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Research article

Incorporating vertical dimensionality improves biological interpretation of hidden Markov model outputs

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Quantifying animal movement is a central component of ecological inquiry. Movement patterns provide insights into how animals make habitat decisions in pursuit of their life-history requirements. Within this context, animals are expected to modulate their movement when navigating landscape complexities like steep or uneven slopes. However, the analytical tendency to predict animal movement as a function of bivariate (x, y) telemetry data (i.e. 2D methods) excludes such complexities and presumes that the landscapes over which this movement occurs are completely flat. Failure to consider vertical dimensionality may inhibit quantification and interpretation of animal behaviors, such as outputs of hidden Markov models (HMMs) built upon geometric measurements of animal movement like step length and turning angle. To explore the analytical consequences of this assumption, we utilized a dataset of GPS collared pumas *Puma concolor* in the Santa Cruz mountains of central California. We fit HMMs using traditional 2D step lengths and turning angles and compared them to HMMs built upon movement geometries in which we incorporated vertical dimensionality (i.e. 2D+). We then used a combination of quantitative inspection of model outputs and visual evaluation in 3D rendering software to understand what new states and biological interpretations can be facilitated by using 2D+ data. We found that 2D+ HMMs outperformed 2D HMMs in their ability to explain variation in vertical dimensionality. Furthermore, 2D+ models were able to isolate distinctive behavioral states associated with vertical dimensionality, such as movements on and off ridgelines. Our results show that 2D+ techniques enable researchers to directly investigate variation in animal movement and behavioral states across complex landscapes. We discuss the implications of our results for future study of animal behavior and energetics as well as illustrate how our methods can be tractably incorporated into HMMs to enable researchers to gain greater insights into animal movement ecology.

Keywords: animal movement, hidden Markov models, *Puma concolor*, spatial dimensionality, state-space modeling, telemetry



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Introduction

The field of movement ecology is centered around quantifying and predicting the complex ways in which animals use their environments to satisfy their life history requirements (Nathan et al. 2008). The mechanisms that underlie such movement decisions depend on intrinsic conditions of the individual animals, as well as the extrinsic biotic and abiotic conditions in the environment (Karasov and Rio 2007, Sibly et al. 2013). Herein, animal movement is representative of dynamic tradeoff decisions that have important implications for survival and reproduction (Hobbs 1989, Benson and Chamberlain 2007, Attum et al. 2013). Consequently, animals are often assumed to make movement decisions that maximize resource intakes while minimizing resource expenditures (Pyke 1984, Fagan et al. 2013). Thus, animals make movement decisions that dynamically consider the availability of resources, prevailing environmental conditions, inter- and intra-species encounters and anthropogenic activity (Kerk et al. 2015, Wilmers et al. 2017, Evans et al. 2020, Montgomery et al. 2020). While animal movement processes are dynamic and complex, so too should be the analytical techniques built and deployed to analyze them (Hebblewhite and Haydon 2010, Montgomery et al. 2010, 2011, Heit et al. 2021).

Coupled growth in remote sensing technologies and quantitative movement modeling has facilitated studies of animal movement ecology at increasingly fine spatio-temporal resolutions (Hazel 2009, Benson 2010). Over time, models fit to describe animal movement have been refined to account for spatial autocorrelation, sample size issues and locational error in telemetry systems (Seaman et al. 1999, Montgomery et al. 2011, Fleming et al. 2014). Despite these efforts, vertical dimensionality remains an important source of bias that, comparatively, has received much less attention in animal movement modeling and home range estimation (Belant et al. 2012, Chandler et al. 2020, Heit et al. 2021). Vertical dimensionality refers to the vertical variation in the physical structure of landscapes (e.g. topography, bathymetry or anthropogenic features; Montgomery et al. 2020). While we may consider the physical space for animal movement to be three-dimensional (3D), for terrestrial animals we prefer to categorize these landscapes as 2D+. We do this because while we can measure an animal's position using three axes (x , y , z), terrestrial animal movement is bound to landscape surfaces via gravity. Without the capability to fly, swim or burrow, terrestrial animal movement is distinct as it takes place not in a volume but on a plane that is bent into the shapes of mountains and valleys (Milne 1997, Tracey et al. 2014). These 2D+ animal movements are important given that navigating landscapes with higher amounts of vertical dimensionality requires greater expenditure of energy in pursuit of resources (Wakelyn 1987, Pe'er et al. 2006, Birn-Jeffery and Higham 2014, Dunford et al. 2020). Vertical dimensionality has also been found to play an important role in mitigating inter- and intra-species interactions, whether they be affiliative, competitive or predatory in nature (Stankowich and

Coss 2007, Farhadinia et al. 2019). Consequently, animal movement models built using only 2D movement data from telemetry tracking may mischaracterize movement behaviors and their subsequent energetic consequences (Jenness 2004, Tracey et al. 2014, Dunford et al. 2020).

Telemetry is a predominate tool used to document animal movement (Cagnacci et al. 2010, Hebblewhite and Haydon 2010). The data returned from telemetry systems typically consist of bivariate coordinate data representing the location of the animal research subject across longitude (x) and latitude (y) dimensions (i.e. 2D). The capability exists for a third dimension: change in elevation (z) to be incorporated, either via altitudinal measurements from telemetry equipment or data extracted from digital elevation models (DEMs) but these data are not often included in the functions used to measure animal movement (McClintock and Michelot 2018, Signer et al. 2019). Hidden Markov models (HMMs) are one tool that has been developed to use telemetry data to quantify animal behavioral states (Patterson et al. 2009, Langrock et al. 2012, McClintock et al. 2014). Herein, states are inferred from geometric measurements of animal movement paths including the distance traveled (step length) and change in bearing (turning angle; Langrock et al. 2012, Zucchini et al. 2017). In this way, an 'encamped' or 'resting' state may be associated with relatively short mean step lengths and unconcentrated turning angles (i.e. undirected movement), while an 'exploratory' or 'transit' state may be inferred from longer step lengths and concentrated turning angles (i.e. more directed movement).

We hypothesized that the nature of these model outputs, however, should be expected to change if the underlying vertical dimensionality is considered. For example, what may look like a short step length in a horizontal direction from a 2D perspective may be representative of a longer energetically-costly climbing movement in reality (Fig. 1). The disparity between 2D and 2D+ steps can also be expected to increase with higher degrees of vertical dimensionality. Thus, climbing and descent movement steps may be consistently underestimated in areas with high vertical dimensionality. We expect, that by using variables in HMMs that capture 2D+ movement, it is possible to distinguish between movement phases occurring in different degrees of vertical dimensionality with different distributions of vertical turning angles, where horizontal movement alone would not have been enough to identify such differences. To test this hypothesis, we fit HMMs to five-minute GPS movement data of pumas *Puma concolor* in California using the traditional 2D approaches and compared the outputs to the 2D+ HMMs in which we directly incorporated vertical dimensionality.

Methods

Hypothesis testing approach

To test our hypothesis that 2D+ HMMs can elucidate complex animal movements and improve the biological

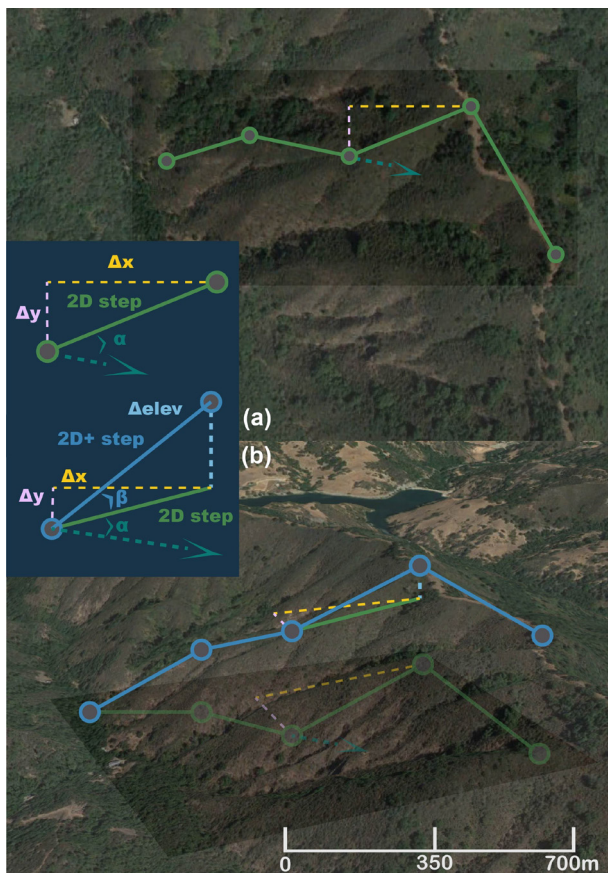


Figure 1. A comparison between two-dimensional (2D) movement geometry and movement geometry that accounts for vertical dimensionality beyond a 2D plane (2D+). Successive 2D movement steps can be calculated as the resultant vector of changes in x and y coordinates (a), while 2D+ movement steps also take changes in elevation resulting from increased vertical dimensionality into account (b). Greek letters alpha and beta represent horizontal and vertical turning angles respectively. Dashed arrow shown in teal represents the trajectory of the previous movement step. Changes in x and y represent changes in latitude and longitude.

interpretation of fitted states we developed a two-phase modeling approach – one to determine how the incorporation of 2D+ data affects the numerical outputs of HMMs, and the second to explore how biological interpretations of HMM states can change between 2D and 2D+ based cases. In the first phase, we fit and compared HMMs based upon 2D and 2D+ cases of our data. The 2D case was based upon the traditional input data of horizontal step length, and horizontal turning angle. The 2D+ case took the 2D case and replaced 2D step length with 2D+ step length, and added the vertical turning angle (Fig. 1). In this phase we were most interested in the effect of including 2D+ variables on the number of states supported by the data. In the second phase, we used linear regression models to determine whether 2D+ states were more significantly associated with variation in vertical dimensionality. Additionally, we used 3D rendering software to visualize fitted states to explore how 2D+ models altered

the biological interpretations of HMMs. We applied this two-phased modeling approach to test our hypothesis using the movement of pumas in California as a case study.

Study area

We positioned our study in a ~1700-km² region of the Santa Cruz Mountains of central California consisting of a diverse matrix of forested patches and open grasslands interspersed among exurban and suburban development between the Pacific Ocean to the west, and the cities of Santa Cruz and San Jose, CA to the south and northeast respectively (Fig. 2). The density of human habitation in the study area ranges from 0 to 1500 buildings km⁻² (Suraci et al. 2020). The forests in the area predominately consist of redwood *Sequoia sempervirens* and Douglas fir *Pseudotsuga menziesii*. Elevation in the study area, characterized by a 3.4 m NASA ASTER digital elevation model (U.S./Japan ASTER Science Team 2020) ranges from sea level to 1155 m with a median terrain ruggedness index (TRI) of 2.57 (range 0–329; Riley et al. 1999; Fig. 2).

Pumas were captured using tracking hounds or cage traps as described in Wilmers et al. (2013). Individual pumas were immobilized using Telazol (Fort Dodge Laboratories) and all capture and handling protocols were approved by the Institutional Animal Care and Use Committee of the University of California – Santa Cruz (Protocol WilmC1612) and the California Department of Fish and Wildlife (Permit SC-11968). We fit each puma with a GPS collar that recorded locations at five-minute time intervals (GPS Plus, Vectronics Aerospace; Suraci et al. 2020).

Multi-dimensional movement path geometry and covariates

To represent vertical dimensionality in our study area we calculated TRI values for each raster cell in the DEM encompassing the extent of our puma dataset. TRI is a function of the sum total of elevation change between raster cells and their eight neighboring cells, giving an index of how complex the landscape terrain is (Riley et al. 1999). We made these calculations using the 'spatialEco' package in R statistical software and then extracted the TRI value for each puma location (Evans and Ram 2015, www.r-project.org).

We prepared two input data streams based on movement path geometry for our 2D HMMs. First, we calculated horizontal step length as the vectoral distance between successive locations, and horizontal turning angle as the horizontal change in bearing between locations. Next, we prepared three input data streams for the 2D+ HMMs. This included the same horizontal turning angle as the 2D models, but additionally we calculated a new 2D+ step length as the distance between successive locations, accounting for changes in elevation indicative of vertical dimensionality for pumas, and a vertical turning angle defined as the vertical change in bearing (Fig. 1). We modeled all step length parameters with a gamma distribution and the angular measures using a von Mises distribution (Zucchini et al. 2017). We calculated these metrics

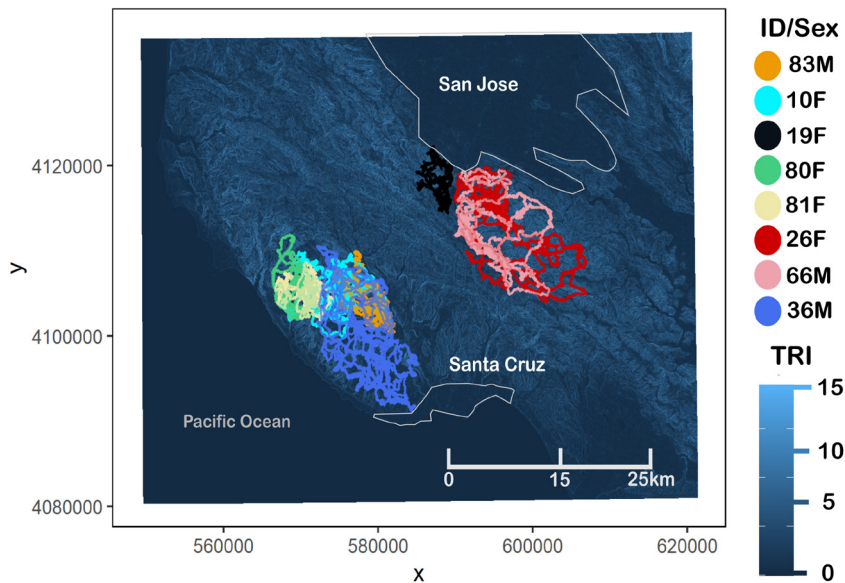


Figure 2. Map of GPS locations from eight collared pumas *Puma concolor* captured and monitored in the Santa Cruz Mountains of California, USA from July 2015 to August 2017. Puma movement occurred between the urban areas of San Jose and Santa Cruz, CA. Colors of locations correspond to different individual pumas. Locations are overlaid on a map of terrain ruggedness index (TRI) values showing a high diversity of vertical dimensionality.

using the 'momentuHMM' package in R (McClintock and Michelot 2018, www.r-project.org).

Hidden Markov models

First, we fit population-level HMMs at two, three, four and five behavioral states for both the 2D and 2D+ data cases, for a total of eight testable models. The choice to use this amount of states was based on prior research on puma movement dynamics we conducted in this system (Dunford et al. 2020). To examine how the fitted behavioral states changed with vertical dimensionality, we included TRI as a spatial covariate on the state transition probabilities in all these models. As 'momentuHMM' uses numerical optimization of the likelihood function to fit the HMMs, the choice of appropriate starting values is imperative (Langrock et al. 2012, Schliehe-Diecks et al. 2012, Pohle et al. 2017). For each of our eight testable models we tested 50 sets of starting values sampled from uniform distributions with bounds chosen based on the empirical distributions of step lengths and turning angles. From these, we retained the model with the lowest negative log-likelihood. We evaluated our models using a combination of Akaike's information criterion (AIC), and model pseudo-residuals (Costa and De Angelis 2010, Schliehe-Diecks et al. 2012), and the distributions showing the relative likelihood of an animal being in a state given values of a spatial covariate, also known as stationary state distributions (Costa and De Angelis 2010, Langrock et al. 2012).

In pursuit of phase two of our hypothesis testing approach, we inspected the stationary state distributions. Next, we used the Viterbi algorithm which uses the fitted models to predict a behavioral state for each puma location and repeated

this process for the eight testable HMMs across both the 2D and 2D+ classes. We then quantified the relationship between the predicted state sequence of each HMM to TRI using an ANOVA. We considered the best-performing and most realistic models to be those with high adjusted R^2 , low standard deviations on state parameters and low AIC values, which has been shown to be a reliable test for HMMs (Costa and De Angelis 2010). Finally, we visually explored random subsets of the predicted state sequences using a 3D rendering of a digital elevation model in QGIS (QGIS Association 2021). This allowed us to verify the distinctions in model output between climbing and non-climbing puma movements

Results

Between 15 May 2015 and 22 August 2017, we GPS-tracked eight adult pumas (four males, four females). In total, there were 151 932 individual GPS locations (range: 14 166–22 434 per individual, μ : 18 991) returned from our telemetry system. Each puma was tracked for between 52 and 79 days per individual animal (μ =66.9, SD =10.6 days, Table 1). We fit a total of eight hierarchical HMMs consisting of two, three, four and five-state models across both the 2D and 2D+ classes (Fig. 3).

HMM parameter estimates (first phase)

In both the 2D and 2D+ cases, the two-state model identified a short-range movement state and a long-range movement state, and the three-state model identified an encamped state (Table 2). In the 2D+ case, we did find variation in vertical

Table 1. Details of pumas *Puma concolor* captured and fixed with GPS collars in the Santa Cruz Mountains of California, USA from July 2015 to August 2017. Identification number, sex, date of first location, date of last location, number of days, number of locations, range of elevation values and mean elevation are given for each individual puma.

ID	Sex	First fix	Last fix	Days	Locations	Elev. range (m)	Mean elev. (m)
80	F	3 Jun 2017	21 Aug 2017	79	22 577	13–614	298
10	F	20 Jul 2016	21 Sep 2016	63	18 084	90–786	346
19	F	15 May 2015	15 Jul 2015	61	17 506	181–785	337
81	F	3 Jun 2017	21 Aug 2017	79	22 312	23–579	341
83	M	3 Jun 2017	21 Aug 2017	79	22 434	13–805	518
26	M	15 May 2015	15 Jul 2015	61	17 402	103–1056	552
66	M	19 Oct 2016	10 Dec 2016	52	14 166	110–1057	479
36	M	15 May 2015	15 Jul 2015	61	17 451	14–804	321

Distributions of 2D and 2D+ input data streams

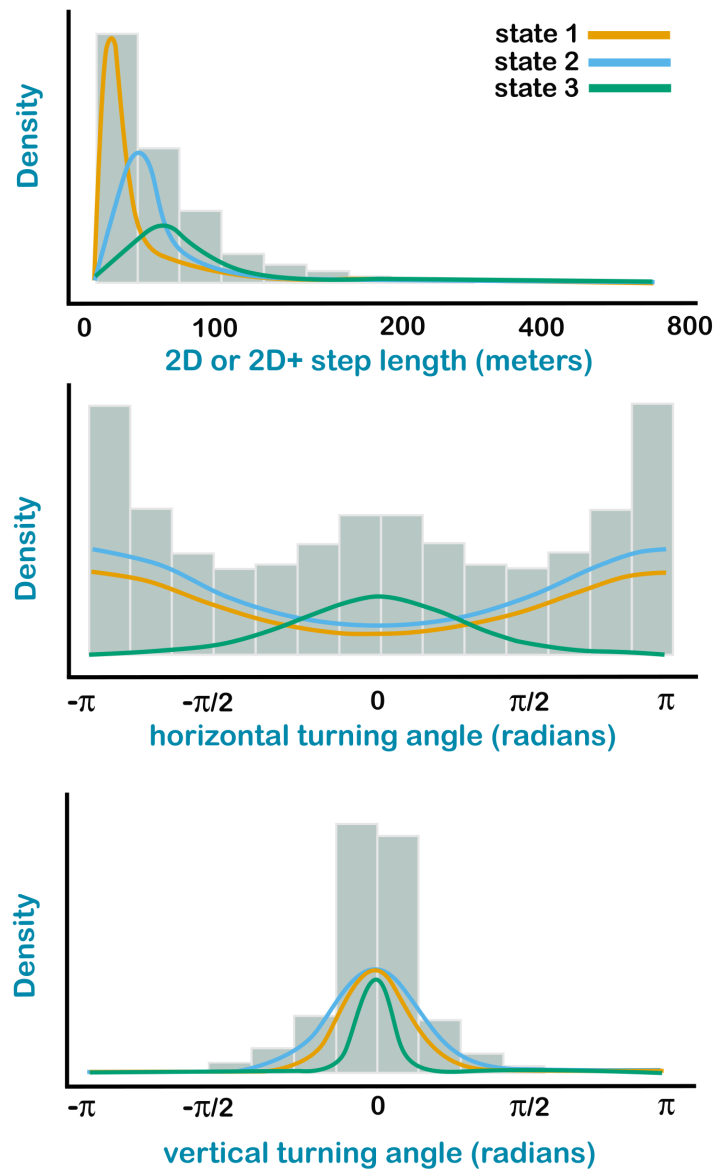


Figure 3. Example distributions of input data streams for hidden Markov models of puma *Puma concolor* the Santa Cruz Mountains of California, USA from July 2015 to August 2017. The first panel (step length) can refer both to both 2D and 2D+ (with vertical dimensionality) step length, though values for 2D+ step length would be higher than 2D step lengths in reality.

Table 2. Parameter estimates from the hidden Markov models of pumas *Puma concolor* tracked in the Santa Cruz Mountains of California, USA from July 2015 to August 2017. Models correspond to one of two cases: two-dimensional data (2D) and data accounting for vertical dimensionality (2D+), as well as differing numbers of fitted states (S). Statistics of fitted parameters that are shown are mean (μ), standard deviation (σ) and angular concentration (κ). Vertical turning angles were modeled with a fixed mean of 0 radians.

Model	State	Step length		Hor. turning angle		Ver. turning angle
2D, S=2	1	$\mu=16.17$	$\sigma=13.48$	$\mu=3.13$	$\kappa=0.67$	–
	2	$\mu=95.97$	$\sigma=59.93$	$\mu=0.00$	$\kappa=1.19$	–
2D+, S=2	1	$\mu=17.88$	$\sigma=14.18$	$\mu=3.13$	$\kappa=0.65$	$\kappa=5.50$
	2	$\mu=102.49$	$\sigma=56.36$	$\mu=0.00$	$\kappa=1.24$	$\kappa=21.91$
2D, S=3	1	$\mu=7.48$	$\sigma=5.21$	$\mu=3.13$	$\kappa=0.60$	–
	2	$\mu=24.59$	$\sigma=16.88$	$\mu=3.13$	$\kappa=0.70$	–
	3	$\mu=103.29$	$\sigma=60.74$	$\mu=0.00$	$\kappa=1.52$	–
2D+, S=3	1	$\mu=8.49$	$\sigma=5.54$	$\mu=3.14$	$\kappa=0.64$	$\kappa=7.46$
	2	$\mu=27.07$	$\sigma=16.59$	$\mu=3.13$	$\kappa=0.62$	$\kappa=4.64$
	3	$\mu=109.27$	$\sigma=56.22$	$\mu=0.00$	$\kappa=1.45$	$\kappa=28.14$
2D, S=4	1	$\mu=5.31$	$\sigma=3.57$	$\mu=3.14$	$\kappa=0.56$	–
	2	$\mu=14.35$	$\sigma=8.73$	$\mu=3.13$	$\kappa=0.68$	–
	3	$\mu=37.00$	$\sigma=24.95$	$\mu=-3.13$	$\kappa=0.58$	–
	4	$\mu=109.59$	$\sigma=61.54$	$\mu=0.00$	$\kappa=1.94$	–
2D+, S=4	1	$\mu=5.75$	$\sigma=3.52$	$\mu=-3.14$	$\kappa=0.60$	$\kappa=8.12$
	2	$\mu=15.37$	$\sigma=8.2$	$\mu=3.13$	$\kappa=0.66$	$\kappa=5.32$
	3	$\mu=40.27$	$\sigma=21.49$	$\mu=-3.13$	$\kappa=0.51$	$\kappa=4.89$
	4	$\mu=115.34$	$\sigma=57.30$	$\mu=0.00$	$\kappa=1.72$	$\kappa=35.83$
2D, S=5	1	$\mu=5.07$	$\sigma=3.40$	$\mu=3.14$	$\kappa=0.56$	–
	2	$\mu=13.03$	$\sigma=7.58$	$\mu=3.12$	$\kappa=0.74$	–
	3	$\mu=39.72$	$\sigma=23.05$	$\mu=3.14$	$\kappa=9.55$	–
	4	$\mu=30.68$	$\sigma=21.67$	$\mu=-0.03$	$\kappa=0.36$	–
	5	$\mu=113.57$	$\sigma=58.07$	$\mu=0.00$	$\kappa=1.82$	–
2D+, S=5	1	$\mu=7.52$	$\sigma=4.53$	$\mu=3.10$	$\kappa=0.465$	$\kappa=3.80$
	2	$\mu=115.69$	$\sigma=56.68$	$\mu=0.00$	$\kappa=1.76$	$\kappa=22.17$
	3	$\mu=11.46$	$\sigma=7.68$	$\mu=-3.12$	$\kappa=0.76$	$\kappa=76.89$
	4	$\mu=27.81$	$\sigma=15.24$	$\mu=3.13$	$\kappa=0.69$	$\kappa=4.09$
	5	$\mu=50.10$	$\sigma=28.85$	$\mu=3.13$	$\kappa=0.23$	$\kappa=292.71$

turning angles between states in both the two- and three-state HMMs, indicating that the long-range movements in both these models were on flatter slopes compared to the short-range movements. Among the four-state HMMs in both the 2D and 2D+ cases, the first two states corresponded to short step lengths and unconcentrated turning angles, but the distributions of each state were overlapping (Table 2). However, the 2D+ model had a larger variation between vertical turning angle concentration among these states, identifying that these states corresponded to similar step distances, but on differing degrees of incline or decline. The three- and four-state HMMs both depicted a short-range movement state and a long-range movement state (Table 2). It was between these states that a pronounced deviation between vertical turning angle concentrations (4.89–39.83) became evident indicating a large difference in the vertical dimensionality of areas in which these behaviors are exhibited. In both the 2D and 2D+ five-state HMMs there were three states associated with moderate-range movements, which had overlapping distributions (Table 2). However, in the 2D+ five-state HMM, the three moderate-range movement states exhibited considerable variation in vertical turning angle (range 4.09–292.71) indicating that the third state corresponded to short range movements on flat slopes, while the fourth state represented short range movements on variable slopes.

Vertical dimensionality (second phase)

The stationary state distributions for each HMM showed that the behavioral states across these models had different relationships with vertical dimensionality. In the two-state model in both cases, the lower activity state was associated with increases in TRI. In the three and four-state models, this changed and variation in TRI was captured by a moderate activity state. However, in the four-state model, moderate activity states were distinct from each other only in their relationship to TRI, as the step length and horizontal turning angle parameters were very similar (Fig. 4). This was supported by a larger variation in vertical turning angle between these states in the 2D+ case. The 2D+ HMMs also had visibly smaller 95% confidence intervals. The five-state HMMs showed the greatest departure between the 2D and 2D+ cases. In the 2D five-state HMM, there were no states clearly associated with increasing TRI values. However, in the five-state 2D+ HMM, the fourth state (in this model a moderate activity state) and its stationary probabilities were positively correlated with TRI values. When we modeled TRI as a function of Viterbi predicted states via an ANOVA model, we found that 2D+ HMMs were better fit as inferred by the AIC and adjusted R^2 values (Table 3). Overall, the ANOVA HMM that explained the most variation in TRI was the 2D+ five-state HMM.

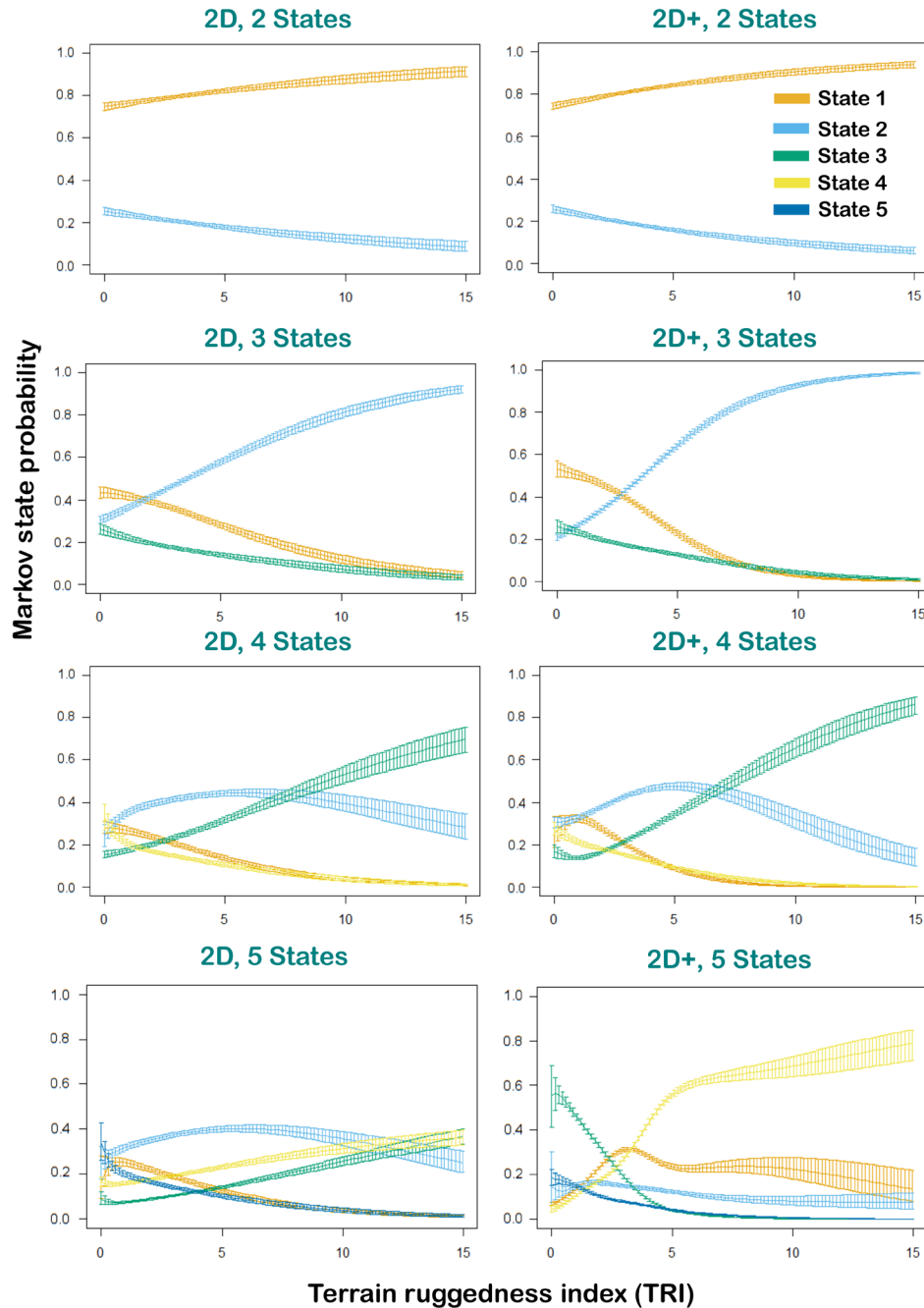


Figure 4. Stationary state probabilities of hidden Markov models of puma *Puma concolor* movement in the Santa Cruz Mountains of California, USA from July 2015 to August 2017. Models correspond to one of two cases: two-dimensional data (2D) and data accounting for vertical dimensionality (2D+), as well as differing numbers of fitted states (S). State probabilities are plotted as a function of terrain ruggedness index (TRI), and vertical bars represent the 95% confidence intervals.

Discussion

In areas with high vertical dimensionality, terrestrial animals, such as pumas, contend with movement decisions with implications for energy expenditure, survival and reproduction (Birn-Jeffery and Higham 2014, Dunford et al. 2020). Thus, the complexity of the landscapes over which these movement decisions occur are fundamental to animal fitness. Our hypothesis that integration of 2D+ HMMs would

facilitate new biological interpretations of these movement decisions was supported. We found that 2D+ HMMs can result in state predictions that include dynamic behaviors such as climbing, descending and navigating complex landscapes that are otherwise obscured by 2D techniques. Via the integration of 2D+ movement into HMMs, we were able to predict behavioral states that more realistically describe puma climbing and descent actions that were missed by conventional 2D HMMs.

Table 3. Results of analysis of variance (ANOVA) models of predicted behavioral states as a function of landscape ruggedness index (TRI). States were obtained from a study of puma *Puma concolor* in the Santa Cruz Mountains of California, USA from July 2015 to August 2017. Models correspond to one of two cases: two-dimensional data (2D) and data accounting for vertical dimensionality (2D+), as well as differing numbers of fitted states (S). For each model, the first state corresponds to the intercept of the model by which other states are compared. Adjusted R² and change in AIC values obtained for the entire model. Change in AIC is calculated from the model with the highest AIC (2D, S=2).

Model	State	β estimate	SE	T statistic	p-value	Adj. R ²	Δ AIC
2D+, S=5	1	3.466	0.009	372.44	< 2e-16	0.2519	0
	2	-0.540	0.015	-36.73	< 2e-16	-	-
	3	-1.576	0.013	-121.82	< 2e-16	-	-
	4	0.851	0.012	71.23	< 2e-16	-	-
	5	-1.311	0.018	-72.12	< 2e-16	-	-
2D, S=5	1	2.654	0.012	224.794	< 2e-16	0.0390	+36 734
	2	0.681	0.014	48.56	< 2e-16	-	-
	3	1.142	0.019	59.72	< 2e-16	-	-
	4	0.852	0.017	50.070	< 2e-16	-	-
	5	0.082	0.017	4.698	2.62e-6	-	-
2D+, S=4	1	2.364	0.011	216.95	< 2e-16	0.0888	+28 913
	2	1.009	0.013	77.20	< 2e-16	-	-
	3	1.598	0.015	108.07	< 2e-16	-	-
	4	0.272	0.017	16.41	< 2e-16	-	-
2D, S=4	1	2.672	0.011	234.78	< 2e-16	0.0409	+36 433
	2	0.666	0.016	49.08	< 2e-16	-	-
	3	1.028	0.015	67.17	< 2e-16	-	-
	4	0.059	0.017	3.49	4.84e-4	-	-
2D+, S=3	1	2.649	0.008	333.71	< 2e-16	0.0849	+29 631
	2	1.147	0.010	108.71	< 2e-16	-	-
	3	0.103	0.014	7.26	4.05e-13	-	-
2D, S=3	1	2.863	0.008	338.97	< 2e-16	0.0357	+37 063
	2	0.718	0.011	65.50	< 2e-16	-	-
	3	-0.043	0.014	-2.987	0.002	-	-
2D+, S=2	1	3.288	0.006	595.52	< 2e-16	0.0076	+41 439
	2	-0.427	0.013	-33.53	< 2e-16	-	-
2D, S=2	1	3.277	0.006	588.69	< 2e-16	0.0053	+41 777
	2	-0.349	0.012	-28.01	< 2e-16	-	-

There are a variety of scenarios in which the 2D+ methods we implemented here would provide valuable insights for practitioners. Pumas, for example, use a variety of strategies to navigate steep slopes, each with their own associated costs and benefits for energy expenditure (Dunford et al. 2020). Depending on the situation, pumas may choose to travel longer distances on flatter slopes rather than shorter distances on steeper slopes (Dunford et al. 2020). Steep movements can be more cost-effective in situations like ambushing prey, where energy is saved by avoiding a lengthy pursuit (Williams et al. 2014, Wang et al. 2015). Differentiating these diverse behaviors has previously been accomplished by using animal-borne accelerometers in combination with direct observation of animal research subjects in captivity. We found that using HMMs and 2D+ movement geometry, the same task can also be accomplished with GPS telemetry data. For instance, the 2D HMMs were not able to make the distinction between longer-distance movements across steep slopes and those along flatter surfaces (i.e. ridgelines) that the 2D+ HMMs could (Fig. 5). In the 2D+ five-state HMM, the state that captured most of the variation in vertical dimensionality (i.e. the climbing state) had longer mean step lengths than the climbing state in the four-state HMM (Table 2). Typically, overlap of standard deviations between

states in 2D HMMs indicates that fewer states are needed to retain biologically reasonable interpretations. In using a 2D+ approach, we found that states with similar less distinguishable step lengths and horizontal turning angles may still be differentiated by vertical turning angles. Upon qualitative inspection, we confirmed that the 2D+ HMMs were capturing entirely distinct behavioral states. For instance, the 2D+ four-state HMM differentiated longer movements on steeper slopes from those on ridgelines (Fig. 5). The 2D+ five-state HMM did not make this distinction. Instead, the climbing state was associated with shorter, more clustered movements in habitat with high vertical dimensionality. Furthermore, the five-state HMM greatly outperformed other HMMs in terms of its ability to predict TRI complexity (Table 3). Together, these results show that 2D+ HMMs could be used to isolate specific types of movement that are of interest to researchers.

Here, we have demonstrated the ability of 2D+ techniques to enhance the biological interpretation of HMM outputs. The next step will be to quantify the corresponding variation in energetic outputs of animals moving over these complex landscapes. Pumas have been found to experience fine-scale energetic costs in movement, which subsequently has implications for their individual animal space use and population-level dynamics (Wang et al. 2017, Dunford et al.

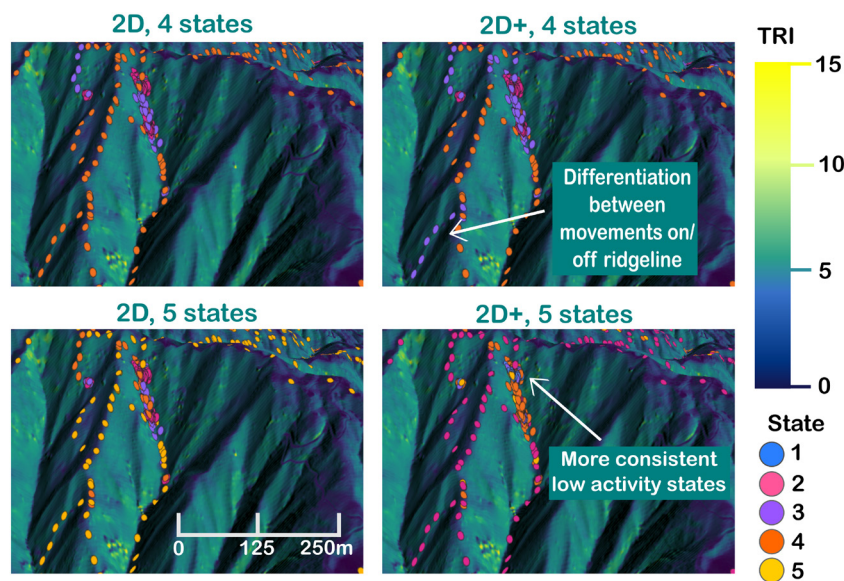


Figure 5. Outputs of the hidden Markov models of puma *Puma concolor* movement in the Santa Cruz Mountains of California, USA from July 2015 to August 2017. Puma locations are color coded by predicted state sequences from four and five state models using two different data types. Two-dimensional (2D) models used horizontal step length and turning angles derived from bivariate telemetry data, and 2D+ models incorporated vertical turning angles and changes in elevation.

2020, Nickel et al. 2021). Studies using HMMs to investigate animal activity and energy budgets would be improved by identifying behavioral states associated with climbing and descent movements. Furthermore, accurately describing animal movement in complex landscapes is increasingly important, as global climate change will necessitate some species to utilize montane areas to escape rising temperatures (Cahill et al. 2014). Anthropogenic sprawl and habitat loss may also push animals into more rugged areas humans cannot as easily develop. Pumas in California, for instance, are predicted to experience a loss of approximately one third of existing habitat on private land by 2030 (Nielsen et al. 2015). If these habitat conversion trends continue, the energetic landscape may make it favorable for pumas to further adapt to more human-dominated landscapes, increasing depredation on domestic animals and negative human–wildlife interactions (Shepard et al. 2013, Wang et al. 2017, Nickel et al. 2021). Thus, the techniques that we describe herein could be very useful to predictive studies seeking to understand the implications of the various futures of animal ecology. Implementing the methods that we outline in this paper is also quite tractable. Fitting a 2D+ HMM requires only the calculation of 2D+ step and vertical turning angle, both of which can be calculated from existing 2D telemetry data with not more than a few lines of R code. We calculated our 2D+ movement data using straightforward trigonometry and elevation values derived from DEMs, which are globally available at a variety of resolutions. The greatest limiting factors to fitting 2D+ HMMs are the availability of fine-scale GPS telemetry data and computational overhead of using more than two input data streams in movement models. However, these issues are readily being alleviated as telemetry systems

have greater temporal resolutions and high-performance computing options are reducing convergence times.

In evaluating the capacity of 2D and 2D+ HMMs to accurately identify behavioral states, we used a relatively simple application of a hidden Markov modeling approach. We have shown how these techniques can be effectively deployed to gain new insights into the movement ecology of pumas. However, these results can also be readily applied to other movement models, as well as to other species. The conceptual bias related to vertical dimensionality is not limited to HMMs, as other studies have shown that vertical dimensionality is influential in estimations of home range size, predatory behavior, prey escape behavior and migration (Kie et al. 2005, Stankowich and Coss 2007, Farhadinia et al. 2019, Heit et al. 2021). Furthermore, with respect to other species, we are not just describing impacts on large mammals inhabiting complex landscapes. Rather, the effects of vertical dimensionality can change with the spatial scale at which that complexity is mapped and also according the temporal scale or fix rate of movement data (Levin 1992, Fleming et al. 2014). As coarser fix rates would aggregate animal behavior to a larger spatial extent, it would not make sense to then model behavior as a function of fine-scale spatial data. Thus, future studies may be able to provide guidance on matching spatial scale of landscape data to the temporal scale of movement locations. Our study provides the basis with which to further explore the incorporation of 2D+ data into HMMs, the most valuable of which would be to use simulated movement data in place of real telemetry locations to evaluate expected versus observed behavioral states.

Animals, and perhaps particularly those that reside in complex landscapes, are expected to make movement decisions

that maximize resource intake and minimize energy expenditure (Pyke 1984, Hobbs 1989). The patterns that arise from these decisions are of key interest to a variety of fields of study. Via a quantitative analysis, 2D+ modeling can account for the increased distances incurred from vertical dimensionality and allows for differentiation between climbing and non-climbing movements. The effects of vertical dimensionality on HMMs depend on a variety of factors including number of fitted states, and likely vary with temporal resolution, and degree of vertical dimensionality across a landscape. Importantly, 2D and 2D+ methods were similar for small numbers of behavioral states, indicating that uses of HMMs for reasons other than understanding energetics are likely unaffected by 2D methods. However, our results provide an example for how vertical dimensionality influences animal movement behavior and reveal exciting new avenues for understanding the dynamics of vertical dimensionality and animal movement in the future.

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Ethics statement – Pumas were captured using tracking hounds or cage traps as described in Wilmers et al. (2013). Individual pumas were immobilized using Telazol (Fort Dodge Laboratories) and all capture and handling protocols were approved by the Institutional Animal Care and Use Committee of the University of California – Santa Cruz (Protocol WilmC1612) and the California Department of Fish and Wildlife (Permit SC-11968). We fit each puma with a GPS collar that recorded locations at five-minute time intervals (GPS Plus, Vectronics Aerospace; Suraci et al. 2020).

Author contributions

David R. Heit: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (equal); Software (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Christopher C. Wilmers:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Software (equal). **Waldemar Ortiz-Calo:** Conceptualization (equal); Writing – review and editing (equal). **Robert A. Montgomery:** Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Supervision (lead); Writing – review and editing (equal).

Data availability statement

The R code for this article are available in the Supporting Information. Raw data are available upon request due to the sensitivity of the subject species.

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Attum, O., Cutshall, C. D., Eberly, K., Day, H. and Tietjen, B. 2013. Is there really no place like home? Movement, site fidelity and survival probability of translocated and resident turtles. – *Biodivers. Conserv.* 22: 3185–3195.
- Belant, J. L., Millsbaugh, J. J., Martin, J. A. and Gitzen, R. A. 2012. Multi-dimensional space use: the final frontier. – *Front. Ecol. Environ.* 10: 11–12.
- Benson, E. 2010. *Wired Wilderness: technologies of tracking and the making of modern wildlife.* – JHU Press.
- Benson, J. F. and Chamberlain, M. J. 2007. Space use, survival, movements and reproduction of reintroduced Louisiana black bears. – *J. Wildl. Manage.* 71: 2393–2403.
- Birn-Jeffery, A. V. and Higham, T. E. 2014. The scaling of uphill and downhill locomotion in legged animals. – *Integr. Comp. Biol.* 54: 1159–1172.
- Cagnacci, F., Boitani, L., Powell, R. A. and Boyce, M. S. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. – *Phil. Trans. R. Soc. B* 365: 2157–2162.
- Cahill, A. E., Aiello-Lammens, M. E., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C. J., Ryu, H. Y., Sbeglia, G. C., Spagnolo, E., Waldron, J. B. and Wiens, J. J. 2014. Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. – *J. Biogeogr.* 41: 429–442.
- Chandler, C. J., Van Helden, B. E., Close, P. G. and Speldewinde, P. C. 2020. 2D or not 2D? Three-dimensional home range analysis better represents space use by an arboreal mammal. – *Acta Oecol.* 105: 103576.
- Costa, M. and De Angelis, L. 2010. Model selection in hidden Markov models: a simulation study. – *Alma Mater Stud. Univ. Bologna*, p. 15.
- Dunford, C. E., Marks, N. J., Wilmers, C. C., Bryce, C. M., Nickel, B., Wolfe, L. L., Scantlebury, D. M. and Williams, T. M. 2020. Surviving in steep terrain: a lab-to-field assessment of locomotor costs for wild mountain lions *Puma concolor*. – *Mov. Ecol.* 8: 34.
- Evans, J. S. and Ram, K. 2015. Package ‘spatialEco.’ – R package. <https://cran.r-project.org/web/packages/spatialEco/spatialEco.pdf>
- Evans, L. J., Goossens, B., Davies, A. B., Reynolds, G. and Asner, G. P. 2020. Natural and anthropogenic drivers of Bornean elephant movement strategies. – *Global Ecol. Conserv.* 22: e00906.
- Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U. E., Tang, W., Papastamatiou, Y. P., Forester, J. and Mueller, T. 2013. Spatial memory and animal movement. – *Ecol. Lett.* 16: 1316–1329.
- Farhadinia, M. S., Heit, D. R., Montgomery, R. A., Johnson, P. J., Hobeali, K., Hunter, L. T. B. and Macdonald, D. W. 2019. Vertical relief facilitates spatial segregation of a high density large carnivore population. – *Oikos* 129: 346–355.
- Fleming, C. H., Calabrese, J. M., Mueller, T., Olson, K. A., Leimgruber, P. and Fagan, W. F. 2014. From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatiotemporal scales. – *Am. Nat.* 183: E154–E167.
- Hazel, J. 2009. Evaluation of fast-acquisition GPS in stationary tests and fine-scale tracking of green turtles. – *J. Exp. Mar. Biol. Ecol.* 374: 58–68.
- Hebblewhite, M. and Haydon, D. T. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. – *Phil. Trans. R. Soc. B* 365: 2303–2312.
- Heit, D. R., Ortiz-Calo, W. and Montgomery, R. A. 2021. Landscape complexity persists as a critical source of bias in terrestrial animal home range estimation. – *Ecology* 102: e03427.

- Hobbs, N. T. 1989 Linking energy balance to survival in mule deer: development and test of a simulation model. – *Wildl. Monogr.* 101: 3–39.
- Jenness, J. S. 2004. Calculating landscape surface area from digital elevation models. – *Wildl. Soc. Bull.* 32: 829–839.
- Karasov, W. H. and Rio, C. M. del 2007. *Physiological ecology: how animals process energy, nutrients and toxins.* – Princeton Univ. Press.
- Kerk, M. van de, Onorato, D. P., Criffield, M. A., Bolker, B. M., Augustine, B. C., McKinley, S. A. and Oli, M. K. 2015. Hidden semi-Markov models reveal multiphasic movement of the endangered Florida panther. – *J. Anim. Ecol.* 84: 576–585.
- Kie, J. G., Ager, A. A. and Bowyer, R. T. 2005. Landscape-level movements of North American elk *Cervus elaphus*: effects of habitat patch structure and topography. – *Landscape Ecol.* 20: 289–300.
- 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.
- Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. – *Ecology* 73: 1943–1967.
- McClintock, B. T. and Michelot, T. 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. – *Methods Ecol. Evol.* 9: 1518–1530.
- McClintock, B. T., Johnson, D. S., Hooten, M. B., Ver Hoef, J. M. and Morales, J. M. 2014. When to be discrete: the importance of time formulation in understanding animal movement. – *Mov. Ecol.* 2: 21.
- Milne, B. T. 1997. Applications of fractal geometry in wildlife biology. – In: Bissonette, J. A. (ed.), *Wildlife and landscape ecology.* Springer, pp. 32–69.
- Montgomery, R. A., Roloff, G. J., Hoef, J. M. V. and Millsaugh, J. J. 2010. Can we accurately characterize wildlife resource use when telemetry data are imprecise? – *J. Wildl. Manage.* 74: 1917–1925.
- Montgomery, R. A., Roloff, G. J. and Hoef, J. M. V. 2011. Implications of ignoring telemetry error on inference in wildlife resource use models. – *J. Wildl. Manage.* 75: 702–708.
- Montgomery, R. A., Heit, D. R. and Ortiz-Calo, W. 2020. Integrating the multi-domain and multi-dimensional nature of animal movement into ecological modelling. – *Ecol. Model.* 436: 109220.
- 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. – *Proc. Natl Acad. Sci. USA* 105: 19052–19059.
- Nickel, B. A., Suraci, J. P., Nisi, A. C. and Wilmers, C. C. 2021. Energetics and fear of humans constrain the spatial ecology of pumas. – *Proc. Natl Acad. Sci. USA* 118: e2004592118.
- Nielsen, C., Thompson, D., Kelly, M. and Lopez-Gonzalez, C. 2015. *Puma concolor.* The IUCN red list of threatened species. <https://www.iucnredlist.org>.
- 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. – *J. Anim. Ecol.* 78: 1113–1123.
- Pe'er, G., Heinz, S. K. and Frank, K. 2006. Connectivity in heterogeneous landscapes: analyzing the effect of topography. – *Landscape Ecol.* 21: 47–61.
- 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. – *J. Agric. Biol. Environ. Stat.* 22: 270–293.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. – *Annu. Rev. Ecol. Syst.* 15: 523–575.
- QGIS Association 2021. QGIS Geographic Information System. <http://www.qgis.org>.
- Riley, S. J., DeGloria, S. D. and Elliot, R. 1999. Index that quantifies topographic heterogeneity. – *Int. J. Sci.* 5: 23–27.
- 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.
- Seaman, D. E., Millsaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. and Gitzen, R. A. 1999. Effects of sample size on kernel home range estimates. – *J. Wildl. Manage.* 63: 739–747.
- Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A. and Vosper, S. B. 2013. Energy landscapes shape animal movement ecology. – *Am. Nat.* 182: 298–312.
- Sibly, R. M., Grimm, V., Martin, B. T., Johnston, A. S. A., Kułakowska, K., Topping, C. J., Calow, P., Nabe-Nielsen, J., Thorbek, P. and DeAngelis, D. L. 2013. Representing the acquisition and use of energy by individuals in agent-based models of animal populations. – *Methods Ecol. Evol.* 4: 151–161.
- Signer, J., Fieberg, J. and Avgar, T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. – *Ecol. Evol.* 9: 880–890.
- Stankowich, T. and Coss, R. G. 2007. Effects of risk assessment, predator behavior and habitat on escape behavior in Columbian black-tailed deer. – *Behav. Ecol.* 18: 358–367.
- Suraci, J. P., Nickel, B. A. and Wilmers, C. C. 2020. Fine-scale movement decisions by a large carnivore inform conservation planning in human-dominated landscapes. – *Landscape Ecol.* 35: 1635–1649.
- Tracey, J. A., Sheppard, J., Zhu, J., Wei, F., Swaisgood, R. R. and Fisher, R. N. 2014. Movement-based estimation and visualization of space use in 3D for wildlife ecology and conservation. – *PLoS One* 9: e101205.
- U.S./Japan ASTER Science Team, A. S. 2020. ASTER DEM Product. <https://doi.org/10.5067/ASTER/ASTGTM.003>.
- Wakelyn, L. A. 1987. Changing habitat conditions on bighorn sheep ranges in Colorado. – *J. Wildl. Manage.* 51: 904–912.
- Wang, Y., Nickel, B., Rutishauser, M., Bryce, C. M., Williams, T. M., Elkaim, G. and Wilmers, C. C. 2015. Movement, resting and attack behaviors of wild pumas are revealed by tri-axial accelerometer measurements. – *Mov. Ecol.* 3: 2.
- Wang, Y., Smith, J. A. and Wilmers, C. C. 2017. Residential development alters behavior, movement and energetics in an apex predator, the puma. – *PLoS One* 12: e0184687.
- Williams, T. M., Wolfe, L., Davis, T., Kendall, T., Richter, B., Wang, Y., Bryce, C., Elkaim, G. H. and Wilmers, C. C. 2014. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. – *Science* 346: 81–85.
- Wilmers, C. C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M. L., Kermish-Wells, J., Yovovich, V. and Williams, T. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. – *PLoS One* 8: e60590.
- Wilmers, C. C., Isbell, L. A., Suraci, J. P. and Williams, T. M. 2017. Energetics-informed behavioral states reveal the drive to kill in African leopards. – *Ecosphere* 8: e01850.
- Zucchini, W., MacDonald, I. L. and Langrock, R. 2017. *Hidden Markov models for time series: an introduction using R*, 2nd edn. – CRC Press.