Ecological Processes

A hierarchical path-segmentation movement ecology framework

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Abstract

This paper lays out a hierarchical, appropriate-complexity framework for conceptualizing movement-path segments at different spatiotemporal scales in a way that facilitates comparative analyses and bridges behavior and mathematical concepts. It then outlines a process for generating a multimode, multiscale stochastic simulation model that can be used to test animal movement hypotheses and make predictions of movement responses to management and global change. Many methods for analyzing movement data begin by generating step-length (SL) and turning-angle (TA) distributions from relocation time-series data, some of which are linked to ecological, landscape, and environmental covariates. The frequency at which these data are collected may vary from sub-seconds to several hours. The kinds of questions that may be asked of these data, however, are very much scale dependent. The hierarchical path-segmentation (HPS) framework presented here clarifies how the scale at which SL and TA data are collected relates to other sub- and super-diel scales. Difficulties arise because the information contained in SL and TA time series are often not directly relatable to the physiological, ecological, and sociological factors that drive the structure of movement paths at longer scales. These difficulties are overcome by anchoring the classification of movement types around the concept of fixed-period (24 h) diel activity routines and providing a bridge between behavioral/ecological and stochastic-walk concepts (means, variances, correlations, individual-state and local environmental covariates). This bridge is achieved through the generation of relatively short segments conceived as characteristic sequences of fundamental movement elements. These short segments are then used to characterize longer canonical-activity-mode segments that emerge through movement at behaviorally relevant sub-diel scales. HPS thus provides a novel system for integrating sub-minute movement sequences into canonical activity modes (CAMs) that, in turn, can be strung together into various types of diel activity routines (DARs). These DARs both vary among individuals within a given day, and for any given individual across time and under the influence of landscape factors. An understanding of how DARs are influenced by environmental inputs will help us predict the response of supra-diel lifetime movement phases (LiMPs) of individuals, as well as their complete lifetime tracks (LiTs), to anthropogenically induced global change.

Keywords: Hierarchical path segmentation (HPS), Fundamental movement elements (FuMEs), Canonical activity modes (CAMs), Diel activity routines (DARs), Life-history movement phases (LiMPS), Multi-CAM metaFuME Markov (M-cubed) models, Biased correlated random walk models

Introduction

A recent paper by Nathan and 36 others in the journal Science (Nathan et al. 2022) discusses how big-data approaches lead to an increased understanding of the ecology of animal movement. In particular, Nathan et al. point out how the introduction of the four-component movement ecology framework (1. internal state;
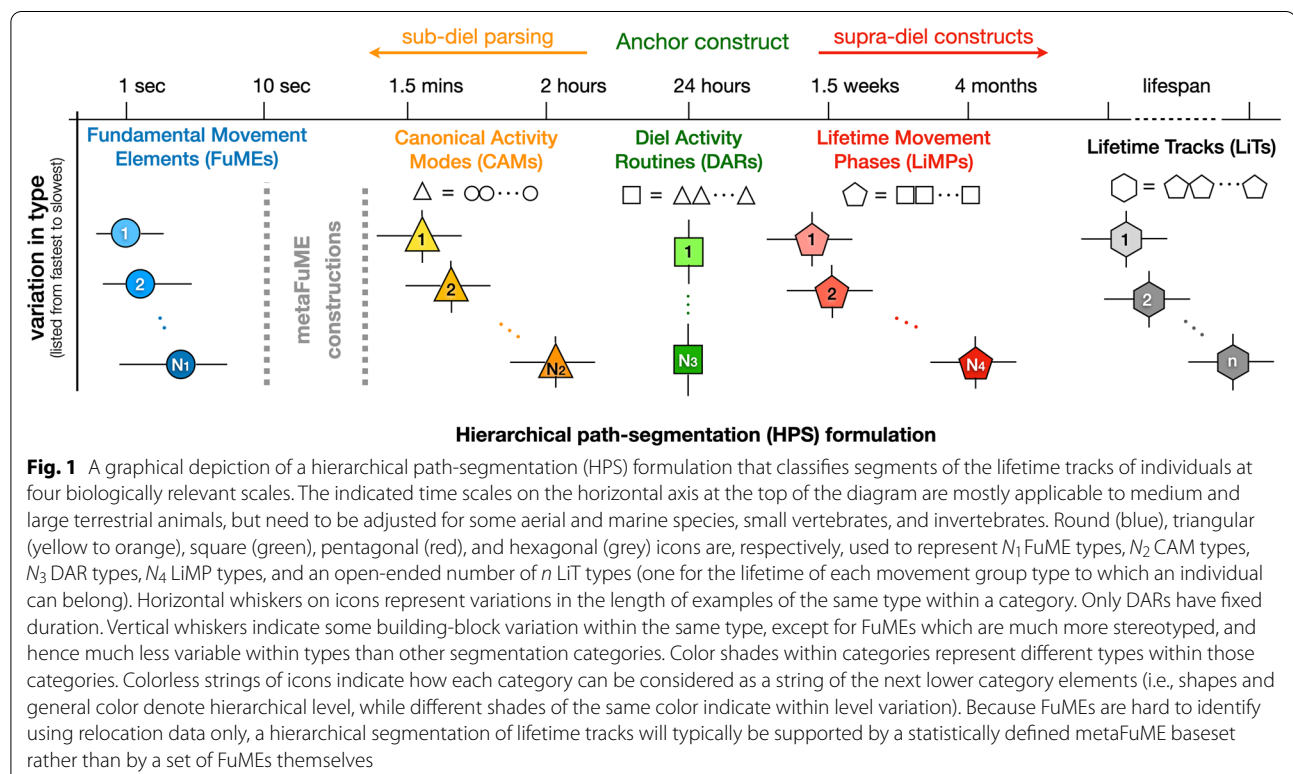
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2. motion capacity; 3. navigation capacity; and 4. external factors), together with the rapid development of new technologies and data processing tools for analyzing these movement paths (Joo et al. 2020; Williams et al. 2020), has led to a recent major upsurge in movement ecology research. One of the important points made by Nathan et al. (2022), in their section on *Patterns and mechanisms across spatiotemporal scales*, is that quantifying how movement patterns and drivers change across scales remains one of the major challenges in movement ecology. Meeting this challenge requires that we develop a hierarchical framework to link discussions of movement processes across different behavioral scales of analysis. In this paper, we propose such a hierarchical path-segmentation (HPS) framework, using the concept of the diel activity routine (DAR) to provide a behavioral anchor to the segmentation of lifetime tracks. Such segmentation, as Nathan et al. (2022) point out, is an important goal "for elucidating how behavior, cognition, and physiology develop across spatial and temporal scales and in relation to environmental changes."

In proposing a hierarchical path-segmentation (HPS) framework for conceptualizing movement behavior across spatiotemporal scales, it is desirable from both computational and behavioral points of view to identify an anchoring scale that is of fixed duration. The 24-h diel time scale provides the only such naturally occurring

anchor (Fig. 1): all others (see Glossary for the definition of acronyms and an explanation of terms)—whether the subdiel canonical activity modes (CAMs) viewed as sequences of fundamental movement elements (FuMEs), or supradiel lifetime movement phases (LiMPs) that can be aligned sequentially to produce the lifetime tracks (LiTs) of individuals—have variable durations of occurrence (Fig. 1). For definiteness, we refer to repeated 24-h movement path segments as diel activity routines (DARs), although the time of day at which these segments begin and end needs to be selected. The most appropriate start/finish times for DARs may vary among species, depending on their behavioral routines. For example, in the case of the black rhino 6 am turns out to be a better start/finish point than noon, 6 pm or midnight from the point of view of reduced variation in spatial displacements over 24-h periods. Such displacements were found to frequently be smaller at dawn than at dusk or at their midday and midnight resting periods (Seidel et al. 2019).

Elaborating on the issue of variable durations for movement path segmentation, at sub-DAR scales (Fig. 1), the length of time that individuals are involved in different canonical activity modes (CAMs) (Getz and Saltz 2008; e.g., periods of rest, feeding/foraging, heading towards a target location some distance away from the current location) is likely be quite variable, with CAM duration depending on environmental factors, motivation

Hierarchical path-segmentation (HPS) formulation

Fig. 1 A graphical depiction of a hierarchical path-segmentation (HPS) formulation that classifies segments of the lifetime tracks of individuals at four biologically relevant scales. The indicated time scales on the horizontal axis at the top of the diagram are mostly applicable to medium and large terrestrial animals, but need to be adjusted for some aerial and marine species, small vertebrates, and invertebrates. Round (blue), triangular (yellow to orange), square (green), pentagonal (red), and hexagonal (grey) icons are, respectively, used to represent N_1 FuME types, N_2 CAM types, N_3 DAR types, N_4 LiMP types, and an open-ended number of n LiT types (one for the lifetime of each movement group type to which an individual can belong). Horizontal whiskers on icons represent variations in the length of examples of the same type within a category. Only DARs have fixed duration. Vertical whiskers indicate some building-block variation within the same type, except for FuMEs which are much more stereotyped, and hence much less variable within types than other segmentation categories. Color shades within categories represent different types within those categories. Colorless strings of icons indicate how each category can be considered as a string of the next lower category elements (i.e., shapes and general color denote hierarchical level, while different shades of the same color indicate within level variation). Because FuMEs are hard to identify using relocation data only, a hierarchical segmentation of lifetime tracks will typically be supported by a statistically defined metaFuME baseset rather than by a set of FuMEs themselves

and physiological states. How far we can drill down to scales finer than the CAMs, depends on the frequency at which the relocation data are collected. At high enough frequencies one can identify the mechanically produced set of fundamental movement elements (FuMEs characterized by single-step sequences involved in walking, running, slithering, undulating in water, flapping wings, etc.), although other kinds of data, such as accelerometer data from multiple points on the body of an individual, may be needed to decide when a particular type of movement step begins and ends. When frequencies are not sufficiently high or appropriate data are not available to decide when a particular FuME begins and ends, statistical quantities—which I refer to as metaFuMEs—can be defined. The construction of metaFuMEs is discussed more fully in the next section (also see Luisa Vissat et al. 2022), where we will see that metaFuMEs provide a basis for constructing all track segments (as portrayed in Figs. 2 and 3; much as nucleic acids are the basis for coding strings of DNA).

At supra-DAR scales (Fig. 1), different lifetime movement phases (LiMPs) consisting of multiple diel activity periods (such as summer versus winter range activities, as well as migrations among such ranges) are also likely to be of variable duration, depending on the severity of winters, mildness of summers, the variation in annual rainfall and temperature conditions, as well as the intensity of competition for resources and pressure from predators and natural enemies (Elith et al. 2010). Ideally, if a relocation data set is available from an individual's birth until its death, than its lifetime track (LiT), which will also vary among individuals of the same species, can be parsed into a sequence of LiMPs, each of variable duration. These LiMPs, in turn, are composed of sequences of DARs of different types, with different LiMPs being

characterized by the frequencies and ordering of their composite DARs.

An example of how an HPS approach provides a link between movement path relocation data and behavioral narratives is provided in Luisa Vissat et al. (2022), where DAR segments were extracted from a population of 44 barn owls (*Tyto alba*), each tracked on average for periods close to half a year. This study identified 7 different types of DARs and analyzed how these different among individuals by gender, age, season and location. The study also identified idiosyncratic behaviors that depended on the particulars of specific family groups. The insights that were obtained in this study could not have emerged without hierarchical path segmentation and the categorization of segments a particular scale—in this case the DAR scale—into several different types.

It is worth stressing that the HPS framework proposed in this paper provides a set of concepts not used in current statistical methods for developing narratives based on comparative analyses of how individual movement within and across species differ: current methods either ignore spatiotemporal scaling or do not emphasize behavioral differences across scales. I also outline how this framework can be used to generate complex random walks (hierarchical, multimodal, biased, correlated; see Morales et al. 2004; Bartumeus et al. 2005; Johnson et al. 2002; Codling et al. 2008; Ahearn et al. 2017; Getz et al. 2020) that span all the hierarchical segmentation levels appropriate for comparison with a particular relocation time series. More specifically, in this paper, the question is addressed of how we may reconcile the fact that the step length (SL) and turning angle (TA) distributions extracted (Kareiva and Shigesada 1983; Turchin 1998) directly from the relocation times series are not directly interpretable in terms of behavioral and ecological
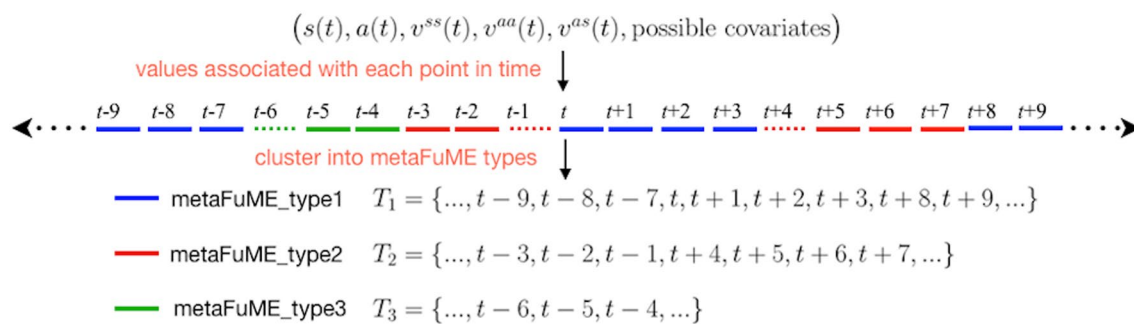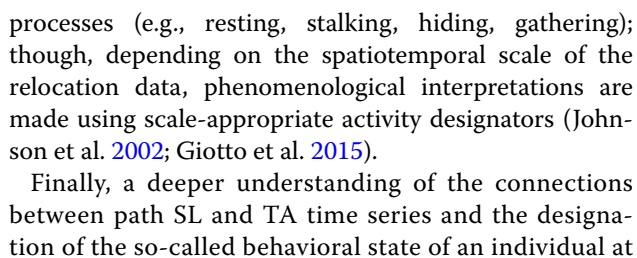

Fig. 2 Parsing the walk *W* into a set of metaFuMEs. Associated with each point *t* is a set of running values $(s(t), a(t), v^{ss}(t), v^{aa}(t), v^{as}(t), \text{other possible covariates})$. Cluster analysis may be used to generate metaFuME categories. For purposes of illustration, we depict three types of metaFuMEs with associated lists of time steps—i.e., metaFuME sequence index sets—that can then be used to define the ensemble of values associated with each metaFuME type: blue $= T_1$, red $= T_2$, and green $= T_3$. Note that we expect transition points between strings of metaFuMEs of one type (broken line segments), such as $t - 6$, $t - 1$ and $t + 4$, could well be outliers in the clustering process. Outliers may be assigned to the cluster to which they are closest in some suitably defined sense (as indicated by the colors of the broken lines)

Fig. 3 The segment structure of movement paths at different scales according to the scheme proposed in Fig. 1. **A** A multi-season lifetime track (LiT) *W* (Eq. 1) can be segmented into different types of lifetime movement phases (LiMPs), each of which can then be segmented into diel activity routines (DARs) and again segmented into canonical activity modes (CAMs). Each CAM is constructed from different proportions of metaFuMEs (aggregates of correlated fundamental movement elements), where each metaFuME is derived from a bivariate step-length/turning-angle distribution derived from time series with specific first-order correlative statistics. Short-duration CAMs (e.g., CAM 3) can easily be missed and averaged into longer duration CAMs (e.g., CAMs 1 and 2), if DAR segmentation analyses are not undertaken at a sufficiently fine scale. **B** An illustrative example of a simple two-CAM *return-to-home-with-a-water-stop* DAR where the two types of metaFuMEs that generate the *traveling* CAM are shown under magnification

processes (e.g., resting, stalking, hiding, gathering); though, depending on the spatiotemporal scale of the relocation data, phenomenological interpretations are made using scale-appropriate activity designators (Johnson et al. 2002; Giotto et al. 2015).

Finally, a deeper understanding of the connections between path SL and TA time series and the designation of the so-called behavioral state of an individual at each of its relocation points requires that we find a way to reconcile narratives constructed using two different kinds of vocabularies. The first is the language of biological designators arising from behavioral and ecological concepts. Our primary tools here are the application of path segmentation methods (Nams 2014; Edelhoff et al. 2016; Seidel et al. 2018) that include hidden Markov models (HMMs; Michelot et al. 2016;

Franke et al. 2004; Langrock et al. 2012; Zucchini et al. 2016) and behavioral change-point analyses (BCPA; Gurarie et al. 2009, 2016; Owen-Smith and Martin 2015). The second is the language of mathematical stochastic walks (Kareiva and Shigesada 1983; Bartumeus et al. 2005; Patterson et al. 2008) that makes no attempt to associate biological concepts with points or segments of the relocation data time series, but uses purely statistical methods to assign best-fitting model parameter values (Chatfield 2016) to movement paths, with the possible inclusion of individual and environmental covariates (Jonsen et al. 2003; Preisler et al. 2004; Johnson et al. 2008; Fleming et al. 2014; Calabrese et al. 2016).

A pragmatic view of HPS

The view that large segments of individual movement paths can be parsed into strings of fundamental movement elements (FuMEs—see glossary; Fig. 1, Table 1) with characteristic frequencies and patterns of occurrence is highly idealized. Identifying FuMES is generally a biomechanical problem that is beyond the scope and capabilities of analyses based on relocation data alone. Other kinds of data, such as audio recordings, have been used to identify FuMEs: e.g., wing flaps of small birds (Sapir et al. 2010; Northrup et al. 2019) or footfalls of foraging ungulates (Northrup et al. 2019). If the frequency of our relocation data, however, spans strings of around 10–100 FuMEs, occurring either repetitively or in correlated groups of a couple of FuME types, then we may be

Table 1 Hierarchical organization of a typical vertebrate lifetime track (LiT)

Scale/segment	Time	Space	Categories	Data	Some approaches and methods
	Constraint level: type of analysis				
FuMEs[*]	0.1–few secs	0–1000 cm	Stride, trot, run, twist, jump, flap	Accelerometer video	Machine learning[*†], Newtonian mechanics
	Highly constrained: biomechanical analyses				
Meta- FuMEs[*]	Resolution of relocation data[*‡]	Average step length	Bivariate SL and TA distributions	SL and TA means, variances and correlations[††]	Cluster analysis ensemble filtering
	Base level: movement ecology analyses				
Short duration CAMs[†]	0.1–10 min	A few meters to a few kms	Resting, browsing, riding thermals	secs to mins,	Path segmentation[**]
	Highly flexible: sub-hourly/hourly analysis			metaFuMEs and covariate data	
Long duration CAMs[†]	10–100 min	A few meters to many kms	Feeding traveling	mins to hours,	
	Highly flexible: sub-diel analysis			Short CAMs and Covariate data	
DARs[‡]	Fixed 24-h	Diel range	Central-place foraging Ranging	24 h of data CAM eequences	Periodograms (Fourier, wavelets)
	Time constrained: diel cycle analysis				
LiMPs[§]	Several days to a few months	Home ranges and their shifts over time	Philopatry, dispersal, migration, nomadic, recursion	DAR sequences	Clustering methods, ideal-free/despotic distribution analyses
	Strongly constrained: lunar and seasonal cycle analyses				
Partial or whole LiTs[#]	Paths encompassing several LiMPs	Habitat types	Territorial ranging, migratory nomadic	LiMP sequences	GIS toolbox, deep-learning[*†], pattern anal.
	Moderately constrained: question-at-hand analysis				

SL step-length, *TA* turning-angle

The indicated spatiotemporal scaling applies best to most medium and large vertebrates, with faster/smaller scales needed for many smaller vertebrates, birds, and invertebrates.)

[*]Fundamental movement elements; [†]canonical activity modes; [‡]diel activity routines

[§]Lifetime movement phases; [#]lifetime tracks

[*†]Machine/deep learning methods can be applied at any scale but may be particularly useful here

[*‡]Around 5 s to 1 min

[**]Includes hidden Markov models (HMMs) and behavioral change-point analyses (BCPA)

[††]See "Stochastic walk statistics" section in main text

able to reliably identify different strings of predominantly one type of FuME, or stereotypical mixed sequences of particular FuMES, which we call "metaFuMEs". With this definition, for relatively high-frequency relocation data, all the different metaFuMEs, in a set of metaFuME types, may have the same or different fixed lengths determined by the time between consecutive relocation points and the number of points in each type used to construct each metaFuME type bivariate SL and TA distribution (e.g., see Getz et al. 2020), and auto- and cross-correlation time-series coefficients (Chatfield 2016). Such sets of metaFuMEs can then be used as a basis for representing different types of identifiable activities (e.g., foraging or focused traveling to a selected location), referred to as canonical activity modes (CAMs—see glossary; Getz and Saltz 2008).

Segmenting relocation data at a metaFuME level only make sense if the data have been sampled at frequencies that lie somewhere between the time it takes to execute several typical FuMEs (i.e., on the order 10 s) and the time it takes to perform a short-period CAM that is relevant to movement ecologists (i.e., on the order of a few minutes, except for sharp burst of movement related to predation or defense). Fortunately, current technologies facilitate the collection of data at frequencies of 0.01 to 1 Hz in birds (Harel et al. 2016b; Harel and Nathan 2018) and mammals (de Weerd et al. 2015; McGavin et al. 2018) of even relatively small size. Beyond GPS methods for collecting high-frequency data are other methods such as reverse GPS (e.g., the Atlas system; Weiser et al. 2016; Toledo et al. 2016); but reverse GPS is generally limited in spatial extent to some tens or hundreds of square kilometers. Also, high-frequency movement data have been collected using video equipment for small (e.g., ants) to moderately sized (e.g., mice) organisms in a laboratory setting (Spink et al. 2001; Kane et al. 2004; Delcourt et al. 2013). From a practical point of view, though, particularly since the size of relocation data sets can be rather large when collected at frequencies of around 0.01 to 1 Hz, it may be useful to carry out a metaFuME identification process on selected segments of the full path (such as CAMs), and then use a suitable method to reconcile disparate identification efforts to obtain a consensus set of metaFuME types that can be applied to the full movement path.

At this point, it is worth emphasizing that the distributions used to characterize directions taken and distances moved per sampling interval, depend on the relocation sampling frequency (Codling and Hill 2005; Codling and Plank 2011). This frequency, in turn, limits the set of questions that can be addressed to those that are compatible with the scale of the collected data. Thus, relocation data collected every 5 min is more than adequate

for estimating the maximum displacement (i.e., maximum distance from the start of a movement segment) of a DAR, as shown by Luisa Vissat et al. (2022) for the barn owl. Such data, however, would be inadequate for estimating the distance moved by an individual searching an area, if that individual changed direction on average more often than every 5 min. This constraint must be kept in mind if high-frequency data are re-sampled to reduce the relocation frequency to a more manageable or appropriate scale.

Assuming that a set of metaFuMEs has been identified, as discussed in more detail below, then it may be possible to stably identify different kinds of short-duration CAMs with periods varying from around 10 metaFuMEs (i.e., a couple of minutes) to a few hours (Fig. 1, Table 1). Following this, longer duration CAMs may be more conveniently parsed in terms of several shorter duration CAMs rather than in terms of metaFuME types. To emphasize this, both short and long duration CAMs are identified in the hierarchical scheme laid out in Table 1. Due to the importance of circadian rhythms as physiological and behavioral drivers (Takahashi et al. 2008; Yerushalmi and Green 2009; Hardin and Panda 2013), the diel cycle provides an empirically obvious segmentation window for the identification of various types of diel activity routines (DARs; set of green boxes in Fig. 1; also see Table 1), although the start and end of a DAR cycle might vary for diurnal, nocturnal and crepuscular species. Several types of DARs may then be identified in terms of differences in the type and frequency of their constituent CAMs. For example, different types of DARs have been identified in terms of the portion of their diel cycle that various groups of lemurs are active (Donati et al. 2016) and of the variation in the diel travel rates of turtles (Jonsen et al. 2006).

DARs, in turn, can be strung together to create life-history movement phases (LiMPs; sets of red pentagons in Fig. 1) that, depending on the longevity of the species, may be periodic (e.g., annual migration; for a review see Milner-Gulland et al. 2011) or episodic (e.g., dispersal; for a review see Bowler and Benton 2005). Finally, a sequence of LiMPs sequentially strung together from the birth-to-death of an individual constitutes its full lifetime track (LiT; Nathan et al. 2008; indicated by the grey pentagons in Fig. 1; also see Table 1). Beyond LiMPs, LiTs from several individuals can be used to map out space-use by populations rather than just the movement path of any single individual (Mueller and Fagan 2008).

Beyond the relevance of diel cycles to movement behavior (Wittemyer et al. 2008), are lunar (Polansky et al. 2010) and seasonal cycles (Marra et al. 2015); and even weekly cycles if the influence of humans has some impact on the movement of animals in urban and

suburban areas. The critical nature of the diel scale in driving movement behavior is reflected in our identification of the fixed-period DAR category as a central construct in our framework, depicted in Fig. 1. In contrast, the lunar cycle may be more relevant to some organisms than others (Polansky et al. 2010). Thus beyond DARs only seasonally or life-history-relevant LiMPs segments are identified with seasonal segments only being relevant to organisms with life-spans long enough to experience several seasonal cycles (Marra et al. 2015; Allen et al. 2018). For some organisms, particular LiMPs, such as dispersal, occur only once; while migration behavior may vary from year to year, influenced by inter-annual variations in climatic conditions—perhaps linked to multiyear marine (Mysterud et al. 2001; Grémillet and Boulinier 2009) or sunspot (Myers 2018) cycles. Further, periodically driven movement patterns may also change with age (e.g., exploration when young) and life-history stage (e.g., elephants in musth). Thus, beyond DARs, other cyclic patterns become either less obvious or more species-specific.

The data compatibility problem

A relocation data time series W consists of a series of two (or in some cases three) dimensional points:

$$W = \left\{ \left(t; x(t), y(t) \right) \middle| t = 0, \ldots, t_f \right\}. \tag{1}$$

The temporal resolution of these data will determine whether it is possible to identify metaFuMEs, short (e.g., vigilance behavior during grazing; Fortin et al. 2004) or long duration CAMs (e.g., heading to water; Polansky et al. 2015), or only movement patterns at diel scales and beyond (Spiegel and O'Farrell 2019; Owen-Smith 2013; Giotto et al. 2015; Seidel et al. 2019).

Parsing a movement path into its elements is somewhat like picking out words from a voice recording. The human brain does this very well, as do modern digital machines using deep-learning methods (Hinton et al. 2012; Zhang et al. 2018). In an extremely crude sense, FuMEs are comparable to syllables, metaFuMEs to words, short duration CAMs to sentences and long duration CAMs to paragraphs. DARs may be thought of as single pages in a book-of-life, where each page can be identified as belonging to one of a rather limited number of types (e.g., a typical winter versus summer day or a day during a migratory versus non-migratory LiMP). Thus, the stories being told are rather boring, page-by-page repetitions, with important cyclic variations, as well as other variations due to environmental influences.

Despite the current, technology driven, exponential growth in the quantity and quality of movement data

(including relocation, accelerometer, physiological, and environmental measurements; Williams et al. 2019), collecting the kind of multi-body-placement accelerometer and relocation data needed to identify the start and finish of individual FuMEs (i.e., with a spatial accuracy of centimeters rather than meters or even decimeters) may still be beyond the budgets of most movement ecology studies. Other technologies, such as audio (Sapir et al. 2010; Hurme et al. 2019; Northrup et al. 2019), magnetometer (Williams et al. 2017; Chakravarty et al. 2019), and video (Spink et al. 2001; Kane et al. 2004; Delcourt et al. 2013) may well be more cost effect in terms of identifying the start and finish times of individual FuMES. Thus, for some time to come, relocation data collected at fixed frequencies slower than around 1 Hz are going to be significantly misaligned in time (at least to within half a second) with the start and finish of each of the FuMEs that make up a path segment of interest.

At this point, it is worth noting that accelerometer data alone have been used to parse out relatively short time scale (order of 10 s) behavioral elements along movement paths using machine learning methods (Nathan et al. 2012; Thessen 2016; Wang et al. 2015). These behavioral elements, which almost certainly include several FuME steps, in reality are partial elements of more extensive short-duration CAMs that typically last tens of seconds to several minutes. Accelerometer data, for example, have been used to categorize standing, running, preening, eating, and active and passive flight CAMs in vultures with 80–90% accuracy (Nathan et al. 2012). It may be possible for some FuMEs, however, such as the time taken to complete a FuME when walking versus running, to be identifiable directly from accelerometer data (as we find in modern digital watches that are able to monitor the number of steps we take while moving).

In summary, location data on their own (i.e., without accompanying subsecond accelerometer, acoustic, magnetometer or video data) are fundamentally incompatible with the identification of FuMEs because FuMEs are characterized by the movement of body parts while location data apply to a body as a whole. For this reason, it is worth reemphasizing the following:

1. Given that the identification of individual FuMEs from relocation data is not generally possible, we are left with the rather challenging task of extracting a set of metaFuME elements, where each metaFuME type is characterized by its own SL–TA distributional pair and correlations with and between consecutive and simultaneous values.

2. The complete set of metaFuME types, once identified, can then be used as a basis for constructing an appropriate complexity (Getz et al. 2018; Larsen et al. 2016), HPS framework of CAM, DAR and LiMP segments, where the latter is used to classify different types of lifetime tracks (Table 1), beginning with CAM sequences constructed using a multi-CAM metaFuME Markov (M-cubed) modeling approach described in more detail below.

Stochastic walk statistics

At any time scale, movement time series may be analyzed using purely statistical methods applied to the SL and TA time series derived from W to generate various running statistics. These statistics may include the means, variance, autocorrelations of SL and TA time series data and cross-correlations between the two (Chatfield 2016; McCulloch and Cain 1989; Bergman et al. 2000; Byers 2001). Running versions of these statistics can then be used to identify points in time where abrupt changes in their values occur, using methods referred to as behavioral change-point analyses (BCPAs; Owen-Smith and

Martin 2015; Chen and Gupta 2011; Matteson and James 2014; Killick and Eckley 2014; Gurarie et al. 2009, 2016) or, more generally, path segmentation methods (PS; Nams 2014; Edelhoff et al. 2016; Seidel et al. 2018). A graphic indicating the most important of these methods and the scale at which they typically are applied is provided in Fig. 4.

As discussed earlier, though, identifying a set of FuMEs is a problem that requires biomechanical (Delp and Loan 2000), audio (Sapir et al. 2010), or other kinds of covariate data (Chakravarty et al. 2019) than relocation data on their own. With relocation data alone, a hierarchical analysis of a path can only be underpinned by elements that are derived statistically from the relocation time series W (Eq. 1).

From this time series, we can extract a 1-D time series of step lengths and another 1-D time series of turning angles as follows:

- Generate the step-length (SL) time series

$$S = \{(t, s(t)) \mid t = 1, \ldots, t_f\}, \qquad (2)$$

Fig. 4 Current scale-dependent analytical methods for analyzing movement paths. The temporal range is only suggestive and best applied to medium and large vertebrates. Also the image placements are not precise and some methods, such as machine learning (Thessen 2016), can be applied to data at any scale, but here are associated with the scale at which they are likely to be most useful. In addition, deep learning (useful for identifying different types of long-term patterns) is actually a subset of machine learning (where other machine techniques, such as random forests and support vector machines have been applied to accelerometer data; Nathan et al. 2012; Fehlmann et al. 2017). Stochastic walks include correlated and biased random walks (Johnson et al. 2008). Space–time residence analyses represent a family of methods that include first-passage-time (FPT; Fauchald and Tveraa 2003; McKenzie et al. 2009) and related approaches (Torres et al. 2017), while recurrence analyses cover a plethora of methods used to identify recursive movement patterns (Berger-Tal and Bar-David 2015; Bar-David et al. 2009). The melange of images is extracted from publications in the literature (Nathan et al. 2012; Panzacchi et al. 2016; Morales et al. 2004; DeCesare et al. 2012; Wittemyer et al. 2008; Lyons et al. 2013; Abrahms et al. 2017; Fleming and Calabrese 2017; Pohle et al. 2017; Torres et al. 2017; Gurarie et al. 2017), as well as created for this publication

using the derived values

$$s(t) = \sqrt{(x(t) - x(t-1))^2 + (y(t) - y(t-1))^2}. \tag{3}$$

- Generate the turning-angle (TA) time series

$$A = \{(t, a(t)) \mid t = 2, \ldots, t_f\}, \tag{4}$$

using the derived values

$$a(t) = \arctan\left(\frac{y(t) - y(t-1)}{x(t) - x(t-1)}\right) \\ - \arctan\left(\frac{y(t-1) - y(t-2)}{x(t-1) - x(t-2)}\right). \tag{5}$$

From these two time series we can obtain their means and variances, respectively, denoted by (μ_ℓ, σ_ℓ), $\ell = s, a$, and then use them compute the following three variation related time series:

- Generate two normalized (by the appropriate variances) "running-term autocorrelation" time series

$$V^{\ell\ell} = \{(t, v^{\ell\ell}(t)) \mid t = t_b, t_b + 1, \ldots, t_f\} \\ \text{for } \ell = s \, (t_b = 2), \, a \, (t_b = 3), \tag{6}$$

where

$$v^{\ell\ell}(t) = \frac{(\ell(t) - \mu_\ell)(\ell(t-1) - \mu_\ell)}{\sigma_\ell}. \tag{7}$$

- Generate a normalized "running-term cross-correlation" time series

$$V^{as} = \{(t, v^{as}(t)) \mid t = 2, \ldots, t_f\}, \tag{8}$$

where

$$v^{as}(t) = \frac{(a(t) - \mu_a)(s(t) - \mu_s)}{\sqrt{\sigma_a \sigma_s}}. \tag{9}$$

We are now challenged with the task of using the five time series above (step length, turning angle, two autocorrelation and one cross-correlation)—and, perhaps, other covariate data when available (e.g., acoustic, accelerometer, local environmental)—to parse W (Eq. 1) into several, say Λ (capital lambda), different single-step metaFuME ensembles (Fig. 2). The most obvious approach is to use clustering methods, but this should be accompanied by some sort of range standardization procedure for each variable to improve the performance of the clustering algorithm (Van Moorter et al. 2010). Each of these Λ ensembles, belonging to the same metaFuME type, can now be regarded as a set of drawings from the same bivariate distribution $D_\lambda(s, a)$, $\lambda = 1, \ldots, \Lambda$. If the relocation sampling period, except for speed bursts, encompasses around 10–50 FuMEs (i.e., more than around 5 s but less than about a minute—e.g, fast walking in humans crudely corresponds to 2 steps per second, though most movement is slower than this); then, in the proposed HPS framework, we are in the metaFuME segment zone (Fig. 1, Table 1). If the relocation sampling period is on the order of tens of minutes to several hours, then each relocation likely encompasses hundreds to tens of thousands of FuMEs. In this case, set of states are more appropriately identified as short or long duration CAMs than as metaFuMEs.

Once a set of metaFuMEs has been identified from a particular ensemble of segments of the same CAM or DAR type, along with the accompanying metaFuME sequence index sets (Fig. 2), we are still faced with the task of reconciling various metaFuME sets obtained from different CAM or DAR ensembles into a comprehensive metaFuME set. Such a set will then underlie all LiMPs of a particular type, but not necessarily across a complete lifetime track, because we might expect metaFuME sets for, say, juveniles versus adults to be different for same species. Many different types of cluster analyses (McGarigal et al. 2016) can be tried to identify metaFuMEs. Also, multicriteria optimization methods using, for example, genetic algorithms or approximate Bayesian computations (Coello 2003; Odu and Charles-Owaba 2013; Marin et al. 2012) could be used to reconcile metaFuME sets obtained from ensembles of different types of segments. Such investigations, however, are well beyond the scope of this "concepts" paper, but are undertaken elsewhere (Getz et al. 2020).

Once the time series W and, hence, the corresponding SL and TA time series have been parsed into ensembles and organized into a set of Λ metaFuMEs, the associated metaFuME sequence index sets T_λ, $\lambda = 1, \ldots, \Lambda$ (Fig. 2) can be identified. The distributions of all the joint pairs $(s(t), a(t))$, where $t \in \mathbf{T}_\lambda$, $\lambda = 1, \ldots, \Lambda$, can then be fitted to an appropriate metaFuME bivariate distributions $D_\lambda(s, a)$, $\lambda = 1, \ldots, \Lambda$ and the metaFuME sequence index set ensemble $\mathscr{T}_\Lambda = \{T_\lambda \mid \lambda = 1, \ldots, \Lambda\}$ can be used to estimate transition rates among metaFuME sequences. In essence, we have estimated a set of bivariate metaFuME distributions:

$$\mathscr{D}_\Lambda = \{D_1(s, a), \ldots, D_\Lambda(s, a)\}, \tag{10}$$

and a matrix of values $(\mathbf{P})_{\lambda\kappa} = p_{\lambda\kappa}$ (with $\lambda, \kappa = 1, \ldots, \Lambda$) that represent the probability of sampling values from the distribution $D_\lambda(s, a)$ when the previous drawing was from the distribution $D_\kappa(s, a)$.

We can now use the set of distributions $\mathscr{D}_\Lambda$ and transition matrix $\mathbf{P}$, essentially as a Markov metaFuME movement model, to construct a CAM segment of a walk $W(t_f)$. We do this by first generating a set of T drawings (the hat notation represents drawings):

$$T \text{ drawings} := \{(\hat{s}_t, \hat{a}_t) \text{ sampled from } D_\kappa(s, a)$$
$$\text{with probability } p_{\lambda\kappa} | t = 0, \dots, t_f - 1\},$$
$$\tag{11}$$

and then generating a segment of $W(t_f)$ from these drawings using the following equations (Patterson et al. 2008), where $\theta(t)$ is the absolute angle of heading at time t:

$$x(t+1) = x(t) + \hat{s}_t \cos\left(\theta(t) + \hat{a}_t\right),$$
$$y(t+1) = y(t) + \hat{s}_t \sin\left(\theta(t) + \hat{a}_t\right), \tag{12}$$
$$\theta(t+1) = \theta(t) + \hat{a}_t.$$

Thus, in short, we use the extracted identified metaFuME-distribution-set and Markov transition-matrix pair $(\mathcal{D}_\Lambda, \mathbf{P})$ to generate a CAM segment of a walk W that is one instantiation of an ensemble of CAM segments generated using Eqs. 11 and 12.

To generate different sets of CAM sequences and string these together to form particular DARs requires that we have additional distributional descriptions for the length of different CAM sequences found in particular DARs, and matrix probabilities for transitioning among CAMs within such DARs. The outlines of model to accomplish this task, referred to as a multi-CAM metaFuME Markov (M-cubed) model is described in the next section. In terms of a single CAM metaFuME Markov model embodied in Eqs. 11 and 12, the appropriate number of metaFuME distribution pairs Λ in the set $\mathcal{D}_\Lambda$ (Eq. 10) is, a priori, unknown. A first guess at this number might be the number of modes in step length time series derived for different types of CAM segments, if such modes are evident. The problem of finding the best mixture of unimodal pairs $(D_\lambda^{\mathrm{SL}}, D_\lambda^{\mathrm{TA}})$ of distributions that best fit such derived empirical data is a challenging estimation problem that can be approached in several ways, including ensemble Kalman filtering (Dovera and Della Rossa 2011) under the assumption that the underlying distributions are log-concave (Walther et al. 2009). A prudent approach may be to proceed by first looking for the two best-fitting pairs of bivariate distributions:

$$\mathcal{D}_2 = \{D_1(s, a), D_2(s, a)\}, \tag{13}$$

and then moving on to three, four, and so on, until no improvement in fit is obtained at the next value for Λ in an information theoretic sense (Symonds and Moussalli 2011). We may then use existing segmentation methods (e.g., BCPA) to identify possible CAMs that may emerge from the simulated data and compare them to the CAMS identified in the original data. If the fit is satisfactory, we may then use our multi-CAM metaFuME Markov (M-cubed) model (Getz et al. 2020) to predict how individuals may respond to management or global change in terms of local and intermediate scale movements. We note, though, that the M-cubed modeling approach described in the next section contains no global directional information. Thus, additional constructs will be needed to obtain movement motivated by headings to specific distant target sites. The performance of M-cubed-type models and their extensions are investigated elsewhere (Getz et al. 2020).

M-cubed model construction

The basis of the M-cubed model is to take ensembles of CAM segments of the same type and identify a set of metaFuMEs that can be used to simulate the local structure of such CAMs. If this is done for all the kinds of CAMs that constitute a particular DAR type, then the model can be used to string several types of CAMs together to conform to observed sequences and frequencies of CAMs characteristic of type of DAR under consideration. This approach to constructing M-cubed models has been explored and evaluated elsewhere (Getz et al. 2020). Such M-cubed models, however, do not account for movement towards specific distant targets. To include such phenomena requires that M-cubed models be appropriately extended to include directional biases induced by an attraction to distant geographic locations or a repulsion related to the existence of boundaries to movement (e.g., landscape topography or water).

Extraction of an M-cubed model from relocation data requires that the frequency of the data be available at the metaFuME scale, which from Table 1 for medium-to-large terrestrial vertebrates is likely to be around 0.01 to 0.1 Hz. Although details of the approach can be found in (Getz et al. 2020), for the sake of completeness, a brief summary of the approach is enumerated here.

Summary of approach

1. Path relocation data, W^{data} (Eq. 1) are parsed into ensembles of DARs of various types, using an appropriate method (e.g., based on net-square daily displacement or other suitable daily measures; see Bunnefeld et al. 2011; Bischof et al. 2012; Abrahms et al. 2017; Owen-Smith and Martin 2015; Owen-Smith et al. 2010).

2. CAM segments are identified from DAR segment ensembles of the same type (Fig. 3), using appropriate methods such as BCPA (Nams 2014; Edelhoff et al. 2016; Seidel et al. 2018) or HMM (Zucchini et al. 2016). In the latter case, the HMM will need to be performed on a subset of the data subsampled at a scale suitable for identifying CAMs of interest (e.g., if CAMs of interest are assumed to last around 20 min

or longer, then data should be subsampled using a consecutive point intervals of, say, at most 5 min).

3. All the data from the ensemble of path segments identified as belonging to the same CAM type within the same DAR type should be strung together into a set of points. If we assume that Φ such CAM-DAR compound types are identified, use W^{ensemble_ϕ}, $\phi = 1, \ldots, \Phi$ to denote these sets of points.

4. Cluster analyses or other type of categorization procedure should be performed, using the values $\left(s(t), a(t), v^{ss}, v^{aa}, v^{as}\right)$ (Eqs. 2–9) for all times t for which there are points in the sets W^{ensemble_ϕ} to identify sets of metaFuME types specific to each of the sets $W^{\text{ensemble}_\phi}, \phi = 1, \ldots, \Phi$ (Fig. 2).

5. For each ensemble type ϕ, distributions $\left(D^\phi_\lambda\right)$, $\lambda_\phi = 1, \ldots, \Lambda_\phi$, should be fitted to each of the Λ_ϕ metaFuME types identified in the previous step, with some effort to reconcile metaFuME types identified across different ensembles $W^{\text{ensemble}_\phi}, \phi = 1, \ldots, \Phi$

6. Distributions $D^\phi_\lambda, \lambda = 1, \ldots, \Lambda_\phi$ can be fitted to each of the metaFuME types identified in ensemble ϕ, $\phi = 1, \ldots, \Phi$, and an associated Markov transmission matrix $\left(\mathbf{P}^\phi\right)$ estimated to obtain the characterizing pairs $\left(\mathcal{D}^\phi_{\Lambda_\phi}, \mathbf{P}^\phi\right)$, which can then be used in a Markov metaFuME movement model to generate CAMs of type ϕ, for $\phi = 1, \ldots, \Phi$.

7. The metaFuME Markov models derived in the previous step for each type of CAM can be combined into a multi-CAM metaFuME Markov (M-cubed) model that produces sequences of CAMs with CAM lengths and CAM-type transition statistics that are extracted from the DAR ensemble data.

8. The performance of the M-cubed model can be evaluated by comparing the CAMs obtained directly from W^{data}, using existing BCPA and HMM methods, with CAMs produced by the M-cubed model simulations.

General discussion

Without an underlying framework to organize information and bridge processes conceived at different spatiotemporal scales, a deep understanding of both our physical and biological worlds is impossible. In the context of movement ecology, the classification of movement types at different spatiotemporal scales is of considerable interest, although approaches to date have been somewhat informal. At the lifetime track level, basic life-history types regarding, *interalia*, dispersal and migration behavior may be identified. In the movement ecology literature, we see many studies interested in diel activity routines (DARs; Rahimi and Owen-Smith 2007;

Owen-Smith 2013; Owen-Smith and Goodall 2014), lifetime movement phases (LiMPs; Fahr et al. 2015; Marra et al. 2015) and over all lifetime tracks (LiTs: Abrahms et al. 2017). Contrasting DAR types may include distinctions among nomadic, central-place foraging, or territorial behavior, where a single lifetime track may have movement phases dominated by one or other diel activity routine. An example is male springboks in Etosha National Park, Namibia, that exhibit territorial behavior during the wet season and nomadic behavior during the dry season, with daily excursions to the same waterhole around midday during the wet season (Lyons et al. 2013). Thus DARs are also very likely to be influenced by seasonal factors, as in pandas that change daily levels of activity in response to seasonal drivers (Zhang et al. 2017).

Extensive effort has also been made to parse diel and longer segments into various types of sub-diel activity modes (Owen-Smith et al. 2010; Donati et al. 2016) that, if stably identifiable across different segments, can be organized into a set of canonical activity modes (CAMs; Getz and Saltz 2008). At finer time scales, however, beyond using accelerometer, acoustic and magnetometer data to identify behavioral states (Williams et al. 2017; Hurme et al. 2019; Nathan et al. 2012; Fehlmann et al. 2017; Chakravarty et al. 2019; Sapir et al. 2010; Zucchini et al. 2016), very little work has been undertaken to identify sets of fundamental movement elements (FuMEs) from which CAMs are constructed. As pointed out in this paper, using relocation data alone, we cannot endeavor to identify an underlying set of FuMEs. The best we can hope for, provided sub-minute relocation data are available, is the identification of a set of metaFuMEs consisting of repeated or correlated strings of FuMES, and characterized by particular step-length and turning-angle distributions.

We should not underestimate the analytical and computational challenge required to extract a comprehensive and stable (across many segments at various scales) set of metaFuME elements. The best methods to do this still remain to be developed and how well this may be accomplished remains to be seen; although satisfying progress has already been made (Getz et al. 2020). Future progress may require many of the ideas presented here to be refined or modified. There is no denying, however, that a formalized, widely accepted HPS framework will greatly facilitate efforts to address outstanding questions in movement ecology, particularly those involving comparative analyses within species (Wittemyer et al. 2019), as well as across species. Within species variation may allow us to assess differences along geographic clines with application to the behavioral adaptation of species under landscape and climate change (Seebacher and Post 2015).

It may help us assess fitness in the context of feeding strategies, social behavior (Harel et al. 2016a, 2017), areas attractive to populations (Giotto et al. 2015), or mapping out landscapes in terms of their overall resistance to movement (Zeller et al. 2012). It may also be diagnostic of changes in movement behavior when individuals are stressed, ill, have genetic defects, or females are pregnant (Spink et al. 2001; Owen-Smith 2013); or it may be predictive in terms of pathogen transmission and the spread of disease (Cross et al. 2007; Tracey et al. 2014; Dougherty et al. 2018; Zidon et al. 2017). Differences in various species' movement profiles at various scales may be critical when it comes to taking a multispecies approach to assessing the impacts of ecosystem management on species conservation (Brodie et al. 2015; Runge et al. 2014).

Additionally, a formalized HPS framework of appropriate complexity (Getz et al. 2018; Larsen et al. 2016) can be used, for example, to address the dozen plus questions that were recently posed regarding the movement ecology of marine megafauna (Hays et al. 2016)—but are equally applicable to all animal species. These questions include: (1) Are there simple rules underlying seemingly complex movement patterns and hence common drivers for movement across species? and (2) How will climate change impact animal movements? An ability to address both of these question, as well as those raised above and others besides, in a comparative way—with a level of consistency and coherency that only a universally accepted classification framework can provide—is needed with great urgency, as the field of movement ecology matures.

Conclusion

The hierarchical path-segmentation (HPS) formulation presented in this paper provides a coherent approach to deconstructing the movement paths of animals into sets of categorized segments at four biological relevant scales, anchored around the fixed 24-h, diel activity routine (DAR) scale. Once an appropriate set of DARs has been identified, as was done by Luisa Vissat et al. (2022) for barn owls (*Tyto alba*), these DARs can then be parsed in sub-diel segments, using various biological change point or hidden Markov methods. These sub-diel segments then provide us with a set of canonical activity modes (CAMs) (Fig. 1), where the duration of the smallest CAMs that may be identified depends on the frequency of the empirical path relocation data. The DARs themselves also provide a basis for defining different lifetime movement phases (LiMPS) in terms of each phase being characterized by a particular frequency and sequence of several DAR types.

If empirical relocation data are available at a sufficiently high frequency to identify a set of statistically defined meta fundamental movement element (metaFuME) constructs,

then these metaFuMEs can be be used as a basis for predicting how movement patterns may respond to environmental change. In particular, the M-cubed modeling approach summarized in this paper can be used to simulate CAM segments (Getz et al. 2020) that, in the presence of particular environmental factors, may be used to assess how the movement behavior of individuals adapt to global change. It will likely take models of this complexity to address the two questions posed in the last paragraph of the "General discussion" section above, as well as those posed elsewhere in the context of theoretical and applied movement ecology. The latter are of particular importance in addressing questions related to conservation biology, resource management, and global change assessment. In short, the HPS formulation presented in this paper, provides a multiscale, spatiotemporal approach to developing models able to meet Nathan et al. (2022)'s stated goal of elucidating how movement behaviors adapt in response to environmental change.

Glossary

BCPA — Behavioral change point analysis. Behavioral change-point analysis refers to a group of methods used to determine how the statistics of a biological variable y (e.g., its mean, variance, autocorrelation, or rate of change in slope or curvature), dependent on a second variable x, switches at threshold points with changes in x [e.g., space, time, or the abscissa in a stress-response relationship; Morales et al. (2004), Andersen et al. (2009), Chen and Gupta (2011), Jonsen et al. (2007)]. Note, more generally, x could be vector-valued.

CAM — Canonical activity mode. This is a stably classifiable subdiel behavioral mode (pattern of movement) such as a foraging bout, resting period, or purposeful heading (i.e., traveling) to a distant target location.

DAR — Diel activity routine. This is a stably classifiable 24-h sequence of CAMs that occur at characteristic frequencies and times of the day. We note that the start and end of a DAR cycle may vary for diurnal, nocturnal and crepuscular species.

FuME — Fundamental movement elements [pronounced "fume" and same as FME defined in Getz and Saltz (2008)]. This is a relatively rapid, highly repeatable, stereotypic set of body movements that forms the basis of the locomotory capacity of an individual (e.g., a walk step, a running step, a wing flap, a jump, etc.)

HMM — Hidden Markov model. A time series of observable values that depend in a probabilistic sense on the values of an associated, but unobservable Markov chain process [a set of states where the transition from one state to another depends only on the value of the current state; Zucchini et al. (2016)]

HPS — Hierarchical path segmentation. This refers to the formulation that is centered around diel activity routines (DARs), which can be parsed in canonical activity modes (CAMs) or strung together to produce lifetime movement phases (LiMPs) (see Figs. 1 and 3).

LiMP — Lifetime movement phase. This is a path segment that typically reflects a life-history relevant movement behavior such as dispersal (episodic), migration (periodic), or other periodic behaviors at a greater-than-diel scale.

LiT — Lifetime track. This is the total movement path of an individual from its birth to its death.

MetaFuME — A correlated stereotypical or characteristic sequence of FuMEs of fixed duration equal to the time between consecutive relocation points (only applicable to relatively high-frequency data: ideally, metaFuMEs should contain no more than several tens of FuMES).

M-cubed   Multi-CAM metaFuME Markov (model). A model based on the metaFuME set $\mathscr{D}_\Lambda$ of CAM-specific distributions (Eq. 10) and CAM-specific Markov transition matrices $P_\lambda, \lambda = 1, \ldots, \Lambda$, derived from the set $\mathscr{T}_\Lambda$ of metaFuME sequence index set ensembles (see Fig. 2). This model contains only local movement information and cannot be used to simulate movement patterns motivated by headings to distant targets.

PS   Path segmentation. This is the process of breaking up a movement path into reliably stable metaFuMEs, CAMs, DARs, and LiMPs using a suite of methods that include BCPA and HMM approaches (Nams 2014, Edelhoff et al. 2016; Seidel et al. 2018).

SL   Step length. The distance between consecutive relocation points, as generated from Eq. 1 using Eq. 3.

TA   Turning angle. The change in the angle of heading across three consecutive relocation points, as generated from Eq. 1 using Eq. 5.

Declarations

Competing interests
The author declares that he has no competing interests

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