A hierarchical framework for segmenting movement paths

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Abstract

Comparative applications of animal movement path analyses are hampered by the lack of a comprehensive framework for linking structures and processes conceived at different spatio-temporal scales. Although many analyses 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, or longer. The kinds of questions that may be asked of these data, however, are very much scale-dependent. It thus behooves us to clarify how the scale at which SL and TA data are collected related to one another and to the kinds of ecological questions that can be asked. Difficulties arise because the information contained in SL and TA time series is not semantically consilient with the physiological, ecological, and sociological factors that influence the structure of movement paths. I address these difficulties by classifying movement types at salient temporal scales using two different kinds of vocabularies. The first is the language derived from behavioral and ecological concepts. The second is the language derived from mathematically formulated stochastic walks. The primary tools for analyzing these walks are fitting time-series and stochastic-process models to SL and TA statistics (means, variances, correlations, individual-state and local environmental covariates), while paying attention to movement patterns that emerge at various spatial scales. The purpose of this paper is to lay out a more coherent, hierarchical, scale-dependent, appropriate-complexity framework for conceptualizing path segments at different spatio-temporal scales. Additionally, this framework is designed to bridge biological and mathematical movement ecology concepts; thereby, hopefully, stimulating the development of conceptually-rooted methods for simulating hypothetical and analyzing empirical data that can be used to test hypothesis regarding mechanisms driving animal movement.

Keywords: Fundamental movement elements, canonical activity modes, diel activity routines, life-history movement phases, life-time tracks

Introduction

The movement of organisms over landscapes can be usefully analyzed from various viewpoints. Four are suggested by the conceptual framework for movement ecology proposed by Nathan et al. (2008), depending on which questions constitute the focal interest—why move? how is movement executed? where to move? and how does the immediate environment, as well as the internal state of individuals, impact movement? Several more viewpoints arise when we focus on the structure of the movement path itself and how this structure may fill space at different spatio-temporal and, hence, ecological relevant scales (Levin 1992)—from the sequencing of various high-resolution movement elements to the emergence of seasonal home ranges and habitat utilization distributions (Worton 1987, Morellet et al. 2013, Torney et al. 2018, Wittemyer et al. 2019). The current lack of a comprehensive framework for linking structures and processes conceived at different spatio-temporal scales, however, hampers the conciliation of these viewpoints and of a comparative meta-analyses of similar questions addressed across disparate species and spatio-temporal scales. With this in mind, a more coherent, hierarchical, scale-dependent, appropriate-complexity framework than currently exists is laid out in this paper for conceptualizing path segments at different spatio-temporal scales. Of considerable importance is that this framework underscores the need for the collection of high resolution relocation data (minute or subminute sampling intervals) whenever possible.

Nathan et al. (2008) argued that movement arises from the interactions of several processes and motivations that can be understood through an analysis of external factors or stimuli, the internal state of an organism (e.g. see Morelle et al. 2015), and the organism's mechanical and navigational capacities. These interactions then result in a movement process that may be characterized by a time series of relocation points that define movement paths (Siniff & Jessen 1969, Edelhoff et al. 2016). From these relocation time series, sequences of step lengths (SL) and turning angles (TA) can be extracted (Kareiva & Shigesada 1983, Turchin 1998). Other data, such as accelerations (Nathan et al. 2012), audio (Sapir et al. 2010, Hurme et al. 2019, Northrup et al. 2019) and magneto (Williams et al. 2017, Chakravarty et al. 2019) data, as well as physiological measurements (e.g., temperature, blood glucose levels) (Wilmers et al. 2015), may be recorded and used in the context of relocation point covariates. Additional covariates may be environmental, including measurements of local resistance to movement caused by landscape topology, vegetation features, and local atmospheric conditions (Shepard et al. 2013, Getz & Saltz 2008, Spiegel et al. 2015), as well as local ecosystem features that are often inferred using remotely sensed electromagnetic spectral data (e.g., visual and infra-red satellite imagery or lidar) (Pettorelli et al. 2011, 2014, Bork & Su 2007).

In this paper, the question is addressed of how we may reconcile the fact that SL and TA distributions are not directly interpretable in terms of behavioral and ecological processes (e.g., resting, stalking, hiding, gathering); but, depending, on the spatio-temporal scale of the relocation data, phenomenological interpretations are made using scale-appropriate activity designators (Johnson et al. 2002, Owen-Smith & Goodall 2019, Giotto et al. 2015). 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 & Martin 2015). The second is the language of mathematical stochastic walks (Kareiva & Shigesada 1983, Bartumeus et al. 2005, Patterson et al. 2008) that treats movement relocation data as a time series of values and applies existing time-series methods (Chatfield 2016) to finding the parameter values that best fit selected time-series models 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).

Moving between stochastic-walk descriptions and biological designators in describing segments of movement paths is akin to translating between phonologic (e.g., Latin, cyrillic) and logographic (e.g., hieroglyphics, Chinese) scripts: much context-dependent interpretation needs to take place. But, in fact, the situation is much more dire, since we do not have access to every character—i.e., fundamental movement element (FuMEs, see glossary; Getz & Saltz 2008)—in the path sequence, but only some kind of "average" value across several characters or potential point-source values. The primary goal of this paper is to flesh out the temporal structure of biological designators of movement-path segments and provide more coherent insights into the relationship between biological designators and stochastic-process models at different temporal scales.

Biological Designators of Path Segments

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, although audio recordings, for example, have been used to identify the wingflaps of small birds (Sapir et al. 2010, 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 able to reliably identify different multiFuME or "metaFuME" aggregates. All metaFuMEs, in a set of several metaFuME types, has a fixed length equal to the time between consecutive relocation points and each metaFuME type has its own characteristic bivariate SL and TA distribution and time-series auto- and cross-correlations (Chatfield 2016). Such metaFuME sets can then be used as a basis for representing different types of identifiable activities (e.g., foraging or focused travelling to a selected location) as canonical activity modes (CAMs—see glossary; Getz & Saltz 2008).

Segmenting relocation data at a metaFuME level only makes 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 ten seconds) 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). Fortunately, new technologies are leading the collection of data at frequencies of around 0.01 to 0.1 Hz, and even 1 Hz in large birds (Harel, Horvitz & Nathan 2016, Harel & Nathan 2018). For example, relocation data at these frequencies is now being collected for small mammals and birds and, indeed for larger mammals as well (de Weerd et al. 2015, McGavin et al. 2018). 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 the latter is limited at this time in spatial extent to some tens or hundreds of square kilometers. Also, high frequency movement data has 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, particularly since the size of relocation data sets can be rather large when collected at frequencies of around 0.01 to 0.1 Hz, it may be useful to carry out a metaFuME identification process on selected segments of the full path W (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. Assuming that a set of metaFuMEs has been identified, as discussed in more detail in succeeding sections, 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, I point to the existence of both short duration and long duration CAMs 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 & Green 2009, Hardin & 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). 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 migration Milner-Gulland et al. 2011) or episodic (e.g., dispersal; for a review see Bowler & Benton 2005). Finally, a sequences of LiMPs sequentially strung together from the birth-to-death of an individual constitute its full lifetime track (LiTT; Nathan et al. 2008) (indicated by the grey pentagons in Fig. 1; also see Table 1). Beyond LiMPs, LiTTs from several individuals can be used to map out space-use by populations rather than just the movement path of any single individual (Mueller & Fagan 2008).

This view of metaFuME, CAM, DAR and LiMP segmentation of LiTTs—in the context of available data and the questions we would like to ask—provides a hierarchical classification system of appropriate complexity (Getz et al. 2018, Larsen et al. 2016) for the parsing of movement paths. It also provides a semantic framework for the quantitative narratives (Getz et al. 2019) needed to explain the role that movement plays in the ecology and evolution of organisms. In the context of evolution, for example, we expect natural selection to hone both the mechanics of performing FuMEs and the way these FuMEs are organized into metaFuMEs, CAMs, DARs, and LiMPs to create LiTTs that maximize the expected lifetime fitness of individuals. In particular, it is of considerable interest how the frequency and sequencing of different FuMEs and CAMs in the production of DARs and LiMPs affect individual fitness (Hein et al. 2016, Cattarino et al. 2016).

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). The critical nature of the diel scale in driving movement behavior is reflected in our creation of the fixed-period DAR category (Fig. 1 for identifying key structures within LiMPs. In contrast, the lunar cycle may be more relevant to some organisms than others (Polansky et al. 2010), while only for relatively long-lived organisms will their LiTTs cover sufficiently many seasonal cycles to support a statistical analyses of repeated LiMP motifs (Marra et al. 2015, Allen et al. 2018). For some organisms, particular LiMPs, such

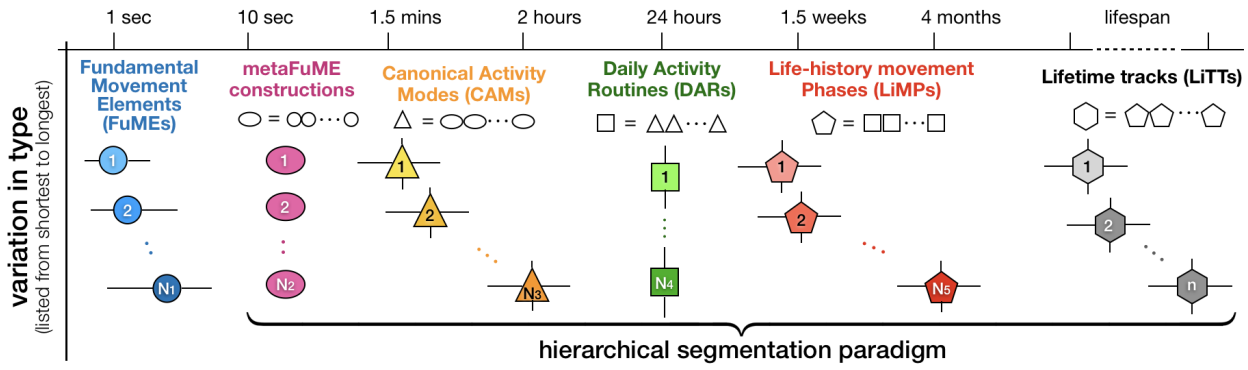

Figure 1: **Scale-dependent path segmentation categories of lifetime track segments.** The time scale applies to typical medium and large terrestrial animals and needs to be adjusted for aerial and marine species, and small animals, including invertebrates. Round (blue), oval (lilac), triangular (yellow to orange), square (green), pentagonal (red), and hexagonal (grey) icons are respectively used to represent N_1 FuME types, N_2 metaFuME types, N_3 CAM types, N_4 DAR types, N_5 LiMP types, and an open-ended number of n LiTT types (one for the life time 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 (except for metaFuMEs which are the length of time between successive relocation points and DARs which are nominally fixed to 24 hours) and 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 and metaFuMEs which are characterized by SL and TA distributions). 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 LiTTs will typically be supported by a metaFuME baseset rather than by a set of FuMEs themselves.

as dispersal, occur only once; while migration behavior may vary from year to year, influenced by interannual variations in climatic conditions—perhaps linked to multiyear marine (Mysterud et al. 2001, Grémillet & 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 less obvious or more species-specific.

The Data Compatibility Problem

Deconstructing 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 a very crude sense, FuMEs are comparable to words, and CAMs to sentences or even paragraphs. However, the number of FuMEs (on the order of 10^1-10^2) is likely four orders of magnitude smaller than the number of words in everyday speech, and the story told is a rather boring repetition of some tens of sentences repeated with moderate variation influenced by an individual's environment. DARs may be thought of as single pages, where each page can be identified as belonging to one of several types (e.g., a typical winter versus summer day, a day during a migratory versus non-migratory life-history movement phase—i.e,

Table 1: Hierarchical organization of a typical vertebrate lifetime track (LiTT). (Spatio-temporal scaling applies best to typical medium to large vertebrates, but not as well to small vertebrates, birds, or invertebrates.)

Scale/ Segment	**Time**	**Space**	**Categories**	**Data**	**Some approaches and methods**
	Constraint level: agency				
true **FuMEs**[*]	0.1–10 secs	0.1–1000 cms	stride, trot, run twist, jump, flap	accelerometer video	machine learning, Newtonian mechanics
	highly constrained: biomechanical analyses				
meta-**FuMEs**[*]	resolution of relocation data sampling: $\geq$ 5 secs, $\leq$ 1 min		bivariate SL & TA[¶] distributions	SL & TA statistics[††]	ensemble filtering on means, variances & correlations
	base level: movement ecology analyses				
short duration **CAMs**[†]	0.1–10 mins	1–100 meters	resting, browsing, riding thermals	secs to mins, metaFuMEs & covariate data	path segmentation[**]
	highly flexible: sub-hourly/hourly focus				
long duration **CAMs**[†]	10-100 mins	0.1-10 kilometers	feeding traveling,	mins to hours, short CAMs & covariate data	
	highly flexible: sub-diel focus				
DARs[‡]	fixed 24-hr	diel range	central-place foraging ranging	mins to hours, CAM sequences	periodograms (Fourier, wavelets)
	time constrained: diel cycle				
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 cycles				
partial or whole **LiTTs**[#]	paths encompassing several LiMPs	habitat types	territorial, migratory, central place foragers, nomads	LiMP sequences	GIS toolbox, deep-learning, pattern anal.
	moderately constrained: question-at-hand				

[*]Fundamental Movement Elements; [†]Canonical Activity Modes; [‡]Diel Activity Routines;
[§]Life-history Movement Phases; [#]Life Time Tracks; [¶]SL=step-length & TA=turning-angle;
[**]Includes Hidden Markov Models (HMMs) and Behavioral Change-Point Analyses (BCPA)
[††]See Section on **Stochastic Walks and MetaFuMEs** in main text

LiMP).

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), we are still far from 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), although relocation using audio (Sapir et al. 2010, Hurme et al. 2019, Northrup et al. 2019) and magneto (Williams et al. 2017, Chakravarty et al. 2019) data show considerable potential in this respect. In short, how different parts of the body move in relationship to one another may well be required for the identification of

certain FuMES. Thus, for some time to come, relocation data collected at fixed frequencies slower than around 1 Hz are going to be temporally misalignment with the approximate (at least to within half a second) of 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 has been used to parse out relatively short time scale (order of 10 secs) behavioral elements along movement paths using machine learning methods (Nathan et al. 2012, Thessen 2016). 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, was able to categorize standing, running, preening, eating, and active and passive flight CAMs in vultures with 80-90% accuracy (Nathan et al. 2012). Another on baboons was able to categorize foraging, lying, sitting, running, standing walking, groom (actor), groom (receiver) with high accuracy ($> 90\%$), except for grooming, which was considerably harder to identify, particularly when the focal individual was the receiver (Fehlmann et al. 2017). In these two examples, sitting, grooming, preening and feeding CAMs are identifiable, but none of the basic FuMEs that are executed during the generation of these CAMs are individually identified. 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) or audio (Sapir et al. 2010, Hurme et al. 2019, Northrup et al. 2019), magneto (Williams et al. 2017, Chakravarty et al. 2019) or video (Spink et al. 2001, Kane et al. 2004, Delcourt et al. 2013) data.

In summary, location data on its own (i.e., without accompanying subsecond accelerometer, accoustic, magneto or video data) is fundamentally incompatible with the identification of FuMEs for two reasons:

- Consecutive point locations alone cannot determine what an individual is doing. What is needed in addition is, at least, the relative position of several different body parts of the individual to its center of gravity and, more usefully, the acceleration of these parts, or other kinds of data such as audio or video recordings.

- Regular sampling is likely to occur during the execution of FuMEs, rather than at the start or finish of a FuME; and, further, different FuMEs generally take different amounts of time to execute.

In light of these reasons, 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 that 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), hierarchical framework of CAM, DAR and LiMP segments, where the latter is used to classify different types of LiTTs (Table 1).

Current Path Analysis Methods

Before considering how to find a set of metaFuME distribution set that provides an appropriately defined best fit to an empirical walk W (defined in terms of its set of observed relocation values)—

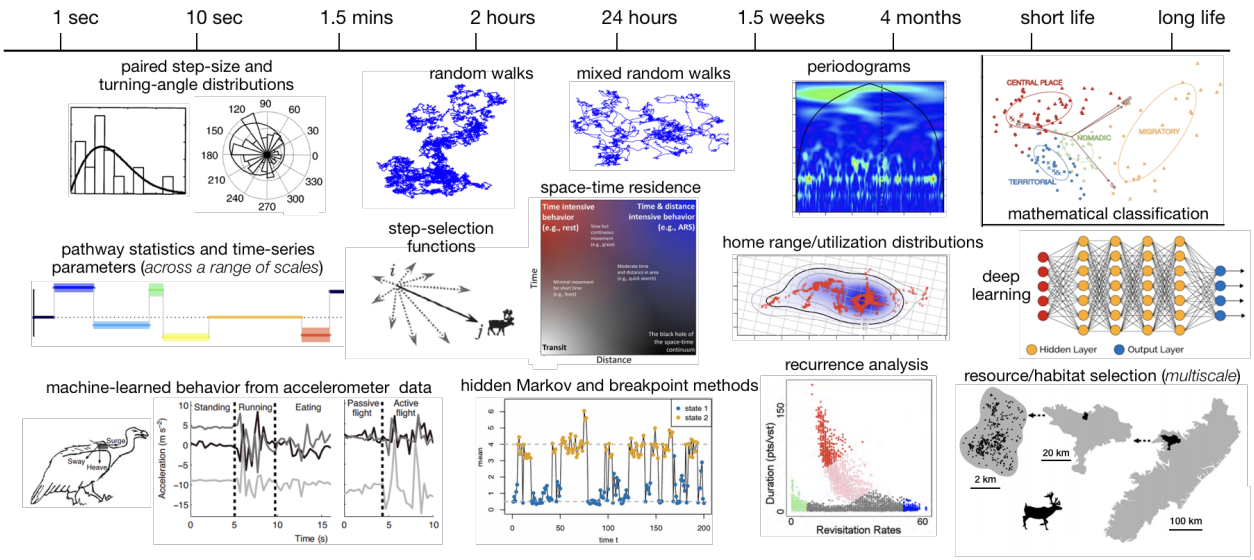

Figure 2: **Current scale-dependent analytical methods for analysing movement paths.** The temporal range is only suggestive and best applied to medium and large vertebrates. Also the image placements are not precise and some methods, such as machine learning (Thessen 2016), can be applied to data at 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 deep-learning 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 represents a family methods that include first-passage-time (FTP; Fauchald & 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 & 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 & Calabrese 2017, Pohle et al. 2017, Torres et al. 2017, Gurarie et al. 2017), as well as created for this publication.

i.e., in 2-D, W is represented by the time series

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

let us briefly review the current state of path analysis that is relevant for analysing relocation data sampled at scales typically appropriate for identifying CAMs and higher-level patterns (Fig. 2). Note that the temporal resolution of the data will determine whether it is possible to identify short duration CAMs (e.g., vigilance behavior during grazing; Fortin et al. 2004), long duration CAMs (e.g., heading to water; Polansky et al. 2015), or only movement patterns at diel scales and beyond (Spiegel & O'Farrell 2018, Owen-Smith 2013, Giotto et al. 2015).

At any time scale, movement time series may be analysed using purely statistical methods applied to the SL and TA time series derived from W, as explicitly described in the next section, 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 & 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 meth-

ods referred to as behavioral change-point analyses (BCPAs; Owen-Smith & Martin 2015, Chen & Gupta 2011, Matteson & James 2014, Killick & Eckley 2014, Gurarie et al. 2009, 2016) (Fig. 2) or, more generally, path segmentation methods (PS; Nams 2014, Edelhoff et al. 2016, Seidel et al. 2018).

Once particular CAM or DAR types of segments have been identified, they can be organized into ensembles of the same type. For clarity in referring to such ensembles, we use upper case calligraphic letters, which contrasts with the italicized uppercase letters used to denote sets of points that are essentially time series, such as W defined in Eq. 1. In particular, $W^{\text{seg_type}}$ will be used to refer to a segment of W of a particular type: e.g., "seg_type"=DAR_1 is a diel activity routine segment of type 1 and $\mathcal{W}^{\text{seg_type}}$ is used to refer to an ensemble or set of segments of this type: viz.,

$$R \text{ instances of a particular segment type:} \qquad \mathcal{W}^{\text{seg_type}} = \{W_r^{\text{seg_type}} | r = 1, ..., R\} \tag{2}$$

Beyond purely statistical characterizations of the SL and TA time series is the notion that some sort of state (typically behavioral; but possibly physiological, disease, etc.) can be associated with each location point in the walk W (Patterson et al. 2008). A very simple example is the stop/move representation of cattle grazing paths (Zhao & Jurdak 2016). The most widely used methods for identifying subsets of points that reflect some underlying state or canonical activity mode (CAM) involve hidden Markov models (HMM) (Michelot et al. 2016, Franke et al. 2004, Langrock et al. 2012, Zucchini et al. 2016) (Fig. 2), although an independent mixture modeling approach has been shown to be equally viable, if not better (Goodall et al. 2017). These methods are particularly germane when covariate data are available at each location, such as accelerometer and temperature data from GPS collars, remotely sensed physiological information (Cross et al. 2016), vegetation structure (Tsalyuk et al. 2019), or physical landscape features that, for example, facilitate or retard movement (Zeller et al. 2012). The task of an HMM is to find a best estimate of which state of a current set of "hidden" states H_i belonging to a set of n possible states $\mathcal{H} = \{H_1, ..., H_n\}$ should be assigned to the individual when at the location $(x(t), y(t))$.

HMMs can be applied at any temporal scale, including the metaFuME scale, depending only on the relocation and covariate data. Other methods, such as step-selection function (SSF) methods, which address the question of where am I likely to move next as a function of landscape covariates, can be applied at any scale (Fortin et al. 2005, Panzacchi et al. 2016, Thurfjell et al. 2014, Avgar et al. 2016). SSFs, however, address different kinds of questions at different scales: they have more of a behavioral interpretation at a 1-minute scale while more of an ecological (e.g., resource use) interpretation at multi-hour scales. On the other hand, habitat or resource-selection function (HSF or RSF) methods (Boyce et al. 2002, McGarigal et al. 2016, DeCesare et al. 2012) are, by their very nature, low resolution models that typically apply at a seasonal level and assume non-autocorrelated location data. When RSFs are evaluated at a life-time level over many individuals in a population, they are called niche models—but such models no longer rely on movement data, only on point location data (Townsend Peterson et al. 2007).

Other general time-series or signal-analysis methods that have been co-opted by movement ecologists include wavelet analysis (Wittemyer et al. 2008, Polansky et al. 2010)—which provides interpretations at the resolution of one to several orders of magnitude greater than the frequency at which data are collected (e.g., daily movement to monthly movement patterns for data collected at the frequency of 1-hour for at least a year)—and machine learning approaches (Thessen 2016, Valletta et al. 2017) that have been applied both to location (Bennison et al. 2018) and accelerometer

data (Nathan et al. 2012) (Fig. 2). These methods, however, do not have an extensive history of application in movement ecology, but are likely to become more ubiquitous as the field of movement ecology matures.

Stochastic Walk Statistics

As discussed earlier, identifying a set of FuMEs is a problem that requires biomechanical (Delp & Loan 2000), audio (Sapir et al. 2010), or other kinds of covariate data (Chakravarty et al. 2019) than relocation data on its 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

$$S = \{(t, s(t))|\ t = 1, ..., t_f\} \tag{3}$$

using the derived values

$$s(t) = \sqrt{(x(t) - x(t-1))^2 + (y(t) - y(t-1))^2} \tag{4}$$

- Generate the turning-angle (TA) time series

$$A = \{(t, a(t))|\ t = 2, ..., t_f\} \tag{5}$$

using the derived values

$$a(t) = \arctan\left(\frac{y(t) - y(t-1)}{x(t) - x(t-1)}\right) - \arctan\left(\frac{y(t-1) - y(t-2)}{x(t-1) - x(t-2)}\right) \tag{6}$$

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

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

$$V^{xx} = \{(t, v^{xx}(t))|\ t = 1, ..., t_f\} \quad \text{for } x = a,\ s, \tag{7}$$

where

$$v^{xx}(t) = \frac{\big(x(t) - \mu_x\big)\big(x(t-1) - \mu_x\big)}{\sigma_x} \tag{8}$$

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

$$V^{as} = \{(t, v^{as}(t))|\ t = 1, ..., t_f\} \tag{9}$$

where

$$v^{as}(t) = \frac{\big(a(t) - \mu_a\big)\big(s(t) - \mu_s\big)}{\sqrt{\sigma_a \sigma_s}} \tag{10}$$

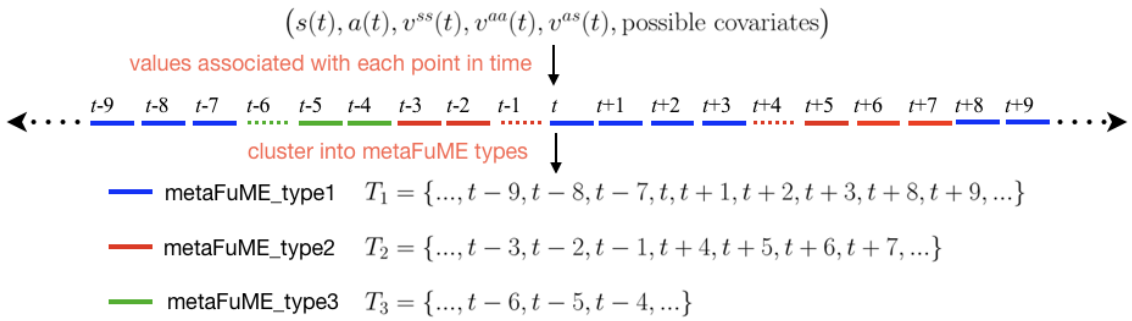

Figure 3: **Parsing the walk W into a set of metaFuMEs.** Associated with each point t is a set of running values $\big(s(t), a(t), v^{ss}(t), v^{aa}(t), v^{as}(t)$, other possible covariates$\big)$. Cluster analysis may be used to generate metaFuME categories. For purposes of illustration, we depict three types of metaFuMEs with associated lists of time steps that can then be used to define the ensemble of values associated with each metaFuME type: blue $= \mathcal{T}_1$, red $= \mathcal{T}_2$, and green $= \mathcal{T}_3$. 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).

We are now challenged with the task of using the five time series above—and, perhaps, other covariate data when available (e.g., acoustic, accelerometer, local environmental)—to parse W into an several, say Φ, different one-step ensembles (Fig. 3). Each of these Φ ensembles can now be regarded as a set of drawings from the same bivariate distribution $D_\phi(s, a)$, $\phi = 1, ..., \Phi$. If the relocation sampling period, except for speed bursts, encompasses around 10-50 FuMEs (i.e., more than around 5 seconds but less than about a minute—fast walking in humans crudely corresponds to 2 steps per second, though most movement is slower than this); then, in the proposed hierarchical segmentation 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 metaFuMEs.

Once a set of metaFuMEs has been identified from a particular ensemble of segments of the same CAM or DAR type, 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 LiTT, 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, multicrietria optimization methods using, for example, genetic algorithms or approximate Bayesian computations (Coello 2003, Odu & 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.

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 Φ metaFuMEs, we then identify the index time sets T_ϕ, $\phi = 1, ..., \Phi$, associated with each ensemble (Fig. 3). The distributions of all the joint pairs $(s(t), a(t))$, where $t \in \mathbf{T}_\phi$, $\phi = 1, ..., \Phi$, may be fitted to appropriate metaFuME bivariate distributions $D_\phi(s, a)$, $\phi = 1, ..., \Phi$. In essence, we have estimated the a set of bivariate metaFuME

distributions

$$\mathcal{D}_\Phi = \{D_1(s,a), ..., D_\Phi(s,a)\}. \tag{11}$$

The final missing piece is now use the set of switching times among the index sets (this would be switching between modes at the finest possible scale (Patterson et al. 2008) rather than at courser scales Morales et al. 2004, Jonsen et al. 2007)

$$\mathcal{T}_\Phi = \{T_\phi | \phi = 1, ..., \Phi\}$$

to estimate a matrix of probabilities $(\mathbf{P})_{\phi\psi} = p_{\phi\psi},\ \phi,\ \psi = 1, ..., \Phi$ of the probability of sampling values from the distribution $D_\phi(s,a)$ when the previous drawing was from the distribution $D_\psi(s,a)$. In this case, any walk $W(t_f)$ can be modeled as a process generated by first undertaking the following T drawings (the hat notation represents drawings)

$$T \text{ drawings} := \quad \{(\hat{s}_t, \hat{a}_t) \text{ sampled from } D_\psi(s,a) \text{ with probability } p_{\phi\psi} | t = 0, ..., t_f - 1\} \tag{12}$$

and then generating $W(t_f)$ from these drawings using the equations (Patterson et al. 2008)

$$\begin{aligned} x(t+1) &= x(t) + \hat{s}_t \cos \hat{a}_t \\ y(t+1) &= y(t) + \hat{s}_t \sin \hat{a}_t \end{aligned} \tag{13}$$

Thus, in short, the drawings are a Markov process that facilitates the construction of a walk W that is one instantiation of an ensemble of walks that can be generated using Eqs. 12 and 13 from a proposed or identified metaFuME-distribution-set and transition-matrix pair $(\mathcal{D}_\Phi, \mathbf{P})$.

A priori, the best-fit number of distribution pairs Φ in the set $\mathcal{D}_\Phi$ (Eq. 11) is unknown. A first guess at this number might be the number of modes in H^{SL} or H^{TA}, if such modes are evident. The problem of finding the best mixture of unimodal pairs $(D_\phi^{\text{SL}}, D_\phi^{\text{TA}})$ of distributions that best fit the empirical data is a challenging estimation problem that has been approached in several ways, including ensemble Kalman filtering (Dovera & Della Rossa 2011) and assuming 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 (the tilde used to indicate that they are "best fitting"):

$$\tilde{\mathcal{D}}_2 = \{\tilde{D}_1(s,a), \tilde{D}_2(s,a)\} \tag{14}$$

and then moving on to three, four, and so on, until no improvement in fit is obtained at the next value for Φ in an information theoretic sense (Symonds & Moussalli 2011).

In a nutshell, the challenge we face is the identification of a set of distributions $\tilde{\mathcal{D}}_\Phi$(where *a priori* the size of the set Φ is unknown) and a Markov transition matrix $\tilde{\mathbf{P}}$ that can then be used to generate N walks $\tilde{W}_i(t_f),\ i = 1, ..., N$ of length T for which our particular empirical walk $W^{\text{data}}(t_f)$ is most likely to belong; or expressed mathematical using uppercase italics to denote individual walks and uppercase calligraphy to denote a set of walks, suppressing the argument in T we have:

$$\tilde{\mathcal{W}}^{\text{ensemble}} = \left\{\tilde{W}_i | i = 1, ..., N\right\} \quad \text{is a "best fitting" ensemble to } \ W^{\text{data}} \tag{15}$$

This of course is an extremely challenging undertaking that can be made more manageable by breaking it down into a series of separate more manageable tasks, as discussed below, to make the identification of the best-fitting pair $\left(\tilde{\mathcal{D}}_\Phi, \tilde{\mathbf{P}}\right)$ possible.

Hierarchical Segmentation of Walks

From a practical point of view, particularly as the size of relocation data sets increases when collected at frequencies of around 0.01 to 0.1 Hz, the following approach might prove useful to carrying out a hierarchical segmentation analysis of relocation data. The goal is to obtain ensembles of similar segments that can then used to identify sets of metaFuMEs, initially ensemble by ensemble of similar segments types (typically, ensembles of particular CAM types), and then through consolidation of various metaFuME sets to obtain single metaFuME set applicable to segments of a particular LiMP type (since different LiMPs may be age dependent and fundamental movement elements may also be age dependent)

1. From plots of a relocation data set W^{data} on landscapes (i.e., eyeballing it)—or using any appropriate identification method, such as net-square-displacement data (Bunnefeld et al. 2011, Bischof et al. 2012)—select one or more subsets of W^{data} that individually appear to belong to particular types of LiMPs (e.g., sort segments of W^{data} into $\text{LiMP}_{\text{type}}$, where type=migratory, wet season-residence, etc.) (Fig. 4). The occurrences and frequencies of different types of LiMPs in a LiTT can be then used to categorize an individual's LiTT type, thereby providing a less adhoc alternative to other approaches that may be used (Abrahms et al. 2017)).

2. Sort 24-hour segments of $W^{\text{LiMP}_{\text{type}}}$ (e.g., midnight to next midnight for diurnal species or midday to next midday for nocturnal species) into one or more DAR types ($W^{\text{DAR}_{\text{type}}}$, type $= 1, 2, ...$) and generate a set of summary statistics relating to the SL and TA time series associated with these DAR segments.

3. Use SL, TA, and derived correlation statistics statistics (Eqs. 3-10) to cluster (McGarigal et al. 2016) these 24-hour DAR segments into a set of g_n DAR types or use machine learning methods (Thessen 2016) to create such sets: i.e., recalling notational definition Eq. 2, create sets $\mathcal{W}^{\text{DAR}_g}$ and fit their summary statistics to appropriate distributions $D^{\text{DAR}_g}(s, a)$, $g = 1, ..., g_n$. Note that different $W^{\text{LiMP}_{\text{type}}}$ may yield the same set of DARs, but in very different proportions over their extents. Alternatively, some of them may have one or more DAR types not found in other $W^{\text{LiMP}_{\text{type}}}$ segments.

4. After stringing together all the data contained in $\mathcal{W}^{\text{DAR}_g}$, use one or more segmentation methods to obtain a consensus on the best way to segment these strings into an optimal number of CAM types (Fig. 4). Depending on the resolution of the data, these may be long or short duration CAMs or both (Owen-Smith & Martin 2015). If the process is first applied to obtain long duration CAMS (e.g., using BCPA based on a relatively wide sliding window of say 30 minutes; Owen-Smith & Martin 2015), then each of these long duration CAMS may then be further segmented into short duration CAMS (e.g., using BCPA based on a narrower sliding window of say 10 minutes, should the data permit), though care has to be taken that short duration CAMs obtained from different long duration CAMs are reconciled to optimize the number of shorter duration CAMs that, in different proportions, constitute long duration CAMs. The same can be said of optimizing the number of CAMs used in different proportions to build up the different types of DARs (Fig. 4)

5. Using various sets of CAMs and, possibly DARs, of the same type, apply "yet to be devised methods" to identify the sets of metaFuMES, using the general approach outlined in the

next section that will likely drawn upon clustering methods (McGarigal et al. 2016) and multicriteria optimization (Odu & Charles-Owaba 2013).

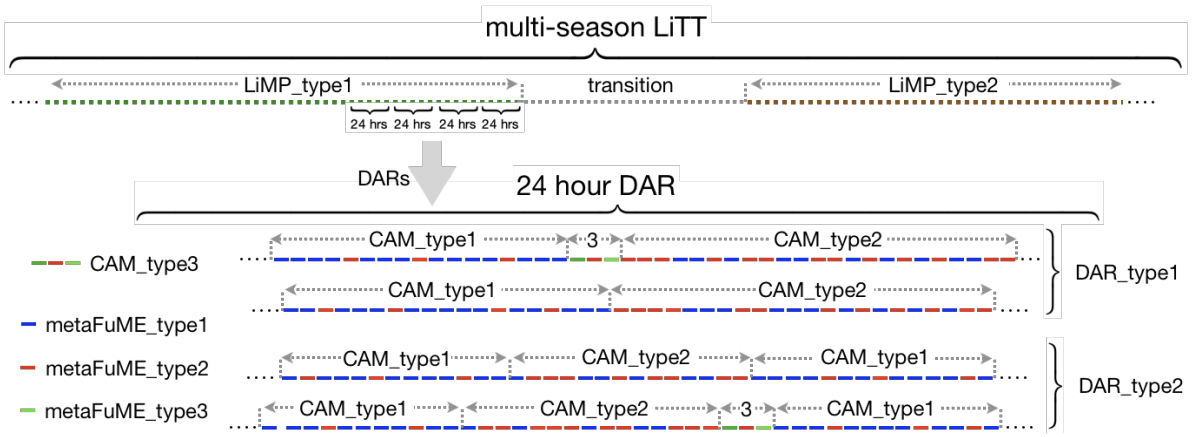

Figure 4: **The structure of a movement path at different scales.** A multi-season lift-time track (LiTT) W (Eq. 1) can be segmented at various scales: first into different types of life-history movement phases (LiMPs), each which can be then be parsed into diel segments that are then classified as being of a particular diel activity routine (DAR) type. These DARs can be parsed into canonical activity mode (CAM) segments, each of which are composed of different proportions of metaFuMEs (aggregates of correlated fundamental movement elements), where each metaFuME is characterized by a joint step-length and turning-angle ((s, a); Eqs 4 and 6) distribution with specific first-order and correlative statistics. Short duration CAMs (e.g., CAM 3) can easily be hidden by being averaged into longer duration CAMs (e.g., CAMs 1 and 2), if DAR segmentation analyses are not done at a sufficient fine scale. For simplicity, only two or three types of path segments are depicted at each identified scale.

Conclusion

Without an underlying framework to organize information, deep comprehension within any scientific field is impossible. Clearly this has been true of the physical sciences with theories of gravity and the structure of matter being central to our current understanding of the physical universe. This is also true of the life sciences where, for example, the Linnaean taxonomic system, with some modifications, has reigned supreme over the past 250 years (Schuh 2003). This reign still holds today, even within the microbial sciences (Rosselló-Móra & Whitman 2019, Moore et al. 2010) where Mayr's biological species concept fails in several critical ways (Gevers et al. 2005).

In the context of movement ecology, the classification of movement types at different spatio-temporal scales is of considerable interest, although approaches to date have been somewhat informal. At the LiTT 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 routine (DARs) (Rahimi & Owen-Smith 2007, Owen-Smith 2013, Owen-Smith & Goodall 2014), life-time phase (LiMPs) (Fahr et al. 2015, Marra et al. 2015) and over-all life time tracks (LiTTs) (Abrahms et al. 2017). Contrasting DAR types may include distinctions among nomadic, central-place foraging, or territorial behavior, where a single LiTT may have LiMPs dominated by one or other of these DARs, as in male springbok in Etosha National Park, Namibia,

exhibiting territorial behavior during the wet season and nomadic behavior during the dry season, with daily excursions to the same water-hole 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 diel 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 & Saltz 2008). At finer time scales, however, beyond using accelerometer, acoustic and magento 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; same as FMEs in Getz & Saltz 2008) from which CAMs are constructed. As pointed out in this paper, using relocation data alone, we cannot endeavour to identify an underlying set of FuMEs. The best we can hope for, provide subminute relocation data is 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. It may require many of the ideas presented here to be refined or modified. But there is no denying, however, that if successful, a formalized, widely accepted, hierarchical-path-segmentation 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 & Post 2015). It may help us assess fitness in the context of feeding strategies or social behavior (Harel et al. 2017, Harel, Duriez, Spiegel, Fluhr, Horvitz, Getz, Bouten, Sarrazin, Hatzofe & Nathan 2016) or mapping out landscapes in terms of their overall resistance to movement (Zeller et al. 2012) (which, for example, has bearing on the amount of energy it takes to travel a given distance) or areas attractive to populations (Giotto et al. 2015). 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' LiMP/DAR/CAM movement profiles 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).

In addition, a formalized, hierarchical-path-segmentation 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. The framework

presented here is a starting point to developing a more comprehensive one that can be fleshed out in the future, supported by analytical and computational methods, some of which still need to be developed or refined from existing methods.

Glossary

An expansion of the various acronyms used in the text are provided here in alphabetical order along with a very brief definition/explanation of their meaning.

BCPA: Biological Change Point Analysis. Biological 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 & 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-hour sequence of CAMs that occur at characteristic frequencies and times of the day.

FuME: Fundamental Movement Elements (also FME; Getz & Saltz 2008). This is a relatively rapid, highly repeatable, steorotypic 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)

LiMP: Life-history 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.

LiTT: Life Time Track. This is the total movement path of an individual from its birth to its death

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. 4.

TA: Turning Angle. The change in the angle of heading across three consecutive relocation points, as generated from Eq. 1 using Eq. 6.

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