Movement of large African savanna herbivores is shaped by intricate interactions between behavioural modes and the spatial-temporal environment

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Abstract

1. Animal movement arises from a complex interaction between an animal and its heterogeneous environment. The large amount of variables involved in that interaction complicates the ecological inference thereof. In order to better understand movement, the myriad of involved variables can be grouped into behavioural, spatial, and temporal components of the movement process (related to the questions of *why*, *where* and *when* to move), which should be addressed simultaneously.
2. We studied the influence of spatial environmental variation on fine-scale movement trajectories of eland antelope, blue wildebeest and plains zebra in a South-African game reserve, in simultaneous consideration with temporal rhythms and behavioural movement modes.
3. We described the animals' movement process as multi-mode random walks using hidden Markov models (HMMs), where both the probabilities of switching between modes as well as the mode-dependent speed and turning angle distributions were a function of time of day, tree cover and terrain slope.

4. The fitted HMMs clustered the trajectories of all three species into a fast and directed "transit" mode and a slow and tortuous "encamped" mode. All movement properties displayed a strong diel pattern, with the effects of tree cover and slope on speed being largest in the evening when animals generally moved faster. Wildebeest and zebra in their transit mode moved faster with increasing tree cover whereas eland moved slower, but only so on steep terrain. In the encamped mode, tree cover had almost no effect on speed, but a strong effect on tortuosity. The animals also generally moved more tortuously with higher tree cover, even more so on sloping terrain.
5. Due to our integrated approach, we showed that the influence of spatial environmental heterogeneity on animal movement varies greatly in diel cycles and between movement modes, reflecting variation in the animals' habitat selection and decision making throughout the day. Thus, focusing on the interactions between *why*, *when* and *where* to move is needed to more truthfully describe and understand animal movement.

Keywords: behavioural thermoregulation; diurnal cycle patterns; foraging; GPS tracking; predator-prey interactions; state space modelling; ungulate movement; wildlife activity

1 Introduction

Movement is ubiquitous to animal life and central to ecological phenomena such as territoriality and home range dynamics (Kie et al., 2002; Moorcroft et al., 1999), predator-prey dynamics (Abrams, 2007; Flaxman & Lou, 2009), distribution patterns (Bailey et al., 1996) and population dynamics (Armsworth & Roughgarden, 2005; Morales et al., 2010; Revilla & Wiegand, 2008). Studying what drives the movement of animals through their environment is thus key to understanding emergent movement properties and their ecological consequences (Morales et al., 2010; Schick et al., 2008). However, this understanding is hampered by the complexity of the interactions between animals and their environment. Namely, similar movement patterns might emerge from different underlying processes that require different ecological interpretations. For example, animals might move slowly through thick vegetation because it physically impedes their movement, because they forage, hide from predators, or seek shelter

from solar radiation. Moreover, the response of animals to their environment may change over time, e.g. via diel, lunar and seasonal patterns (e.g. de Knegt et al., 2021). Therefore, the animal movement process has generally been divided into several components in an effort to alleviate the interpretation issues: an internal motive regarding *why* to move and its temporally and spatially varying environment influencing *when* and *where* to move (Nathan et al., 2008).

First, "*why to move*" relates to the internal motives for movement (e.g. reproduction, resource acquisition and threat avoidance), which are often manifested in different behaviours (e.g. mating, foraging and fleeing) that produce distinct movement modes (e.g. distributions of speed and turning angle) (McClintock et al., 2012; Morales et al., 2004; Nathan et al., 2008). Distinguishing different movement modes in animal trajectories has yielded insights in different foraging strategies within individuals (McClintock et al., 2017), predator-prey interactions (Forester et al., 2007) and effects of anthropogenic disturbance on behaviour (van Beest et al., 2019). Acknowledging the internal motives and their emergent movement modes is thus key to the interpretation of animal movement, specifically regarding how this movement interacts with the environment (Jonsen et al., 2006; McClintock et al., 2012, 2017; Morales et al., 2004).

Second, regarding *"when to move"*, animal movement often shows pronounced temporal variation and even cyclic patterns. For example, seasonal migratory movements (e.g. Dingle, 2014; Dingle & Drake, 2007) have long been recognized, as well as the influence of lunar rhythms (e.g. Polansky et al., 2010; Riotte-Lambert & Matthiopoulos, 2020). Moreover, many animals show strong diel activity patterns (e.g. Ensing et al., 2014; Forester et al., 2007; Green & Bear, 1990; Massé & Côté, 2013; Owen-Smith & Goodall, 2014; Vazquez et al., 2019), which can arise directly due to variation in light and thermal conditions (Dussault et al., 2004) or indirectly due to predation risk and human activity (Ensing et al., 2014; Fischhoff et al., 2007; Owen-Smith & Traill, 2017; Skarin et al., 2010). Temporal periodicity is thus a central characteristic in the movements of animals (Riotte-Lambert et al., 2013).

Third, the focus on *"where to move"* relates the movement of animals to the characteristics of their spatial surroundings. Especially the effects of vegetation and topography on the movement of large terrestrial herbivores have received much attention. Vegetation-rich environments often coincide with lower movement speeds (Avgar et al., 2013; de Knegt et al., 2007, 2021; Frair et al., 2005; Fryxell et al., 2008). Topography can influence movement through energetic costs associated with moving through sloping or rugged terrain (Dailey & Hobbs, 1989; Parker et al., 1984; White & Yousef, 1978). Perhaps surprisingly, ungulates have been found to increase movement speed on slopes, possibly to reduce their time spent in energetically costly surroundings (Frair et al., 2005). Furthermore, ungulates can select slopes for foraging since elevation differences increase the diversity of encountered vegetation and thereby the chance of finding high quality forage (Leblond et al., 2010). Daily cycles can also interact strongly with the landscape to affect animal movement (Ager et al., 2003; Fischhoff et al., 2007; Leblond et al., 2010). For example, ungulates can select areas with high vegetation cover during daytime and more open areas during the night to decrease predation risk (Ager et al., 2003; Leblond et al., 2010). These examples illustrate that relationships between spatial environmental characteristics and movement patterns are conditional on the context of internal motive and time, as this context determines the costs and benefits that these spatial environmental characteristics represent.

Internal motives, temporal rhythms and spatial environmental heterogeneity are thus three intricately linked components of the animal movement process. However, animal movement research has often been hampered by the focus on univariate analyses (Eikelboom et al., 2020), while ideally the relationships between animal movement and each of these three components should be modelled and interpreted within each other's context (Nathan et al., 2008). Only when interpreting animal movement relative to these three components acting in concert can we advance our understanding of the processes shaping animal movement.

Here we study how movement modes, diel patterns and spatial environmental heterogeneity interact to shape the movement of large ungulates by modelling the movement process explicitly as a composite of these components. We use a large amount of fine-scale (10 minute resolution) GPS tracking data of

eland antelope, blue wildebeest and plains zebra in a South-African game reserve to fit Hidden Markov Models (HMMs) with input from the time of day, tree cover and terrain slope. HMMs can describe the movement process as a multi-mode random walk comprised of step lengths and turning angles, with input from both temporal variation and environmental heterogeneity (McClintock et al., 2020), thereby making them an ideal model for our purpose. We aim to quantify the interactive effects of movement mode (as a proxy for internal motive), diel patterns and spatial environmental heterogeneity on movement properties, and how these differ between our study species. In doing so, we address the questions of *why*, *when* and *where* to move, thereby trying to advance our understanding of the movements of our study species and demonstrating ways to analyse these components in concert.

2 Materials and methods

2.1 Animals and study area

From June to August 2017, 34 eland antelope (*Taurotragus oryx*), 34 blue wildebeest (*Connochaetes taurinus*) and 35 plains zebra (*Equus quagga*) were captured in Welgevonden Game Reserve, Limpopo, South Africa (24°13'S, 27°54'E), and equipped with neck collars containing GPS and accelerometer sensors. For more details about the collaring process and sensors, see de Knegt et al. (2021). The animals were released in a fenced study area of 1200 hectares at the northern edge of the reserve (Fig. 1). As a part of the Waterberg mountain massif and Bushveld ecoregion (Mucina et al., 2006), the study area is characterised by nutrient poor sandy soils in the lower northern part and rocky, flat hilltop plateaus dissected by ravines extending towards the south. Woody vegetation varies from mixed to open dry deciduous woodland, with the rocky plateaus being the most open.

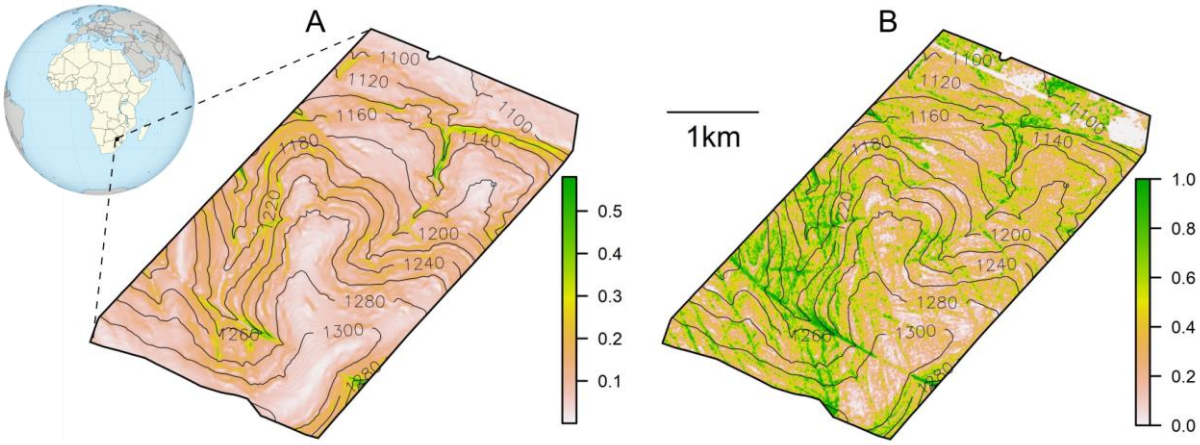

Figure 1. Overview of the study area and its environmental heterogeneity with A) terrain slope (radians) and B) fractional tree cover. Numbers at the isoclines denote elevation from sea level (m).

2.2 Animal movement data

The GPS sensors collected spatial positions with a frequency ranging between 15 and 2 minutes, depending on the amount of body activity as determined by the accelerometer (see de Knegt et al., 2021). The position data were corrected, smoothed and modelled to regular ten-minute resolution trajectories as described in de Knegt et al. (2021). Due to sensor failures, we selected from each species only the ten individuals with the most recorded data in the period from September to December 2017 (the first four months of the study period, during which the sensors collected most data). Our subset contained a total of 357,815 positions across 30 individuals of the three species, comprising 481 bouts (i.e. an uninterrupted and regular sequence of positions of a single individual) with a median bout length of 496 positions (3.4 days).

2.3 Environmental data

A digital elevation model of the study area with resolution 2x2 m was available, from which terrain slope (hereafter referred to as slope) was calculated (Fig. 1A). We used aerial images of the study area from August 2013 to create an orthomosaic with a 0.25x0.25 m resolution, which we then used to classify the pixels into trees, grass, bare ground and other/built up area using the Semi-Automatic Classification Plugin for QGIS (Congedo, 2021). After having applied an isotropic Gaussian kernel smoother with a 10 m standard deviation to the classified pixels, we derived fractional tree cover

(hereafter referred to as tree cover) and fractional grass cover maps of the study area at a 2x2 m resolution (Fig. 1B). Tree cover was strongly negatively correlated with grass cover (r = 0.95), so we decided to use only tree cover in our analyses and consider it a measure for the inverse of grass cover as well. We extracted tree cover and slope values for each animal position.

2.4 Movement model structure

We constructed a Hidden Markov Model (HMM) for each species separately to examine how their movement properties were shaped by movement modes, diel patterns and environmental heterogeneity. We described the movement process as a random walk consisting of steps (distances between subsequent positions) with lengths s and turning angles φ (change between subsequent movement headings). Since intervals between steps were constant at ten minutes, we refer to s as speed throughout. s and φ were fitted to *gamma* (Γ) and *von Mises* (*vM*) distributions, respectively, which were unique to each discrete movement mode z. Thus, z was defined as a unique combination of three movement parameters: the mean μ and standard deviation σ of the speed (converted from the shape and scale parameter of the Γ distribution for easier interpretation) and the *vM* concentration parameter κ of the turning angle (the *vM* mean was fixed at 0 since there was no reason to assume a movement bias to either the right or left direction). μ, σ and κ were in turn modelled as functions of several covariates using a log-link (see section *Movement model covariates*). Mode switching between the steps was governed by switching matrix M, where the off-diagonal elements are logit-linear functions of covariates. We considered a three-mode, two-mode and a one-mode HMM, i.e. 3x3, 2x2 and 1x1 dimensions for M respectively. Thus, the HMM had the general form:

$$M = \begin{bmatrix} \gamma_{1\to1} = 1 - \sum_{z=2}^{n} \gamma_{1\to\mathrm{z}} & \cdots & \gamma_{1\to\mathrm{n}} = f_a(\boldsymbol{\theta}_a, \boldsymbol{\xi}_a) \\ \vdots & \ddots & \vdots \\ \gamma_{\mathrm{n}\to1} = f_b(\boldsymbol{\theta}_b, \boldsymbol{\xi}_b) & \cdots & \gamma_{\mathrm{n}\to\mathrm{n}} = 1 - \sum_{z=1}^{n-1} \gamma_{\mathrm{n}\to\mathrm{z}} \end{bmatrix}$$

$$s_{z=i} \sim \Gamma\left(\mu = f_c(\boldsymbol{\theta}_{c,i}\, \boldsymbol{\xi}_c), \sigma = f_d(\boldsymbol{\theta}_{d,i}, \boldsymbol{\xi}_d)\right)$$

$$\phi_{z=i} \sim vM\left(\mu = 0, \kappa = f_e(\boldsymbol{\theta}_{e,i}, \boldsymbol{\xi}_e)\right)$$

Where $\gamma_{i\to j}$ is the probability of switching from mode $z = i$ to $z = j$ between consecutive steps, f_n are functions for step switching probabilities and Γ and *vM* parameters, $\boldsymbol{\theta}_n$ are sets of to-be-fitted coefficients of function f_n (and for mode $z = i$ in case of $\boldsymbol{\theta}_{n,i}$), and $\boldsymbol{\xi}_n$ are sets of covariates (see next section).

2.5 Movement model covariates

Within the HMMs, we modelled the parameters μ, σ and κ and the mode switching probabilities $\gamma_{i\to j}$ each as a function of three covariates. Two of those were the spatial environmental covariates tree cover and slope. The third covariate was a constructed daily cyclic pattern covariate (DCC) that describes the diel patterns in μ, σ and κ (driven by e.g. ambient temperature, solar position, perceived predation risk and internal diel rhythm). To determine those diel patterns, we binned the GPS position data per time of day (144 bins of 10 minutes) and fitted Γ distributions (μ and σ) to speeds and *vM* distributions (κ) to turning angles within a centred moving window of three bins wide. This yielded empirical diel patterns in parameters μ, σ and κ (Fig. S1). We constructed DCC by first rescaling and averaging the empirical diel patterns in μ, σ and κ to one aggregate diel pattern per species (Fig. 2), given that these separate empirical diel patterns were strongly correlated within species (Fig. S2). We then fitted to that aggregate diel pattern a mixture of a cosine and four wrapped normal (*WN*) distributions with 24 h periods to compute the final DCC values per species, with the wrapped normal distributions representing two peaks and two lows per day that were fixed at the peaks and lows of the aggregate diel patterns (Fig. 2). Thus, DCC had the following form:

$$DCC = \alpha + \beta \cos\left(t_{day} + \gamma\right) + \sum_{n=1}^{4} \delta_n f_{WN}(\mu_n, \sigma_n)$$

Where t_{day} is the time of day (range $0 - 2\pi$), f_{WN} is the probability density function of the *WN* distribution with a 24 h period (describing 1 out of 4 peaks or lows per day in the aggregate diel pattern), and δ_n are scalars for those distributions. As a result, each animal position had a corresponding DCC value, which depended on the time of day and the species (Fig. 2). We then scaled tree cover, slope and DCC to a

mean of 0 and standard deviation of 1, and included the three variables and their two-way interactions as covariates of μ, σ and κ in the HMMs. We included tree cover, slope and DCC without interactions as covariates of the mode switching probabilities $\gamma_{i \to j}$.

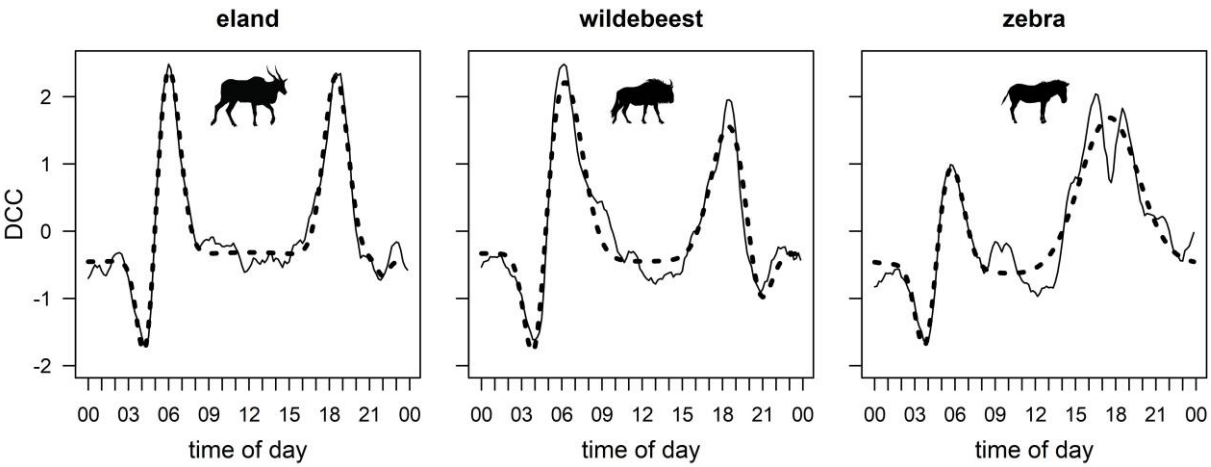

Figure 2. Aggregate diel patterns averaged from μ, σ and κ for eland, wildebeest and zebra (solid line). We fitted a daily cycle covariate (DCC, dashed line) to those aggregate diel patterns, which summarizes the diel activity patterns per species as expressed in movement properties μ, σ and κ. DCC is a mixture distribution of a cosine and four wrapped normal distributions with 24 h periods.

2.6 Model fitting workflow

We fitted the HMM per species and per unique number of movement modes separately in eleven iterations (Table 1), by numerical maximisation of the log-likelihood function, using the *fitHMM* routine from the R package *momentuHMM* (McClintock & Michelot, 2018). For the initial iteration, we fitted a baseline HMM without any covariates to speed μ and σ, turning angle κ and mode switching probabilities $\gamma_{i \to j}$. For the second to tenth iterations, we added covariates and/or interactions between covariates to the distribution parameters and switching probabilities (Table 1). The full model in the eleventh iteration included tree cover, slope and DCC as covariates to $\gamma_{i \to j}$, and these three variables and their two-way interactions as covariates to μ, σ and κ. The fitted parameter values from each iteration were used as starting values for the next; starting values for other parameters were set to 0 (note that all covariates had been scaled to mean 0 and standard deviation 1). For each iteration, four sets of perturbations of those starting values β were sampled from $\sim N(\beta, \sigma = 0.25 \cdot \beta)$. The model fit with the

highest likelihood out of all starting sets was taken to be the optimal fit and subsequently used to initiate the model fit of the next iteration. However, in practice all sets of fitted models converged to almost identical coefficient values and model likelihoods. We used the Akaike information criterion (AIC) to assess model parsimony throughout the workflow. The model structure and fitting workflow were identical for all three species and number of modes.

All analyses were performed in R 3.6.1 (R Core Team, 2019), using the packages *raster* 3.4-5 (Hijmans, 2021) for map plotting and covariate extraction and *momentuHMM* 1.5.1 (McClintock & Michelot, 2018) for model fitting and calculation of model AIC and stationary mode probabilities.

3 Results

3.1 Hidden Markov Models

We explored Hidden Markov Models (HMMs) with one, two and three movement modes. The single-mode HMMs were far inferior to the two-mode HMMs in terms of model fit, with the best single-mode models being outperformed by the worst two-mode models (ΔAIC = 74,117; 105,847 and 146,886 for eland, wildebeest and zebra respectively) and even more by the best two-mode models (ΔAIC = 85,049; 114,821 and 154,458 for eland, wildebeest and zebra respectively). The best three-mode HMMs were better still than the best two-mode HMMs in terms of model fit, albeit with a smaller difference (ΔAIC = 32,093; 29,170 and 27,381 for eland, wildebeest and zebra respectively). Both the two- and three-mode HMMs detected two modes that were qualitatively similar in terms of speed and turning angle distributions, with the three-mode HMMs detecting an additional slow and directional mode (Fig. S3). This third mode responded very little to both the temporal and spatial environmental variables, while the response displayed by the other two modes was qualitatively similar for both the two- and three-mode HMMs (Figs. S4-S6). Therefore, we visualized only the results from the two-mode HMMs in the main text. However, to strengthen the reliability of our analysis, we only formulated results and conclusions that were supported by both the two- and three-mode HMMs (Wagenmakers et al., 2022). The likelihood of all two-mode HMMs, which were fitted in eleven iterative steps for each species, are

presented in Table 1. The models including only one DCC covariate (step 6) were superior to all previous models including tree cover and slope, indicating that DCC was the dominant explanatory variable, accounting for a lot of temporal variation which is not accounted for by tree cover and slope alone. For each species the full model (step 11), which includes all covariates and interactions, was the most parsimonious model according to AIC value. We therefore analysed the data further using the full models.

Table 1. Overview of iteratively fitted two-mode HMMs and their ΔAIC per species. ΔAIC was calculated for each species separately relative to the best model of that species. tc = tree cover, sl = terrain slope, DCC = daily cycle covariate, μ, σ and κ are movement parameters and $\gamma_{i \to j}$ = mode switching probability. Powers of 2 indicate all two-way interactions among the covariates between brackets. The AIC of the full models (step 11) was 1,305,636; 1,304,360 and 1,286,972 for eland, wildebeest and zebra respectively.

Predictor set	Model step	μ, σ and κ covariates	$\gamma_{i \to j}$ covariates	ΔAIC Eland	ΔAIC Wildebeest	ΔAIC Zebra
none	1	–	–	10,932	8,974	7,572
spatial	2	tc, sl	–	10,354	8,451	5,782
	3	tc, sl	tc, sl	10,278	8,405	5,727
	4	$(\text{tc, sl})^2$	–	10,233	8,267	5,362
	5	$(\text{tc, sl})^2$	tc, sl	10,157	8,219	5,327
temporal	6	DCC	–	882	978	2,299
	7	DCC	DCC	822	918	2,240
spatial + temporal	8	tc, sl, DCC	–	256	678	787
	9	tc, sl, DCC	tc, sl, DCC	145	432	677
	10	$(\text{tc, sl, DCC})^2$	–	114	241	67
	11	$(\text{tc, sl, DCC})^2$	tc, sl, DCC	0	0	0

3.2 Movement modes

All species displayed one faster, more directed mode and one slower, more tortuous mode (Fig. S3). We labelled these as “transit” and “encamped” movement modes, thereby avoiding to project too specific

behavioural annotations on the modes. For example, while slower and more tortuous movement could be associated with foraging, actual foraging behaviour cannot be concluded from speed and turning angle alone due to overlap of those movement properties among different behaviours (McClintock et al., 2020). We considered "transit" and "encamped" to be reasonable abstractions while retaining spatially descriptive meaning. Overall, zebra moved markedly faster in the transit mode compared to the other two species (zebra: 0.62 ± 0.50SD km/h, eland: 0.25 ± 0.28SD km/h, wildebeest: 0.32 ± 0.30SD km/h) and wildebeest moved markedly slower in the encamped mode compared to the other two species (zebra: 0.13 ± 0.13SD km/h, eland: 0.10 ± 0.17SD km/h, wildebeest: 0.04 ± 0.05SD km/h). Contrarily, the movement tortuosity was more similar between the two modes for wildebeest (transit mode κ = 1.41, encamped mode κ = 0.89) and zebra (transit mode κ = 4.80, encamped mode κ = 1.19) than for eland (transit mode κ = 18.00, encamped mode κ = 0.68).

3.3 Movement related to covariates

The main effects of time of day, tree cover and slope only partly described speed (parameters μ and σ) and turning angle (parameter κ). Speed differed greatly throughout the day, being low just before sunrise and peaking around sunrise and in the evening (Fig. 3; the sunrise peak is not pictured). Higher tree cover resulted in slower eland movement, but faster wildebeest and zebra movement (Figs. S7-S9). Furthermore, all species moved slower at steeper slopes, with their movement tortuosity increasing slightly for eland but decreasing for wildebeest and zebra. Time of day, tree cover and slope interacted to varying degrees to more accurately predict the movement parameters (Fig. 3). On flat terrain, effects of tree cover on speed were generally small to negligible for all three species. On steeper terrain, an increase in tree cover caused eland to move slower in both modes, but wildebeest and zebra in the transit mode to move faster. This interaction was generally more pronounced in the evening (18:00) than in the morning (04:00) and at noon. Likewise, tree cover had an effect on movement tortuosity predominantly on steeper terrain, where it generally caused animals to move more tortuous (Fig. 4). In their transit mode, eland and zebra moved more tortuous than wildebeest, but eland tortuosity was not affected by tree cover or slope. Movement tortuosity was quite stable throughout the day for eland and zebra, but for wildebeest it differentiated more between the internal modes in the evening than in the morning.

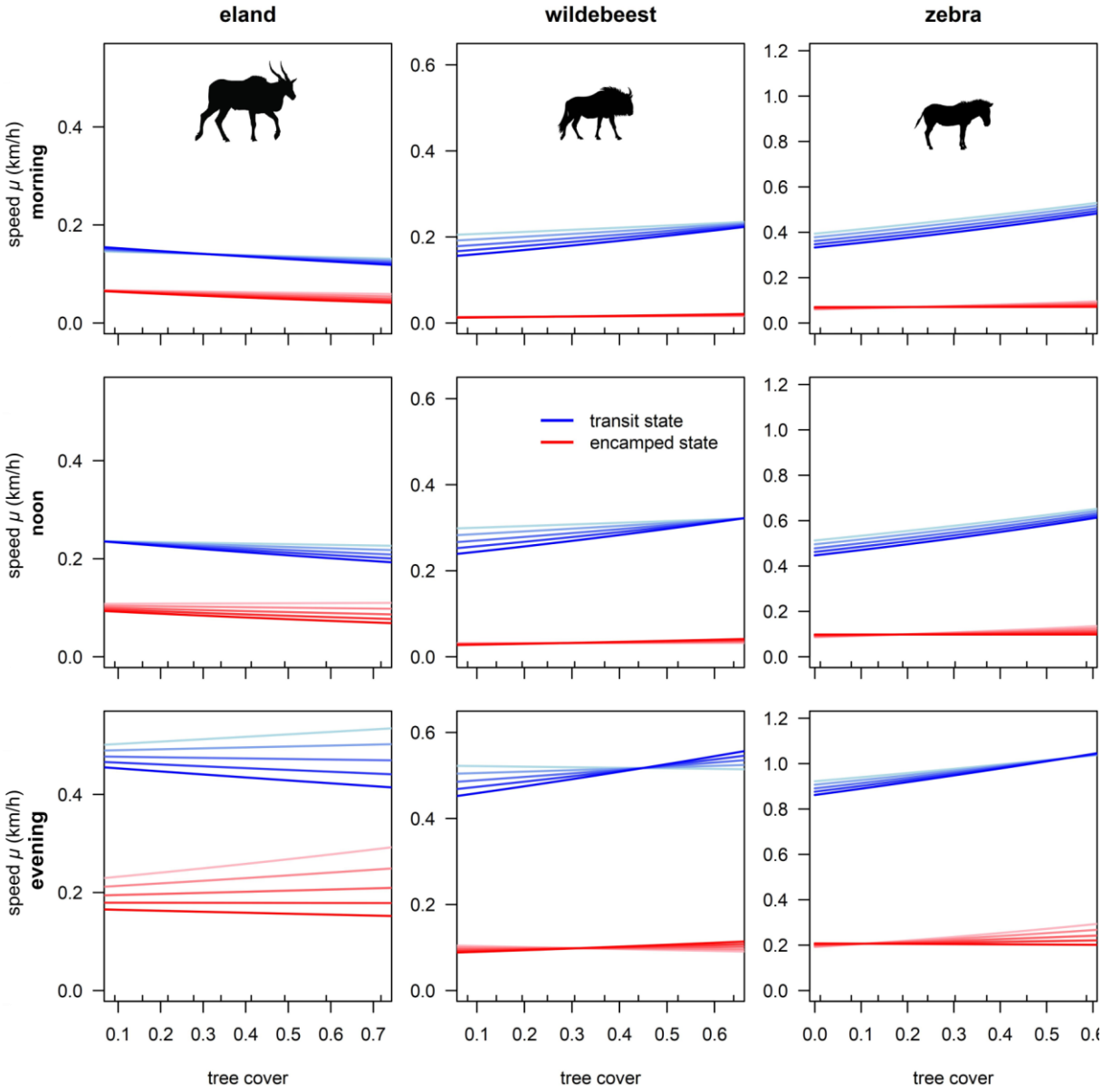

Figure 3. Model predictions of movement speed μ as a result of tree cover and slope in the morning (04:00, top row), at noon (12:00, middle row) and in the evening (18:00, bottom row) for eland, wildebeest and zebra. The times were chosen to capture a dip, baseline and peak in DCC (see Fig. 2). Blue and red indicate the transit and encamped mode respectively. Colour mapping within blue and red indicates a progression of slope from 0 (light) till 0.15 (the 90th percentile of slope values in the complete dataset; dark). Small ticks at the inside of tree cover axes mark the 10th, 20th … 90th percentile values of tree cover in the respective data sets. Note that the y-axis scales differ between species. Confidence intervals have been omitted for visual clarity, but they were generally small. For speed σ, see Fig. S5.

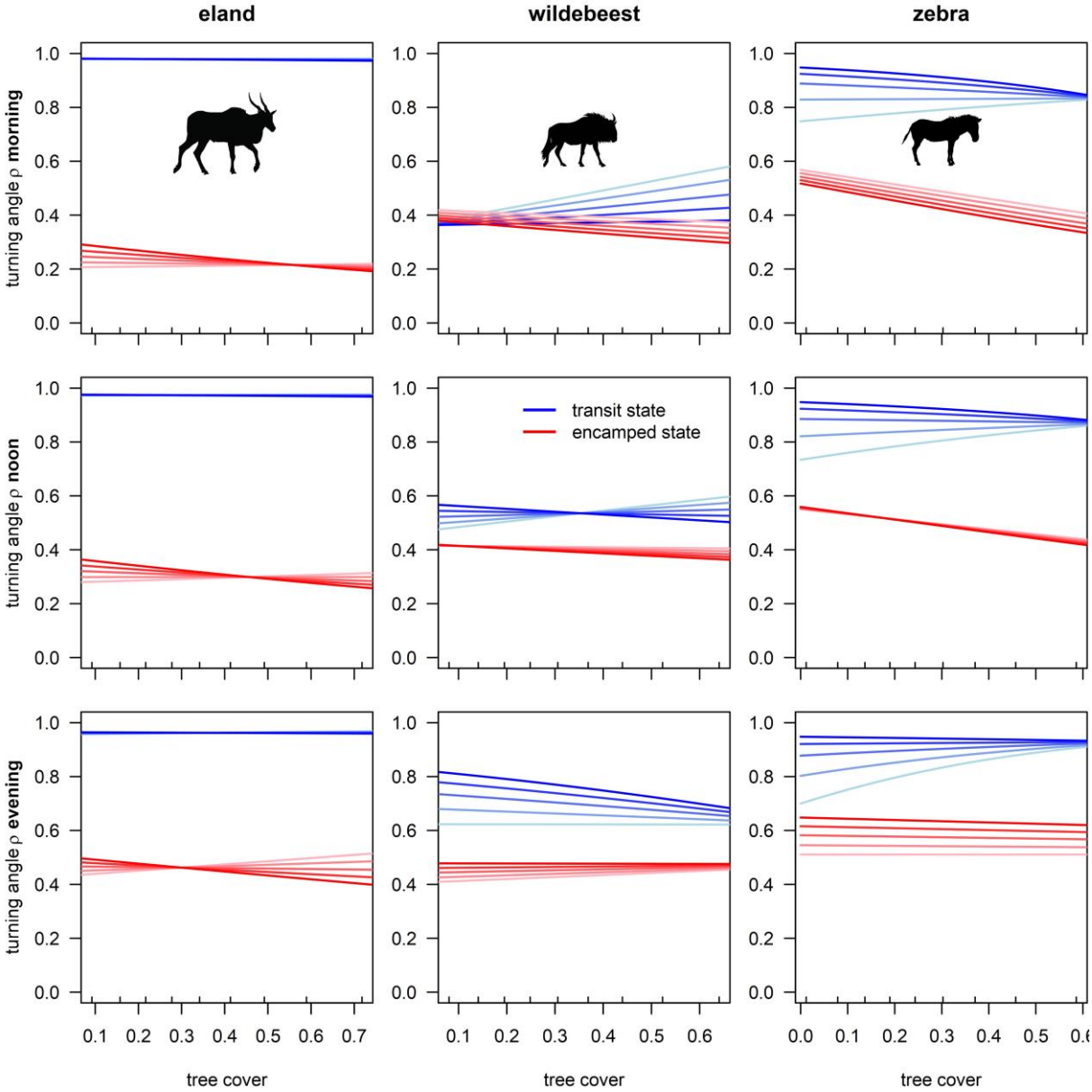

Figure 4. Model predictions of turning angle concentration as a result of tree cover and slope in the morning (04:00, top row), at noon (12:00, middle row) and in the evening (18:00, bottom row) for eland, wildebeest and zebra. Concentration parameter κ (which ranges from 0-infinity) has been converted to ρ (range 0-1) in this figure for visualization purposes. The times were chosen to capture a dip, baseline and peak in DCC (see Fig. 2). Blue and red indicate the transit and encamped mode respectively. Colour mapping within blue and red indicates a progression of slope from 0 (light) till 0.15 (the 90th percentile value of slope in the complete dataset; dark). Small ticks at the inside of tree cover axes mark the 10th, 20th … 90th percentile values of tree cover in the respective data sets. Confidence intervals have been omitted for visual clarity, but they were generally small.

3.4 Movement mode occupancy

Time of day had little influence on the stationary mode probabilities of all species (Fig. S10). Wildebeest showed some diel variation, being more likely to move in its encamped state but the difference being smaller in the evening than before sunrise. Tree cover also had little influence on the mode probabilities of eland and wildebeest, while zebra became slightly more likely to move in their transit mode when in areas with a higher tree cover. On steeper slopes, wildebeest became considerably less likely to display their transit mode, while the other species did not.

4 Discussion

We investigated how the movements of three large African savanna ungulate species arise from the interplay between movement modes and temporal and spatial environmental heterogeneity, thereby adressing the questions of *why*, *when* and *where* to move. We show that these three components of the movement process explained a large amount of variation in the emergent movement properties, but especially that there were strong interactions between those components. All movement properties displayed a strong diel pattern, with the effects of tree cover and slope on speed being largest in the evening when animals generally moved faster. Wildebeest and zebra in their "transit" mode moved faster with increasing tree cover whereas eland moved slower, but only so on steep terrain. In the "encamped" mode, tree cover had almost no effect on speed, but a strong effect on tortuosity. The animals also generally moved more tortuous with higher tree cover, even more so on sloping terrain. Tree cover did not influence the probability of being in a certain movement mode, and slope made only wildebeest more likely to be in the encamped mode. All our results and conclusions were supported by both the two- and three-mode HMMs, thereby disregarding those results for which the models did not agree and thus strengthening the reliability of our conclusions (Wagenmakers et al., 2022).

The daily cycle covariate (DCC), our proxy for temporal variation on a diel scale, was the most important factor in explaining variation in the movement properties (Table 1, Fig. 3). There was some level of correlation between variation in DCC on the one hand and spatial environmental variation (tree cover

and slope) on the other hand (Fig. S1, Table S1). This implies that DCC in our analysis captured both the *direct*, space-invariant, effect of time of day on the movement properties of the animals (i.e. endogenous rhythms and/or rhythms that are related to temporal variation without a clear spatial pattern), as well as an *indirect* effect of time of day through temporal variation in habitat selection, given that habitat influenced the movement properties as well (Figs. 3-4). The purely spatial influence of environmental heterogeneity on movement (i.e. the fitted time-invariant influence of the tree cover and slope covariates on movement) was small compared to both the temporal DCC proxy and the interactions between DCC and the spatial covariates. These results imply that the movements of our study species are driven mostly by processes that operate along temporal and spatial-temporal dimensions, rather than along a time-invariant spatial dimension (i.e. behavioural temporal patterns that arise from either internal diel rhythms or temporal variation in habitat selection throughout the day, or both).

The purely temporal, space-invariant patterns likely arise from various diel determinants, such as variation in ambient temperature and perceived predation risk (Palmer et al., 2022). High ambient temperatures generally suppress movement activity (Ditmer et al., 2018; Owen-Smith, 1998) and many ungulates show crepuscular activity cycles (Ensing et al., 2014; Forester et al., 2007; Green & Bear, 1990; Vazquez et al., 2019), resting through midday when temperatures are highest (Ben-Shahar, 1987; Owen-Smith et al., 2010; Owen-Smith & Goodall, 2014; Shrestha et al., 2014). Eland, wildebeest and, to a lesser extent, zebra in our study conformed to this diel pattern (Fig. 2). Furthermore, movement as an aspect of antipredator behaviour can show diel patterns in response to daily variability in predation risk (Bonnot et al., 2013; Fischhoff et al., 2007; Owen-Smith & Traill, 2017; Ross et al., 2013). Activity during the night can be suppressed by higher predation risk, yielding activity peaks around dawn and dusk (Crawford et al., 2019). Although our study area was largely predator-free, predator-avoidance behaviour due to perceived predation risk in low-visibility areas (Riginos, 2015; Riginos & Grace, 2008) might still have influenced movement in a pattern similar to that of temperature.

Wildebeest and zebra moved faster with increasing tree cover in their transit mode, but not in their encamped mode. The movement of eland in relation to the environment differed less between its modes, with eland generally moving slower with increasing tree cover. These patterns can have arisen through differences in predation risk between the species. Eland is much larger than wildebeest and zebra and adult elands are less vulnerable to predation from all but the largest predators. Leopards were present in the study area and they select somewhat bushy surroundings for ambushing their prey (Balme et al., 2007). Areas with higher tree or shrub cover may thus present a larger perceived risk of predation than open grassland for wildebeest and zebra, whereas for eland the difference in perceived risk between the habitats would be smaller. Differences in diet could be another possible explanation for these movement differences between the species: grazing wildebeest and zebra generally forage in areas with high grass cover (Groom & Harris, 2010) (i.e. low tree cover in our study area), and may thus increase their speed in areas with higher tree cover due to the lower likelihood of encountering available forage there. For eland, a mixed feeder (McNaughton & Georgiadis, 1986), bushy areas provide forage and may hence cause less of a speed increase.

The animals generally moved slower in their transit mode with increasing slope. Previous research has found deer more likely to move faster on steeper terrain, assumedly due to energetic costs rendering slopes less preferable to reside on (Frair et al., 2005). Our results show that responses to spatial environmental heterogeneity depend on the movement mode and hence partly on the motive for moving. Especially when in transit, slopes pose increased energetic costs or injury risk associated with moving through such terrain (Dailey & Hobbs, 1989; Parker et al., 1984; White & Yousef, 1978). Moreover, tree cover interacted with slope to make eland and wildebeest move slower and more tortuously. Interestingly, on flat terrains tree cover had very little influence, indicating that movement resistance caused by the environment can accumulate from different components of that environment, which underpins the importance of considering multiple sources of spatial environmental heterogeneity simultaneously when investigating their effect on movement.

The discrete movement modes combined various behaviours that resemble each other in terms of movement properties, rather than perfectly representing single behaviours. The encamped mode might for example include resting, foraging and slow explorative movements, where the occurence of these behaviours may vary during the day. The behaviour(s) that are represented by the fitted movement modes can thus differ between models and, in our case, species. This could explain why wildebeest movement in the encamped mode was much slower than that of the other species, as it perhaps did not include e.g. foraging behaviour in contrast to the other two species. This is supported further by the fact that wildebeest, unlike eland and zebra, became much more likely to be in the transit mode on sloping terrain, as highly sloping terrain might be less suitable foraging habitat. The effect of slope on stationary mode probability was smaller for zebra and virtually absent for eland, and tree cover had no significant effect on any of the species. Moreover, mode occupancy in eland and zebra showed very little variation throughout the day, but wildebeest showed some (Fig. S10). This suggests that the diel patterns in movement properties were for a large part caused by within-mode behavioural variability instead of diel patterns in mode switching. These results indicate that, in line with our finding that diel patterns are a much stronger driver than spatial (time-invariant) environmental heterogeneity, movement of our study species is predominantly driven by the animals' pre-existing internal motives (e.g. to translocate, feed or rest), which vary during the day and thus lead to temporal variation in spatial behaviour.

5 Conclusion

We demonstrated how behavioural movement modes and temporal and spatial environmental heterogeneity (the different components of the movement process relating to the quesions of *why*, *when* and *where* to move) interact in an intricate way to drive ungulate movement. Within a movement mode, the movements of our study species were driven largely by temporal patterns in their behaviour that resulted from internal diel rhythms and temporal variation in habitat selection throughout the day, as opposed to time-invariant environmental heterogeneity. Future research should specifically investigate to what extent factors such as temperature and predation risk interact to drive diel variation in habitat selection, to further assess the role of habitat selection in determining movement properties throughout

the day. Moreover, studying animals in larger or multiple areas and combining data from multiple ungulate species would allow for a comparison with the specific effects and interactions that we found, which will provide insight in the ungulate movement process across a wider range of applications. Understanding the drivers of animal movement, and ultimately of ecological phenomena that emerge from it, critically depends on considering the various components of the movement process in concert and especially the interactions between them.

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Conflict of interest

All authors declare to have no conflict of interest.

Author contributions

H.L., H.J.d.K. and J.A.J.E. conceived the ideas for the study and designed its methods; H.J.d.K. and J.A.J.E. provided the data; H.L. analysed the data and led the writing of the manuscript. All authors (H.L., H.J.d.K. and J.A.J.E.) contributed critically to the drafts and gave final approval for publication.

Data availability statement

Our data and code will be made publicly available via the 4TU.ResearchData repository after acceptance of the manuscript.

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