


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 (*Synceus caffer*; in Kruger National Park, South Africa) recharge dynamics.

Keywords

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

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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 (Ingraham & 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.* 2012; McKellar *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’ (Laundré *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 (*Synceus caffer*) in South Africa. We also discuss possible ways to extend the model to account for conspecific and allospecific 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 $\mathbf{w}'(\boldsymbol{\mu})\boldsymbol{\theta}(v)$ for any location $\boldsymbol{\mu} \equiv (\mu_1, \mu_2)'$ in region \mathcal{D} (e.g. the study area).

The coefficients $\boldsymbol{\theta}(v) \equiv (\theta_1(v), \dots, \theta_p(v))'$ appropriately weight each of the landscape variables (e.g. elevation, land type, etc.) in $\mathbf{w}(\boldsymbol{\mu}) \equiv (w_1(\boldsymbol{\mu}), \dots, w_p(\boldsymbol{\mu}))'$ 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 $\mathbf{w}'(\boldsymbol{\mu}(t))\boldsymbol{\theta}(v)$ represents the physiological landscape value that influences the energy recharge dynamics as the individual under study moves to position $\boldsymbol{\mu}(t)$ at time t .

In fact, for a given individual trajectory $\boldsymbol{\mu}(t)$ (for all $t \in \mathcal{T}$ in the study period), the physiological landscape $\mathbf{w}'(\boldsymbol{\mu}(t))\boldsymbol{\theta}(v)$ 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

$$g(v, t) = g_0(v) + \int_0^t \mathbf{w}'(\boldsymbol{\mu}(\tau))\boldsymbol{\theta}(v)d\tau, \quad (1)$$

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. $v \in \mathcal{V}$) 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 & Hobbs 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 (Laundré *et al.* 2001; Bleicher 2017). Thus, we can express an aggregated physiological recharge process as an integral over the

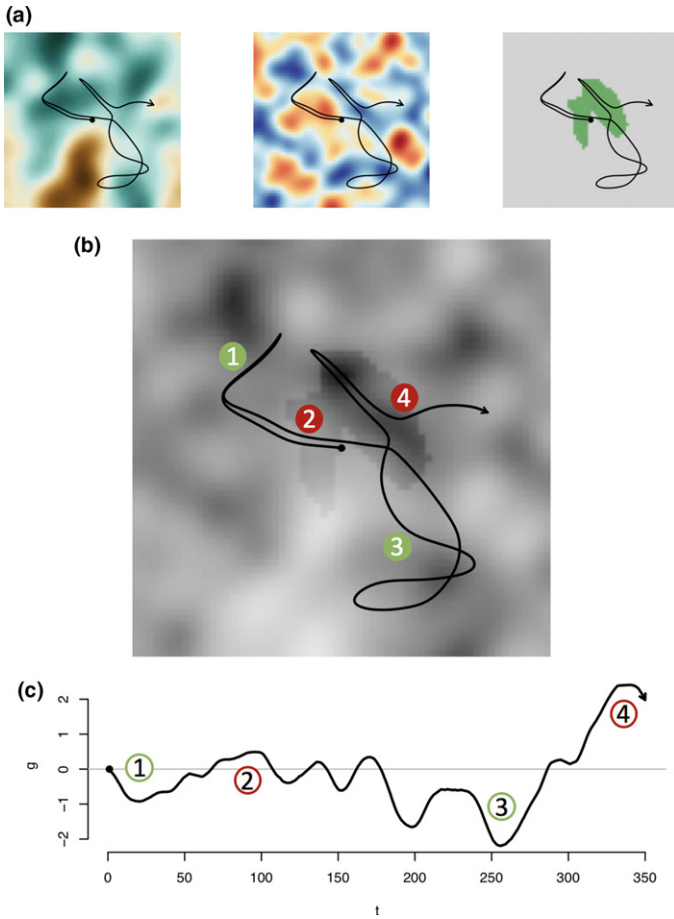


Figure 1 (a) Simulated environmental covariates $w(\mu)$ that may influence the recharge function (left: large scale spatial process, middle: small scale spatial process, right: patch); (b) an example physiological landscape based on the environmental covariates with example individual trajectory ($\mu(t)$, for all $t \in T$) shown as solid line beginning at solid point and ending at the arrow; (c) physiological recharge function arising from the path integral of the physiological landscape associated with trajectory. Numbered circles represent time points at which the simulated individual is charged (red) and discharged (green).

set of all physiological processes \mathcal{V} :

$$g(t) = \int_{\mathcal{V}} g(v, t) dv, \tag{2}$$

$$= g_0 + \int_0^t w'(\mu(\tau))\theta d\tau, \tag{3}$$

where we show that the initial aggregated charge is

$$g_0 \equiv \int_{\mathcal{V}} g_0(v) dv, \tag{4}$$

and the aggregated recharge coefficients are

$$\theta \equiv \int_{\mathcal{V}} \theta(v) dv \tag{5}$$

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 $z(t_i)$ 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 $i = 1, \dots, n$) and associated trajectory $\mu(t_i)$ we formulate the hierarchical model

$$s(t_i) \sim [s(t_i)|\mu(t_i)], \tag{6}$$

$$\mu(t_i) \sim \begin{cases} \mathcal{M}_0, & z(t_i) = 0, \\ \mathcal{M}_1, & z(t_i) = 1, \end{cases} \tag{7}$$

for $i = 1, \dots, n$, where the bracket notation ‘ $[\cdot]$ ’ 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

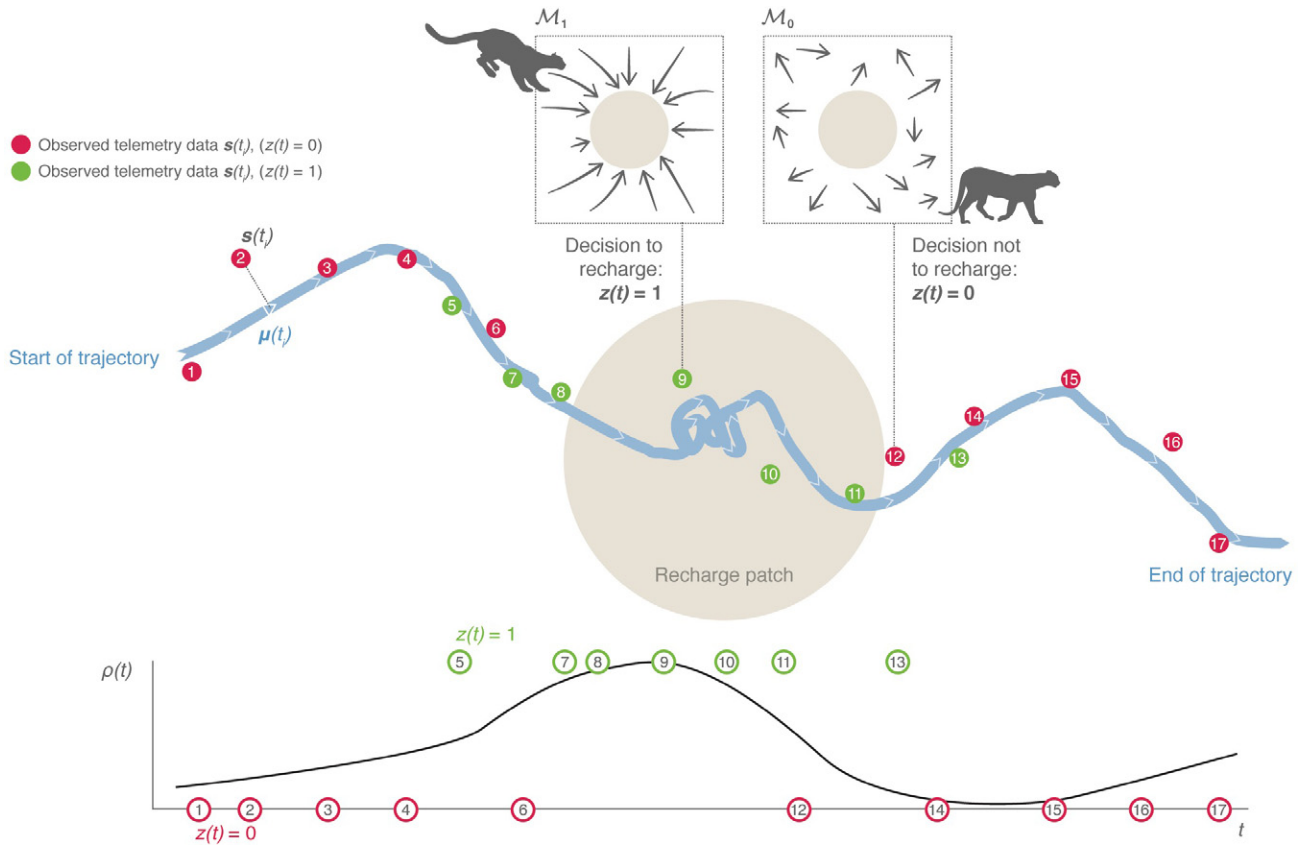


Figure 2 Schematic of recharge and movement model components. The observed telemetry data ($s(t_i)$, red and green points along trajectory) at time t_i are measurements (with error) of the true positions $\mu(t_i)$ (blue triangle, left, for a given observation time t_i). The underlying continuous-time trajectory $\mu(t)$ is shown as the solid blue line and is conditionally modelled based on the movement dynamics (incorporated in models \mathcal{M}_0 and \mathcal{M}_1) and possibly changes in the environment (incorporated in model \mathcal{M}_1). In this example, the brown circle in the middle of the study area represents a recharge region or patch where the individual may recharge its energy (e.g. a prey kill area). The binary decision $z(t)$ to recharge indicates when the individual responds to the underlying landscape (in this case, it may be attracted to the recharge region). While $z(t)$ is represented as a continuous-time binary process in our model, this figure shows the subset of decisions associated with the observed telemetry data (numbered points in bottom plot). In the figure, decisions to recharge ($z(t) = 1$) are green and are otherwise shown in red ($z(t) = 0$). The stochastic binary decision process is governed by the probability function $\rho(t)$ (shown as solid black line in bottom plot), which is, in turn, a function of the recharge process $g(t)$ (not shown).

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 $\rho(t)$ 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 $s(t_i) \sim N(\mu(t_i), \sigma_s^2 \mathbf{I})$ (for $i = 1, \dots, n$) and a mixture SDE with components

$$d\mu(t) = \begin{cases} \sigma_0 d\mathbf{b}_0(t), & z(t) = 0 \\ -\nabla p(\mu(t), \beta) dt + \sigma_1 d\mathbf{b}_1(t), & z(t) = 1 \end{cases} \quad (8)$$

for the set of times in the study period $t \in \mathcal{T}$, 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 β . The diffusion aspects of the movement process are controlled by the two Gaussian white noise terms $d\mathbf{b}_0(t)$ and $d\mathbf{b}_1(t)$ that are scaled by σ_0 and σ_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; \mathcal{M}_1 in Fig. 2). Conversely, when $z(t) = 0$, the individual may roam freely without needing to respond to the environment (\mathcal{M}_0 in Fig. 2). Thus, in this particular model specification, we would obtain biased inference

about the movement parameters β if the individual was assumed to move according to the SDE with potential function $p(\mu(t), \beta)$ 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 approach proposed by Hooten & Johnson (2017) to connect the telemetry data to the underlying trajectory. This 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 $\mu(t)$ 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 $\mu(t_j)$ in eqn 7 can be written as $\mathcal{M}_0 = N(\mu(t_{j-1}), \sigma_0^2 \mathbf{I} \Delta t)$ and $\mathcal{M}_1 = N(\mu(t_{j-1}) - \nabla p(\mathbf{x}'(\mu(t_{j-1}))\beta)\Delta t, \sigma_1^2 \mathbf{I} \Delta t)$ for a fine grid of time points, t_1, \dots, t_m , spaced Δt 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 $\mu(t_j)$ for all $j = 1, \dots, m$, as well as three sets of parameters: (1) the drift coefficients in the potential function, β , (2) the initial recharge state g_0 and recharge coefficients θ and (3) the variance parameters σ_s^2 , σ_0^2 and σ_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

$$\begin{aligned}
 & [\{\mu(t_j), \text{ for } j = 1, \dots, m\}, \beta, g_0, \theta, \sigma_s^2, \sigma_0^2, \sigma_1^2 | \{s(t_i), i = 1, \dots, n\}] \propto \\
 & \prod_{i=1}^n [s(t_i) | \mu(t_i), \sigma_s^2] \prod_{j=1}^m [\mu(t_j) | \mu(t_{j-1}), \sigma_0^2]^{1-z(t_j)} \\
 & [\mu(t_j) | \mu(t_{j-1}), \beta, \sigma_1^2]^{z(t_j)} [z(t_j) | g_0, \theta] \\
 & \times [\beta] [g_0] [\theta] [\sigma_s^2] [\sigma_0^2] [\sigma_1^2],
 \end{aligned} \tag{9}$$

for a fine discretisation of the latent position process $\mu(t_j)$ at times t_1, \dots, 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).

RESULTS

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 (Hussemann *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 $p(\mu(t), \beta) = \mathbf{x}'(\mu(t))\beta$ to account for drift when discharged. To formulate the recharge component of the full model, we used an intercept (θ_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 β_j

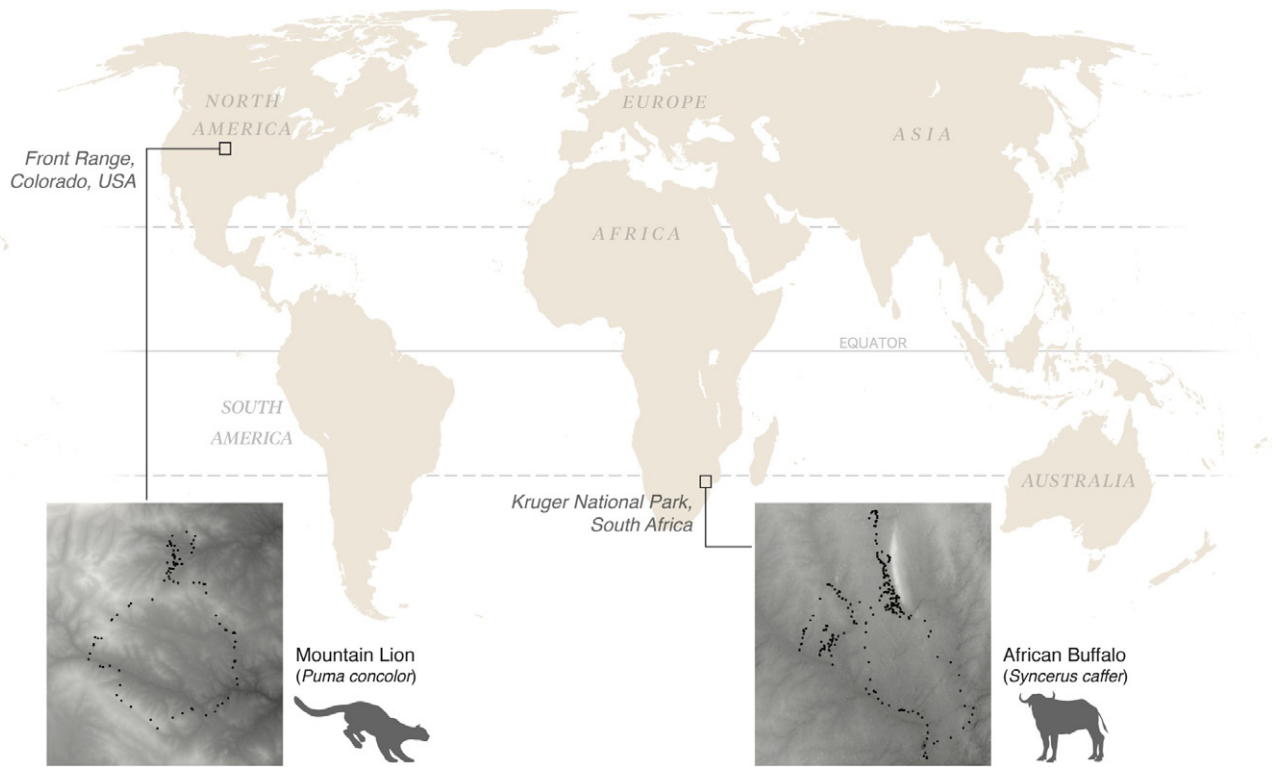


Figure 3 World map depicting the regions where the telemetry data in our examples arise from a global positioning system collared mountain lion and African buffalo. Telemetry data are shown as black points on blown up maps, with elevation shown as background shading; high (relative) elevations shown as lighter shading.

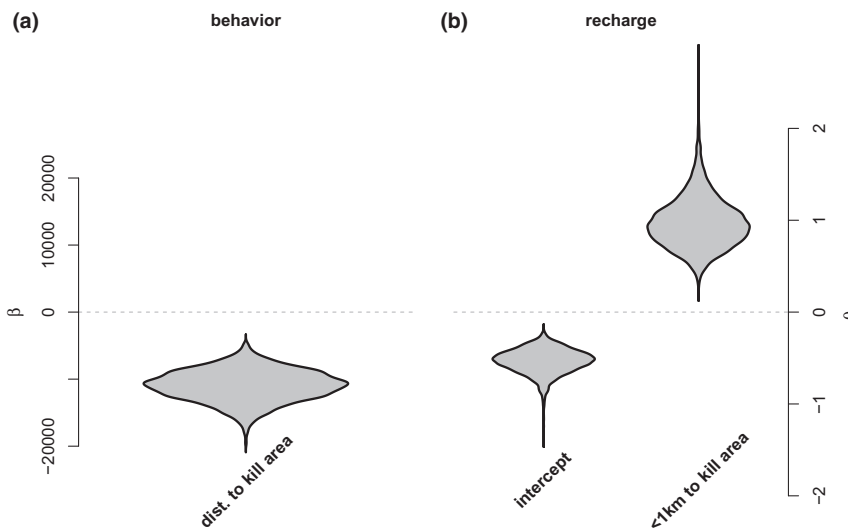


Figure 4 Marginal posterior violin plots for the mountain lion model parameters (a) β and (b) θ .

(coefficient for distance to prey kill area), θ_0 (recharge intercept coefficient) and θ_1 (coefficient for inside prey kill area) are shown in Fig. 4.

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

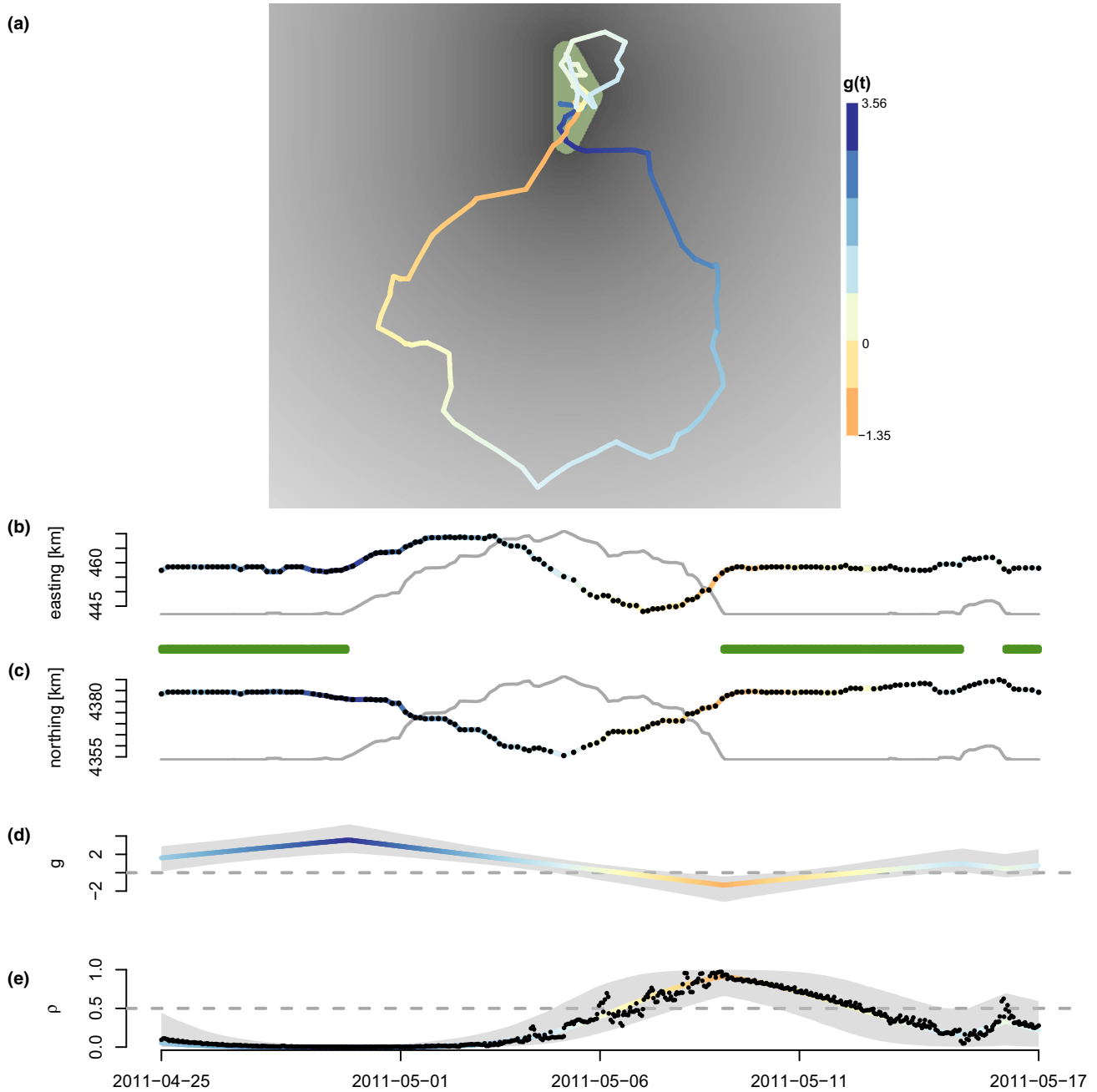


Figure 5 Posterior median associated with the mountain lion data analysis for the a) recharge function $g(t)$ shown as colour on top of the posterior median trajectory $\mu(t)$. Prey kill area (i.e. convex polygon with 1 km buffer from prey kill site clusters) shown as green region indicating area associated 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 (Cornélias *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 buffalo 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; Cornélias *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 extent of the region during the 2 weeks time period, but travelled *c.* 15 km between major surface water sources to the southeastern portion of the region during 7–9 October 2005.

We specified the recharge function to include an intercept (θ_0) and covariates for elevation, slope, surface water proximity (< 0.5 km buffer to nearest surface water) and an interaction for elevation \times slope to examine the evidence for an effect of water and other resources for which topography may serve as a surrogate on physiological recharge during a time when it is difficult to predict the widespread availability of water and forage during the transition from dry to wet season in this region. For movement covariates, we used elevation, slope and distance to nearest surface water.

We fit recharge-based hierarchical movement models to the African buffalo telemetry data shown in Fig. 3. The full set of

priors and hyperparameter settings, as well as pseudocode and computational details to fit the full recharge-based movement model, are provided in Online Appendix C. As in the mountain lion data analysis, we also examined a set of simpler models, including hierarchical models that incorporate \mathcal{M}_0 and \mathcal{M}_1 separately with all covariates as well as \mathcal{M}_1 with only surface water covariates both together with \mathcal{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 orients 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 $\rho(t)$ 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 $\rho(t)$ 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 $z(t) = 1$ 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 (\mathcal{M}_0 and \mathcal{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-

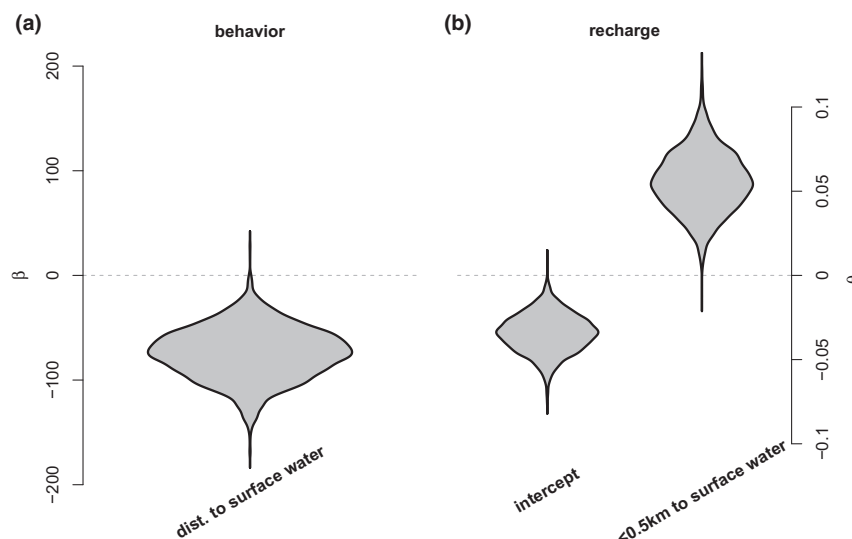


Figure 6 Marginal posterior violin plots for the African buffalo model parameters (a) β and (b) θ .

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 (\mathcal{M}_0) represents random diffusive movement and the other term (\mathcal{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

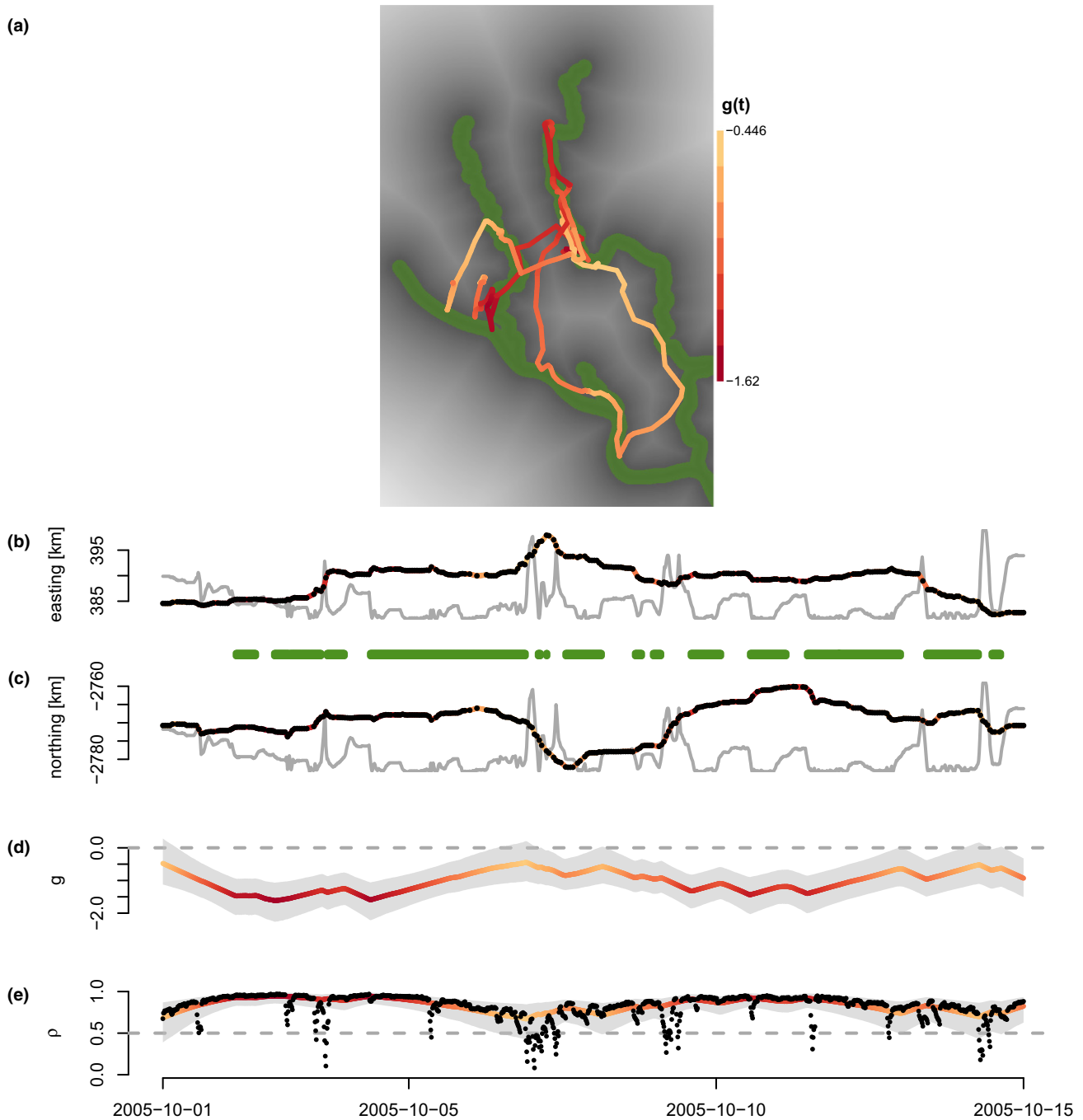


Figure 7 Posterior median associated with the African buffalo data analysis for the (a) recharge function $g(t)$ shown as colour on top of the posterior median trajectory $\mu(t)$. Distance to surface water is shown in the background for reference (with small distances indicated by darker shades) and green indicating inferred areas associated with recharge. 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. Distance to surface water profile shown as grey line in (b) and (c) for reference. Green rug at the bottom of (b) represents times when the recharge function is increasing.

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. \mathcal{M}_0 and \mathcal{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.

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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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