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Hidden semi-Markov models reveal multiphasic movement of the endangered Florida panther

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Summary

1. Animals must move to find food and mates, and to avoid predators; movement thus influences survival and reproduction, and ultimately determines fitness. Precise description of movement and understanding of spatial and temporal patterns as well as relationships with intrinsic and extrinsic factors is important both for theoretical and applied reasons.

2. We applied hidden semi-Markov models (HSMM) to hourly geographic positioning system (GPS) location data to understand movement patterns of the endangered Florida panther (*Puma concolor coryi*) and to discern factors influencing these patterns.

3. Three distinct movement modes were identified: (1) Resting mode, characterized by short step lengths and turning angles around 180°; (2) Moderately active (or intermediate) mode characterized by intermediate step lengths and variable turning angles, and (3) Traveling mode, characterized by long step lengths and turning angles around 0°.

4. Males and females, and females with and without kittens, exhibited distinctly different movement patterns. Using the Viterbi algorithm, we show that differences in movement patterns of male and female Florida panthers were a consequence of sex-specific differences in diurnal patterns of state occupancy and sex-specific differences in state-specific movement parameters, whereas the differences between females with and without dependent kittens were caused solely by variation in state occupancy.

5. Our study demonstrates the use of HSMM methodology to precisely describe movement and to dissect differences in movement patterns according to sex, and reproductive status.

Key-words: dwell time distribution, hidden semi-Markov models, movement patterns, multiphasic animal movement, Puma concolor coryi, Viterbi algorithm

Introduction

Animal movement within heterogeneous landscapes is a key process influencing many aspects of ecology, because survival depends on food acquisition and predator avoidance, and successful reproduction depends on finding mates (Morales & Ellner 2002). Moreover, resource and space use patterns emerge from individual movement behaviour and can have significant implications for population dynamics (Turchin 1998). Animal movement is the result of a complex interaction between an animal's external environment and internal state and varies depending on an animal's sex, age and reproductive status (Jonsen, Myers & Flemming 2003; Favreau 2006). Understanding movement patterns can help understand home range and territorial dynamics (Moorcroft, Lewis & Crabtree 1999), animals' ability to exploit spatially and temporally variable resources (Clobert *et al.* 2009), and their interactions with conspecifics (Dickson, Jenness & Beier 2005). It is also essential for assessing a species' ability to respond to threats such as habitat fragmentation and

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climate change (Clobert *et al.* 2009). Some species confine their movements in space and, through time, develop home ranges and/or territories (Powell 2012). Territoriality constrains movement behaviours within a certain area and adds behaviours such as territory defence to movement patterns. Territorial animals commonly also have a life stage without territoriality (e.g. dispersal), during which they may exhibit different movement patterns.

It has been recently proposed that animals alter movement patterns as a complex function of internal states and social, ecological and environmental factors (Fryxell *et al.* 2008; Nathan *et al.* 2008). This multiphasic movement idea (Fryxell *et al.* 2008) provides a framework for understanding why animals exhibit different movement patterns depending on intrinsic states (e.g. sex, residency and reproductive status) and extrinsic environmental cues. Quantifying and describing statistically discernible and biologically meaningful numbers of movement modes, and their behavioural correlates, has been challenging due to the lack of high-resolution location data and/or an appropriate modelling framework. Many central questions in animal movement analysis remain unresolved. How can we determine biologically meaningful numbers of behaviourally distinct movement phases exhibited by animals? How are the movement phases influenced or modulated by extrinsic environmental factors? In what way do these movement phases differ? It is generally well known that animals of different sex, age or reproductive status exhibit different movement patterns. Do these differences arise because of sex-, age- or reproductive status-specific differences in movement modes, the amount of time spent in each mode, or because of differences in mode-specific movement parameters depending on sex, age or reproductive status?

The hidden Markov Model (HMM), a discrete-time time-series model, has been used to study animal movement and space use patterns (Franke, Caelli & Hudson 2004; Franke *et al.* 2006; Patterson *et al.* 2009). One limitation of HMM for modelling animal movement is that dwell times (i.e. time spent in a specific state) are assumed to follow a geometric distribution; this assumption may not always hold (Langrock *et al.* 2012). The hidden semi-Markov model (HSMM), an extension of HMM, relaxes this assumption and permits explicit modelling of dwell times using alternative statistical distributions (Langrock *et al.* 2012). Like HMMs, HSMMs also allow for the use of the Viterbi algorithm (Zucchini & MacDonald 2009) to assign a movement state for each move segment (Langrock *et al.* 2012).

In this study, we investigated the movement patterns of the Florida panther (*Puma concolor coryi*), an endangered subspecies of puma that exhibits territorial behaviour. Using long-term (2005–2012) global positioning system (GPS) data, our goal was to understand Florida panther movement patterns, and factors influencing these patterns. We applied hidden semi-Markov models (HSMM) and the Viterbi algorithm to hourly GPS location data to discern behaviourally distinct movement modes exhibited by 13 Florida panthers and to quantify differences in movement patterns exhibited by panthers of different sex, and reproductive and residency status. The implementation of HSMM within a maximum-likelihood framework allowed us to fit alternative statistical distributions for step length, turning angle, and dwell time, consider a range (2–6) of behavioural modes, and to apply an information-theoretical approach to identify the appropriate statistical distribution for HSMM parameters as well as the appropriate number of behavioural modes. Finally, we decomposed differences in overall movement patterns into differences due to variation in time spent in different movement modes, and within-mode differences in movement behaviours.

Materials and methods

STUDY SPECIES AND AREA

The Florida panther, an endangered subspecies of north American pumas, previously inhabited all of Florida and much of southeastern United States (Young & Goldman 1946). Currently, only one small population remains in South Florida, south of Lake Okeechobee, with limited dispersal potential due to landscape barriers (Maehr 1997). Florida panthers are nocturnal and crepuscular, with activity peaks around sunset and sunrise, while diurnal periods generally involve episodes of rest in daybeds (Maehr *et al.* 1990; Land *et al.* 2008). Panthers are solitary and territorial. The currently occupied range of the Florida panther is topographically flat, has a subtropical climate, and is characterized by permanent and ephemeral wetlands influenced by seasonal rains from May through October (Duever *et al.* 1986). A more detailed description of the area can be found in Kautz *et al.* (2006) and Onorato *et al.* (2011).

FIELD METHODS

Male and female panthers were captured and fitted with GPS collars. By Florida Fish and Wildlife Conservation Commission (FWC) staff using trained hounds and houndsmen. Panthers were treed and immobilized with a combination of ketamine hydrochloride (HCl; 10 mg kg^{-1}; Congaree Veterinary Pharmacy, Cayce, SC), xylazine HCl (1 mg kg^{-1}; Congaree Veterinary Pharmacy) and midazolam HCl (0·03 mg kg^{-1}; Abbott Laboratories, North Chicago, IL), using a 3-ml compressed air dart fired from a CO_2-powered rifle (JM special; Dan-inject ApS, Børkop, Denmark). Immobilized panthers were lowered to the ground with a rope, or caught on the ground with a net or wildlife cushion (McCown, Maehr & Roboski 1990; Land *et al.* 2008). Panthers were fitted with GPS collars programmed with different fix schedules (Onorato *et al.* 2011), but we only used location data obtained at hourly intervals.

DATA ANALYSIS

Animal movements are typically characterized by metrics such as step lengths, turning angles and mean-squared displacement

(MSD); these movement descriptors may vary over time and differ among individuals depending on sex, age and residency or reproductive status. Detailed analyses of Florida panther movement descriptors are presented in Appendix S1 (Supporting information). Using observations of adult females and/or kittens from tracking aircraft and camera traps, we identified females that had no kittens, females with young kittens in the den, and females with older dependent kittens. We also used sex, age and MSD to distinguish between dispersing and resident or territorial males; movement of dispersing males is not constrained in space, whereas that of territorial males is generally restricted within their territories. We compared movement patterns between males and females, between territorial and dispersing males, and for a female who successfully raised kittens during our study, among periods prior to birth, when she was accompanied by young kittens in den, and when she was with older but still dependent kittens. Finally, we compared movement between dry and wet seasons, and across the diel period. Results of these analyses are presented in Appendix S1.

Of 18 Florida panthers GPS-tracked in hourly intervals, data were sufficient for 13 panthers to permit HSMM modelling. We used HSMMs, and not HMMs, for modelling Florida panther movement because HSMMs allow flexible modelling of the dwell time distributions (Langrock *et al.* 2012). We considered two to six underlying movement states for HSMM fitting, as well as alternative distributions for step length (log-normal, gamma and Weibull), turning angle (wrapped normal and wrapped Cauchy) and dwell times (Poisson and negative binomial). Technically, the algorithm developed by Langrock *et al.* (2012) implements an approximation to a given dwell time distribution that is only exact up to the dimension of the matrix used to parameterize the HSMM; beyond maximum dwell time corresponding to the dimension of the approximating transition matrix, the dwell time distribution decays geometrically. A matrix dimension of 10 was used, which we considered large enough because the mean dwell time was never greater than five. We experimented with matrix sizes of up to 30, but this substantially increased computation time and did not change the parameter estimates.

An information-theoretical approach (Burnham & Anderson 2002) using the Bayesian information criterion (BIC) was used for multimodel comparison and statistical inference. BIC was used as an appropriate information criterion because we were primarily interested in explaining the data generation process by identifying the 'true' number of underlying movement states. The appropriate number of movement states for each panther was determined based on BIC values and biological interpretability of movement states.

To facilitate the comparison of parameter estimates among panthers, the movement states were ordered based on the Weibull scale parameter, which is equivalent to ordering the states based on the mean step length (see Appendix S2, Supporting information for details). We tested for sex-specific differences in each state-specific parameter for the step length, turning angle and dwell time distributions using a Mann–Whitney *U*-test (Conover 1999) (Appendix S2). We assessed the fit of the 3-state HSMM models to Florida panther movement data using three complementary approaches. First, we examined Quantile–Quantile (q–q) plots for step length and turning angle distributions to visually assess the fit of HSMM models to movement data for each panther. Secondly, we compared observed movement descriptors (step lengths and turning angles) of each panther with descriptors that were simulated using parameter estimates obtained from a particular model. Finally, we examined the temporal autocorrelation functions of observed and simulated step lengths. For details on these three approaches, please refer to Appendix S2.

Using the Viterbi algorithm, which predicts the most likely sequence of movement states based on observed movement characteristics (Zucchini & MacDonald 2009; Langrock *et al.* 2012), a movement mode was assigned to every observed move segment for each panther (Appendix S3, Supporting information). We then examined which movement modes panthers were likely to occupy depending on time of the day, season and reproductive status.

Male and female Florida panthers exhibited different movement patterns with distinctly different average hourly step lengths (Appendix S1); such sex-specific differences may arise due to differences in distribution of state-specific step lengths, turning angles or dwell times, or a combination of these. For example, males could have longer average hourly step lengths overall either because they have a longer hourly step length when they travel, or because males spend more time travelling than females. To decompose the observed differences in average step length between males and females (step length or time spent travelling), we simulated movement descriptors (step lengths and turning angles) using different combinations of state-specific average parameters for all panthers, and for males and females separately. Percentile-based parametric bootstrap confidence intervals were estimated for mean simulated step lengths based on 100 bootstrap samples (Efron & Tibshurani 1993).

Depending on the underlying behaviour (e.g. resting or active modes), the proportion of time spent in each movement state could be different. Thus, we also estimated the stationary distribution (i.e. the 'state occupancy'; the proportion of time spent in a state) from the transition probability matrix used to approximate the HSMM. This matrix was constructed from the dwell time distributions and state transition probabilities. Using 3-state HSMM models, we estimated state occupancy and compared it between males and females.

One female (FP94) in our study produced a litter during the 24 months that she was GPS-tracked, and the presence of her kittens was confirmed visually soon after birth and when kittens were ca. 2 months old. Data for this female were used to examine to what extent the presence of kittens influenced state-specific movement parameters and state occupancy probabilities.

The package move.HMM (Augustine & Langrock 2014) for R (R Development Core Team 2011) was used for fitting HSMM models, simulating step lengths and turning angles using the estimated parameters, and for estimating states with the Viterbi algorithm.

Results

During 2005–2012, 18 Florida panthers were GPS-tracked at hourly intervals for a total of 3200 panther days. We only used locations that were successfully acquired at hourly intervals, resulting in 48 825 hourly locations of 13 males (32 468 total locations) and 5 females (17 357). Of these, sample sizes were sufficient for MSD calculation and HSMM modelling for 13 panthers (10 males: 32 316 locations; three females: 17 164 locations). Males generally had longer step lengths than females, and movement descriptors for all panthers varied over a diel period. The MSD increased steadily and reached an asymptote for all panthers except for a dispersing male, suggesting that movement of panthers is generally constrained within home ranges except when they are dispersing. Detailed analysis of Florida panther movement descriptors is presented in Appendix S1.

The HSMM modelling revealed that distributions that consistently had the best fit were Weibull for step length, wrapped Cauchy for turning angle, and negative binomial for dwell time. Using these three distributions, we fitted HSMM models for every panther with the number of behavioural states ranging from 2 to 6 and used BIC values to compare models for each panther. The number of states that yielded lowest BIC values varied among individuals, but 3–4 state models were well supported for most panthers (Fig. 1).

Models with >3 states were difficult to interpret biologically, especially because it was not possible to make behavioural observations at the time GPS locations were obtained. On the other hand, 3-state models were generally statistically well-supported and biologically interpretable. Based on the ordered state-specific parameters, three states representing specific behavioural modes were identi-

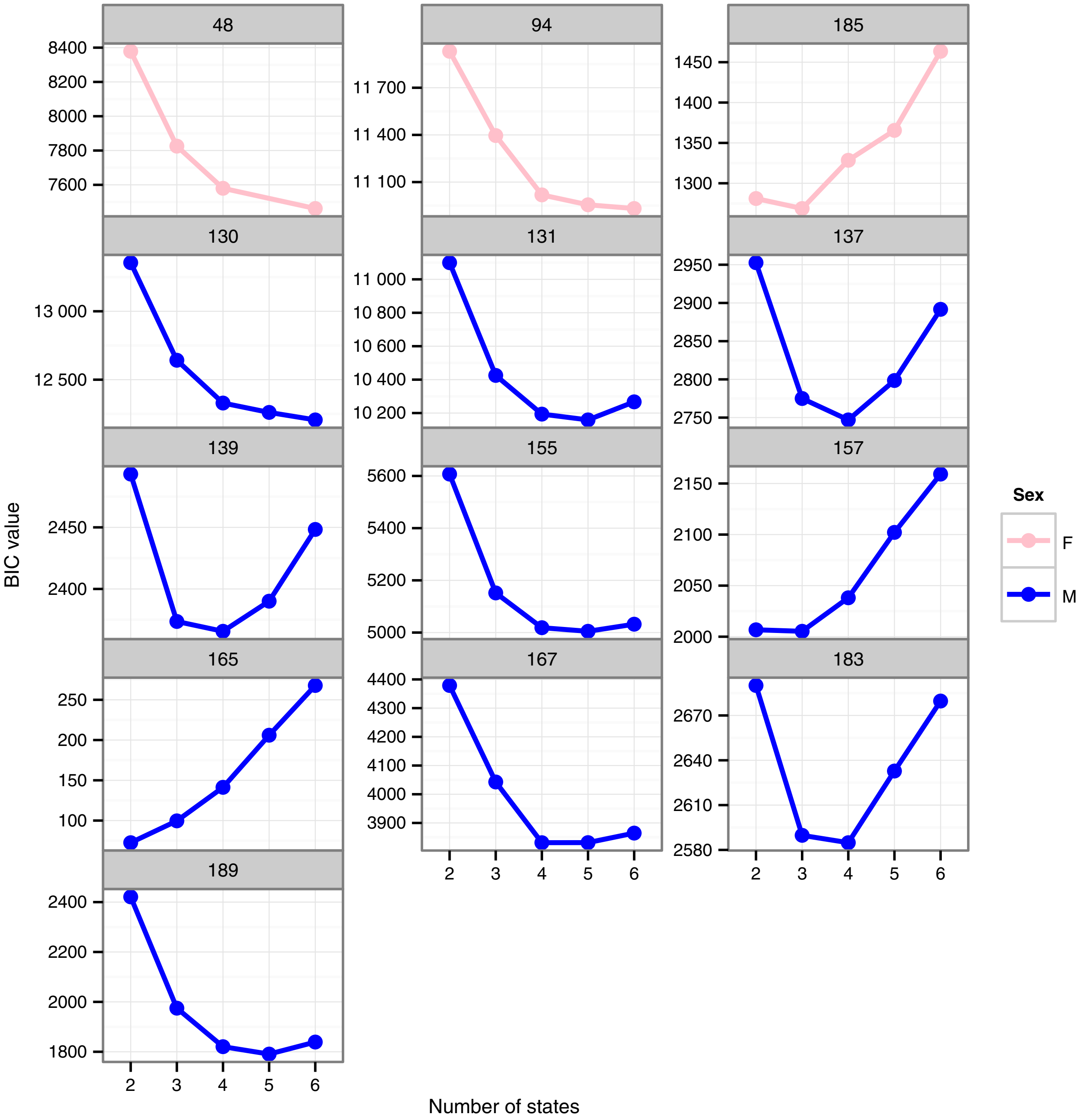

Fig. 1. Bayesian information criterion (BIC) values for 2–6 state hidden semi-Markov models fitted to movement data for each Florida panther. Each panel presents the results for one individual and is labelled with that panther's identification number.

fied: (i) a resting mode, with short step lengths and turning angles around 180°; (ii) a moderately active (or intermediate) mode characterized by intermediate step lengths and variable turning angles; and (iii) a travelling mode characterized by long step lengths and turning angles around 0° (Fig. 2a). Average step lengths in the resting mode were similar for males and females, but step lengths for males were substantially longer than those of females in the intermediate and the travelling modes (Fig. 2b).

We concluded that 3-state models represented statistically discernible and biologically interpretable behavioural modes, and thus used 3-state models for further analysis and evaluation of model fit (Appendix S2). For each panther, we obtained state-specific estimates of parameters for the distributions used to model step lengths, turning angles and dwell times (Fig. 3). The negative binomial shape parameters were close to 1 for most panthers, indicating that the dwell time distributions were close to geometric, and hence that a HMM would have sufficed for these individuals. Observed and simulated distributions were very similar for all panthers, indicating adequate model fit, and the fit generally improved with sample size (i.e. the number of GPS locations). The residual plots for step length, turning angle and dwell time distributions also indicated that that the 3-state HSMM models fit our data well (Appendix S2). Temporal autocorrelation functions (ACFs) of the observed and simulated step lengths showed that the HSMMs accurately captured the short-term (<10 h) autocorrelation but not the diurnal periodicity in movement (Appendix S2).

Next, the Viterbi algorithm was used to assign a specific state to every observed move segment for each panther in our data set (Appendix S3); we then examined the distribution of these states during a diel period and across different weeks of the year. Panthers were primarily in the resting mode during the day and in travelling mode during the night (Fig. 4a). Males exhibited a very strong diurnal pattern and were mostly in the resting mode during the day, whereas state occupancies for females were much less variable over a diel period. Females spent more time in the resting mode during mid-summer than during the rest of the year, whereas males spent more time resting during the second half of the year (Fig 4b).

Both observed and simulated average step lengths were longer for males than for females. This difference can be caused by longer step lengths for males in the intermediate and travelling modes, by males spending more time in behavioural modes with longer step lengths, or by a combination thereof. By simulating step lengths with different combinations of average step length and dwell time

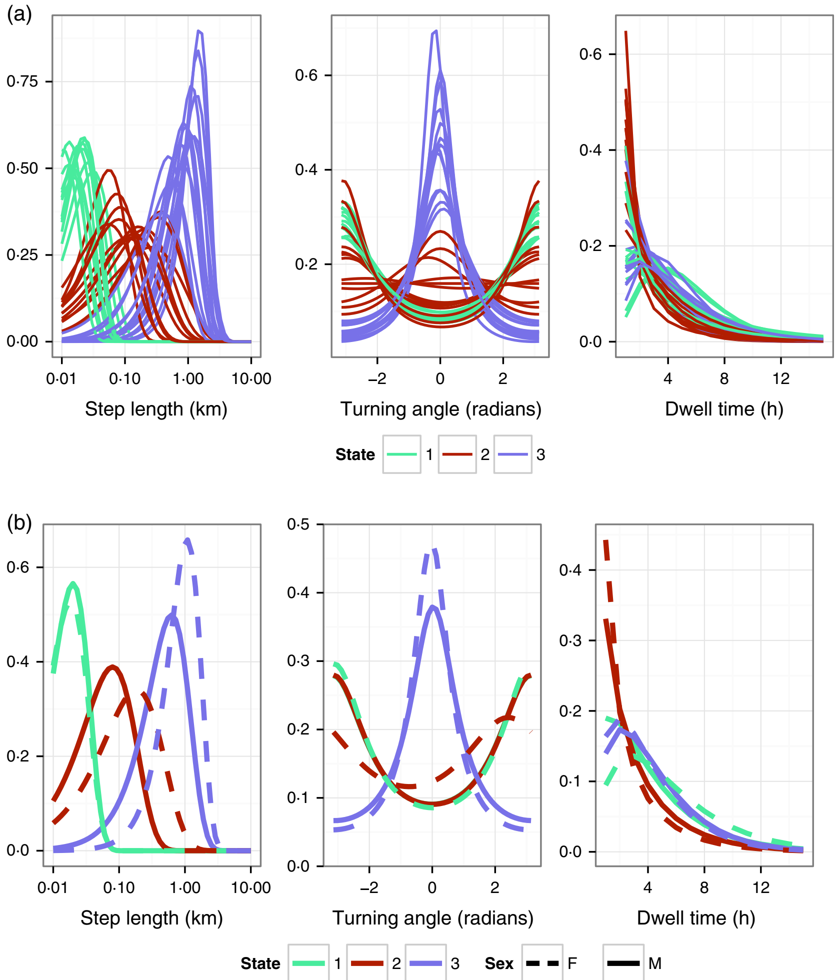

Fig. 2. (a) Distribution of hidden semi-Markov movement model (HSMM) parameters (step length, turning angle and dwell time) for each of the three movement states for 3-state HSMM models. State 1 represents the resting state, state 2 is intermediate or moderately active state, and state 3 is travelling state, and (b) the same plot of the three different states but now with the average distributions for males and females.

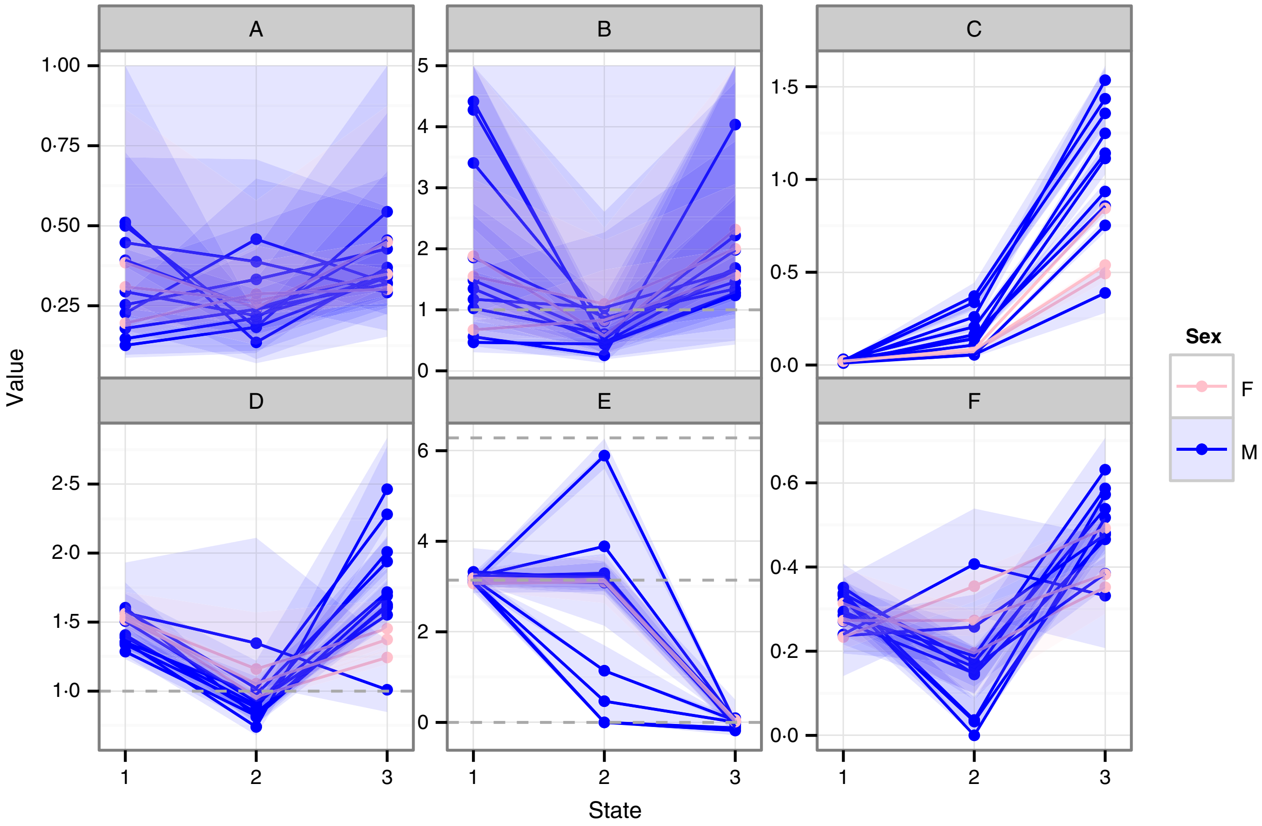

Fig. 3. Average state-specific parameter estimates with shaded 95% CI for the 3-state hidden semi-Markov models (HSMMs) fitted to Florida panther movement data. Each line represents an individual panther, and each panel represents a parameter. Panels a and b present the probability and size parameters defining the binomial distribution used to model step lengths. Panels c and d present the scale and shape parameters defining the Weibull distribution used to model turning angles. Panels e and f represent the mean and concentration parameters defining the wrapped Cauchy distribution used to model dwell times.

distribution for all panthers, and for males and for females separately, we found that females generally spent more time in state 3 (i.e., travelling mode), but that males had longer steps in that mode (Fig. 5). The estimated state occupancies also indicated that males spent the highest proportion of time in the resting mode, whereas females divided their time more equally between travelling and resting modes (Fig. 6). Furthermore, state-specific step length distributions were similar whether a female was with or without kittens, but she spent more time in resting mode when she had kittens (Fig. 6).

To examine the robustness of our results, we also fitted 2–6 state HSMMs to data that were pooled for all panthers, and for males and females separately. The BIC values for these models continued to decrease as the number of states increased, most likely due to increased sample sizes. Parameter estimates and ordering of states, as well as sex-specific differences in movement descriptors, were similar to those based on individual-based analyses (Appendix S4, Supporting information).

Discussion

Despite the intuitive appeal of the multiphasic movement idea (Fryxell *et al.* 2008; Nathan *et al.* 2008), discerning and quantifying behaviourally distinct movement modes have been challenging. The application of the hidden semi-Markov modelling framework (Langrock *et al.* 2012) and the Viterbi algorithm to long-term GPS telemetry data allowed us to identify statistically discernible and biologically interpretable movement modes for Florida panthers, to estimate state-specific movement parameters and to decompose overall variation in movement pattern into differences in probability of occupancy of different movement modes vs. differences in behaviour within modes.

Our analyses revealed that Florida panthers exhibited three distinct movement modes: resting, travelling and moderately active modes. Although it was not possible to make direct behavioural observations at the time GPS locations were obtained, estimates of state-specific movement parameters, diurnal activity patterns and a closer examination of movement trajectories on landscapes offer biological interpretation of behaviours underlying each movement mode. The resting mode was characterized by very short step lengths and near-uniform turning angles; panthers spent the majority of the day in this mode. These results, along with the observation that pumas are least active during the day (Beier, Choate & Barrett 1995; Dickson, Jenness & Beier 2005), indicate that panthers are generally resting in daybeds or otherwise inactive

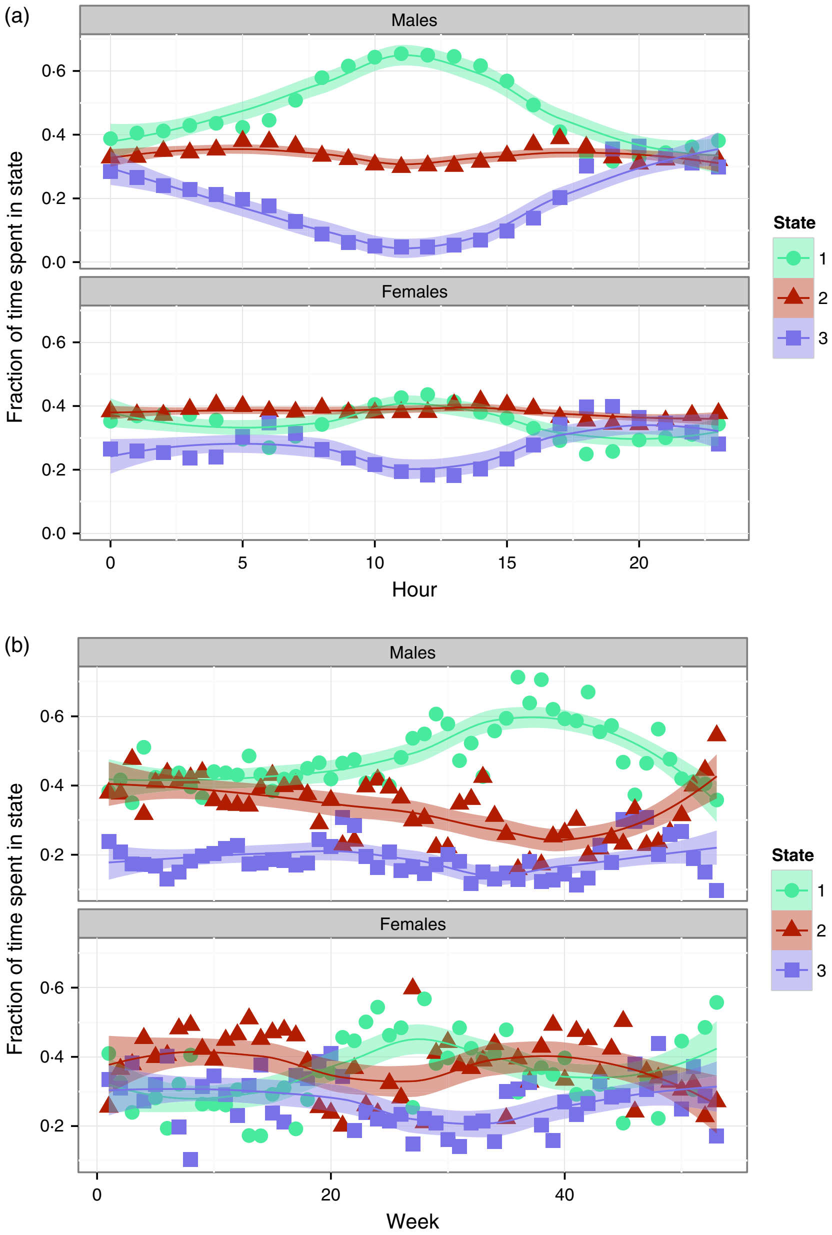

Fig. 4. Amount of time spent in each of the three movement states (a) during every hour over the diel period and (b) during every week of the year with a shaded smoothed mean, for males and females. State 1, 2 and 3 indicate the resting, intermediate and travelling state, respectively.

while in the resting mode. Both travelling and moderately active modes were characterized by long step lengths, but panthers had substantially longer step lengths while in travelling mode, suggesting that panthers are on the move in both of these states but that they travel at higher speeds when in travelling mode versus moderately active mode. Furthermore, panthers travelled in near-straight-line while in travelling state (indicating persistent, directional movement), whereas the moderately active mode was characterized by variable turning angles. These results suggest that Florida panthers exhibit travelling mode while travelling among habitat patches and patrolling home ranges/territories; while in this movement mode, panthers travel efficiently and fast in a straight line. In contrast, panthers exhibit moderately active movement mode during intrapatch movements and/or when searching for prey; although active, panthers in this movement mode travel slower and lack directionality.

Overall, male Florida panthers had substantially longer step lengths than females (Appendix S1). This difference can be due to longer step lengths for males while active, males spending more time in behavioural modes with longer step lengths (i.e. travelling and intermediate modes), or a combination of the two. Interestingly, we found that females actually spent proportionately more time in the travelling mode than males, and even had longer average step lengths than males during some day time hours (Fig. S1a). However, males had substantially longer step lengths than females while in travelling mode especially during the night, leading to significantly longer average hourly step lengths for males. Furthermore, males spent a majority of time (~65%) during the day in resting

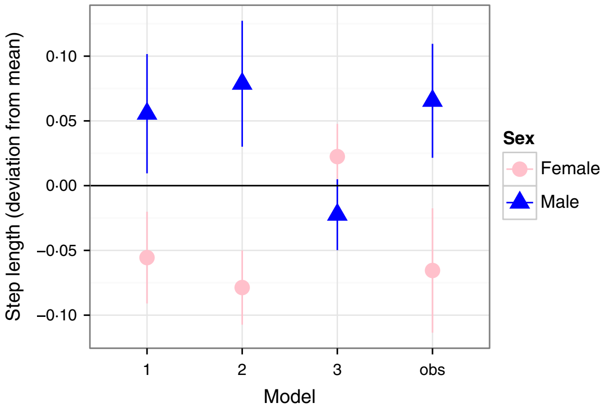

Fig. 5. Step lengths estimated from simulations using different combinations of parameters presented as the mean (± SD) deviation from the observed mean step lengths for male and female Florida panthers. Model 1 = all sex-specific parameters; model 2 = sex-specific step lengths and turning angles only; model 3 = sex-specific transition probability matrices and dwell times only. Also shown are the observed average step lengths for male and female Florida panthers (obs).

mode, whereas females spent approximately equal amounts of time in resting and moderately active modes (~40% each) (Fig. 4). Males spent little or no time in travelling mode around mid-day, whereas females spent ≥20% of time in that state even during the hottest time of the day (Fig. 4). Sex-specific differences in Florida panther movement patterns are a consequence of complex interplays between differences in movement behaviours over a diel period as indicated by variation in diurnal pattern of state occupancy and in state-specific movement parameters.

Only one GPS collared female gave birth during this study; our comparison of female movement patterns based on reproductive status is solely derived from her data set. This female exhibited substantially different movement behaviours depending on her reproductive status. She moved fastest with longer average step lengths when she did not have kittens and moved slowest with shortest average step lengths when she was with older (>2 months) dependent kittens. Her movement parameters (step length and turning angles) in each mode were similar among the reproductive states, but when caring for kittens, she spent 22% more time in resting mode than when she was without kittens, leading to shorter average step lengths. Florida panther kittens generally stay in their natal dens for the first 8 weeks of their lives, during which period movements of their mothers are restricted to areas close to the den. Kittens older than ca. 8 weeks of age can follow their mothers (Hemker, Lindzey & Ackerman 1984; Beier, Choate & Barrett 1995), but their limited mobility may constrain movement speed of their mothers, leading to shorter average step lengths.

Based on age and MSD, we identified one male that was dispersing during our study (Appendix S1). This male had longer average step lengths than resident males, possibly because dispersers must traverse longer distances to look for available territories. Our data were insufficient to tease apart overall differences in movement patterns of dispersing and resident males into state occupancy and movement behaviour within modes.

Multistate HSMM models and the Viterbi algorithm allowed us to identify statistically discernible and biologically interpretable movement modes and to resolve differences in movement patterns more precisely than was previously possible. Although the application of H(S) MMs to study animal movement is not new (Franke, Caelli & Hudson 2004; Franke *et al.* 2006; Patterson *et al.* 2009; Langrock *et al.* 2012), our study is novel because we fit HSMMs with more than two movement states and decompose sex- or reproductive status-specific differences in movement patterns into separate underlying components. While the three-state models are biologically interpretable and statistically defensible, even more complex models are apparently statistically optimal for some Florida panthers with larger data sets. For two (out of 11) males and two (out of three) females, the BIC curves even suggest that the best model is more complex than the most complex (6-state) models that we fitted to

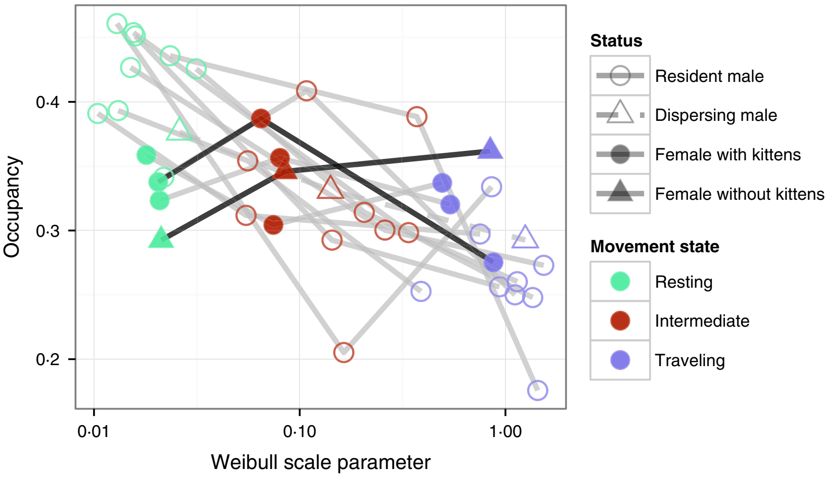

Fig. 6. Weibull scale parameter and state occupancy probability for each of the three movement states for each Florida panther. Females generally spent a smaller proportion of time in resting state than males. Black lines represent trajectories of female 94 split into the periods with and without kittens. The Weibull scale parameter was fairly similar when female 94 was with and without kittens, but the state occupancy differed substantially depending on reproductive status.

the data (Fig. 1). Although these results may suggest that panthers exhibit highly complex movement behaviours (indicated by potentially a large number of movement states), we found it difficult to identify movement states in these more complex models with biologically interpretable behaviours, or to find regular patterns in the parameters across individuals or across models with different numbers of states.

Although H(S)MM and the Viterbi algorithm offer an objective approach to quantifying movement states and permit precise decomposition of differences in movement behaviours, as illustrated by our study, several challenges must be overcome for their potentials to be fully realized. Current implementations of the H(S)MM framework assume strictly diffusive movement. In order to appropriately account for home-ranging behaviours, it may be desirable to incorporate Ornstein–Uhlenbeck-like movement, with drift towards a home range centre, into one or more movement modes (Blackwell 1997; Fryxell *et al.* 2008). Also, current implementations of H(S)MMs assume that both among-state transitions and movement parameters within states are temporally homogeneous and independent of environmental covariates; permitting temporal heterogeneity as a function of biologically meaningful covariates could add more realism. Current implementations of H(S)MM are formulated in terms of discrete, evenly spaced movement steps that create a challenge when handling data that are temporally gappy or collected on multiple time scales. Finally, most GPS telemetry studies provide a large amount of location data for each individual (although not necessarily as much independent *information* as suggested by naïve information-theoretical measures), but the number of individuals tends to be small owing to expense and logistical difficulties. In such cases, treating individuals as random samples from a population with common properties (i.e., using mixed- or hierarchical-modelling techniques) may allow better estimation than fitting each individual's parameters separately as we have done here, although it adds considerable computational complexity (Schliehe-Diecks, Kappeler & Langrock 2012; Bolker *et al.* 2013). While H(S)MM (and state-space models generally) are flexible and can in principle be extended to handle a wide range of biological complexities, addressing the aforementioned complexities represents substantial technical and computational challenges. Even simple approaches to address these limitations tend to be computationally challenging. For example, fitting HSMMs by pooling all panthers, and males and females separately required >300 h of high-performance computer time; however, estimates of parameters did not differ substantially (Appendix S4).

It has long been recognized that movement patterns differ among individuals, depending on their sex, reproductive state, and residency status. However, discerning mechanisms that underlie differences in movement patterns has been challenging. Through a creative use of HSMM and the Viterbi algorithm, we have shown that differences in movement patterns of male and female Florida panthers are a consequence of sex-specific differences in diurnal patterns of state occupancy and sex-specific differences in state-specific movement parameters, whereas that between females with and without dependent kittens are caused solely by variation in state occupancy. Our study is the first, to our knowledge, to decompose differences in movement behaviours into its separate components and to pinpoint whether the differences arise from variations in occupancy or in behaviour within movement modes. Despite technical challenges, multistate HSMMs and the Viterbi algorithm have much to offer; our study provides a comprehensive example of how these tools can be successfully applied to advance the field of movement ecology.

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Data accessibility

Hourly step lengths and turning angles of male and female Florida panthers available at: http://ufdc.ufl.edu//IR00004241/00001.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Descriptive analysis of Florida panther movement.

Appendix S2. Assessment of the fit of 3-state hidden semi-Markov models to Florida panther movement data.

Appendix S3. Movement trajectories for selected Florida panthers with movement state assigned to each move segment based on the Viterbi algorithm.

Appendix S4. Results of 2–6 state hidden semi-Markov models (HSMMs) fitted to pooled data.