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 and relate to one another, as well as 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 theoretical 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 [1], 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 [2]—from the sequencing of various high-resolution movement elements to the emergence of seasonal home ranges and habitat utilization distributions [3, 4, 5, 6]. 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 [7]), 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 [8, 9]. From these relocation time series, sequences of step lengths (SL) and turning angles (TA) can be extracted [10, 11], and organized into time-stamped pairs of values. Other data, such as accelerations [12], audio [13, 14, 15] and magnetometer [16, 17] data, as well as physiological measurements (e.g., temperature, blood glucose levels) [18], 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 [19, 20, 21], as well as local environmental features that are often inferred using remotely sensed electromagnetic spectral data (e.g., visual and infra-red satellite imagery or lidar) [22, 23, 24].

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 [25, 26, 27]. 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 [28, 9, 29] that include hidden Markov models (HMMs; [30, 31, 32, 33]) and behavioral change-point analyses (BCPA; [34, 35, 36]). The second is the language of mathematical stochastic walks [10, 37, 38] that treats movement relocation data as a time series of values and applies existing time-series methods [39] to finding the parameter values that best fit selected time-series models to movement paths, with the possible inclusion of individual and environmental covariates [40, 41, 42, 43, 44].

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; [20])—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.

A Pragmatic View of Path Segmentation

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., wingflaps of small birds [13, 15] or footfalls of foraging ungulates [15]. 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 "meta-FuME" 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 [39]. 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; [20]).

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, current technologies are promoting the collection of data at frequencies of 0.01 to 1 Hz in birds [45, 46] and mammals [47, 48] 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 [49, 50]); but currently reverse GPS is limited 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 [51, 52, 53]. 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 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 [54, 55, 56], 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 [57] and of the variation in the diel travel rates of turtles [58].

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 [59]) or episodic (e.g., dispersal; for a review see [60]). Finally, a sequences of LiMPs sequentially strung together from the birth-to-death of an individual constitute its full lifetime track (LiTT; [1]) (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 [61].

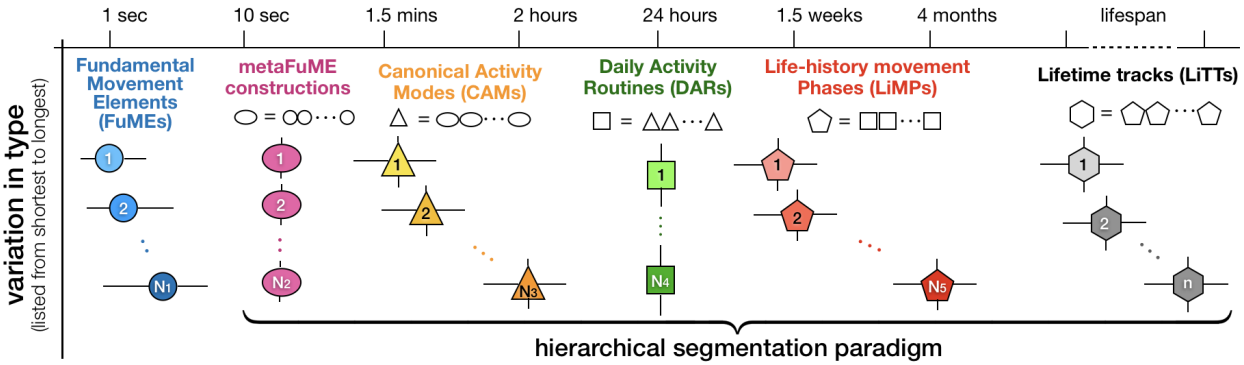

Figure 1: **Scale-dependent path segmentation categories of lifetime track segments.** The time scale applies to typical medium and large terrestrial animals and needs to be adjusted for aerial and marine species, and small animals, including invertebrates. Round (blue), oval (lilac), triangular (yellow 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). 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.

This pragmatic 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 [62, 63] for the parsing of movement paths. It also provides a

semantic framework for the quantitative narratives [64] 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 [65, 66].

Beyond the relevance of diel cycles to movement behavior [67], are lunar [68] and seasonal cycles [69]; and even weekly 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 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 [68], while only for relatively long-lived organisms will their LiTTs cover sufficiently many seasonal cycles to support a statistical analyses of repeated LiMP motifs [69, 70]. For some organisms, particular LiMPs, such 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 [71, 72] or sunspot [73] 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 [74, 75]. 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; [76]), 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 [13, 14, 15], magnetometer [16, 17], and video [51, 52, 53] may well be more cost effect in terms 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 has been used to parse out relatively short time scale (order of 10 secs) behavioral elements along movement paths using machine learning methods [12, 77, 78]. These behavioral elements, which almost certainly include several FuME steps, in reality are partial elements of more extensive short-duration CAMs that

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: type of analysis				
FuMEs[*]	0.1–few secs	0–1000 cms	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 & TA[¶] distributions	SL & TA means, variances & correlations[††]	cluster analysis ensemble filtering
	base level: movement ecology analyses				
short duration **CAMs**[†]	0.1–10 mins	a few meters to a few kms	resting, browsing, riding thermals	secs to mins, metaFuMEs & covariate data	path segmentation[**]
	highly flexible: sub-hourly/hourly analysis				
long duration **CAMs**[†]	10-100 mins	a few meters to many kms	feeding traveling	mins to hours, short CAMs & covariate data	
	highly flexible: sub-diel analysis				
DARs[‡]	fixed 24-hr	diel range	central-place foraging ranging	24 hrs of data CAM sequences	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 **LiTTs**[#]	paths encompassing several LiMPs	habitat types	territorial ranging, migratory nomadic	LiMP sequences	GIS toolbox, deep-learning[*†], pattern anal.
	moderately constrained: question-at-hand analysis				

[*]Fundamental Movement Elements; [†]Canonical Activity Modes; [‡]Diel Activity Routines

[§]Life-history Movement Phases; [#]Life Time Tracks; [¶]SL=step-length & TA=turning-angle

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

[*‡]Around 5 secs to 1 min

[**]Includes Hidden Markov Models (HMMs) and Behavioral Change-Point Analyses (BCPA)

[††]See Section on **Stochastic Walks and MetaFuMEs** in main text

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 [12]. Another analysis 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 [79]. In pumas, accelerometer has been used to identify low versus high acceleration

movement phases, resting, eating and grooming [78]. In these examples, sitting/resting, 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 [13, 14, 15], magnetometer [16, 17] or video [51, 52, 53] data.

In summary, location data on its own (i.e., without accompanying subsecond accelerometer, acoustic, magnetometer or video data) is 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 [62, 63], 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)—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; [80]), long duration CAMs (e.g., heading to water; [81]), or only movement patterns at diel scales and beyond [82, 83, 27].

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 [39, 97, 98, 99]. 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; [36, 100, 101, 102, 34, 35]) (Fig. 2) or, more generally, path segmentation methods (PS; [28, 9, 29]).

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

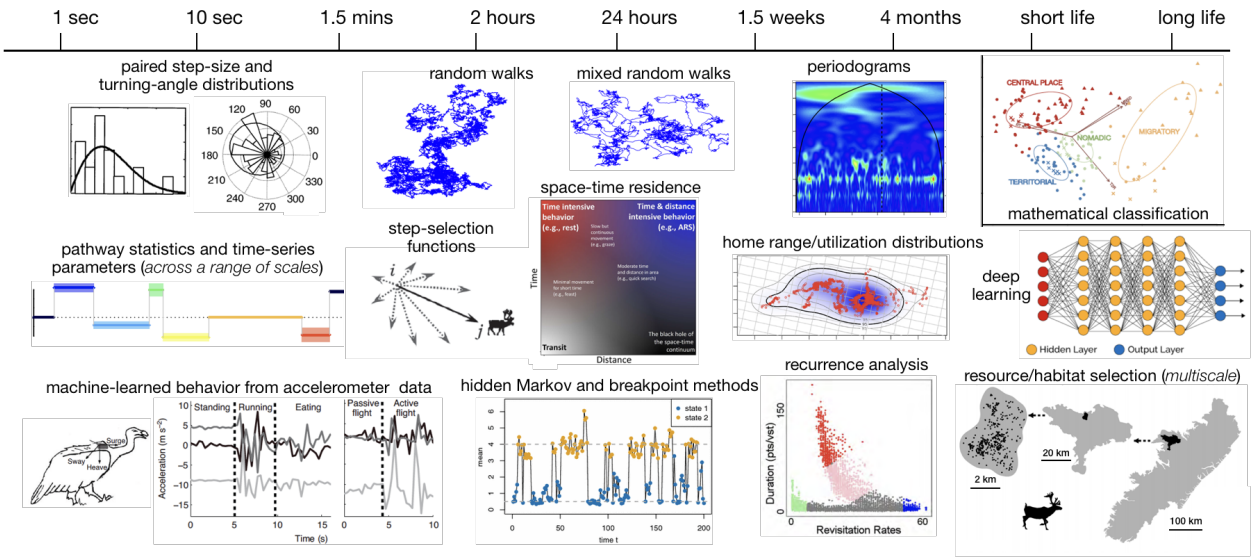

Figure 2: **Current scale-dependent analytical methods for analysing movement paths.** The temporal range is only suggestive and best applied to medium and large vertebrates. Also the image placements are not precise and some methods, such as machine learning [77], can be applied to data at any scale, 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; [12, 79]). Stochastic walks include correlated and biased random walks [42]. Space-time residence analyses represents a family methods that include first-passage-time (FTP; [84, 85]) and related approaches [86], while recurrence analyses cover a plethora of methods used to identify recursive movement patterns [87, 88]. The melange of images is extracted from publications in the literature [12, 89, 90, 91, 67, 92, 93, 94, 95, 86, 96], as well as created for this publication.

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 [38]. A very simple example is the stop/move representation of cattle grazing paths [103]. 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) [30, 31, 32, 33] (Fig. 2), although an independent mixture modeling approach has been shown to be equally viable, if not better [104]. 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 [105], vegetation structure [106], or physical landscape features that, for example, facilitate or retard movement [107]. 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 [108, 89, 109, 110]. 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 [111, 112, 91] 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 [113].

Other general time-series or signal-analysis methods that have been co-opted by movement ecologists include wavelet analysis [67, 68]—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 [77, 114] that have been applied both to location [115] and accelerometer data [12] (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 [116], audio [13], or other kinds of covariate data [17] 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

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

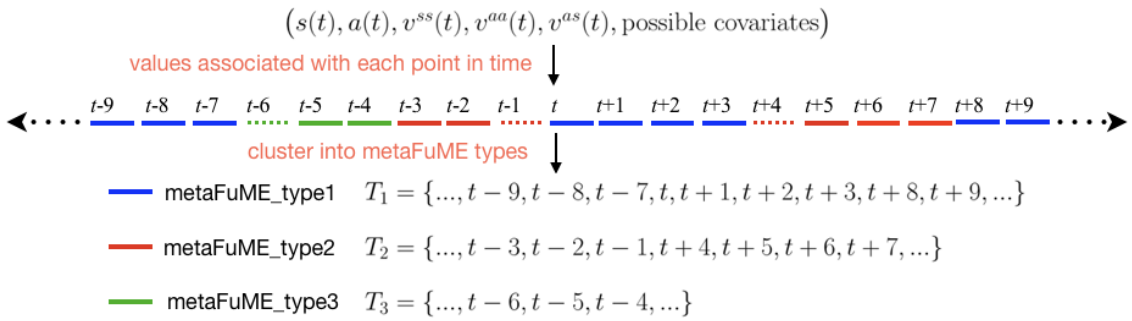

Figure 3: **Parsing the walk W into a set of metaFuMEs.** Associated with each point t is a set of running values $\big(s(t), a(t), v^{ss}(t), v^{aa}(t), v^{as}(t)$, other possible covariates$\big)$. Cluster analysis may be used to generate metaFuME categories. For purposes of illustration, we depict 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).

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
$$V^{\ell\ell} = \{(t, v^{\ell\ell}(t))|\ t = t_b, t_b+1, ..., t_f\} \quad \text{for } \ell = s\,(t_b = 2),\ a\,(t_b = 3), \tag{7}$$
where
$$v^{\ell\ell}(t) = \frac{\big(\ell(t) - \mu_\ell\big)\big(\ell(t-1) - \mu_\ell\big)}{\sigma_\ell} \tag{8}$$

- Generate a normalized "running-term cross-correlation" time series
$$V^{as} = \{(t, v^{as}(t))|\ t = 2, ..., t_f\} \tag{9}$$
where
$$v^{as}(t) = \frac{\big(a(t) - \mu_a\big)\big(s(t) - \mu_s\big)}{\sqrt{\sigma_a \sigma_s}} \tag{10}$$

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 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 [112] can be tried to identify metaFuMEs. Also, multicriteria optimization methods using, for example, genetic algorithms or approximate Bayesian computations [117, 118, 119] 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 a set of bivariate metaFuME distributions

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

The final missing piece is to now use the set of switching times among the index sets (this would be switching between modes at the finest possible scale [38] rather than at courser scales [90, 120])

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

to estimate a matrix of probabilities $(\mathbf{P})_{\phi\psi} = p_{\phi\psi}$, ϕ, $\psi = 1, ..., \Phi$ 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 [38]

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

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 [121] and assuming the underlying distributions are log-concave [122]. 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 [123].

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:

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

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 be used to identify sets of metaFuMEs, initially ensemble by ensemble of similar segment 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 [124, 125]—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 ad-hoc alternative to other approaches that may be used [93]).

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 [112] these 24-hour DAR segments into a set of g_n DAR types or use machine learning methods [77] 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 $\mathcal{W}^{\mathrm{DAR}_g}$, 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 [36]. 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; [36]), 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 [112] and multicriteria optimization [118].

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 [126]. This reign still holds today, even within the microbial sciences [127, 128] where Mayr's biological species concept fails in several critical ways [129].

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) [130, 83, 131], life-time phase (LiMPs) [132, 69] and over-all life time tracks (LiTTs) [93]. 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 [92]. 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 [133].

Extensive effort has also been made to parse diel and longer segments into various types of sub-diel activity modes [134, 57] that, if stably identifiable across different segments, can be organized into a set of canonical activity modes (CAMs; [20]). At finer time scales, however, beyond using accelerometer, acoustic and magnetometer data to identify behavioral states [16, 14, 12, 79, 17, 13, 33], very little work has been undertaken to identify sets of fundamental movement elements (FuMEs; same as FMEs in [20]) from which CAMs are constructed. As pointed out in this paper,

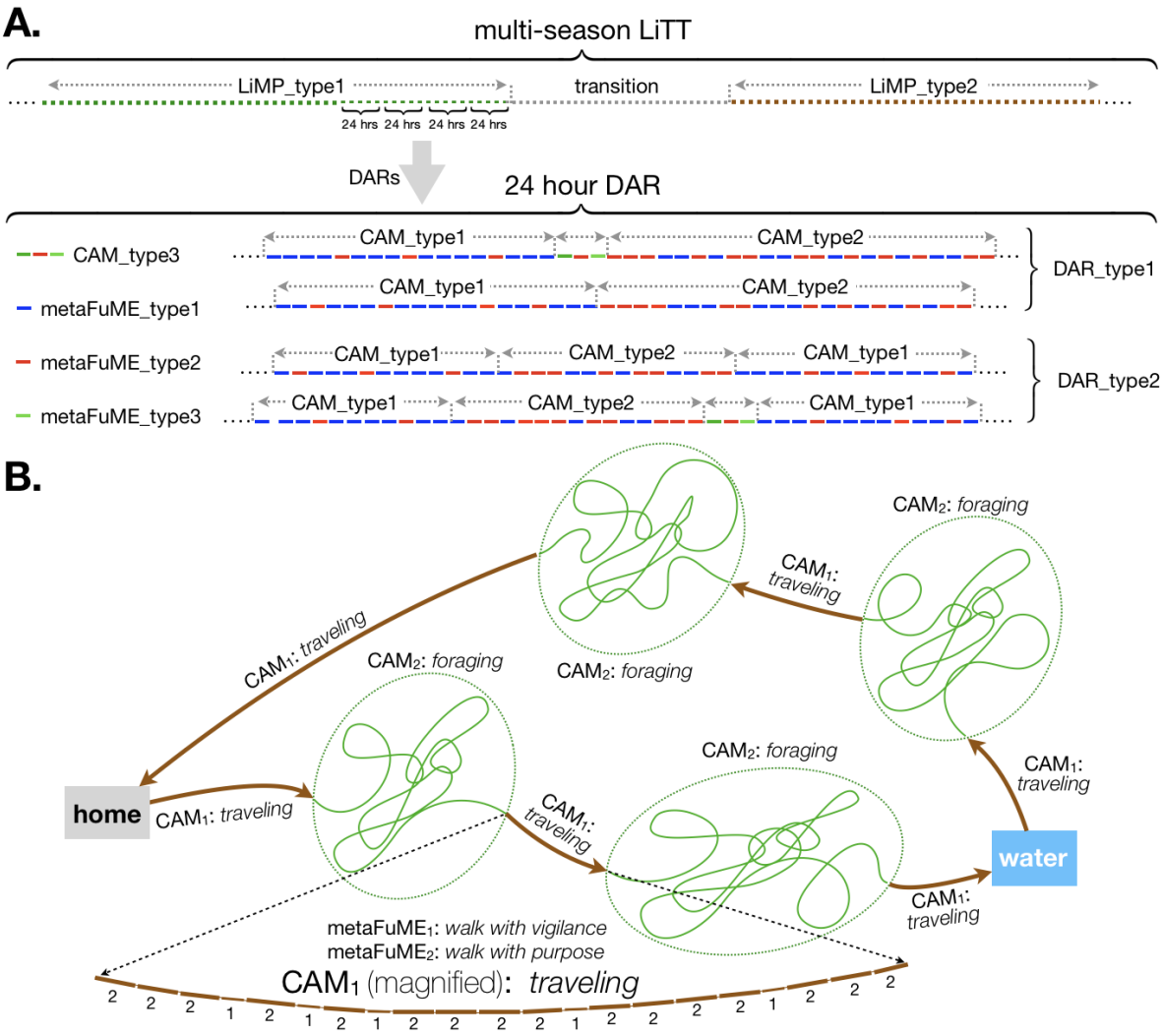

Figure 4: **The segmentation structure of movement paths at different scales. A.** A multi-season life-time track (LiTT) W (Eq. 1) can be segmented into different types of life-history movement phases (LiMPs), each of which can then be segmented into diel activity routines (DARs) and again segmented 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 is 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.

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 [6], 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 [135]. It may help us assess fitness in the context of feeding strategies or social behavior [136, 137] or mapping out landscapes in terms of their overall resistance to movement [107] (which, for example, has bearing on the amount of energy it takes to travel a given distance) or areas attractive to populations [27]. It may also be diagnostic of changes in movement behavior when individuals are stressed, ill, have genetic defects, or females are pregnant [51, 83]; or it may be predictive in terms of pathogen transmission and the spread of disease [138, 139, 140, 141]. 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 [142, 143].

In addition, a formalized, hierarchical-path-segmentation framework of appropriate complexity [62, 63] can be used, for example, to address the dozen plus questions that were recently posed regarding the movement ecology of marine megafauna [144]—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: 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) [90, 145, 100, 120]. 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; [20]). 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) [33]

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 [28, 9, 29].

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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References

[1] Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, et al. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences. 2008;105(49):19052–19059.

[2] Levin SA. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology. 1992;73(6):1943–1967.

[3] Worton B. A review of models of home range for animal movement. Ecological modelling. 1987;38(3-4):277–298.

[4] Morellet N, Bonenfant C, Börger L, Ossi F, Cagnacci F, Heurich M, et al. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within E urope. Journal of Animal Ecology. 2013;82(6):1326–1339.

[5] Torney CJ, Hopcraft JGC, Morrison TA, Couzin ID, Levin SA. From single steps to mass migration: the problem of scale in the movement ecology of the Serengeti wildebeest. Philosophical Transactions of the Royal Society B: Biological Sciences. 2018;373(1746):20170012.

[6] Wittemyer G, Northrup JM, Bastille-Rousseau G. Behavioural valuation of landscapes using movement data. Philosophical Transactions of the Royal Society B. 2019;374(1781):20180046.

[7] Morelle K, Podgórski T, Prévot C, Keuling O, Lehaire F, Lejeune P. Towards understanding wild boar *Sus scrofa* movement: a synthetic movement ecology approach. Mammal Review. 2015;45(1):15–29.

[8] Siniff DB, Jessen C. A simulation model of animal movement patterns. In: Advances in ecological research. vol. 6. Elsevier; 1969. p. 185–219.

[9] Edelhoff H, Signer J, Balkenhol N. Path segmentation for beginners: an overview of current methods for detecting changes in animal movement patterns. Movement ecology. 2016;4(1):21.

[10] Kareiva P, Shigesada N. Analyzing insect movement as a correlated random walk. Oecologia. 1983;56(2-3):234–238.

[11] Turchin P. Quantitative analysis of movement. Sinauer assoc. Sunderland (mass.); 1998.

[12] Nathan R, Spiegel O, Fortmann-Roe S, Harel R, Wikelski M, Getz WM. Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. Journal of Experimental Biology. 2012;215(6):986–996.

[13] Sapir N, Wikelski M, McCue MD, Pinshow B, Nathan R. Flight modes in migrating European bee-eaters: heart rate may indicate low metabolic rate during soaring and gliding. PLoS One. 2010;5(11):e13956.

[14] Hurme E, Gurarie E, Greif S, Flores-Martínez JJ, Wilkinson GS, Yovel Y, et al. Acoustic evaluation of behavioral states predicted from GPS tracking: a case study of a marine fishing bat. Movement ecology. 2019;7(1):21.

[15] Northrup JM, Avrin A, Anderson CR, Brown E, Wittemyer G. On-animal acoustic monitoring provides insight to ungulate foraging behavior. Journal of Mammalogy. 2019;.

[16] Williams HJ, Holton MD, Shepard EL, Largey N, Norman B, Ryan PG, et al. Identification of animal movement patterns using tri-axial magnetometry. Movement ecology. 2017;5(1):6.

[17] Chakravarty P, Maalberg M, Cozzi G, Ozgul A, Aminian K. Behavioural compass: animal behaviour recognition using magnetometers. Movement Ecology. 2019;7(1):28.

[18] Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. Ecology. 2015;96(7):1741–1753.

[19] Shepard EL, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB. Energy landscapes shape animal movement ecology. The American Naturalist. 2013;182(3):298–312.

[20] Getz WM, Saltz D. A framework for generating and analyzing movement paths on ecological landscapes. Proceedings of the National Academy of Sciences. 2008;105(49):19066–19071.

[21] Spiegel O, Harel R, Centeno-Cuadros A, Hatzofe O, Getz WM, Nathan R. Moving beyond curve fitting: using complementary data to assess alternative explanations for long movements of three vulture species. The American Naturalist. 2015;185(2):E44–E54.

[22] Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jedrzejewska B, Lima M, et al. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research. 2011;46(1):15–27.

[23] Pettorelli N, Laurance WF, O'Brien TG, Wegmann M, Nagendra H, Turner W. Satellite remote sensing for applied ecologists: opportunities and challenges. Journal of Applied Ecology. 2014;51(4):839–848.

[24] Bork EW, Su JG. Integrating LIDAR data and multispectral imagery for enhanced classification of rangeland vegetation: A meta analysis. Remote Sensing of Environment. 2007;111(1):11–24.

[25] Johnson CJ, Parker KL, Heard DC, Gillingham MP. A multiscale behavioral approach to understanding the movements of woodland caribou. Ecological Applications. 2002;12(6):1840–1860.

[26] Owen-Smith N, Goodall V. Movement informatics of large mammalian herbivores across hierarchical scales: inferring biology from statistics. Under review. 2019;.

[27] Giotto N, Gerard JF, Ziv A, Bouskila A, Bar-David S. Space-use patterns of the Asiatic wild ass (*Equus hemionus*): complementary insights from displacement, recursion movement and habitat selection analyses. PloS one. 2015;10(12):e0143279.

[28] Nams VO. Combining animal movements and behavioural data to detect behavioural states. Ecology letters. 2014;17(10):1228–1237.

[29] Seidel DP, Dougherty E, Carlson C, Getz WM. Ecological metrics and methods for GPS movement data. International Journal of Geographical Information Science. 2018;32(11):2272–2293.

[30] Michelot T, Langrock R, Patterson TA. moveHMM: An R package for the statistical modelling of animal movement data using hidden Markov models. Methods in Ecology and Evolution. 2016;7(11):1308–1315.

[31] Franke A, Caelli T, Hudson RJ. Analysis of movements and behavior of caribou (Rangifer tarandus) using hidden Markov models. Ecological Modelling. 2004;173(2-3):259–270.

[32] Langrock R, King R, Matthiopoulos J, Thomas L, Fortin D, Morales JM. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. Ecology. 2012;93(11):2336–2342.

[33] Zucchini W, MacDonald IL, Langrock R. Hidden Markov models for time series: an introduction using R. Chapman and Hall/CRC; 2016.

[34] Gurarie E, Andrews RD, Laidre KL. A novel method for identifying behavioural changes in animal movement data. Ecology letters. 2009;12(5):395–408.

[35] Gurarie E, Bracis C, Delgado M, Meckley TD, Kojola I, Wagner CM. What is the animal doing? Tools for exploring behavioural structure in animal movements. Journal of Animal Ecology. 2016;85(1):69–84.

[36] Owen-Smith N, Martin J. Identifying space use at foraging arena scale within the home ranges of large herbivores. PloS one. 2015;10(6):e0128821.

[37] Bartumeus F, da Luz MGE, Viswanathan GM, Catalan J. Animal search strategies: a quantitative random-walk analysis. Ecology. 2005;86(11):3078–3087.

[38] Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J. State–space models of individual animal movement. Trends in ecology & evolution. 2008;23(2):87–94.

[39] Chatfield C. The analysis of time series: an introduction. Chapman and Hall/CRC; 2016.

[40] Jonsen ID, Myers RA, Flemming JM. Meta-analysis of animal movement using state-space models. Ecology. 2003;84(11):3055–3063.

[41] Preisler HK, Ager AA, Johnson BK, Kie JG. Modeling animal movements using stochastic differential equations. Environmetrics. 2004;15(7):643–657.

[42] Johnson DS, London JM, Lea MA, Durban JW. Continuous-time correlated random walk model for animal telemetry data. Ecology. 2008;89(5):1208–1215.

[43] Fleming CH, Calabrese JM, Mueller T, Olson KA, Leimgruber P, Fagan WF. From fine-scale foraging to home ranges: a semivariance approach to identifying movement modes across spatiotemporal scales. The American Naturalist. 2014;183(5):E154–E167.

[44] Calabrese JM, Fleming CH, Gurarie E. ctmm: an r package for analyzing animal relocation data as a continuous-time stochastic process. Methods in Ecology and Evolution. 2016;7(9):1124–1132.

[45] Harel R, Horvitz N, Nathan R. Adult vultures outperform juveniles in challenging thermal soaring conditions. Scientific reports. 2016;6:27865.

[46] Harel R, Nathan R. The characteristic time-scale of perceived information for decision-making: Departure from thermal columns in soaring birds. Functional ecology. 2018;32(8):2065–2072.

[47] de Weerd N, van Langevelde F, van Oeveren H, Nolet BA, Kölzsch A, Prins HH, et al. Deriving animal behaviour from high-frequency GPS: tracking cows in open and forested habitat. Plos one. 2015;10(6):e0129030.

[48] McGavin SL, Bishop-Hurley GJ, Charmley E, Greenwood PL, Callaghan MJ. Effect of GPS sample interval and paddock size on estimates of distance travelled by grazing cattle in rangeland, Australia. The Rangeland Journal. 2018;40(1):55–64.

[49] Weiser AW, Orchan Y, Nathan R, Charter M, Weiss AJ, Toledo S. Characterizing the accuracy of a self-synchronized reverse-GPS wildlife localization system. In: Information Processing in Sensor Networks (IPSN), 2016 15th ACM/IEEE International Conference on. IEEE; 2016. p. 1–12.

[50] Toledo S, Kishon O, Orchan Y, Shohat A, Nathan R. Lessons and experiences from the design, implementation, and deployment of a wildlife tracking system. In: Software Science, Technology and Engineering (SWSTE), 2016 IEEE International Conference on. IEEE; 2016. p. 51–60.

[51] Spink A, Tegelenbosch R, Buma M, Noldus L. The EthoVision video tracking systema tool for behavioral phenotyping of transgenic mice. Physiology & behavior. 2001;73(5):731–744.

[52] Kane AS, Salierno JD, Gipson GT, Molteno TC, Hunter C. A video-based movement analysis system to quantify behavioral stress responses of fish. Water Research. 2004;38(18):3993–4001.

[53] Delcourt J, Denoël M, Ylieff M, Poncin P. Video multitracking of fish behaviour: a synthesis and future perspectives. Fish and Fisheries. 2013;14(2):186–204.

[54] Takahashi JS, Hong HK, Ko CH, McDearmon EL. The genetics of mammalian circadian order and disorder: implications for physiology and disease. Nature reviews genetics. 2008;9(10):764.

[55] Yerushalmi S, Green RM. Evidence for the adaptive significance of circadian rhythms. Ecology letters. 2009;12(9):970–981.

[56] Hardin PE, Panda S. Circadian timekeeping and output mechanisms in animals. Current opinion in neurobiology. 2013;23(5):724–731.

[57] Donati G, Campera M, Balestri M, Serra V, Barresi M, Schwitzer C, et al. Ecological and anthropogenic correlates of activity patterns in Eulemur. International Journal of Primatology. 2016;37(1):29–46.

[58] Jonsen ID, Myers RA, James MC. Robust hierarchical state–space models reveal diel variation in travel rates of migrating leatherback turtles. Journal of Animal Ecology. 2006;75(5):1046–1057.

[59] Milner-Gulland E, Fryxell JM, Sinclair AR. Animal migration: a synthesis. Oxford University Press; 2011.

[60] Bowler DE, Benton TG. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews. 2005;80(2):205–225.

[61] Mueller T, Fagan WF. Search and navigation in dynamic environments–from individual behaviors to population distributions. Oikos. 2008;117(5):654–664.

[62] Getz WM, Marshall CR, Carlson CJ, Giuggioli L, Ryan SJ, Romañach SS, et al. Making ecological models adequate. Ecology letters. 2018;21(2):153–166.

[63] Larsen LG, Eppinga MB, Passalacqua P, Getz WM, Rose KA, Liang M. Appropriate complexity landscape modeling. Earth-science reviews. 2016;160:111–130.

[64] Getz WM, Salter R, Tallam K. A quantitative narrative on movement, disease and patch exploitation in nesting agent groups. bioRxiv. 2019;Available from: `https://www.biorxiv.org/content/early/2019/10/03/791400`.

[65] Hein AM, Carrara F, Brumley DR, Stocker R, Levin SA. Natural search algorithms as a bridge between organisms, evolution, and ecology. Proceedings of the National Academy of Sciences. 2016;113(34):9413–9420.

[66] Cattarino L, McAlpine CA, Rhodes JR. Spatial scale and movement behaviour traits control the impacts of habitat fragmentation on individual fitness. Journal of Animal Ecology. 2016;85(1):168–177.

[67] Wittemyer G, Polansky L, Douglas-Hamilton I, Getz WM. Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. Proceedings of the National Academy of Sciences. 2008;p. pnas–0801744105.

[68] Polansky L, Wittemyer G, Cross PC, Tambling CJ, Getz WM. From moonlight to movement and synchronized randomness: Fourier and wavelet analyses of animal location time series data. Ecology. 2010;91(5):1506–1518.

[69] Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM. A call for full annual cycle research in animal ecology. Biology letters. 2015;11(8):20150552.

[70] Allen RM, Metaxas A, Snelgrove PV. Applying movement ecology to marine animals with complex life cycles. Annual Review of Marine Science. 2018;10:19–42.

[71] Mysterud A, Stenseth NC, Yoccoz NG, Langvatn R, Steinheim G. Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. Nature. 2001;410(6832):1096.

[72] Grémillet D, Boulinier T. Spatial ecology and conservation of seabirds facing global climate change: a review. Marine Ecology Progress Series. 2009;391:121–137.

[73] Myers JH. Population cycles: generalities, exceptions and remaining mysteries. Proceedings of the Royal Society B: Biological Sciences. 2018;285(1875):20172841.

[74] Hinton G, Deng L, Yu D, Dahl GE, Mohamed Ar, Jaitly N, et al. Deep neural networks for acoustic modeling in speech recognition: The shared views of four research groups. IEEE Signal processing magazine. 2012;29(6):82–97.

[75] Zhang Z, Geiger J, Pohjalainen J, Mousa AED, Jin W, Schuller B. Deep learning for environmentally robust speech recognition: An overview of recent developments. ACM Transactions on Intelligent Systems and Technology (TIST). 2018;9(5):49.

[76] Williams HJ, Taylor LA, Benhamou S, Bijleveld AI, Clay TA, de Grissac S, et al. Optimising the use of bio-loggers for movement ecology research. Journal of Animal Ecology. 2019;.

[77] Thessen A. Adoption of machine learning techniques in ecology and earth science. One Ecosystem. 2016;1:e8621.

[78] Wang Y, Nickel B, Rutishauser M, Bryce CM, Williams TM, Elkaim G, et al. Movement, resting, and attack behaviors of wild pumas are revealed by tri-axial accelerometer measurements. Movement Ecology. 2015;3(1):2.

[79] Fehlmann G, ORiain MJ, Hopkins PW, OSullivan J, Holton MD, Shepard EL, et al. Identification of behaviours from accelerometer data in a wild social primate. Animal Biotelemetry. 2017;5(1):6.

[80] Fortin D, Boyce MS, Merrill EH, Fryxell JM. Foraging costs of vigilance in large mammalian herbivores. Oikos. 2004;107(1):172–180.

[81] Polansky L, Kilian W, Wittemyer G. Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state–space models. Proceedings of the Royal Society B: Biological Sciences. 2015;282(1805):20143042.

[82] Spiegel O, O'Farrell S. Spatial Orientation and Time: Methods. 2018;.

[83] Owen-Smith N. Daily movement responses by African savanna ungulates as an indicator of seasonal and annual food stress. Wildlife Research. 2013;40(3):232–240.

[84] Fauchald P, Tveraa T. Using first-passage time in the analysis of area-restricted search and habitat selection. Ecology. 2003;84(2):282–288.

[85] McKenzie HW, Lewis MA, Merrill EH. First passage time analysis of animal movement and insights into the functional response. Bulletin of mathematical biology. 2009;71(1):107–129.

[86] Torres LG, Orben RA, Tolkova I, Thompson DR. Classification of animal movement behavior through residence in space and time. PloS one. 2017;12(1):e0168513.

[87] Berger-Tal O, Bar-David S. Recursive movement patterns: review and synthesis across species. Ecosphere. 2015;6(9):1–12.

[88] Bar-David S, Bar-David I, Cross PC, Ryan SJ, Knechtel CU, Getz WM. Methods for assessing movement path recursion with application to African buffalo in South Africa. Ecology. 2009;90(9):2467–2479.

[89] Panzacchi M, Van Moorter B, Strand O, Saerens M, Kivimäki I, St Clair CC, et al. Predicting the continuum between corridors and barriers to animal movements using Step Selection Functions and Randomized Shortest Paths. Journal of Animal Ecology. 2016;85(1):32–42.

[90] Morales JM, Haydon DT, Frair J, Holsinger KE, Fryxell JM. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology. 2004;85(9):2436–2445.

[91] DeCesare NJ, Hebblewhite M, Schmiegelow F, Hervieux D, McDermid GJ, Neufeld L, et al. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications. 2012;22(4):1068–1083.

[92] Lyons AJ, Turner WC, Getz WM. Home range plus: a space-time characterization of movement over real landscapes. Movement Ecology. 2013;1(1):2.

[93] Abrahms B, Seidel DP, Dougherty E, Hazen EL, Bograd SJ, Wilson AM, et al. Suite of simple metrics reveals common movement syndromes across vertebrate taxa. Movement ecology. 2017;5(1):12.

[94] Fleming CH, Calabrese JM. A new kernel density estimator for accurate home-range and species-range area estimation. Methods in Ecology and Evolution. 2017;8(5):571–579.

[95] Pohle J, Langrock R, van Beest FM, Schmidt NM. Selecting the number of states in hidden Markov models: pragmatic solutions illustrated using animal movement. Journal of Agricultural, Biological and Environmental Statistics. 2017;22(3):270–293.

[96] Gurarie E, Fleming CH, Fagan WF, Laidre KL, Hernández-Pliego J, Ovaskainen O. Correlated velocity models as a fundamental unit of animal movement: synthesis and applications. Movement ecology. 2017;5(1):13.

[97] McCulloch C, Cain M. Analyzing discrete movement data as a correlated random walk. Ecology. 1989;70(2):383–388.

[98] Bergman CM, Schaefer JA, Luttich S. Caribou movement as a correlated random walk. Oecologia. 2000;123(3):364–374.

[99] Byers JA. Correlated random walk equations of animal dispersal resolved by simulation. Ecology. 2001;82(6):1680–1690.

[100] Chen J, Gupta AK. Parametric statistical change point analysis: with applications to genetics, medicine, and finance. Springer Science & Business Media; 2011.

[101] Matteson DS, James NA. A nonparametric approach for multiple change point analysis of multivariate data. Journal of the American Statistical Association. 2014;109(505):334–345.

[102] Killick R, Eckley I. changepoint: An R package for changepoint analysis. Journal of statistical software. 2014;58(3):1–19.

[103] Zhao K, Jurdak R. Understanding the spatiotemporal pattern of grazing cattle movement. Scientific reports. 2016;6:31967.

[104] Goodall V, Fatti L, Owen-Smith N. Animal movement modelling: independent or dependent models? South African Statistical Journal. 2017;51(2):295–315.

[105] Cross PC, Almberg ES, Haase CG, Hudson PJ, Maloney SK, Metz MC, et al. Energetic costs of mange in wolves estimated from infrared thermography. Ecology. 2016;97(8):1938–1948.

[106] Tsalyuk M, Kilian W, Reineking B, Getz WM. Temporal variation in resource selection of African elephants follows long-term variability in resource availability. Ecological Monographs. 2019;89(2):e01348.

[107] Zeller KA, McGarigal K, Whiteley AR. Estimating landscape resistance to movement: a review. Landscape ecology. 2012;27(6):777–797.

[108] Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology. 2005;86(5):1320–1330.

[109] Thurfjell H, Ciuti S, Boyce MS. Applications of step-selection functions in ecology and conservation. Movement ecology. 2014;2(1):4.

[110] Avgar T, Potts JR, Lewis MA, Boyce MS. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution. 2016;7(5):619–630.

[111] Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FK. Evaluating resource selection functions. Ecological modelling. 2002;157(2-3):281–300.

[112] McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA. Multi-scale habitat selection modeling: a review and outlook. Landscape ecology. 2016;31(6):1161–1175.

[113] Townsend Peterson A, Papeş M, Eaton M. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography. 2007;30(4):550–560.

[114] Valletta JJ, Torney C, Kings M, Thornton A, Madden J. Applications of machine learning in animal behaviour studies. Animal Behaviour. 2017;124:203–220.

[115] Bennison A, Bearhop S, Bodey TW, Votier SC, Grecian WJ, Wakefield ED, et al. Search and foraging behaviors from movement data: a comparison of methods. Ecology and evolution. 2018;8(1):13–24.

[116] Delp SL, Loan JP. A computational framework for simulating and analyzing human and animal movement. Computing in Science & Engineering. 2000;2(5):46–55.

[117] Coello CAC. Evolutionary multi-objective optimization: A critical review. In: Evolutionary optimization. Springer; 2003. p. 117–146.

[118] Odu G, Charles-Owaba O. Review of multi-criteria optimization methods–theory and applications. IOSR Journal of Engineering (IOSRJEN). 2013;3(10):1–14.

[119] Marin JM, Pudlo P, Robert CP, Ryder RJ. Approximate Bayesian computational methods. Statistics and Computing. 2012;22(6):1167–1180.

[120] Jonsen ID, Myers RA, James MC. Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. Marine Ecology Progress Series. 2007;337:255–264.

[121] Dovera L, Della Rossa E. Multimodal ensemble Kalman filtering using Gaussian mixture models. Computational Geosciences. 2011;15(2):307–323.

[122] Walther G, et al. Inference and modeling with log-concave distributions. Statistical Science. 2009;24(3):319–327.

[123] Symonds MR, Moussalli A. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaikes information criterion. Behavioral Ecology and Sociobiology. 2011;65(1):13–21.

[124] Bunnefeld N, Börger L, van Moorter B, Rolandsen CM, Dettki H, Solberg EJ, et al. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology. 2011;80(2):466–476.

[125] Bischof R, Loe LE, Meisingset EL, Zimmermann B, Van Moorter B, Mysterud A. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? The American Naturalist. 2012;180(4):407–424.

[126] Schuh RT. The Linnaean system and its 250-year persistence. The Botanical Review. 2003;69(1):59.

[127] Rosselló-Móra R, Whitman WB. Dialogue on the nomenclature and classification of prokaryotes. Systematic and applied microbiology. 2019;42(1):5–14.

[128] Moore ER, Mihaylova SA, Vandamme P, Krichevsky MI, Dijkshoorn L. Microbial systematics and taxonomy: relevance for a microbial commons. Research in microbiology. 2010;161(6):430–438.

[129] Gevers D, Cohan FM, Lawrence JG, Spratt BG, Coenye T, Feil EJ, et al. Re-evaluating prokaryotic species. Nature Reviews Microbiology. 2005;3(9):733.

[130] Rahimi S, Owen-Smith N. Movement patterns of sable antelope in the Kruger National Park from GPS/GSM collars: a preliminary assessment. African Journal of Wildlife Research. 2007;37(2):143–152.

[131] Owen-Smith N, Goodall V. Coping with savanna seasonality: comparative daily activity patterns of A frican ungulates as revealed by GPS telemetry. Journal of Zoology. 2014;293(3):181–191.

[132] Fahr J, Abedi-Lartey M, Esch T, Machwitz M, Suu-Ire R, Wikelski M, et al. Pronounced seasonal changes in the movement ecology of a highly gregarious central-place forager, the African straw-coloured fruit bat (Eidolon helvum). PloS one. 2015;10(10):e0138985.

[133] Zhang J, Hull V, Ouyang Z, He L, Connor T, Yang H, et al. Modeling activity patterns of wildlife using time-series analysis. Ecology and evolution. 2017;7(8):2575–2584.

[134] Owen-Smith N, Fryxell J, Merrill E. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philosophical Transactions of the Royal Society B: Biological Sciences. 2010;365(1550):2267–2278.

[135] Seebacher F, Post E. Climate change impacts on animal migration. Climate Change Responses. 2015;2(1):5.

[136] Harel R, Spiegel O, Getz WM, Nathan R. Social foraging and individual consistency in following behaviour: testing the information centre hypothesis in free-ranging vultures. Proceedings of the Royal Society B: Biological Sciences. 2017;284(1852):20162654.

[137] Harel R, Duriez O, Spiegel O, Fluhr J, Horvitz N, Getz WM, et al. Decision-making by a soaring bird: time, energy and risk considerations at different spatio-temporal scales. Philosophical Transactions of the Royal Society B: Biological Sciences. 2016;371(1704):20150397.

[138] Cross PC, Edwards WH, Scurlock BM, Maichak EJ, Rogerson JD. Effects of management and climate on elk brucellosis in the Greater Yellowstone Ecosystem. Ecological Applications. 2007;17(4):957–964.

[139] Tracey JA, Bevins SN, VandeWoude S, Crooks KR. An agent-based movement model to assess the impact of landscape fragmentation on disease transmission. Ecosphere. 2014;5(9):1–24.

[140] Dougherty ER, Seidel DP, Carlson CJ, Spiegel O, Getz WM. Going through the motions: incorporating movement analyses into disease research. Ecology letters. 2018;21(4):588–604.

[141] Zidon R, Garti S, Getz WM, Saltz D. Zebra migration strategies and anthrax in Etosha National Park, Namibia. Ecosphere. 2017;8(8):e01925.

[142] Brodie JF, Giordano AJ, Dickson B, Hebblewhite M, Bernard H, Mohd-Azlan J, et al. Evaluating multispecies landscape connectivity in a threatened tropical mammal community. Conservation Biology. 2015;29(1):122–132.

[143] Runge CA, Martin TG, Possingham HP, Willis SG, Fuller RA. Conserving mobile species. Frontiers in Ecology and the Environment. 2014;12(7):395–402.

[144] Hays GC, Ferreira LC, Sequeira AM, Meekan MG, Duarte CM, Bailey H, et al. Key questions in marine megafauna movement ecology. Trends in ecology & evolution. 2016;31(6):463–475.

[145] Andersen T, Carstensen J, Hernandez-Garcia E, Duarte CM. Ecological thresholds and regime shifts: approaches to identification. Trends in Ecology & Evolution. 2009;24(1):49–57.