

Incorporating movement patterns to discern habitat selection: black bears as a case study

Dana L. Karelus^{ID A,E,*}, J. Walter McCown^B, Brian K. Scheick^B, Madelon van de Kerk^C, Benjamin M. Bolker^D and Madan K. Oli^A

^ADepartment of Wildlife Ecology and Conservation, and School of Natural Resources and Environment, 110 Newins-Ziegler Hall, University of Florida, Gainesville, FL 32611, USA.

^BFlorida Fish and Wildlife Conservation Commission, 1105 SW Williston Road, Gainesville, FL 32601, USA.

^CSchool of Environmental and Forest Sciences, 114 Winkenwerder, University of Washington, Seattle, WA 98195, USA.

^DDepartments of Mathematics & Statistics and Biology, McMaster University, 314 Hamilton Hall, Hamilton, Ontario L8S 4K1, Canada.

^ECorresponding author. Email: dana.karelus@sulross.edu

Abstract

Context. Animals' use of space and habitat selection emerges from their movement patterns, which are, in turn, determined by their behavioural or physiological states and extrinsic factors.

Aim. The aims of the present study were to investigate animal movement and incorporate the movement patterns into habitat selection analyses using Global Positioning System (GPS) location data from 16 black bears (*Ursus americanus*) in a fragmented area of Florida, USA.

Methods. Hidden Markov models (HMMs) were used to discern the movement patterns of the bears. These results were then used in step-selection functions (SSFs) to evaluate habitat selection patterns and the factors influencing these patterns.

Key results. HMMs revealed that black bear movement patterns are best described by three behavioural states: (1) resting (very short step-lengths and large turning angles); (2) encamped (moderate step-lengths and large turning angles); and (3) exploratory (long step-lengths and small turning angles). Bears selected for forested wetlands and marsh wetlands more than any other land cover type, and generally avoided urban areas in all seasons and when in encamped and exploratory behavioural states. Bears also chose to move to locations farther away from major roads.

Conclusions. Because habitat selection is influenced by how animals move within landscapes, it is essential to consider animals' movement patterns when making inferences about habitat selection. The present study achieves this goal by using HMMs to first discern black bear movement patterns and associated parameters, and by using these results in SSFs to investigate habitat selection patterns. Thus, the methodological framework developed in this study effectively incorporates state-specific movement patterns while making inferences regarding habitat selection. The unified methodological approach employed here will contribute to an improved understanding of animal ecology as well as informed management decisions.

Implications. Conservation plans focused on preserving forested wetlands would benefit bears by not only providing habitat for resting and foraging, but also by providing connectivity through fragmented landscapes. Additionally, the framework could be applied to species that follow annual cycles and may provide a tool for investigating how animals are using dispersal corridors.

Additional keywords: black bear movement, hidden Markov models, step-selection functions, step-length, *Ursus americanus*.

Received 30 October 2017, accepted 4 November 2018, published online 15 February 2019

Introduction

As animals traverse the landscape, they make choices about where and how to move as they search for resources and mates,

and seek safety from predators or disturbance. Their choices regarding where to move, the pattern of movement within their home ranges and the amount of time spent in each

*Dana L. Karelus is now affiliated with Borderlands Research Institute, Sul Ross State University, C-21, Alpine, TX 79832, USA.

habitat component defines space- and habitat-use patterns. In essence, space-use and habitat selection by animals are emergent properties of their movement patterns. Therefore, a thorough understanding of space- and habitat-use patterns requires knowledge of animals' movement patterns (Moorcroft and Barnett 2008; Forester *et al.* 2009; Moorcroft 2012; van Moorter *et al.* 2016; Patterson *et al.* 2017). This understanding is particularly important in human-dominated landscapes where higher quality habitats are typically separated by degraded habitats, thus requiring animals to move more extensively, which can increase mortality risks from vehicular collision and other anthropogenic factors (Forman and Alexander 1998; Tigas *et al.* 2002; Buchmann *et al.* 2012; Beyer *et al.* 2016; Karelus *et al.* 2017).

Internal physiological and behavioural states of animals are important determinants of animal movement patterns (Fryxell *et al.* 2008; Nathan *et al.* 2008; Schick *et al.* 2008; Gurarie *et al.* 2015). For example, finding mates may be the primary motivation for movement during breeding season, whereas finding food or avoiding predators may be the primary drivers of movement during non-breeding seasons. Likewise, behavioural states such as travelling from one section of the home range to another, hunting for prey or resting will leave signatures in movement patterns that may be indicative of the relevant movement states. The observed movement patterns, therefore, are determined by the interactive effects of animals' internal physiological or behavioural states, as well as extrinsic factors such as time of the year, habitat quality or barriers to movements (Jonsen *et al.* 2003; Nathan *et al.* 2008; Martin *et al.* 2013). Although many of the extrinsic factors can be measured, animals' behavioural states are often difficult to quantify, especially for species that are nocturnal, travel widely, occupy forested or other dense habitats or are otherwise difficult to observe. A practical solution to this problem is offered by hidden Markov models (HMMs), which have been recently applied to animal movement studies because they permit identification of hidden behavioural states based on observed movement trajectories (Langrock *et al.* 2012; Schliehe-Diecks *et al.* 2012; van de Kerk *et al.* 2014; Patterson *et al.* 2017).

The HMMs are discrete-time, discrete-state, state-space models that use serially observed data to explore the underlying, unobservable states causing the observed patterns and the probabilities of transitioning among the states (Schick *et al.* 2008; Patterson *et al.* 2009; Langrock *et al.* 2012; Zucchini and Macdonald 2016). When applying HMMs to animal movement, the observed data typically consist of the animals' step-lengths (distance between successive locations) and turning angles (exterior angle made by three successive locations). The underlying unobservable states represent the behavioural states. Using HMMs, it is possible to discern the number of states and estimate the probability of transitioning between states and associated parameters, which in turn permits inferences regarding behavioural states (Schick *et al.* 2008; Visser 2011; Langrock *et al.* 2012). HMMs have been applied to animal movement studies with biologically insightful results (Franke *et al.* 2004, 2006; Boyd *et al.* 2014; van de Kerk *et al.* 2014; McKellar *et al.* 2015; Ditmer *et al.* 2017). However, there have been limited studies attempting to integrate state-specific movement patterns to habitat selection.

Because animals may select habitats differently depending on their behavioural state or their motivation for movement, explicit consideration of the behavioural states underlying movement phases is essential for meaningful inferences regarding habitat selection by animals (Cozzi *et al.* 2016; Abrahms *et al.* 2017). Therefore, our objective was to investigate the pattern of habitat selection by a large carnivore, the American black bear (*Ursus americanus*), inhabiting a highly fragmented landscape in Florida, USA, while explicitly incorporating state-specific movement. Although black bear habitat-use patterns have been studied in Florida and elsewhere in North America (Onorato *et al.* 2003; Dobey *et al.* 2005; Benson and Chamberlain 2007; Moyer *et al.* 2008; Karelus *et al.* 2016), no studies have considered state-specific movement patterns while making inferences about habitat selection. We fitted HMMs to high-resolution Global Positioning System (GPS) location data to identify the appropriate behavioural states underlying observed black bear movement patterns and to estimate the relevant model parameters. Then we applied Viterbi algorithms to assign the most likely behavioural state to each step of individual bears' movement paths (Zucchini and Macdonald 2016). For each step, we simulated possible steps the bear could have taken based on the distribution of step-lengths and turning angles corresponding to the assigned state. Finally, to make inferences regarding black bear habitat selection, we used step-selection functions (SSFs) to compare each movement step with the matched simulated alternative steps that a bear might have taken (Fortin *et al.* 2005; Thurfjell *et al.* 2014). Thus, our analysis of habitat selection adequately incorporates state-specific movement patterns.

Methods

Study species and site

Historically, black bears were distributed throughout most of North America, but they have been extirpated from a large section of their former range (Servheen *et al.* 1999; Pelton 2003; Scheick and McCown 2014). However, black bear populations are growing in many parts of their range (Garshelis and Hristienko 2006; Hristienko and McDonald 2007; Scheick and McCown 2014), including in Florida, USA (Karelus *et al.* 2016). In Florida, there are seven isolated bear populations (Florida Fish and Wildlife Conservation Commission 2012). Two of these populations occur in Ocala National Forest and in Osceola National Forest and bears recently colonised the area between them (Fig. 1; Karelus *et al.* 2016). The population density of black bears in our study area was ~ 0.1 bears km^{-2} (Humm *et al.* 2017). Female bears typically have smaller home ranges and tend to move with shorter step-lengths than male bears (Alt *et al.* 1980; Hellgren and Vaughan 1990; Dobey *et al.* 2005; Karelus *et al.* 2017). Bears also change their movements among seasons and by time of day (Garshelis and Pelton 1980; Garshelis *et al.* 1983; Bridges *et al.* 2004; Karelus *et al.* 2017). Black bears often have larger home ranges in the fall (1 September – 31 December) than in other seasons because they increase their caloric intake and thus increase foraging to prepare for winter (Garshelis 1978; Hellgren *et al.* 1989; Noyce and Garshelis

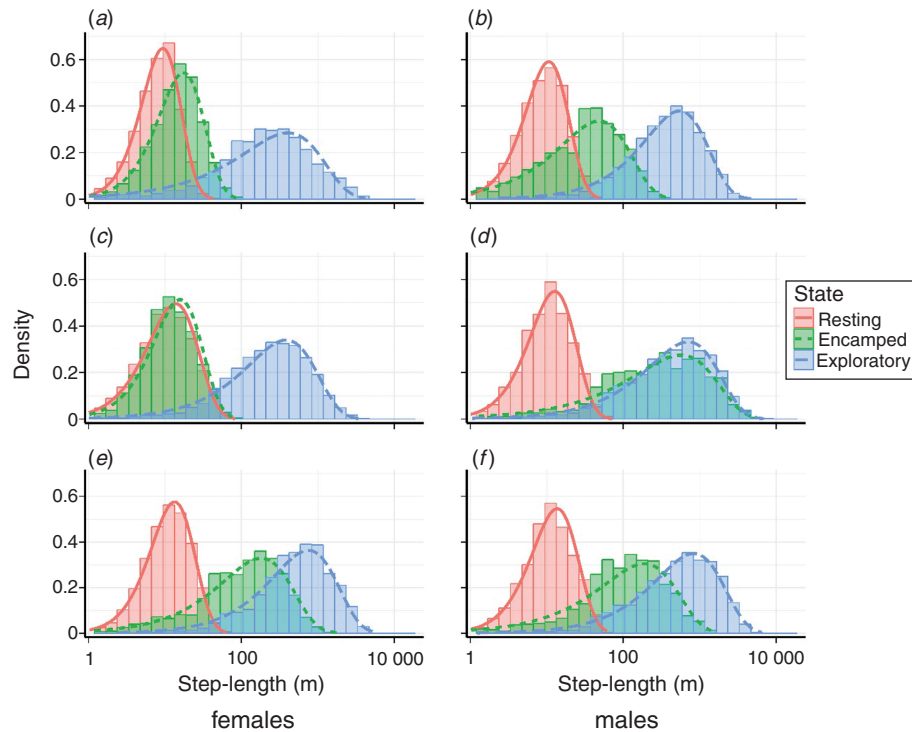


Fig. 1. Plots of step-length parameter distributions from three-state Hidden Markov models (HMMs) for Florida black bears in north-central Florida for (a) females in winter, (b) males in winter, (c) females in summer, (d) males in summer, (e) females in fall and (f) males in fall. All distributions of step-lengths were from the Gamma distribution. Note that the *x*-axis is on the log scale.

2011). In Florida, male bears and non-pregnant females are not obliged to den in the winter because of the mild climate and food availability (Wooding and Hardisky 1992; Garrison *et al.* 2012).

Our study site was at the Camp Blanding Joint Training Center (295 km²) and surrounding private lands in north-central Florida. The area lies in what is referred to as the Ocala to Osceola corridor (Hector *et al.* 2000), although the area is not officially designated as a wildlife corridor. Natural habitats in the area are dominated by mesic flatwoods and sandhill uplands and scrub, as well as mixed hardwood hammocks and cypress swamps (Karelus *et al.* 2016). Several creeks and drainages traverse the site. Anthropogenic land uses, including tree plantations, agriculture and rural and urban developments fragment the habitat (Karelus *et al.* 2016). The area is likely to become more fragmented in the coming years due to the anticipated human population growth in the state and the sprawling suburbs of the Jacksonville area (Carr and Zwick 2016).

Field methods

We captured bears using Aldrich spring-activated foot snares (Margo Supplies, High River, AB, Canada) with a double anchor 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 anaesthetised each captured bear with Telazol (3.5–5 mg kg⁻¹), removed a premolar for age estimation (Willey 1974), fitted them with GPS transmitting collars (Lotek WildCell MG,

Newmarket, ON, Canada), and then released them within 60 min at the capture sites. The collars were programmed to obtain GPS locations every 2 hours 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 following approved protocols.

Habitat covariates

We extracted the landcover type for each location from the Florida Vegetation and Land Cover 2014 geographic information system (GIS) raster layer (10 × 10 m-resolution; Redner and Srinivasan 2014). We grouped landcover types with similar vegetation and combined minimally available land cover types into six landcover categories: (1) forested wetlands; (2) marsh-wetland; (3) rural-agricultural areas; (4) tree plantations; (5) urban areas; and (6) woodland-scrub (see details in Karelus *et al.* 2016).

We calculated the distances from bear locations to the nearest creek, major road and minor road using shapefiles for both creeks and roads from the Florida Geographic Data Library (<http://www.fgd.org/>). We classified primary routes (i.e. interstates and national highways) and secondary routes (state highways and county roads) as major roads. We classified all other roads as minor roads (e.g. neighbourhood roads or private roads that were either paved or made from native materials). We calculated the distances from each bear location to the nearest creek, major road

and minor road using the package 'rgeos' (Bivand and Rundel 2016) in R (R Core Team 2016). Because bears undergo seasonal physiological shifts (Hellgren *et al.* 1989), we defined three 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).

Movement metrics and identification of movement states

Using only successive bihourly locations, we calculated the step-lengths and turning angles. The turning angle of an animal continuing in the same direction would equal 0 radians (i.e. 0°), and the turning angle of an animal going back to where it came from would equal π radians (i.e. 180°) along each bear's trajectory. We then used the step-lengths and turning angles as bivariate input data in HMMs with various candidate distributions for step-length (gamma, Weibull, log-normal and exponential distributions) and for turning angle (von Mises and wrapped Cauchy distributions). To ensure that our models were numerically stable, we compared HMM results from 30 different sets of randomly chosen starting values for each candidate distribution and number of state. The number of states in an HMM must be specified before running the model, and model comparison statistics can be employed to determine fit of models with different number of states to data. However, HMMs generally tend to favour models with more states; therefore, best practice dictates that users should only test models with biologically meaningful numbers of states (van de Kerk *et al.* 2014; Li and Bolker 2017; Pohle *et al.* 2017). We expected that the bears' movement patterns would include the signature of a resting state (very short step-lengths and high degrees of turning) and of an exploratory state (long step-lengths and more directed travel), and potentially also include a state with moderate step-lengths, which could represent an encamped state (potentially foraging). Thus, we tested HMMs with two and three biologically meaningful movement states.

Black bear home-range sizes and movements typically vary between the sexes and among seasons (Alt *et al.* 1980; Garshelis and Pelton 1981; Hellgren *et al.* 1989; Powell *et al.* 1997; Moyer *et al.* 2007; Karelus *et al.* 2017); their movements also vary across the diel period (Garshelis *et al.* 1983; Lewis and Rachlow 2011; Karelus *et al.* 2017). Therefore, we expected sex-specific and season-specific differences in the movement parameters corresponding to each movement state and differences in state transition probabilities throughout the diel period. We tested for additive main effects of sex, season and time of day on the probability of transitioning among states. We used an information-theoretic approach with Akaike's Information Criterion (AIC) to make statistical inferences regarding the number of states and effect of covariates, and to select the most parsimonious model (Burnham and Anderson 2002). Then, based on the most parsimonious model, we used the Viterbi algorithm to assign the most likely state to each step in the trajectories for all animals (Langrock *et al.* 2012; Zucchini and Macdonald 2016). The Viterbi algorithm is a recursive, optimal solution to the problem of finite-state discrete-time Markov process (Forney 1973; Zucchini and Macdonald

2016), and provided an efficient way of assigning the most likely state to each step in black bear movement paths.

Step-selection functions

Habitat selection by animals is often studied using resource selection functions (RSFs; Boyce *et al.* 2002; Manly *et al.* 2002). Despite many advantages, RSFs do not explicitly incorporate movement patterns and also have been criticised for the manner in which habitat availability is defined (Johnson and Nielsen 2006; Martin *et al.* 2008; Fieberg *et al.* 2010; Thurfjell *et al.* 2014). A solution to these issues is provided by the step-selection functions (SSFs), which take into account the animal's movements and the serial structure of GPS location data (Fortin *et al.* 2005; Forester *et al.* 2009; Squires *et al.* 2013; Latombe *et al.* 2014; Thurfjell *et al.* 2014). SSFs use a modelling framework in which each step in an animal's trajectory ('used') is compared with multiple 'unused' steps an animal might have taken during that time step (Forester *et al.* 2009; Thurfjell *et al.* 2014). Thus, SSFs specifically consider where the animal chose to move from available options. We incorporated HMMs into the SSF framework by selecting unused steps based on the sex- and season-specific movement parameters defining the respective behavioural state that was assigned to the step by the Viterbi algorithm (Langrock *et al.* 2012; Zucchini and Macdonald 2016). For example, if the Viterbi algorithm assigned a step in a female's trajectory during summer as state 2, we would randomly select a turning angle and a step-length from their respective distributions to create an unused step.

Although there are no widely accepted guidelines regarding the number of unused steps with which to compare each used step in SSFs, Thurfjell *et al.* (2014) advised against using too many unused steps. Thus, we selected six unused steps corresponding to each used step by randomly choosing turning angles and step-lengths from the respective distributions of those parameters of the observed steps corresponding to the assigned movement state. We designated a unique step ID to each observed step and its corresponding unused steps. We then performed mixed-effects conditional logistic regression by using a two-step estimation approach (Duchesne *et al.* 2010; Craiu *et al.* 2011). The first step in this analytical approach estimates the cluster- or individual-specific parameters, whereas the second step uses the expectation maximisation (EM) algorithm in conjunction with conditional restricted maximum likelihood to estimate the population parameters. This approach has been shown to work well, while avoiding computational challenges and complexities inherent in nonlinear mixed-effects models (Duchesne *et al.* 2010; Craiu *et al.* 2011).

In our analyses, the individual bear was set as the cluster, the step ID as the strata, and a binary response was marked as chosen or not chosen (used versus unused). We fit a model with additive fixed- and random-effects of landcover type, distance to creeks, distance to major roads, and distance to minor roads and an unstructured variance-covariance matrix across clusters. By fitting a mixed effect model, we were able to account for heterogeneous habitat selection among animals, essentially treating each individual bear as a unit of study and permitting us to make population-level inference regarding habitat

selection by black bears (Revelt and Train 1998; Duchesne *et al.* 2010; Craiu *et al.* 2011). We first performed two-step conditional logistic regression using all the data collected from all bears included in our study. We then performed the two-step conditional logistic regression for each season and for each movement state to investigate differences in seasonal habitat selection or differences in selection based on behavioural states. Random effects of distance to minor roads or to creeks could not be included because this caused the design matrix to be singular and, consequently, caused computational problems.

We used the R package *moveHMM* (Michelot *et al.* 2016) to calculate the movement path descriptors, fit HMMs and to assign the most likely states to the steps with the Viterbi algorithm and the package *CircStats* (Lund and Agostinelli 2012) to calculate the average turning angles. We fitted the mixed conditional logistic regression models with the function 'Ts.estim' in the package *TwoStepCLogit* (Craiu *et al.* 2016). Due to the estimation methods used in the two-step conditional logistic regression, we could not use an information-theoretic approach based on AIC scores for model selection and statistical inference (Craiu and Duchesne 2018). All analyses were performed in program R (version 3.3.1; R Core Team 2016). Our R code is provided as Supplementary Material to this paper.

Results

We tracked 16 bears (6 females, 10 males) for 5812 bear-days from July 2011 to March 2014, which resulted in a total of 58 951 bi-hourly 3D-validated GPS locations (mean \pm s.e.: 2907.3 \pm 1033.2 per bear). From these data, we estimated movement descriptors for 28 485 locations for females and 23 773 locations for males.

Average step-lengths and turning angles differed between females and males and both varied among seasons (Table 1). Females generally travelled shorter bi-hourly distances and turned more frequently than males across all seasons. Females and males travelled with the longest bi-hourly step-lengths and most directly in the fall, and with the slowest bi-hourly step-lengths and least directly in the winter. Bears of both sexes exhibited differences in movement patterns throughout the diurnal cycle, with the longest step-lengths at dawn and dusk for females, and at night for males, and the shortest step-lengths at midday for both sexes (see Karelus *et al.* 2017).

We found that HMM models with three states, a Gamma distribution for step-length, a wrapped Cauchy distribution for turning angle, and additive effects of sex, season, and hour of day were most supported (Table 2). However, due to the large differences in movement patterns between females and males and among seasons, we then fitted three-state HMMs separately for each sex in each season; all models included a covariate of hour of day and the Gamma distribution for step-length and the wrapped Cauchy distribution for turning angle. We identified the following three general movement states: (1) a state with short step-lengths and turning angles around π radians (180°; likely behavioural state: resting); (2) a state with moderate step-lengths and turning angles around 3.14 radians (180°; likely behavioural state: encamped; though turning angles for this state for males in the summer instead averaged around

Table 1. Average step-lengths (\pm s.e.) and turning angles by season for female and male bears in the Camp Blanding area in Florida based on GPS locations between 2011 and 2014

Sex	Season	Number of bears	Number of locations	Average step-length \pm s.e. (m)	Average turning angle (°)
Females	Winter	9	9519	90.21 \pm 36.73	105.42°
	Summer	13	8877	248.95 \pm 24.51	49.85°
	Fall	10	10 089	352.96 \pm 21.98	30.37°
Males	Winter	7	7933	212.92 \pm 44.48	78.50°
	Summer	15	6778	385.73 \pm 41.71	25.78°
	Fall	11	9062	425.7 \pm 35.19	18.91°

Table 2. Model selection results from hidden Markov models (HMMs) testing for the number of movement states and factors that influenced the transition probabilities among movement states by Florida black bears in north-central Florida from 2011 through 2014

Only two and three states were tested because at the bihourly scale of the data without direct observations of behaviour, discerning the biological relevance of 4 or more states would be difficult. The top 10 models are sorted based on the Δ AIC (Akaike Information Criterion) values in an ascending order. The weight indicates the Akaike weight or model probability

Rank	Model	Δ LogLik	Δ AIC	Weight
1	3 State: Sex + Season + Hour	0.00	0.00	1.00
2	3 State: Season + Hour	372.65	733.30	0.00
3	3 State: Sex + Hour	1183.74	2343.47	0.00
4	3 State: Hour	1577.16	3118.31	0.00
5	3 State: Sex + Season	2115.89	4207.78	0.00
6	3 State: Season	2325.33	4614.65	0.00
7	3 State: Sex	3024.15	6000.29	0.00
8	2 State: Sex + Season + Hour	3124.18	6190.36	0.00
9	2 State: Season + Hour	3172.07	6282.14	0.00
10	3 State: Null	3332.07	6604.13	0.00

0 radians); and (3) a state with long step-lengths and turning angles around 0 radians (0°; likely behavioural state: travelling or exploratory; Figs 1, 2). However, for females in the winter and for both sexes in the summer, the distributions for both step-lengths and turning angles in the encamped state overlapped highly with those in either the resting state or the exploratory state (Figs 1, 2). In the fall for both sexes, the resting, encamped and exploratory states were the most distinct from each other (Figs 1 and 2). Bears typically travelled during morning and evening hours but males also travelled during the night in the winter and fall (Fig. 3). During winter, when the distributions of the resting and encamped states were similar, females exhibited less of a diurnal pattern (Fig. 3).

Ignoring seasonal variation, there was substantial evidence that black bears selected for forested wetlands (which included freshwater forested wetlands, cypress and other coniferous wetlands, wet flatwoods, baygall, freshwater and floodplain swamps, and dome and basin swamps) or marsh wetlands (which included freshwater non-forested wetlands, prairies and bogs, marshes, natural lakes and ponds, cultural lakes, riverine, natural rivers and streams) and that they tended to avoid habitats closer to major roads. Considered seasonally, evidence for habitat selection was strong in all seasons; bears

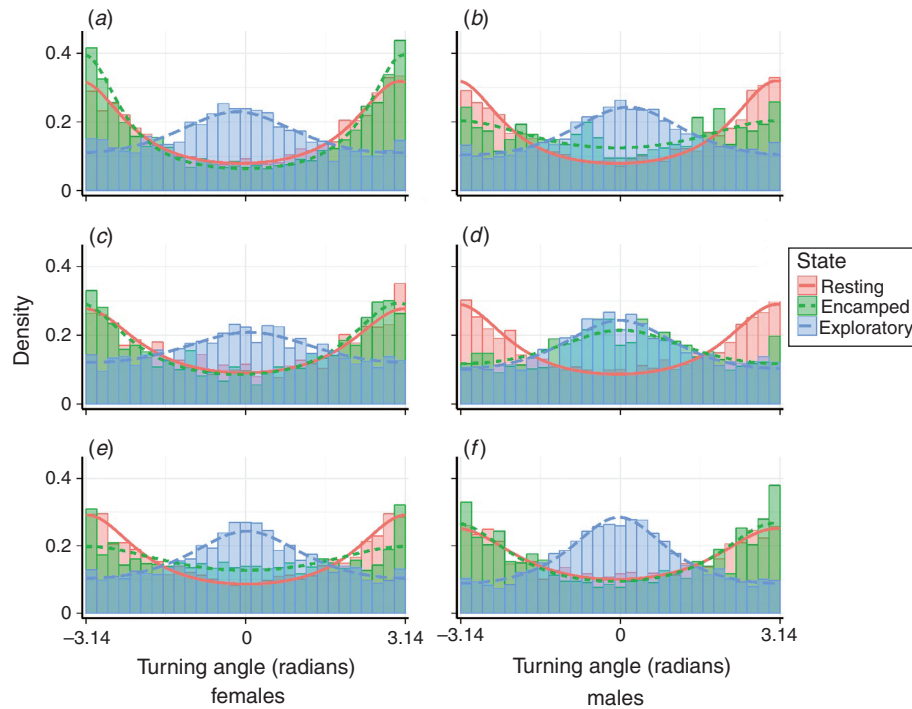


Fig. 2. Plots of turning angle parameter distributions from three-state Hidden Markov models (HMMs) from Florida black bears in north-central Florida for (a) females in winter, (b) males in winter, (c) females in summer, (d) males in summer, (e) females in fall, and (f) males in fall. All distributions of turning angles were from the wrapped Cauchy distribution.

selected for forested wetlands or marsh wetlands in the summer and all but for forested wetlands or rural/agricultural areas in the winter. The effect of distances to roads and creeks also varied across seasons. During winter, distances to roads and creeks had no significant effect on black bear habitat selection whereas distance to major roads positively affected habitat selection by black bears during summer (bears chose to use areas farther from roads); in fall, major roads again had a positive effect on habitat selection and distance to creeks had a negative effect (bears chose to use areas closer to creeks; Table 3). Overall and in the summer and fall, bears chose forested wetlands and marsh wetlands more than any other landcover type (Fig. 4). In the winter, bears selected for forested wetlands and rural/agricultural land covers (Table 3; Fig. 4).

Animals can select for different habitats while in different behavioural states (Abrahms *et al.* 2017). Thus, we also tested for state-specific habitat selection patterns. The model for bears in state 1 (resting) indicated that there was an effect of land cover, but distances to roads and creeks had no effect on bears' habitat selection. The model for states 2 (encamped) and 3 (exploratory) revealed significant effects of land cover type and distances to major roads, and of distance to creeks while in state 3. Bears preferentially chose forested wetlands and marsh wetlands over other land cover types while in the encamped and travelling states. While in the resting state, they chose forested wetlands but their preference for forested wetlands, marsh wetlands, urban areas and rural and agricultural areas did not differ substantially (Table 3). However, confidence intervals for some of the predictive odds for this state were large, indicating substantial

uncertainty (Fig. 4). Distance to major roads had a positive effect in the encamped and exploratory states (they chose areas farther from major roads) and there was a weak negative effect of distance to creeks in the exploratory state (they chose areas closer to major roads; Table 3).

Discussion

Many wildlife species exhibit annual cycles in their behaviours and physiology, and thus different movement patterns in different seasons. For example, species that hibernate or den in the winter must gather resources in the fall to prepare for winter and then reduce their movements in the winter. Also, males and females can exhibit different movement patterns, especially during the breeding season, due to sex-specific differences in reproductive strategies. Therefore, sex and season must be considered when investigating animal movement and habitat selection patterns. Because black bears exhibit strong seasonal patterns in physiology, and females and males have different reproductive strategies (Garshelis *et al.* 1983; Hellgren *et al.* 1989), we sought to understand how movement patterns differ between sexes and vary among seasons and how these translate into variation in habitat selection. To achieve these goals, we first applied HMMs to identify behavioural states and tested for differences in those states by sex and season. Then we linked state-specific movement patterns to their habitat selection by incorporating our HMM results into SSFs.

An HMM with three movement states and covariates of sex, season, and hour of day was best supported by data. In our models, covariates only affected the probability of transitioning

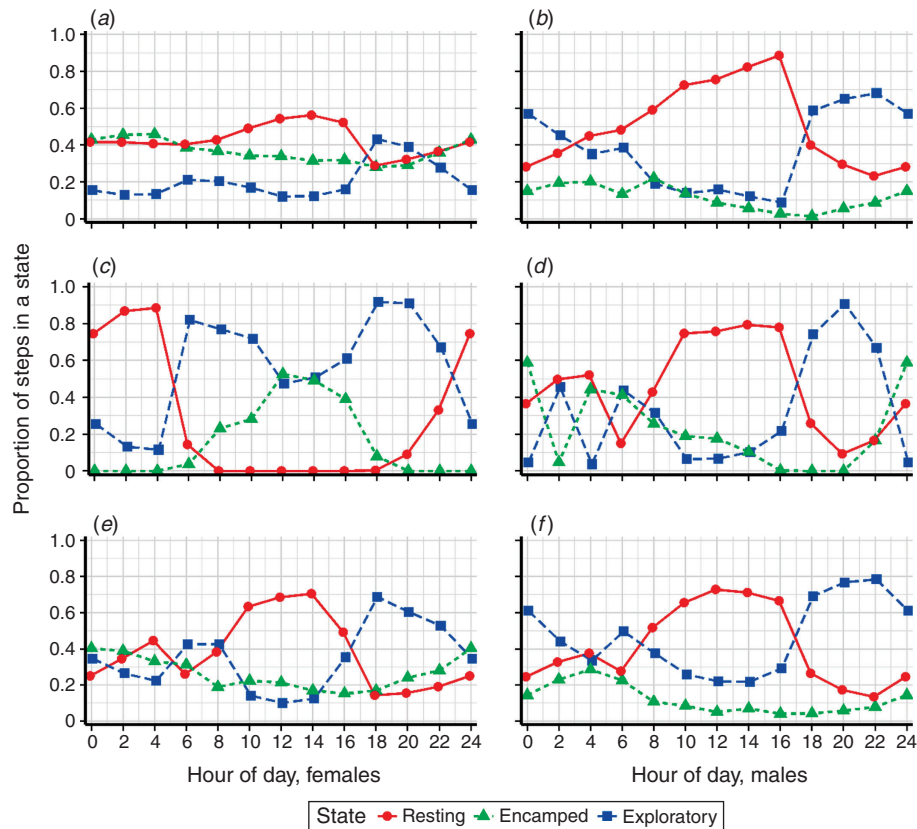


Fig. 3. Proportion of steps in each movement state across the diel period as assigned by the Viterbi algorithm for Florida black bears in north-central Florida by sex and season: (a) females in winter; (b) males in winter; (c) females in summer; (d) males in summer; (e) females in fall; and (f) males in fall.

among states; therefore, we fit sex and season-specific HMMs with three states and a covariate of hour of day. However, the distribution of step-lengths and turning angles were essentially the same for two of the three states for both sexes in the winter and summer. In the fall, all three states were more distinct from each other. The two clear movement states in the winter and summer likely represented the behavioural states of resting (a movement state with very short step-lengths and sharp turns) and travelling or exploratory (a movement state with long step-lengths and directed travel). In the fall, we interpreted the additional state as encamped (a movement state with moderate step-lengths and sharp turns). Similar patterns have been found for other species (Franke *et al.* 2004; Pohle *et al.* 2017), though the interpretation of a movement state with moderate step-lengths (what we defined as encamped) may differ among species. For Florida panthers (*Puma concolor coryi*), this state was simply considered 'moderately active' (van de Kerk *et al.* 2014). This type of state was considered 'locally active at a kill site' for wolves (*Canis lupus*; Franke *et al.* 2006). For black bears, 'foraging' is a fitting interpretation for the encamped state because their diet is composed of mostly plant matter and they spend much of their time eating, especially in the fall (Maehr and Brady 1984; Stratman and Pelton 1999; Dobej *et al.* 2005).

In the winter, females were more likely to be in the resting/encamped states throughout the entire diel period whereas males tended to be in the resting/encamped states in midday

and in the exploratory state through the evening and nighttime hours. In Florida, only pregnant females must den in the winter, whereas males and non-pregnant females do not necessarily den (Wooding and Hardisky 1992; Garrison *et al.* 2012); however, all bears reduce their movements (Karelus *et al.* 2017). Only three females gave birth during our study, so our results provide evidence that non-pregnant females may have been using day beds (Rayl *et al.* 2014) for extended bouts throughout the winter and spent little time travelling.

In the summer, females changed their movements to a crepuscular pattern of activity whereby they spent the night and midday in resting/encamped states and were in exploratory states in the morning and evening. The step-lengths in each behavioural state were similar to those in the winter. Conversely, males were more likely to be in an exploratory state throughout the night and had longer distance movements in their exploratory state compared with those in the winter. Males may have increased their movements in the summer as they were looking for mates, whereas females may have only been responding to increased food availability after winter denning (Powell *et al.* 1997).

In the fall, both sexes exhibited faster bi-hourly movements in the exploratory state than in the other seasons and the encamped state was distinct from the resting and exploratory states. Again, both sexes were most likely to rest during midday and males were more likely than females to be in an exploratory

Table 3. Coefficient estimates ± standard error and 95% confidence intervals for the variables included in the mixed conditional logistic models from all seasons and all behavioural states, all states in the winter, all states in the summer, all states in the fall, state 1 (resting) in all seasons, state 2 (encamped) in all seasons and state 3 (exploratory) in all seasons

Land cover types with coefficients less than 0 and confidence intervals that do not include 0 indicate that the landcover type was less likely to be chosen than the reference category, forested wetlands. Coefficients greater than 0 and confidence intervals that do not include 0, would indicate that the category is preferred over forested wetlands. For distance variables, positive coefficients indicate the bears chose to move away from the feature and negative coefficients indicate the bears chose to move closer to the feature. In some cases, bears were removed from the analyses due to zero-variance among variables. The number of bears included in each model is given by *n*

Model	Variable	Coefficient ± s.e. (95% CI)
Overall, <i>n</i> = 16	Marsh wetland	-0.29 ± 0.16 (-0.61, 0.03)
	Wood/scrub	-0.32 ± 0.06 (-0.44, -0.20)
	Tree plantation	-0.57 ± 0.06 (-0.69, -0.46)
	Rural/agricultural	-0.63 ± 0.12 (-0.87, -0.39)
	Urban	-0.86 ± 0.17 (-1.2, -0.53)
	Major roads	0.12 ± 0.02 (0.07, 0.17)
	Minor roads Creeks	0 ± 0 (0, 0) 0 ± 0 (0, 0)
Winter, <i>n</i> = 12	Rural/agricultural	-0.30 ± 0.23 (-0.75, 0.16)
	Marsh wetland	-0.37 ± 0.17 (-0.71, -0.03)
	Wood/scrub	-0.47 ± 0.14 (-0.75, -0.19)
	Tree plantation	-0.75 ± 0.16 (-1.07, -0.43)
	Urban	-1.12 ± 0.31 (-1.73, -0.52)
	Major roads	0.06 ± 0.05 (-0.05, 0.17)
	Minor roads Creeks	0 ± 0 (0, 0) 0 ± 0 (0, 0)
Summer, <i>n</i> = 16	Wood/scrub	-0.22 ± 0.1 (-0.41, -0.03)
	Marsh wetland	-0.23 ± 0.14 (-0.50, 0.04)
	Tree plantation	-0.48 ± 0.09 (-0.65, -0.31)
	Rural/agricultural	-0.84 ± 0.15 (-1.13, -0.54)
	Urban	-1.37 ± 0.24 (-1.84, -0.90)
	Major roads	0.13 ± 0.04 (0.06, 0.21)
	Minor roads Creeks	0 ± 0 (0, 0) 0 ± 0 (0, 0)
Fall, <i>n</i> = 16	Wood/scrub	-0.37 ± 0.07 (-0.5, -0.23)
	Marsh wetland	-0.39 ± 0.21 (-0.79, 0.02)
	Rural/agricultural	-0.58 ± 0.13 (-0.83, -0.34)
	Urban	-0.60 ± 0.17 (-0.92, -0.28)
	Tree plantation	-0.64 ± 0.06 (-0.76, -0.52)
	Major roads	0.14 ± 0.02 (0.10, 0.19)
	Minor roads Creeks	0 ± 0 (0, 0) 0 ± 0 (0, 0)
State 1, <i>n</i> = 10	Urban	0.23 ± 0.67 (-1.08, 1.53)
	Marsh wetland	-0.02 ± 0.16 (-0.34, 0.29)
	Tree plantation	-0.47 ± 0.17 (-0.8, -0.13)
	Wood/scrub	-0.50 ± 0.19 (-0.88, -0.12)
	Rural/agricultural	-0.53 ± 0.29 (-1.1, 0.04)
	Major roads	0.76 ± 1.26 (-1.71, 3.22)
State 2, <i>n</i> = 16	Marsh wetland	-0.21 ± 0.16 (-0.53, 0.10)
	Wood/scrub	-0.51 ± 0.07 (-0.65, -0.37)

(continued next column)

Table 3. (continued)

Model	Variable	Coefficient ± s.e. (95% CI)
	Tree plantation	-0.66 ± 0.08 (-0.81, -0.50)
	Rural/agricultural	-0.76 ± 0.16 (-1.08, -0.44)
	Urban	-0.88 ± 0.21 (-1.3, -0.46)
	Major roads	0.27 ± 0.07 (0.12, 0.41)
	Minor roads	0 ± 0 (0, 0)
	Creeks	0 ± 0 (0, 0)
State 3, <i>n</i> = 16	Wood/scrub	-0.29 ± 0.07 (-0.42, -0.16)
	Marsh wetland	-0.30 ± 0.18 (-0.64, 0.05)
	Tree plantation	-0.59 ± 0.06 (-0.71, -0.47)
	Rural/agricultural	-0.62 ± 0.13 (-0.86, -0.37)
	Urban	-0.82 ± 0.18 (-1.18, -0.47)
	Major roads	0.11 ± 0.02 (0.06, 0.16)
Minor roads	0 ± 0 (0, 0)	
Creeks	0 ± 0 (0, 0)	

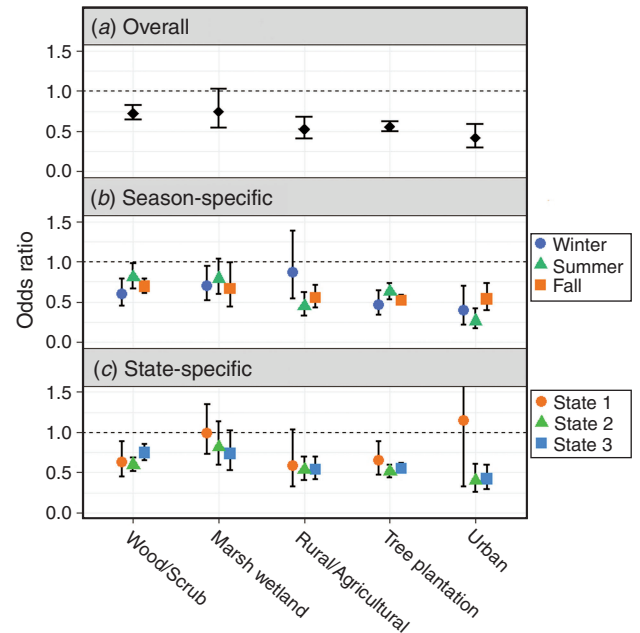


Fig. 4. Predictive odds with 95% confidence intervals of a bear choosing a land cover type based on (a) the mixed-conditional logistic models for the overall data, and (b) by season and (c) by state where the states represent the resting, encamped and exploratory states, respectively. Values for each land cover type are in reference to forested wetlands where values greater than 1 along with confidence intervals that do not cross 1 indicate the bears chose this land cover over forested wetlands, and values less than 1 with confidence intervals less than 1 indicate bears chose forested wetlands over the respective landcover. In cases where the confidence interval crosses 1, the land cover is selected similarly to forested wetlands.

state at night. Bears in the south-east USA tend to have the largest home ranges in the fall when they increase their caloric intake to prepare for the winter (Hellgren *et al.* 1989; Powell *et al.* 1997; Moyer *et al.* 2007). Our results indicate that bears in our study area not only increase their bi-hourly speeds of travel, but also were more likely to be in an encamped state (i.e. move moderate distances and turn around; potentially foraging) at night in fall.

Determining the appropriate number of states for HMMs is challenging because information theoretic approaches for model selection tend to favour HMMs with more states (van de Kerk *et al.* 2014; Li and Bolker 2017; Pohle *et al.* 2017). However, additional states may not relate to an actual underlying biological process, but instead may be a product of noise in the data, temporal autocorrelation, correlation within a state or individual heterogeneity (Li and Bolker 2017; Pohle *et al.* 2017). Black bears exhibited variation in their movements throughout the day; therefore, we accounted for temporal autocorrelation by including hour of the day as a covariate in our HMMs (Li and Bolker 2017) and we attempted to account for correlation within a state by running season-specific models. However, considerable overlap in step-length and turning angles between the resting and encamped states in the winter for both sexes and in the summer for females, and overlap between the encamped and exploratory state for males in the summer may indicate possible overfitting. The overlap in model parameters between encamped and exploratory states indicates these two states may not be distinct in some seasons, and/or that circannual rhythm of black bears affects movement states. It may be worthwhile to allow for seasonal variation in the number of states, depending on species biology. Additional information on animal movement (e.g. accelerometer data; Ditmer *et al.* 2017; Leos-Barajas *et al.* 2017) can also be helpful in differentiating states with similar distributions of step-lengths and turning angles.

We found that bears consistently chose to move to forested wetlands, significantly more than to human-modified land cover types, across all seasons and generally in any behavioural state. These results suggest that the bears actively avoid human-dominated, highly modified areas within the landscape. An exception to the trend was that bears also moved to rural and agricultural areas and urban areas while resting. Many of the rural and agricultural areas where the bears rested were within the Camp Blanding Joint Training Center, not on the adjacent agricultural lands. These areas on Camp Blanding had sparse human structures or open fields and were therefore likely to have received limited human-use throughout the day for most of the year. However, our results more properly represent where bears chose to move to while resting, and not so much where they chose to rest. We had to remove some bears from our analysis in the resting state because, in this state, many of their unused steps were in the same land cover type as the used step; this in turn likely contributed to the large confidence intervals in the resting state. Bears likely chose to move to forested wetland and marsh wetland habitats because these areas provide them with food, water and also with cover in the forested areas (Powell *et al.* 1997). These results are consistent with previous findings that black bears in south-eastern USA tend to select for forested wetlands (Hellgren *et al.* 1991; Wooding and Hardisky 1994; Stratman *et al.* 2001) and generally travel at a slower speed (i.e. shorter step-lengths) while in the forested wetlands (Karelus *et al.* 2017).

We also found that bears chose to move away from major roads, and this result was again consistent in summer and fall and when in the encamped or exploratory state. Our previous analyses indicated that the bears exhibited shorter step-lengths when near major roads (Karelus *et al.* 2017) and that the bears selected areas closer to major roads than at random (Karelus

et al. 2016). Taken together, our previous results regarding bears' selection of areas closer to roads may have been influenced by bears in the resting state, or may have been due to the configuration of the bears' home ranges within the landscape. We also found that minor roads and creeks had little to no effect on bears' habitat selection. However, it is likely that bear movement is more strongly influenced by major roads, minor roads and creeks at finer temporal scales; this may help to partially explain why other studies have found different results regarding bear selection of habitat in relation to roads (Reynolds-Hogland and Mitchell 2007; Coster and Kovach 2012; Costello *et al.* 2013; Karelus *et al.* 2016).

Conclusions

In summary, our study provided a general framework for explicitly incorporating sex-specific, seasonal and diurnal variation in movement patterns while investigating habitat selection. Our results showed that bear movement varied across seasons and they generally chose to move to forested wetlands and marsh wetlands over all other available land cover types. Although some of these findings are not substantially different from past studies, we also were able to show that the bears exhibited behavioural state-specific habitat selection patterns. These results highlight the importance of incorporating information on movement patterns and underlying behavioural states while making inferences about black bear habitat selection patterns. For example, bears avoided urban, rural, and agricultural areas while they were in the encamped and exploratory states, but they were among the selected land cover types when bears were in the resting state. Without explicit consideration of behavioural states, this detail would have been missed. Our findings regarding how bears are selecting habitat in the fragmented landscape could be an important consideration for managers seeking to increase connectivity among populations (Clark *et al.* 2015).

How animals move in the landscape and the time they spend in various habitat components defines their space- and habitat-use patterns. The movement patterns, on the other hand, are affected both by animals' internal states and where in space the animals are located. For example, animals foraging for high-energy food resources in preparation for hibernation would spend less time travelling and more time foraging once a high-quality habitat patch is located; they would spend more time travelling in search of resources in poor-quality habitats. Likewise, it is easy to imagine differences in movement patterns when animals are searching for mates during the breeding season versus when they are foraging in preparation for hibernation. Thus, habitat selection by animals emerges from how they move, but how they move in the landscape is affected by their intrinsic state and various extrinsic factors. Therefore, a thorough understanding of space- and habitat-use patterns requires knowledge of animals' movement patterns but understanding movement patterns necessitates knowledge of motivation for movement and factors influencing them (Moorcroft and Barnett 2008; Forester *et al.* 2009; Moorcroft 2012; van Moorter *et al.* 2016). Because animals may select habitats differently depending on motivation for movement or behavioural state underlying their movement patterns,

ignoring behavioural states underlying movement patterns can potentially obscure important details regarding which habitat components are for different activities or while in different behavioural states (Cozzi *et al.* 2016; Abrahms *et al.* 2017). Thus, studies of habitat-selection should include movement patterns and underlying behavioural states whenever feasible.

Although the ideas of discerning state-specific movement patterns, investigating the potential influence of covariates on transition probabilities between behavioural states and using step-selection functions in habitat selection studies are not new (Morales *et al.* 2004; Latham *et al.* 2011; McGreer *et al.* 2015; Zeller *et al.* 2016; Gilbert *et al.* 2017; Patterson *et al.* 2017), these approaches have not been effectively integrated. The novel analytical approach we developed and employed in this study effectively integrates these concepts by utilising hidden Markov models and the Viterbi algorithm to quantify state-specific movement patterns, and the step-selection function to subsequently discern habitat selection and possible behavioural mechanisms underlying the selection. It is now possible to discern animals' behavioural states based on movement metrics and ask refined questions regarding state-specific movement and habitat selection patterns. Using this approach, one can identify and manage for habitats that animals preferentially use, and identify habitats they avoid, while in specific behavioural states (e.g. foraging, dispersing, raising young). We believe that the unified methodological approach that we have presented here will lead to improved understanding of animal ecology, as well as informed management decisions.

Data accessibility

Florida black bear movement data are available at: <http://ufdc.ufl.edu/IR00010695/00001>.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Acknowledgements

We thank Camp Blanding Joint Training Center, Florida Fish and Wildlife Conservation Commission, the School of Natural Resources and Environment and the Department of Wildlife Ecology and Conservation, University of Florida for providing funding. We would like to thank Paul Catlett of Camp Blanding for providing logistical support. We would also like to express our thanks to the private land owners who took interest in our study and kindly allowed us on their properties. For assisting with data collection, we thank J. Burford, A. Casavant, D. Colbert, K. Malachowski, T. McQuaig and E. Troyer. We thank E. Hellgren D. Reed and P. White for many helpful comments on this manuscript, and T. Thernaue and T. Duchesne for help regarding the implementation of mixed-effects conditional logistic regression.

References

- Abrahms, B., Sawyer, S. C., Jordan, N. R., McNutt, J. W., Wilson, A. M., and Brashares, J. S. (2017). Does wildlife resource selection accurately inform corridor conservation? *Journal of Applied Ecology* **54**, 412–422. doi:10.1111/1365-2664.12714
- Alt, G. L., Matula, G. J. Jr, Alt, F. W., and Lindzey, J. S. (1980). Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. *International Conference on Bear Research and Management* **4**, 131–136.
- Benson, J. F., and Chamberlain, M. J. (2007). Space use and habitat selection by female Louisiana black bears in the Tensas River Basin of Louisiana. *The Journal of Wildlife Management* **71**, 117–126. doi:10.2193/2005-580
- Beyer, H. L., Gurarie, E., Börger, L., Panzacchi, M., Basille, M., Herfindal, I., Van Moorter, B., Lele, S. R., and Matthiopoulos, J. (2016). “You shall not pass!”: quantifying barrier permeability and proximity avoidance by animals. *Journal of Animal Ecology* **85**, 43–53. doi:10.1111/1365-2656.12275
- Bivand, R., and Rundel, C. (2016). rgeos: interface to Geometry Engine – Open Source (GEOS). R package version 0.3–20. Available at <https://CRAN.R-project.org/package=rgeos> [Verified December 2018]
- Boyce, M. S., Vernier, P. R., Nielsen, S. E., and Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecological Modelling* **157**, 281–300. doi:10.1016/S0304-3800(02)00200-4
- Boyd, C., Punt, A. E., Weimerskirch, H., and Bertrand, S. (2014). Movement models provide insights into variation in the foraging effort of central place foragers. *Ecological Modelling* **286**, 13–25. doi:10.1016/j.ecolmodel.2014.03.015
- Bridges, A. S., Vaughan, M. R., and Klenzendorf, S. (2004). Seasonal variation in American black bear *Ursus americanus* activity patterns: quantification via remote photography. *Wildlife Biology* **10**, 277–284.
- Buchmann, C. M., Schurr, F. M., Nathan, R., and Jeltsch, F. (2012). Movement upscaled – the importance of individual foraging movement for community response to habitat loss. *Ecography* **35**, 436–445. doi:10.1111/j.1600-0587.2011.06924.x
- Burnham, K. P., and Anderson, D. R. (2002). ‘Model Selection and Multimodel Inference: a Practical Information-theoretic Approach.’ 2nd edn. (Springer: New York.)
- Carr, M. H., and Zwick, P. D. (2016). Florida 2070: mapping Florida’s future—alternative patterns of development in 2070. Technical Report to Florida Department of Agriculture and Consumer Services & 1000 Friends of Florida. Geoplan Center, University of Florida, Gainesville, Florida, USA.
- Clark, J. D., Laufenberg, J. S., Davidson, M., and Murrow, J. L. (2015). Connectivity among subpopulations of Louisiana black bears as estimated by a step selection function. *The Journal of Wildlife Management* **79**, 1347–1360. doi:10.1002/jwmg.955
- Costello, C. M., Cain, S. I., Nielson, R. M., Servheen, C., and Schwartz, C. C. (2013). Response of American black bears to the non-motorized expansion of a road corridor in Grand Teton National Park. *Ursus* **24**, 54–69. doi:10.2192/URSUS-D-11-00027.1
- Coster, S. S., and Kovach, A. I. (2012). Anthropogenic influences on the spatial genetic structure of black bears. *Conservation Genetics* **13**, 1247–1257. doi:10.1007/s10592-012-0368-4
- Cozzi, G., Chynoweth, M., Kusak, J., Coban, E., Coban, A., Ozigul, A., and Sekercioglu, C. (2016). Anthropogenic food resources foster the coexistence of distinct life history strategies: year-round sedentary and migratory brown bears. *Journal of Zoology* **300**, 142–150. doi:10.1111/jzo.12365
- Craiu, R. V., and Duchesne, T. (2018). A scalable and efficient covariate selection criterion for mixed effects regression models with unknown random effects structure. *Computational Statistics & Data Analysis* **117**, 154–161. doi:10.1016/j.csda.2017.07.011
- Craiu, R. V., Duchesne, T., Fortin, D., and Baillargeon, S. (2011). Conditional logistic regression with longitudinal follow-up and individual-level random coefficients: a stable and efficient two-step estimation method. *Journal of Computational and Graphical Statistics* **20**, 767–784. doi:10.1198/jcgs.2011.09189
- Craiu, R. V., Duchesne, T., Fortin, D., and Baillargeon, S. (2016). TwoStepCLogit: conditional logistic regression: a two-step estimation method. R package version 1.2.5. Available at <https://CRAN.R-project.org/package=TwoStepCLogit> [Verified December 2018]

- Ditmer, M. A., Moen, R. A., Windels, S. K., Forester, J. D., Ness, T. E., and Harris, T. R. (2017). Moose at their bioclimatic edge alter their behavior based on weather, landscape, and predators. *Current Zoology* **64**, 419–432.
- Dobey, S., Masters, D. V., Scheick, B. K., Clark, J. D., Pelton, M. R., and Sunquist, M. E. (2005). Ecology of Florida black bears in the Okefenokee–Osceola ecosystem. *Wildlife Monographs* **158**, 1–41.
- Duchesne, T., Fortin, D., and Courbin, N. (2010). Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology* **79**, 548–555. doi:10.1111/j.1365-2656.2010.01670.x
- Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M. S., and Frair, J. L. (2010). Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **365**, 2233–2244. doi:10.1098/rstb.2010.0079
- Florida Fish and Wildlife Conservation Commission (2012). Florida black bear management plan. Florida Fish and Wildlife Conservation Commission, Tallahassee, FL.
- Forester, J. D., Im, H. K., and Rathouz, P. J. (2009). Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology* **90**, 3554–3565. doi:10.1890/08-0874.1
- Forman, R. T. T., and Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29**, 207–231. doi:10.1146/annurev.ecolsys.29.1.207
- Forney, G. D. Jr (1973). The Viterbi algorithm. *Proceedings of the IEEE* **61**, 268–278. doi:10.1109/PROC.1973.9030
- Fortin, D., Morales, J. M., and Boyce, M. S. (2005). Elk winter foraging at fine scale in Yellowstone National Park. *Oecologia* **145**, 335–343. doi:10.1007/s00442-005-0122-4
- Franke, A., Caelli, T., and Hudson, R. J. (2004). Analysis of movements and behavior of caribou (*Rangifer tarandus*) using hidden Markov models. *Ecological Modelling* **173**, 259–270. doi:10.1016/j.ecolmodel.2003.06.004
- Franke, A., Caelli, T., Kuzyk, G., and Hudson, R. J. (2006). Prediction of wolf (*Canis lupus*) kill-sites using hidden Markov models. *Ecological Modelling* **197**, 237–246. doi:10.1016/j.ecolmodel.2006.02.043
- Fryxell, J. M., Hazell, M., Börger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., McIntosh, T., and Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 19114–19119. doi:10.1073/pnas.0801737105
- Garrison, E. P., McCown, J. W., Barrett, M. A., and Oli, M. K. (2012). Denning ecology of Florida black bears in north-central Florida. *Southeastern Naturalist* **11**, 517–528. doi:10.1656/058.011.0314
- Garshelis, D. L. (1978). Movement ecology and activity behavior of black bears in the Great Smokey Mountains National Park. Masters Thesis, University of Tennessee.
- Garshelis, D. L., and Hristienko, H. (2006). State and provincial estimates of American black bear numbers versus assessments of population trend State and provincial estimates of American black bear numbers versus assessments of population trend. *Ursus* **17**, 1–7. doi:10.2192/1537-6176(2006)17[1:SAPEOA]2.0.CO;2
- Garshelis, D. L., and Pelton, M. R. (1980). Activity of black bears in the Great Smoky Mountains National Park. *Journal of Mammalogy* **61**, 8–19. doi:10.2307/1379952
- Garshelis, D. L., and Pelton, M. R. (1981). Movements of black bears in the Great Smoky Mountains. *The Journal of Wildlife Management* **45**, 912–925. doi:10.2307/3808099
- Garshelis, D. L., Quigley, H. B., Villarrubia, C. R., and Pelton, M. R. (1983). Diel movements of black bears in the southern Appalachians. *International Conference on Bear Research and Management* **5**, 11–19.
- Gilbert, S. L., Hundertmark, K. J., Person, D. K., Lindberg, M. S., and Boyce, M. S. (2017). Behavioral plasticity in a variable environment: snow depth and habitat interactions drive deer movement in winter. *Journal of Mammalogy* **98**, 246–259. doi:10.1093/jmammal/gyw167
- Gurarie, E., Bracis, C., Delgado, M., Meckley, T. D., Kojola, I., and Wagner, C. M. (2015). What is the animal doing? Tools for exploring behavioral structure in animal movements. *Journal of Animal Ecology* **85**, 69–84. doi:10.1111/1365-2656.12379
- Hellgren, E. C., and Vaughan, M. R. (1990). Range dynamics of black bears in Great Dismal Swamp, Virginia–North Carolina. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* **44**, 268–278.
- Hellgren, E. C., Vaughan, M. R., and Kirkpatrick, R. L. (1989). Seasonal patterns in physiology and nutrition of black bears in Great Dismal Swamp, Virginia–North Carolina. *Canadian Journal of Zoology* **67**, 1837–1850. doi:10.1139/z89-262
- Hellgren, E. C., Vaughan, M. R., and Stauffer, D. F. (1991). Macrohabitat use by black bears in a southeastern wetland. *The Journal of Wildlife Management* **55**, 442–448. doi:10.2307/3808972
- Hector, T. S., Carr, M. H., and Zwick, P. D. (2000). Identifying a linked reserve system using a regional landscape approach: The Florida Ecological Network. *Conservation Biology* **14**, 984–1000. doi:10.1046/j.1523-1739.2000.99075.x
- Hristienko, H., and McDonald, J. E. (2007). Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. *Ursus* **18**, 72–88. doi:10.2192/1537-6176(2007)18[72:GITSCA]2.0.CO;2
- Humm, J. M., McCown, J. W., Scheick, B. K., and Clark, J. D. (2017). Spatially explicit population estimates for black bears based on cluster sampling. *The Journal of Wildlife Management* **81**, 1187–1201. doi:10.1002/jwmg.21294
- Johnson, C., and Nielsen, S. (2006). Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *The Journal of Wildlife Management* **70**, 347–357. doi:10.2193/0022-541X(2006)70[347:RSFBOU]2.0.CO;2
- Jonsen, I. D., Ransom, A. M., and Flemming, J. M. (2003). Meta-analysis of animal movement using state-space models. *Ecology* **84**, 3055–3063. doi:10.1890/02-0670
- Karelus, D. L., McCown, J. W., Scheick, B. K., van de Kerk, M., and Oli, M. K. (2016). Home ranges and habitat selection by black bears in a newly colonized population in Florida. *Southeastern Naturalist (Steuben, ME)* **15**, 346–364. doi:10.1656/058.015.0215
- Karelus, D. L., McCown, J. W., Scheick, B. K., van de Kerk, M., Bolker, B. M., and Oli, M. K. (2017). Effects of environmental factors and landscape features on movement patterns of Florida black bears. *Journal of Mammalogy* **98**, 1463–1478.
- Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., and Morales, J. M. (2012). Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology* **93**, 2336–2342. doi:10.1890/11-2241.1
- Latham, A. D. M., Latham, M. C., Boyce, M. S., and Boutin, S. (2011). Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications* **21**, 2854–2865. doi:10.1890/11-0666.1
- Latombe, G., Parrott, L., Basille, M., and Fortin, D. (2014). Uniting statistical and individual-based approaches for animal movement modelling. *PLoS One* **9**, e99938. doi:10.1371/journal.pone.0099938
- Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T. A., Watanabe, Y. Y., Murgatroyd, M., and Papastamatiou, Y. P. (2017). Analysis of animal accelerometer data using hidden Markov models. *Methods in Ecology and Evolution* **8**, 161–173. doi:10.1111/2041-210X.12657
- Lewis, J. S., and Rachlow, J. L. (2011). Activity patterns of black bears in relation to sex, season, and daily movement rates. *Western North American Naturalist* **71**, 388–395. doi:10.3398/064.071.0306

- Li, M., and Bolker, B. M. (2017). Incorporating periodic variability in hidden Markov models for animal movement. *Movement Ecology* **5**, 1–12. doi:10.1186/s40462-016-0093-6
- Lund U., and Agostinelli. C. (2012). CircStats: Circular Statistics. R package version 0.2-4. Available at <https://cran.r-project.org/package=CircStats> [Verified 16 January 2019].
- Maehr, D. S., and Brady, J. R. (1984). Food habits of Florida black bears. *The Journal of Wildlife Management* **48**, 230–235. doi:10.2307/3808478
- Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., and Erickson, W. P. (2002). 'Resource Selection by Animals: Statistical Design and Analysis for Field Studies.' 2nd edn. (Kluwer Academic Publishers: Boston, MA.)
- Martin, J., van Moorter, B., Revilla, E., Blanchard, P., Dray, S., Quenette, P. Y., Allainé, D., and Swenson, J. E. (2013). Reciprocal modulation of internal and external factors determines individual movements. *Journal of Animal Ecology* **82**, 290–300. doi:10.1111/j.1365-2656.2012.02038.x
- Martin, J., Calenge, C., Quenette, P.-Y., and Allainé, D. (2008). Importance of movement constraints in habitat selection studies. *Ecological Modelling* **213**, 257–262. doi:10.1016/j.ecolmodel.2007.12.002
- McGreer, M. T., Mallon, E. E., Vander Vennen, L. M., Wiebe, P. A., Baker, J. A., Brown, G. S., Avgar, T., Hagens, J., Kittle, A. M., Mosser, A., Street, G. M., Reid, D. E. B., Rodgers, A. R., Shuter, J., Thompson, I. D., Turetsky, M. J., Newmaster, S. G., Patterson, B. R., and Fryxell, J. M. (2015). Selection for forage and avoidance of risk by woodland caribou (*Rangifer tarandus caribou*) at coarse and local scales. *Ecosphere* **6**, art288. doi:10.1890/ES15-00174.1
- McKellar, A. E., Langrock, R., Walters, J. R., and Kesler, D. C. (2015). Using mixed hidden Markov models to examine behavioral states in a cooperatively breeding bird. *Behavioral Ecology* **26**, 148–157. doi:10.1093/beheco/aru171
- Michelot, T., Langrock, R., and Patterson, T. A. (2016). moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution* **7**, 1308–1315. doi:10.1111/2041-210X.12578
- Moorcroft, P. R. (2012). Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. *Journal of Mammalogy* **93**, 903–916. doi:10.1644/11-MAMM-S-254.1
- Moorcroft, P. R., and Barnett, A. (2008). mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology* **89**, 1112–1119. doi:10.1890/06-1985.1
- Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., and Fryxell, J. M. (2004). Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* **85**, 2436–2445. doi:10.1890/03-0269
- Moyer, M. A., McCown, J. W., and Oli, M. K. (2007). Factors influencing home range size of female Florida black bears. *Journal of Mammalogy* **88**, 468–476. doi:10.1644/06-MAMM-A-165R1.1
- Moyer, M. A., McCown, J. W., and Oli, M. K. (2008). Scale-dependent habitat selection by female Florida black bears in Ocala National Forest, Florida. *Southeastern Naturalist (Steuben, ME)* **7**, 111–124. doi:10.1656/1528-7092(2008)7[111:SHSBFF]2.0.CO;2
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 19052–19059. doi:10.1073/pnas.0800375105
- Noyce, K. V., and Garshelis, D. L. (2011). Seasonal migrations of black bears (*Ursus americanus*): causes and consequences. *Behavioral Ecology and Sociobiology* **65**, 823–835. doi:10.1007/s00265-010-1086-x
- Onorato, D. P., Hellgren, E. C., Mitchell, F. S., and Skiles, J. R. Jr (2003). Home range and habitat use of American black bears on a desert montane island in Texas. *Ursus* **14**, 120–129.
- Patterson, T. A., Basson, M., Bravington, M. V., and Gunn, J. S. (2009). Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology* **78**, 1113–1123. doi:10.1111/j.1365-2656.2009.01583.x
- Patterson, T. A., Parton, A., Langrock, R., Blackwell, P. G., Thomas, L., and King, R. (2017). Statistical modelling of individual animal movement: an overview of key methods and a discussion of practical challenges. *ASStA. Advances in Statistical Analysis* **101**, 399–438. doi:10.1007/s10182-017-0302-7
- Pelton, M. R. (2003). Black bears (*Ursus americanus*). In 'Wild Mammals of North America'. 2nd edn. (Eds G. A. Feldhamer, B. C. Thompson and J. A. Chapman.) pp. 547–556. (Johns Hopkins University Press: Baltimore, MD.)
- Pohle, J., Langrock, R., van Beest, F. M., and Schmidt, N. M. (2017). Selecting the number of states in hidden Markov models: pragmatic solutions illustrated using animal movement. *Journal of Agricultural Biological & Environmental Statistics*. doi:10.1007/s13253-017-0283-8
- Powell, R. A., Zimmerman, J. W., and Seaman, D. E. (1997). 'Ecology and Behaviour of North American Black Bears: Home Ranges, Habitat and Social Organization.' (Chapman and Hall: London, UK.)
- R Core Team (2016). R: a language and environment for statistical computing. (R Foundation for Statistical Computing, Vienna, Austria.) Available at <http://www.r-project.org/> [Verified December 2018]
- Rayl, N. D., Fuller, T. K., Organ, J. F., McDonald, J. E., Otto, R. D., and Mahoney, S. P. (2014). Den abandonment and transitional day bed use by black bears (*Ursus americanus*) in Newfoundland. *Wildlife Biology* **20**, 222–228. doi:10.2981/wlb.00020
- Redner, J., and Srinivasan, S. (2014). Florida vegetation and land cover 2014. Final Report. Fish and Wildlife Research Institute grant #6207. (Florida Fish and Wildlife Conservation Commission: Tallahassee, FL.)
- Revelt, D., and Train, K. (1998). Mixed logit with repeated choices: households' choices of appliance efficiency level. *The Review of Economics and Statistics* **80**, 647–657. doi:10.1162/003465398557735
- Reynolds-Hogland, M. J., and Mitchell, M. S. (2007). Effects of roads on habitat quality for bears in the southern Appalachians: a long-term study. *Journal of Mammalogy* **88**, 1050–1061. doi:10.1644/06-MAMM-A-072R1.1
- Scheick, B. K., and McCown, W. (2014). Geographic distribution of American black bears in North America. *Ursus* **25**, 24–33. doi:10.2192/URSUS-D-12-00020.1
- Scheick, B. K., Cunningham, M. W., McCown, J. W., and Orlando, M. A. (2009). Anchor modification for a foot-hold snare to capture American black bears. *Ursus* **20**, 47–49. doi:10.2192/08GR013R.1
- Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., Halpin, P. N., Joppa, L. N., McClellan, C. M., and Clark, J. S. (2008). Understanding movement data and movement processes: current and emerging directions. *Ecology Letters* **11**, 1338–1350. doi:10.1111/j.1461-0248.2008.01249.x
- Schliehe-Diecks, S., Kappeler, P. M., and Langrock, R. (2012). On the application of mixed hidden Markov models to multiple behavioural time series. *Interface Focus* **2**, 180–189. doi:10.1098/rsfs.2011.0077
- Servheen, C., Herrero, S., and Peyton, B. (1999). Bears: status, survey and conservation action plan. IUCN/SSC Action Plans for the Conservation of Biological Diversity. (IUCN/SSC Bear Specialist Group: Gland, Switzerland.)
- Squires, J. R., DeCesare, N. J., Olson, L. E., Kolbe, J. A., Hebblewhite, M., and Parks, S. A. (2013). Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. *Biological Conservation* **157**, 187–195. doi:10.1016/j.biocon.2012.07.018
- Stratman, M. R., and Pelton, M. R. (1999). Feeding ecology of black bears in northwest Florida. *Florida Field Naturalist* **27**, 95–102.
- Stratman, M., Alden, C., Pelton, M., and Sunquist, M. (2001). Habitat use by American black bears in the sandhills of Florida. *Ursus* **12**, 109–114.

- Thurfjell, H., Ciuti, S., and Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology* **2**, 4. doi:10.1186/2051-3933-2-4
- Tigas, L. A., Van Vuren, D. H., and Sauvajot, R. M. (2002). Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biological Conservation* **108**, 299–306. doi:10.1016/S0006-3207(02)00120-9
- van de Kerk, M., Onorato, D. P., Criffield, M. A., Bolker, B. M., Augustine, B. C., McKinley, S. A., and Oli, M. K. (2014). Hidden semi-Markov models reveal multiphasic movement of the endangered Florida panther. *Journal of Animal Ecology* **84**, 576–585. doi:10.1111/1365-2656.12290
- van Moorter, B., Rolandsen, C. M., Basille, M., and Gaillard, J.-M. (2016). Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology* **85**, 21–31. doi:10.1111/1365-2656.12394
- Visser, I. (2011). Seven things to remember about hidden Markov models: a tutorial on Markovian models for time series. *Journal of Mathematical Psychology* **55**, 403–415. doi:10.1016/j.jmp.2011.08.002
- Willey, C. H. (1974). Aging black bears from first premolar tooth sections. *The Journal of Wildlife Management* **38**, 97–100. doi:10.2307/3800203
- Wooding, J. B., and Hardisky, T. S. (1992). Denning by black bears in northcentral Florida. *Journal of Mammalogy* **73**, 895–898. doi:10.2307/1382213
- Wooding, J. B., and Hardisky, T. S. (1994). Home range, habitat use, and mortality of black bears in north-central Florida. *International Conference on Bear Research and Management* **9**, 349–356.
- Zeller, K. A., Mcgarigal, K., Cushman, S. A., Beier, P., Vickers, T. W., and Boyce, W. M. (2016). Using step and path selection functions for estimating resistance to movement: pumas as a case study. *Landscape Ecology* **31**, 1319–1335. doi:10.1007/s10980-015-0301-6
- Zucchini, W., and Macdonald, I. L. (2016). 'Hidden Markov Models for Time Series: an Introduction Using R.' 2nd edn. (Chapman and Hall/CRC Press: Boca Raton, FL.)