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Aggregating the conceptualisation of movement data better captures real world and simulated animal-environment relationships.

Habitat selection analysis is a widely applied statistical framework used in spatial ecology. Many of the methods used to generate movement and couple it with the environment are strongly integrated within GIScience. The choice of movement conceptualisation and environmental space can potentially have long-lasting implications on the spatial statistics used to infer movement-environment relationships. The aim of this study was to explore how systematically altering the conceptualisation of movement, environmental space, and temporal resolution affects the results of habitat selection analyses using both real-world case studies and a virtual ecologist approach. Model performance and coefficient estimates did not differ between the finest conceptualisations of movement (e.g., vector and move), while substantial differences were found for the more aggregated representations (e.g., segment and area). Only segments modelled the expected movement-environment relationship with increasing linear feature resistance in the virtual ecologist approach, and altering the temporal resolution identified inversions in the movement-environment relationship for vectors and moves. The results suggest that spatial statistics employed to investigate movement-environment relationships should advance beyond conceptualising movement as the (relatively) static conceptualisation of vectors and moves and replace these with (more) dynamic aggregations of longer-lasting movement processes such as segments and areal representations.

Keywords: habitat selection; movement; segments; trajectories; virtual ecology;

Introduction

Movement data are becoming ubiquitous in GIScience, and this spatiotemporal geographic information has improved our understanding of many of the geographic processes we study. While time geography (Hägerstrand 1970; Miller 1991; Neutens et al. 2011) and temporal GIS (Yuan 1996; Christakos et al. 2012) have become regular focal points of research within the discipline, the concept of time has never been wholly resolved (Goodchild 2013). In particular, the static representation of space and time has

limited the development of approaches and methods to study movement across sub-disciplines (Gudmundsson et al. 2012; Laube 2014). Despite this, GIScience is well placed to address such challenges associated with studying movement across an array of thematic topics, including spatial ecology (Holloway and Miller 2018), with frameworks emerging that unify these methodological and conceptual matters within a GIScience context (Dodge 2016).

Movement is a pervasive ecological process that is inherently linked with the spatial configuration of organisms and the underlying environment (Nathan et al. 2008); for example, barriers, corridors and land cover can all have a driving influence on where organisms can move, while goal-orientated movement towards resources determine the end location of movement steps (Holloway and Miller 2018). Subsequently, studies investigating the environmental drivers of movement have increased in abundance in recent years (Long and Nelson 2013; Dodge et al. 2014; Miller et al. 2019), with numerous statistical approaches employed to model movement-environment processes pertaining to home range utilisation patterns (Spiegel et al. 2016), social network patterns (Fisher et al. 2017), dispersal in response to climate change (Holloway et al. 2016) and habitat selection (Hooten et al. 2014). Despite these investigations, the moving object and movement space (e.g., environmental space) are subject to a number of conceptual and methodological challenges, including the sampling regime (e.g., continuous *v* noncontinuous), the idiosyncrasies of the sample, the semantic level of the moving object (e.g., fix or move), the structure of the movement spaces (e.g., discrete or continuous), as well as how the moving object and movement space are coupled in statistical models.

Laube (2017) recently described six semantic levels of quantifying movement in a GIScience context (Figure 1) that range from an instantaneous level (e.g., local time-

stamped location; ‘fix’, ‘vector’), to an interval aggregated level (e.g., connections between static fixes; ‘move’, ‘segment’), to a global aggregation (e.g., the probability of space use; ‘area’, ‘density’). These varied conceptualisations of the moving object all represent slightly different movement processes and different conceptualisations have all been used within movement ecology studies. Moreover, the conceptualisation of the moving object cannot exist independently of the environmental space. The environment is inextricably linked with animal movement (Nathan et al. 2008) and is regularly incorporated as covariates in statistical models. For example, in habitat selection studies, movement and the environment have been coupled together as ‘vectors’ (e.g., environmental value at the end of the movement step – Viejou et al. 2018), ‘moves’ (e.g., the proportion of an environmental value along the step – Mason and Fortin, 2017), and ‘segments’ (e.g., the proportion of an environmental value along parts of the movement segment – Zeller et al. 2016). Furthermore, these conceptualisations can be used interchangeably to investigate animal-environment interactions within the same statistical model (e.g., Fortin et al. 2005).

These decisions are pertinent because the choice of movement conceptualisation can alter the inferences made from such statistical models. For example, Zeller et al. (2016) identified substantial differences in regression coefficients for several land covers when puma habitat selection was conceptualised using hourly ‘segments’ and five-minute ‘moves’, with segments generating larger regression coefficients. Similarly, Holloway and Miller (2018) found that the area of landscape that was accessible to simulations of 25 brown hyenas over a year period was 60,000km^2 larger when movement was conceptualised as ‘moves’ compared to ‘vectors’.

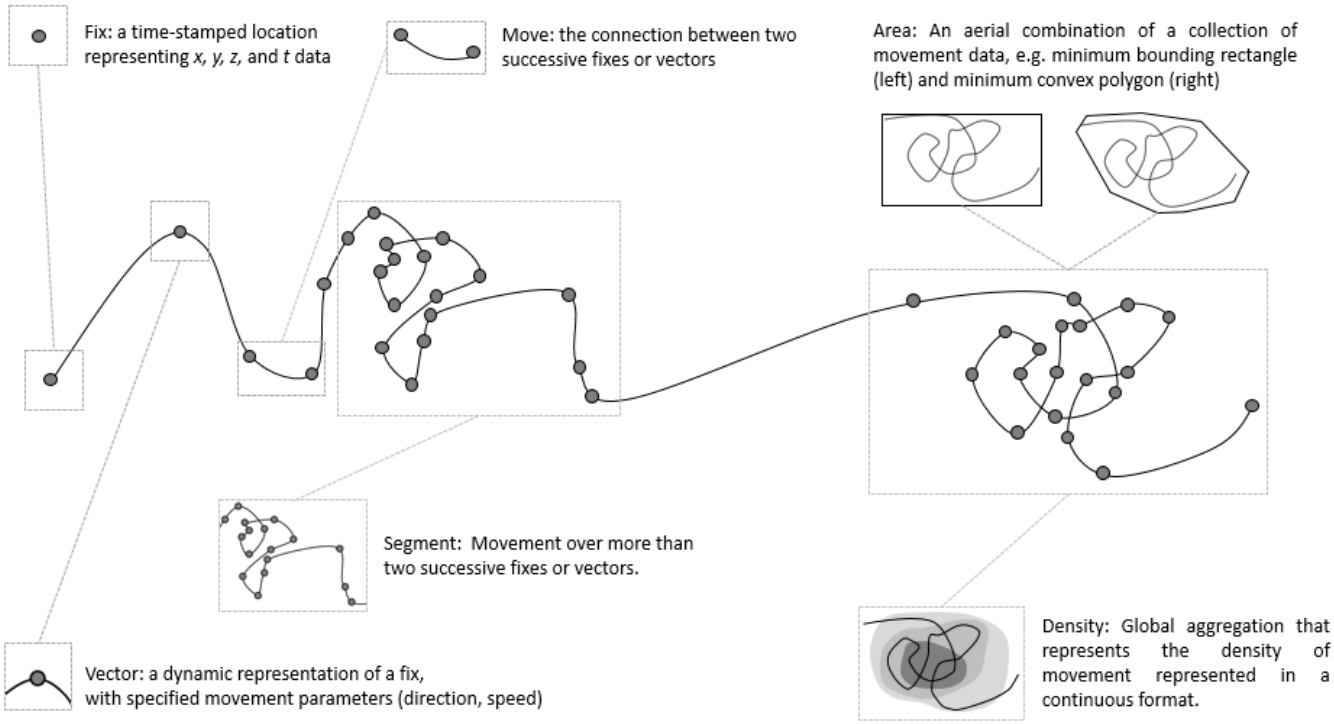


Figure 1. Diagram to illustrate the different conceptualisations of movement along a single movement trajectory.

The coupling of the environment and moving objects has been suggested as being greatest when individuals react to linear features (LFs) (Thrufjell et al. 2014). In particular, the methods proposed for quantifying movement in response to LFs may not reliably capture the underlying behaviour. The assumption that animals move in a straight line between two successive 'fixes' is necessary for analysing movement at coarser aggregations; however, it can introduce uncertainties where LFs are considered. For example, when organisms use LFs as corridors, the amount of time the 'move' or 'segment' is recorded on the LF may be small due to the need to record the movement as a straight line. Using such a covariate could result in an assumption of avoidance as the fix is never located on the LF, despite there being a strong movement-environment relationship (Thurfjell et al. 2014). Several methods have been suggested to measure the relationship between movement and LFs (see Methodology), and with such wide

variation in their implementation, it is likely that resulting inferences from models will vary markedly.

The choice of movement conceptualisation and environmental space can potentially have long-lasting implications on any management strategy resulting from these spatial statistics; however, no formal analysis has investigated how the conceptualisation of movement in relation to the movement space influences movement-environment inferences. Subsequently, the aim of this study is to explore how systematically altering the conceptualisation of movement and environmental space affects the results of habitat selection analyses using both real-world case studies and a virtual ecologist approach. This study will explore three main questions: 1) does the conceptualisation of the moving object and environmental space influence a) the model performance and b) the environmental preference of habitat selection? 2) does the habitat selection methodology correctly identify environmental preferences of animal movement using a virtual ecologist approach? and 3) does systematically varying the temporal resolution of the virtual data used in the statistical model change the environmental preference identified?

Methodology

Habitat Selection Analysis

Habitat selection is defined simply as the probability that a specific habitat will be used by an animal when it encounters it (Lele et al. 2013). Habitat selection analysis develops a function that is proportional to the probability of the use of a resource unit by an organism (Manly et al. 2002). The ‘used’ observations are compared to a set of ‘alternative’ observations that the animal theoretically could have selected, with a set of environmental variables that characterise ‘selection’ identified from the statistical model

(Figure 2). Habitat selection has been implemented across multiple conceptualisations of movement, including ‘fixes’ (Figure 2a; resource selection analysis – RSA), ‘vectors’ and ‘moves’ (Figure 2b; step selection analysis – SSA), and ‘segments’ and ‘areas’ (Figure 2c; path selection analysis – PathSA).

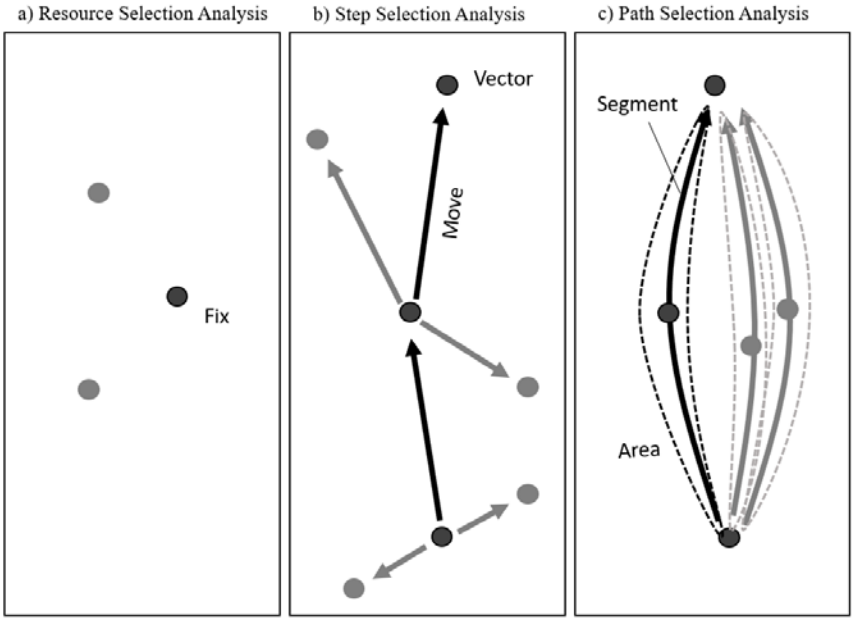


Figure 2. Habitat selection analyses that compare an observed (black) movement observation to a set of alternative (grey) movement observations that an individual could have theoretically taken. Black dots represent successive telemetry locations of an individual (in step-selection analysis and path-selection analysis), with five different movement conceptualisations (fix, vector, move, segment, area) represented as the moving object.

In RSA (Figure 2a), habitat selection measures a used ‘fix’ with a set of alternative ‘fixes’. However, the methodologies to generate alternative fixes do not limit resource availability to an accessible distance of current animal location (Fortin et al. 2005; Forrester et al. 2009). In SSA, an observed step between two successive telemetry locations is compared to alternatively generated steps (created from an empirical distribution of movement parameters) that the animal theoretically could have taken (Thurfjell et al. 2014). In SSA (Figure 2b), the alternative steps have been represented as ‘vectors’ (e.g., environmental value at the end of the move – Viejou et al. 2018), and

‘moves’ (e.g., the proportion of an environmental value along the move – Mason and Fortin, 2017). PathSA (Figure 2c) compares segments of the movement trajectories with alternatively simulated trajectories of the same time period. PathSA has been represented as ‘segments’ (e.g., mean value along the movement segment – Elliot et al. 2014), and ‘areas’ (e.g., mean proportion of the environmental values within a Pareto-weighted kernel around each vector in the segment – Zeller et al. 2014; 2016).

While different statistical methods have been used to investigate habitat selection (e.g., Dickson et al. 2005); the prevailing methodology that has been used across RSA, SSA, and PathSA is conditional logistic regression (Thurfjell et al. 2014). Using this approach, habitat selection $\widehat{w}(x)$ is defined as:

$$\widehat{w}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ ... \ + \beta_n x_n) \qquad (1.0)$$

where β_n is the coefficient estimated by the conditional logistic regression for the variable x_n. Observations with higher $\widehat{w}(x)$ values have a higher likelihood of being chosen by the animal, meaning such an approach can identify the influence the environment can have on habitat selection and animal movement. Habitat selection can be extended to all conceptualisations of movement (Figure 1; Figure 2) and the following sections will outline the methodological steps involved in generating the alternative movement conceptualisations for use in the statistical analysis. Figure 3 illustrates a conceptual workflow of the methodology to support the description. While animal positional data has been used to parameterise RSAs, due to the relatively static nature of the ecological process under study, this research will focus on habitat selection analyses with a more explicit consideration of movement (i.e., SSA and PathSA).

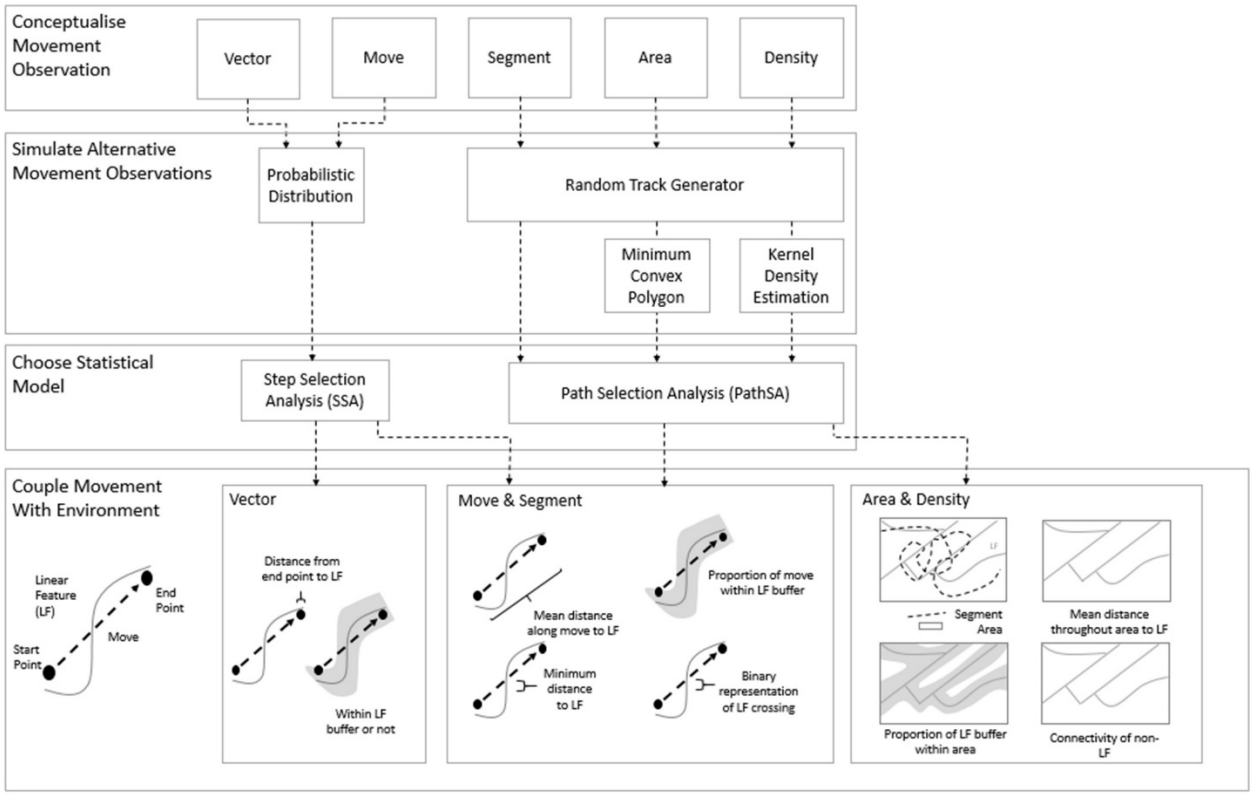


Figure 3. Conceptual diagram of the habitat selection analysis undertaken within this study.

Step-Selection Analysis (SSA) - Vector and Move

SSA compares the observed step with a set of alternative steps the individual theoretically could have taken (Figure 2b). Alterative steps were generated by drawing turn angles and step lengths from the probability distribution of all observed steps in the dataset. Drawing movement parameters from the probability distribution to generate the alternative steps creates more representative steps, simultaneously reducing the bias associated with using less constraining distributions (e.g., random and quantile - Holloway and Miller 2014). All movement observations that do not move (e.g., distance of zero) were removed from the analysis as these do not represent movement but possibly ‘stops’ or ‘stationary processes’. The number of alternative steps does not bias results (Thurfjell et al. 2014); therefore, three alternative steps were generated based on

the derived movement parameters. From these alternative steps, both vectors and moves were then incorporated in the analysis.

Path-Selection Analysis (PathSA) - Segment, Area, Density

PathSA compares the observed movement segment with a set of alternative movement segments the individual theoretically could have taken (Figure 2c). Observed trajectories were split to create segments of daily movement. Alternative segments were simulated following the random trajectory generator (RTG) algorithm proposed by Technitis et al. (2015). This method simulates random movement between a fixed origin (A) and destination (B), using a two-dimensional representation of the space-time prism, maximum speed, and movement time. To overcome unrealistic trajectories, a random order of time-step generation was implemented (Technitis et al. 2015). The start- and end-points of the alternative segments match those of the corresponding observed segment. This algorithm generates alternative segments that individual animals could use. Again, three alternative segments were generated for use in the statistical model.

Three areal aggregations of movement were generated from these segments. A minimum bounding rectangle (MBR) and a minimum convex polygon (MCP) represent the spatial extent of the movement, and a 50% kernel density estimation (KDE) was converted to an areal polygon to allow direct comparison with the two aforementioned aggregations. Due to the simplistic geometry and the subsequent overlapping of MBRs, it was found that the statistical models would not converge due to the high similarity of data contained within them; therefore, the areal aggregations of movement discussed herein refer only to MCP and KDE.

Environmental Space

In habitat selection studies, land cover has predominantly been measured as a binary variable recorded at the exact coordinate of the vector (e.g., Bjorneraas et al. 2011; Ewald et al. 2014; Street et al. 2015; Scharf et al. 2016; de la Torre et al. 2017; Cozzi et al. 2017; Hradsky et al. 2017; Brennan et al. 2018; Martin et al. 2018; DeMars and Boutin 2018; Viejou et al. 2018), while studies have also measured the proportion of land cover along the move or segment (Elliot et al. 2014; Panzachhi et al. 2016; Mason and Fortin, 2017), or the proportion of land cover within a buffer surrounding the vector, move or segment (Reding et al. 2013; Street et al. 2016; Zeller et al. 2016).

LFs have been incorporated in the statistical model by using the mean distance along the move or segment to the LF (LF_mean - Coulon et al. 2008), the shortest distance of the move or segment to the LF (LF_min - Fortin et al. 2005), a binary representation of whether the LF has been crossed (LF_cross - Panzachhi et al. 2016; Marchand et al. 2017), and as the distance from the end vector (equivalent of LF_mean - Clark et al. 2015; Brennan et al. 2018; Holloway 2018).

Table 1 outlines six methods of incorporating LFs used in this study, the ecological justification for use as an environmental covariate, and the movement conceptualisation that the method can be coupled with. Land cover was incorporated in a consistent manner across all six models in Table 1 following the predominant method used in habitat selection studies; value or proportion of land cover along or within the movement conceptualisation.

Table 1. Outline of the six models that investigate the relationship between movement and linear features (LFs). Description of the methodology to measure LF environmental covariates, the ecological reasoning for their inclusion, and the five conceptualisations of movement that can be coupled with the method.

Model	*Description*	*Reasoning*	*Conceptualisation*
LF_mean	Measures the mean value to the LF from, along, or within the movement conceptualisation	Used to identify movement towards (negative coefficient), away (positive coefficient), or in parallel to roads (equal to reference).	Vector; Move; Segment; Area; Density
LF_prop	Measures the proportion of the movement conceptualisation that is within a buffer of the LF (distance to correspond with suggested movement step lengths and impact distances)	Proportion of time within a LF buffer indicates usage of LF, proposed to overcome limitation of unlikely nature of movement step falling exactly on the one-dimensional line.	Vector; Move; Segment; Area; Density
LF_min	Measures the minimum distance to the LF from the movement conceptualisation	Used to identify movement towards (negative coefficient), away (positive coefficient), or in parallel to LFs (equal to reference).	Move; Segment
LF_cross	Binary value representing whether the LF has been crossed by the movement conceptualisation	Used to indicate whether animals will use or cross LF (1), or whether they avoid them (0).	Move; Segment
Non-LF_agg	Landscape reclassified into a binary space (linear or non-linear). The degree of aggregation of non-linear patches in the area., calculated from the adjacency matrix, which shows the frequency with which different pairs of patch types appear side-by-side in the landscape. prop.like.adjacencies in *spatialEco* (Evans 2017)	Used as a measure of connectivity for non-linear landscapes in the study area. A higher aggregation indicates less LFs, with linear landscapes used more (negative coefficient) or less (positive coefficient) by animals.	Area; Density
Non-LF-conn	Landscape reclassified into a binary space (linear or non-linear). Metric describing the physical connectedness of the non-linear patches. patch.cohesion.index in *SpatilEco* (Evans 2017)	Used as a measure of connectivity for non-linear landscapes in the study area. A higher cohesion indicates less LFs, with linear landscapes used more (negative coefficient) or less (positive coefficient) by animals.	Area; Density

Real-World Case Study

Telemetry data of oilbirds (*Steatornis caripensis*) in Venezuela and Burchill's zebra (*Equus quagga burchelli*) in Botswana were obtained from Holland et al. (2009) and Bartlem-Brooks et al. (2013a) respectively via Movebank (Holland et al. 2012; Bartlem-Brooks et al. 2013b). Table 2 summarises the information pertaining to these datasets, and Supplementary Information 1 contains maps of the movement trajectories. Land cover type data product (MCD12Q1) from the Moderate Resolution Imaging

Spectroradiometer (MODIS) was obtained from the Global Land Cover Facility (Friedl et al. 2010; Channan et al. 2014) to match the start date of the telemetry datasets. Global Roads Open Access Data Set, Version 1, was obtained from the Center for International Earth Science Information Network (CIESIN, 2013). Veterinary fence lines in Botswana were also identified and digitised.

Table 2. Information on species datasets used within this study.

Species	Number of Individuals	Time-step (mins)	Total Fixes	Start Date	End Date
Oilbirds	4	10	790	13-10-2007	18-10-2007
Zebra	6	60	29,687	25-10-2007	27-05-2009

For both oilbirds and zebras, land cover was categorised into three classes to match hypotheses surrounding habitat selection (Holland et al. 2009; Bartlem-Brooks et al. 2013a; Holloway and Miller 2014). For oilbirds the environment consisted of evergreen broadleaf forest, cropland, and other habitat, and for zebras the environment consisted of savanna, shrubland, and other habitat. Primary preference for evergreen broadleaf forests and savannas and secondary preference for cropland and shrublands compared to the reference land cover of other habitat was hypothesised for oilbirds and zebras respectively. LFs for both animals consisted of roads; however, following the impact of veterinary fences on zebra movement identified by Bartlem-Brooks et al. (2013a), these were also included in the LF layer for Botswana. It was hypothesised that both animals would exhibit behaviours associated with preference for these linear features. A buffer of 4000 m was applied around the LFs to incorporate the 99th percentile of step lengths, to ensure use of LFs was detected (as opposed to fitting a too restrictive buffer distance).

Analysis

Habitat selection was estimated using conditional logistic regression using the *survival* package (Therneau 2015) in R 3.5.1 (R Development Core Team 2008). Coefficients were standardised with the exception of the variables represented by binary values. Akaike's Information Criterion (AIC) was calculated to investigate model performance and select the best-fit theoretical distribution across all models. This identifies the environmental covariates that best fit the movement data. However, due to variation in sample sizes between SSA and PathSA, AIC should only be compared directly between SSA vector and move, and directly among PathSA segment, MCP and KDE. Standardised coefficients of the environmental covariates were then compared to investigate whether certain movement conceptualisations resulted in larger selection preferences. For the land cover variables, the coefficients indicate the log odds for that movement conceptualisation being chosen relative to a reference habitat (e.g., other habitat), and for LFs the coefficients indicate the log odds for selecting a movement option as the independent variable changes.

Virtual Ecologist Case Study

The virtual ecologist approach generates data by simulating the ecological processes that give rise to the patterns subsequently analysed (Zurell et al. 2010; Miller 2014; Avgar et al. 2016). This approach allows researchers to evaluate the ability of readily employed spatial statistics to model the expected movement-environment relationship. By simulating movement trajectories in response to the underlying environment, the ability of habitat selection analyses to identify the known patterns can be explicitly tested. Furthermore, by systematically altering the conceptualisation of the moving object, we can test how aggregating movement to coarser conceptualisations affects results.

Fine-scale movement was simulated using a discrete-step process of one-minute time-steps over 24-hours on a 665 x 591 rectangular grid of 100m cells in the *SiMRiv* package (Quaglietta and Porto 2018). Land cover was generated by creating a random raster of three categories, with each land cover attributed a value representing resistance to movement of 0.75, 0.25, and 1.00. The decision to simulate one low resistance (0.25), one high resistance (0.75) and one completely avoidable (1.00) land cover mimics the inferences from the two case studies that animals have a primary, secondary, and an avoidable land cover preference. The LF network from Botswana was scaled to fit within the overall landscape extent. The decision to use a real-world linear-network as opposed to a random one was to reduce the risk of generating overly simplified virtual movements that might result from unrealistic linear-networks (Miller 2014). A buffer of 100m was placed around the LF in the generation of the resistance raster to represent the 20^{th} percentile of the simulated step lengths. Due to the simulations reflecting a known-truth, a more restrictive movement-LF relationship was incorporated in the model, due to the fact there would be less noise than in the real-world case studies. Simulations were calculated using five resistance to movement values for the LF (0.00, 0.25, 0.50, 0.75, and 1.00). These values allowed a systematic investigation from use of LF (0.00) to avoidance of LF (1.00), meaning the statistical framework and environmental covariates could be assessed for how well they captured the underlying processes relating to LFs. Further details regarding the methodological steps and R code for SiMRiv simulations are in Supplementary Information 2.

In total, 500 simulations were run for the five landscape configurations of land cover and LF resistance, which resulted in 2500 simulations. These simulations were treated as the ‘observed’ movement features, with ‘alternative’ movement features generated including vectors, moves, and segments using the same methodology as

outlined for the real-world case studies. These movement conceptualisations were coupled with the underlying environment using the LF_mean and LF_prop methods outlined in Table 1, and again, habitat selection was calculated using conditional logistic regression (equation 1).

Finally, each simulation was sampled at 1- 2-, 5-, 10-, 15-, 30-, 60-, 90-, and 120-minute time-steps to represent different temporal resolutions that animal trajectory data are commonly collected at and used in the statistical framework. This allowed the habitat selection analyses to be investigated for how well the known movement processes were captured once the temporal resolution of the input data was coarsened from that at which it was simulated.

The coefficient values were then compared for each variable using the Wilcoxon matched pairs signed rank test according to the number of comparisons made. This test converts scores to ranks and compares them across the two conditions. The effect size of the test was calculated by dividing the z score by the square root of *n* and using the Cohen (1988) criteria of 0.1 = small effect, 0.3 = medium effect and 0.5 = large effect.

Results

Model Performance and Environmental Preferences

Performance between SSA models with movement coupled with LFs did not differ for either oilbirds or zebras (Figures 4a-b). Similarly, when coefficient values and standard errors for both land cover variables and LFs were compared between vectors and moves, minimal differences were observed (Figures 4c-d), suggesting that the ability of the statistical models and parameterised environmental covariates to best fit the movement data does not differ between the interval aggregation conceptualisations of movement. The model parameterised with minimum distance to LFs (LF_min)

appears to outperform those parameterised with mean distance (LF_mean), proportion within LF buffer (LF_prop), and a binary value indicating whether the LF has been crossed (LF_cross) when movement was conceptualised as segments (Figures 4a-b); however, when the coefficient values were explored (Figures 4c-d), the coefficients for minimum distance to LFs were substantially larger than the land cover values, with very wide standard errors reported. This pattern appears to occur due to the structure of the LF network within both environments (Supplementary Information 1), meaning that for the majority of segments, the minimum value is found at the start or end point, which subsequently means the models overfit the data.

The MCP and KDE conceptualisations of movement reported lower AIC values when the landscape was parameterised as the aggregation (N-LF_agg) and connectedness (N-LF_conn) of the non-LF landscape (Figures 4a-b) compared with the LF_mean and LF_prop parameterisations within the same area. When coupled with the standardised coefficient results (Figures 4c-d), both species were more likely to select movement paths with a lower aggregation or connectivity than the alternative movement option. This suggests that both species are using landscapes that are fragmented by LFs more so than those that are not, inferring a preference for landscapes dominated by LFs. While similar preferences for movement towards LFs was identified across movement and environmental conceptualisations for oilbirds (with the exception of LF_min), both avoidance of LFs using LF_mean, LF_prop, and LF_min parameterisations, and attraction to LFs using LF_cross, N-LF_agg, and N-LF_conn was identified for zebras.

Furthermore, when preference for shrubland habitat was explored for zebras (Figure 4d) the MCP and KDE conceptualisations (proportion of land cover in area) for models N-LF_agg and N-LF_conn, a preference for the reference habitat (other land

cover) was identified, which contradicts every other inference made from vectors, moves, and segments. Similar results were observed for oilbird selection of cropland (Figure 4c) when the conceptualisation of movement becomes more aggregated, although not as exaggerated. Such an inversion in the relationship between movement and the hypothesised 'secondary' habitat as movement conceptualisation was aggregated suggests that either the species' preference for this habitat is scale dependent (preference for selection on an individual-level, but avoidance across an aggregated global space use) or that a change in the movement conceptualisation is causing a methodological artefact to arise in the statistical model.

An inversion in the movement-environment relationship was also identified when LFs were measured as mean distances (LF_mean) and proportion within the buffer (LF_prop) for zebras (Figure 4d). Selection of movement away from LFs for all movement conceptualisations of zebras was recorded when the environmental space was represented as mean distance; however, when LFs were represented as proportions, positive coefficients suggest a preference for such landscapes. This inversion in the movement-environment relationship was not recorded for the different movement-environment conceptualisations for oilbirds (Figure 4c), suggesting this trend may be species-specific. When the movement data of the zebra are explored, the movement consists of two states (seasonal migration and foraging), with the seasonal migration strongly associated with the north-south veterinary fence line (Supplementary Information 1). Such a relationship is not identified when the mean distance is reported but is when a 4 km buffer is applied around the LF.

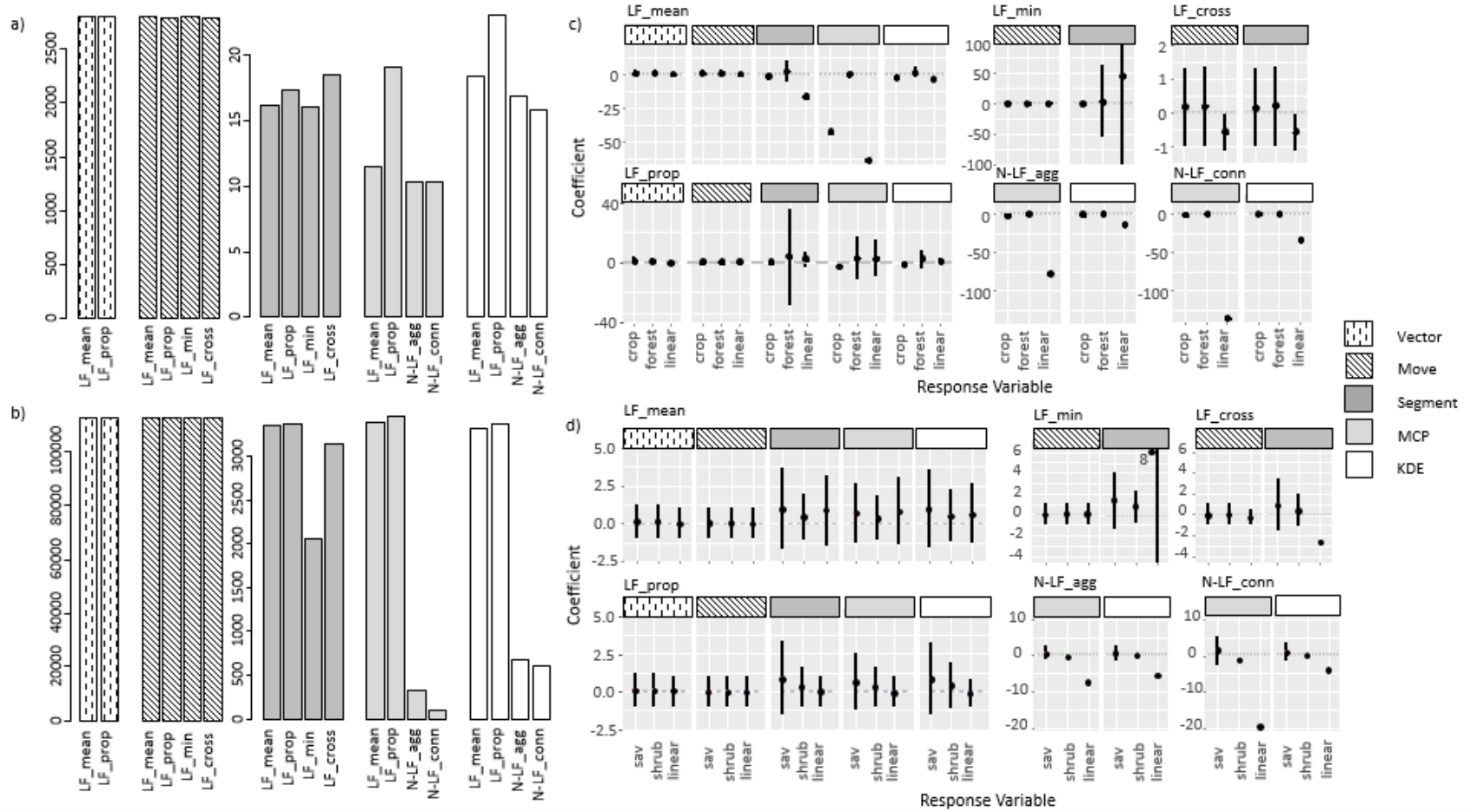


Figure 4. Akaike Information Criterion (AIC) scores for the different movement conceptualisations and linear feature (LF) representations for a) oilbirds and b) zebras. Standardised coefficient values with standard errors for the different models parameterised on movement conceptualisations and LF representation for c) oilbirds and d) zebras.

Virtual Ecologist – Environmental Preference and Temporal Resolution

Figures 5 and 6 illustrate the coefficient values of the environmental covariates for the different movement conceptualisations and LF resistance values at each time-step derived from the virtual ecologist approach. The expected relationship for the model LF_mean (Figure 5) is for LF selection preference to increase positively as resistance increases (e.g., selection preference increases as the distance increases away from LFs), while the expected relationship for the model LF_prop (Figure 6) is for LF selection preference to increase negatively as resistance increases (e.g., selection preference for movement that has a lower proportion within the LF buffer). It was also expected that the land cover (LC1, LC2) coefficients would not change as the LF resistance was increased, as the resistance values for both LC1 and LC2 were held constant. Given the resistance values of 0.75 and 0.25 for LC1 and LC2, it was expected that selection into both of these habitats would be positive to reflect selection over LC3 (the reference habitat).

Segments were the only conceptualisation that accurately captured this expected pattern across all time-steps for both models (Figures 5 and 6), while vectors and moves resulted in habitat selection that identified both attraction and avoidance for all LF resistance values between 0.00 (attraction) and 1.00 (avoidance). For the vector and move conceptualisations, it was the shorter time-steps (1-minute, 2-minutes) that incorrectly modelled the movement-environment relationship as attraction when LF resistance was specified as 1.00, and it was the longer time-steps (5-minutes to 120-minutes) that correctly modelled the expected relationship. As the virtual data was simulated at 1-minute time-steps, the assumption was that the shorter temporal resolution would reliably capture the underlying relationship. Coarser time-steps of vectors and moves are characteristic of simplified (albeit linear) segments, suggesting

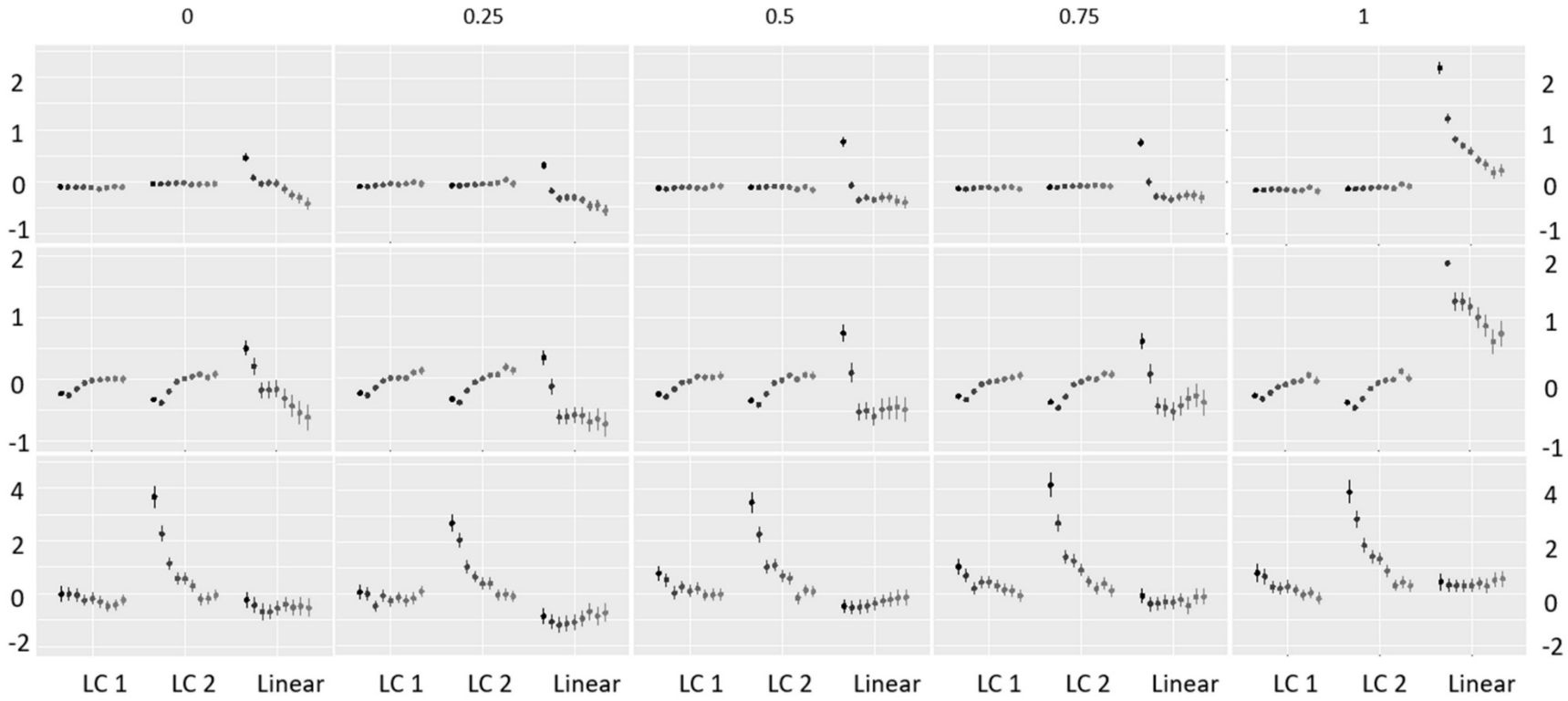


Figure 5. Standardised coefficient values for land cover (LC) and linear features (LFs) with 95% confidence intervals for the LF_mean (mean distance to LFs) for the virtual species. Results include the movement conceptualisations of vectors, moves, and segments. Resistance values (0, 0.25, 0.5, 0.75, 1) correspond to the resistance of linear features to movement in the simulations, with the expected movement-LF relationship to increase in selection preference as resistance increases (e.g., selection preference increases as the distance increases away from LFs), while movement-LC relationships should remain consistent as LF resistance is increased. For each variable, coefficient scores for 1-, 2-, 5-, 10-, 15-, 30-, 60-, 90-, and 120-minute time steps are reported left to right.

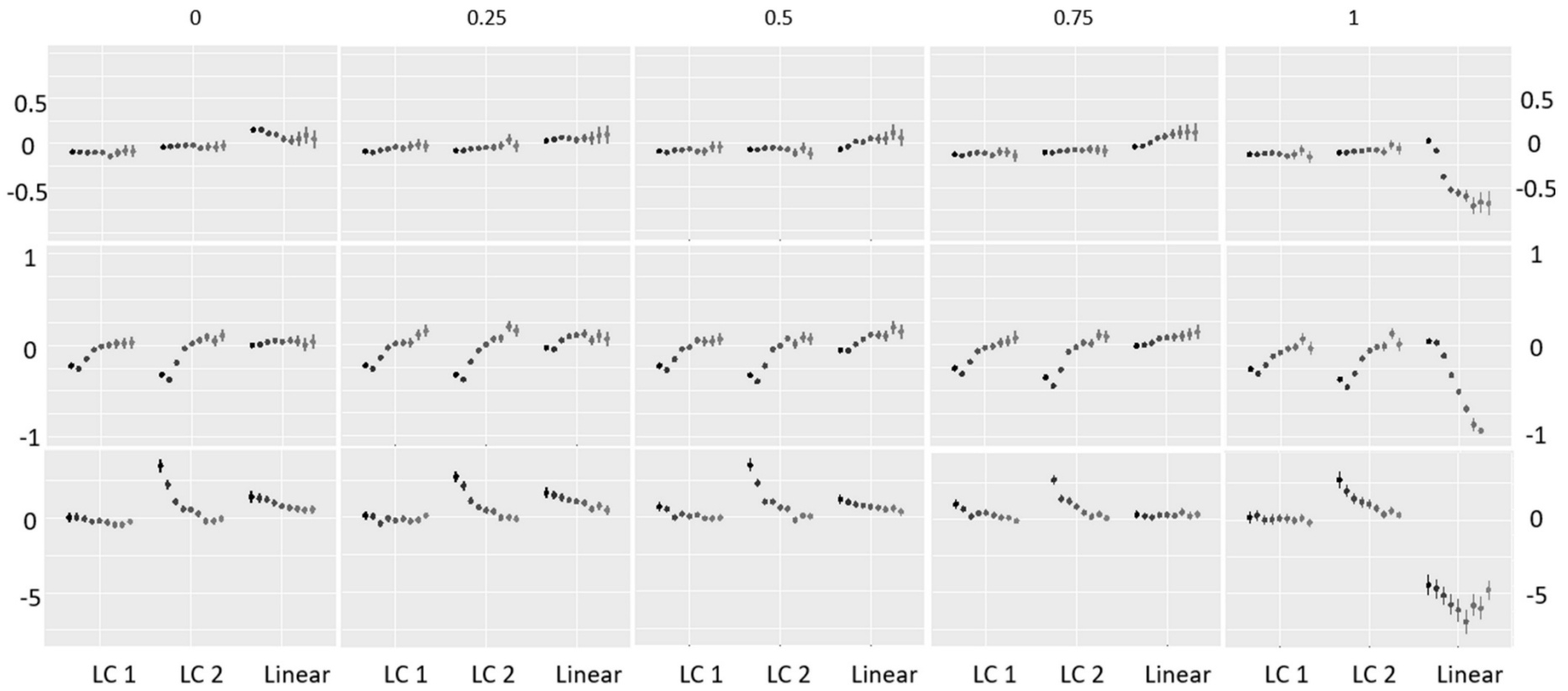


Figure 6. Standardised coefficient values for land cover (LC) and linear features (LFs) with 95% confidence intervals for the LF_prop (proportion of movement observation within LF buffer) for the virtual species. Results include the movement conceptualisations of vectors, moves, and segments. Resistance values (0, 0.25, 0.5, 0.75, 1) correspond to the resistance of linear features to movement in the simulations, with the expected movement-LF relationship to decrease in selection preference as resistance increases (e.g., selection preference for movement that has a lower proportion within the LF buffer), while movement-LC relationships should remain consistent as LF resistance is increased. For each variable, coefficient scores for 1-, 2-, 5-, 10-, 15-, 30-, 60-, 90-, and 120-minute time steps are reported left to right.

that movement-LF relationships are only observable at the more aggregated movement conceptualisations. Due to longer time-steps of vectors and moves covering more of the spatial variation in the overall movement trajectory, the conceptualisations are capturing the extreme relationship, but as a construct of the temporal resolution.

The expectation that the LC1 and LC2 coefficients would not change was generally found to be true when altering the LF resistance (Figures 5 and 6), suggesting that preference for land covers remains when resistance to other features in the landscape is altered. However, figures 5 and 6 do identify increases in the LC1 and LC2 coefficient values for vectors and moves and a decrease in the LF coefficient values for segments as the time-steps were increased from 1-minute to 120-minutes. For moves, the LC1 and LC2 values appeared to invert from negative to positive as the temporal resolution increased. Preference of LC1 (resistance 0.75) and LC2 (resistance 0.25) over LC3 (resistance 1.00) was expected (i.e., positive coefficients) for all movement coefficients; however, the finer time-steps of the move identified preference for the reference habitat (i.e., negative coefficients). While segments identified a decrease in coefficient size as the time-steps increased, in only a few instances did the relationship invert.

Tables 3, SI3.1, and SI.3.2 (Supplementary Information 3) identify the results of the Wilcoxon matched pairs signed rank for the two models. The differences between coefficient values for LC1 and LC2 as the time-step was altered was generally not significant, nor did the values change sign (Tables SI3.1 and SI3.2). However, Table 3 identifies significant differences between the coefficient values when vectors, moves, and segments were directly compared. Segments were found to generate higher coefficient values for land cover preference compared to vectors and moves, with Cohen's criteria identifying a large effect between vectors and segments for both

models (Table 3). Furthermore, it can be seen from Table 3 that this difference resulted in an inversion of the movement-environment relationship, with segments identifying a positive relationship, while vectors identified a negative relationship.

Table 3. Confusion matrix of Wilcoxon matched pairs signed rank for both the LF_mean (mean distance to linear feature) and LF_prop (proportion of movement within linear feature buffer) models comparing coefficient values among movement conceptualisations. Value refers to second group in the comparison. *medium effect, **large effect.

Inversion of Coefficients from Positive to Negative

Inversion of Coefficients from Negative to Positive

LF_mean

Linear Features (LFs) Coefficients			
	Vector	Move	Segment
Vector			
Move	n.s.		
Segment	Lower**	Lower**	

Land Cover 1 (LC1) Coefficients			
	Vector	Move	Segment
Vector			
Move	Higher**		
Segment	Higher**	Higher	

Land Cover 2 (LC2) Coefficients			
	Vector	Move	Segment
Vector			
Move	n.s.		
Segment	Higher**	Higher**	

LF_prop

Linear Features (LFs) Coefficients			
	Vector	Move	Segment
Vector			
Move	n.s.		
Segment	n.s.	n.s.	

Land Cover 1 (LC1) Coefficients			
	Vector	Move	Segment
Vector			
Move	Higher**		
Segment	Higher**	n.s.	

Land Cover 2 (LC2) Coefficients			
	Vector	Move	Segment
Vector			
Move	Higher**		
Segment	Higher**	Higher**	

Discussion

Habitat selection is a widely applied statistical framework that investigates spatial ecology, yet many of the methods used to generate movement and couple it with the environment are deep-rooted in GIScience concepts and frameworks (e.g., computational movement analysis; analysis of movement data). The challenges associated with applying geographic context to movement data, as well as identifying how different object and space conceptualisations influence movement-environment inferences are GIScience challenges that must be addressed in future research (Dodge 2016; Holloway and Miller 2018; Miller et al. 2019). Subsequently, the aim of this study was to explore how systematically altering the conceptualisation of movement and environmental space affects the results of habitat selection analyses (e.g., SSA and PathSA).

PathSA has been less readily implemented than SSA, and subsequently less is understood about the inclusion of segments as the movement conceptualisation in habitat selection. In general, PathSA models resulted in larger (independent of sign) coefficient values than SSA for oilbirds (Figure 4c), zebras (Figure 4d), and the virtual species (Figures 5-6, Table 3), corroborating the findings of Zeller et al. (2016). Exceptions to this trend were identified, with no significant differences being observed among conceptualisations for the LF variable in the LF_prop model (Table 3); however, Figure 5 identified that vectors and moves incorrectly specified the expected LF-movement relationship at finer temporal scales. Moreover, the coefficient values for PathSA more accurately captured the expected relationships for all variables, as vectors and moves incorrectly identified preference for the reference habitat (Figures 5-6). These results suggest that PathSA better captures the underlying processes associated with animal-movement decisions than vectors or moves that are commonly implemented in SSA.

The relatively static treatment of movement in vectors and moves could explain the ability of segments to outperform these conceptualisations. When movement is represented as discrete entities, the underlying processes are masked as movement is not considered a process but an isolated event that is not directly informed by the movement decisions preceding or succeeding it. The ability of segments to correctly inform movement-environment (both land cover and LF) preferences (Figures 5 and 6) at all time-steps coupled with the inability of vectors and moves to inform on these preferences suggests that PathSA is required to effectively model the expected movement-environment relationships when investigating habitat selection.

Model performance varied across the three PathSA conceptualisations of movement for both oilbirds and zebras (Figures 4a-b), with models N_LF_agg and N_LF_conn performing the best based on AIC. Coefficient values were large for movement-LF relationships for the two areal representations of movement (Figures 4c-d) suggesting a preference for less aggregated or connected landscapes. Edge habitat provides more opportunities (including increased food and ease of movement) for many species (Laurance 2000) and it was hypothesised that both oilbirds and zebras would utilise LF habitats in part for these reasons. While results from the areal models support this, landscape measures of non-linear features potentially incorporate a number of confounding variables not related to movement-LF interactions. Subsequently, the two areal aggregations were not incorporated in the virtual ecologist approach so a more focused investigation could be directed explicitly towards the more established methods. However, these results suggest that areal aggregations could be utilised within PathSA analyses. Areal aggregations have not readily been incorporated within SSA or PathSA, despite their potential. Therefore, new methods conceptualising movement as areas and densities need to be explored within the habitat selection framework (e.g.,

time geography density estimator, Downs 2010; Downs et al. 2018) as well as the coupling of this movement with LFs.

Systematically altering the resistance of movement to LFs in the virtual ecologist approach allowed for the movement-environment relationship calculated from the conditional logistic regression to be examined. Expected movement-environment relationships were observed for segments when behaviour was complete avoidance (1.00) or attraction (0.00), yet inverted relationships were recorded across all resistance values for both vectors and moves as the time-steps were altered (Figures 5 and 6). These results suggest that vectors and moves are not suitable for modelling movement-LF relationships when individuals also made decisions on other land cover variables. This is particularly pertinent in landscapes where preference for LFs exists, but movement is not fixed to a LF network with discrete step choices based on other environmental factors masking movement-environment relationships at the individual aggregations in the statistical model. Subsequently, movement should be viewed at aggregated conceptualisations for the movement-LF relationships to be reliably modelled.

Increasing the temporal resolution of the simulations within the virtual ecologist approach resulted in the coefficient values for vectors and moves approaching the expected movement-environment relationship, while for segments it generally resulted in a decrease in the coefficient value (Figures 5 and 6). Both vectors and moves incorrectly specified the expected virtual movement-environment relationships at the finer temporal scales for land cover and LFs, suggesting that if these conceptualisations are to be used, coarser resolutions are a necessity. Coarser temporal resolutions of moves potentially reflect the dynamic nature of movement more so that the discrete finer temporal resolutions as they consist of several smaller movement steps (albeit

simplified). This further emphasises that many movement-environment relationships are only observable at an aggregated level (e.g., segments). Even with movement simulated using only three environmental variables in the virtual ecologist approach, the movement preferences of individuals are not identifiable when vectors and moves are incorporated in SSA. Such results question the ability of using SSA parameterised on vectors and moves using real-world data, particularly given the fact that movement will likely be influenced by more than three factors. However, given the resolution of real-world telemetry datasets (Table 2), the resolution may be such that the broader scale spatial patterns are still identifiable. With several methods for simulating movement in continuous-time (e.g., Harris and Blackwell 2013), further research should investigate whether such discrete step spatial statistics can capture the drivers of continuous simulations, or whether similar patterns of relationship inversion replicate.

Recent studies have advocated for incorporating movement parameters (e.g., step-length) into the statistical framework to relax the assumption that resource selection is independent of movement attributes (Forrester et al. 2009; Avgar et al. 2016; Signer et al. 2018). Similarly, studies have also called for memory to be incorporated within the statistics for the same reasons (Oliveira-Santos et al. 2016; Holloway 2018). The decision to omit both movement parameters and memory from the analysis meant that the focus of the results and subsequent discussion could centre on the movement-environment interactions. Despite this, these are important determinants in habitat selection, and future studies should continue to explore the interactions among all components of the movement process. This is particularly relevant given that external factors (e.g., the environment) are just one of the driving forces of animal movement specified in Nathan et al.'s (2008) movement ecology paradigm (internal state, navigational capacity, motion capacity). The inclusion of movement parameters

and memory begin to respectively address the ‘how’ (motion capacity) and ‘where’ (navigational capacity) questions associated with animal movement. Therefore, while this research focused on the external factors of movement, the results borne out are applicable to an integrated movement ecology framework.

Conclusion

The static representation of space and time in GIScience and spatial ecology has limited the development of the statistical methodologies implemented to explore species-environment relationships. Representing movement as a static entity does not reliably account for the complex dynamic relationships that exists between movement and the environment. Movement conceptualisations that represented a more ‘aggregated’ definition (e.g., segment) informed animal-movement relationships more reliably compared to vectors and moves. The virtual ecologist approach allowed resistance to the environment to be systematically altered, meaning the ability of habitat selection analyses to accurately inform on these relationships could be tested. In particular, the PathSA models that used a linear representation of movement were the only conceptualisation of movement that captured the expected relationship between movement and linear features as the resistance to this landscape was increased (Figures 5 and 6). Systematically changing the temporal resolution that movement was sampled at also substantially changed the strength of the coefficients representing selection for binary land cover variables (Table 3), with finer time-steps incorrectly specifying movement-environment relationships (Figures 5 and 6). These results suggest that statistical approaches that are employed to investigate movement-environment relationships should advance beyond conceptualising movement as the (relatively) static aggregations of vectors and moves and replace these with (more) dynamic aggregations of longer-lasting movement processes such as segments and areal representations.

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Table 1. Information on species datasets used within this study.

Table 2. Methodology to measure the environmental covariate for the five conceptualisations of movement used in the analysis. Step-Selection Analysis (SSA), and Path-Selection Analysis (PathSA).

Table 3. Confusion matrix of Wilcoxon Matched Pairs Signed Rank for both the LF_mean and LF_prop models comparing coefficient values among movement conceptualisations. Value refers to second group in the comparison. *medium effect, **large effect.

Figure 1. Diagram to illustrate the different semantic conceptualisations of movement along a single movement trajectory.

Figure 2. Habitat selection analyses that compare an observed (black) movement observation to a set of alternative (grey) movement observations that an individual could have theoretically taken. Black dots represent successive telemetry locations of an individual (in step-selection analysis and path-selection analysis), with five different movement conceptualisations (fix, vector, move, segment, area) represented as the moving object.

Figure 3. Conceptual diagram of the habitat selection analysis undertaken within this study.

Figure 4. Akaike Information Criterion (AIC) scores for the different movement conceptualisations and linear feature (LF) representations for a) oilbirds and b) zebras. Standardised coefficient values with standard errors for the different models parameterised on movement conceptualisations and LF representation for c) oilbirds and d) zebras.

Figure 5. Standardised coefficient values for land cover (LC) variables and linear features (LFs) with 95% confidence intervals for the LF_mean (mean distance to LFs) for the virtual species. Results include the movement conceptualisations of vectors, moves, and segments. Resistance values (0, 0.25, 0.5, 0.75, 1) correspond to the resistance of linear features to movement in the simulations, with the expected movement-LF relationship to increase in selection preference as resistance increases (e.g., selection preference increases as the distance increases away from LFs), while movement-LC relationships should remain consistent as LF resistance is increased.

For each variable, coefficient scores for 1-, 2-, 5-, 10-, 15-, 30-, 60-, 90-, and 120-minute time steps are reported left to right.

Figure 6. Standardised coefficient values for land cover (LC) variables and linear features (LFs) with 95% confidence intervals for the LF_prop (proportion of movement observation within LF buffer) for the virtual species. Results include the movement conceptualisations of vectors, moves, and segments. Resistance values (0, 0.25, 0.5, 0.75, 1) correspond to the resistance of linear features to movement in the simulations, with the expected movement-LF relationship to decrease in selection preference as resistance increases (e.g., selection preference for movement that has a lower proportion within the LF buffer), while movement-LC relationships should remain consistent as LF resistance is increased. For each variable, coefficient scores for 1-, 2-, 5-, 10-, 15-, 30-, 60-, 90-, and 120-minute time steps are reported left to right.