



Effects of environmental factors and landscape features on movement patterns of Florida black bears

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A greater understanding of how environmental factors and anthropogenic landscape features influence animal movements can inform management and potentially aid in mitigating human–wildlife conflicts. We investigated the movement patterns of 16 Florida black bears (*Ursus americanus floridanus*; 6 females, 10 males) in north-central Florida at multiple temporal scales using GPS data collected from 2011 to 2014. We calculated bi-hourly step-lengths and directional persistence, as well as daily and weekly observed displacements and expected displacements. We used those movement metrics as response variables in linear mixed models and tested for effects of sex, season, and landscape features. We found that step-lengths of males were generally longer than step-lengths of females, and both sexes had the shortest step-lengths during the daytime. Bears moved more slowly (shorter step-lengths) and exhibited less directed movement when near creeks, in forested wetlands, and in marsh habitats, possibly indicating foraging behavior. In urban areas, bears moved more quickly (longer step-lengths) and along more directed paths. The results were similar across all temporal scales. Major roads tended to act as a semipermeable barrier to bear movement. Males crossed major roads more frequently than females but both sexes crossed major roads much less frequently than minor roads. Our findings regarding the influence of landscape and habitat features on movement patterns of Florida black bears could be useful for planning effective wildlife corridors and understanding how future residential or commercial development and road expansions may affect animal movement.

Key words: black bear movement, expected displacement, mean squared displacement, movement ecology, observed displacement, random walk, step-length, *Ursus americanus*

Movement is fundamental for animals to obtain resources, escape threats, disperse, and find mates. Therefore, movement affects population dynamics and genetic connectivity among populations as well as affecting an individual animal's fitness (Morales et al. 2010). Knowledge of movement patterns can be used to improve our understanding of animals' habitat requirements, to predict future range expansions, and to plan potential wildlife corridors in a more informed way (Colchero et al. 2011; Buchmann et al. 2012; Avgar et al. 2013; Clark et al. 2015; Allen and Singh 2016). Additionally, as more land is altered for human use, understanding animal movement in fragmented,

human-dominated landscapes may provide important insights into the potential impact of human disturbance on wildlife (Belotti et al. 2012; Martin et al. 2013) and suggest ways to reduce conflict with humans (May et al. 2010; Jachowski et al. 2013; Russell et al. 2013; Vasudev and Fletcher 2015).

Many factors affect an animal's movement patterns. Individuals within a species may exhibit different movement patterns depending on their sex, age or life-history stage, and reproductive status (Aschoff 1966; Nathan et al. 2008; Laidre et al. 2013; Martin et al. 2013; van de Kerk et al. 2014). Extrinsic factors such as habitat quality, resource availability

and access, as well as anthropogenic features on the landscape, also influence animal movement (McClellan et al. 2001; Ager et al. 2003; Fahrig 2007; Kauhala et al. 2007; Belotti et al. 2012; Kozakai et al. 2013). For example, many animals move more slowly in resource-rich habitats than in poor quality or fragmented habitats (Fryxell et al. 2008; Avgar et al. 2013; Ehlers et al. 2014; van Moorter et al. 2016). Additionally, anthropogenic features may impede or facilitate animal movement. Animals may avoid crossing roads or traversing through areas with high levels of human activity or buildings (Tigas et al. 2002; Revilla and Wiegand 2008; Holderegger and Di Giulio 2010; Beyer et al. 2016). Alternatively, animals may use roads or other human-made linear features as travel paths and thus may exhibit increased movement rates and higher directionality in these areas (Tigas et al. 2002; Dickson et al. 2005; Roever et al. 2010). Animals also may exhibit different movement patterns if they are attracted to anthropogenic areas due to the availability of human foods (Rogers 1987; Tigas et al. 2002; Merkle et al. 2013; Lewis et al. 2015). Because large carnivores are highly mobile, require relatively large spaces and a large amount of resources, and because they can potentially come into serious conflict with humans, knowledge of their movement patterns may be particularly useful for species and land management.

The Florida black bear (*Ursus americanus floridanus*) is a subspecies of American black bear that currently occurs in 7 relatively isolated populations across the state (Larkin et al. 2004; Dixon et al. 2007; Florida Fish and Wildlife Conservation Commission 2012). The statewide population is thought to be increasing and bears are recolonizing portions of their former range (Pelton et al. 1999; Dobey et al. 2005; Hostetler et al. 2009; Florida Fish and Wildlife Conservation Commission 2012). However, the human population in Florida is also increasing (U.S. Census Bureau 2017). Black bears are omnivorous habitat generalists, and therefore may utilize a wide variety of habitats, including residential areas, which may lead to human–bear conflicts. Threats to Florida black bears include habitat loss (due to habitat fragmentation and residential and commercial development), road-related mortalities, and, in smaller populations, low genetic diversity (Larkin et al. 2004; Dixon et al. 2007; Florida Fish and Wildlife Conservation Commission 2012).

Space use by black bears varies widely across their geographic range, with home range size typically showing an inverse relationship with habitat productivity (Alt et al. 1980; Smith and Pelton 1990; Oli et al. 2002). Sex also influences space use by bears; males generally use larger home ranges than females (Alt et al. 1980; Hellgren and Vaughan 1990; Dobey et al. 2005). Furthermore, space use by bears of both sexes varies seasonally in response to the bears' physiological cycles and food availability; for example, bears generally use larger home ranges in the fall when hyperphagia causes them to forage more actively in preparation for winter denning (Garshelis and Pelton 1981; Hellgren et al. 1989; Noyce and Garshelis 2011). In the southeastern United States, bears tend to select riparian forests over more open habitats (Hellgren et al. 1991; Wooding and Hardisky 1994; Stratman et al. 2001; Dobey et al. 2005;

Karelus et al. 2016). Florida black bears rely heavily on saw palmetto (*Serenoa repens*) and other hard and soft mast as food sources, but also eat insects (Maehr and Brady 1984; Stratman and Pelton 1999; Dobey et al. 2005).

While patterns of space and habitat use of bears are generally well understood (Garshelis and Pelton 1980; Masters 2002; Lewis and Rachlow 2011; Guthrie 2012), few studies have directly investigated movement patterns based on fine temporal scales, such as hourly or bi-hourly locations. Fewer still have tested for additive and interactive effects of spatial or temporal factors on movement patterns, and investigated how these patterns vary across temporal scales. Habitat and other extrinsic environmental factors can affect animal movement (Fryxell et al. 2008; Nathan et al. 2008) but the temporal scale at which data are collected may influence the results. Avgar et al. (2013) developed a framework for quantifying the effect of environmental factors on movement of woodland caribou (*Rangifer tarandus caribou*) at various temporal scales using the expected squared displacement, $E(R^2)$, as a primary movement metric. This summary statistic can be used to describe movement patterns and to make predictions at different temporal scales (Kareiva and Shigesada 1983; Morales and Ellner 2002; Nouvellet et al. 2009). How environmental factors affect movement metrics such as step-length, turning angles, and expected squared displacement can provide insights into habitat quality for black bears, or predict how landscape features might affect space use and dispersal.

We studied the movement patterns of Florida black bears in north-central Florida at various temporal scales and, using the analytical framework developed by Avgar et al. (2013), tested for the effects of intrinsic and extrinsic environmental factors thought to influence animal movement. We predicted that 1) males would travel at higher speeds (i.e., with longer step-lengths) and exhibit more directed movements than females; and 2) black bears would travel faster in fall than in summer or winter. In terms of environmental factors, we expected that black bears would 3) travel more slowly in forested habitats and when near creeks; and 4) move shorter distances near major roads.

MATERIALS AND METHODS

Study site.—Our study site was in north-central Florida at Camp Blanding Joint Training Center (295 km²) and adjacent private lands (Fig. 1). Several creeks and drainages run through the area. Natural habitats consist of mesic flatwoods, sand hill uplands and scrub, as well as mixed hardwood hammocks and cypress swamps (Karelus et al. 2016). The natural vegetation communities are fragmented by roads, tree plantations, agriculture, and human communities. Human disturbance on Camp Blanding varies throughout the year. Military training activities occur at the base multiple times per year. When military operations are not occurring, hunting, fishing, wildlife viewing, and hiking are allowed on a portion of the property. Bears were not hunted in Florida during our study.

Field methods and data collection.—We captured bears using Aldrich spring-activated foot snares—with a double anchor

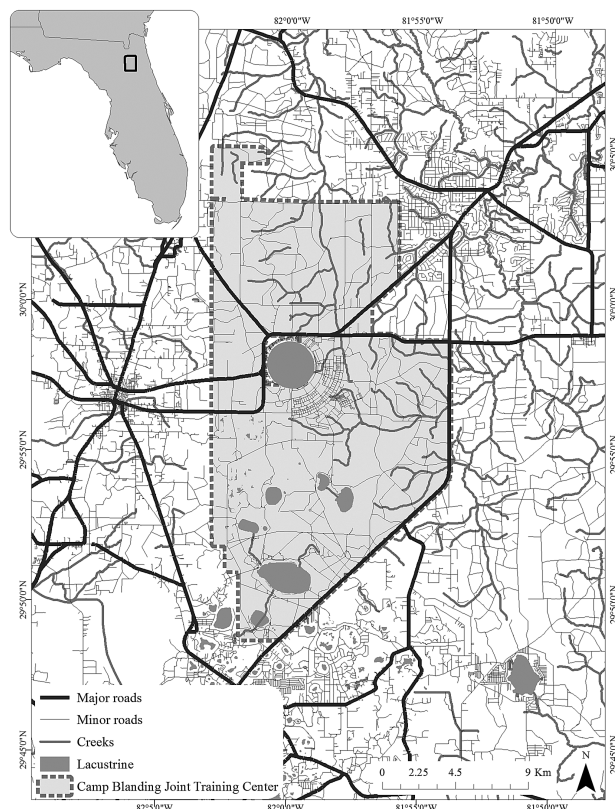


Fig. 1.—Map of the study site at Camp Blanding Joint Training Center, Florida. Roads and creeks are also shown.

cable set (Scheick et al. 2009) and with culvert traps. The double anchor set reduced the potential of injury to captured bears resulting from wrapping the cable around a tree. We anesthetized each captured bear with Telazol (3.5–5 mg/kg), removed a premolar for aging (Willey 1974), fitted them with GPS (Lotek WildCell MG; Lotek Wireless, Inc., Newmarket, Ontario, Canada) transmitting collars, then released them at the capture sites. The collars obtained GPS locations every 2 h and were programmed to fall off after 2 years. The collars were accurate to a 20-m radius for 95% of the locations (Karelus et al. 2016). We visited the sites of suspected denning females to document reproduction. Animals were handled by Florida Fish and Wildlife Conservation Commission staff using methods that conform to the American Society of Mammalogy guidelines (Sikes et al. 2016).

We recorded the landcover type, and distance to creeks, major roads, and minor roads for each bear location. We used the Florida Vegetation and Land Cover 2014 geographic information system (GIS) raster layer (Redner and Srinivasan 2014), which has a resolution of 10×10 m. We grouped landcover types with similar vegetation and combined minimally available land cover types into 6 land cover categories: forested wetlands, marsh wetland, rural-agricultural areas, tree plantations, urban areas, and woodland-scrub (details in Karelus et al. 2016). We obtained the shapefiles for both creeks and roads from the Florida Geographic Data Library (<http://www.fgdl.org/>). We classified primary routes (i.e., interstates and U.S. highways)

and secondary routes (state highways and county roads) as major roads. We classified all other roads as minor roads (e.g., neighborhood roads or private roads that were either paved or native materials). We calculated the distances from each bear location to the nearest creek, major road, and minor road using the package “rgeos” (Bivand et al. 2016) in R (R Core Team 2016).

We divided the day into dawn (0501–0900 h), midday (0901–1700 h), dusk (1701–2100 h), and night (2101–0500 h) to investigate diurnal variation in movement. Because bears undergo seasonal physiological shifts (Hellgren et al. 1989), we defined 3 seasons based on bear biology in Florida: winter (1 January–30 April; when bears typically den), summer (1 May–31 August; when breeding occurs), and fall (1 September–31 December; when hard mast becomes available). We compared winter movements of females with newborn cubs to females without newborn cubs and summer movements for mothers with and without cubs, redefining the summer season as 1 May–31 July based on the known survival of the cubs from VHF collars, game cameras, and sightings. VHF collars on cubs were lightweight and expandable to accommodate the cubs’ growth (Garrison et al. 2007).

Movement metrics.—We investigated bear movements at bi-hourly (every 2 h), daily, weekly, and monthly temporal scales. We defined a day as starting at 0800 and ending at the same time on the consecutive morning. If a location was missing at 0800, we used the next location closest in time from between 0600 and 1000. If no locations from an individual were obtained in that time frame on a day, both that day and the previous day were removed from the daily-scale data. We defined the beginning and the ending of each respective week and month for an individual as the bear’s 1st and last location within the time scale. We removed a day, week, or month for an individual if more than half of the expected number of bi-hourly locations were missing within that time frame (e.g., daily required at least 6 locations per day). We calculated the following movement metrics for all bi-hourly locations: step-length, directional heading, and directional persistence. Step-length, l , is the straight-line distance between 2 successive bi-hourly locations. Directional heading, θ , is the angular difference between the direction of the step and 0° . Directional persistence, c , is the cosine of the difference between 2 consecutive θ s (Avgar et al. 2013). At the daily, weekly, and monthly scales, we calculated the observed displacement (straight-line distance between the 1st and last location for each bear), and overall heading, γ (angle made from the trajectory of the displacement and 0°). We calculated the directional bias, q , as $\cos(\gamma - \theta)$.

We used the expected squared displacement, $E(R^2)$, to assess overall movement patterns at daily, weekly, and monthly scales while incorporating the statistical properties of the movements (Nouvellet et al. 2009; Avgar et al. 2013). The method for calculating $E(R^2)$ depended on the type of movement the animal displayed at each temporal scale: either a biased random walk (BRW) or a correlated random walk (CRW). We determined the type of movement by calculating the correlation between c and q over each time scale for each individual; intervals with a

positive and significant correlation were classified as BRW, all others were considered to be CRW (Benhamou 2006). We calculated $E(R^2)$ for BRW (Codling et al. 2008; Avgar et al. 2013) and for CRW (Benhamou 2006; Avgar et al. 2013), respectively, as:

$$E(R^2) = nE(l^2) + n(n-1)E(q)^2 E(l)^2 \quad (1)$$

$$E(R^2) = nE(l^2) + E(l)^2 \frac{2E(c)}{(1-E(c)) \left(1 - \frac{1-E(c)^n}{1-E(c)}\right)} \quad (2)$$

where n is the expected number of time steps in the given interval (e.g., 12 bi-hourly locations in a day and 84 bi-hourly locations in a week); $E(l)$ is the average bi-hourly step-length over the respective temporal scale; $E(c)$ is the weighted average directional persistence; and $E(q)$ is directional bias. The directional persistence and directional bias were weighted by the average step-length to account for potential correlation between travel speed and direction (Avgar et al. 2013).

For each bear, we calculated the mean squared displacement (MSD), a measure of how far an animal moves within a certain time interval (Kareiva and Shigesada 1983; Benhamou 2006; Codling et al. 2008), as:

$$\text{MSD}(\Delta t) = \frac{1}{N - \Delta t} \sum_{k=1}^{N-\Delta t} (x_{t_{k+\Delta t}} - x_{t_k})^2 + (y_{t_{k+\Delta t}} - y_{t_k})^2 \quad (3)$$

where N is the number of locations for each bear, x and y are Universal Transverse Mercator (UTM) coordinates of each location, and Δt represents the time interval. MSD provides information about distance moved over a certain window of time (i.e., extent of movement), and about whether or not the animal exhibited bounded movement (Singh et al. 2016). The MSDs of individuals exhibiting confined movement (e.g., within a home range) will reach a plateau with longer time intervals, whereas MSDs of individuals exhibiting unconstrained movement (e.g., dispersal) will continue to increase monotonically.

Statistical analysis of movement.—We used linear mixed models with a random effect of individual bear to examine the effect of environmental covariates on the bi-hourly step-lengths and other movement metrics at the bi-hourly, daily, and weekly temporal scales (Avgar et al. 2013). We tested for the additive fixed effects of sex, season, distance to creeks, distance to major roads, and distance to minor roads on the following movement metrics: bi-hourly step-length l , average step-length $E(l)$, observed displacement, and the square root of expected displacement $E(R^2)$ (hereafter, expected displacement), directional persistence $E(c)$ and directional bias $E(q)$. All variables except $E(c)$ and $E(q)$ were natural log-transformed. Additionally, we tested for 2- and 3-way interactions between season, sex, and each of the distance covariates. For models at the bi-hourly scale, we also included the fixed effects of land cover and an interactive effect of time of day. We incorporated 1st-order autoregressive error in all models to account for autocorrelation in the data. The distances to creeks and roads in all models were standardized by subtracting the mean and dividing

by the standard deviation, thus centering the mean on 0 and reducing convergence problems (Bolker et al. 2009).

We selected the most parsimonious model for each response variable at the weekly and daily scales, while respecting marginality in the interactive terms by including the respective main effects in each model, based on an information-theoretic approach using the Akaike Information Criterion (AIC—Burnham and Anderson 2002; Klar et al. 2008). We assessed the fit of the models using the conditional coefficient of determination ($R^2_{\text{GLMM}(c)}$)—Nakagawa and Schielzeth 2013). The $R^2_{\text{GLMM}(c)}$ was calculated using the R package MuMIn (Barton 2015).

Analysis of road crossing.—Roads can act as semipermeable barriers to animal movement. To assess whether, or to what extent, major and minor roads within the bears' home ranges affected their movement patterns, we analyzed the frequency of road crossing by bears. We recorded the number of times each bear crossed either a major or minor road between each successive bi-hourly location using ArcGIS (ESRI 2015) and Geospatial Modeling Environment (Beyer 2015). We used 95% kernel density estimates as derived in Karelus et al. (2016) for home ranges and used ArcGIS (ESRI 2016) to calculate the length of each of the major and minor roads within each bear's home range. We analyzed the number of road crossings for each road type separately using generalized linear mixed models with a negative binomial distribution with linear-variance parameterization due to overdispersion in Poisson models. We first tested for the fixed effect of sex alone; we then tested for the additive effect of sex and linear road length (log transformed and scaled to a mean of 0) to test for the effect of sex while accounting for the length of the roads. The number of weeks that each bear was tracked was used as an offset; thus, in effect, our response variable was the number of road crossings per week.

We used the R package adehabitatLT (Calenge 2006) to calculate the movement path descriptors. We fitted the mixed effect models with function "lme" in the package "nlme" (Pinheiro et al. 2015) and generalized linear models with a negative binomial response with the function "glmmTMB" in the package "glmmTMB" (Magnusson et al. 2017); all analyses were performed in program R (version 3.3.1—R Core Team 2016).

RESULTS

We collared 16 bears (6 females, 10 males; ages 1.5 to 9.5, all of potential breeding age) and tracked them for 5,812 bear-days between 2011 and 2014, yielding 58,951 bi-hourly 3D-validated GPS locations (mean \pm SE: $2,907.3 \pm 1,033.2$ per bear). When only considering high-quality, 3D-validated bi-hourly locations, the average fix rate at which the locations were obtained was 0.84 ± 0.01 (range: 0.74–0.93). After aggregating data at longer temporal scales, there were 4,628 daily (289.3 ± 103.6 per bear), 711 weekly (44.4 ± 5.61 per bear), and 169 monthly (10.6 ± 3.9 per bear) locations.

Overall, females moved with shorter step-lengths than males, with average bi-hourly step-lengths (mean \pm 1 SE) of $228.45 \pm$

21.88 m for females compared to 346.77 ± 41.46 m for males (Supplementary Data SD1a). Step-lengths of both sexes varied across the diel period during all seasons, with females having the longest step-lengths between 2000 and 2400 h and the shortest step-lengths between 1400 and 1800 h. Males showed a similar pattern but had a longer period of shortest step-lengths (1000–1800 h), which were more similar over the seasons. Bears of both sexes traveled the farthest distances during dusk in the fall and the shortest in the winter (Fig. 2). During our study, only 2 mothers had sufficient GPS location data after leaving their dens for analysis of movement during summer. In the winter, females with cubs had shorter step-lengths than females without cubs across the diel period; however, in the summer their step-lengths were similar (Fig. 3).

Based on MSD, all but 2 bears exhibited confined movement over time (Fig. 4), with males reaching their maximum displacement after approximately 160 h and females after approximately 80 h. The 2 bears with unbounded movements were 2-year-old males, suggesting that these bears were dispersing. Directional persistence and bias for females and males across all temporal scales and seasons were close to zero indicating frequent turns throughout movement trajectories (Supplementary Data SD1a; Figs. 5A and 5B).

A total of 95.2%, 94.4%, and 95.3% of bi-hourly locations were classified as CRW at daily, weekly, and monthly scales, respectively, with the remaining locations classified as BRW. Observed and expected displacements increased with temporal scale for both males and females, and displacements were larger for males than females across all temporal scales (Supplementary Data SD1a). The daily, weekly, and monthly expected displacement explained 59.9%, 55.2%, and 46.0% of the variation in the respective observed displacement (Fig. 6). The expected weekly displacements were longer than observed weekly displacements for females in fall and summer but were similar in winter; however, the expected and observed weekly displacements were similar for males in all seasons (Figs. 5C and 5D).

We further analyzed weekly locations using linear mixed models (results based on bi-hourly and daily locations are presented in Supplementary Data SD1c and SD2d–SD2j). The small sample size of monthly locations precluded more detailed statistical analyses at that temporal scale. The most parsimonious model for $E(l)$ at the weekly scale included an effect of distance to creeks and 3-way interactions among season, sex, and major roads as well as season, sex, and distance to minor roads (Supplementary Data SD1b). The top model for observed weekly displacement included the 3-way interaction between

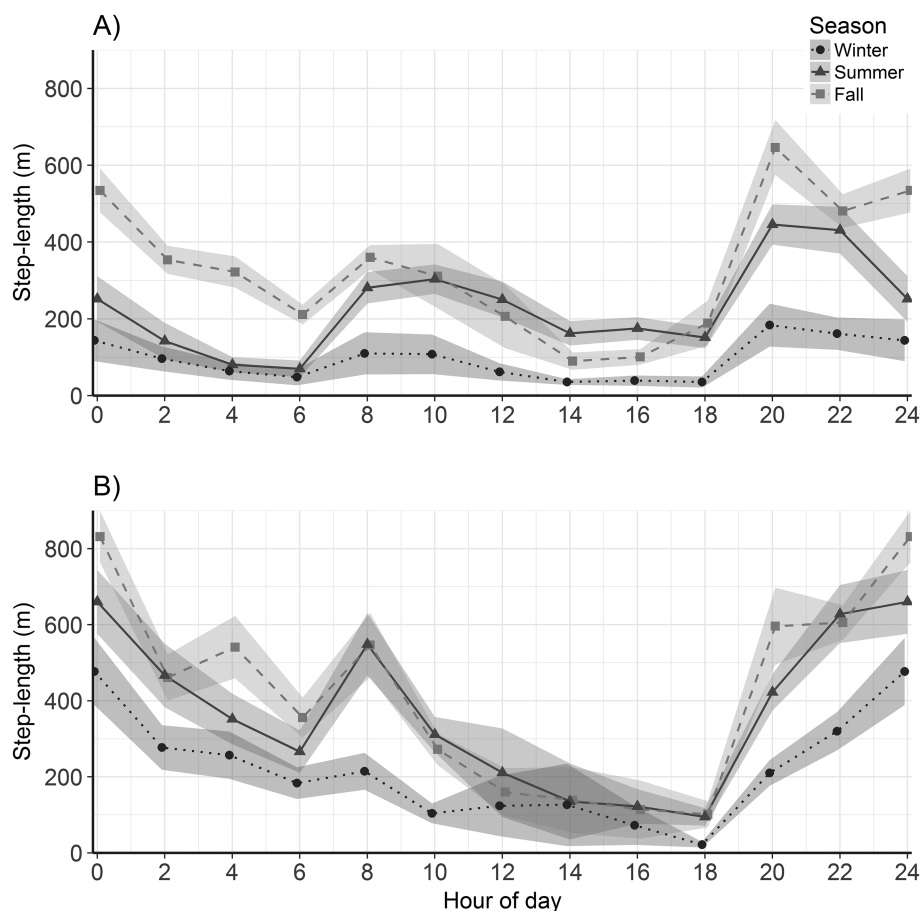


Fig. 2.—Average bi-hourly step-length (\pm 95% CI) in meters throughout the diel period for Florida black bears (*Ursus americanus floridanus*) in north-central Florida for: A) females by season (summer [7,450 locations], fall [8,124 locations], and winter [8,456 locations]; $n = 6$ for all seasons), and B) males by season ($n = 10$ in fall [5,820 locations] and summer [7,495 locations], $n = 7$ in winter [7,126 locations]). Winter was defined as 1 January–30 April, summer as 1 May–31 August, and fall as 1 September–31 December based on the biology of Florida black bears (see text).

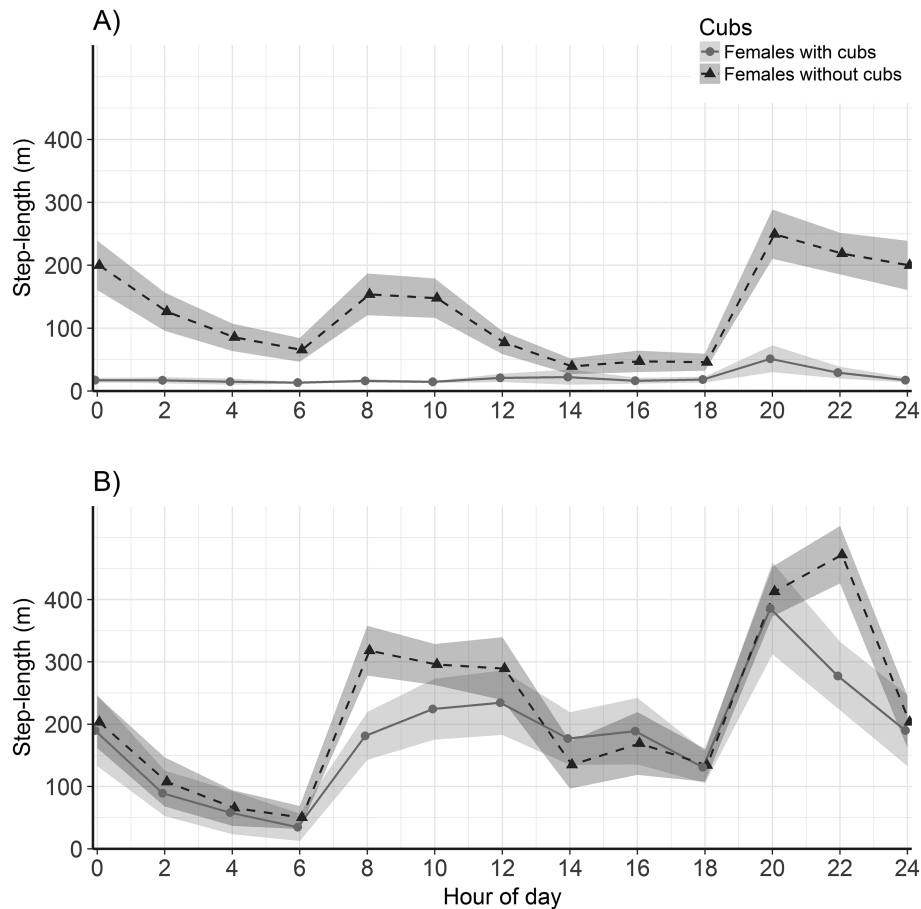


Fig. 3.—Average bi-hourly step-length (\pm 95% CI) in meters throughout the diel period for female Florida black bears (*Ursus americanus floridanus*) in north-central Florida with and without cubs of the year during: A) winter (denning mothers: $n = 3$ [1,666 locations]; females without newborn cubs: $n = 6$ [6,492 locations]), and B) summer (mothers with new cubs: $n = 2$ [1,589 locations]; females without new cubs: $n = 4$ [3,772 locations]). Winter was defined as 1 January–30 April, summer as 1 May–31 August, and fall as 1 September–31 December based on the biology of Florida black bears (see text).

season, sex, and distance to major roads, and the 2-way interaction of sex with minor roads, but did not include distance to creeks (Table 1; Supplementary Data SD1b). The top model for the weekly expected displacement included 2-way interactions between season and distance to creeks, and a 3-way interaction between season, sex, and distance to major roads (Table 1; Supplementary Data SD1b). The same variables generally were the most influential at the daily scale (Supplementary Data SD1c).

The most parsimonious models for movement metrics revealed the following patterns: males had longer step-lengths compared to females; bears of both sexes had shorter step-lengths in winter than in summer or fall; and bears exhibited shorter average step-lengths and displacements when they were closer to creeks (Figs. 7 and 8). Also, females generally traveled shorter bi-hourly distances near minor roads, whereas males generally traveled longer bi-hourly distances near minor roads. Both sexes tended to have shorter step-lengths near major roads but females generally responded more drastically to major roads than males (Figs. 7 and 8). The most parsimonious model for directional persistence at the weekly scale indicated that bears of both sexes turned more near creeks and

females turned more near major roads. Males, on the other hand, exhibited more directed travel, especially during the winter, when near major roads (Supplementary Data SD2a). The most parsimonious model for directional bias indicated that females traveled in a more directed manner over the entire week when they were closer to creeks and farther from minor roads, whereas males traveled in a more directed manner over the week when closer to minor roads and when farther from creeks. However, there were some seasonal differences. In the summer and winter, bears traveled along more directed paths over the week when farther away from creeks (Supplementary Data SD2b). Models for expected weekly displacement and other movement metrics at daily and bi-hourly scales indicated similar trends (Supplementary Data SD2c–SD2j). Analyses at bi-hourly scales also indicated that bears generally traveled with the shortest step-lengths when in forested wetlands and marsh wetlands, and with the longest step-lengths when in rural, agricultural, and urban areas (Supplementary Data SD2j).

Collectively, females crossed major roads 11 times and males crossed major roads 120 times (Table 2). There were 4 females and 3 males that did not cross major roads; however, 2 of those females did not have any major roads within their home range and

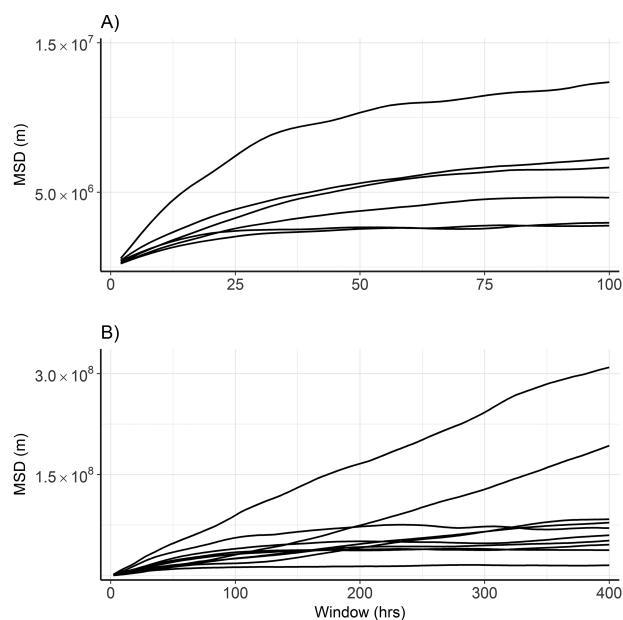


Fig. 4.—The mean squared displacement (MSD) over different time intervals for: A) individual female ($n = 6$; 24,030 locations) and B) male ($n = 10$; 20,441 locations) Florida black bears (*Ursus americanus floridanus*) in north-central Florida. The MSDs reaching asymptotes indicate confined movement (i.e., within a home range).

were removed from further analysis of major road crossings. All bears crossed minor roads. Females crossed minor roads 2,928 times (range: 59–793) and males crossed minor roads 4,033 times (Table 2). Generally, males crossed roads more frequently than females (Table 2). However, when we included the length of roads within each individual's home range as a covariate, the sex-specific differences in the frequency of road crossing disappeared for major roads (slope parameters: β [Male] = -0.61 , 95% CI: $-2.72, 1.50$, β for road length = 1.49 , 95% CI: $0.56, 2.43$), as well as for minor roads: β [Male] = -0.17 , 95% CI: $-0.96, 0.63$, β for road length = 0.39 , 95% CI: $0.04, 0.75$).

DISCUSSION

Male bears in our study area travelled at higher speeds (i.e., with longer step-lengths) than females (Fig. 2); these findings agree with results of earlier studies of black bear movement (Garshelis et al. 1983; Masters 2002; Lewis and Rachlow 2011; Guthrie 2012) and home range dynamics (Hellgren and Vaughan 1990; Dobey et al. 2005; Karelus et al. 2016). Both female and male black bears traveled the least during the day; females tended to exhibit more crepuscular movements, whereas movements by males were more nocturnal. Activity patterns of black bears in natural areas (using active–non-active signals on VHF collars) generally follow a crepuscular pattern, with bears being less active during the day or night (Amstrup and Beecham 1976; Garshelis and Pelton 1980; Masters 2002). A predominantly nocturnal activity pattern is generally thought to be a strategy to avoid human disturbance (Lariviere et al. 1994; Beckmann and Berger 2003; Lyons 2005; Matthews et al. 2006; Ordiz et al. 2012). In our fragmented study area, male bears may have

exhibited greater nocturnal movements than females because males travel more widely and therefore are likely to experience a greater degree of anthropogenic disturbance.

We expected that black bears would move faster in the fall than in summer or winter because bears may have to travel greater distances to acquire sufficient food resources during fall hyperphagia (Garshelis et al. 1983). Whereas females exhibited the expected movement patterns, differences in travel speed of males during summer and fall were less dramatic. Bears in the southern Appalachians traveled greater distances in the fall than in the summer in only 1 of the 3 study sites (Garshelis et al. 1983). Females in the Okefenokee–Osceola area of Florida did not exhibit variation in their movement speeds among seasons; however, some bears made notable long-distance moves outside their home range in the fall (Masters 2002). Mate-seeking behavior by males during the summer breeding season may lead to faster travel speeds (Alt et al. 1980; Smith and Pelton 1990; Lewis and Rachlow 2011), and could potentially have masked the expected seasonal movement patterns.

Our results indicated a substantial reduction in travel speed during winter for both females and males. We confirmed the birth of cubs to 3 collared females during our study and females with newborn cubs consistently exhibited restricted movements in the winter. In contrast, males and females without newborn cubs typically remained more mobile in the winter throughout our study (Fig. 3). This pattern was expected because pregnant females must den in the winter, but all other cohorts of Florida black bears do not necessarily den (Wooding and Hardisky 1992; Garrison et al. 2012).

For animals moving within the bounds of an established home range, the MSD plot reaches an asymptote as the time interval (Δt) is increased. The MSD plot indicated that the movements of female bears reached a maximum distance after approximately 80 h (3 days) and those of males after about 160 h (or 6 days; Fig. 3), suggesting that females cover their home range in about half the time taken by males to complete the same action. The MSD of dispersing individuals tends to continue to increase after that of other individuals has plateaued, reflecting the fact that their movements are not restricted within confined areas. While two 2-year-old males appeared to be dispersing (Costello 2010), we could not confirm that these movements represented dispersal rather than exploratory movements because both bears lost their collars after approximately 3 months. More studies of dispersal such as that conducted by Lee and Vaughan (2003) are needed.

The expected squared displacement incorporates several movement descriptors into a single value (Kareiva and Shigesada 1983; Morales and Ellner 2002; Nouvellet et al. 2009; Avgar et al. 2013), providing information that is not contained in any other single movement descriptor; furthermore, it allows predictions of an animal's movement pattern. The framework developed by Avgar et al. (2013) allows for the expected squared displacement to be calculated assuming either a CRW or BRW, thus accounting for periods when an animal may be exhibiting markedly different movement patterns. Bears were unlikely to travel in a fixed direction or

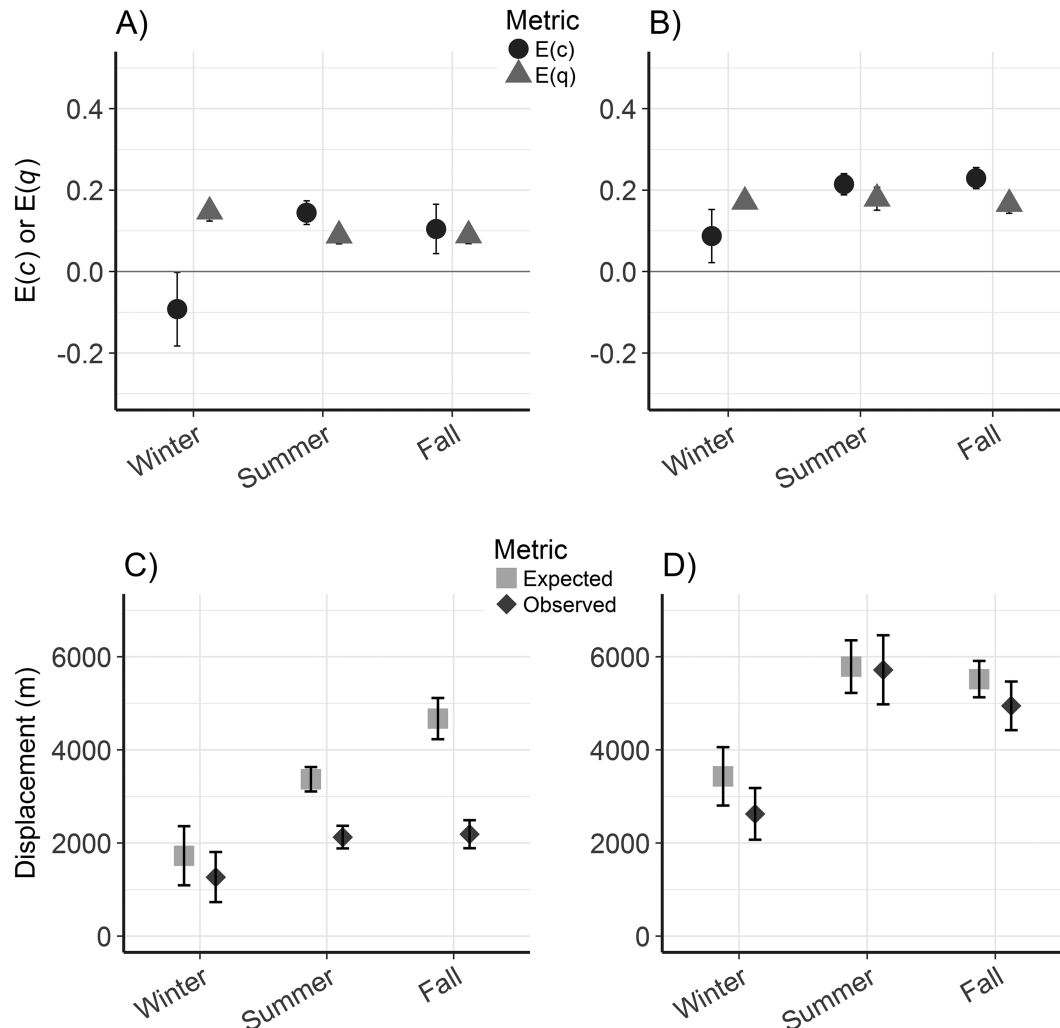


Fig. 5.—Weekly average directional persistence, $E(c)$, and directional bias, $E(q)$, for: A) female and B) male Florida black bears (*Ursus americanus floridanus*). Also presented are weekly average observed displacement and average expected displacement for: C) female and D) male Florida black bears.

exhibit a strong directional bias in their movement paths; consequently, only a small proportion of trajectories were classified as BRW. This matches search strategy theory (Zollner and Lima 1999) in that movements while foraging generally correspond to CRW (e.g., woodland caribou—Avgar et al. 2013).

For both CRW- and BRW-designated bear movement paths, the expected displacement tended to be larger than the respective observed displacement. Avgar et al. (2013) attributed the overestimates of expected displacements of woodland caribou to high primary productivity, which likely led the caribou to increase their foraging activities. The average difference between expected and observed displacements for bears was the highest in the fall, when Florida black bears forage intensely (Wooding and Hardisky 1994; Moyer et al. 2007). However, the strength of the relationship between observed and expected displacements also weakened with an increasing temporal scale, highlighting the importance of temporal scales in the study of animal behavior (McCann et al. 2017). The mismatch between the observed and expected displacements, especially at high

temporal scales, is likely due to the fact that CRW models do not account for confined movements (Bergman et al. 2000; Fryxell et al. 2008; Auger-Méthé et al. 2016).

Results of mixed model analyses suggested that most movement metrics differed between sexes and varied across seasons either in an additive or interactive fashion. Distance to landscape features such as creeks and roads varied in their effect on the movement metrics. Male bears traveled at higher speeds than females, and both sexes traveled faster in fall than in winter. Movements of both sexes were least directed in the winter and most directed in the summer. Directed travel may be advantageous to an animal while searching for new resources or mates (Bailey and Thompson 2006; Bartumeus et al. 2008; Gurarie and Ovaskainen 2013; Laidre et al. 2013; Wilson et al. 2013); thus, our results may indicate that the bears may be searching for highly dispersed food resources in our fragmented study area or for mates in the summer.

We expected that bears would travel with slower speeds in high-quality habitats because they should spend more time in these areas while foraging or resting, and should travel faster

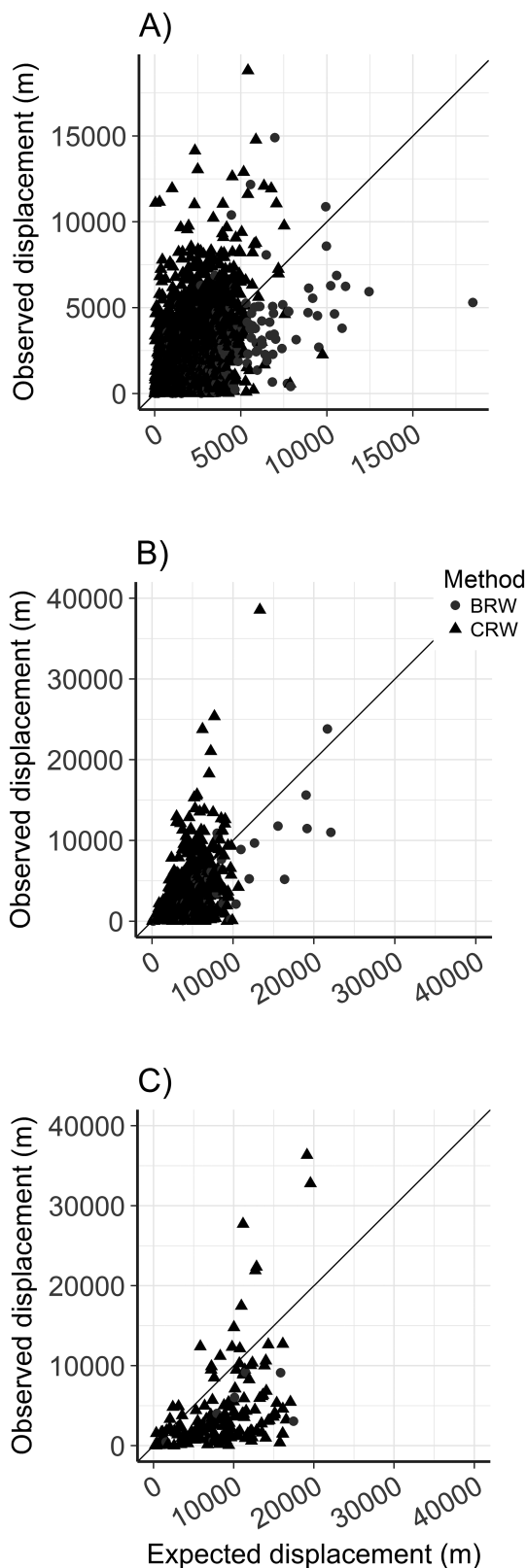


Fig. 6.—Observed versus expected displacements for bi-hourly location data from Florida black bears (*Ursus americanus floridanus*) in north-central Florida at: A) daily, B) weekly, and C) monthly temporal scales for both biased random walks (BRW) and correlated random walks (CRW). The line on each graph indicates a perfect correlation between the observed and expected values.

through poor-quality habitat (Franke et al. 2004; Shepard et al. 2013). In general, bears moved more slowly and turned more frequently in forested wetlands and marsh habitats, and areas near creeks. Forested wetlands generally are resource-rich and provide cover and food (Hellgren et al. 1991; Wooding and Hardisky 1994; Karelus et al. 2016), and creeks are an important source of water. In contrast, bears moved with faster speeds in urban and rural or agricultural areas (Supplementary Data SD2j). Faster travel speeds with longer step-lengths in human-dominated landscapes may be a strategy to minimize anthropogenic disturbance. Bears increase movement speeds and have heightened stress responses when in open agricultural areas without edible crops (Ditmer et al. 2015a). However, with experience, bears can learn to use anthropogenic food sources (Ditmer et al. 2015b), which may change how they move through urban areas.

Animals should reduce their travel speed when encountering landscape features that increase resistance to movement and animals should move faster if some feature of the landscape facilitates movement (Zeller et al. 2012; Avgar et al. 2013; Beyer et al. 2016). Black bears in our study generally exhibited slower movement rates and displacements when near major roads. Shorter step-lengths near major roads were either because of edge effects (Hellgren et al. 1991) or due to a semi-permeable barrier effect of the roads (Whittington et al. 2005; Beyer et al. 2016).

In our study area, field observations of bear tracks persisting along stretches of dirt roads suggested that bears used minor roads as travel pathways (J. W. McCown, pers. obs.). In fact, many large mammals including cougars (*Puma concolor*), bison (*Bison bison*), and wolves (*Canis lupus*) use low-traffic roads as travel pathways (Hellgren et al. 1991; Dickson et al. 2005; Bruggeman et al. 2007; Gurarie and Ovaskainen 2011; Zimmermann et al. 2014). Bears may exhibit seasonal differences in how they use areas near roads due to increased use by humans, such as hunting (Stillfried et al. 2015). When near minor roads, males traveled faster and more directedly, especially in the summer.

Spatial heterogeneity can profoundly influence many aspects of an animal's ecology, including movement, with individuals occupying small habitat fragments being most adversely affected. For example, using an experimental approach, Diffendorfer et al. (1995) found that several species of small mammals travelled substantially longer distances in small fragments; MSDs for individuals inhabiting small fragments were ~2-fold greater than individuals inhabiting large fragments. Conversely, propensity to move decreased as the patch size decreased (Diffendorfer et al. 1995). Roads present an additional challenge to wildlife inhabiting urban areas because they often act as barriers to animal movement and animals inhabiting such habitats tend to avoid roads (National Research Council 2005; Leblond et al. 2013). Our analysis of road crossings indicated that males were more likely to cross roads than females. This is likely because males have larger home ranges and travel greater distances than females and are therefore more prone to encounter roads in a fragmented habitat. However, when we included the length of roads within individual home

Table 1.—Model selection statistics testing for the effect of various covariates on movement metrics of black bears (*Ursus americanus floridanus*) in north-central Florida: A) weekly average bi-hourly step-length, $E(l)$; B) weekly average directional persistence, $E(c)$; C) weekly average directional bias, $E(q)$; D) weekly observed displacement; and E) weekly expected displacement, $\sqrt{E(R^2)}$. Models appear in order of the difference in the Akaike Information Criterion corrected for small sample sizes (ΔAICc). The difference in the log-likelihood from the top model (ΔLL), model probability (Weight), conditional coefficient of determination ($R^2_{\text{GLMM}(c)}$), and the number of parameters (K) are also given. A plus sign (+) indicates an additive effect, whereas a colon (:) indicates an interactive effect. Covariates are: Creeks, Minor roads, Major roads (distances from each location to the respective feature); Sex (females or males), and Season (summer, fall, and winter). See Supplementary Data SD1 for a complete list of models.

Rank	Model	K	Deviance	ΔLL	ΔAICc	Weight	$R^2_{\text{GLMM}(c)}$
A. Weekly average step-length, $E(l)$							
1	Creeks + Major roads + Minor roads + Season + Sex + Major roads:Season + Major roads:Sex + Minor roads:Season + Minor roads:Sex + Season:Sex + Major roads:Season:Sex + Minor roads:Season:Sex	22	1112.32	0.00	0.00	0.17	0.46
2	Creeks + Major roads + Season + Sex + Creeks:Season + Major roads:Season + Major roads:Sex + Season:Sex + Major roads:Season:Sex	18	1121.79	-4.73	0.98	0.10	0.45
B. Average weekly directional persistence, $E(c)$							
1	Creeks + Major roads + Season + Sex + Major roads:Season + Major roads:Sex + Season:Sex + Major roads:Season:Sex	16	-95.70	0.00	0.00	0.23	0.30
2	Creeks + Major roads + Season + Sex + Creeks:Sex + Major roads:Season + Major roads:Sex + Season:Sex + Major roads:Season:Sex	17	-95.77	0.04	2.02	0.08	0.30
C. Average weekly directional bias, $E(q)$							
1	Creeks + Minor roads + Season + Sex + Creeks:Season + Creeks:Sex + Minor roads:Sex	13	-527.65	0.00	0.00	0.03	0.09
2	Creeks + Minor roads + Sex + Creeks:Sex + Minor roads:Sex	9	-519.36	-4.14	0.02	0.03	0.07
D. Weekly observed displacement							
1	Major roads + Minor roads + Season + Sex + Major roads:Season + Major roads:Sex + Minor roads:Sex + Season:Sex + Major roads:Season:Sex	17	2532.32	0.00	0.00	0.10	0.29
2	Creeks + Major roads + Season + Sex + Major roads:Season + Major roads:Sex + Season:Sex + Major roads:Season:Sex	16	2534.67	-1.17	0.25	0.08	0.29
E. Weekly expected displacement							
1	Creeks + Major roads + Season + Sex + Creeks:Season + Major roads:Season + Major roads:Sex + Season:Sex + Major roads:Season:Sex	18	1383.93	0.00	0.00	0.20	0.48
2	Creeks + Major roads + Minor roads + Season + Sex + Creeks:Season + Major roads:Season + Major roads:Sex + Minor roads:Sex + Season:Sex + Major roads:Season:Sex	20	1381.52	1.20	1.83	0.08	0.48

ranges as a covariate in our analysis, the differences in frequency of road crossings between males and females disappeared. Indeed, males tended to have more major roads within their home ranges than did females; 2 of the females included in our study did not have major roads within their home ranges (Table 2). Thus, females avoided crossing roads by establishing home ranges away from major roads, which was not necessarily the case for males. Therefore, the major roads in the Camp Blanding area likely acted as a semipermeable barrier to bear movement, an observation also reported by other studies of bear movement (Brody and Pelton 1989; Beringer et al. 1990; McCown et al. 2009; van Manen et al. 2012). In contrast, minor roads appear to have no effect on bear movement. Bears

of both sexes crossed minor roads with much greater frequency than major roads, and there was no difference in this frequency between males and females. Unlike major roads, the length of minor roads within each bear's home range had no effect on the road crossing rates, suggesting that minor roads present no resistance to movement of bears of either sex.

Knowledge of movement ecology has direct implications for wildlife conservation and management, because movement determines species' geographic range and animals' ability to survive and reproduce (Nathan et al. 2008; Owen-Smith et al. 2010; Barton et al. 2015). Allen and Singh (2016) suggested that linking animal movement ecology with conservation requires knowing movement attributes of the animals and

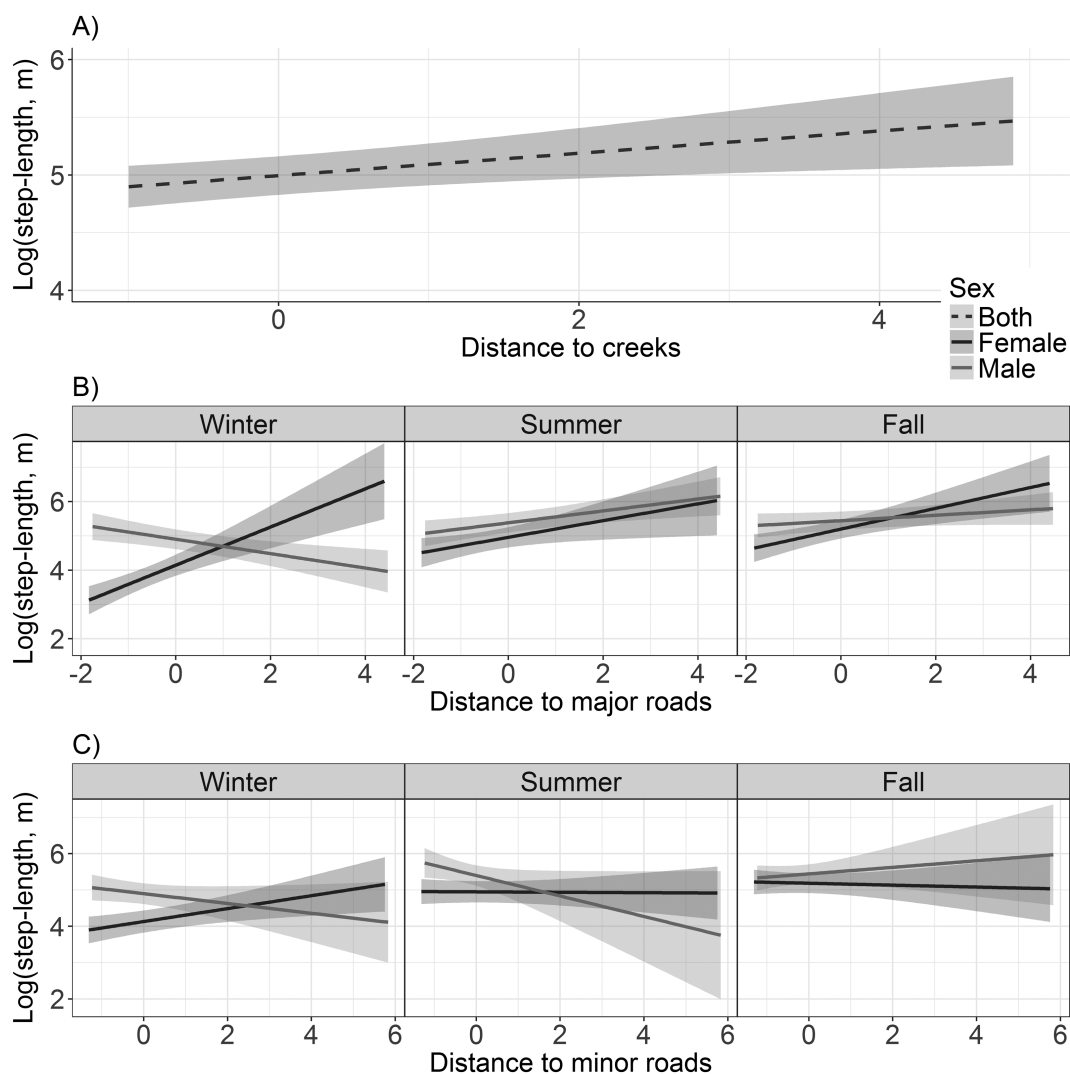


Fig. 7.—Effect of covariates on the weekly average bi-hourly step-length (\pm 95% CI) for Florida black bears (*Ursus americanus floridanus*) in north-central Florida: A) main effect of distance to creeks, B) 3-way interaction among sex, season, and distance to major roads, and C) 3-way interaction among sex, season, and distance to minor roads. All weekly average step-lengths are on the log scale and all distances are standardized.

how this knowledge can be used for the planning and implementation of management actions. Understanding movement patterns may be even more important for the management of large mammals inhabiting anthropogenically fragmented landscapes where they may come into conflict with humans (Tigas et al. 2002; Kertson et al. 2011; Goswami et al. 2015) or die from vehicular collisions (Hostetler et al. 2009; McCown et al. 2009; Benson et al. 2011; Basille et al. 2013). In this study, we provided data on movement patterns of Florida black bears inhabiting a highly fragmented landscape, and showed that male and female black bears exhibit fundamentally different movement patterns, that reproductive status strongly influences movement of females, and that bears may alter their movement patterns depending on habitat quality and anthropogenic disturbance. Bears of both sexes travelled at slower speeds and exhibited less directed movements when near creeks, marshes, or forested wetland habitats, highlighting the importance of forested wetlands for black bears inhabiting human-dominated

landscapes. Because forested wetlands provide foraging and denning habitats, conservation planners should consider mitigating the impacts of future road development on forested wetlands as a priority for bear conservation and for promoting genetic connectivity.

Conservation of species that travel long distances, such as migratory species, often requires managing the entire ecological network, which includes breeding and wintering grounds as well as stopover areas (Faaborg et al. 2010; Brower et al. 2012; Allen and Singh 2016). We suggest that management of highly mobile species inhabiting fragmented landscapes necessitates a similar approach, whereby management efforts should not only focus on habitat patches, but also the linkages among those patches. Such an approach would not only benefit the target species but also promote ecological connectivity and contribute to a broader goal of biodiversity conservation in anthropologically fragmented landscapes (LaPoint et al. 2015).

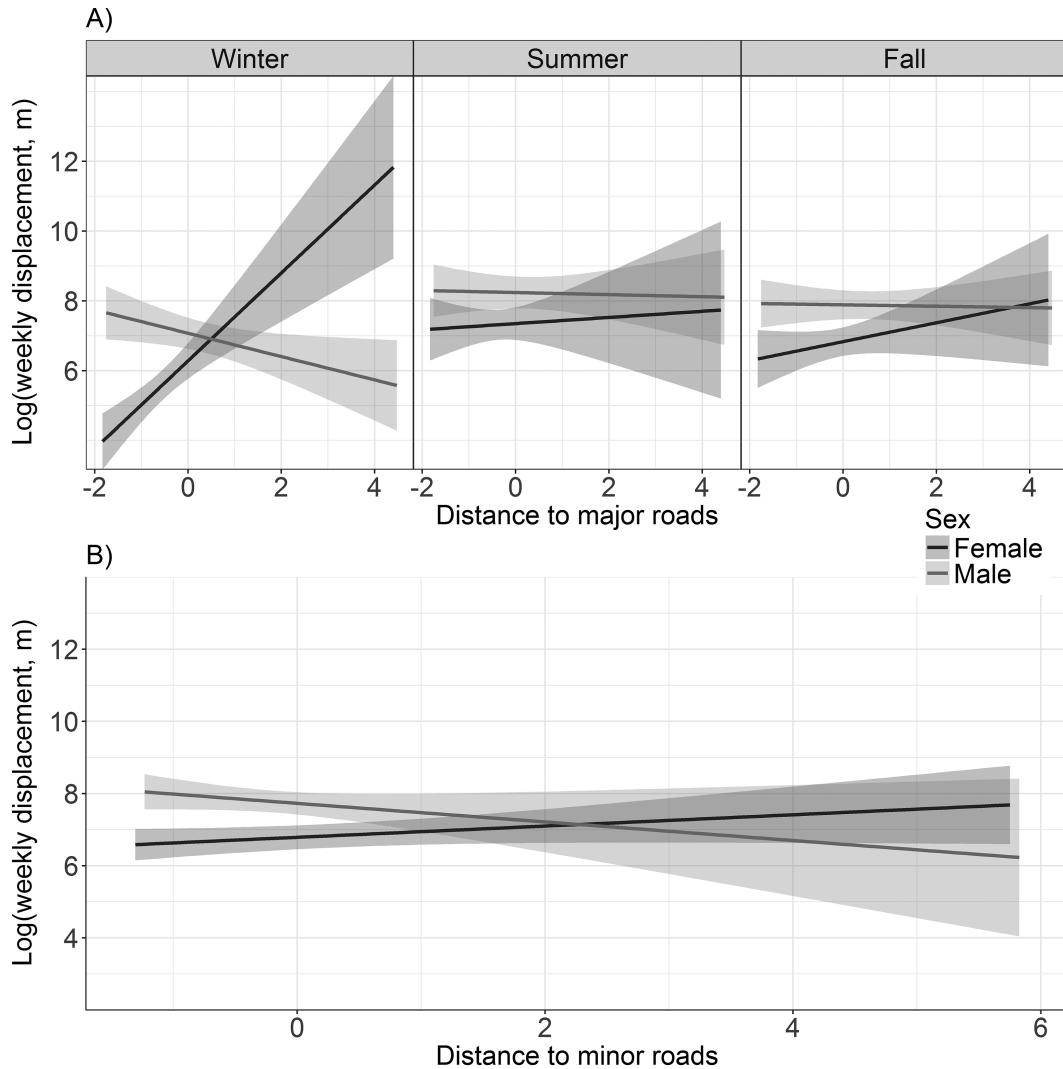


Fig. 8.—Effect of covariates on the weekly observed displacement (\pm 95% CI) for Florida black bears (*Ursus americanus floridanus*) in north-central Florida: A) 3-way interaction among sex, season, and distance to major roads, and B) 2-way interaction between sex and distance to minor roads. All weekly displacements are on the log scale and all distances are standardized.

Table 2.—Average number of weeks that bears were monitored, average road length within individual home ranges (km), and the average number of road crossings by female and male Florida black bears (*Ursus americanus floridanus*) in north-central Florida. All values are shown \pm SE (minimum to maximum).

	Weeks monitored	Road length (km)		Number of road crossings	
		Major roads	Minor roads	Major roads	Minor roads
Females	74.4 \pm 5.8 (51.9, 88.9)	3.2 \pm 1.3 (0, 8.4)	58.3 \pm 19.8 (24.4, 154.9)	1.8 \pm 1.3 (0, 8)	488 \pm 110.2 (59, 793)
Males	36.4 \pm 5.7 (6.3, 59)	35.5 \pm 7.8 (10.4, 88)	436.5 \pm 57.1 (170.7, 790.3)	12 \pm 6.1 (0, 65)	403.3 \pm 77.3 (44, 790)
Combined	50.6 \pm 6.2 (6.3, 8.2)	23.4 \pm 6.3 (0, 88)	294.7 \pm 59.2 (24.4, 790.3)	8.2 \pm 4 (0, 65)	435.1 \pm 62.2 (44, 793)

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Tables showing averages for each movement metric and additional model selection tables for movement metrics at weekly and daily temporal scales.

Supplementary Data SD2.—Figures showing model results for weekly movement metrics that are not shown in the manuscript and for the model results from daily and bi-hourly temporal scales.

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