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Modelling non-Euclidean movement and landscape connectivity in highly structured ecological networks

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Summary

1. Movement is influenced by landscape structure, configuration and geometry, but measuring distance as perceived by animals poses technical and logistical challenges. Instead, movement is typically measured using Euclidean distance, irrespective of location or landscape structure, or is based on arbitrary cost surfaces. A recently proposed extension of spatial capture-recapture (SCR) models resolves this issue using spatial encounter histories of individuals to calculate least-cost paths (ecological distance: *Ecology*, **94**, 2013, 287) thereby relaxing the Euclidean assumption. We evaluate the consequences of not accounting for movement heterogeneity when estimating abundance in highly structured landscapes, and demonstrate the value of this approach for estimating biologically realistic space-use patterns and landscape connectivity.

2. We simulated SCR data in a riparian habitat network, using the ecological distance model under a range of scenarios where space-use in and around the landscape was increasingly associated with water (i.e. increasingly less Euclidean). To assess the influence of miscalculating distance on estimates of population size, we compared the results from the ecological and Euclidean distance based models. We then demonstrate that the ecological distance model can be used to estimate home range geometry when space use is not symmetrical. Finally, we provide a method for calculating landscape connectivity based on modelled species-landscape interactions generated from capture-recapture data.

3. Using ecological distance always produced unbiased estimates of abundance. Explicitly modelling the strength of the species-landscape interaction provided a direct measure of landscape connectivity and better characterised true home range geometry. Abundance under the Euclidean distance model was increasingly (negatively) biased as space use was more strongly associated with water and, because home ranges are assumed to be symmetrical, produced poor characterisations of home range geometry and no information about landscape connectivity.

4. The ecological distance SCR model uses spatially indexed capture-recapture data to estimate how activity patterns are influenced by landscape structure. As well as reducing bias in estimates of abundance, this approach provides biologically realistic representations of home range geometry, and direct information about species-landscape interactions. The incorporation of both structural (landscape) and functional (movement) components of connectivity provides a direct measure of species-specific landscape connectivity.

Key-words: abundance, animal movement, dendritic ecological network, density, ecological distance, functional connectivity, habitat network, stream distance, structural connectivity

Introduction

Animal movement is a feature of almost all ecological and evolutionary theory and is the result of complex and, in many cases, difficult to observe interactions between individuals and their environment. Organisms typically use areas closely associated with their specific habitat requirements rather than moving indiscriminately through heterogeneous landscapes (Ricketts 2001; Bender & Fahrig 2005). This is particularly true in highly structured landscapes where movement can be deter-

mined exclusively by the spatial configuration and geometry of the habitat (Beier & Noss 1998; Fagan 2002; Grant, Lowe & Fagan 2007). However, measuring distances as perceived by animals (i.e. ecological distance) poses both logistical and technical challenges. Instead, arbitrarily defined, or statistically convenient, models of animal movement based on Euclidean distance, and that lack biological realism, are often adopted when movement is not the primary inference objective (Zeller, McGarigal & Whiteley 2012).

The effects that highly structured habitat networks can have on biological processes such as demography, population and community structure, extinction, movement, and connectivity have been demonstrated both theoretically (Fagan 2002) and

empirically (Grant, Green & Lowe 2009; Grant *et al.* 2010) using dendritic ecological networks (DENs: e.g. stream, cave, hedgerow and transport networks). Grant, Lowe & Fagan (2007) describe this as a conceptual shift from a lattice network approach towards acknowledging the natural structure of ecological networks. However, describing patterns in linear networks has a strong focus on measuring distance strictly along linear features ('within-network' movement), whereas movement away from the linear feature ('out-of-network' movements) are considered secondary in importance (Rissler, Wilbur & Taylor 2004; Ver Hoef, Peterson & Theobald 2006; Grant, Lowe & Fagan 2007). The DEN approach is therefore limited in application, especially when movement within a network is *associated with* rather than *restricted to* landscape features. Terrestrial species using riparian corridors are perhaps the canonical example of such a case. Understanding the biological processes that play out in spatially structured ecological systems requires bridging the conceptual domains of node-based lattice networks and branch-based linear networks (Grant, Lowe & Fagan 2007; Beier, Majka & Spencer 2008; Swan & Brown 2011).

Spatial capture-recapture models (SCR: Efford 2004; Borchers & Efford 2008; Royle & Young 2008) offer a natural and flexible framework for investigating a wide range of ecological processes while simultaneously modelling space use. However, a major criticism of the approach is that almost all applications of SCR use encounter probability models based on Euclidean distance that imply symmetric and stationary home ranges, irrespective of an individual's location or the surrounding landscape structure. Royle *et al.* (2013) proposed a model for jointly estimating density and landscape connectivity using patterns of spatial encounters of individuals to calculate least-cost paths, and by doing so, estimate 'ecological' distance rather than assuming Euclidean animal movement (the ecological distance model). Cost surfaces, although widely used in ecology, are usually user-defined based on expert opinion, or arbitrarily selected and subjected to *post hoc* sensitivity analysis (Beier & Noss 1998; Zeller, McGarigal & Whiteley 2012). It would be preferable to use parametric models to explicitly quantify such cost surfaces using empirical data (e.g. using landscape genetics data: Hanks & Hooten 2013). The promise of the approach of Royle *et al.* (2013) is that capture-recapture data, perhaps the most commonly collected ecological monitoring data, can be used to directly *estimate* parameters of cost functions. Moreover, the ability to measure ecological distance in this way is exactly analogous to describing landscape connectivity, that is, 'the degree to which the landscape facilitates or impedes movement' (Taylor *et al.* 1993), a linchpin of biological conservation (Tischendorf & Fahrig 2000).

Royle *et al.* (2013) demonstrated that misspecifying the SCR encounter model using Euclidean distance results in negative bias in estimates of abundance due to unmodelled heterogeneity in encounter probability. However, the simulations were conducted using two semi-structured landscape configurations (systematic and fragmented) using only a single, low cost parameter value relating activity to landscape structure. It

is yet unclear whether the ecological distance model performs equally well when the landscape is highly structured (e.g. stream or road networks, habitat corridors). Moreover, it is important to understand the relationship between such biases in abundance estimates and the degree to which animal movement is associated with landscape features (i.e. the degree of violation of the Euclidean distance assumption). To address these issues, we simulate SCR data across a range of scenarios where movement is increasingly associated with water in a complex river network to investigate how different levels of species-landscape association, which results in varying degrees of violation of the Euclidean assumption, affect estimates of population size in a highly structured riparian network. We then demonstrate the utility of the model by using model estimates to derive biologically interesting metrics of home range geometry (shape and size), effective distances and, most importantly, of landscape connectivity.

Methods

A STANDARD SCR MODEL

The general setting for a spatial capture-recapture analysis is that there exists a population of I individuals, each having an activity centre with easting (E) and northing (N) coordinates $S_i = (s_{i,E}, s_{i,N})$. The goal is to estimate the number of individuals (or activity centres) within a region of interest \mathcal{S} , which is to say we wish to estimate density: $D = N/|\mathcal{S}|$, where $|\mathcal{S}|$ is the area of \mathcal{S} . We assume that activity centres are distributed uniformly throughout the region of interest:

$$S_i \sim \text{Uniform}(\mathcal{S}).$$

The population is subjected to sampling via a collection of $j = 1, \dots, J$ detectors or traps resulting in observations $y_{i,j}$, which are the encounter frequencies of individual $i = 1, \dots, I$ at trap j across K sampling occasions. In most SCR studies, observations are assumed to be binomially distributed with sample size K (the number of sampling occasions):

$$y_{i,j} \sim \text{Binomial}(K, p_{i,j}),$$

where $p_{i,j}$ is the encounter probability of individual i in trap j which depends on the distance between the trap location (x_j) and the individual's activity centre (s_i) as follows:

$$p_{i,j} = p_0 \times e^{-\alpha_1 d_{\text{euc}}(x_j, s_i)^2}. \quad \text{eqn 1}$$

This is the bivariate normal encounter model where $\text{logit}(p_0) = \alpha_0$ is the baseline encounter probability, $\alpha_1 = 1/(2\sigma^2)$ controls the shape of the function, and $d_{\text{euc}}(x_j, s_i)$ is the Euclidean distance between trap j and the activity centre of individual i . Parameters α_0 and α_1 are parameters to be estimated. This is the standard SCR model which is based on Euclidean distance (SCR_{euc}). Use of SCR_{euc} implies that home ranges of all individuals are stationary (i.e. home ranges are identical regardless of location), and that space use is symmetrical around an activity centre regardless of local landscape structure. Although many other encounter models exist, they are all based on Euclidean distance, and imply symmetric and stationary mod-

els of space use, and therefore the use of ecological distance (see below) as an alternative distance measure is directly applicable to them all.

A MODEL FOR NON-STATIONARY HOME RANGES

A model proposed by Royle *et al.* (2013) uses an identical formulation of the encounter model above with the exception that Euclidean distance, $d_{\text{euc}}(x_j, s_i)$, is substituted with length of the least-cost path, $d_{\text{lep}}(x_j, s_i)$. This allows a relaxation of the Euclidean assumption implied when using traditional encounter models. Calculating least-cost paths requires that a landscape \mathcal{V} be discretised into pixels v_p , each of which has associated covariate values $z(v_p)$ corresponding to some measure of the landscape (e.g. percent cover, distance from a feature, elevation etc.). We make the distinction between the region of interest \mathcal{S} , and the cost covariate surface \mathcal{V} , because it is not necessary for the resolution of both to be identical, although the resolution of \mathcal{V} must be at least as fine as that of \mathcal{S} . Now, given a discrete landscape \mathcal{V} , let $\mathcal{L}_w^{v, v'} = \{v, v_{1,w}, \dots, v_{m_w, w}, v'\}$ denote the $w = 1, \dots, W$ th path, consisting of any set of adjacent king's neighbourhood cells, $(v_p, v_{p+1, w}) \in \mathcal{L}_w^{v, v'}$, that connect any two points v and v' . Each path $\mathcal{L}_w^{v, v'}$ therefore consists of m_w line segments connecting m_w+1 cells from cell center to cell center, and the cost weighted distance is the product of the distance (path length) and the associated cost (see Eq. 2 below). Evaluating all reasonable paths, the one that incurs the lowest cumulative cost is considered the *least* cost path:

$$d_{\text{lep}}(v, v') = \min_{\mathcal{L}_1, \dots, \mathcal{L}_W} \sum_{p=1}^{m+1} \text{cost}(v_p, v_{p+1}) \times d_{\text{euc}}(v_p, v_{p+1}). \quad \text{eqn 2}$$

For a given covariate/cost surface we identify the least cost path using Dijkstra's (path finding) algorithm, implemented in the R package `gdistance` (van Etten 2012).

Following Royle *et al.* (2013), we define the cost function $[\text{cost}(v_p, v_{p+1})]$ as a log-linear function of the average of the two covariate values:

$$\log[\text{cost}(v_p, v_{p+1})] = \alpha_2 \frac{z(v_p) + z(v_{p+1})}{2}. \quad \text{eqn 3}$$

This formulation of the SCR model involves estimating the additional parameter, α_2 , which is a parameter that defines the resistance surface, $\mathcal{R} = \exp(\alpha_2 \mathcal{V})$, through which least cost paths are chosen. Moreover, α_2 is a direct measure of species- and landscape-specific connectivity and has a convenient and biologically intuitive interpretation that, when $\alpha_2 = 0$, that is, when there is no landscape resistance, the cost function evaluates to $\exp(0) = 1$ and distance is exactly Euclidean, and, as α_2 increases, the landscape becomes more structured and the least cost path becomes increasingly associated with preferred landscape features.

This is the model for non-stationary home ranges using ecological distance [SCR_{ecol}, see also Royle *et al.* 2013]. Parameters α_0 , α_1 and α_2 are estimated using maximum likelihood and least cost paths are evaluated at each iteration of the maximum likelihood optimisation. The use of maximum likelihood also

allows formal comparisons to be made between models SCR_{ecuc} and SCR_{ecol} using AIC. We note that it is also straightforward to extend the cost function to include more than one covariate, or even to define alternative, user defined cost functions (see van Etten 2012).

SIMULATION STUDY: A RIPARIAN HABITAT NETWORK

We assess the consequences of misspecifying the model of space use with Euclidean distance by comparing estimates of abundance from the two models described above (SCR_{ecuc} vs. SCR_{ecol}), when space use is increasingly associated with water in a linear habitat network (i.e. as α_2 gets increasingly larger than 0). The focus on a riparian species in a river network provides a general, and biologically appealing, setting whereby movement has an association with the structure of the landscape. This is in contrast to the restrictive cases where movement is considered to be symmetrical around an activity centre and therefore can be measured in Euclidean distance (Raabe & Gardner 2013), or the dendritic network approach where distance along the stream is often the focus (Fagan 2002; Grant 2011; Van Looy *et al.* 2014). As a motivating example, consider otters (Van Looy *et al.* 2014) that move in and around river networks and not strictly along the water.

We generated a discrete 'distance-to-water' surface consisting of 32,745 100 m \times 100 m cells (extent = 17.7 km \times 18.57 km) by calculating the distance from the centroid of each cell to the nearest stream (Fig. 1). We then simulated a population of $N = 200$ individuals with activity centres (s) that were uniformly distributed as outlined above (Fig. 1). Using a trapping array consisting of 64 traps arranged in a regular grid on approximately the inner 10 km \times 10 km square (Fig. 1), spatial

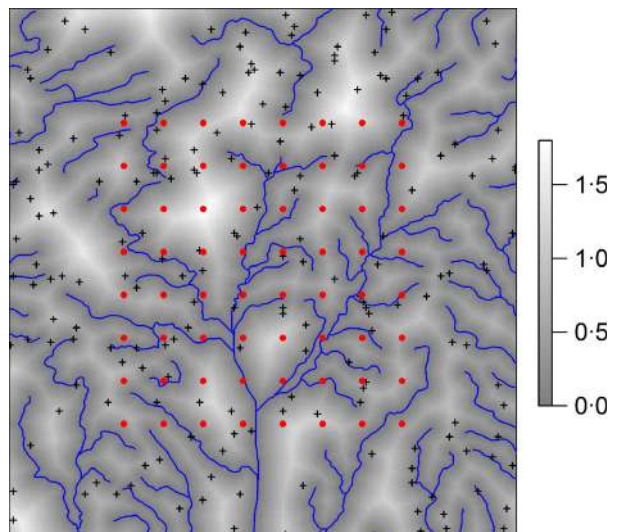


Fig. 1. A visual representation of the riparian network used in our simulation study. Blue lines represent the stream network, red points show 64 traps arranged in a regular trapping grid in the central 10 km \times 10 km² and the landscape is classified as a 'distance-to-stream' surface where the light grey to dark grey gradient denotes farthest to closest distance to water respectively (legend in kilometers). For demonstrative purposes, the black crosses are a single realisation of $N = 200$ randomly generated individual activity centers.

encounter histories were simulated from model SCR_{ecol} setting parameter values to $\alpha_0 = -1$, $\sigma = 1.4$, and $K = 10$, across a range of costs controlling how structured the landscape was, and therefore how strongly space use was associated with water: $\alpha_2 = 0, 1, 2, 3, 4, 5, 6, 7, 8, 9$ and 10 (see above for parameter definitions). Simulations were carried out assuming individuals could be detected in multiple traps in any occasion but only once at each trap in each occasion. We conducted 500 simulations for each of the α_2 scenarios.

We fitted models SCR_{euc} and SCR_{ecol} to the simulated data using likelihood analysis implemented in R using the integrated likelihood functions provided as supplementary material. We note that, while SCR_{euc} can be analysed using likelihood methods implemented in the R package `SECR` (Efford 2013), or using Bayesian methods (Royle *et al.* 2014), SCR_{ecol} cannot currently be analysed using either due to the iterative calculation of the least-cost paths. For consistency and completeness, we provide R functions to implement both models and a working example as supplements.

DERIVING BIOLOGICAL METRICS

Home range size and shape

The kernel of the encounter probability model is directly related to space use (Royle *et al.* 2014), and as such, the expected probability that an individual with activity centre s_i uses any $s_u \in \mathcal{S}$ cells can be derived by evaluating the SCR_{ecol} encounter model at the maximum likelihood estimates (mle) for α_1 and α_2 and setting $p_0 = 1$. We refer to this probability as $\text{Pr}(g[s_u, s_i])$ and make the distinction between cell *use* (g) and imperfect encounters within a cell (y). The approximate $\mathcal{H}\%$ home range size can therefore be derived by computing the number of cells that meet the condition $\text{Pr}(g[s_u, s_i]) \geq (1 - \mathcal{H}/100)$ and multiplying that by the area of a single pixel of the covariate surface, a :

$$\text{HR}_{\mathcal{H}\%} = a \sum_{s_i \in \mathcal{S}} \mathbf{I}(\text{Pr}(g[s_u, s_i]) \geq \frac{\mathcal{H}}{100}). \quad \text{eqn 4}$$

Here, $\mathbf{I}(\text{Pr}(g[s_u, s_i]) \geq \mathcal{H}/100)$ is an indicator function that equals one when the condition is satisfied and zero otherwise. Home range geometry can then be visualised by simply plotting this spatially indexed binary surface.

Landscape connectivity

The natural extension of the home range estimator above is to consider the probability of cell use given any number of activity centers \mathbf{s} , and for all cells in the landscape, which is a direct measure of landscape connectivity. Cell-specific connectivity values, $\mathcal{C}(s_u)$, are calculated by computing the expected cell-specific probability of use, as above, but for any particular set of activity centres. Here we define two useful measures of connectivity. First, *potential connectivity*, $\mathcal{C}^P(s_u)$, which is the expected probability of using cell s_u when each cell in \mathcal{S} contains a single individual activity centre:

$$\mathcal{C}^P(s_u) = \sum_{s_i \in \mathcal{S}} \text{Pr}(g[s_u, s_i]). \quad \text{eqn 5}$$

Second, because cell specific density estimates are an output from the SCR_{euc} model, this can be extended further to calculate *realised connectivity*, $\mathcal{C}^R(s_u)$, which is the potential connectivity, calculated above, weighted by the model estimated density in each cell $D(s_i)$:

$$\mathcal{C}^R(s_u) = \sum_{s_i \in \mathcal{S}} \text{Pr}(g[s_u, s_i]) \times D(s_i). \quad \text{eqn 6}$$

Relative frequency of use

When $\alpha_2 > 0$ the frequency of use of any point on the landscape (e.g. a pixel) at a given distance, say d , from an activity centre s_i is determined not by Euclidean distance but by the *effective* distance given the cost surface. Here, we derive an intuitive measure to first compare the effective distances of a point located d km away from an individual's activity centre in two directions around a hypothetical stream section, d_f ; (i) along the water (least resistant, $r = 0$), and (ii) perpendicularly away from the water (most resistant, $r = 1$). Then, evaluating the encounter probability model for these two distances, we compute the relative frequency of use, \mathcal{F} , for the points:

$$\mathcal{F}_r = e^{-\alpha_1 d_f^r}, \quad \text{eqn 7}$$

where

$$d_f = d \times e^{\alpha_2 (r \cdot d)/2}. \quad \text{eqn 8}$$

Evaluating the above for both $r = 0$ and $r = 1$ for any value of d and taking the ratio, $\mathcal{F}_{r=0}/\mathcal{F}_{r=1}$, provides a measure of how much more frequently a point *along* the stream is expected to be used than a point the same Euclidean distance *away* from the stream. For example, when $\alpha_2 = 3$ and for a point $d = 1$ km away from the stream (i.e. $r = 1$), $\mathcal{F} = 4.48$, whereas for a point the same Euclidean distance along the stream, and which incurs no additional cost, $\mathcal{F} = 1$. Therefore, the use frequency of a point *away* from the stream is $1/4.48 = 0.22$ times the frequency of a point *along* the stream and highlights the potential for home range asymmetry.

Simulation results

In simulations where $\alpha_2 = 0$, least-cost path distance is exactly Euclidean distance and is reflected in the comparable and negligible bias in estimated abundance (\hat{N}) across both models (c. 0%, Table 1, Fig. 2). Increasing values of α_2 generate space use patterns that are more closely associated with the water which increases the degree of home range asymmetry. The flexibility of model SCR_{ecol} to account for such asymmetry resulted in practically unbiased estimates of abundance for all values of α_2 (<3% in all cases). However, because of the Euclidean assumption, the encounter probability model of SCR_{euc} is misspecified and resulted in extremely negatively biased (up to 69% bias) estimates of N that increased markedly with increasing α_2 values (Fig. 2). In fact, even at low cost values ($\alpha_2 = 2$)

Table 1. Simulation results from fitting both a Euclidean distance SCR model, SCR_{euc} , and the least-cost path distance SCR model, SCR_{ecol} to simulated data. Simulated SCR data were generated using model SCR_{ecol} with fixed parameters $\alpha_0 = -1$, $\sigma = 1.4$ (and hence $\alpha_1 = 0.26$), $K = 10$, and varying values of α_2 . Values for α_2 were integer values $0, \dots, 10$, where increasing values represent increasing cost associated with moving away from water (0 is ‘no cost’ and is equivalent to Euclidean distance). Summary statistics are provided for the estimators for N . We also compare the derived 95% home range size (km^2) for two individuals with randomly selected activity centers (Ind. 1 and Ind. 2, see also Fig. 3) based on the maximum likelihood estimate of α_1 using the approach described in the text (see *Home range size and shape*).

α_2	\hat{N}				95%HR size (km^2)			
					Ind. 1		Ind. 2	
	Mean	SD	%bias	%coverage	Truth	Estimate	Truth	Estimate
SCR_{euc}								
0	199.85	9.05	-0.08	95	33.77	33.15	33.77	33.11
1	190.79	11.95	-4.61	90	21.65	20.01	17.06	19.94
2	168.30	13.42	-15.85	42	15.33	15.35	11.01	15.41
3	143.57	13.97	-28.21	3	11.25	13.15	7.76	13.10
4	125.22	14.04	-37.39	0	7.98	11.76	6.22	11.72
5	107.79	13.24	-46.10	0	5.53	10.86	5.25	10.87
6	93.48	13.18	-53.26	0	3.70	10.16	4.55	10.21
7	81.37	12.27	-59.31	0	2.45	9.65	3.94	9.62
8	74.03	12.18	-62.99	0	1.46	9.15	3.27	9.18
9	67.78	12.33	-66.11	0	0.64	8.90	2.78	8.91
10	63.91	11.51	-68.05	0	0.08	8.77	2.20	8.82
SCR_{ecol}								
0	199.41	9.03	-0.29	95	33.77	33.35	33.77	33.05
1	198.99	12.34	-0.51	96	21.65	21.61	17.06	17.03
2	200.12	15.99	0.06	95	15.33	15.33	11.01	10.98
3	199.71	19.80	-0.14	96	11.25	11.22	7.76	7.74
4	200.76	24.06	0.38	94	7.98	7.98	6.22	6.22
5	201.57	27.16	0.78	95	5.53	5.45	5.25	5.23
6	202.40	29.36	1.20	96	3.70	3.59	4.55	4.48
7	200.84	32.69	0.42	96	2.45	2.27	3.94	3.85
8	202.13	35.98	1.06	95	1.46	1.34	3.27	3.21
9	203.06	38.32	1.53	96	0.64	0.49	2.78	2.68
10	205.49	39.80	2.75	95	0.08	0.06	2.20	2.13

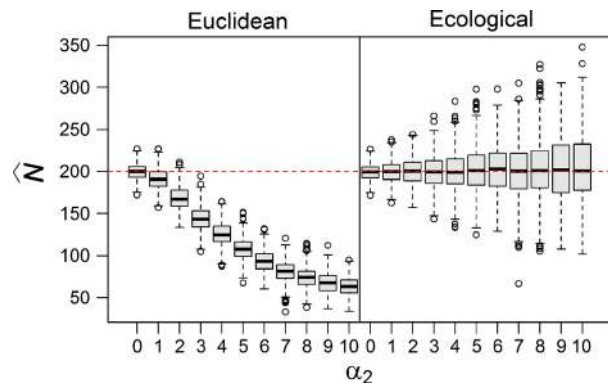


Fig. 2. Estimated abundance under both the Euclidean distance model SCR_{euc} (left) and the ecological distance model SCR_{ecol} (right) based on data simulated using increasing values of the cost parameter α_2 ($\alpha_2 = 0, \dots, 10$). Results are based on 500 simulations of each cost scenario and show that bias in estimated N is negative and increases as α_2 increases.

bias in N was extreme ($>15\%$). While the lack of bias in \hat{N} using SCR_{ecol} is encouraging, it was expected given that it was the data-generating model, although it is encouraging that the bias remains low even in extreme cases of home range asymmetry.

Similarly, estimates of α_2 generated from model SCR_{ecol} were unbiased and well estimated across all scenarios (Table 2).

Although N was fixed at 200 in each simulation, introducing increasing levels of structure to the landscape resulted in fewer individuals detected, and of those detected, fewer unique locations per individual detected (Table 2). This reduction in data quality (i.e. reduced sample size), while expected given the simulation study settings, demonstrates that even when SCR data are limited and space use is strongly influenced by landscape structure, the model can generate reliable estimates of the landscape resistance parameter α_2 .

To demonstrate how home range geometry can be estimated using model SCR_{ecol} , and to evaluate the performance of both models in recovering simulated home range statistics, we generated two individual activity centres within our riparian landscape (Ind. 1 and Ind. 2; Fig. 3). Using the data generating values and the activity centres of these two simulated individuals, we computed and visualised the true $\mathcal{H} = 95\%$ home range shape and size as outlined above. We then compared those to the home range shape and size generated using maximum likelihood estimates from both distance models ($\theta_{\text{euc}} = [\alpha_0, \alpha_1, (\alpha_2 \equiv 0)]$ and $\theta_{\text{ecol}} = [\alpha_0, \alpha_1, \alpha_2]$) for the same two individuals. For $\alpha_2 = 0$, movement is Euclidean and, as expected, both models predict home range shape and size close to the true value (Table 1, Fig. 3). For all non-zero values of α_2 , home range shapes and sizes remained well characterised using

Table 2. Simulation results for the performance of the estimator of the resistance parameter α_2 under model SCR_{ecol} across a range of known values ($\alpha_2 \in 1, 2, 3, 4, 5, 6, 7, 8, 9, 10$). The summary statistics are the simulated mean, standard deviation (SD) and % bias (%bias) of α_2 based on 500 simulations of each of the α_2 scenarios. Also provided are simulation average encounter history summaries of: the mean number of individuals observed at least once (m_{total}), the number of individuals observed at least 2 unique spatial locations ($m_{\text{loc} > 1}$), and the average number of unique spatial locations each $m_{\text{loc} > 1}$ individual was observed at (μ_{loc}).

α_2	$\hat{\alpha}_2$			Sample size (n)		
	Mean	SD	%bias	m_{total}	$m_{\text{loc} > 1}$	μ_{loc}
0	0.03	0.04	–	144.52	118.85	5.71
1	1.00	0.09	0.00	113.85	86.44	3.97
2	2.00	0.16	0.00	90.28	60.60	3.27
3	3.02	0.28	0.01	73.26	45.71	2.91
4	4.00	0.40	0.00	60.90	34.93	2.75
5	5.04	0.53	0.01	50.66	27.61	2.64
6	6.08	0.64	0.01	43.27	22.55	2.56
7	7.16	0.76	0.02	37.46	18.87	2.51
8	8.16	0.91	0.02	33.28	16.30	2.46
9	9.23	1.21	0.03	30.52	13.85	2.42
10	10.11	1.39	0.01	27.34	12.02	2.40

model SCR_{ecol} (Table 1, Fig. 3). Importantly, SCR_{ecol} allows home range geometry to change according to an individuals' location and surrounding landscape (Ind. 1 vs. Ind. 2 in Fig. 3 and Table 1; red line in Fig. 3). Because the Euclidean distance model can only reproduce symmetrical home ranges which are the same for individuals irrespective of location, as movement becomes more associated with the water (i.e. less Euclidean), the model overestimates home range size (Table 1) and poorly characterises the home range shape (black line in Fig. 3).

To demonstrate the calculation of landscape connectivity metrics, we computed potential and realised connectivity surfaces for a single simulated SCR data with $\alpha_2 = 3$. Using the resulting connectivity surfaces, areas of high connectivity (green in Fig. 4a,b) and low connectivity (white in Fig. 4a,b) in the landscape can be easily identified. Interestingly, despite streams not being physically connected, areas of high connectivity can be maintained by out-of-network movements in areas with a high density of branches in close proximity (Fig. 4a,b).

Discussion

A general feature of capture-recapture (CR) methods is negative bias in abundance estimates associated with unmodelled heterogeneity in capture probability (Otis *et al.* 1978). The novelty of spatial CR is the development of an explicit model of space use to account for an important source of heterogeneity – variation in the distances between individuals and traps that affects capture probability (Efford 2004; Borchers & Efford 2008; Royle & Young 2008; Royle *et al.* 2014). However, such models are based exclusively on Euclidean distance and have attracted some criticism because they largely ignore the, often complex, structure of the landscape. Perhaps more fundamentally though, as measures of ecological distance and Euclidean distance diverge, Euclidean distance provides progressively poorer measures of *effective* distance, and distance-related capture heterogeneity remains unaccounted for. As such, misspecification of the model for space use is likely to result in biased estimates of abundance (Royle *et al.* 2013). Our simulations show that this is indeed the case. When space use is more strongly associated with landscape structures, and home ranges become increasingly asymmetric and non-stationary, estimates of abundance based on Euclidean distance models become more negatively biased (Fig. 2). The flexibility of the ecological distance model, SCR_{ecol} , allows the strength of the association between space use and landscape structure to be estimated directly for data. Space use can therefore be modelled in terms of *ecological* distance using estimated least cost paths, ultimately providing better estimates of abundance.

Ecological networks with linear geometries such as streams have been shown to constrain local patterns of movement (dendritic ecological networks DENs: Grant, Green & Lowe 2009, Grant *et al.* 2010) and it is likely that most species are subjected to similar constraints related to associations with preferred habitats (Swan & Brown 2011). The ecological distance model represents a general model of space use for which the Euclidean and dendritic models can be considered special cases: Euclidean distance is equivalent to SCR_{ecol} with $\alpha_2 = 0$, whereas strictly stream distance (dendritic) is equivalent to SCR_{ecol} with $\alpha_2 \gg 0$. This flexibility is appealing because no restrictive assumptions need to be made about the geometry

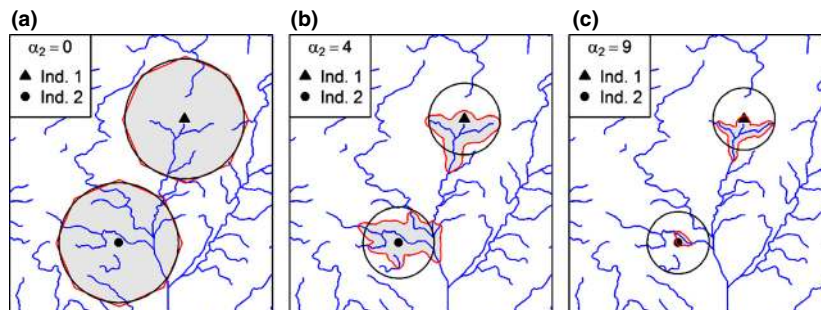


Fig. 3. Having obtained mle's of parameters α_1 and α_2 under model SCR_{ecol} and α_1 under model SCR_{euc} , it is possible to compute and visualise home range extent and geometry for any activity centre on the landscape. Here we randomly select 2 activity centers (Ind. 1 and Ind. 2) and, using mle's from a single realisation of simulated SCR data, compare the true 95% home range geometry (grey shaded area), to that estimated under the SCR_{ecol} (red contour line) and SCR_{euc} (black contour line) models. The figure shows estimated home ranges of Ind. 1 and Ind. 2 for simulations where $\alpha_2 = 0$ (a), $\alpha_2 = 4$ (b), and $\alpha_2 = 9$ (c).

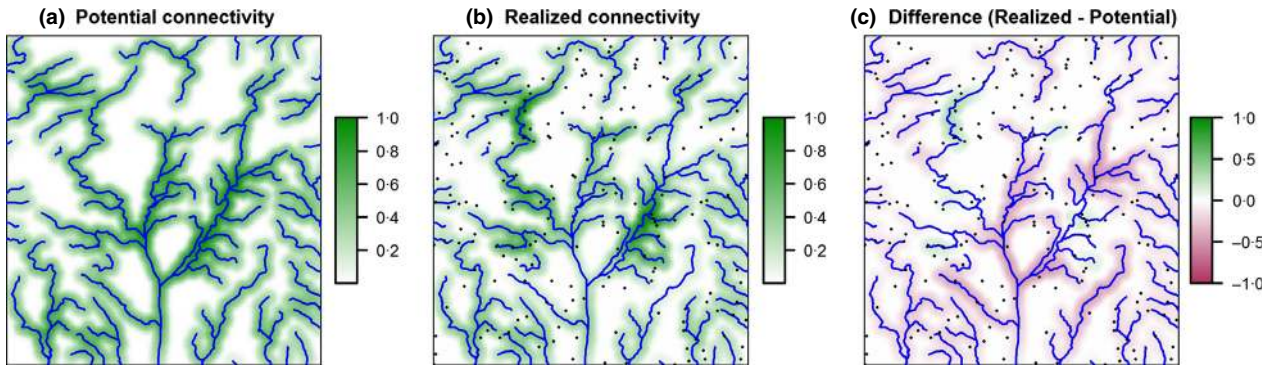


Fig. 4. Using maximum likelihood estimates from model SCR_{eco1} fitted to a single realisation of SCR data simulated using $\alpha_2 = 3$, potential connectivity [C^P , (a)], and realized connectivity [C^R , (b)] were computed. The colour scale (green to white) represents the gradient in connectivity values where green areas denote highly connected cells in the landscape whereas white areas are least connected parts of the landscape. We present the scaled connectivity surfaces ($C_i/\max(C)$) for ease of comparison of both measures. (c) the difference between *Realized* and *Potential* connectivity identifies areas that are more (green) or less (red) utilized than expected under the fitted model. The points in (b,c) represent the single realisation of $N = 200$ individual activity centres used to simulate SCR data.

of individual home ranges and α_2 can be estimated directly using widely collected (spatial) capture-recapture data. When data are insufficient to estimate α_2 , the model will simply reduce to the Euclidean distance model, however, when estimable it is a direct measure of the strength of species–landscape interactions. We do note, however, that it is encouraging that the model provided robust estimates of α_2 even when data were relatively sparse, that is, low numbers of detected individuals and few spatial recaptures, and space use is strongly influenced by the structure of the landscape (Table 2). As a result, it is possible to derive biologically realistic characterisations of home range geometries (shape and size) that are both location specific (i.e. are non-stationary) and that explicitly incorporate information about surrounding landscape structure (i.e. can be asymmetric). The ability to estimate ecological distance represents a liberating model development that allows specific hypotheses to be tested about space use and the strengths of associations with landscape features while also providing estimates of population density.

We compared abundance and home range estimates from the Euclidean and ecological distance based models using a stream network and a range of possible landscape cost values that represented movement with varying degrees of association with water (from none to extremely strong). It is unclear what values of α_2 would be expected in a natural setting, and therefore, difficult to say how cautionary our findings should be in terms of biased inference when the model is misspecified. However, a preliminary analysis of a small data set collected on a semi-aquatic riparian specialist species produced values of $\alpha_2 \approx 3-5$ which, based on our simulations, would produce substantially biased estimates if unaccounted for (A. Fuller, C. Sutherland, M. Hare and J.A. Royle, unpublished data). Interestingly, bias in \hat{N} from our simulations in the highly structured stream network was lower than reported by (Royle *et al.* 2013) in semi-structured ‘fragmented’ or ‘gradient’ habitats using very similar simulation settings and specifically, $\alpha_2 = 1$ (22% and 30% respectively vs. 4.5%). The suggestion that landscape configuration may also influence the magnitude of bias lends more support for the ecological distance

model because it explicitly accounts for the structure/configuration of the landscape.

In addition to influencing patterns of space use locally, the structure, configuration and/or geometry of the landscape determines the degree of larger-scale landscape connectivity (Isaak *et al.* 2014; Peterson *et al.* 2013; Beier & Noss 1998; Fagan 2002; Ver Hoef, Peterson & Theobald 2006; Grant, Lowe & Fagan 2007). Because α_2 is a direct estimate of the species–landscape interaction strength, the ecological distance model is exactly a model for estimating landscape connectivity. That is, it is an estimate of the ‘degree to which the landscape facilitates or impedes movement’ (Taylor *et al.* 1993). To date, connectivity models have been based on arbitrarily defined or opinion based cost surfaces (Beier & Noss 1998; Zeller, McGarigal & Whiteley 2012). Moreover, they generally focused on either landscape structure (structural connectivity, e.g. Beier & Noss 1998) or animal movement (functional connectivity, e.g. Tischendorf & Fahrig 2000) alone, in fact, the link between the two is not straightforward (Goodwin & Fahrig 2002) and they are often poorly correlated (Moilanen & Nieminen 2002; Bender, Tischendorf & Fahrig 2003; Winfree *et al.* 2005). The ecological distance approach explicitly models the relationship between landscape structure (i.e. α_2) and animal movement (i.e. σ), integrating both components of connectivity (structural and functional, Fig. 4).

We developed the link between the species–landscape interaction and landscape connectivity formally based on the expected frequency of use of any cell given any particular spatial configuration of individuals under the fitted model of space use. For example, if we consider a population of $N = 1$ individual, the connectivity surface would be identical to that individual’s home range (Fig. 3), which would in turn depend its’ location. The next obvious case would be to consider a discrete landscape where each point represents a single individual activity centre which we call *potential connectivity* (C^P). This measure provides a theoretical measure of cell specific connectivity (Fig. 4a). Animals are rarely distributed uniformly and identically in space however, so we provide a second measure of connectivity that multiplies pixel specific

potential connectivity (C_i^P) by spatially explicit estimates of density derived from the SCR model [$D(s_i)$], which we call *realised connectivity* (C^R). Realised connectivity is a metric that integrates estimates of density, species specific space use patterns and the structure of the landscape (Fig. 4b). An interesting and potentially powerful application of this approach is that the difference between C^P and C^R provides direct information about areas that are used more or less frequently than expected (Fig. 4c) that would be useful for prioritising landscape/habitat conservation and/or restoration, and even areas for potential translocation and/or assisted migration.

Our measures of landscape connectivity are based on expected use frequency of any part of the landscape and are based on estimated relationships between space use and landscape structure. This highlights the important contribution of out-of-network movements to landscape connectivity such that connected areas are not restricted to connected waterways, but rather, connectivity can be maintained by movement between close proximity but distinct stream sections (out-of-network). In our example we assume a closed population with fixed activity centres, therefore, connectivity is based on expected local space use and provides a measure of habitat suitability or availability. The development of open SCR models allows dispersal to be modeled based on variation through time of activity centre locations using a similar distance-based model used to model space use. In the same way we generate connectivity surfaces using α_2 , dispersal based connectivity can easily be derived using an ecological distance based model of dispersal in an open SCR model.

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