

Fitting Probability Distributions to Animal Movement Trajectories: Using Artificial Neural Networks to Link Distance, Resources, and Memory

Benjamin D. Dalziel,^{1,*} Juan M. Morales,^{2,†} and John M. Fryxell^{1,‡}

1. University of Guelph, Guelph, Ontario N1G 2W1, Canada;
2. Laboratorio Ecotono, Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue, Quintral 1250 (8400) Bariloche, Argentina

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ABSTRACT: Animal movement paths are often thought of as a confluence of behavioral processes and landscape patterns. Yet it has proven difficult to develop frameworks for analyzing animal movement that can test these interactions. Here we describe a novel method for fitting movement models to data that can incorporate diverse aspects of landscapes and behavior. Using data from five elk (*Cervus canadensis*) reintroduced to central Ontario, we employed artificial neural networks to estimate movement probability kernels as functions of three landscape-behavioral processes. These consisted of measures of the animals' response to the physical spatial structure of the landscape, the spatial variability in resources, and memory of previously visited locations. The results support the view that animal movement results from interactions among elements of landscape structure and behavior, motivating context-dependent movement probabilities, rather than from successive realizations of static distributions, as some traditional models of movement and resource selection assume. Flexible, nonlinear models may thus prove useful in understanding the mechanisms controlling animal movement patterns.

Keywords: animal movement, *Cervus canadensis*, elk, model, random walk, resource selection.

* E-mail: ben.dalziel@gmail.com.

† E-mail: pajaron@gmail.com.

‡ E-mail: jfryxell@uoguelph.ca.

To survive and reproduce, animals must successfully cope with changes in the landscape over space and time. Movement is an important tool for confronting spatiotemporal variability (e.g., Fryxell et al. 2004). But how do patterns observed in the movements of animals correspond to the patterns we see in landscapes? For instance, the path of a fish swimming upstream in a river contains motifs from both the shape of the river and the fish's own trajectory within it. When we watch the movement path, it is difficult to tell which elements of its structure derive from the river and which derive from the fish. Similarly, in terrestrial animals, movement paths are often affected by the distribution of resources such as food and shelter, but trajectories also maintain an internal order resulting from physiological constraints governing the distance between successive locations and cognitive behaviors that translate landscape and trajectory structures into future movement decisions. Because movement is a key process affecting population and community dynamics (Tilman and Kareiva 1997; Turchin 1998; Cuddington and Yodzis 2000), exploring how structure is transmitted between elements of an ecosystem (e.g., between the river and the trajectory of the fish) may improve our understanding of ecology.

Yet it has proven challenging to decompose animal movement patterns into their motivating landscape and behavioral processes. Inspiring research from behavioral and landscape ecology has illuminated much, but the resulting hypotheses are rarely contrasted on common ground (Lima and Zollner 1996). We attempt to address this issue here by presenting a new framework for analyzing animal movement trajectories in a behavior-landscape context.

The framework has a couple of features. First, in order to create a common ground where disparate aspects of landscape structure and behavior can be considered, we use the concept of effective landscape structure (ELS). An ELS is defined here as a measure that expresses an interaction between an aspect of the state of the animal (e.g., its location or gut fullness) and an aspect of the structure

of the landscape (e.g., its spatial coordinates or the distribution of resources). A simple example of ELS is the Euclidean distance to each point on the landscape from the animal's current location. This is a function of the coordinates of the landscape, but it also changes with the location of the animal. By "landscape" we mean here the geographic region that, for the duration of the study period, includes the animal's home range and extends far enough from it so that the probability of the animal dispersing to the edge approaches 0.

The benefit of capturing landscape-behavior interactions using ELS is that its mathematical domain—the landscape—is the same regardless of what aspect of ELS is being considered. So, although the measures used to derive a particular ELS may be diverse, different ELSs may be readily combined in a model by superposing them. Movement predictions over these composite landscapes can then be phrased by mapping the elements of ELS to movement probability. The likelihood of such a model, given movement data, is then easily assessed by calculating the probability of each move in the data set, given the model.

The second feature of our approach is as follows. Traditionally, mapping landscape structure to movement probability would be done using parametric equations. This is problematic, since a fundamental framework for understanding animal movement that would allow the derivation of such equations from first principles has not yet fully emerged, although considerable progress has been made by Grünbaum (1999), Moorcroft and Lewis (2006), and others. We avoid this problem by using artificial neural networks (ANNs; Hecht-Nielsen 1990; Ripley 1994; Huse et al. 1999; Morales et al. 2005; Yu et al. 2006) to estimate ELS-based movement kernels. ANNs project vectors of inputs (the "input layer") onto a series of other vectors (the "hidden layer[s]") via nonlinear transformations. The last in the series of these vector layers represents the "output layer"—the variable whose relationship to the inputs is being investigated. A useful feature of ANNs is their mathematically proven capacity, under certain conditions, to reproduce arbitrary functions of input variables (Hecht-Nielsen 1990). The ability of ANNs to adopt arbitrary functional forms relieves the need to express hypotheses using equations specified a priori, while an ELS-based likelihood function improves the model-fitting algorithm's ability to efficiently explore parameter space, despite the diversity of the underlying landscape-behavioral mechanisms.

We explored our approach by applying it to movement data from five elk (*Cervus canadensis*) reintroduced to southern Ontario and fitted with tracking collars. This was combined with data from the Ontario Landcover Database, which uses Landsat Thematic Mapper data to classify the cover type of each 25-m² pixel of the landscape (fig. 1).

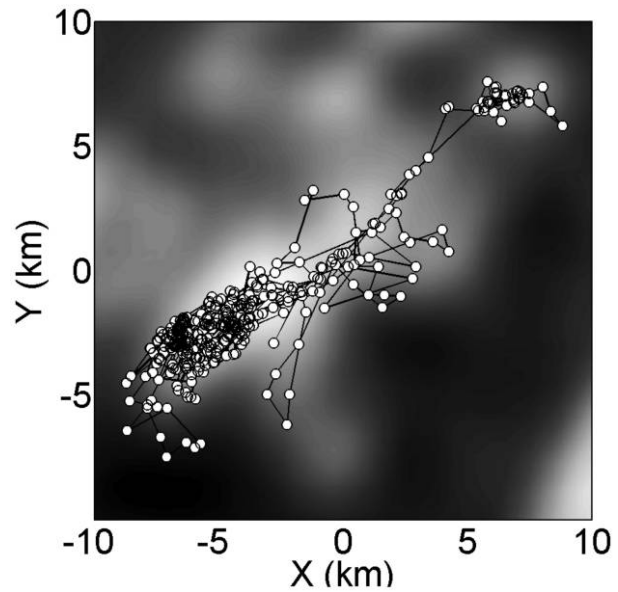


Figure 1: Daily satellite telemetry fixes for elk 721, released near Bancroft, Ontario, in 2003 as part of a provincewide reintroduction program. Mid-night fixes are represented by white circles, and successive fixes are connected with black lines. Background shading shows the results of resource structure analysis for this landscape using principal-components analysis (see app. A in the online edition of the *American Naturalist*).

Using these data, we applied the approach outlined above to examine the role of three landscape-behavioral variables in determining movement patterns: the distance to each point on the landscape from the animal's current location (hereafter "distance"); the spatial distribution of resources, estimated from the landcover data (hereafter "resources"); and memory of previously visited locations, estimated from the movement history of each animal (hereafter "memory"). We formed a suite of seven models consisting of combinations of these variables fitted these to the data and compared their likelihood and ability to predict novel observations. While these processes are often invoked to explain animal movement, they are seldom rigorously considered in combination and therefore represent a good context for exploring our approach.

Material and Methods

Models

We wished to estimate the probability of an elk moving to a given place on the landscape at a certain time. The predictor variables are the three elements of ELS we considered: distance, resources, and memory.

These variables were included in different combinations in each of a series of models. In specifying the models, we

followed a fully factorial design, so that each possible treatment combination (save the trivial one, where all variables are absent) was represented as a model. Some of the models represent traditional approaches to modeling animal movement that have seldom been compared using the same data, while others represent relatively new directions of inquiry.

The modeling took place on a lattice whose elements each had a spatial coordinate (x) and properties that could change over discrete time (t). Each point in the lattice was described by three functions, corresponding to the respective input variables. Let $d(x, t)$ be the Euclidean distance from the animal's location at time t to the point with coordinate x . Let $r(x, t)$ be the resource structure at location x and time t (in our analysis, resource structure did not change over time). Because memory, $m(x, t)$, was difficult to observe directly, we used information about the probability that an animal had previously visited a given location as a surrogate. We measured this using the minimum distance to x attained by the animal over a time window extending back from the present. Strong memory was characterized by low values of $m(x, t)$, indicating a high probability that the animal had previously visited that location within the specified window of time. Thus,

$$m(x, t) = \min_{\tau} d(x, \tau), \quad (1)$$

where $\tau = t - k, \dots, t$ and k determines the size of the memory window over which minimum distance is calculated. The structure of the model landscape as a whole can be described by the vector-valued function

$$\mathbf{s}(x, t) = \begin{bmatrix} d(x, t) \\ r(x, t) \\ m(x, t) \end{bmatrix}, \quad (2)$$

so that elements of $\mathbf{s}(x, t)$ represent layers of information about how the elements of ELS vary over space and time.

To link landscape structure to animal movement, imagine that \mathbf{s} affects the animal's trajectory via a movement kernel, $k(\mathbf{s})$, that maps landscape structure to displacement probability (for an example of movement models featuring displacement kernels, see Kot et al. 1996). Specifically, k is the probability density function that predicts the likelihood of the animal moving to a location with structure \mathbf{s} at time $t + 1$ (fig. 2). Although the domain of the displacement kernel is landscape structure, this structure depends on space and time, so we will sometimes write $k(x, t)$ to avoid clutter. If $x^*(t)$ represents the location of an animal moving over the landscape, we can then write $x^*(t + 1) \sim k(x, t)$. In other words, the location of the animal one unit of time in the future is distributed over the landscape according to the function $k(x, t)$.

To fit k to data, one must have a method of evaluating the goodness of fit. The likelihood of a certain displacement kernel, given an observed trajectory, is equal to the product of the displacement probabilities at each point in the trajectory,

$$L(k|x^*) = \prod_{t=1}^{T-1} k(x^*(t + 1), t), \quad (3)$$

where there are T points in the trajectory described by $x^*(t)$.

Artificial Neural Networks (ANNs)

We used ANNs trained with trajectory data to fit $k(x, t)$. The ANN had a three-layer feed-forward structure including an input layer with three nodes (to hold different treatment combinations of distance, resource structure, and memory) and a hidden layer with seven nodes. We found that using fewer hidden nodes prevented model convergence, while using more increased computing time and the danger of overfitting (results not shown). The output layer of the ANN had one node, corresponding to the displacement probability for a particular combination of inputs.

Information from the input layer was projected onto each node of the hidden layer as a weighted average of the elements of the input layer plus a constant. After transformation with a sigmoid function (eq. [5]), the hidden layer was projected to the output layer in a similar fashion and modified again with the sigmoid function. Thus, we approximated the probability of moving to a particular point on the landscape at a particular time in terms of its structure, $s(x, t)$, using

$$k(\mathbf{s}) \propto f(\mathbf{U}f(\mathbf{W}\mathbf{s} + \mathbf{b})), \quad (4)$$

where \mathbf{W} is a 7×3 matrix corresponding to the connection strengths between the nodes of the input layer and the nodes of the hidden layer, \mathbf{b} is a seven-element column vector that adjusts the relative strength of the contribution of each element of the hidden layer to the output layer, \mathbf{U} is a 1×7 matrix corresponding to the connection strengths between the nodes of the hidden layer and the nodes of the output layer, and f is the sigmoid function

$$f(z) = \frac{1}{1 + e^{-z}}, \quad (5)$$

which operates element-wise on the hidden and output layers. After it had been evaluated at each point on the landscape, $k(\mathbf{s})$ was multiplied by a constant so as to satisfy $\sum k(\mathbf{s}) = 1$, as required for probability density functions.

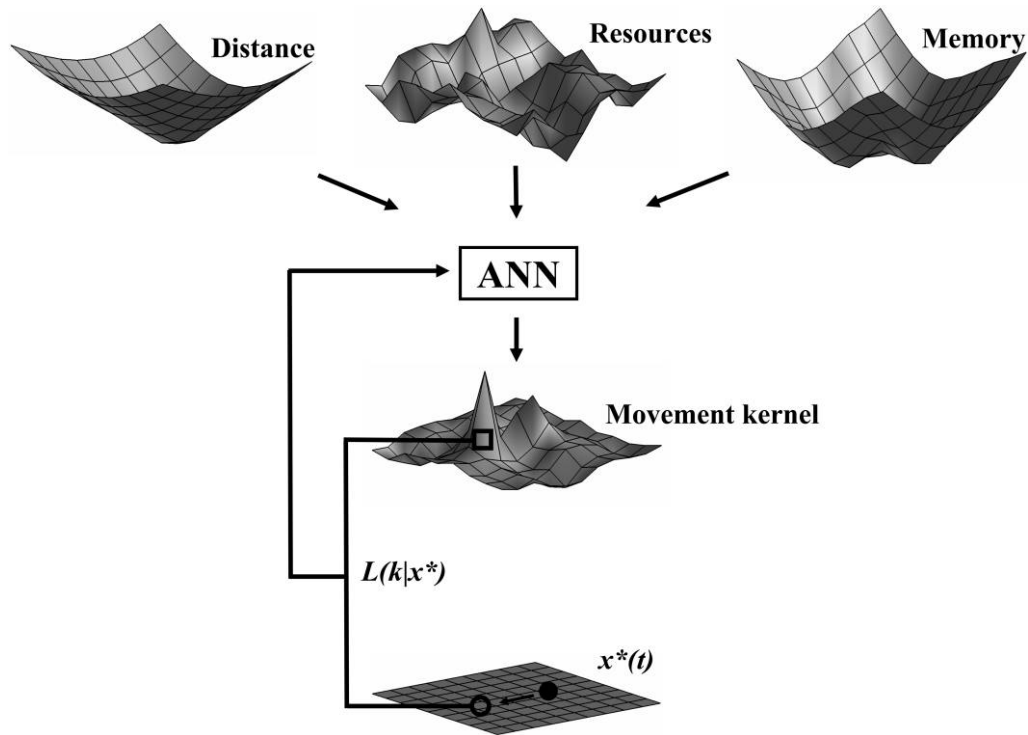


Figure 2: Combining elements of effective landscape structure (ELS) to form hypothetical movement kernels. The surfaces labeled “Distance,” “Resources,” and “Memory” represent three measures of ELS, mapping three types of landscape-behavior interaction into the spatial domain. These were combined at each time step, using an artificial neural network (ANN), to form a movement kernel estimating the probability density for the animal’s next location. The likelihood of these kernels was evaluated using their probability densities at 50 randomly chosen points in the observed trajectory $x^*(t)$. The solid marker in $x^*(t)$ is the animal’s current location, and the open marker is its location at time $t + 1$. The likelihood of this move, given the current displacement kernel, is fed back into the ANN, and the way the elements of ELS are combined is iteratively adjusted using a genetic algorithm.

The animal movement kernel for a given time is this probability density taken over the whole landscape.

The connection strengths for the ANN for each of the seven models—each model being a function of distance, resource, and/or memory information—were decided using a genetic algorithm (GA) that attempted to maximize the likelihood of a displacement kernel, using equation (3), given the inputs supplied to that kernel (see “Genetic Algorithm”). The likelihoods of the models were then compared.

Data

The elk we studied were transported in 2001 from Elk Island National Park, Alberta, to south-central Ontario as part of provincewide reintroduction program. Female elk were captured by helicopter net-gunning in January of 2003 and fitted with radio collars containing global positioning systems (GPSs) that recorded the location of the animal every 4 h for approximately a year, at which time

they dropped off automatically and could be retrieved by triangulating their radio beacons. From these data we selected five elk with enough fixes to fit and compare the models and extracted daily locations by using the fix closest to midnight.

The landscape through which the elk moved is dominated by mixed forest with areas of exposed bedrock. It is relatively flat, and the main topographical features are valleys because of the substantial network of rivers and lakes. This creates a gradient of moist low-lying areas, populated by coniferous species, and more arid highland deciduous communities. This is punctuated with agricultural areas, both abandoned and contemporary, and logged areas of variable size and age.

Landscape structure and the ensuing displacement kernels in the models were represented on a 10×10 grid. The amount of computing power required to run the GAs and ANNs made finer resolutions with more grid cells expensive in terms of computing time. Also, our primary interest was in mid- rather than fine-scale movement de-

cisions. The value of $d(x, t)$ was calculated as the Euclidean distance from the coordinates taken by the GPS collar to the center of each grid cell; $r(x, t)$ was calculated for each elk using data obtained from the Ontario Provincial Land-cover Database (see app. A in the online edition of the *American Naturalist*); $m(x, t)$ was calculated from $d(x, t)$ using equation (1), with a memory window that extended to the beginning of the data set.

When distance, resource structure, or memory did not appear in a model, we replaced the appropriate input node with 0s. This did not affect the fitting ability of the model, since ANNs with more than twice as many hidden nodes as inputs can fit any smooth function of those inputs exactly (Hecht-Nielsen 1990). All inputs were standardized to be between 0 and 1.

Genetic Algorithm (GA)

The algorithm we used to implement this analysis in Matlab is available in the online edition. For each elk, a population of 1,000 solutions, each representing a possible set of connection strengths for the ANN, was generated by drawing from a uniform distribution between -5 and 5 . Each individual solution in the population was assigned a fitness determined by the likelihood of the resulting displacement kernel, evaluated using equation (3), at 50 points randomly chosen from the elk's path. The first 100 fixes were excluded from this sample to allow observable long-term memory to accumulate. The population of solutions was then divided at random into groups of four. Within each group, the two individuals with the highest fitness combined elements of their respective solutions to form two offspring, who replaced the two individuals with the lowest fitness in that group. Each offspring then underwent a mutation event, where a random number, drawn from a normal distribution with a variance of 0.1 , was added to each of the weights and biases associated with a randomly chosen node in the ANN. The values for all weights and biases were constrained to be between -5 and 5 . We used this tournament style of selection coupled with a high mutation rate to increase the algorithm's power to explore parameter space by favoring diversity over selectivity (Ashlock 2005). This process was repeated for 100 generations. One can never guarantee that the best solution discovered using the GA is a global optimum: this is a universal drawback of the approach (Ashlock 2005). However, we defend the ability of the GA we used to explore parameter space with a speed and agility that makes the existence of better solutions unlikely.

Other methods exist for adapting the weights and biases of an ANN. For example, one can back-propagate differences between actual and desired outputs to create directional change in weight and bias vectors (Rumelhart et al.

1986). But these methods require a set of training data, and the desired output must be known. On the other hand, we were interested only in finding the best-fitting displacement kernel for each movement data set and had no prior expectations about the direction this exploration would take (Huse et al. 1999; Capi and Doya 2005; Morales et al. 2005).

Results

Each ANN model found a solution within about 30 iterations, which was not significantly improved on within the remaining generations (fig. 3). Each model thus displayed a characteristic likelihood ceiling. Comparing the ceilings across models at the hundredth generation allowed inference into which models offered better explanations of the data (table 1). Models having two- or three-way interactions among distance, resource structure, and memory typically had higher likelihoods than their single-input counterparts. For four of the five elk, the model with the highest likelihood featured all three variables, although this likelihood was often very close to the distance-memory model, which was also the model with the highest likelihood for elk 721. Among the single-input models, the distance and memory models were more likely choices than the resource-based model. Similarly, adding resource information to the other models usually resulted in a relatively small increase in likelihood.

ANNs with more than twice the number of hidden nodes as input nodes have the ability to fit any smooth function of the input variables exactly (Hecht-Nielsen 1990). Because each model had the same fitting ability, models competed solely on the basis of their input domains, and it is possible to compare models using raw likelihoods despite the fact that some models had more input information than others. This is in contrast to many wildlife ecology models that are fitted to data, where model complexity—resulting in improved fitting ability independent of biologically plausible mechanism—can affect the statistical likelihood of a model as much or more than the invoked biological mechanisms per se (Burnham and Anderson 1998).

To shed more light on the performance of the models, we assessed their predictive power by performing stochastic simulations. For each model, we ran 1,000 simulations of 50 moves each. During the simulations, the animals moved first according to the kernels fitted by one of the seven models and then to a random location within the selected grid cell. For each resulting path, we calculated a few "probes" designed to highlight various aspects of the trajectory, which could then be compared to similarly calculated probes on the data (e.g., Kendall et al. 1999). In other words, the probes represent statistical descriptors by

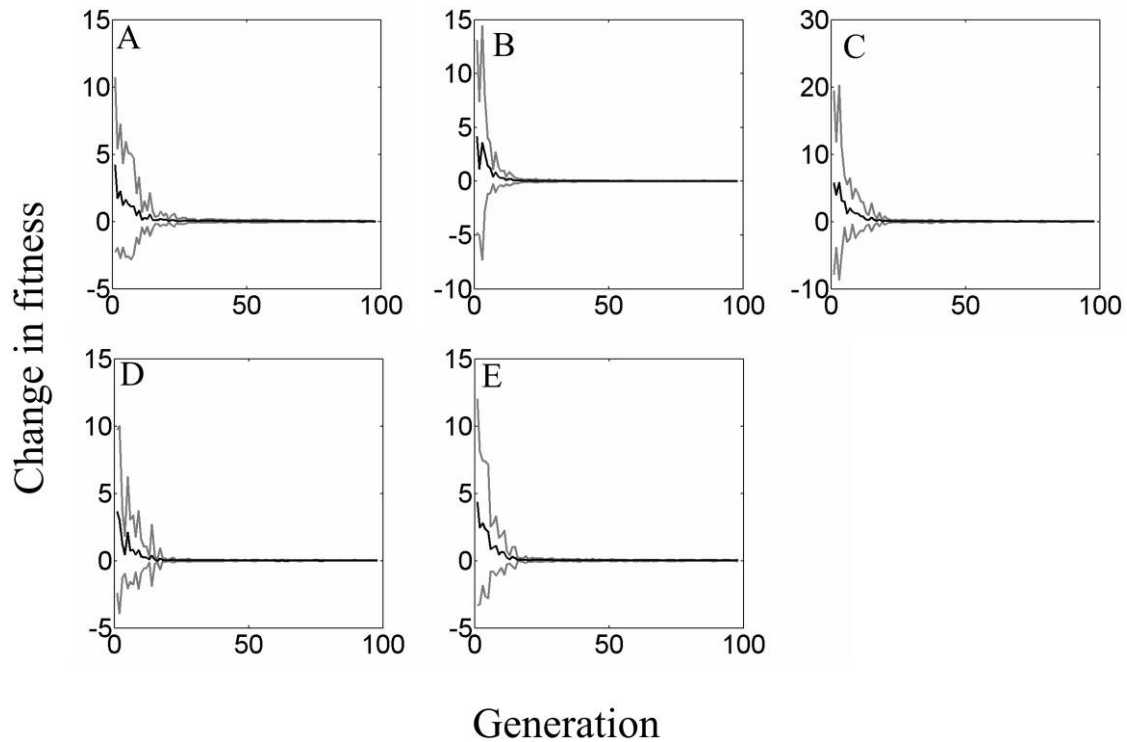


Figure 3: Change in fitness between successive generations averaged over the models. Each panel shows the results for a different elk: from A to E, elks 287, 480, 800, 520, and 721. The black line in each panel represents the average change in fitness over the models, while the enclosing gray lines show 95% confidence intervals.

which the data and model output can be contrasted, by assuming that models employing processes most similar to those that generated the data will also have the closest probe values. Each probe was oriented toward one of our measures of ELS. As a measure of the distance-based dynamics of the simulated paths, we extracted the distribution of daily displacements (starting with those greater than the grid resolution). To measure resource-related dynamics, the resource selection function (RSF) for each trajectory was calculated by logistic regression:

$$p(x^*(t) = x) = \frac{\exp[\beta_0 + \beta r(x)]}{1 + \exp[\beta_0 + \beta r(x)]}. \quad (6)$$

Finally, as a memory-based probe, we calculated the probability that, in a given step, the animal would return to a previously visited location. This statistic is similar to the return parameter described by Gautestad and Myrsetrud (2005) in their memory-based model. The distribution of probe values from the models was compared to the data using 1,000 bootstrapped samples of 50 locations each (fig. 4). The bootstrapping was done by random sampling with replacement from the entire trajectory data set for each

respective elk. Each of these 50-location samples was thus analogous to the training set used to fit the model. As an illustrative example, we calculated the movement kernels for two hypothetical situations (fig. 5).

Each of the univariate models predicted the data better when evaluated with its corresponding probe (e.g., the distance-based model predicted the distribution of dis-

Table 1: Negative log likelihoods for seven movement models and five elk

Model	480	721	520	800	287
m	115.54	137.50	127.71	76.47	89.46
r	217.84	187.01	209.79	217.75	166.49
rm	108.26	134.46	107.80	75.23	90.12
d	102.11	98.05	127.27	68.91	122.61
dm	83.75	86.49	112.78	55.46	85.99
dr	94.00	95.36	120.91	65.50	112.97
drm	82.59	88.19	103.23	53.97	85.36

Note: Numbers in bold represent the model with highest likelihood (least negative log likelihood) for each elk. d = distance, r = resource structure, m = memory. Thus, the drm model is the full model, including interactions between distance, resources, and memory, while model dr captures interactions between distance and resource structure in the absence of memory.

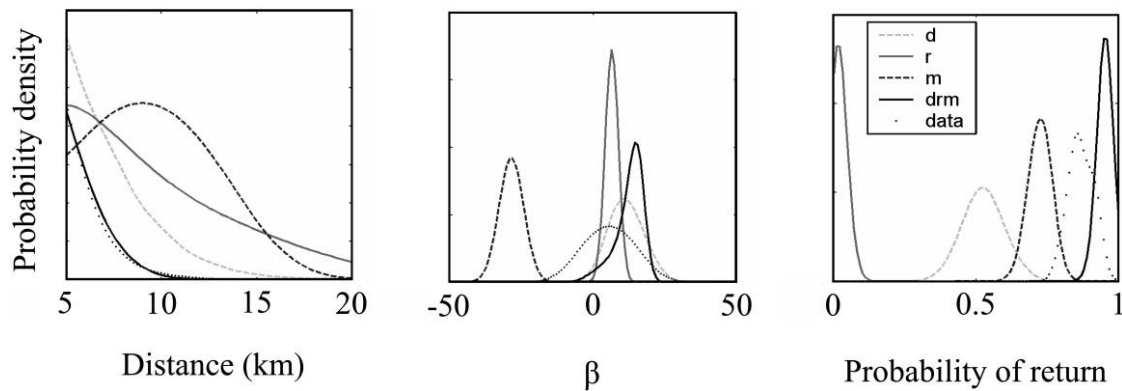


Figure 4: Distributions of three probes comparing four models of elk movement to new data for elk 480. The probes were (left to right) the distribution of the magnitude of daily displacements larger than the grid size, the slope coefficient for a resource selection function, and the probability that a given move returned the animal to a previously visited pixel. Probes were calculated on the actual movement data using 1,000 bootstrapped samples of 50 moves each and on 1,000 50-step simulations of the distance (d), resource (r), memory (m), and full-interaction (drm) models. The distributions were smoothed to make the figure easier to read.

placement distances better than the resource-based model, but vice versa for the RSF probe). However, the full model, featuring interactions between distance, resource structure, and memory (drm), performed well against the data with each respective probe, although sometimes the corresponding univariate model made more precise and accurate predictions.

Discussion

How do interactions between landscape properties and behavioral processes determine animal movement trajectories? This question is challenging, in part because it calls for diverse measures of landscapes and behavior. Another difficulty is the lack of a theoretical basis for marrying or contrasting diverse models. We attempted to confront these issues here by exploring a novel method of fitting models to animal movement data. We used artificial neural networks (ANNs) to estimate movement probability kernels that incorporated measures of three landscape-behavioral processes. These encompassed the structure of the landscape in physical space, the distribution of resources, and animals' memory of the landscape. These variables were measured using the concept of effective landscape structure (ELS): combining an aspect of the landscape with an aspect of the state of an animal moving over it, so that, while these measures incorporated behavior, their mathematical domain was always the landscape itself. We then used the ANNs to dynamically superpose multiple layers of ELS to form hypothetical behavioral-ecological landscapes that could be mapped directly to movement probability.

When multiple ELSs were included in a single model,

the fit usually improved, and sampling from the resulting probability distributions produced movement trajectories that matched new data according to diverse measures. In contrast, single-input models tended to fit only the data according to probes based on the same metric as the model itself. For example, when confronted with new data, the model including only resource information predicted correlations with resources well but failed to predict the velocities by which specific resource patches were visited (distance information) or the preference for previously visited patches (memory information).

It has long been acknowledged that most current movement models are profound simplifications, representing an attempt to trade realism in favor of tractability (Lima and Zollner 1996). Behavioral processes not explicitly included in a model are often represented as unexplained variability in the statistical distributions from which movement velocities are sampled (e.g., Turchin 1991). Comparing more detailed models with those that have been simplified by the addition of stochastic noise, accomplished here by selectively excluding variables from the input layer of the ANNs, might provide a way of examining the consequences of excluding various behavioral processes or landscape properties from movement models, allowing a data-driven approach to building parsimonious models based on multiple aspects of landscape-behavior interaction. In general, the increased fit and predictive power of the interaction models we tested suggest that dynamic movement kernels motivated by multiple landscape-behavioral contexts may prove useful in constructing more realistic models of animal movement.

The input variables we considered all have strong lineages in ecological hypotheses. We wish to review this

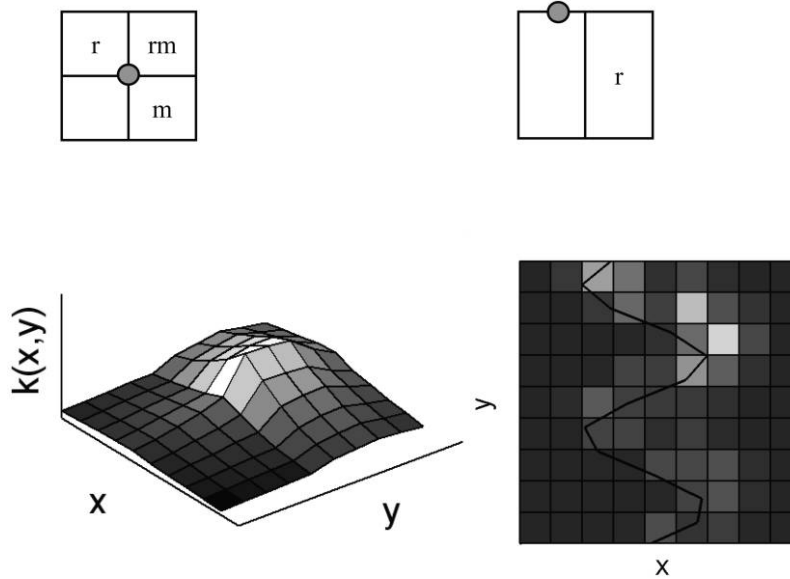


Figure 5: Movement kernels predicted by the full-interaction model for two hypothetical landscapes. On the left, the animal is at the center of a landscape divided into four quadrants. Clockwise from the upper left, these quadrants represent rich resources, rich resources and strong memory, strong memory, and neither rich resources nor strong memory. On the right is a landscape divided into resource-poor and resource-rich areas (left and right sides, respectively). The animal is at the top of the landscape, having followed the trajectory indicated by the curved line.

history briefly. The first input variable we considered, distance, is usually included in hypotheses via random-walk models (RWs). The RWs use movement data to estimate probability density functions for the velocities associated with successive animal displacements and then attempt to predict novel observations by sequentially sampling from these distributions (Turchin 1998). Distance, via the mechanisms of the RW, is present in a wide body of ecological theory because it is the microscopic basis for the diffusion processes implied by many spatial hypotheses (Okubo 2001). Distance is also important because it is a measure of the scale, defined by resolution and extent (Turner et al. 2001), at which movement and resource selection occur. Grazers, such as elk, can move differently at different spatiotemporal scales (Johnson et al. 2002; Ager et al. 2003; Morales et al. 2004) and achieve distributions that are correlated with the distribution of resources in a way that varies over short (diel; Ager et al. 2003) and long (seasonal; Ager et al. 2003; Boyce et al. 2003) times and over varying spatial extents (Boyce et al. 2003). Distance also determines the probability that an animal encounters a particular location (Dusenbery 1989). The spatial structure of the landscape also affects life histories indirectly since many movement strategies rely on the expected resource density in the landscape (possibly determined by which locations have been previously encountered) as a decision variable,

for example, in deciding when to leave a patch (Charnov 1976; Fryxell et al. 2004).

Resource structure, our second input variable, is often investigated using resource selection functions (RSFs). The RSFs calculate the correlation between the distribution of resources and the presence or absence of the animal within some bounded landscape (Manly et al. 2002). If the movement decisions that motivate the animal's distribution are made with complete knowledge of the whole landscape and infinite powers of movement, then the resulting RSF converges to the ideal free distribution, where fitness is maximized (Farnsworth and Beecham 1999). At the other extreme, with minute powers of movement and no knowledge of the landscape, the RSF will capture the results of resource selection only at very small scales, and, if the distribution of resources is stationary, the trajectory will more strongly resemble a RW (Farnsworth and Beecham 1999). There is a growing understanding that the correlations observed between animals and their resources are the results of complex behavioral decisions responding to stochastic landscapes (Stamps et al. 2005; Buskirk and Millsbaugh 2006). In these circumstances, the information gleaned from traditional RSFs can be difficult to interpret in a mechanistic way. But because of their ability to accurately predict animal distributions in specific landscapes (something many movement models cannot do), RSFs are

a valuable tool for wildlife conservation and management (Mladenoff et al. 1999).

Our final input variable, memory, is observed in a wide range of taxa, including birds (Hurly 1996), insects (Schatz et al. 1999), and mammals (Mendl et al. 1997; Janson 1998). Animals' powers of movement are often greater than their powers of perception (Skellam 1951), and relying on stored information about the landscape can aid in confronting spatiotemporal variation in resources (Benhamou 1994), provided that the metabolic and opportunity costs of relying on memory do not outweigh the fitness benefits (McNamara and Houston 1987; Dukas 1999; Dumont and Hill 2001). The physiological and behavioral mechanisms by which memory works are diverse (Mackney and Hughes 1995; Benhamou and Poucet 1996; Blum and Abbott 1996; Wilkie et al. 1996; Benhamou 1997; Hughes and Blight 1999; Bisch-Knaden and Wehner 2003; Collett et al. 2003; Thiele and Winter 2005), making it a ubiquitous but somewhat enigmatic variable in behavioral ecology.

Memory has been the subject of some fruitful theoretical research. Short-term memory is most commonly incorporated into movement models using correlated random walks, which are RWs that incorporate autocorrelation between the directions of successive displacements (Kareiva and Shigesada 1983; Turchin 1998). Long-term memory has also received some attention via RWs that exhibit long-term autocorrelation in position (Blackwell 1997; Tan et al. 2001, 2002; Gautestad and Mysterud 2005). The effects of the interactions between distance and short- or long-term autocorrelations in position on animal movement patterns are not well understood, except in the simplest cases (e.g., Patlak 1953), nor is there a mechanistic understanding of how these dynamics create emergent properties in animal movement paths, such as home range formation (Parrish and Edelstein-Keshet 1999).

Of the models we tested, both the single-input memory model and the full interaction model fitted the data well in terms of our memory-based probe (return probability). This probe was loosely based on the work of Gautestad and Mysterud (2005). The fact that one of the best-fitting models in terms of this probe included interactions with other variables emphasizes the fact that this memory-based measure of pattern may derive from processes other than memory. This supports the view that the statistical distributions associated with many single-input movement models should, at least initially, be seen as the results of animal movement and not the causes. The probability distributions associated with RWs or RSFs can be challenging to interpret as mechanistic models because vastly different behaviors can produce the same trajectories in a given landscape and because, conversely, the same behaviors can produce different movement paths in different landscapes.

Models that incorporate mixtures of RWs in response to landscape structure may be useful in bridging the gap between statistical mechanics and behavior (Morales et al. 2004).

The influence of resource structure in the models we tested provides another example of the sometimes ambiguous divide between statistical fit and ecological mechanism in movement models. Surprisingly, including resource structure in the models we tested provided relatively small increases in likelihood despite the importance of resource structure in determining the ecology of elk (Boyce et al. 2003). It is possible that the measure of resource structure we used (variation in landcover) was not sensitive to the resources that matter to elk. In this case, the relatively low importance of resource information in our models may be simply attributable to the fact that we measured the wrong variables. On the other hand, while landcover itself represents a relatively narrow measure of the myriad of important elk resources, including food, shelter, mates, decreased risk of predation, density of conspecifics, etc., variation in landcover is probably well correlated with variations in many of these resources. Since our measure of resource structure captured up to 61% of the total variation in the landscapes over which the elk moved, it seems likely that there is more occurring here than can be explained by the lack of measurement accuracy.

Another possible explanation for the relative unimportance of resource structure in our models is that patterns in resource structure are transmitted into animal movement paths indirectly, through other landscape and behavioral processes. For example, when resource information was included in the memory models, it may have had little effect because of a correlation with memory. Observations of spatial memory are necessarily correlated with resource selection, since foraging elk embed the resource structure of the landscape into their trajectory.

Using flexible, nonlinear models such as ANNs to estimate the shapes of movement kernels may prove useful in further study of the ways information is transmitted between a landscape and the trajectories of the animals that inhabit it.

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