of time during the functional life of the collar. Field trials assessing location error associated with GPS collar models used in this study revealed a mean error of 33.9 ± 8 m (*SE*; $n = 3{,}210$ fixes—Onorato et al. 2011). Canopy cover, among other factors, can affect the GPS fix success for collars (Frair et al. 2004), but this affect is reduced when fix schedules are set for rapid locations (e.g., hourly).

*Covariates.*—We assessed the influence of a habitat selection coefficient, index of risk, and season on sex-specific movement parameters. We combined 43 land-cover classes in a GIS habitat layer (Kautz et al. 2007) into 6 classes and assigned habitat selection values according to GPS location results described by Onorato et al. (2011). Habitat classes included upland forest, wetland forest, dry-prairie grassland, marsh-shrub, agriculture, and other (a class that included all remaining habitats, including open water, mangrove swamps, exotic plants, urban areas, etc.). Onorato et al. (2011) found panthers selected (in order of preference) upland forest, wetland forest, marsh-shrub-swamp, and prairie grassland habitats. Agricultural and the "other" land-cover classes were used in proportion to their availability and no class was avoided. Forested habitats provide a variety of critical attributes for panthers such as den sites, rest sites, and stalking cover that may improve hunting success (Onorato et al. 2011). We used minimum convex polygons (MCP) to delineate use areas for panthers for several movement metrics. We quantified selected habitat within 100% MCP use areas of individual panthers by: 1) tabulating the percentage composition of the 6 cover types within the use area; 2) multiplying each percentage by the corresponding selection ratio value from Onorato et al. (2011:table 2; upland forest: 0.532, wetland forest: 0.620, dry-prairie grassland: 0.785, marsh-shrub: 0.799, agriculture: 1.039, and other: 1.047 [smaller selection values equate to habitats more preferred by panthers]); and 3) averaging these values for an overall habitat selection (suitability) coefficient for the individual use area using the same scale. Per Onorato et al. (2011), habitat selection coefficients < 1 are selected and > 1 are avoided. Habitat coefficients that are not significantly different from 1 are used in proportion to their availability.

We created an index of risk layer in GIS to assess how habitats predicted to be avoided by panthers, due to traffic volume and road density, affect movement. Roads are a significant cause of mortality for panthers and we were interested to see how roads within individual home ranges altered movement because of associated risk of an accident. The index of risk was calculated using a geostatistical analysis in ArcGIS 9.3 (ESRI 2008) following a methodology similar to that used by McClintock et al. (2015:appendix S2). First, 1-km$^2$ grid cells were overlaid on a 100% MCP encompassing all GPS fixes collected for all collared panthers. This polygon was designated as the study area. The index of risk coefficient (RR) for each 1-km$^2$ grid cell $i$ was then calculated as:

$$\mathrm{RR}_i = \frac{a_i - \mathrm{mean}(a_i)}{sd(a_i)} + \frac{b_i - \mathrm{mean}(b_i)}{sd(b_i)},$$

where $a_i$ is the average annual daily traffic volume (AADT) for roadways within a particular 1-km$^2$ cell $i$, mean($a_i$) and $sd(a_i)$ are the mean and standard deviation of $a_i$ across the study area, $b_i$ is the total length of road contained in a particular 1-km$^2$ cell $i$, and mean($b_i$) and $sd(b_i)$ are the mean and standard deviation of $b_i$ for the total length of road within the study area. To determine the index of risk assigned to each panther, we used Hawth's Tools (polygon-in-polygon analysis; http://www.spatialecology.com/htools) in ArcGIS 9.3 (ESRI 2008) to calculate the weighted average index of risk for all 1-km$^2$ cells intersected by a panther's 100% MCP use area. The cells that contained the most roads had the highest index of risk values.

*Calculation of movement metrics.*—We removed location data for the first and last 48 h for each individual panther to exclude potentially abnormal movements due to capture, radio malfunctions, or death. To quantify movement patterns, we calculated 7 movement metrics: daily movement distance (DMD), weekly movement range (WMR), step length, directional persistence, directional bias, and observed (OD) and expected displacement (ED) distances (Jedrzejewski et al. 2002; Benhamou 2006; Avgar et al. 2013). We calculated DMD, an estimate of the total distance traveled during a 24-h period, by taking all locations recorded in the universal transverse mercator (UTM) coordinate system from that period and calculating the distance between sequential points, then summing all the distances between points during the 24-h period. When hourly fix attempts within a 24-h period were unsuccessful, we calculated the straight-line distance from the previous successful fix to the next successful fix. The WMR is the proportion of the home range that was covered by an individual panther each week. This involved calculating the 95% MCP use area value for each panther using all locations collected while being monitored with a GPS collar and comparing them with the 95% MCP use area value for locations collected over weekly periods (WMR = weekly 95% MCP/overall 95% MCP).

Step length was the straight-line distance between 2 consecutive hourly GPS locations. When hourly fix attempts were unsuccessful, corresponding step lengths could not be calculated and thus were treated as missing values. Directional persistence is a metric that describes an animal's propensity to maintain its previous movement heading and is calculated as the cosine of the angular difference between the directions of 2 consecutive steps, while directional bias is a metric that relates to an animal's propensity to maintain its average weekly movement heading and is calculated via the cosine of the angular difference between the overall weekly direction and the individual step's direction (Avgar et al. 2013). Because animals tend to move faster when traveling toward a preferred direction, directional persistence and directional bias are not independent of step length. Thus, means of directional persistence and directional bias were calculated as weighted means, weighted by the corresponding step length (Avgar et al. 2013).

The ED (expected straight-line distance traveled after a certain number of steps assuming either a biased random walk or correlated random walk movement model) is a central concept of animal movement analyses (Kareiva and Shigesada 1983) and has recently been suggested as a robust summary statistic for capturing key properties of animal movements (Nouvellet et al. 2009). Avgar et al. (2013) demonstrated the utility of ED in linking the impacts of extrinsic factors to animal movement metrics. To calculate ED, we assessed the trajectory of each animal as a correlated random walk or biased random walk based on the level of correlation between directional persistence and directional bias (Benhamou 2006). If there was a significantly positive correlation between directional persistence and directional bias, the trajectory was classified as a biased random walk, and the ED within a specific time frame was calculated as:

$$\mathrm{ED} = \sqrt{nE(\mathrm{SL}^2) + n(n-1)E(\mathrm{DB})^2\,E(\mathrm{SL})^2},$$

where ED is the expected displacement; $E(\mathrm{SL})$ and $E(\mathrm{SL}^2)$ are the mean step length and mean squared step length, respectively; DB is the directional bias; and $n$ is the number of hourly steps during a specific time frame (Codling et al. 2008; Avgar et al. 2013). If there was no significant correlation, the trajectory was classified as a correlated random walk, and ED was calculated as:

$$\mathrm{ED} = \sqrt{nE(\mathrm{SL}^2) + E(\mathrm{SL})^2 \frac{2E(\mathrm{DP})}{1 - E(\mathrm{DP})\dfrac{1 - E(\mathrm{DP})^n}{1 - E(\mathrm{DP})}}}$$

where DP is the directional persistence (Benhamou 2006; Avgar et al. 2013). ED can be compared with OD (the straight-line distance traveled within a certain time frame) using linear regression analysis. We calculated daily, weekly, and monthly OD and ED for each panther.

We used generalized linear mixed-effects models (GLMMs), assuming a gamma-distributed error structure and log link function to test for the effect of spatiotemporal covariates on weekly movement metrics (step length, OD, ED, DMD, WMR). Mixed models were applied to weekly averages of response variables to minimize autocorrelation. We included individual panther ID as a random effect and fixed effects of sex, season, habitat selection coefficient, and index of risk as well as the interaction between season and index of risk, season and habitat selection coefficient, sex and index of risk, and sex and habitat selection coefficient. We used an information-theoretic approach using the Akaike information criterion (AIC—Burnham and Anderson 2002; Klar et al. 2008) for model comparison and to quantify model parsimony. The influence of a covariate was assessed by comparing AIC values for models with and without a covariate, and by examining if 95% confidence intervals on the regression coefficient included zero. The relationship between ED and OD was assessed using a simple linear regression; the coefficient of determination ($R^2$) used as a measure of the percentage of variance in OD that was explained by ED.

We performed all analyses in program R v3.1.1 (R Core Team 2014). GLMMs were fitted using glmer() function in the R package lme4 (Bates et al. 2015).

## Results

We compiled GPS collar data from 10 male and 3 female panthers captured between 2005 and 2012 for a total of 4,750 panther-days and 60,304 hourly locations. Age of male and female panthers when initially collared averaged 2.9 ± 0.50 and 7.2 ± 3.36 years, respectively. Step lengths and DMD were longer for males than for females but these varied between seasons, with panthers of both sexes traveling faster during the dry season than the wet season (Table 1; Figs. 2, 3a, and 3d). We found the same pattern for directional persistence, which was slightly higher for males than for females, and higher for both sexes during the dry season than the wet season (Table 1; Fig. 3b). The pattern was the opposite for directional bias, which was lower for males than for females, and higher in the wet season than the dry season (Fig. 3c). Males covered a larger part of their home range weekly than did females (Table 1), and both sexes covered a larger part each week in the dry season than in the wet season (Fig. 3e). The longest DMD recorded during the study was a 24.02-km journey by an adult male.

**Table 1.**—Sex- and season-specific step length (mean ± *SE*), directional persistence, directional bias, daily movement distance (m), and weekly movement range (%) of Florida panthers (*Puma concolor coryi*). See Table 2 for statistical inference. Means for step length, daily movement distance and weekly movement range are weekly averages to minimize issues related to autocorrelation.

| Sex | Parameter | Season | | | |
|---|---|---|---|---|---|
| | | Dry | | Wet | |
| | | Mean | Range | Mean | Range |
| Male | Step length (m/h) | 371.80 ± 0.94 | 31.13–794.19 | 289.35 ± 1.52 | 23.97–620.87 |
| | Directional persistence | 0.46 ± 0.00 | –0.08–0.72 | 0.40 ± 0.00 | –0.23–0.71 |
| | Directional bias | 0.17 ± 0.00 | –0.19–0.71 | 0.18 ± 0.00 | –0.23–0.62 |
| | Daily movement distance (m) | 6,701 ± 17 | 667–14,636 | 4,616 ± 25 | 476–11,796 |
| | Weekly movement range (%) | 26.53 ± 0.14 | 0.06–80.48 | 10.76 ± 0.13 | 0.04–44.81 |
| Female | Step length (m/h) | 280.34 ± 1.23 | 94.91–641.54 | 185.65 ± 1.43 | 66.37–471.03 |
| | Directional persistence | 0.38 ± 0.00 | –0.05–0.66 | 0.23 ± 0.00 | –0.51–0.73 |
| | Directional bias | 0.19 ± 0.00 | –0.03–0.60 | 0.22 ± 0.00 | –0.27–0.67 |
| | Daily movement distance (m) | 5,249 ± 28 | 1,688–14,114 | 2,629 ± 24 | 553–6,719 |
| | Weekly movement range (%) | 11.81 ± 0.10 | 0.73–41.19 | 4.06 ± 0.08 | 0.00–23.32 |

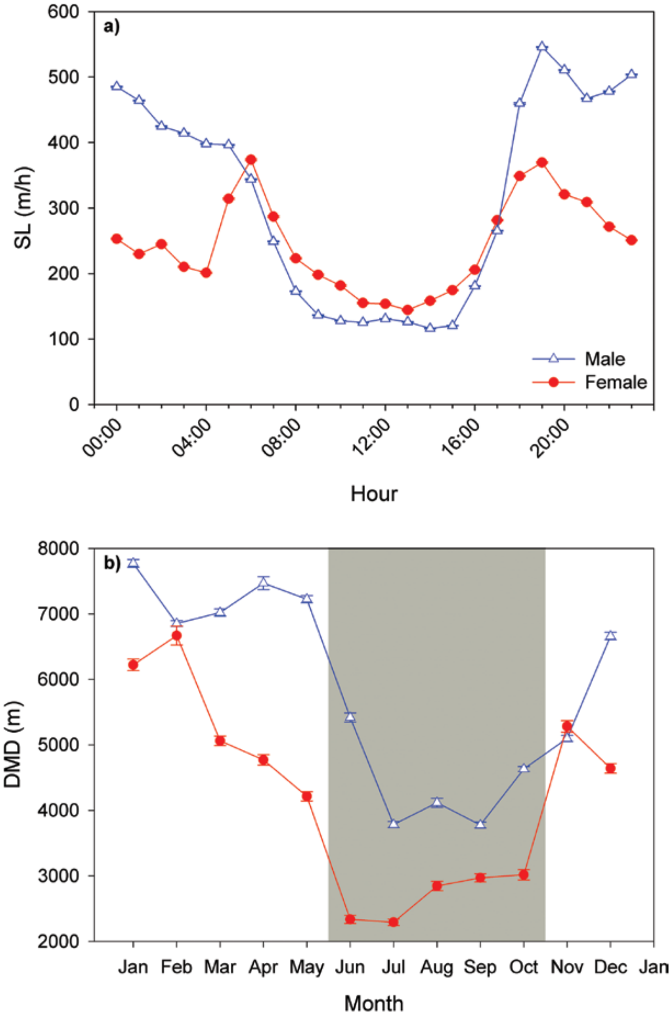

**Fig. 2.**—Sex-specific mean (a) hourly step length (SL) during the diel period; and (b) daily movement distance (DMD) by month. Shaded area indicates wet season.

We evaluated the relationships between the index of risk and the habitat selection coefficient on movement metrics using the best model that included these covariates. The index of risk was related negatively to DMD and positively to OD; its relationship to other movement metrics was inconsistent (Table 2; Fig. 4). The habitat selection coefficient, for which lower values equate to higher habitat selection rankings, was related positively to OD, ED, and DMDs (i.e., DMD decreased as habitat selection coefficient decreased), but negatively to step length (i.e., speed increased as habitat selection coefficient decreased; Table 2; Fig. 4).

Observed and expected displacements were larger for males than for females, and within each sex, larger during the dry than wet season (Table 3). Daily and weekly ED was similar to OD and explained 66% ($R^2 = 0.658$, slope = 0.869, $SE = 0.018$), and 47% ($R^2 = 0.469$, slope = 0.737, $SE = 0.040$) of the observed variability, respectively (Figs. 5a and 5b). Monthly ED explained 61% ($R^2 = 0.614$, slope = 0.08, $SE = 0.007$) of the observed variation, but OD was consistently lower than ED (Fig. 5c).

All well-supported generalized linear mixed models for movement metrics included an effect of season, suggesting that all movement parameters differed between dry and wet seasons (Table 2). The most parsimonious model for step length and DMD included an interaction effect of season and index of risk, although the habitat selection coefficient also appeared as an effect in well-supported models for these parameters. OD was affected by season and habitat selection coefficient; a competing model that received similar support ($\Delta\text{AIC} < 1$) also included sex as a covariate, highlighting sex-specific differences in this metric. Although the most parsimonious models for ED included season, other models with $\Delta\text{AIC} < 2$ suggested that season and sex also substantially affected ED (Table 2). The patterns of seasonal and sex-specific differences in movement metrics were as expected.

## Discussion

*Florida panther movement patterns.*—Using high-resolution GPS location data, our goal was to discern and quantify factors that influence movement patterns of Florida panthers. We expected movement patterns to differ between males and females due to differences in reproductive behaviors. In theory, movement by males should manifest itself in 2 forms: territoriality and transitory movements. Territoriality is a trait exhibited by dominant males guarding their home ranges to control access to resources and females (Logan and Sweanor 2001). Territoriality is recognizable by constant, regular movement from one end of the home range to the other. Transitory movement is typically associated with younger males that lack a home range. These young males move to find food and avoid conflicts with resident males that may result in injury or death. Transitory movement is characterized by irregular, large, straight-line movements punctuated by lengthy stationary periods (Sandell 1989; Beier et al. 1995; Jedrzejewski et al. 2002; van de Kerk et al. 2015). Movement of females, on the other hand, is dictated by their reproductive chronology and is influenced by the presence of young. Gravid females establish a den within their home range just before parturition. Births can occur during any month of the year, but peak in the spring (Hostetler et al. 2012). For 2 months post parturition, feeding and caring for young anchors the mother to the den except for short jaunts to hunt and feed (Hemker et al. 1984; Maehr 1990; Beier et al. 1995). After young reach 2 months of age, the dam abandons the den and leads young on short movements to kills (Maehr et al. 1989) and temporary cache sites. Movements become progressively longer until the young disperse, at approximately 14 months of age (Hemker et al. 1984; Maehr et al. 1989, 2002; Beier et al. 1995; Hostetler et al. 2010). After the young have dispersed, females typically have a short period of less-constrained movement until they mate again and the cycle repeats.

Consistent with these expected patterns, movements of male panthers were characterized by approximately 33% longer step lengths, 28% longer DMD, and more directional persistence than movements of females. These movement metrics seem to reflect the behavior of territorial males that require rapid movement with a high degree of directional persistence to traverse their home range as quickly and frequently as possible to

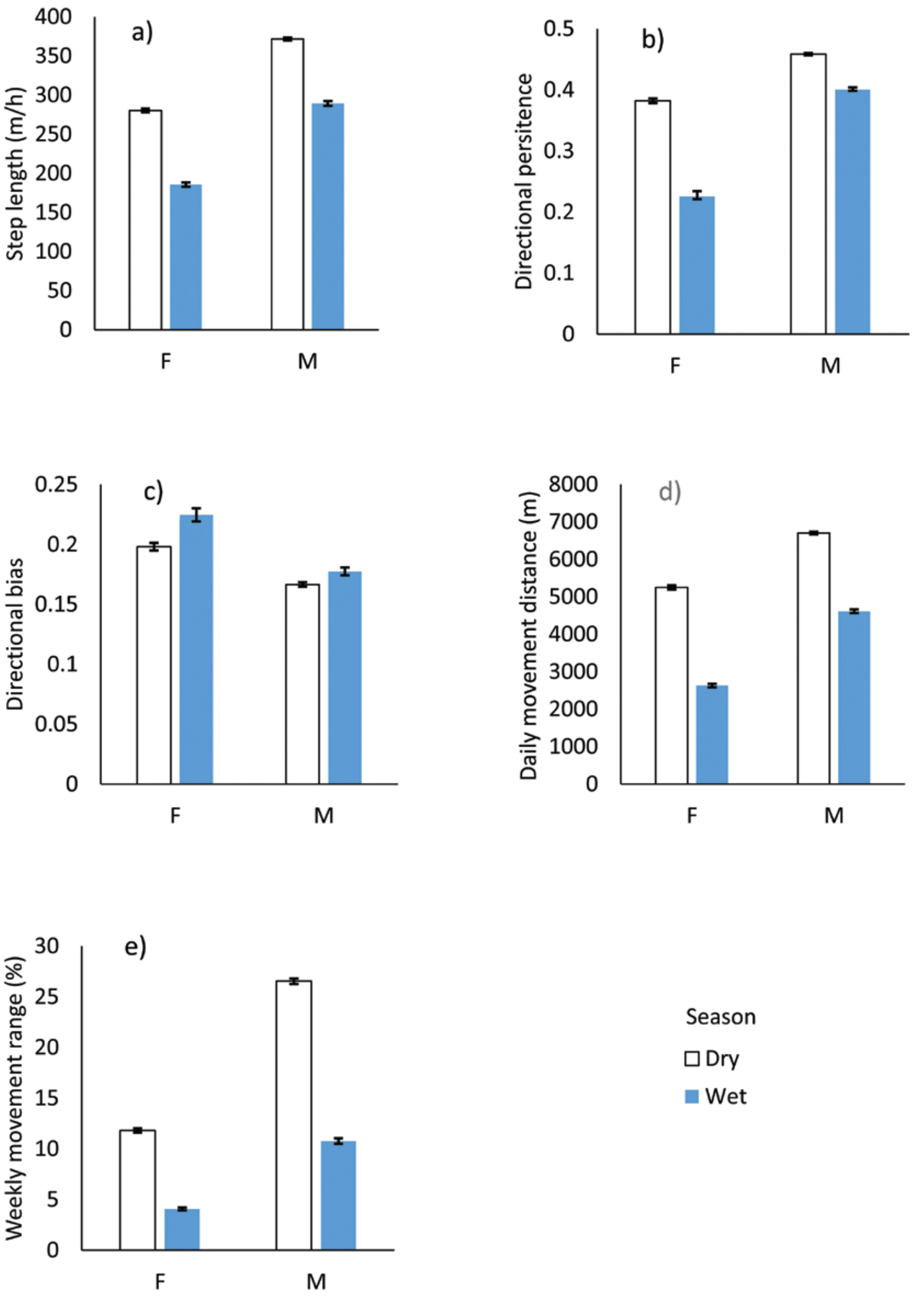

**Fig. 3.**—Sex- and season-specific step length (a), directional persistence (b), directional bias (c), daily movement distance (d), and weekly movement range of Florida panthers (*Puma concolor coryi*) in southern Florida, 2005–2012, aggregated by week (e).

defend against male challengers and to locate resident females that are in estrous (Logan and Sweanor 2010). The movement metrics we calculated for female panthers suggest the kind of movement pattern that would be expected for individuals caring for and accompanied by young much of the time: slower movement with shorter step lengths and less directional persistence. The territorial behavior of adult males resulted in their covering on average 27% of their home range (while monitored) weekly, whereas females, whose movement can be impacted by maternal behavior, covered only 12% of their home range weekly. We note our sample of GPS-collared panthers was skewed toward young males and included only a small number of GPS-collared females, with only 1 female who was reproductively active when monitored (van de Kerk et al. 2015). This may have influenced metrics by homogenizing differences due to sex and age as movements by older females may more closely resemble those of subadult males. Even though our sample of females was small, it represented 3 demographic age groups (subadult, adult, and older adult). Female panthers are more important for monitoring long-term demographic patterns of population growth and persistence (Hostetler et al. 2013), so less-reliable GPS collars with a maximum life expectancy

**Table 2.**—Model selection results testing for the effect of sex, season, habitat selection coefficient (HQ), and index of risk (RR, "road risk" as the index is based on road density and traffic volume) on Florida panther (*Puma concolor coryi*) movement metrics: step length (SL), observed displacement (OD), expected displacement (ED), daily movement distance (DMD), and weekly movement range (WMR) aggregated by week. Number of parameters (*k*), log likelihood (LL), difference in AICc (Akaike information criterion corrected for small sample size) between a given model and the best supported model in the set (ΔAICc), and AICc weights are presented. A plus sign (+) indicates additive effects and an asterisk (*) indicates additive and interactive effects. The number of parameters includes the intercept as well as residuals and random-effect variance terms. We only present models with a ΔAICc < 4 along with the null model.

| | Model | *k* | LL | ΔAICc | Weight |
|---|---|---|---|---|---|
| SL | Season * RR | 6 | −2,346.63 | 0.00 | 0.33 |
| | Sex + season | 5 | −2,348.58 | 1.84 | 0.13 |
| | Season | 4 | −2,349.62 | 1.86 | 0.13 |
| | Season * RR + HQ | 7 | −2,346.61 | 2.05 | 0.12 |
| | Season * HQ | 6 | −2,348.09 | 2.93 | 0.08 |
| | Sex + season + HQ | 6 | −2,348.48 | 3.70 | 0.05 |
| | Season + HQ | 5 | −2,349.59 | 3.87 | 0.05 |
| | Season + RR | 5 | −2,349.60 | 3.88 | 0.05 |
| | Null | 3 | −2,370.80 | 42.20 | 0.00 |
| OD | Season + HQ | 5 | −3,780.04 | 0.00 | 0.37 |
| | Sex + season + HQ | 6 | −3,779.48 | 0.95 | 0.23 |
| | Season * HQ | 6 | −3,780.03 | 2.06 | 0.13 |
| | Season + RR | 5 | −3,781.15 | 2.23 | 0.12 |
| | Season * RR | 6 | −3,780.98 | 3.96 | 0.05 |
| | Null | 3 | −3,793.05 | 21.93 | 0.00 |
| ED | Season | 4 | −3,710.87 | 0.00 | 0.25 |
| | Sex + season | 5 | −3,710.27 | 0.85 | 0.17 |
| | Sex + season + HQ | 6 | −3,709.34 | 1.06 | 0.15 |
| | Season + HQ | 5 | −3,710.48 | 1.26 | 0.14 |
| | Season * RR | 6 | −3,709.83 | 2.03 | 0.09 |
| | Season + RR | 5 | −3,710.87 | 2.05 | 0.09 |
| | Sex + season + RR | 6 | −3,710.27 | 2.91 | 0.06 |
| | Season + HQ + RR | 6 | −3,710.37 | 3.10 | 0.05 |
| | Null | 3 | −3,724.53 | 25.27 | 0.00 |
| DMD | Season * RR | 6 | −3,466.71 | 0.00 | 0.58 |
| | Sex + season + HQ + RR | 7 | −3,467.17 | 3.00 | 0.13 |
| | Null | 3 | −3,516.33 | 93.07 | 0.00 |
| WMR | Sex + season | 5 | −1,320.30 | 0.00 | 0.20 |
| | Sex + season + HQ | 6 | −1,319.36 | 0.18 | 0.18 |
| | Season * HQ | 6 | −1,319.63 | 0.72 | 0.14 |
| | Season + HQ | 5 | −1,320.79 | 0.98 | 0.12 |
| | Season | 4 | −1,322.03 | 1.41 | 0.10 |
| | Sex + season + RR | 6 | −1,320.07 | 1.60 | 0.09 |
| | Season * HQ + RR | 7 | −1,319.62 | 2.79 | 0.05 |
| | Season + HQ + RR | 6 | −1,320.79 | 3.04 | 0.04 |
| | Season + RR | 5 | −1,321.94 | 3.27 | 0.04 |
| | Null | 3 | −1,361.51 | 78.32 | 0.00 |

of 1 year in South Florida were often not optimal for concurrent studies that required long-term data on females. Such data could only be obtained with VHF collars that typically have an average operational life span of 5 years, hence our smaller sample of females with GPS collars.

The DMD estimated for Florida panthers (males: 6.7 ± 17 [*SE*] km during the dry season, 4.6 ± 25 km during the wet season; females: 5.2 ± 28 km during the dry season, 2.6 ± 24 km during the wet season) was similar to that reported for pumas in southern California (6.4 ± 4.2 [*SD*] km—Beier et al. 1995), but was smaller than estimates for pumas in cool, arid landscapes along the Utah–Idaho border (16.1 ± 0.8 km—Laundré 2005) and Patagonia, Chile (13.4 ± 2.5 km—Elbroch and Wittmer 2012). Elbroch and Wittmer (2012) suggested that the shorter DMDs in Patagonia than in Utah–Idaho were due to higher prey density in Patagonia. Southern California and Florida are characterized by Mediterranean and tropical climates, respectively, with more stable temperatures. We hypothesize that the combination of warmer climate and different prey assemblages shortened the DMD even further for Florida panthers compared with the findings of Laundré (2005) and Elbroch and Wittmer (2012) because they may allow for higher panther densities and smaller home ranges that can reduce travel distances. Our results also show that the varied hydrological conditions experienced in South Florida throughout the year have an impact on the DMD of panthers (see below). Finally, perhaps DMDs in Florida are shortened by dense human populations that border the panther breeding range and by the abundance of roadways.

*Relationships between covariates and movement metrics.*—Movement patterns of panthers were highly seasonal; virtually all well-supported models for each movement metric included the effect of season. South Florida's tropical climate and latitude reduce variation in seasonal daylight and temperature (Duever et al. 1986). Thus, panthers depend less on photoperiod and temperature differences to cue their annual cycles than do western pumas and are more influenced by seasonal hydroperiod (McCarthy and Fletcher 2015), highlighted by large differences in every movement parameter compared between dry and wet seasons. During the wet season (May–October), South Florida experiences frequent afternoon thunderstorms. Additionally, water levels can rise significantly when a tropical depression or hurricane makes landfall during the wet season. These seasonal changes in precipitation, in conjunction with South Florida's low elevation and flat topography, result in a sheet-flow of water across much of the landscape that can remain deep (0.5 m or more) for months (Duever et al. 1986; MacDonald-Beyers and Labisky 2005). The dry season is characterized by reduced precipitation, mild weather, and the drawdown of water across the previously saturated landscape. This hydrologic shift effectively dominates the ecology of South Florida and influences the organisms dwelling there. Home ranges for all panthers we studied were subjected to this flooding.

For most terrestrial mammals, energetic costs associated with travel by wading or swimming are greater than walking and running. Therefore, when water levels are elevated, panthers move shorter distances. White-tailed deer (*Odocoileus virginianus*), feral hogs (*Sus scrofa*), raccoons (*Procyon lotor*), and other prey species are also restricted by high water levels and may congregate on upland "islands" dominated by pines and hardwood hammocks with somewhat dry soil (MacDonald-Beyers and Labisky 2005). This concentration of prey likely benefits panthers, because it allows them to move to high ground and hunt for extended periods in a small portion of their home range. During the dry season, previously flooded land becomes traversable to most prey species, which in turn leads

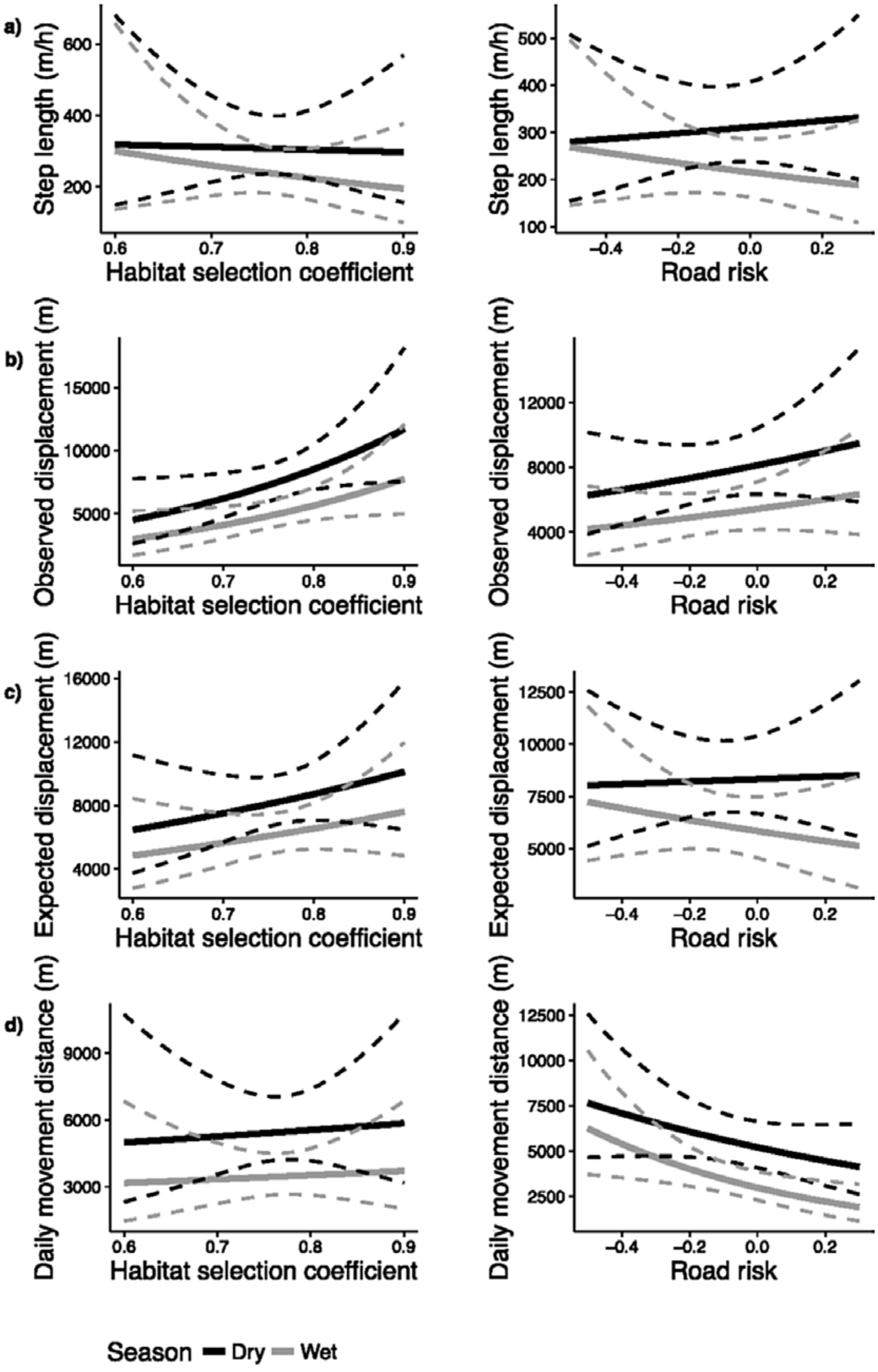

**Fig. 4.**—The effect of habitat selection coefficient (higher-selected habitat indicated by a lower coefficient value) and road risk on Florida panther (*Puma concolor coryi*) movement metrics: a) step length, b) observed displacement, c) expected displacement, and d) daily movement distance These relationships were assessed based on the most parsimonious model including the covariate (Table 2), and are depicted separately for dry and wet seasons.

to panthers moving farther to acquire prey, which now can disperse. Similar predator–prey dynamics resulting from seasonal flooding have been documented in jaguars on the Pantanal of Brazil (Crawshaw and Quigley 1991; Cavalcanti and Gese 2009, 2010).

The relationships of the index of risk to movement were difficult to discern. The index of risk was related positively to step length during the dry season and negatively during the wet season. This pattern parallels our findings regarding step length differences between seasons and may result from the significant interaction we identified between these 2 covariates on step length. Conversely, the index of risk was negatively related to DMD regardless of season. Our index of risk is based on road density and traffic volume, and the influence of roads on

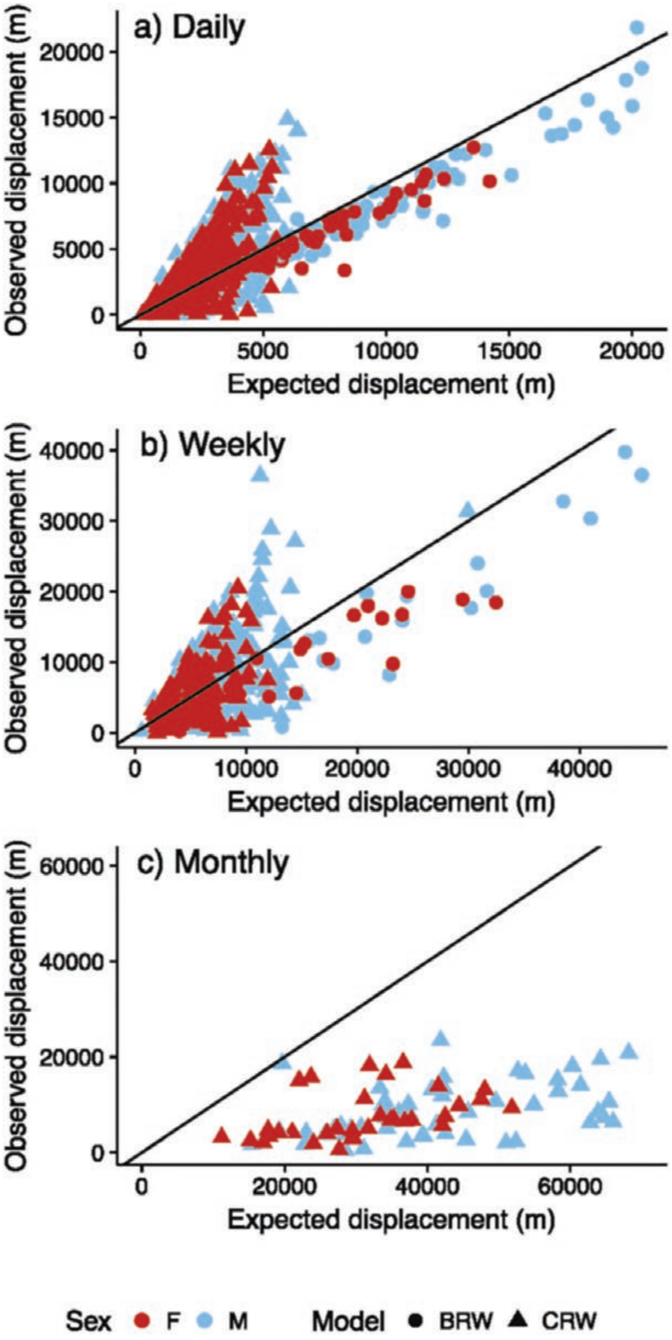

**Fig. 5.**—Observed versus expected displacement of male and female Florida panthers (*Puma concolor coryi*) in a) daily, b) weekly, and c) monthly time intervals. The diagonal line represents a perfect match. Expected displacements were calculated using either biased random walk (BRW) or correlated random walk (CRW) models.

movement metrics could be clarified by increasing the number of panthers monitored in areas with varied levels of risk from roads. Our sample is biased by panthers that often roam large parcels of public land and may only intermittently encounter roads. The presence of the index of risk in many, if not all, of our most parsimonious models for DMD and step length demonstrates that additional research to determine the impact of roads on panther movement is warranted.

**Table 3.**—Sex- and season-specific daily, weekly, and monthly observed (OD) and expected (ED) displacement of Florida panthers (*Puma concolor coryi*). Mean values are in meters.

| Sex | Season | Parameter | Daily ($\bar{X}$ ± *SE*) | Weekly ($\bar{X}$ ± *SE*) | Monthly ($\bar{X}$ ± *SE*) |
|---|---|---|---|---|---|
| Male | Dry | OD | 3,795 ± 5.5 | 9,691 ± 53.8 | 12,346 ± 371.0 |
| | | ED | 3,379 ± 5.3 | 10,172 ± 48.2 | 92,337 ± 3,965.5 |
| | Wet | OD | 2,818 ± 11.0 | 5,977 ± 47.6 | 9,005 ± 231.5 |
| | | ED | 2,689 ± 11.1 | 7,125 ± 39.5 | 43,636 ± 1,520.7 |
| Female | Dry | OD | 3,232 ± 9.7 | 7,378 ± 61.0 | 8,045 ± 305.4 |
| | | ED | 2,860 ± 8.2 | 7,811 ± 54.4 | 35,961 ± 569.7 |
| | Wet | OD | 1,952 ± 28.2 | 49,688 ± 67.3 | 7,245 ± 319.5 |
| | | ED | 1,958 ± 28.2 | 5,808 ± 92.7 | 26,123 ± 536.3 |

Panthers generally covered longer DMDs but did so at a slower step length (m/h) in habitats known to have higher selection coefficients (less-selected habitat classes) for panthers. Our step length results differ from those of Dickson et al. (2005), who denoted faster step lengths in California for pumas when using habitats that had low selection rankings. This difference may be due to the extreme hydrological fluctuations that characterize the tropical ecosystems of South Florida. For example, during the wet season, panthers moved faster in higher-selected habitat, while step length during the dry season did not vary extensively with habitat selection coefficient. Some possible explanations for these observations include: 1) during the dry season, when more of the landscape is easily traversed, panthers can quickly pass through less-selected habitat to reach better habitat with more prey; and 2) when water levels rise, panthers may be forced to limit their movement and will avoid less-selected habitat altogether and concentrate movement in higher-selected habitats, such as upland forests. Upland forests are more likely to remain dry during the wet season, whereas less-selected habitat (e.g., marsh-shrub-swamp) may be inundated, which would impede movement (Cox et al. 2006; Onorato et al. 2011).

Our findings demonstrate that sex, selected habitat, season, and road risk affect patterns of Florida panther movement. These results may assist managers in developing more effective policies to address challenges currently facing the panther population due to habitat loss and mortality associated with vehicle collisions (Onorato et al. 2010, 2011; Frakes et al. 2015). Furthermore, our results regarding movement metrics of panthers could prove useful to planners in the delineation of effective corridors between remnant areas of habitat. Such information is especially critical given Florida's rapidly growing human population. Improving our knowledge of such factors as habitat selection and movement patterns can help limit the impact of development and road construction on the recovery of the Florida panther.

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