METHOD

Running on empty: recharge dynamics from animal movement data

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Abstract

Vital rates such as survival and recruitment have always been important in the study of population and community ecology. At the individual level, physiological processes such as energetics are critical in understanding biomechanics and movement ecology and also scale up to influence food webs and trophic cascades. Although vital rates and population-level characteristics are tied with individual-level animal movement, most statistical models for telemetry data are not equipped to provide inference about these relationships because they lack the explicit, mechanistic connection to physiological dynamics. We present a framework for modelling telemetry data that explicitly includes an aggregated physiological process associated with decision making and movement in heterogeneous environments. Our framework accommodates a wide range of movement and physiological process specifications. We illustrate a specific model formulation in continuous-time to provide direct inference about gains and losses associated with physiological processes based on movement. Our approach can also be extended to accommodate auxiliary data when available. We demonstrate our model to infer mountain lion (Puma concolor; in Colorado, USA) and African buffalo (Syncerus caffer; in Kruger National Park, South Africa) recharge dynamics.

Keywords

Animal movement, animal physiology, continuous-time model, energetics.

INTRODUCTION

Energetics has been a dominant theme in ecological and biological science for centuries (Zuntz 1897; Nussbaum 1978) because an improved understanding of metabolics and energy acquisition provides insights about fundamental similarities and differences among species (Taylor et al. 1982). An understanding of the connection between energetics and movement is critical for all aspects of biology and leads to improved management and conservation of wildlife because physiological processes and vital rates are indicative of animal health (Nathan et al. 2008; Wilmers et al. 2017). Healthy wildlife individuals and populations are an essential ecosystem service and have intrinsic anthropogenic and ecosystem value (Ingram & Foster 2008).

While much research has focused primarily on the ties between energy and locomotion, myriad other factors influence animal decision-making processes (Alcock 2009). Decisions made by animals directly affect their movement rates and hence indirectly affect their energy as well as other physiological processes (Houston & McNamara 1999; Morales et al. 2005, 2010). In what follows, we use the term ‘recharge’ as a general reference to physiological processes that require replenishment for an organism to maintain its physical health and normal activities. The recharge concept is a simplification of complex physiological changes over time; it reduces the complexity enough that we can account for aggregate physiological signals while inferring environmental influences on animal movement given telemetry data. We describe examples of physiological processes that may be connected with animal movement decisions and show how they accumulate in a recharge function that can be statistically inferred using tracking data. Our approach to account for recharge dynamics relies on a long-memory statistical model specified to mimic physiological processes and can be applied to animal tracking data to test hypotheses about animal behaviour as well as estimate parameters associated with changes in physiological processes over time.

Many former studies of animal movement have used experimental laboratory approaches to measure oxygen intake and energy expenditure directly (Alexander 2003; Halsey 2016). These studies provided a foundational kinematic understanding of animal movement in controlled environments (Full et al. 1990). More recent research has examined connections between movement and energetics in natural settings (Karasov 1992) and how terrain and environmental factors influence movement (e.g. Humphries & Careau 2011; Shepard et al. 2013; Williams et al. 2014). Biotelemetry technology has facilitated regular measurement of movement and led to improved understanding of individual-based physiological processes (e.g. Cooke et al. 2004; Green 2011).

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Improvements in high-quality animal tracking data are occurring at an increasing rate (Cagnacci et al. 2010). Wildlife tracking devices have allowed researchers to collect unprecedented data sets that contain valuable information about animal movement, and hence energetics and other physiological processes that require recharge (Kays et al. 2015; Wilmers et al. 2015). Statistical approaches have been developed to characterise the variation within and among individual animal trajectories (Scharf et al. 2016, 2018; Hooten et al. 2017; Hooten & Johnson 2019). These approaches include the use of environmental information and methods to identify the portions of animal trajectories that indicate distinctly different patterns (e.g. Whoriskey et al. 2017). For example stochastic differential equations (SDEs; Brillinger 2010) allow researchers to make inference on the importance of environmental covariates on movement in continuous time. Some discrete-time models also incorporate covariates and focus on phenomenological clustering of movement processes that are linked to possible behavioural changes over time (e.g. Morales et al. 2004; Langrock et al. 2012; McClintock et al. 2015).

Despite the proliferation of statistical animal movement models, few are based on specific mechanisms related to physiology (e.g. Schick et al. 2013). In contrast, purely mathematical animal movement models are almost always mechanistically motivated (Turchin 1998), but are often too complex to allow for statistical learning using location-based telemetry data alone. Some statistical models have been used to make post hoc inferences concerning physiological processes such as memory (e.g. Avgar et al. 2013; Oliveira-Santos et al. 2016) and energetics (e.g. Merkle et al. 2017; Hooten et al. 2018), including some that rely on auxiliary data from accelerometers (e.g. Wilson et al. 2012). However, they often lack the mechanistic mathematical specifications to account for recharge dynamics directly when inferring movement dynamics. Demographic models based on capture-recapture data, such as Cormack–Jolly–Seber (CJS) models, explicitly consider individual health and body condition when inferring vital rates (Pollock 1991; Lebreton et al. 1992), but are often focused on large spatial and temporal scales (Schick et al. 2013).

In what follows, we broaden the current scope of ‘energy landscapes’ (Wilson et al. 2012; Shepard et al. 2013) and ‘landscapes of fear’ (Laudrè et al. 2001; Bleicher 2017) to include all physiological processes that require recharge. We consider accumulations of these physiological landscapes that result in individual-based recharge functions and link them to decision-making processes of individual organisms as they move. We show how to use telemetry data to make inference about both the decision and recharge processes in heterogeneous environments and account for their effect on movement. We demonstrate our recharge movement model with case studies involving telemetry data for a mountain lion (Puma concolor) in Colorado, USA and African buffalo (Syncerus caffer) in South Africa. We also discuss possible ways to extend the model to account for conspecific and allo-specific interactions among individuals as well as accommodate auxiliary data sources such as individual-level health and accelerometer data.

MATERIAL AND METHODS

Physiological landscapes

Critical to our approach is the concept of recharge, a time-varying process involving an individual physiological characteristic \( v \). Physiological recharge can be expressed as a function \( g(v, t) \) that increases (i.e. charges) and decreases (i.e. discharges) over time depending on the decision-making process of the individual, the resulting behaviour, and the environmental conditions it encounters. We refer to a combination of spatially explicit covariates that affect the recharge function \( g(v, t) \) over time as the ‘physiological landscape’. For a physiological characteristic \( v \), we define the physiological landscape as \( w(\mathbf{u}) \theta(v) \) for any location \( \mathbf{u} \equiv (\mu_1, \mu_2)^T \) in region \( D \) (e.g. the study area).

The coefficients \( \theta(v) \equiv (\theta_1(v), \ldots, \theta_p(v))^T \) appropriately weight each of the landscape variables (e.g. elevation, land type, etc.) in \( w(\mathbf{u}) \equiv (w_1(\mathbf{u}), \ldots, w_p(\mathbf{u}))^T \) so that they combine to result in a surface that modulates the state of the physiological process \( v \) as an individual moves throughout the space (Fig. 1). For example if \( v \) refers to the energetic component of a larger suite of physiological processes, then \( w(\mathbf{u})(t) \theta(v) \) represents the physiological landscape value that influences the energy recharge dynamics as the individual under study moves to position \( \mathbf{u}(t) \) at time \( t \).

In fact, for a given individual trajectory \( \mathbf{u}(t) \) (for all \( t \in T \) in the study period), the physiological landscape \( w(\mathbf{u}(t)) \theta(v) \) is accumulated as the individual moves. This accumulation over time results in what we refer to as a physiological recharge function that can be expressed as the line integral of the physiological landscape

\[
g(v, t) = g_0(v) + \int_0^t w(\mathbf{u}(v)) \theta(v)dv, \tag{1}
\]

where the lower limit (i.e. zero) on the integral in eqn 1 corresponds to the beginning of the study period. Fig. 1c depicts the physiological recharge function as the line integral associated with the trajectory. At times when \( g(v, t) \) is large, the individual is in a charged state with respect to physiological process \( v \). Conversely, when the physiological recharge function \( g(v, t) \) is small, it indicates that the physiological process \( v \) is discharged and the individual may alter its behaviour in an attempt to recharge.

While energy is among the most commonly studied physiological characteristic (Wilson et al. 2012), there exists a large set of other individual-based physiological characteristics (i.e. \( v \in V \)) that contribute to individual, population, community and ecosystem health and larger scale vital rates (Matthiopoulos et al. 2015). For example in addition to energy intake and expenditure (Spalinger & Hobb 1992; Stephens et al. 2007), most animals require periodic hydration (e.g. Tshipa et al. 2017), sleep (Savage & West 2007), heat (Humphries & Carreau 2011) and shelter (Eggleston & Lipcius 1992). Less obvious physiological processes requiring recharge that transcend the individual level may include activities such as reproduction (Proaktor et al. 2008), care for young (Dudeck et al. 2018) and ‘security’ in the context of landscapes of fear (Laudrè et al. 2001; Bleicher 2017). Thus, we can express an aggregated physiological recharge process as an integral over the
set of all physiological processes $\mathcal{V}$:

$$g(t) = \int_V g(v, t) dv, \quad (2)$$

$$= g_0 + \int_0^t w(\mu(\tau)) \theta d\tau, \quad (3)$$

where we show that the initial aggregated charge is

$$g_0 \equiv \int_V g_0(v) dv, \quad (4)$$

and the aggregated recharge coefficients are

$$\theta \equiv \int_V \theta(v) dv \quad (5)$$

in Online Appendix A. As we describe in what follows, the aggregated recharge process in eqn 3 provides a fundamental mechanistic link between environmental characteristics and the physiology and sociality of moving individuals as they seek to recharge – a link that is missing in most other contemporary models for animal movement and one that allows us to examine the evidence for physiological signals in animal movement trajectories. Furthermore, in the absence of a strict connection to specific physiological processes, the recharge function in eqn 3 can be used to generalise movement models to accommodate long-range temporal dependence that may go unaccounted for otherwise. Finally, the recharge function we specified in eqn 3 can be generalised easily to accommodate time-varying coefficients (i.e. $\theta(t)$), nonlinearity in the physiological landscape and alternatives to the convolution form of aggregation (e.g. based on the principle of limiting factors). For example to account for optima in the environmental gradients that comprise the physiological landscape, we can include polynomial transformations of environmental variables $w$ as we would in a conventional regression model.

### Movement decisions based on physiological processes

#### General framework

Most modern statistical models for animal trajectories account for both measurement error and movement dynamics using a hierarchical framework (Schick et al. 2008; Hooten et al. 2017). Thus, we employ a hierarchical structure to build a general modelling framework that reconciles animal trajectories and physiological processes while accounting for measurement error and uncertainty in movement dynamics (Fig. 2). To develop a general recharge-based movement modelling framework, we consider a model for the telemetry data that depends on the true, underlying animal trajectory. Our movement model characterises the structure of the trajectory, and hence the perception of the landscape by the animal, depending on a binary decision process $\mathbf{z}(t)$ of the animal over time. This decision process arises stochastically according to a probability function that depends on the underlying aggregated physiological process. For telemetry observations $s(t_i)$ (for $i = 1, \ldots, n$) and associated trajectory $\mathbf{u}(t)$ we formulate the hierarchical model

$$s(t_i) \sim [s(t_i)|\mathbf{u}(t_i)], \quad (6)$$

$$\mathbf{u}(t_i) \sim \{\mathcal{M}_0, \quad z(t_i) = 0, \quad \mathcal{M}_1, \quad z(t_i) = 1\}, \quad (7)$$

for $i = 1, \ldots, n$, where the bracket notation ‘[ · ]’ denotes a generic probability distribution (Gelfand & Smith 1990) that may include additional parameters. We introduce continuous-time models for $\mathcal{M}_0$ and $\mathcal{M}_1$ in the example specification that follows.

The mixture movement model in eqn 7 depends on a latent binary decision $z(t)$ that represents the individual’s choice to recharge when $z(t) = 1$ (where $z(t) = 1$ corresponds to a discharged state and $z(t) = 0$ corresponds to a charged state). The instantaneous probability of the decision to recharge ($\rho(t)$) can be related to the latent physiological recharge process $g(t)$ through an appropriate link function. Thus, in the case studies that follow, we express $z(t) \sim \text{Bern}(\rho(t))$ with $\rho(t) = 1 - \Phi(g(t))$, where $\Phi(\cdot)$ represents the standard normal cumulative distribution function (i.e. the inverse probit function; another option is the logit). This relationship between $\rho(t)$ and $g(t)$ implies that the decision to recharge will increase

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in probability when the aggregated physiological process \( g(t) \) decreases. For example, as an individual ventures far from resources that allow it to recharge, \( g(t) \) will decline and the individual will eventually need to make an effort to replenish its physiological processes, hence increasing \( q(t) \) and changing its movement behaviour (Fig. 2). By connecting an animal decision process \( z(t) \) with movement and resources, our model formulation explicitly accounts for the relationship between stimuli and motivation, which is a primary focus of ethology (Colgan 1989).

A continuous-time recharge-based movement model

In the continuous-time setting, SDE models are a popular option to account for diffusion and drift across heterogeneous landscapes (Brillinger 2010). Thus, we provide an example specification using the hierarchical framework by formulating the specific components of our recharge-based movement model in eqns 6–7. We consider Gaussian error for telemetry observations such that \( s(t_i) \sim N(\mu(t_i), \sigma_i^2 I) \) (for \( i = 1, \ldots, n \)) and a mixture SDE with components

\[
\begin{align*}
\frac{d\mu(t)}{dt} &= \left\{
\begin{array}{ll}
-\nabla p(\mu(t), \beta) dt + \sigma_0 \mathbf{d}_0(t), & z(t) = 0 \\
0 + \sigma_1 \mathbf{d}_1(t), & z(t) = 1
\end{array}
\right. \quad (8)
\end{align*}
\]

for the set of times in the study period \( t \in T \), where, \( p \) represents a potential function (so-called because of its connections to potential energy in physics; Preisler et al. 2013) controlling the drift of the individual trajectory \( \mu(t) \) based on landscape covariates and associated coefficients \( \beta \). The diffusion aspects of the movement process are controlled by the two Gaussian white noise terms \( \mathbf{d}_0(t) \) and \( \mathbf{d}_1(t) \) that are scaled by \( \sigma_0 \) and \( \sigma_1 \).

The movement process model in eqn 8 can be interpreted in the following way. When the decision to recharge is made \( (z(t) = 1) \) at time \( t \), the individual will respond to the environment as dictated by the potential function \( p(\mu(t), \beta) \) by taking steps that are aligned approximately with its gradient surface (i.e. downhill on the surface; \( M_1 \) in Fig. 2). Conversely, when \( z(t) = 0 \), the individual may roam freely without needing to respond to the environment (\( M_0 \) in Fig. 2). Thus, in this particular model specification, we would obtain biased inference.
about the movement parameters $\bm{\beta}$ if the individual was assumed to move according to the SDE with potential function $p(\bm{\mu}(t), \bm{\beta})$ without considering the underlying physiological process (i.e. $z(t) = 1$ always). Most studies investigating resource selection assume only a single movement model. Thus, the movement model specification in eqn 8 allows us to infer when a physiological signal is present in our telemetry data (i.e. when $z(t)$ switches between zero and one at some point along the trajectory).

It is worth noting that our model formulation fits into a broader class of models for movement using the basis function framework provides opportunities to extend the model in future studies to accommodate other types of smoothness and heterogeneity in the trajectory process (see Scharf et al. 2018 and Hooten et al. 2018 for further details). Also, to fit the model to data, we must solve the SDE for $\bm{\mu}(t)$ based on a discrete approximation. This solution is more intuitive than the SDE itself because it assumes a discrete-time form where the process components of the model for $\bm{\mu}(t)$ in eqn 7 can be written as $\mathcal{M}_0 = \mathcal{N}(\bm{\mu}(t_{j-1}), \sigma_0^2\bm{I}_d)$ and $\mathcal{M}_1 = \mathcal{N}(\bm{\mu}(t_{j-1}) - \mathcal{E}\mathcal{P}(\bm{x}'(\bm{\mu}(t_{j-1})))\bm{\beta}_d, \sigma_1^2\bm{I}_d)$ for a fine grid of time points, $t_1, \ldots, t_m$, spaced $\Delta t$ apart, using an Euler-Maruyama discretisation scheme (Kloeden & Platen 1992).

As a result of our specifications for the hierarchical model, the full parameter set includes the latent position process $\bm{\mu}(t_j)$ for all $j = 1, \ldots, m$, as well as three sets of parameters: (1) the drift coefficients in the potential function, $\bm{\beta}$, (2) the initial recharge state $g_0$ and recharge coefficients $\bm{\theta}$ and (3) the variance parameters $\sigma_0^2$, $\sigma_0^2$ and $\sigma_1^2$. To estimate the parameters and make inference, we can fit the model using maximum likelihood if we are able to derive the integrated likelihood, or we can use Bayesian methods. In what follows, we use a Bayesian approach that allows us to specify priors for the three sets of parameters described above (Online Appendix C) and obtain a Markov chain Monte Carlo (MCMC) sample from the posterior distribution

\[
[(\bm{\mu}(t_j), \text{ for } j = 1, \ldots, m), \bm{\beta}, g_0, \bm{\theta}, \sigma_0^2, \sigma_0^2, \sigma_1^2][s(t_i), i = 1, \ldots, n] \propto \prod_{i=1}^n [s(t_i)]_{\mu(t_i)} , \sigma_0^2 \prod_{j=1}^m [\mu(t_j)]_{\mu(t_{j-1})} \sigma_0^{2z(t_j)-z(t_j)} \times \sigma_1^2 \times [\mu(t_j)]_{\mu(t_{j-1})} \cdot \sigma_0^2 \cdot \sigma_1^2 \cdot \sigma_0^2 \cdot \sigma_1^2,
\]

for a fine discretisation of the latent position process $\bm{\mu}(t_j)$ at times $t_1, \ldots, t_m$.

We applied specific formulations of our hierarchical movement model to infer recharge dynamics based on telemetry data for two contrasting species: a mountain lion in the Front Range of the Rocky Mountains in Colorado, USA and an African buffalo in Kruger National Park, South Africa (Fig. 3). Also, for illustration, we demonstrate the approach based on simulated data in Online Appendix B. Using simulated data, we showed that the modelling framework allows us to recover parameters and identify the data generating model compared to a set of alternatives that consider only $\mathcal{M}_0$ and $\mathcal{M}_1$ individually (Online Appendix B).

\section*{RESULTS}

\subsection*{Mountain lion}

In the western USA, mountain lions ($P.\ concolor$) are apex predators that mostly seek mule deer ($Odocoileus hemionus$) as prey. In the Front Range of the Rocky Mountains in Colorado, USA (Fig. 3), many approaches have been used to model the individual-based movement of mountain lions (e.g. Hanks et al. 2015; Hooten & Johnson 2017; Buderman et al. 2018), but none have modelled connections between physiological dynamics and movement. Front Range mountain lions navigate a matrix of public and privately owned land comprised of wildland-urban interface, roads and trail systems (Blecha 2015; Buderman et al. 2018). Previous research has shown that prey availability and cached carcasses are important factors influencing mountain lion movement (Husseman et al. 2003; Blake & Gese 2016). Thus, we specified a recharge-based movement model for the telemetry data (global positioning system [GPS] with 3 h fixes; $n = 150$) from an adult male mountain lion in Colorado during 25 April 2011 – 17 May 2011 (Fig. 3).

This particular trajectory includes a period at the beginning and end of the time interval where the individual occupied a prey kill area (top centre of mountain lion data in Fig. 3; using methods to identify kills sites described by Knopff et al. 2009). On c. 1 May 2011, the individual mountain lion left the prey kill area to traverse a large loop to the south before returning to the prey kill area. After a few more days at the prey kill area, the individual left again to traverse a small loop to the north. We hypothesised that the mountain lion individual recharged at the prey kill area and mostly discharged otherwise.

We used the same movement model structure as specified in the previous section, with $\mathcal{M}_0$ implying no drift when charged and $p(\bm{\mu}(t), \bm{\beta}) = \mathcal{N}(\bm{x}(\bm{\mu}(t))\bm{\beta})$ to account for drift when discharged. To formulate the recharge component of the full model, we used an intercept ($\theta_0$), and six spatial covariates: presence in the prey kill area, elevation, slope, sine and cosine of aspect and the interaction of elevation and slope. For movement covariates in the full model, we used five: elevation, slope, sine and cosine of aspect and distance to prey kill area.

We fit the full recharge-based movement model to the mountain lion telemetry data shown in Fig. 3. The set of priors and hyperparameter settings, as well as pseudocode and computational details to fit the recharge-based movement model, are provided in Online Appendix C. We also examined a set of simpler models including model $\mathcal{M}_0$ and $\mathcal{M}_1$ separately as well as the recharge-based model with only prey kill area covariates and the associated submodel $\mathcal{M}_1$ with only the prey kill area covariates. We scored each of the models using the negative log posterior predictive score based on cross-validation (Hooten & Hobbs 2015; Online Appendix C) and found the recharge-based model with only prey kill area covariates was the best predictive model. The associated marginal posterior distributions for the model parameters $\beta_1$
In this case, the left half of Fig. 4 (labelled ‘behaviour’) indicates that there is evidence for the individual to move toward the prey kill area when the decision to recharge is made (because of the negative coefficient associated with distance to prey kill area) and the recharge function itself (and hence the decision to recharge) increased with the individual’s presence in the prey kill area (i.e. convex polygon with 1 km buffer from kill site clusters). In terms of the estimated recharge function for the individual mountain lion, the posterior median for $g(t)$ is shown superimposed on the trajectory in Fig. 5. The results of fitting
the recharge-based movement model to the mountain lion telemetry data indicate that the individual is charged (blue) when near the prey kill area (green region) and discharges as it moves farther from the kill area, both to the south and the north (Fig. 5a).

Visualised longitudinally, the posterior marginal trajectories as well as posterior median for $g(t)$ and $\rho(t)$ are shown in Fig. 5. The posterior inference indicates that the mountain lion individual we analysed was mostly recharging during the early portion of the study period (25 April 2011 – 1 May 2011). However, as the recharge function $g(t)$ exceeded a value of approximately three, the individual left the prey kill area. During the week that the individual was away from the prey kill area, our analysis shows that the aggregated physiological process discharged until the behavioural decision process was dominated by $z(t) = 1$, at which point the individual actively

![Figure 5](https://example.com/figure5.png)

**Figure 5** Posterior median associated with the mountain lion data analysis for the a) recharge function $g(t)$ shown as colour on top of the posterior median trajectory $\mu(t)$. Prey kill area (i.e. convex polygon with 1 km buffer from prey kill site clusters) shown as green region indicating area associated with recharge. Distance to prey kill area is shown in the background for reference (with small distances indicated by darker shades). Map in (a) oriented such that north is up. Posterior median trajectories (b, c) and (d) recharge function $g(t)$ and (e) decision probability $\rho(t)$ with 95% credible intervals shown in grey with posterior mean for the decision $z(t)$ shown as black points. Colour corresponds to the value of the recharge function. Profile of distance to prey kill area shown as grey line in (b) and (c) for reference. Green rug at the bottom of (b) represents times when recharge occurred.
sought to recharge. This decision process was characterised largely by a tendency of the individual to orient back toward the prey kill area on 9 May 2011 (Fig. 5). Then, after another few days of recharging at the original prey kill area, the individual left the prey kill area again (this time to the north) and its physiological process began to discharge again until near the end of the study period when the individual returned to the prey kill area (Fig. 5).

African buffalo

In contrast to the western hemisphere predator we described in the previous section, the African buffalo is a large grazing ungulate that ranges throughout sub-Saharan Africa (Sinclair 1977). In Kruger National Park, South Africa, the African buffalo is an important species because it fills a niche in terms of tall and coarse grazing preference (Cornélis et al. 2014), is a source of prey for lions (Panthera leo; Sinclair 1977; Prins 1996; Radloff & Du Toit 2004), and is one of the desirable species for tourism in the region. African buffalos are strongly water dependent because they lack the capacity to subsist on the moisture available from their forage alone (Prins & Sinclair 2013). Previous studies of the movement of African buffalo found that water resources can strongly influence their space use (Redfern et al. 2003). In some cases, African buffalo may undergo large interseasonal movements when resources are limited (e.g. Naidoo et al. 2012), but there is variability in dry vs. wet season movement characteristics across regions (Ryan et al. 2006; Cornélis et al. 2014). Repetitive use of areas is common among African buffalo and some of these patterns in space use may be a result of maintaining physiological balance among resources (Bar-David et al. 2009).

We used the same movement model (8) that we applied to the mountain lion data (but with different environmental variables) to analyse a set of telemetry data arising from an adult female African buffalo in southern Kruger National Park (Getz et al. 2007) obtained using hourly GPS fixes \( n = 361 \) and spanning the period from 1 October 2005 – 14 October 2005 (Fig. 3). The transition from dry to wet season typically occurs during late September and October in South Africa, and the year 2005 had slightly more rainfall than the climate average for Kruger National Park (MacFadyen et al. 2018). The African buffalo movement data we analysed indicates that the individual mostly occupied the northern and western areas near the Sabie River and tributaries are associated with low lying green. This spatially explicit inference indicates that surface water covariates both together with \( M_0 \) and \( M_1 \) separately with all covariates as well as \( M_1 \) with only surface water covariates both together with \( M_0 \) and separately.

Similar to our mountain lion results, the reduced recharge model based only on surface water covariates had a better predictive score than the other models we fit (Online Appendix C). The left half of Fig. 6 (labelled ‘behaviour’), which shows the marginal posterior distribution for the movement parameter, indicates that the African buffalo orient toward surface water when it makes the decision to recharge during this time period. Furthermore, the right half of Fig. 6 indicates that surface water proximity increased the recharge function itself. These results agree with previous findings (e.g. Redfern et al. 2003) that surface water in this region is an important predictor of African buffalo movement.

Displayed in the same way as the mountain lion results, Fig. 7 shows the posterior marginal trajectories as well as posterior median for \( g(t) \) and \( p(t) \) for the African buffalo. The posterior inference indicates that the African buffalo individual we analysed needed to recharge regularly throughout the time period based on the large values for \( p(t) \) overall. However, brief and fairly regular periods where the posterior mean for \( z(t) \) dropped below 0.5 in Fig. 7e indicate short forays away from water resources. One such period where the decision process was not dominated by \( z(t) \) occurred when the individual looped to the southeast of the study area (7–8 October 2005). Our analysis shows that the recharge function started high (near zero) and then mostly decreased as the individual ventured farther from surface water until eventually looping back to the north at which point the recharge function increased again (Fig. 7a,d). In fact, Fig. 7a shows the areas associated with increases in the recharge function in green. This spatially explicit inference indicates that low lying areas near the Sabie River and tributaries are associated with recharge for the African buffalo individual we analysed (Fig. 7a). Furthermore, the fact that the recharge model including surface water proximity covariates had a better predictive score than the simpler models (\( M_0 \) and \( M_1 \)) fit separately, suggests that a physiological recharge signal related to the covariates is present in the movement trajectory for the African buffalo.

**DISCUSSION**

Our example data analyses provided evidence that both the mountain lion and African buffalo data sets contained a physiological signal whose variation is at least partially explained by environmental features. In the case of the mountain lion, a model comparison indicated that proximity to prey kill area was the primary factor influencing the recharge and movement processes. This result agrees with other recent studies (i.e. Buderman et al. 2018) that mountain lion movement patterns are strongly influenced by predatory behaviour. Our analysis of the African buffalo data suggested that recharge-
based dynamics were important because the simpler models that do not directly account for an underlying physiological process had worse predictive scores. In the case of the African buffalo data we analysed, the inferred spatial pattern associated with recharge in Fig. 7a indicated a clear relationship between probable surface water and recharge and this was confirmed by the posterior distributions for movement and recharge parameters (Fig. 6). Previous studies of African buffalo indicate that, while movement is largely driven by water resources, other factors such as forage, social dynamics and cover may also influence space use (Ryan et al. 2006; Winnie et al. 2008). These additional factors could be examined in more detailed studies that combine recharge and social dynamics with plant ecology and energetics.

In general, the feedback between animal decision making, physiology and movement is a complex process that involves both intrinsic and extrinsic factors (Morales et al. 2005, 2010; Nathan et al. 2008). For example, connections between energetics, memory and movement directly influence the way we infer animal home ranges (Börger et al. 2008). Despite calls for more thoughtful frameworks to model movement that consider mechanisms explicitly, many modern approaches to modelling animal trajectories are still purely phenomenological. Recent advances in biotelemetry technology have given rise to massive repositories of high-resolution individual-based data (‘auxiliary data’) that often accompany more conventional position-based telemetry data (Brown et al. 2013). These auxiliary data are collected to measure characteristics of individual fitness and behaviour (e.g. Elliott et al. 2013; Leos-Barajas et al. 2017) and may provide a more direct link to understand physiological recharge.

Leveraging the hierarchical modelling framework to combine data sources (Hobbs & Hooten 2015), we can integrate auxiliary data into the recharge-based animal movement model (Online Appendix E). Such model structures have become common in population and community ecology where they are referred to as ‘integrated population models’ (Schaub & Abadi 2011). When we have auxiliary accelerometer data, it may be possible to connect the fine-scale measurements of micro-movement to the change in position directly (Wilson et al. 1991). In that case, it is sensible to let the auxiliary data inform both the trajectory process and the physiological recharge process directly. In situations where multiple forms of auxiliary data are recorded (e.g. accelerometer and body condition measurements), we can augment the integrated movement model with additional data models that are connected to the latent model components, partitioning the recharge functions further as needed (Online Appendix E).

Overall, the framework we present allows researchers to connect the mechanisms related to known physiological characteristics with more conventional telemetry data to account for latent physiological and individual-based decision processes. Our approach is flexible and allows for modifications to the form of both movement (6)–(7) and recharge functions (1) and (3). As with any mixture model, some structure allows the data to better separate model components so that parameters are identifiable. In our case studies, we specified the movement model such that one term ($M_0$) represents random diffusive movement and the other term ($M_1$) captures movement in response to environmental variables. This helps us learn about the recharge function in a way that corresponds to our pre-existing knowledge about the physiology of these species. In Online Appendix E, we show how to extend the recharge-based movement model to accommodate various sources of auxiliary data to better recognise and estimate the physiological process components depending on available data.

For some species, it may be appropriate to consider additional stochasticity in the recharge process because of unobservable interactions with conspecifics, allospecifics, or other dynamic environmental conditions. Our framework can readily accommodate these sources of overdispersion by specifying the recharge functions $g(v, t)$ as SDEs (in addition to the movement process). Statistical inference in these settings relies
on our ability to observe enough data to successfully estimate the various sources of uncertainty in the model. Auxiliary data, such as those described above, may be helpful to partition and estimate parameters in these more general models.

We formulated the recharge-based movement models in continuous time for our applications to account for irregular telemetry and auxiliary data when available, but, like all continuous-time models that require numerical solutions, our model is fit using an intuitive discrete time approximation. In cases where the telemetry data are high-resolution and temporally regular, the movement models (i.e. $M_0$ and $M_1$) themselves can be formulated directly in discrete time using either the velocity vectors (e.g. Jonsen et al. 2005) or polar coordinates associated with discrete moves (e.g. Morales et al. 2004;...
Langrock et al. 2012; McClintock et al. 2012). In this setting, the movement process and physiological recharge function are limited to the chosen temporal resolution and the associated inference is resolution-dependent.

While our recharge-based movement modelling framework facilitates the inclusion of mechanisms related to physiology, it can also be used as a way to accommodate latent sources of dependence. The physiological recharge functions we specified in eqns 1 and 3 impart a type of long memory in the stochastic process models that we exploit to learn about the influences of landscape and other spatial features on movement. However, time series analyses have relied on long-memory processes to account for dependence in data for many other applications (Beran 1994). In terms of animal memory explicitly, its influence on movement has been investigated separately (e.g. Avgar et al. 2013; Fagan et al. 2013; Bracis et al. 2015; Bracis & Mueller 2017; Merkle et al. 2017), but it has not been accommodated in the way we describe herein, especially in the context of physiological processes.

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AUTHORSHIP
MH, HS and JM designed the modelling methodology and HS performed analyses. MH and HS wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY
Data are included with the computer code at: https://github.com/henryrscharf/Hooten_et_al_EL_2018.

REFERENCES

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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