




A General Approach to Model Movement in (Highly) Fragmented Patch Networks

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Landscape heterogeneity can often be represented as a series of discrete habitat or resource patches surrounded by a matrix of non-habitat. Understanding how animals move in such networks of patches is important for many theoretical and applied questions. The probability of going from one patch to another is affected in a non-trivial way by the characteristics and location of other patches in the network. Nearby patches can compete as possible destinations, and a particular patch can be shadowed by neighboring patches. We present a way to account for the effects of the spatial configuration of patches in models of space use where individuals alternate between spending time in a patch and moving to other patches in the network. The approach is based on the original derivation of Ovaskainen and Cornell (J Appl Probab 40:557–580, 2003) for a diffusion model that considered all possible ways in which an individual leaving a particular patch can eventually reach another patch before dying or leaving the patch network. By replacing the theoretical results of Ovaskainen and Cornell by other appropriate functions, we provide generality and thus make their approach useful in contexts where diffusion is not a good approximation of movement. Furthermore, we provide ways to estimate time spent in the non-habitat matrix when going from patch to patch and implement a method to incorporate the effect of the history of previous visits on future patch use. We present an MCMC way to fit these models to data and illustrate the approach with both simulated data and data from sheep moving among seasonally flooded meadows in northern Patagonia.

Supplementary materials accompanying this paper appear online.

Key Words: Metapopulation; Patch transition; Spatial configuration; Landscape connectivity; Memory.

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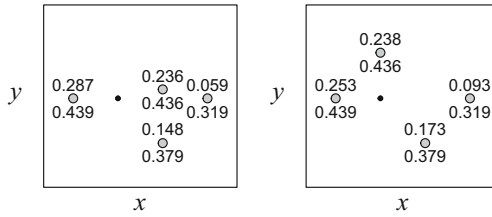


Figure 1. Spatial effects on the probabilities of going from patch to patch (represented as *circles*). The *left panel* shows the probabilities of reaching next each patch in the network when an animal is leaving the small black patch located at the center of the plot. The *right panel* shows how those probabilities change when the position of one of the patches is moved. *Numbers* below each patch give the probabilities of reaching that patch assuming no other patches are present. *Numbers* above patches are probabilities after considering the effects of other patches in the network. Probabilities were calculated assuming diffusion in the non-habitat matrix (Eq. 1) and setting $\alpha = 0.1$.

1. INTRODUCTION

Landscape heterogeneity can often be represented as a series of discrete habitat or resource patches surrounded by a matrix of non-habitat (Hanski 1999a; Hanski and Ovaskainen 2000; Urban and Keitt 2001). Understanding how animals move in such networks of patches is important for many theoretical and applied questions. At the individual level, space use by many animals is usually characterized by an alternation between more or less directed movement among patches, and more tortuous and smaller-scale movements within patches (e.g., Morales et al. 2010; McClintock et al. 2012). Within populations, pollen flow, for example, is non-randomly structured because groups of mother trees and donor trees are located in spatially well-defined modules (Fortuna et al. 2008; Gómez and Perfectti 2012). Similarly, patterns of seed dispersal by birds are the consequence of animals moving among plants and perches (Morales and Carlo 2006; Morales et al. 2013; Carlo et al. 2007). Metapopulation studies have shown that local population densities, gene flow and patch (re)colonization probabilities in fragmented landscapes are greatly affected by the exchange of individuals among patches (Benton and Bowler 2012; Hanski 1999b). Furthermore, the restoration of ecosystem services many times depend on establishing connections between habitat patches (Montoya et al. 2012).

Modeling movement within a patch network is not a simple task. Besides the many factors that can affect how animals move in a landscape, the probability that an individual goes from one patch to another is affected in a non-trivial way by the characteristics and location of other patches in the network. Nearby patches can compete as possible destinations, and a particular patch can be “shadowed” by neighboring patches (see Fig. 1, and figure 4 in Ovaskainen and Cornell 2003). These effects are the result of how patches are located in space, that is, of the so-called spatial configuration (Forman and Godron 1981) of the patch network. If we can take into account the effect of the spatial configuration of the network, we will have better predictive power when attempting to apply what we learn from studying movement in a particular patch network to a different network, or when considering adding or removing patches to an existing network. This would be especially important when assessing connectivity in other patch networks or in modified versions of the original one due to management or restoration.

Earlier attempts to quantify movement among habitat patches relied on capture–recapture or tag recovery data and estimated transition probabilities for all pairs of sites (e.g., Schwarz et al. 1993; Brownie et al. 1993). These approaches have improved notably in their capacity to handle individual and landscape heterogeneity, turning them into very useful and powerful tools (see, for example, Royle and Young 2008; Borchers and Efford 2008; Fuller et al. 2016). Another set of very useful tools was developed around the estimation of gene flow (Sork et al. 1999; Coulon et al. 2004; Waples and Gaggiotti 2006; Chapuis and Estoup 2007). Furthermore, lots of metrics have been developed to characterize and estimate connectivity in landscapes (reviewed in Calabrese and Fagan 2004; Belisle 2005; Saura and Pascual-Hortal 2007), but these are mostly concerned with an overall metric of the ease with which species can move through the network of patches. Network approaches to landscape connectivity are also useful for identifying modularity (clusters of patches) and nestedness (hierarchies of patch use), or they aim at describing the importance of particular patches for overall connectivity (Urban and Keitt 2001; Rayfield et al. 2011; Palmer et al. 2011). Other approaches have relied on assumptions about movement costs or habitat preference in the landscape in order to predict connectivity (e.g., LaPoint et al. 2013; Pullinger and Johnson 2010; Koen et al. 2014; McRae and Beier 2007). In this paper, we are not concerned with network-level measures, but with the patch-to-patch probabilities by which an individual leaving one patch will next encounter another patch. As far as we are aware, there is no general way to assess how the size and location of patches in a network will affect such probabilities (but see Ovaskainen 2008). That is, there is no easy way to account for the competition and shadowing among patches shown in Fig. 1. As a result, these effects are usually ignored.

Beyond the effects of the spatial location of patches, it is increasingly being recognized that most animals can adapt their space use patterns based on previous experiences at particular patches (e.g., Fagan et al. 2013; Merkle et al. 2014). Thus, to model movement in a network of patches we should also consider the potential importance of previous visits to a patch as a factor affecting the probability of its use in the future. Here we present a statistical framework aimed at taking into account the effect of the spatial structure of a patch network on how animals move from patch to patch. We follow the approach used by Ovaskainen and Cornell (2003) for the derivation of the formula for diffusion in highly fragmented landscapes but replace some of their analytic results with general statistical (i.e., not derived from theory) functions whose parameters can be estimated from data. Our approach includes diffusion as a special case at a particular parameter limit. We also derive functions to model time spent in the non-habitat matrix and to account for the effect of memory on the patch-to-patch movement decisions.

2. MODELING FRAMEWORK

2.1. ASSUMPTIONS

Our approach depends on the following assumptions:

- The animals are moving in a network which consists of a finite number n of disjoint circular habitat patches surrounded by a non-habitat matrix. Patches are characterized by their radius r_i (i in $1, \dots, n$) and possibly other attributes such as resource abundance. The centroid-to-centroid distance between patches i and j is denoted by

$d_{i,j}$. The network of patches forms a “highly fragmented landscape” in the sense that each patch is much smaller than the distances between patches, that is $r_i \ll d_{i,j} \forall i, j$ (Ovaskainen and Hanski 2004).

- We assume that the animals spend a variable amount of time within a patch before they decide to leave it. This can be a function of habitat quality, patch size or any other attributes of the patch such as resource abundance, predation risk, density of conspecifics. In contrast to Ovaskainen and Cornell (2003), we do not explicitly model movement inside the patches, and for this manuscript, we will not consider time spent within patches. Extending our models to include time in patch is straightforward for the cases in which it does not affect the probability of going from one patch to another nor the time taken to do so.
- Given that an individual has decided to leave patch i , it will go next to patch j with probability $P_{i,j}$ and it will spend on average a total of $G_{i|j}$ time in the non-habitat matrix as it goes from patch i to patch j . The quantity $G_{i|j}$ is conditional on the animal reaching patch j before it visits any other patch, dies or emigrates from the patch network.
- Once an individual has left a patch, it can either go to another patch, die or leave the patch network. That is, we set $P_{i,i} = 0$ as we do not consider the possibility of the animal returning to the same patch it left once it got into the non-habitat matrix.
- Mortality occurs mainly in the non-habitat matrix and is taken into account, together with the possibility of the animal leaving the patch network, by the fact that $\sum_{j \neq i} P_{i,j} < 1$. In cases where no mortality or emigration occurs during the duration of the study (e.g., GPS tracking of long-lived animals), we can normalize P so that $\sum_{j \neq i} P_{i,j} = 1$.

These assumptions may sound overly restrictive, but they contain enough realism to capture the main problem that we want to address. Also, they apply to many ecological situations such as movement within a metapopulation, foraging in patchy environments and general connectivity in a habitat patch network. An important limitation though is that we are so far ignoring the possible effects of habitat heterogeneity in the non-habitat matrix. For a comparison of diffusion results between a realistic description of a landscape and its approximation based on circular patches, see Zheng et al. (2009).

2.2. DERIVATION OF PATCH-TO-PATCH PROBABILITIES AND TIME SPENT IN THE NON-HABITAT MATRIX

We start by considering a matrix \mathbf{H} holding the probabilities $H_{i,j}$ by which an animal that is currently at the location of patch i would ever (before dying or emigrating) move to patch j , assuming that the animal ignores any other patches in the network. That is, assuming that the animal moves as if the landscape consisted of only the non-habitat matrix and patch j . The elements of \mathbf{H} are a function of the distance between patches $d_{i,j}$, but can also depend on other attributes such as patch size (A), quality ($H_{i,j} = f(d_{i,j}, A_j, \dots)$). As we define the probabilities $H_{i,j}$ for the hypothetical case where no other patches than j would be present,

they do not depend on the locations or the size of those other patches. In essence, H depends on how the animal moves while in the non-habitat matrix. For some types of movement, it will be possible to obtain solutions for these probabilities. Ovaskainen and Cornell (2003, equation 4.1) showed that if movement is modeled as a simple diffusion, then

$$H_{i,j} = \frac{K_o(\alpha_m [r_j + d_{i,j}])}{K_o(\alpha_m r_j)} \quad (1)$$

where K_o is the modified Bessel function of second kind and zero order, r_j is the radius of the destination patch, and $d_{i,j}$ is the distance from the starting point i to the centroid of patch j . The constant α_m is equal to $\sqrt{\frac{c_m}{a_m}}$, with c_m and a_m being mortality and diffusion rate in the non-habitat matrix, respectively.

From \mathbf{H} , we want to obtain the probabilities $P_{i,j}$ of visiting next patch j given that the individual has just left patch i . If we assume that $P_{i,j}$ depends only on the animal just leaving patch i but not on the full history of previous movements, we can write $H_{i,j}$ as a combination of these $P_{i,j}$ (Ovaskainen and Cornell 2003):

$$H_{i,j} = P_{i,j} + \sum_{k \neq i \text{ or } j}^n P_{i,k} H_{k,j} \quad (2)$$

where the summation is over all patches different than i or j . As we condition on actually emigrating from a patch, we set $H_{i,j} = 0$ for all $i = j$. For example, if the network is comprised of just three patches, an individual leaving from patch 1 can eventually reach patch 2 by either going directly there ($P_{1,2}$), or going first to patch 3 and eventually going from patch 3 to patch 2 ($P_{1,3}H_{3,2}$). From Eq. (2), we can use a linear solver to obtain these probabilities of *going next* to a particular patch. These quantities can then be connected to movement or capture–recapture data. For the cases where individuals can die or leave the patch network during the course of the study period, we can set the probability of an animal dying or emigrating from the network given that it has just left patch i as $1 - \sum_{k \neq i} P_{i,k}$. For example, for a three-patch network, we have:

$$\begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & H_{3,2} & 0 & 0 & 0 & 0 & 0 \\ 0 & H_{2,3} & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & H_{3,1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & H_{1,3} & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & H_{2,1} \\ 0 & 0 & 0 & 0 & 0 & 0 & H_{1,2} & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \times \begin{bmatrix} P_{1,1} \\ P_{1,2} \\ P_{1,3} \\ P_{2,1} \\ P_{2,2} \\ P_{2,3} \\ P_{3,1} \\ P_{3,2} \\ P_{3,3} \end{bmatrix} = \begin{bmatrix} 0 \\ H_{1,2} \\ H_{1,3} \\ H_{2,1} \\ 0 \\ H_{2,3} \\ H_{3,1} \\ H_{3,2} \\ 0 \end{bmatrix}$$

Given the eventual movement probabilities $H_{i,j}$, we can use this equation to solve the probabilities $P_{i,j}$ by which the animal goes next to a particular patch. These probabilities are used in the likelihood function as detailed in *Parameter estimation* section below.

We also want to consider the time spent in the non-habitat matrix while going from one patch to another. To do so, we first consider a landscape consisting of patch j only, and define

$U_{i,j}$, the expected time the animal spends in the matrix when moving to patch j given that the animal started moving at location i and will eventually reach patch j . For an animal moving in a patch network, we define $G_{i|j}$ as the mean time spent in the non-habitat matrix given that the animal moves from patch i to j before dying or hitting any other patch. We can decompose the product between the probability of the animal moving eventually from patch i to j and the expected time the animal spends in the non-habitat matrix during this movement as follows:

$$H_{i,j}U_{i,j} = P_{i,j}G_{i|j} + \sum_{k \neq i \text{ or } j} P_{i,k}H_{k,j} (G_{i|k} + U_{k,j}). \quad (3)$$

Again, if the network is comprised of just three patches, an individual leaving from patch 1 can eventually reach patch 2 by either going directly there ($P_{1,2}$) and spending $G_{1|2}$ time in the non-habitat matrix, or going first to patch 3 and eventually from patch 3 to patch 2. This happens with probability $P_{1,3}H_{3,2}$, and the expected time for it is $G_{1|3} + U_{3,2}$. To solve for the expected travel times between patches, we first solve for all the $P_{i,j}$ using a linear solver on Eq. (2) as before. Then, we arrange them in a vector \mathbf{p} and set $\mathbf{H}[\mathbf{p} \circ \mathbf{g}] = \mathbf{h} \circ \mathbf{u} - \mathbf{U}\mathbf{p}$ (where \circ is the Hadamard product, the element-by-element product of vectors) and solve for the product $\mathbf{p} \circ \mathbf{g}$ from where we can obtain \mathbf{g} , a vector with all the $G_{i|j}$.

2.3. GENERAL FUNCTIONS FOR \mathbf{H} AND \mathbf{U}

The main idea behind the work we present here is that Eq. (1), which was derived analytically for the case of diffusion, can be replaced with other functions in order to capture “statistically” the properties of other types of movement. For example, more flexible dependencies on distance and patch size can be taken into account by setting

$$H_{i,j} = \frac{K_o ([a_1 r_j]^{q_1} + [a_2 d_{i,j}]^{q_2})}{K_o ([a_1 r_j]^{q_1})} \quad (4)$$

where a_1 and a_2 can be considered scale parameters and q_1 and q_2 control the shape of the curve (all these parameters have to be > 0). The flexibility of Eq. (4) is illustrated in Fig. 2a showing how q_1 and q_2 control the shape of the decay of the probability of hitting a patch as a function of the distance to it. The case of simple diffusion is recovered when both parameters are set equal to 1, and $a_1 = a_2$. We want to emphasize that Eq. (4) has no theoretical foundation and that other functional forms could be employed based on theoretical or practical considerations.

For the time traveling from patch to patch, we set $U_{i,j}$ as a power law of distance with rate being a linear function of the size of patch j :

$$U_{i,j} = (1 + b_1 r_j) (b_2 d_{i,j})^{q_3} \quad (5)$$

but some other function could be used as long as it ensures that expected travel times are always positive. For diffusion, $U_{i,j}$ does not have a closed-form general solution, but numerical results suggest that it increases linearly with $d_{i,j}$ for moderate to large distances (see examples in the first column of Fig. 4).

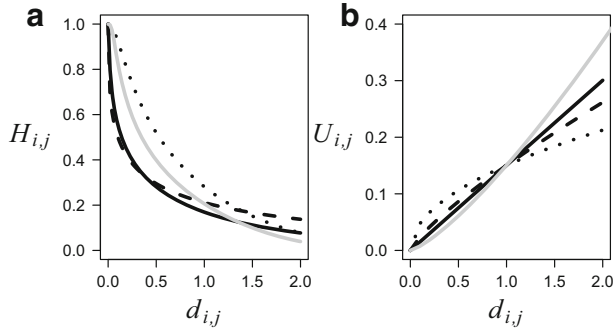


Figure 2. Examples of changes in probability of reaching a patch (a) and time taken to reach it (b) as a function of distance to it. In all cases, the diameter of the target patch is 0.01 units and $a_1 = a_2 = 0.5$, $b_1 = 0.2$, and $b_2 = 0.15$. Solid black line corresponds to a_2 and q_2 equal to 1, and $q_3 = 1$. Dashed line for q_2 and $q_3 = 0.5$, and $q_3 = 0.8$, dotted line $q_2 = 2$ and $q_3 = 0.5$, and gray line to $q_1 = 2$, $q_2 = 3$, and $q_3 = 1.3$.

2.4. THE EFFECT OF MEMORY IN PATCH CHOICE

So far we have considered cases where $P_{i,j}$ does not depend on what the individual experienced before. In fact, that is why the expression in Eq. (2) above is valid. However, most animals are capable of using their past experiences to adapt their patterns of space use (e.g., Fagan et al. 2013; Merkle et al. 2014). We can modify the probability of going to a patch based on the visiting history by adding weights to all the $P_{i,j}$ once we have solved for them. For example, we could have

$$w_j = \exp(\alpha n_j) \quad (6)$$

where n_j is the number of previous visits to patch j , and α is a parameter controlling the effect of previous visits. If $\alpha > 0$, those patches visited before will have more weight and will be more likely to be visited next, but if $\alpha < 0$, the animal will avoid previously visited patches. Another option would be to set $w_j = \exp(\alpha o_j)$, where o_j is an indicator of whether patch j was visited or not in the past (thus ignoring the total number of visits). Any other formulation could be used as long as the resulting weights are non-negative numbers. To obtain the patch-to-patch transition probabilities conditioned on the weights (Z), we may define, for example, $Z_{i,j} = a_i w_j P_{i,j}$, where $a_i = 1/(\sum_j w_j P_{i,j})$ is a scaling constant to normalize the total probability to one. In this case, the relative probability (compared to the case without considering history) of moving from i to j instead of moving from i to k would be w_j/w_k .

2.5. PARAMETER ESTIMATION

We consider the case where available data consist of sequences of the identities of the visited patches (\mathbf{z}) and sequences of the times spent in the non-habitat matrix while going from one patch to another (\mathbf{m}). These sequences run from $\tau = 1, \dots, T$. The identity of the τ -th patch visited is held in z_τ , and the time spent while going from z_τ to $z_{\tau+1}$ is held in $m_{\tau+1}$. Under some conditions as in the simulation study presented below, it is possible that

an animal “goes missing” because it either dies or it leaves the patch network. For a network of n patches, the event of an animal going missing is recorded as if the animal went to “patch” $n + 1$. The first and last patch visited by an individual are not associated with time spent in the non-habitat matrix. The joint probability of $y_{\tau+1} = [z_{\tau+1}, m_{\tau+1}]$ is given by the product of a multinomial and a gamma distribution: $MN(\mathbf{P}[z_{\tau}, z_{\tau+1}]) \Gamma(s, s/\mathbf{G}[z_{\tau}, z_{\tau+1}])$. The gamma distribution is used to allow variability in time spent in the non-habitat matrix.

The values of all $P_{i,j}$ and $G_{i|j}$ are obtained by solving Eqs. (2) and (3) as explained above, parameterized according to Eqs. (4) and (5), and including Eq. (6) in the case where memory effects are considered. Thus, we aim to estimate parameters a_1 , a_2 , q_1 and q_2 in Eq. (4) that control how patch radii and the distance among patches affect movement probabilities. Parameters b_1 , b_2 , q_3 in Eq. (5) are estimated to obtain the expected time spent in the non-habitat matrix via Eq. (3). The shape parameter for the gamma distribution (s) is a free parameter that is also estimated. When memory effects are included, we also estimate the parameter α in Eq. (6) that controls how the number of previous visits to patches affects movement probabilities.

We fitted our models to animal trajectory data on a patch network in the Bayesian framework, using adaptive Metropolis–Hastings MCMC (Brooks et al. 2011) to sample the posterior distribution. The dimension of the matrix \mathbf{H} grows with the square of the number of patches and contains a lot of zeros. To better handle these matrices, we used the sparse matrix tools from the `Matrix` package (Bates and Maechler 2010). For a particular combination of parameters, the following steps are performed to obtain the likelihood. First, Eqs. (4) and (5) are computed based on patch radii and the distance among patch centroids. With these values, the sparse matrices \mathbf{H} and $\mathbf{H} \circ \mathbf{U}$ are built. The function `solve` from the `Matrix` package was used to obtain the patch-to-patch movement probabilities ($P_{i,j}$) and the expected time spent going from one patch to another one ($G_{i|j}$). A check is made to ensure that no $P_{i,j} < 0$ and that row sums of P are ≤ 1 . Depending on whether we allow for animals to leave the patch network (emigrating or dying), the patch-to-patch transition probability matrix will have an extra column where for each row i , we compute $1 - \sum_{j=1}^n P_{i,j}$. For the case of long-lived animals tracked with GPS, it is possible to exclude the possibility of individuals dying or leaving the patch network, and hence, we set $P_{i,j} = P_{i,j} / \sum_{k=1}^n P_{i,k}$. If the effect of memory is considered, this transition probability matrix is then updated based on weights, which are a function of previous visits to patches, to obtain a \mathbf{Z} matrix as detailed above.

For the MCMC algorithm, we initiated three chains at random parameter combinations (sampled from their priors). Parameters were updated one at a time using normal proposal distributions whose variance was updated every 50 iterations in order to achieve about 23% acceptance rate. Following this first adaptive phase, parameters were updated together using a multivariate normal with covariance calculated from the most recent half of the previous iterations. After this second adaptive phase was concluded, the chains were updated using a multivariate normal proposal distribution with the covariance fixed to the value estimated from the second phase. Convergence of the chains was assessed using Gelman and Rubin’s diagnostics (Gelman and Rubin 1992) as implemented in the `Coda` package (Plummer et al. 2006).

3. SIMULATION EXPERIMENT

We performed a simulation study to test the capacity our approach to recover general properties of movement (Eq. 4) regardless of the particular patch network where data were collected. The simulation illustrates the case of individuals moving in the non-habitat matrix following correlated random walks (CRW) subject to mortality risk, and movement not affected by memory.

3.1. SETUP

We simulated patch networks consisting of circular patches (with radii sampled from a uniform distribution with minimum of 0.0002 and a maximum of 0.25) where patches were placed randomly in space but constrained to be within a 10 by 10 square, and at least 1 unit apart from the edge of other patches (i.e., at least twice as the maximum patch diameter). We run simulations on 100 replicated patch networks of 10, 30 and 50 patches.

For each patch network, we simulated the movement of 30 individuals which each started at the edge of a randomly chosen patch and followed a correlated random walk with initial movement direction orthogonal to the edge of the patch. Step length was sampled from a Weibull distribution with shape = 2 and scale = 0.1 (mean = 0.089). Turning angles followed a von Mises distribution with mean 0 and concentration parameter κ set to represent different degrees of directional persistence 0 (no persistence), 5 (moderate persistence) and 50 (high persistence).

Movement speed was set to 0.1 time units per distance unit. Whenever a simulated animal got to a distance ≤ 0.01 from the edge of a patch different from the most recently visited one, it moved there. That is, we assume that once an animal leaves a patch, it does not want to return to it immediately. Time spent within a patch was drawn from an exponential distribution with a mean of 10 time units. This was done for completeness, but here we concentrate on how animals move from patch to patch and we do not consider time spent in patches when analyzing the simulated data.

When a simulated animal left a patch, a random point of exit from the perimeter of the patch was chosen and the animal resumed moving within the non-habitat matrix with initial direction orthogonal to the edge of the patch. Movement stopped once the animal died, which occurred with probability of 0.00001 per move. From the realized movement trajectory, we obtained a time series with the sequence of the identities of the visited patches and a sequence of times moving between patches. With these data, we fitted Eqs. (4) and (5) using MCMC as described in *Parameter estimation* above.

To contrast the results of the approach proposed here with one where the effects of the spatial configuration of the patch network are not taken into account, we fitted a model where the probability of going from patch i to patch j depended only on the distance between patches and on the size of the target patch. For this, we just set $P_{i,j} = H_{i,j}$, where $H_{i,j}$ was calculated from Eq. (4) and where we set $H_{i,i} = 0$. We also contrasted the proposed general formulation with the original one obtained for simple diffusion (results for this latter case are reported in Appendix A).

To compare the estimates of Eq. (4) obtained from the observed movements in the patch networks with the probability of reaching a patch when there are no competing patches, we simulated 10,000 random walkers that started moving at increasing distances from a single patch of radius = 0.1. We used the same CRW parameters and mortality rate as in the previous section, and we recorded the frequency of successful patch arrivals at different starting distances and different degrees of directional persistence (governed by parameter κ). We consider that our approach is successful if Eqs. (4) and (5) fitted to the patch-to-patch movement data are able to capture the patterns of probabilities of reaching a patch, and the expected time to do so, obtained from these CRW simulations. The R code used for simulations and for data analysis can be found in supplement 1.

3.2. RESULTS

Applying the proposed method to simulated data showed that it is possible to recover general movement properties from patch-to-patch movement data even though transition probabilities among patches depend on the particular spatial configuration of the network studied (solid lines in Fig. 3). In contrast, ignoring the effect of the spatial configuration of the patch network (dashed lines in Fig. 3) resulted in overestimation at short distances and underestimations at larger ones. Furthermore, when the spatial configuration of the network was not taken into account, estimates changed visibly when data came from different patch networks (compare dashed lines in the top panels of Fig. 3 which correspond to replicated patch networks of 10 patches, with those of the bottom ones corresponding to networks of 50 patches). As expected, using the equations for simple diffusion from Ovaskainen and Cornell worked well when there was no directional persistence in the CRW, but this model underpredicted transition probabilities for $\kappa > 0$ (results are shown in figure A.1 in Appendix A).

Our method was also capable of recovering the general pattern of increase in travel time in the matrix with distance to a patch (solid lines in Fig. 4). Again, ignoring the effect of the spatial configuration of the patch network resulted in poor and more variable estimates (dashed lines in Fig. 4).

4. CASE STUDY OF SHEEP MOVEMENT

To showcase the application of the methods presented here, we apply them to data from six Merino sheep from Patagonia. The sheep data illustrate the application of our approach where there is no mortality or emigration, and where past experiences are suspected of playing an important role in patch use. The R code used for data analysis can be found in supplement 1.

4.1. SHEEP DATA

Sheep movement data were collected at Fortín Chacabuco Ranch (~40°58'S, 71°08'W) located in Los Lagos department and belonging to the pre-mountain range ecological area

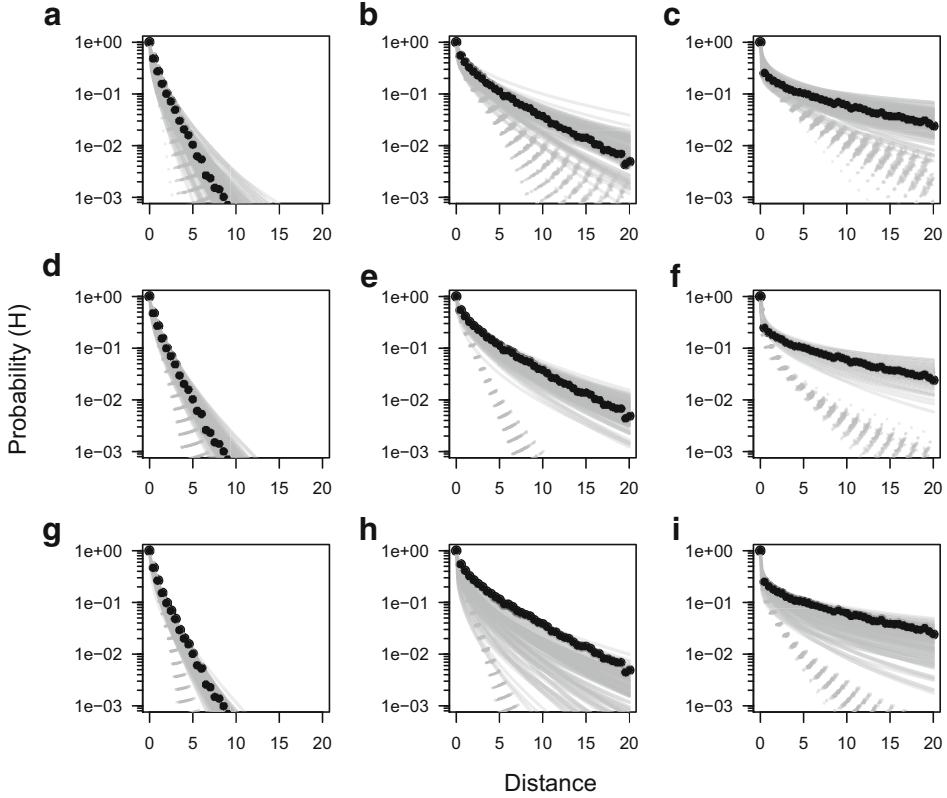


Figure 3. Estimated decay with distance in the probability of finding a patch ($H_{i,j}$) for individuals performing a CRW in the matrix. Our approach (*solid gray lines*) captures the general shape of the decay much better than one ignoring the effects of the spatial configuration of the patch network (*dashed lines*). *Black dots* show the true function $H(d)$ estimated from the frequency of successful arrivals of 10,000 simulated random walkers that started at increasing distances from a patch of 0.1 units in diameter. From *left to right*, *panels* show results for increasing directional persistence ($\kappa = 0, 5$ and 50 respectively). From *top to bottom*, *panels* show results from patch networks of 10, 30 and 50 patches.

of the Argentinean Patagonia (Cabrera 1976). The landscape is characterized by mountain chains and hills, crossed by several rivers and water streams. The weather is cold, with mean annual temperatures of $10\text{ }^{\circ}\text{C}$ and annual precipitations that range from 300 to 700 mm, concentrated during the cold season (May–August). Vegetation corresponds to the Sub-Andean district (León et al. 1998), composed by grasslands (dominated by *Pappostipa speciosa* in lower lands and by *Festuca pallescens* in upper lands), and mallines of different extensions. The farm covers approximately 4300 ha and consists of several paddocks of different sizes ranging from 4 ha to up to 1000 ha.

For this example, we used data from 6 Merino ewes equipped with GPS collars (CatLog-B, Perthold Engineering, link, USA) programmed to register locations every 5 min, from January 26 to March 31, 2015. The total area of the paddock was 994 ha, and included 7 distinct seasonally flooded meadows, with areas of 16.46, 40.37, 2.38, 4.67, 10.74, 3.24, and 5.54 ha, respectively. These meadows, which are called “mallines” in Patagonia (mallín for singular) offer the highest quality forage, and it is important for management to understand

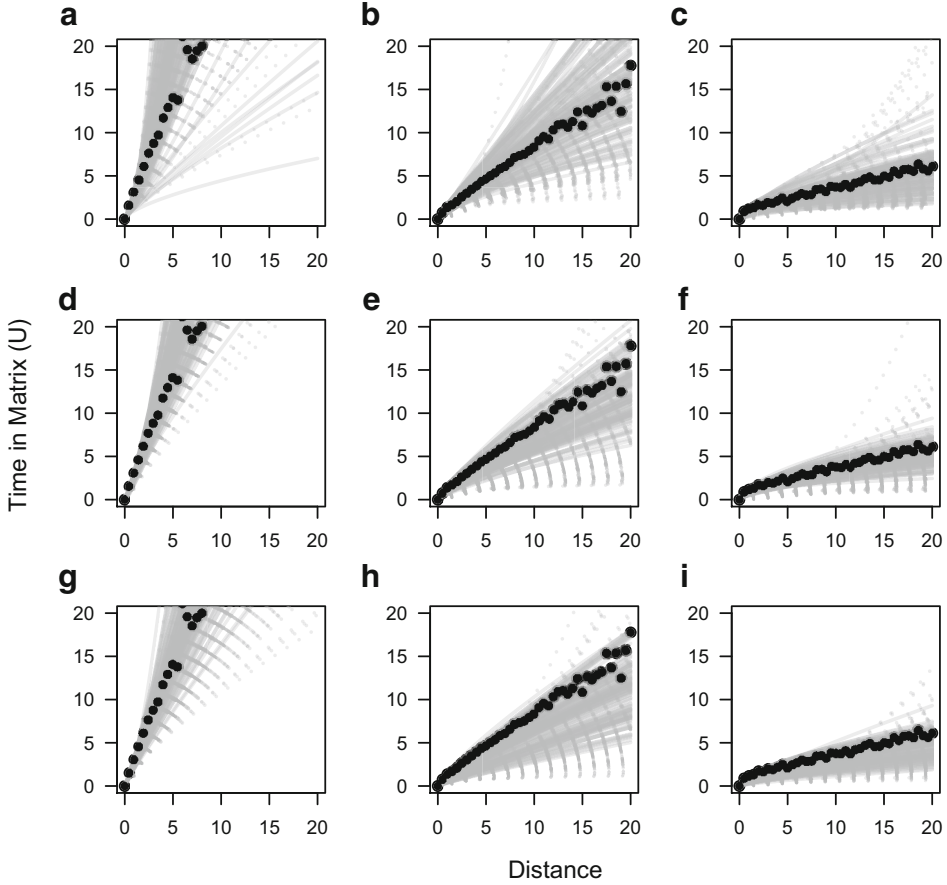


Figure 4. Average time in matrix needed to reach a patch ($U_{i,j}$) as a function of distance to it for animals performing CRW. Our approach (*solid gray lines*) captures the general increase with distance than one ignoring the effects of the spatial configuration of the patch network (*dashed lines*). *Black dots* show the true function $U(d)$ estimated from average time taken for successful arrivals of 10,000 simulated random walkers that started at increasing distances from a patch of 0.1 units in diameter. From *left to right*, panels show results for increasing directional persistence ($\kappa = 0, 5$ and 50 respectively). From *top to bottom*, panels show results from patch networks of 10, 30 and 50 patches.

how animals use these patches (diVirgilio and Morales 2016). The data correspond to a grazing period after weaning, and it was the first time that the flock used this particular paddock. That is, the area was unknown to them and we expect to see the effect of previous visits to patches to unfold over time (Fig. 5).

4.2. DATA PREPARATION

We constructed a shape file with polygons that contained each mallín and then projected them in UTM 19S. This file was converted into a spatial polygon data frame including a variable that contained the identity of each mallín, using the function `SpatialPolygonDataFrame` from the R package `sp` (Pebesma and Bivand 2005).

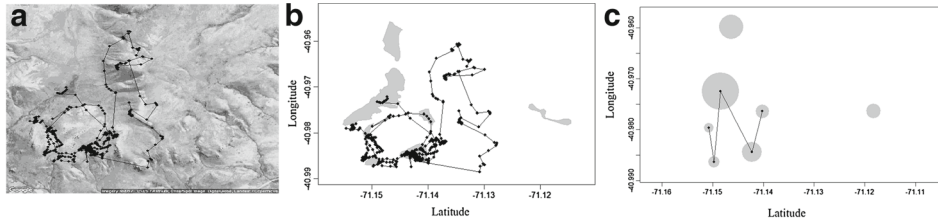


Figure 5. Examples of how a trajectory on a map was simplified to “patch-to-patch” movements. **a** Trajectory of an ewe recorded every 5 min for a week and overlaid on satellite image. **b** Same trajectory over a map where all mallines were identified, and the rest of the area is considered as “matrix.” Finally, **c** further simplification where the mallines are reduced to *circles* and the movement trajectory to transitions between habitat patches.

To consider the possibility that a point is outside patch boundaries due to GPS errors or movements around the edges, we generated a buffer of 5 meters around each patch using the function `gBuffer` from R package `rgeos` (Bivand and Rundel 2012). We projected the GPS in UTM 19S and then transformed it into a spatial points data frame that included the date and time in POSIX format for each location. This transformation was made using the function `SpatialPointsDataFrame` from the `sp` package. Then, we used the function `over` from the same package to determine which locations were included inside each patch and its buffer and which corresponded to displacements between patches. We then use the function `rle` to obtain the sequence of mallines visited for each individual each day. From that sequence, we extracted the initial and the final time of the points inside each visited mallín, and the initial and final time of time spent between mallines. We used the function `difftime` to account the time spent in each patch and the time moving from one patch to the other in minutes.

4.3. MODELS FOR SHEEP MOVEMENT AMONG PATCHES

For the sheep patch-to-patch movement data, we fitted three alternative models: (i) one where the probability of going from one patch to another was a function of distance between patches and the size of the target patch (using Eq. 4); (ii) one including distance and sizes of patches as in the previous one but also considering the number of previous visits to a patch (using Eq. 6 for weights), and (iii) one where the probabilities of going to a particular patch depended on distance, size, and the number of previous visits but where the effect of the spatial configuration of the network was taken into account using Eq. (2).

4.4. RESULTS

Sheep quickly adapted to the new paddock and established a pattern of use of mallines with a clear effect of previous visits in the transition probabilities among patches. The effect of the spatial configuration and the history of previous visits are summarized in Fig. 6 which shows, for day 45 (i.e., after animals had time to build a memory of the paddock), the probabilities that an ewe that is currently leaving mallín number 2 will go next to any of the other patches in the paddock. The spatial configuration of the network leaves the probability of most mallines almost unchanged, but it increases that of the second nearest one and

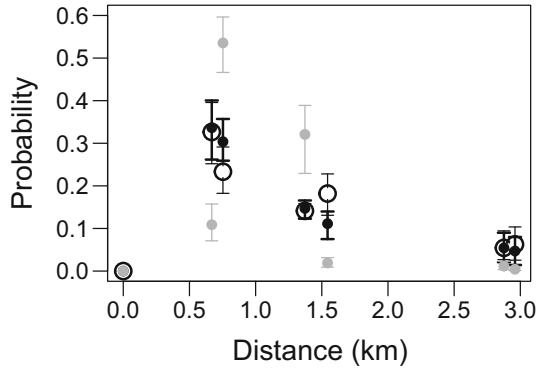


Figure 6. Example of changes in the probability of choosing a particular meadow when the spatial configuration of the patch network and the history of previous visits are considered. *Open symbols* show probabilities for six meadows based on their size and distance to current location for an ewe currently leaving meadow number 2. *Black circles* show how these probabilities change once the effect of the spatial configuration is taken into account, and the *gray circles* show how probabilities increase or decrease once the history of previous 50 visits is taken into account.

decreases the probability of the fourth (see difference between black and open circles). However, previous visits to patches result in substantial increases in the probabilities of a visit to the second and third nearest mallines in detriment of the probabilities of all other patches (gray dots in Fig. 6).

To further examine the consequences of different modeling options, we compared the frequency with which different models predicted the exact next patch (mallín) used by sheep in the time series of patch-to-patch movements. To validate the models with independent data, we calculated the average success rate of a model by fitting the model to all but one sheep and making predictions with the fitted model for the data corresponding to the sheep left out. We repeated this procedure for all six sheep and averaged the success rate across all sheep. The simplest model with only patch size and distance (no spatial effects nor memory) had a frequency of success of 20.76% (credible interval = 9.38, 32). The model with spatial effects but no memory had an average success rate very similar but better than that of the simplest model (21.11%, ci = 9.38, 32.69), and the full model increased this to 26.6 % (ci = 14.63, 40.38).

Even though there is considerable overlap between the ability of the models to predict the exact patch to be visited next, the estimates for parameter α are clearly positive (posterior mean = 0.63, ci = 0.54, 0.71), implying that previous visits to a meadow increase the probability of future visits to it. We can also check for the effect of memory on patch-to-patch transition probabilities by looking at expected patterns of patch use in models with and without memory (Fig. 7). The model without memory resulted in sheep quickly visiting all available meadows in the paddock, which contrasted with the predictions from the model including the effect of previous visits and with what was observed in the data (Fig. 7).

5. DISCUSSION

We have presented a way to account for the effects of the spatial configuration of patches in models of space use where individuals alternate between spending time in a patch and

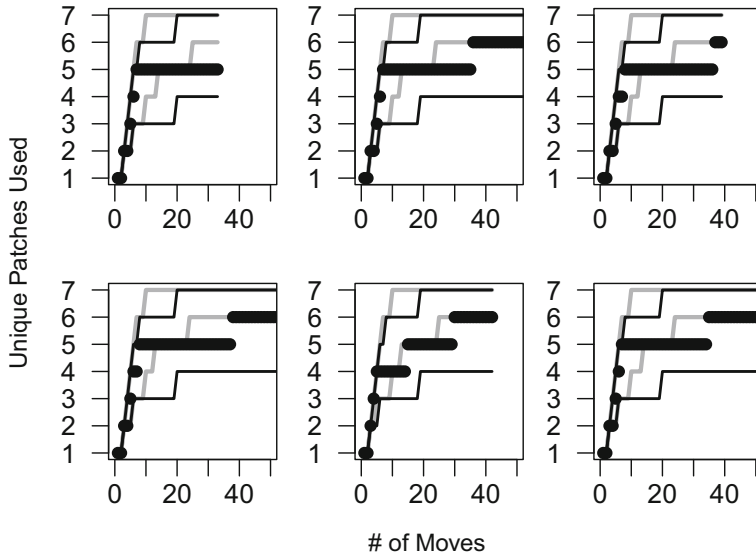


Figure 7. Mallin (patch) use by six ewes after being released in a new paddock. Dots show how each individual increased the number of patches used as they moved from patch to patch. Gray lines are the 95% credible intervals for a model without memory, and black lines for a model with memory. Each panel corresponds to one of the six ewes tracked.

moving to other patches in the network. The approach is based on the original derivation of [Ovaskainen and Cornell \(2003\)](#) for a diffusion model that considered all possible ways in which an individual leaving a particular patch can eventually reach another patch before dying or leaving the patch network (Eq. 2). Replacing the theoretical results of Ovaskainen and Cornell by other “appropriate” functions can provide generality and thus make their approach useful in contexts where diffusion is not a good approximation of movement. Furthermore, we provide ways to estimate time spent in the matrix when going from patch to patch and implement a method to incorporate the effect of the history of previous visits on future patch use.

The way we modeled the probability of eventually reaching a patch as a function of distance to it and its radius (Eq. 4) could be replaced by other functions. Also, one could use model selection techniques to decide, for example, whether it is justified to have different scalings for patch radius and distance (i.e., if $q_1 \neq q_2$).

The analysis of simulated movement in a network of habitat patches (Fig. 3) illustrates how the proposed approach is capable of recovering general properties of movement that are independent of the particular network of patches where data were collected. That is, we obtain a function describing how the size of a patch and the distance to it affect the probability of reaching such patch if it were the only patch in the landscape. This is important because it means that parameter estimates are much less contingent to the spatial properties of the landscape where the data were collected. In contrast, naive analyses where only distance and size of patches are taken into account severely underestimate the probabilities of reaching patches located far (dotted lines in Fig. 3). This result is similar to the findings of [Saura and Pascual-Hortal \(2007\)](#) regarding the importance of “stepping stones” when considering

landscape connectivity. Furthermore, estimates that do not consider the spatial configuration of the patch network are very sensitive to the particular data used (dashed lines in Fig. 3).

The expected time spent in the non-habitat matrix while going from one patch to another was also captured well by our approach (solid lines in Fig. 4)). The estimation of time in the matrix using a naive approach varied a lot between replicated data and in general, underestimated how time in the matrix grew with distance among patches (dashed lines in Fig. 4). In general, the matrix is considered risky for animals so that underestimating the expected time spent in it and how this is affected by the particular structure of a patch network could be quite relevant for metapopulation dynamics (Fahrig 2002; Hanski et al. 2006).

An important assumption for deriving Eq. (2) is that the effects of distance among patches override any potential effect of the point of exit from the patch (it does not matter where exactly the animal leaves a patch). This is the main reason why the approach is proposed for what Hanski (1998) has called “highly fragmented landscapes” where the distance among patches is much larger than the size of patches. However, the bias introduced when this assumption is not met might be much smaller than that obtained when the spatial configuration of the network is ignored (see, for example, figure A.2 in Appendix A).

For a practical application, the user must also consider whether it is safe to ignore the potential effects of habitat heterogeneity while the animals move between patches, and if animals are allowed to return to the patch they just left once they get into the non-habitat matrix. Furthermore, it is relevant to consider the computational issues that arise when a large number of patches is involved (the dimension of the \mathbf{H} matrix grows with the square of the number of patches). When dealing with landscapes with many patches (say several hundred or more), it might be more efficient to consider an approach based on simulating movement and to estimate parameters using approximate Bayesian computation (Grimm and Berger 2016; Fasiolo et al. 2016; Vaart et al. 2015). Furthermore, such simulation-based approaches could be used when the shapes of patches deviate substantially from approximately circular or when there is relevant heterogeneity in the matrix (e.g., Revilla and Wiegand 2008).

The analyses of the sheep data showed that for this particular dataset, there were little differences between a naive approach and ours (open dots vs solid black dots in Fig. 6), but they highlight the importance of including the history of previous visits in models of space use. Further refinements to this model could be made by considering the time spent since last visit to a patch. For example, we could set the weights in Eq. (6) to be negative just after a visit to a patch and then to increase with time to become positive. Besides how we formulate these models, it is quite likely that all of the animals that we are able to track exhibit some capacity to use previous experiences to improve their performance. Several modeling efforts have been aimed at representing how previous visits to a particular place affect the chances of future visits (e.g., Dalziel et al. 2008; Boyer and Walsh 2010; Merkle et al. 2014; Avgar et al. 2015; Riotte-Lambert et al. 2015). Our example here shows how these effects can be taken into account after considering the spatial configuration of the patch network.

Advances in tracking technology and remote sensing are allowing us to obtain increasingly detailed data on landscapes and the movement of a variety of organisms (Kays et al. 2015). While the techniques to deal with such detailed data to model movement are been

developed fast (e.g., [Hooten et al. 2017](#)), many spatiotemporal ecological processes can be conceptualized as involving the movement of animals within a network of patches. By considering such movements within a network of patches, we have proposed a way to deal with the effects of the spatial configuration of the network. In our approach, we also consider how past experience can modify the probabilities of going from one patch to another. We believe that being able to model such effects will contribute to a better understanding of the connection between landscape ecology, behavior and population dynamics ([Morales et al. 2010](#); [Matthiopoulos et al. 2015](#)).

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