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The time frame of home-range studies: from function to utilization

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ABSTRACT

As technological and statistical innovations open new avenues in movement ecology, I review the fundamental implications of the time frame of home-range studies, with the aim of associating terminologies consistently with research objectives and methodologies. There is a fundamental distinction between (*a*) extrapolations of stationary distributions, associated with long time scales and aiming at asymptotic consistency, and (*b*) period-specific techniques, aiming at specificity but typically sensitive to the sampling design. I then review the difference between function and utilization in home-range studies. Most home-range studies are based on phenomenological descriptions of the time budgets of the study animals, not the function of the visited areas. I highlight emerging trends in automated pattern-recognition techniques for inference about function rather than utilization.

Key words: territory, utilization distribution, functional habitat, buffer size, space use, movement scale, step selection function, network theory.

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I. INTRODUCTION

The home-range concept, i.e. the notion that individual animals are spatially restricted, occurs in every branch of ecology and evolution, from the study of the underlying cognitive and behavioural mechanisms that lead to spatial fidelity (Schmidt, 2004; Hinsch & Komdeur, 2017; Hulse, Fowler, & Honig, 2018), to the genetic (Spear *et al.*, 2010), demographic (Fretwell & Lucas, 1969), and macroecological (Kelt & Van Vuren, 2001) consequences. Accordingly, the home-range concept is one of the most prevalent concepts in the ecological literature (>200,000 *Google Scholar* hits, 6550 in 2018 alone). Almost all species are predicted to exhibit some form of spatial fidelity associated with the way they perceive, access, and use resources. Indeed even species that traditionally were considered nomadic are increasingly recognized actually to perform recursions within a finite range, albeit at a slow pace, and also to exhibit short-term site fidelities (Owen-Smith, 2014; Webb *et al.*, 2014; Nandintsetseg *et al.*, 2019). Yet, the concept remains significantly blurred, as evidenced by a number of recent reviews whose titles are framed as questions (Börger *et al.*, 2008; Kie *et al.*, 2010; Fieberg & Börger, 2012; Powell & Mitchell, 2012; Walter, Onorato, & Fischer, 2015).

The seminal article about the home-range concept was written by Burt (1943). Burt (1943) clearly separated two aspects or functions of the home range: on the one hand there was the territory, defended against conspecifics, and on the other hand, the area that encompasses the resources necessary for maintenance and reproduction. As is often reported in mammals, Burt (1943) represented the resource-based home range as larger than the territory, and

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encompassing it (Mertl-Millhollen, 1988; Grant, Chapman, & Richardson, 1992). Another important notion that many ecologists have retained from Burt's (1943) seminal article is that home ranges should not include the locations that are visited during 'excursions' (Olson *et al.*, 2015), which are interpreted as forays to acquire information but not resources directly (Doligez *et al.*, 2003). This essentially resource-based definition of the home range later raised a number of conceptual issues about the significance of territorial behaviours for home-range studies (Fieberg & Börger, 2012; Riotte-Lambert, Benhamou, & Chamaillé-Jammes, 2015; Hinsch & Komdeur, 2017; Kirk *et al.*, 2018). Species and individuals may exhibit spatial fidelity without being territorial, or may defend access to mating opportunities but not food resources (Maher & Lott, 1995; Low, 2005; Hinsch & Komdeur, 2017).

In addition, the framework laid out by Burt (1943) did not specifically associate a time frame with the home-range concept. Space use, by definition, can only increase with time (Rivrud *et al.*, 2009; Van Beest *et al.*, 2011), but nevertheless the observed patterns of visits and revisits and the density of use may change over time (Benhamou & Riotte-Lambert, 2012; Benhamou, 2014). Some authors employ the concept of 'daily home range', which makes intuitive sense given the widespread occurrence of circadian cycles in animal activities (e.g. Russo, Massei, & Genov, 1997). Macroecologists, on the other hand, tend to favour a whole-lifespan definition of the home range to enable comparisons across species with different lifespans and different movement rates (Lindstedt, Miller, & Buskirk, 1986). Conservation biologists also favour a long time frame, because space use measured over a short period of time will not be as inclusive of critical habitats necessary for population and species conservation than space use measured over a long period of time (McDonald, Olsen, & Baker-Gabb, 2003; Schofield *et al.*, 2010; Fleming *et al.*, 2015). Indeed, resource requirements may vary over time with environmental drivers, for example droughts or cold spells (Frafjord & Prestrud, 1992; Foley, Pettorelli, & Foley, 2008; Tuqa *et al.*, 2014). Lastly, the influence of the time frame depends on movement rates. Some species and individuals never stray more than a few hours away from their core roosting site (Sheldon & Daugherty, 1982). For such species a few hours of monitoring will give a good idea of their space requirements. Others may spend more than a year between visits to different parts of their home range (Webb *et al.*, 2014; Nandintsetseg *et al.*, 2019), keep a multi-year memory of resource locations to be able to respond to emergency situations (Foley *et al.*, 2008), or suddenly move long distances in response to environmental challenges (Péron *et al.*, 2011). All these evolved responses to spatial and temporal variance in the environment (Mueller *et al.*, 2011) mean that for some populations, multiple years of monitoring are required to represent the use of space.

A last limitation to Burt's (1943) framework is that he did not explicitly address the role of physical and cognitive constraints. Yet, moving is energy-demanding (Terrier, Aminian, & Schutz, 2001; Yamada *et al.*, 2013) and moving into unfamiliar areas is risky and bears a social cost (Eason & Hannon, 1994; Geffen, Anderson, & Wayne, 2004; Gautestad, 2011), so that some areas are in practice barely reachable (Soberón, 2007; Fig. 1). Clearly not all species and individuals have the same intrinsic movement ability, and this should impact the way they form home ranges. Overall, this complexity has led to increasingly phenomenological approaches to the home-range concept (Worton, 1989; Laver & Kelly, 2008; Powell & Mitchell, 2012). However, recently, fine-resolution long-term tracking technologies have motivated a surge in innovative data-analysis methods that go beyond the description of animal time budgets. These statistical innovations often pertain to new quantities that become available for scrutiny, sometimes before their biological relevance is fully or widely understood (Patterson *et al.*, 2017). Herein I will illustrate my points using an analysis of tracking data from a plains zebra (*Equus quagga*). Methods for that case study are provided as online Supporting Information in Appendix S1.

II. TIME SCALES IN HOME-RANGE STUDIES

As reviewed above, space use is associated with a time frame. Yet, out of more than 200,000 hits for the phrase 'home range' in *Google Scholar* (May 13, 2019) and 13,073 hits for which the full text was available *via* the INEE-CNRS literature search database (http://web.a.ebscohost.com.inee.bib.cnrs.fr), only 8,850 and 702, respectively (5.3%) used a temporal modifier such as 'summer (home) range' or 'daily (home) range', and 9,230 and 613, respectively (4.8%) associated 'home range' with 'timescale', 'time frame', 'temporal scale' or similar phrases. In most other cases, the time frame of the study was determined implicitly by logistical constraints such as the battery life of the tracking unit, the longevity of the study individuals, or the timing of field operations. This is further emphasized by the relative prevalence of studies that quantified weekly or monthly home ranges (791 studies in *Google Scholar*), two timescales with arguably little biological underpinning, and whose choice was probably motivated by logistical constraints and the need to standardize analyses across individuals.

If we return to the fundamental objectives of movement ecology, one is to understand how individual movement responses to environmental change give rise to emergent patterns like species range shifts and demographic fluctuations (Soberón, 2007). This requires the choice of a time frame that captures the cumulative effect of instant resource acquisition rate on demographic parameters that typically pertain to a long time scale, e.g. annual survival. Many species have evolved strategies for storing energy and resources (Drent & Daan, 1980), meaning that the lack of resources at any given time may not correlate with overall performance in the long term. In other words, ideally the time scale for home-range studies should be the same as the scale used to measure individual demographic performance, that is the breeding cycle, the generation time, or the

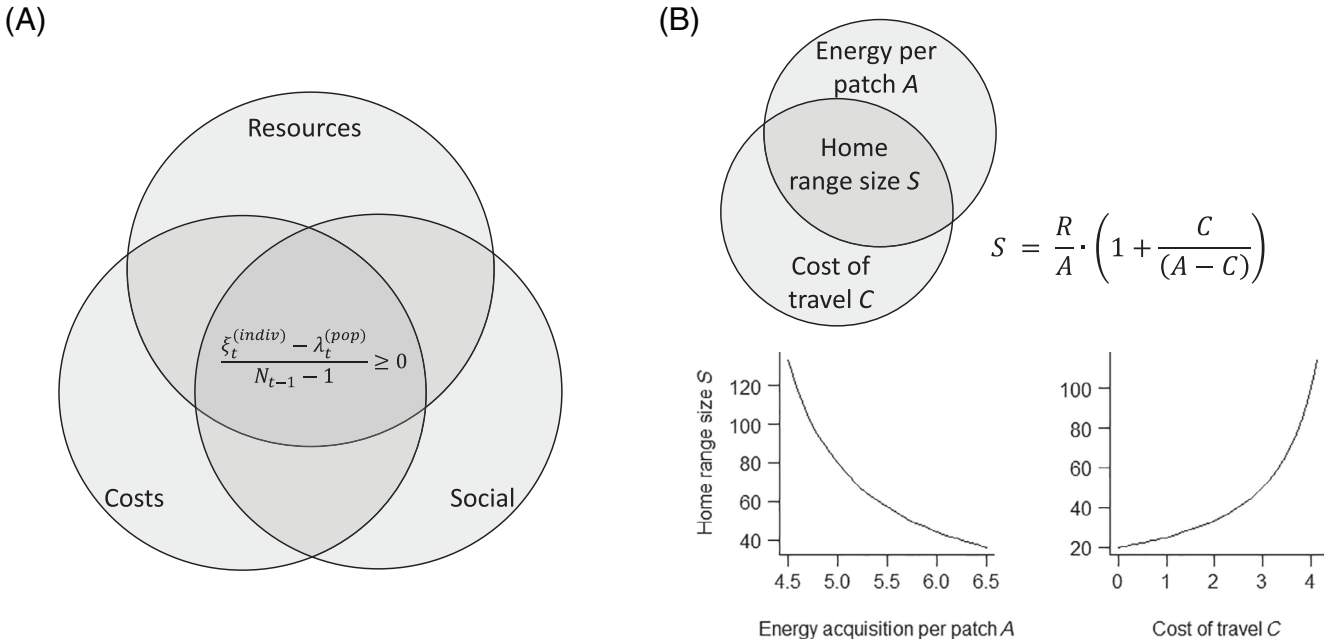


Fig. 1. (A) Three main classes of factors are expected to influence animal movement decisions shaping the home range: (1) food and shelter resources for maintenance and reproduction; (2) social interactions with congeners, including reproduction, competition, and sociality; (3) costs of and constraints on movement, including energy expenditure, environmental barriers and cognitive biases. In this Venn diagram inspired by an analogy with the mechanistic drivers of species distribution (Soberón, 2007), the illustrated principle is that individuals look for the intersection that contains enough resources, that can be acquired at a low-enough cost, for the individual to perform as good as or better than its competitors, as measured by its contribution to population growth rate (*sensu* Coulson *et al.*, 2006). ξ denotes the sum of the individual's survival plus its surviving offspring at the end of the focal time period t. λ denotes the population growth rate over that period. N here denotes the population size at the beginning of the period. The comparison with competitors in the population may be removed, in which case the home range is defined as the location that provides enough resources for a positive contribution to the population growth rate. With that proposed link to demography, home-range properties, such as home-range size, centroid location, or landcover selection coefficients, could eventually be treated like quantitative individual life-history traits that co-vary with population growth ('integral projection model'; Coulson, Tuljapurkar, & Childs, 2010). Once modified to include environmental forcing (Ozgul *et al.*, 2010), this framework would make it possible to project the future distribution of home-range size and composition in a population, thereby paving the way for space-use-based mechanistic models of species distributions. (B) A simplistic variant. The model animal must meet a given need for resource, R, covering maintenance and reproduction. The resources are patchily distributed with A resources per patch. If movement is costless, the home-range size is R/A (Wolf, 1985). If movement is costly, with a cost C to travel from one patch to the next, the animal must acquire $R + C$ resources to offset the cost of movement (McNab, 1963; Ford, 1983) leading to an exponential increase in space use. Note the units on the x-axis: a travel cost of $C = 4$ means that almost all the resources acquired in a patch are allocated to traveling to the next patch. In practice, C might not be that large relative to A, because resources are concentrated enough, or are self-renewable.

total lifespan. At such scales, biodemographic tools can be used to articulate space use with demographic performance (Fig. 1). Another more practical and immediate argument in favour of choosing a demographically relevant time frame to study the home range lies in the presence of an asymptote in the net squared displacement of home-range-bounded animals (Spencer, Cameron, & Swihart, 1990; Giuggioli *et al.*, 2006; Bunnefeld *et al.*, 2011; Börger & Fryxell, 2012; Bastille-Rousseau *et al.*, 2016). This emphasis on the asymptotic behaviour neatly aligns with the above arguments about the choice of a long time frame. Studying the asymptote also makes it more straightforward to compare across species and individuals with different transitory dynamics and different sampling schedules. In practice, the meaning of 'a long time' depends on the duration of the transitory period and therefore on the intrinsic movement rates of the focal animal (Johnson *et al.*, 2008*a*; Fleming *et al.*, 2014). Importantly, this long time frame may exceed the monitoring period, calling for extrapolative and model-based methodologies. In the continuous-time stochastic modelling framework, the asymptote can be further explained as the balance between attraction to a central position and random diffusion drawing the animal away from that central position (Dunn & Gipson, 1977; Blackwell, 1997). Fitting such a continuous-time stochastic process makes it possible to estimate its asymptotic Gaussian distribution whose spread, called the movement variance σ^2, also constitutes a direct measure of the scale of the home range (Giuggioli *et al.*, 2006; Fleming *et al.*, 2014). In addition, the position autocorrelation time τ measures the rate at which the semivariance of the

modelled positions increases with the time lag between positions, before reaching the σ^2 asymptote (Giuggioli *et al.*, 2006; Fleming *et al.*, 2014). τ can be interpreted as the home-range crossing time, effectively capturing the relationship of the focal animal to space: if τ is small, the animal has a relatively small home range with respect to its movement abilities, and *vice versa*. One of the key advantages of this type of model-based metrics of home-range scale is the robustness to variation across individuals in sampling rates and in the amount of telemetry error (Johnson *et al.*, 2008*a*; Fleming *et al.*, 2017). This make these metrics suitable for comparative analyses across individuals, populations, or time periods. However, while these metrics (σ and τ) capture the scale of the home range, they do not measure its precise shape or composition. Similarly, methods geared to extrapolate the stationary utilization distribution, such as the autocorrelated kernel density estimation (AKDE) (Fleming *et al.*, 2015; Fig. 2) or the mechanistic home-range estimator (Moorcroft & Lewis, 2004), are geared towards robustness to variation in sampling design and asymptotic consistency with respect to monitoring duration (Noonan *et al.*, 2019). They thus ensure that the time scale associated with the home-range estimate is consistently long irrespective of the actual time frame of the data, but they often lack the specificity required to delineate precise home-range contours (Péron, 2019; Fig. 3; but see Moorcroft, Lewis, & Crabtree, 2006).

Taking all of this into consideration, I suggest a restrictive use for the phrase 'home range', only for situations where the time frame makes demographic sense (Fig. 1). At other time scales, I advocate for a choice of more generic, available terms like 'space use', 'movement domain' (e.g. Johnson *et al.*, 2008*b*), 'points of interest' (e.g. Benhamou & Riotte-Lambert, 2012), or 'movement amplitude' (e.g. Péron, 2019), rather than 'home range'. Thereby, one would for example talk about seasonal variation in the amplitude of the movements within the home range, instead of seasonal variation in the home-range size itself (White, Saunders, & Harris, 1996; Rivrud, Loe, & Mysterud, 2010; Walter *et al.*, 2015). Within the home-range terminology, I further suggest reserving the phrase 'home-range scale' for the asymptotic variance of the movement process and similar second-moment metrics. Lastly, I emphasize the powerful inference about emergent processes and the comparative analyses that the choice of a demographically relevant time scale would eventually make possible.

III. THE DIFFERENCE BETWEEN UTILIZATION AND FUNCTION

The vast majority of home-range studies are based on the phenomenological description of where the animals spend their time or are predicted to spend their time (Laver & Kelly, 2008). But, the time spent at a location is not necessarily representative of its biological importance (Powell & Mitchell, 2012). For example, preferred travel corridors that connect points of interest are essential for the home range to function as such, but the animals do not spend much time in them (Panzacchi *et al.*, 2016; Jesmer *et al.*, 2018; Scharf *et al.*, 2018; compare Fig. 3A with Fig. 3B). By contrast, roosting sites are often over-represented in animal tracking data (Te Wong, Servheen, & Ambu, 2004; Körtner, Pavey, & Geiser, 2007), but this concentration of use of a few places does not systematically reflect the rarity of the features that led the animals to select these locations. Indeed, the selection process is typically constrained by the way the animals access and acquire information about potential roosting sites (Midford, Hailman, & Woolfenden, 2000; Aplin *et al.*, 2012), perceive risk in novel places (Brown *et al.*, 1999; Gaynor *et al.*, 2019), and also by physiological and ecological constraints on the response to new information (Fig. 1).

In this context, recently available automated pattern-recognition algorithms pave the way for function-based definitions of the home range, *via* the detection of different types of points of interest in animal tracking data. There are two main categories of automated pattern-recognition algorithms. *Unsupervised* algorithms essentially look for patterns in the data using a threshold of dissimilarity to delineate clusters. The user then needs to interpret the final outcome. In the zebra case study, I drew from that philosophy when performing a graph analysis of the movement track (Bastille-Rousseau *et al.*, 2018; Appendix S1). In the graph that the zebra movement steps created, I isolated pixels of high 'betweenness' [*sensu* Cohen & Havlin, 2011: the frequency with which a pixel is on the shortest path between two recorded locations] but low 'centrality' [*sensu* Cohen & Havlin, 2011: the number of steps that start or depart from a pixel]. I then incorporated them into a minimum spanning tree connecting the pixels with a high ratio of betweenness/centrality (Fig. 3A; see Appendix S1 for methods). Some of the branches of that tree connected clusters of high centrality (Fig. 3A). I intuitively interpreted these as corridors between foraging areas. These corridors may correspond to natural features in the landscape that provide safety during travel, to features that are used as landmarks in the cognitive map, maybe as a form of animal culture, or simply to energetic least-cost paths between foraging areas. Other branches of that tree did not end in an area of high centrality (Fig. 3A). The interpretation of these branches is more speculative: they may correspond to excursions as part of the fission–fusion social system (Olson *et al.*, 2015), preferential travel routes when foraging for thinly distributed low-quality resources (Schmidt *et al.*, 2016), immediate response to predator attacks (Courbin *et al.*, 2016), prospection for mates (Lovari *et al.*, 2008), or possibly visits to rarely needed resources such as self-medication and trace elements (Villalba, Provenza, & Shaw, 2006).

On the other hand, *supervised* algorithms require a training data set that the user (or perhaps a neural network) must pre-process, e.g. if the objective is to identify barriers to movement, by specifying which movement step corresponds to an interaction with an obstacle and which corresponds

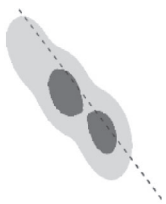
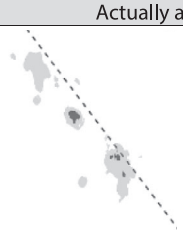
	Interpolation	Extrapolation
	Period-specific time budget	Asymptotically consistent time budget
Phenomenological	 Kriging (Fleming et al., 2016), Brownian Bridge (Horne et al., 2007; Kranstauber et al., 2012), Local Convex Hull (Getz & Wilmers, 2004; Getz et al., 2007), Maximum Convex Polygon (Calenge, 2006)	 Kernel Density Estimator (Worton, 1989), robustized by adaptive data thinning (Hansteen et al., 1997), or with a bandwidth optimizer that takes autocorrelation into account (AKDEc; Fleming & Calabrese 2017)
	Actually accessed resources	Potentially accessible resources
Mechanistic	 Movement-based Kernel Density Estimator (Benhamou & Cornélis, 2010; Benhamou, 2011)	 Mechanistic Home Range Estimator (Moorcroft et al., 1999; Moorcroft & Lewis, 2004), simplified into Synoptic model (Horne et al., 2008), Individual-based simulations (Wang & Grimm, 2007; Signer et al., 2017)

Fig. 2. A classification of the utilization-based home-range estimators. The illustrations are from the zebra case study, using the estimator indicated in bold (see Appendix S1 for methods) Dark and light grey areas respectively represent the 50% and 95% isopleths of the estimated utilization distribution. The diagonal dashed line represents a railway that acts as a partly permeable border to the national park where the zebra was captured. Landcover data for the movement-based kernel density estimator (MKDE) and individual-based simulation (IBS) were extracted from Arraut *et al.* (2018).

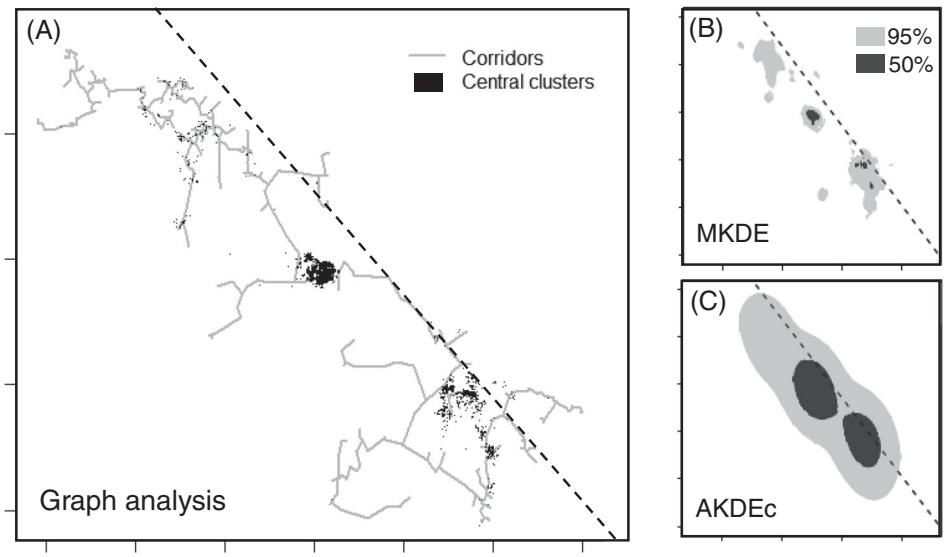


Fig. 3. (A) Graph analysis of the zebra tracking data showing the location of functional elements: clusters of high degree centrality ('central clusters') and minimum spanning tree connecting pixels of high betweenness/centrality ratio ('corridors') (B) 50% and 95% isopleths of the movement-based kernel density estimator (MKDE)-estimated utilization distribution (Benhamou, 2011). (C) 50% and 95% isopleths of the autocorrelated kernel density estimator corrected for the reference function approximation bias (AKDEc)-estimated utilization distribution (Fleming & Calabrese, 2017). The diagonal dashed line represents a railway that acts as a partly permeable border to the national park where the zebra was captured. Landcover data for C were extracted from Arraut *et al.* (2018).

to unimpeded travel. The task of the supervised algorithm is then to find criteria to discriminate between user-defined categories, e.g. what is an obstacle as seen through the lens of animal movement (Valletta *et al.*, 2017). Eventually the algorithm uses these criteria to clusterize the rest of the data set, yielding a map of movement-detected obstacles. Such a framework is probably more promising for non-parametric tasks, like identifying territory borders that are not systematically made tangible by a physical feature, than for parametric tasks like identifying the relative effects of different mapped features (Appendix S1). Currently however, to the best of my knowledge, movement ecologists lack a user-friendly framework to implement supervised machine learning for specific movement ecology applications.

Both these options are data-driven, meaning that they are by construct limited to the information contained in the relocation data. The special case of resources that are critical to animal fitness but are seldom visited represents a strong limit to this type of approach (Powell & Mitchell, 2012). Examples of such resources include salt licks that the animals may only visit after ingesting toxic forage (Villalba *et al.*, 2006). Visits to salt licks may be too far apart in time to be recorded. However, as long as adequate information is available to parameterize the simulating model, e.g. knowledge about physiological requirements for trace elements (Villalba *et al.*, 2006), they can be simulated using individual-based models (Wang & Grimm, 2007; Signer, Fieberg, & Avgar, 2017; Fig. 2D). The flexibility of individual-based simulations could also offer ways to weigh the density of use according to factors other than the time budget, e.g. according to the internal state, as a way to further the difference between function and utilization.

Even if maintaining the focus on utilization, the choice of method should be made according to two major dichotomies, depending on the time frame of the inference and the objectives of the research (e.g. broad space requirements *versus* specific points of interest; Fig. 2). First, the utilization distribution, that is the probability $p(\boldsymbol{r})$ that location $\boldsymbol{r}$ is used at any given time, can be either extrapolated or interpolated. The leading home-range methodology, kernel density estimation (KDE) (Worton, 1989), unambiguously belongs to the class of extrapolation methods (Silverman, 1986; Turlach, 1993), but importantly, its standard implementation can yield flawed results when naively applied to animal tracking data (De Solla, Bonduriansky, & Brooks, 1999; Fleming *et al.*, 2015). The robustized version of KDE offers asymptotic consistency (Fleming *et al.*, 2015; Fleming & Calabrese, 2017; Noonan *et al.*, 2019), but typically lacks the level of specificity that biologists may expect from a home-range delineation technique (Benhamou & Cornélis, 2010; Slaght *et al.*, 2013; compare Fig. 3C with Fig. 3A). By contrast, interpolations focus on one single realization of the movement path during a finite period of time, affording them more specificity especially with regard to customizing the time frame and delineating specific points of interest (Benhamou & Riotte-Lambert, 2012; Kranstauber *et al.*, 2012). However, the spread of the interpolated distribution quantifies the process uncertainty around the interpolated movement path (*sensu* De Valpine & Hastings, 2002), not the home-range size (Horne *et al.*, 2007; Benhamou, 2011; Fleming *et al.*, 2016).

The second dichotomy pertains to the level of mechanistic realism in the models that underlie the interpolations or extrapolations (Fig. 2). Phenomenological approaches only use the tracking data, they assume that the movements are purely stochastic, and that space is homogeneous. They are not designed to accommodate landcover selection rules for example, but instead to compute statistically robust buffers around the recorded locations. As a side note, adding arbitrary buffers around recorded locations is something that many spatial ecologists are clearly not reluctant to do (Ostro *et al.*, 1999; Long & Nelson, 2015), but it seems warranted to find ways to make the choice less arbitrary, for example by considering how flight distances and risk avoidance (Dill & Houtman, 1989; Brown *et al.*, 1999) impact on the functionality of points of interest. On the other hand, mechanistic approaches start by fitting an empirical mechanistic movement model, typically using ancillary environmental data (e.g. Johnson *et al.*, 2008*b*). Examples of movement mechanisms include selection for specific landcover types, reluctance to cross linear features, attraction for the home range of potential mates, and repulsion for the presence of territorial neighbours (Moorcroft & Lewis, 2004; Horne, Garton, & Rachlow, 2008). One of the weaknesses of mechanistic approaches is however that they are sensitive to the fit of the underlying mechanistic model. For example, in the zebra case study (Fig. 3), I used a time-constant landcover selection model, but in reality landcover selection was temporally variable (Courbin *et al.*, 2016), and this likely led to overestimating the use of bushland. Another particular caveat is that some mechanistic methods rely strongly on an equilibrium assumption (Moorcroft & Lewis, 2004) whereas space use may not be stationary. To address these non-stationarities, individual-based simulations again appear promising (Wang & Grimm, 2007). More generally, the main usage for mechanistic extrapolations might be to compare them to observed space use, as a way to assess the realism and parsimony of the set of movement rules that were used to extrapolate.

IV. CONCLUSIONS

(1) Space-use studies are by construction associated with a time frame. I advocate for the systematic reporting of that time frame in publication abstracts, for the increased use of standardized time frames, and whenever possible, for the use of demographically relevant time scales such as the breeding cycle, generation time, and total lifespan. I also suggest restricting the use of the phrase ‘home range’ to studies that are performed at demographically relevant time scales.

(2) The extrapolation of stationary utilization distributions and the model-based estimation of movement variance pertain to long time scales. They correct for the effect of the actual duration of the monitoring period and are more likely to match demographic schedules than period-specific estimates.

(3) I recommend a more consistent association between terminology, methodology and research objectives. For example, model-based extrapolations of stationary utilization distribution lend themselves to comparative analyses because of their asymptotic consistency, and to conservation biology applications because they extrapolate space requirements over representative periods of time. By contrast, interpolations are geared for period-specific inference and for the quantification of process uncertainty.

(4) Automated pattern-recognition techniques, such as those based on the graph analysis of movement tracks, pave the way for a function-based definition of the home range instead of, or in complement to, utilization-based definitions. Examples of functions that can readily be mapped out include roosting, foraging, and travelling.

(5) Individual-based simulations offer a potentially important way to fine-tune that inference by (*a*) incorporating features not documented during the monitoring period, e.g. rarely visited yet critical resources such as trace elements; and (*b*) furthering the distinction between utilization and function by incorporating a process about the internal state of the animal and its effect on movement rates.

V. ACKNOWLEDGMENTS

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