Mechanisms of functional connectivity: the case of free-ranging bison in a forest landscape

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Abstract. Functional connectivity is a key determinant of animal distributions in heterogeneous landscapes. Patch connectivity depends on both patch preference and accessibility, but few studies have integrated habitat selection and movement analyses to gain a general understanding of functional connectivity. In this paper, we define functional connectivity by identifying which factors influence the choice of the patch that is visited next, the location from which animals leave the current patch, and the inter-patch trajectory. Our study provides tools to anticipate movement trajectories and, therefore, animal distribution in patchy landscapes. We followed 23 radio-collared bison across the meadow network of Prince Albert National Park between 2005 and 2008. Selection of the next meadow visited over available meadows was assessed by comparing their characteristics and land cover composition of the area separating them from the departure meadow. Additionally, we used 196 bison trails originating from 29 meadows to evaluate movement rules during inter-patch travels. Bison preferred to travel in deciduous rather than in conifer stands during summer and fall but displayed no preference during winter and spring. They also selected meadows offering higher plant biomass in winter than in other seasons. Throughout the year, meadow proximity was an important determinant of meadow selection. Inter-patch trajectory was influenced by directional persistence, as well as movement biases toward the next meadow and toward canopy gaps. Unlike the choices individuals made in selecting their next meadow, bison displayed no preference between forest stands during inter-meadow travel, indicating that functional connectivity involves hierarchical movement decisions. We showed that the behavioral determinants of functional connectivity varied over spatiotemporal scales. First, forest stand composition between meadows influenced the next target, but not the trajectory during inter-meadow travels. Second, meadow selection varied among seasons. Therefore, although structural connectivity may be immutable to these behaviorally induced changes in inter-patch movements, functional connectivity would adequately account for such modifications in animal spatial dynamics.

Key words: bison; directional persistence; functional connectivity; habitat selection; inter-patch trajectory; movement bias; Prince Albert National Park, Saskatchewan, Canada; radiotelemetry; structural connectivity.

INTRODUCTION

Functional connectivity of habitat patches is recognized as a major determinant of animal distribution in heterogeneous landscapes (Crooks and Sanjayan 2006). The propensity of animals to travel toward a given patch depends on its intrinsic quality and its accessibility (Arthur et al. 1996, Rhodes et al. 2005, Martin et al. 2008). Few studies have integrated analyses of habitat selection and animal movement to gain a general understanding of functional connectivity. Here, we propose a method that integrates patch selection and inter-patch movement decisions to provide a mechanistic understanding of functional connectivity, and therefore, to gain valuable information for predicting animal distribution.

Understanding the link between animal distributions and landscape properties is a central theme of ecological research. This relationship has implications in a wide range of fields, such as population ecology (Johnson and Seip 2008, Schick et al. 2008), landscape ecology (Wiens et al. 1993), and conservation biology (Vane-Wright et al. 1991, Fernandez et al. 2003). Animal distribution often results from individuals making selective use of habitat patches in order to achieve high fitness (Morris and Davidson 2000, McLoughlin et al. 2006). Patch selection can be influenced by factors such as conspecific abundance (e.g., Fletcher 2009), presence of limited resources (e.g., Redfern et al. 2003), and the abundance of forage and its nutritional attributes (e.g., Hebblewhite...
The use of high-quality patches, however, may be modulated by their accessibility (Wiens et al. 1993, Mapelli and Kittlein 2009, Schooley and Branch 2009), a principle central to island biogeography and metapopulation theories (MacArthur and Wilson 1967, Hanski 1998). Accessibility also determines patch use within home ranges. For example, elk (*Cervus elaphus*) tend to select aspen patches in winter, unless they need to negotiate >65° slopes to reach them, in which case they would favor open grasslands (Fortin et al. 2005a).

By understanding movement decisions, we can characterize inter-patch movements and, hence, patch connectivity. Patch connectivity can be defined on both structural and functional bases (With et al. 1997, Tischendorf and Fahrig 2000, Moilanen and Hanski 2001, Goodwin 2003, Crooks and Sanjayan 2006). Structural connectivity involves the spatial contagion of habitat types, which accounts for patch size and inter-patch distances, but it does not consider behavioral processes influencing animal movement (Dunning et al. 1992, Crooks and Sanjayan 2006). In contrast, functional connectivity involves how landscapes influence the movement of organisms among patches (Taylor et al. 1993, Kadoya 2009). There is now a general recognition that functional connectivity should reflect animal spatial dynamics more faithfully by accounting for their responses to landscape structure and composition (With et al. 1997, Bélisle 2005).

A faithful characterization of functional connectivity should be based on a detailed understanding of animal movements. The growing interest in animal movement analysis has led to the emergence and improvement of multiple quantitative methods, such as step-selection functions (Fortin et al. 2005b), mechanistic home range analysis (Moorcroft et al. 2006), biased random walks (Schultz and Crone 2001), and least-cost paths (Adriaensen et al. 2003). Few of these methods specifically address how movement can be integrated into a framework aimed at understanding patch connectivity. Least-cost path (LCP) analysis is one of the few. This approach uses computer algorithms to identify the path that requires the least cumulative costs to move from a source to a target patch. Individual habitat units are assigned a cost, and animals are assumed to use the path of least resistance to travel between two patches. Cost attribution and the functional link between these costs and animal movement, however, are rarely validated from field observations (Fahrig 2007).

Also, LCP overlooks the potential influence of internal movement biases, such as directional persistence (i.e., the propensity for animals to keep moving ahead), and external biases toward or away from landscape features that are located farther than the adjacent habitat units (Fahrig 2007). Not accounting for these biases may lead to incorrect interpretation of the influence of habitat heterogeneity on animal movements (Turchin 1998, Schultz and Crone 2001). Biased correlated random walk models (BCRW) account for both the directional persistence and the attraction of animals to other stimuli, such as high-quality resource patches (Schultz and Crone 2001), topography (Fortin et al. 2005b, Moorcroft et al. 2006), or olfactory and visual cues (Zollner and Lima 1999, Moorcroft and Lewis 2006). Although BCRWs can be a powerful approach to understanding animal distributions (Farnsworth and Beecham 1999), this information is generally not integrated into functional connectivity studies (but see McIntrye et al. 2007).

Overall, functional connectivity depends on an animal's perceptions and use of individual patches, as well as on its movements among them (Kadoya 2009). By describing movement behavior based on the influence of multiple land cover types, together with internal and external biases, we should be able to provide a more realistic depiction of functional connectivity by identifying the most probable routes among patches (Fahrig 2007). However, because departure and arrival points will not be automatically identified, as with the cumulative cost trajectory determined through LCP, we need to determine whether animals select these two locations or place them randomly along patch edges. In summary, to understand mechanisms of functional connectivity based on the animal's responses to landscape features, we need to gain information on factors influencing patch selection, trail–patch anchorage locations, and movement trajectories toward the target patch.

Our objective was to develop a mechanistic understanding of functional connectivity by integrating patch selection and inter-patch movement decisions. We proposed a three-step approach: first, we identified factors influencing the probability of a patch being visited next; second, we determined the locations from which animals are most likely to leave the current patch; and third, we evaluated the determinants of movement trajectories between the current and target patches. Inter-patch trajectories were assessed using a grid-based approach that can account for internal biases, as well as external movement biases caused by the characteristics of adjacent and remote cells. The three-step approach was implemented based on extensive spatial information on plains bison (*Bison bison bison*) traveling among meadow patches in Prince Albert National Park, Saskatchewan, Canada.

Functional connectivity pertains to an animal's perception of its surroundings and, as such, it should reflect cost–benefit trade-offs consistent with energy maximization principles. We therefore selected variables likely to influence energy expenditures or gains during inter-meadow travel. Specifically, we expected bison to maintain low travel costs by orienting their movements toward the nearest meadow, and by moving across relatively open forest understory (e.g., deciduous stands relative to conifer stands). Further, we expected bison to
increase their energy gains by using large meadows where a high concentration of forage is available, as well as meadows where snow conditions are favorable to foraging. Given that bison require daily water intake (McHugh 1958), they may also orient their movements toward meadows in which water is readily available (e.g., presence of a pond).

**Methods**

**Bison population and study area**

Prince Albert National Park (53°44' N, 106°40' W) occupies 3875 km² of central Saskatchewan, Canada. Located at the southern edge of the boreal forest biome, the park has a mean annual daily temperature of 0.4°C (−18°C in January and 16°C in July), and an annual average precipitation of 430 mm, of which 50% falls as rain in summer (Evans et al. 2009). The bison population of Prince Albert National Park was estimated at 385 individuals in 2006 (Fortin et al. 2009). The core area of the bison range is located in the southwestern corner of the park, an area dominated by conifer and deciduous stands (85%), meadows (10%), and water bodies (5%). Because bison strongly select meadows that are rich in grasses and sedges (Fortin et al. 2003), meadows can be considered as high-quality patches imbedded within a forest matrix (see Plate 1).

**Field data collection**

Two sets of data were collected in the field. First, we followed radio-collared bison to identify meadows that were successively visited. Second, bison trails were mapped from field surveys to identify trail–meadow anchorage points (i.e., the locations where bison trails meet the meadow edge), and trail trajectories between meadows.

**Radio-collared bison.**—Global positioning system (GPS) collars (4400M, Lotek Engineering, Newmarket, Ontario, Canada) were installed on 23 female bison. Individuals were followed for periods ranging from 82 to 997 days (mean 454 days) between March 2005 and August 2008. Differences in period lengths were due to animal mortality, collar malfunctions, or battery exhaustion. GPS locations were taken every three hours five days a week and every hour two days a week, but only hourly locations were used to identify meadows that were successively visited.

**Bison trails.**—Bison are gregarious animals that travel within extensive networks of trails (McHugh 1958). In summer, bison trails are large, conspicuous, and denuded of vegetation. They can be easily distinguished from those of other ungulates by their large, rounded hoof prints and presence of feces (Elbroch 2003), although other species also use bison trails. During the summer of 2008, bison trails (number 9.2 ± 1.1 trails per meadow, mean ± SE; range 2–28 trails, N = 196) were systematically located by walking around the edge of 29 meadows (meadow area 8.5 ± 1.94 ha; range 0.08–33.7 ha). All trails were followed using a handheld Global Positional System unit (GPS76, Garmin International, Olathe, Kansas, USA) until they reached another meadow (Fig. 1). The information was then transferred to a Geographic Information System, GIS (ArcGIS 9.3, Environmental Systems Research Institute, Redlands, California, USA).

**Remote sensing and geographic information system of bison habitat.**—A supervised classification of a SPOT5 multispectral image (August 2008; 10 × 10 m pixel resolution) was performed to define landscape attributes over the bison range, based on 310 random field locations. Each field location was taken in a 30 × 30 m area composed of a single land cover type. The resulting map depicted, with an accuracy of 89% (N = 310), six different landscape covers: WATER, AGRICULTURE, CONIFER stands, DECIDUOUS stands, MIXED stands, and open areas. Open areas were subsequently transformed into two categories: MEADOW and canopy GAP. A meadow was an aggregation of at least five pixels (>0.04 ha), whereas a gap included fewer than five aggregated pixels (Fig. 1). Groups of MEADOW pixels were then transformed into a polygon layer. The area of each of these patches was estimated using Hawth’s analysis tools for ArcGIS (Beyer 2004).

To obtain a general indication of plant abundance over the bison range, we followed the example of Anderson et al. (2005) and sampled vegetation when the biomass was at its highest (i.e., August 2008). We collected five vegetation samples of 0.25 m² of above-ground vegetation at 24 sites of 30 × 30 m, one in the center and four −5 m from each edge toward the center. Samples were oven-dried to constant mass. We then established a relationship between total above-ground dry biomass and the normalized difference vegetation index, NDVI: NDVI = (NIR − RED)/(NIR + RED), with surface reflectance values for near-infrared (NIR) and red bands (RED) that were obtained from the SPOT5 image. The relationship between total dry biomass (in kilograms per square meter) and NDVI was as follows: total dry biomass = 1.55 × NDVI − 0.77, ($R^2 = 0.47$, $N = 24$, $P < 0.01$). This relationship was used to estimate average biomass in each meadow.

We characterized snow conditions in meadows across the bison range based on the snow model described by Fortin et al. (2009). In brief, snow depth and density were measured every 10 m along a 70-m transect located in each of 18 open areas during the winters of 2006 (four surveys), 2007 (five surveys), and 2008 (four surveys). Snow water equivalent (SWE) was then estimated from the product of snow depth and density. An inverse distance-weighting function was used to extrapolate SWE to unsampled areas (Schloeder et al. 2001). Model cross-validation indicates a robust relationship between predicted and observed values ($R^2 = 0.76$). A different map was created for every snow survey. Because snow surveys were taken approximately every two weeks, a given snow map was associated with all observations of radio-collared bison taken from a week before the snow
survey to the week after the survey. Snow maps were thus used to estimate SWE in meadows from January to mid-March.

Analysis of functional connectivity

Meadow selection.—We used sequences of GPS locations (1-h relocation interval) from radio-collared bison to characterize their successive use of meadows. We first identified a meadow with at least one bison GPS location (i.e., the source meadow), and then determined which meadow was visited next (i.e., the target meadow). We then characterized this target meadow, together with 10 meadows randomly chosen (random meadow) within a 2 km radius of the source meadow (Fig. 2A). The 2-km limit encompasses >95% of the distances between successively visited meadows.

We characterized each meadow by its area, average plant biomass, squared biomass (second order, to test for a possible quadratic relationship between use and plant biomass; Wilmshurst et al. 1995), presence of a water body within the meadow (e.g., a pond) and, for the winter model, the average SWE of the meadow. We centered biomass estimates to avoid multicollinearity in subsequent statistical models. We also determined the Euclidean distance linking the edge of the source meadow and the edge of target or random meadows. To account for the environmental characteristics of the area between the source and the target meadows or the source and the random meadows, we created a circular buffer with a diameter equal to the shortest distance linking a given pair of meadows and centered on the midpoint of this vector (Fig. 2A; see Johnson et al. 2002b). The proportion of the different land cover types within the buffers was estimated. Because the proportions of the land cover types were nonindependent, we used a principal component analysis (PCA) to reduce the dimensions of the data to two independent components (PC1 and PC2) that identified the major spatial gradients among the land cover types (Graham 2003).

We contrasted the characteristics of target (score = 1) and random (score = 0) meadows with conditional logistic regression (Compton et al. 2002, Fortin et al. 2005a), for which each stratum consisted of one target meadow and its 10 associated random meadows. To account for uncertainty in our estimates of dry biomass, the error distribution associated with the total dry biomass model previously described was included in our analysis. For each meadow, we randomly used a biomass value drawn from the error distribution of the estimated value of the total dry biomass model. This process was repeated 999 times and the average parameter of the conditional logistic regression is reported. Models were built for each season (summer, June–August; fall, September–November; winter, January to mid-March; spring, mid-March to the end of May). Winter did not include December because of the lack of snow data. Model robustness was evaluated

Fig. 1. Graphical representation of the bison trail network (dotted lines) among the meadows (dark gray) and canopy gaps (light gray) of Prince Albert National Park, central Saskatchewan, Canada. Bison trails were followed using a handheld global positioning system.
for each season with $k$-fold cross-validation for conditional logistic regression (Fortin et al. 2009). For validation, each model was built utilizing 80% of randomly selected stratum and, using the parameter derived from this portion of the data, the relative probability of use ($w(x)$) was evaluated for the remaining 20% of the stratum. A high Spearman rank correlation ($r_S$) indicates high model robustness (cf., Fortin et al. 2009). The process was repeated 999 times for this study. We present the average $r_S$ ($\bar{r}_S$) resulting from the 1000 randomizations.

Anchorage points between bison trails and meadows.—To evaluate whether or not bison trails were randomly established along meadow edges, we calculated the proportion of the different land cover types (i.e., deciduous stands, conifer stands, mixed stands, meadows, canopy gaps, and water) in a 20-m buffer around pixels (i.e., 24 adjacent pixels) where a trail connected the meadow (i.e., anchorage point, coded as 1). For each trail found at the edge of a meadow, we also randomly selected pixels along the meadow edge where trails were absent (i.e., coded as 0) and characterized the propor-

Fig. 2. Methodological design used to evaluate mechanisms of functional connectivity for plains bison (Bison bison bison) in a meadow network. (A) Meadow selection. Ten available meadows (light gray polygons; four are visible in the section displayed) were randomly selected within a 2-km buffer zone (dashed arc) from the source meadow (black polygon) and were compared to the meadow that was actually visited next (i.e., target meadow). Meadow characteristics included: meadow area, average snow water equivalent (SWE, winter model), average plant biomass, shortest Euclidean distance between the source meadow and either a random meadow (e.g., straight black line) or the selected target meadow and the land cover types contained within a circular buffer between the source meadow and either a random meadow or the target meadow (e.g., small-dashed circle). (B) Anchorage point between bison trail and meadow. The land cover types within a 20-m buffer (dashed square) around a pixel (central square of $10 \times 10$ m, outlined in solid white) containing a bison trail (Anchorage) were compared to the land cover types around pixels randomly selected among those without a bison trail (Random). (C) Inter-meadow movement through a forest matrix. A representation of the grid-based approach describing inter-meadow trajectories from bison trails. The current location along the trail is represented by a white dot. The surrounding pixels ($10 \times 10$ m) are composed of six unused pixels (pixels 1, 2, 3, 4, 6, and 7) and one used pixel (pixel 5, reached by the solid black arrow representing the observed bison trail), which altogether form a stratum in statistical analysis. The animal arrived from pixel 8, which was not included in the stratum. $E_{DP}$ (long-dashed arrow) represents the bearing expected according to directional persistence, $E_{CG}$ (dotted arrow) is the expected direction toward the nearest canopy gap, and $E_{TM}$ (dot-dashed arrow) is the expected direction toward the target meadow.
tion of land cover types around them (Fig. 2B). When there were sufficient pixels of meadow edge, we randomly selected five pixels without trail for each pixel with trail; otherwise, all pixels without trails were included in the analysis. Again, because the proportions of the land cover types were nonindependent, we used a principal component analysis (PCA) and estimated PC1 and PC2 scores. We then used a conditional logistic regression to contrast PC scores of pixels with and without trails. Because each meadow was characterized by more than one bison trail, all anchorage points and associated random pixels of a given meadow were grouped into the same stratum in the regression (i.e., each stratum had multiple 1’s, each representing a bison trail, with multiple 0’s). This approach accounted for the statistical nonindependence of all the trails reaching a given meadow.

Estimated parameters of the model were used to calculate the likelihood of finding an anchorage point at any given pixel along the meadow edge (i.e., random and anchorage points). With a robust model, pixels with the highest probabilities should have an actual anchorage point (i.e., be coded as 1). We thus evaluated the number of times that pixels with the highest probabilities were anchorage points. This was done separately for each of the 29 meadows; for example, for a meadow with five anchorage points, we identified the five pixels with the highest probabilities and determined whether they had an anchorage point. We then reported the percentage of times that anchorage points were successfully identified. A high percentage is indicative of a robust model. Additionally, to evaluate the improvement of our model over random establishment of anchorage points, a null model that assumed completely random establishment of anchorage points on the meadow’s edge (i.e., 1’s were randomly attributed among the pixels) was also constructed. Random assignment of anchorage points was repeated 1000 times, and the mean percentage is reported for the null model.

*Inter-meadow movements through the forest matrix.*—We developed a grid-based approach to assess the simultaneous effects of land cover type preferences and movement biases on animal movement. We considered that biases of bison movement could include directional persistence, a bias toward the target meadow, and a bias toward canopy gaps, which could be used as stepping stones during inter-meadow travel. Bison trails were split into 10-m segments (i.e., 10-m steps). The current location was surrounded by eight pixels: one pixel where the animal came from, one that was subsequently used, and six unused pixels. A choice set (a stratum) thus includes the used pixel (coded as 1) and the six related unused pixels (coded as 0). We compared the characteristics of used and unused pixels (Fig. 2C).

Pixels were characterized through a set of dummy variables, each representing a given land cover type (i.e., *DECIDUOUS* stand, *CONIFER* stand, *MIXED* stand, *MEADOW*, or canopy *GAP*). *WATER* was not included in the analysis because it was unavailable along the bison trails. We also considered that when an animal is exhibiting directional persistence, the expected direction of the current step, $E_{DP}(\theta)$, equals that of the previous step: $E_{DP}(\theta) = \theta_{i-1}$ where $i$ is time and $\theta$ is the angle (direction) of the step. We calculated the cosine of the difference between $E_{DP}(\theta)$ and the direction toward each of the seven neighboring pixels ($X_{DP}$). For example, pixel 2 would have $X_{DP}$ value of cosine 125° (i.e., −0.57), whereas pixel 3 would be assigned a $X_{DP}$ value of cosine 85° (i.e., 0.09; Fig. 2C).

The expected step direction in the case of a bias toward the target meadow ($E_{TM}(\theta)$) corresponds to the bearing direction between the current location and the target meadow (Fig. 2C). Each pixel of a stratum was then assigned a value corresponding to the cosine of the difference between $E_{TM}(\theta)$ and the bearing of the vector going from the current location to the pixel ($X_{TM}$). For example, pixel 1 would be assigned an $X_{TM}$ value of cosine 170° (i.e., −0.98) and pixel 2, a $X_{TM}$ value of cosine 125° (i.e., −0.57). Because the strength of the bias could vary with distance (Barton et al. 2009), we also accounted for the Euclidean distance ($D_{TM}$) to the target meadow by multiplying $X_{TM}$ by $D_{TM}^{0.0}$ (no distance effect), $D_{TM}^{0.5}$ (effect increasing with distance), or $D_{TM}^{-0.5}$ (effect decreasing with distance); see Eq. 1.

Finally, we also considered an external bias toward canopy gaps. The expected step direction toward canopy gaps ($E_{CG}(\theta)$) was the bearing direction between the current location and the nearest canopy gap (Fig. 2C). Because gaps could be used as stepping stones while traveling toward the target patch, we assumed that bison would be influenced only by canopy gaps possibly encountered in front of them during travel toward the target meadow (i.e., $E_{CG}(\theta)$ can only be within 90° on either side of the previous step bearing direction). Each pixel of a stratum was then assigned a value ($X_{CG}$) corresponding to the cosine of the difference between $E_{CG}(\theta)$ and the bearing of the vector going from the current location to the pixel. We also accounted for potential changes in the strength of this external bias with the Euclidean distance ($D_{CG}$) to the canopy gap (Eq. 1).

We used conditional logistic regression to evaluate the combined influence of movement biases (i.e., directional persistence, bias toward target meadow, and bias toward canopy gaps) and land cover types on the probability of pixel use. The regression model was based on a paired design whereby each pixel actually used (i.e., pixel part of the trail, coded as 1) was associated with the six unused pixels available from that location (pixels adjacent to the trail, coded as 0’s) to form a stratum. Robust 95% confidence intervals of regression parameters were estimated using generalized estimating equations (GEE; Craiu et al. 2008, Koper and Manseau 2009) to control for the lack of independence in the information along each trail. All strata associated with a
Table 1. Parameter estimates (coefficient ± robust SE) of habitat variables predicting which meadow radio-collared bison of Prince Albert National Park will visit next among those available within a 2-km radius.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Summer</th>
<th>Fall</th>
<th>Winter</th>
<th>Spring</th>
</tr>
</thead>
<tbody>
<tr>
<td>Covariate</td>
<td>β ± SE</td>
<td>P</td>
<td>β ± SE</td>
<td>P</td>
</tr>
<tr>
<td>Area (ha)</td>
<td>0.07 ± 0.01</td>
<td>&lt;0.001</td>
<td>0.07 ± 0.01</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Plant biomass (kg/m²)</td>
<td>−3.31 ± 1.11</td>
<td>0.003</td>
<td>−2.16 ± 0.88</td>
<td>0.011</td>
</tr>
<tr>
<td>Plant biomass</td>
<td>−65.85 ± 10.33</td>
<td>&lt;0.001</td>
<td>−29.77 ± 6.45</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Deciduous–conifer gradient</td>
<td>−0.11 ± 0.06</td>
<td>0.07</td>
<td>−0.12 ± 0.06</td>
<td>0.03</td>
</tr>
<tr>
<td>Water gradient</td>
<td>−0.15 ± 0.06</td>
<td>0.01</td>
<td>−0.08 ± 0.07</td>
<td>0.26</td>
</tr>
<tr>
<td>Distance (km)</td>
<td>−2.66 ± 0.14</td>
<td>&lt;0.001</td>
<td>−2.90 ± 0.13</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Presence of water</td>
<td>0.31 ± 0.16</td>
<td>0.06</td>
<td>0.20 ± 0.14</td>
<td>0.14</td>
</tr>
<tr>
<td>SWE in meadow (cm)</td>
<td></td>
<td></td>
<td>−0.25 ± 0.84</td>
<td>0.76</td>
</tr>
<tr>
<td>k-fold cross-validation (f₅)</td>
<td>0.95</td>
<td></td>
<td>0.87</td>
<td></td>
</tr>
</tbody>
</table>

Notes: Parameter estimates were assessed by conditional logistic regression during the different seasons of the year. Distance is the distance between the departure meadow and the next or random meadow. The deciduous–conifer gradient is determined by PCA (see Methods: Analysis of functional selection: Meadow selection). Presence of water is a dichotomous variable, determined through GIS analysis, where 1 indicates presence of water and 0 indicates no water within the meadow. SWE is the product of snow height (cm) and density (a proportion, where 1 corresponds to 1 g/cm³).

To investigate distance effects on the strength of external biases, we tested a model with no distance effect (c = 0, model 1), as well as models based on the two different functional forms of distance effects: a decreasing effect (c = −0.5, model 2), and an increasing effect (c = 0.5, model 3).

The next model (w_cover(x)), model 4, included only dummy variables representing the land cover types:

\[
    w_{\text{cover}}(x) = \exp(\beta_{\text{CONIFER}} \times \text{CONIFER} + \beta_{\text{DECIDUOUS}} \times \text{DECIDUOUS} + \beta_{\text{MIXED}} \times \text{MIXED} + \beta_{\text{GAP}} \times \text{GAP})
\]  

(2)

with MIXED stands being the reference category.

The last three models included both land cover types and movement parameters with varying effects of distances (w_total(x)):

\[
    w_{\text{total}}(x) = w_{\text{move}}(x) \times w_{\text{cover}}(x) = \exp(\beta_{\text{DP}} \times \text{DP} \times \beta_{\text{SWE}} \times \text{SWE} + \ldots + \beta_{\text{GAP}} \times \text{GAP})
\]

where c varied as previously described to create three additional candidate models: no distance effect (c = 0, model 5), decreasing effect (c = −0.5, model 6), and increasing effect (c = 0.5, model 7).

Because trails could be used in both directions, all estimates of bearing direction associated with potential internal and external biases could vary depending on which way we considered the animals to be moving. To get a general assessment of factors influencing inter-patch movement trajectories, we randomly selected a direction for each of the 196 bison trails and estimated the regression parameters. We repeated this randomization procedure 999 times and reported average regression parameters with 95% confidence intervals for the 1000 runs. For each randomization, the seven candidate models were contrasted based on the quasi-likelihood under independence criterion, QIC (Pan 2001, Craiu et al. 2008), and we reported the percentage of the 1000 runs for each model that had the lowest QIC. The model with the lowest QIC was considered the best one among the seven candidate models and, therefore, the model with the highest percentage was considered to have received the most empirical support.

Results

Meadow selection

Models of meadow selection revealed that multiple habitat characteristics influenced which meadow bison visited next. In all seasons, bison leaving a meadow were more likely to end up in a large rather than a small meadow, among those that were available within a 2 km radius (Table 1). This effect could have been expected simply by chance, but needed to be accounted for before assessing the response of bison to other habitat variables. Throughout the year, bison were also more likely to visit meadows closer to their current location. The presence of water was an important determinant of meadow selection in winter and spring; it was marginally important in summer, but it did not seem to influence bison in the fall (Table 1). Also, snow water equivalent (SWE) did not influence meadow selection.

Bison were most likely to visit a meadow offering an intermediate amount of plant biomass (Fig. 3) within the estimated range (0.02–0.75 kg/m²). The relative probability of use of meadows was highest when biomass was −0.50 kg/m² during snow-free seasons, and 0.59 kg/m² in winter. Bison also selected their next meadow based on the matrix present between the source and target meadow. The first two PCA axes explained 63% of the
variance in the land cover types located between the source meadow and the available ones. PC1 reflected a gradient of forest types from deciduous to conifer stands, whereas PC2 mostly represented a water gradient (Table 1). In winter and spring, forest types did not significantly affect selection of the next meadow (Table 1). However, in the fall and to some extent in summer, bison were more likely to travel toward meadows separated from their current location by a high proportion of deciduous rather than conifer forest. In summer and spring, bison avoided areas consisting of a high proportion of water (i.e., negative association with PC2). Models of meadow selection were robust to cross-validation during any season (≥0.83; Table 1).

**Anchorage points of bison trails**

We characterized the area surrounding the anchorage points of bison trails with the first two PCA axes, which altogether explained 57% of the variation in land cover types. The first principal component (PC1) mostly distinguished meadows from conifer stands and water bodies, whereas the second component (PC2) represented a gradient from deciduous stands to meadows (Table 3). The relative probability of finding trail anchorage points along a meadow edge was influenced by both PC1 (β ± SE = 0.13 ± 0.06, N = 250, P = 0.02) and PC2 (β ± SE = −0.74 ± 0.07, N = 250, P < 0.0001). PC1 indicated that anchorage points are more likely to be found in areas with a low proportion of meadows and a high proportion of coniferous stands and water bodies. We suggest that this relationship with PC1 was largely driven by a response to meadows and had little to do with conifer stands and water bodies. First, a univariate analysis confirmed that the likelihood of finding an anchorage point at a given location decreased with the proportion of meadow around that location (β ± SE = −5.55 ± 0.56, N = 250, P < 0.0001), but was independent of conifer stands (β ± SE = −3.95 ± 2.87, N = 250, P = 0.16) or water bodies (β ± SE = −1.80 ± 1.69, N = 250, P = 0.28). Second, PC2 also indicated that trail anchorage points were selectively placed in areas characterized by a small proportion of meadow. PC2 further revealed that trails were most likely to connect meadows in areas with a high proportion of deciduous stands. The presence of deciduous stands at anchorage points was confirmed through a univariate analysis (β ± SE = 5.85 ± 0.60, N = 250, P < 0.0001).

Our model correctly identified pixels with a trail anchorage point 39% of the time, which exceeds random expectations (mean 21%; range 15–28%). Model parameters thus significantly improved our ability to predict where bison trails connect to meadows.

**Inter-meadow movement through forest matrix**

We estimated the difference between the bearing direction at a trail anchorage point and the arrival point in the next meadow, together with the bearing direction of the first 10-m segment of the trail. This difference in bearing direction averaged 2.54° ± 1.34° (mean ± SE, N = 392), with a 95% confidence interval that included 0° (Fig. 4). The length of the mean vector (r) was 0.9, indicating a high concentration around the mean and the distribution of the differences in bearing direction was not uniform (Rayleigh test of uniformity, P < 0.001 N = 392). Bison thus tended to leave directly in the direction of their arrival point in the target meadow. Anchorage points of bison trails were rarely located in the areas corresponding to the shortest

**Table 2. Factor loadings for the first two principal component axes resulting from PCA conducted on proportions of land cover types characterizing the areas between meadows that radio-collared bison occupied in Prince Albert National Park and meadows that were available within a 2-km radius.**

<table>
<thead>
<tr>
<th>Land cover type</th>
<th>PC1: Conifer–deciduous gradient</th>
<th>PC2: Water gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion of water</td>
<td>0.09</td>
<td>0.84</td>
</tr>
<tr>
<td>Proportion of conifer stands</td>
<td>0.58</td>
<td>−0.03</td>
</tr>
<tr>
<td>Proportion of deciduous stands</td>
<td>−0.64</td>
<td>−0.23</td>
</tr>
<tr>
<td>Proportion of mixed stands</td>
<td>0.49</td>
<td>−0.41</td>
</tr>
<tr>
<td>Proportion of canopy gaps</td>
<td>−0.02</td>
<td>0.27</td>
</tr>
</tbody>
</table>

Note: PC1 and PC2 have eigenvalues of 2.0 and 1.2, respectively; collectively, they explain 63% of variation in the correlation matrix.
Euclidean distance between the two meadows. The Euclidean distance that linked the anchorage points of the two meadows was $135.9\% \pm 25.3\%$ longer (mean $\pm$ SE; median 23.8%, $N = 196$, range 0–2252.1%) than the minimum distance between the two meadows. This indicates that, although bison leave directly toward the target meadow, they do not use the shortest trajectory to reach it.

Among the seven candidate models that investigated the factors shaping the trajectory of bison trails, model 5 received the greatest empirical support. Its QIC was the lowest 99.6% of the time ($N = 1000$). Model 5 implied that bison trail trajectories resulted from the influences of land cover types, directional persistence, and external biases without a distance effect (average QIC weight $>0.99$, $N = 1000$; Table 4). Models that only accounted for

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**TABLE 3.** Factor loadings for the first two principal component axes resulting from PCA conducted on land cover type proportions around the edges of meadows in Prince Albert National Park.

<table>
<thead>
<tr>
<th>Land cover type</th>
<th>PC1: meadow to conifer and water gradient</th>
<th>PC2: deciduous to meadow gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion of water</td>
<td>0.58</td>
<td>0.14</td>
</tr>
<tr>
<td>Proportion of coniferous stands</td>
<td>0.57</td>
<td>0.15</td>
</tr>
<tr>
<td>Proportion of mixed stands</td>
<td>0.30</td>
<td>0.09</td>
</tr>
<tr>
<td>Proportion of deciduous stands</td>
<td>-0.09</td>
<td>-0.76</td>
</tr>
<tr>
<td>Proportion of meadow</td>
<td>-0.47</td>
<td>0.56</td>
</tr>
<tr>
<td>Proportion of canopy gaps</td>
<td>-0.04</td>
<td>0.21</td>
</tr>
</tbody>
</table>

*Note:* PC1 and PC2 have eigenvalues of 1.81 and 1.61, respectively; collectively, they explain 58% of the variation in the correlation matrix.

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*Fig. 4.* Frequency histograms (with frequencies of 20–80 given by the respective concentric circles) and mean vector direction (thin line with error bar showing 95% CI) of differences in bearing between anchorage points of the source and target meadows, and the observed bearing of the first 10-m segment for each of the 196 bison trails mapped in Prince Albert National Park in the summer of 2008. A difference of $0^\circ$ indicates that bison left the source meadow directly toward the anchorage point on the target meadow.
land cover types or movement biases had poor empirical support (QIC weight < 0.01, in both cases). Also, considering that effects of external biases increased or decreased with distance did not improve model fit (QIC weight < 0.03 for models 3, 4, 6 or 7; Table 4).

The top-ranking model (model 5) indicated that, along their paths, bison were not more likely to use deciduous or conifer stands than mixed stands (Table 5). Trails also bypassed meadows that were located between the source and target meadows. Meadow avoidance simply pointed out that, although bison tended to select meadows that were in relatively close proximity (Table 3), trails did not always connect the two nearest meadows.

We found that bison trails were more likely to go through canopy GAPS than other land cover types. Moreover, we detected positive taxis of bison in response to gaps (Table 5). Bison also significantly biased their movements toward target meadows (Table 5), which was expected because the target meadows were the predetermined end points of the trails. However, the model indicated that this external bias, although significant, had nine times less influence on trail trajectory than did directional persistence (4.43/0.49; Table 5). Bison thus tended to keep traveling in the same direction as their previous steps. Despite generally leaving a meadow directly toward the anchorage point of the target meadow (Fig. 4), and despite strong directional persistence, cumulative movement biases along the inter-meadow path were such that the path was, on average, 8.4% ± 1.4% longer (mean ± SE; median 4.1%, range 0–257%) than the Euclidean distance between the trail’s departure and arrival anchorage points. The percentage difference in distance was higher for meadows that were farther apart (mixed-effects model accounting for nonindependence of multiple trails linking the same two meadows among the 196 trails surveyed; regression parameter for arcsine (proportion distance⁰·⁵): 0.00027 ± 0.00006; \( F_{1,72} = 20.47, P < 0.001 \)). Therefore, as the distances for bison to cross increased, their trajectories appeared to deviate farther away from a straight line leading directly to the target meadow.

### DISCUSSION

Our study evaluated meadow selection and inter-meadow movement decisions of free-ranging plains bison in an integrative framework of functional connectivity. This is one of the first studies combining patch selection and empirically derived movement behavior to assess the likelihood that habitat patches are connected. Kadoya (2009) suggested that differences in functional connectivity among landscapes relate to how animals perceive, utilize, and move among patches. Accordingly, we present a way, first to evaluate the relative probability of use of the next patch based on patch and matrix attributes, then to identify potential locations from which individuals leave the patch, and finally, to depict the most probable trajectory for reaching the next patch. This information on inter-patch movement decisions provides a mechanistic definition of functional connectivity.

#### Meadow selection

As expected, bison were more likely to transit to meadows that were closer to their current location. For example, a meadow would be two times more likely to be the next target in the fall if it were located at 50 m than at 300 m (Table 1). Similar distance effects have been reported in many vertebrates, including birds (Lynch and Whigham 1984, Andersson and Bodin 2009), mammals (Rodríguez and Andrén 1999), and

### Table 4. Candidate models assessing the influence of landscape composition, directional persistence, bias toward the target meadow, and bias toward canopy gaps along inter-meadow trajectories of bison in Prince Albert National Park.

<table>
<thead>
<tr>
<th>Model no. and description</th>
<th>( K )</th>
<th>( \Delta QIC )</th>
<th>QIC weight</th>
<th>Runs with lowest QIC (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Movement biases only (Eq. 1, with ( c = 0 ))</td>
<td>3</td>
<td>25.65</td>
<td>&lt;0.01</td>
<td>0</td>
</tr>
<tr>
<td>2. Movement biases only (Eq. 1, with ( c = 0.5 ))</td>
<td>3</td>
<td>52.21</td>
<td>&lt;0.01</td>
<td>0</td>
</tr>
<tr>
<td>3. Movement biases only (Eq. 1, with ( c = -0.5 ))</td>
<td>3</td>
<td>39.51</td>
<td>&lt;0.01</td>
<td>0</td>
</tr>
<tr>
<td>4. Land cover only (Eq. 2)</td>
<td>4</td>
<td>8109.59</td>
<td>&lt;0.01</td>
<td>0</td>
</tr>
<tr>
<td>5. Movement biases and land cover (Eq. 3, with ( c = 0 ))</td>
<td>7</td>
<td>0</td>
<td>0.99</td>
<td>99.6</td>
</tr>
<tr>
<td>6. Movement biases and land cover (Eq. 3, with ( c = 0.5 ))</td>
<td>7</td>
<td>29.69</td>
<td>&lt;0.01</td>
<td>0</td>
</tr>
<tr>
<td>7. Movement biases and land cover (Eq. 3, with ( c = -0.5 ))</td>
<td>7</td>
<td>8.78</td>
<td>0.01</td>
<td>0.4</td>
</tr>
</tbody>
</table>

**Notes:** The distance effect, \( c \), is described in Methods: Analysis of functional connectivity: Inter-meadow movement through the forest matrix. \( \Delta QIC \), QIC weights, and percentage with lowest QIC (quasi-likelihood under independence criterion) are calculated based on the average QIC of 1000 randomizations of directionality in the 196 bison trails.

### Table 5. Average parameter estimates (\( \hat{b} \)) with 95% confidence intervals for the most parsimonious model (model 5, Table 4) of bison inter-meadow trajectories.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>( \hat{b} )</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>MIXED (reference category)</td>
<td>0</td>
<td>0.04 to 0.06</td>
</tr>
<tr>
<td>CONIFER</td>
<td>-0.01</td>
<td>-0.07 to -0.009</td>
</tr>
<tr>
<td>DECIDUOUS</td>
<td>-2.18</td>
<td>-2.71 to -1.60</td>
</tr>
<tr>
<td>MEADOW</td>
<td>6.66</td>
<td>4.43 to 8.93</td>
</tr>
<tr>
<td>GAP</td>
<td>4.43</td>
<td>4.35 to 4.52</td>
</tr>
<tr>
<td>Directional persistence</td>
<td>0.49</td>
<td>0.44 to 0.54</td>
</tr>
<tr>
<td>Bias toward target meadow</td>
<td>0.17</td>
<td>0.07 to 0.26</td>
</tr>
<tr>
<td>Bias toward canopy gaps</td>
<td>-0.25 to 0.34</td>
<td></td>
</tr>
</tbody>
</table>

**Note:** We estimated \( \hat{b} \) and CI based on 1000 randomizations of the direction of the 196 bison trails that were followed in Prince Albert National Park.
amphibians (Chan-McLeod and Moy 2007). There could be multiple nonexclusive explanations for this observation. First, bison might be more likely to reach a nearby meadow than one located far away simply by chance. Second, bison should be able to detect an opening in the canopy at relatively close distance, which again favors movements to nearby meadows. Finally, bison could maintain relatively low travel costs by selecting meadows that were relatively close, a behavior that would be consistent with energy maximization principles.

Meadow selection also depended on matrix composition. For example, bison selectively traveled toward their next meadow in fall and to some extent in summer by crossing areas dominated by deciduous stands with a low proportion of conifers, while also avoiding water holes in summer and spring. The meadows found on the winter range are mostly surrounded by conifer or mixed-forest stands. Avoiding those stands would largely restrict the movement of bison in winter, which might explain why they do not respond negatively to conifer stands as they do in summer and fall. The observed behavioral response seems to reflect a trade-off between an avoidance of conifer stands during travel and a search for short paths that can lead to vegetation-rich meadows. Unlike many other habitat selection studies (e.g., Boyce et al. 2003, Fortin et al. 2009, Janin et al. 2009), we directly considered what animals would have to cross to get to their next patch. Johnson et al. (2002a) showed that such considerations can improve our understanding of animal distributions.

In winter and spring, bison favored meadows in which water bodies were available. Fortin et al. (2009) explained that bison have access to vegetation emerging from deep water once the ice can support individuals. Important amounts of vegetation that were not consumed in summer, because bison avoid grazing in deep water (Fortin et al. 2009), then become available during the cold season, which may attract bison to meadows with water bodies. We also found a tendency for bison to select meadows with easy access to water in summer, an observation consistent with Fortin et al. (2003).

We did not detect an influence of snow water equivalent (SWE) on meadow selection. This result is rather surprising, given previous reports of snow effects on bison movement and distribution (Fortin et al. 2003, 2009).
2009). Perhaps this lack of response can be explained by the fact that, in the context of our study, SWE was averaged over entire meadows, and average snow conditions might not have varied enough over the 2-km spatial extent to be able to detect an effect.

As we expected, food characteristics also determined which meadow bison would select next. Domestic sheep Ovis aries (Edwards et al. 1996) and elk (Wolf et al. 2009) have the ability to use past experience to orient their search and foraging decisions. Bison also seem to have preharvest information about patch quality because they selectively orient themselves toward meadows offering an intermediate amount of plant biomass. Spatial memory thus seems to influence patch connectivity in large mammals. Our statistical design implies that some of the meadows considered as the reference point (i.e., used to define availability) were never visited by the radio-collared bison. Spatial memory thus might not be the only factor associated with this selection. Perhaps bison navigate using olfactory and visual cues (e.g., Zollner and Lima 1999, Schooley and Wiens 2003). A better understanding of a bison’s perceptual range is certainly needed in order to gain a more comprehensive explanation for the observed behavioral pattern.

The preference for intermediate biomass of vegetation observed in plains bison has also been reported in captive wood bison Bison bison athabascae (Bergman et al. 2001), as well as in other ungulates such as elk and cattle (Wilmshurst et al. 1995, Drescher et al. 2006, Hebblewhite et al. 2008). Bison might select meadows with intermediate biomass of vegetation because they trade off food digestibility and availability. Large plants are often less digestible than small ones because the former include greater amounts of lignin for mechanical support, and because lignin is a cell wall structural component that limits digestibility (Buxton and Redfearn 1997). On the other hand, herbivores may experience slower intake rates at feeding stations offering relatively low plant biomass (Bergman et al. 2000). The combined effects of these availability and digestive constraints are such that herbivores can often maximize their energy intake rate by feeding at locations offering an intermediate amount of vegetation (Fryxell 1991, Wilmshurst et al. 1995, Bergman et al. 2001, Hebblewhite and Merrill 2009).

To identify these determinants of patch selection, we evaluated inter-meadow movement decisions based on the locations of 23 bison that were followed throughout the year for up to three years. This intensive sampling emphasized seasonal variation in the determinants of inter-patch movements, which implies that functional connectivity differs among seasons. In contrast, structural connectivity should remain consistent across seasons because the spatial arrangement of patches should not change. Therefore, conclusions based solely on structural measures of connectivity might not detect potentially important changes in patch connectivity during the course of the year (Crooks and Sanjayan 2006).

Given that habitat selection varies with group size in bison (Fortin et al. 2009), we could expect functional connectivity to vary with fusion–fission dynamics characterizing bison social system. This hypothesis demands further investigation. For now, our findings probably best reflect functional connectivity of the median bison group size (i.e., 40 bison in summer and 20 in winter).

**Patch–trail anchorage point**

Once the target meadow has been identified, the next step in understanding the mechanisms of patch connectivity would be to identify environmental factors that influence the choice of departure locations from the current meadow. The thick forest stands and flat terrain that characterize most of Prince Albert National Park make it generally impossible to determine, from visual cues, the shortest distance to travel between meadows. Bison should therefore rely on certain meadow attributes to establish a trail anchorage point. As expected, we identified some attributes that bison used to establish a trail. Bison favored meadow tips (i.e., the proportion of meadow was lower around anchorage points than around meadow edges where trails were absent) surrounded by deciduous forest. Trails may be selectively placed at meadow tips because the openings in the forest canopy that they create might often be the first ones seen by individuals approaching the meadow, depending on their trajectory. Also, perhaps before entering the forest, bison try to maintain easy travel and access to high-quality food for as long as possible by leaving at a meadow tip.

This nonrandom distribution of trail anchorage points in meadows was such that Euclidean distances between the beginning and end of bison trails were, on average, twice as long as the shortest distance between the two meadows. Connectivity studies are commonly based on estimates of the shortest Euclidean distance linking adjacent patches (e.g., With and King 1999, Urban and Keitt 2001, Andersson and Bodin 2009). The longer observed travel distances should lead, for example, to residency times longer than expected based on the average shortest distance between patches (Charnov 1976). Quantitative differences in expected residence time should be biased further by the fact that actual distance traveled between patches further depended on adjustment of bison movements to forest matrix attributes.

**Inter-meadow trajectories**

We found that movement trajectories from one meadow to the next were, on average, 8% longer (range 0–25%) than the Euclidean distance linking the beginning and end of the trail. This longer path can be explained by adjustments in movements of individuals to habitat heterogeneity. Our approach accounts for the additive effects of a preference among land cover types and movement biases on the relative probability of use.
of habitat units encountered during inter-meadow travels. Unlike bison choices of which meadows they would next visit, we detected no preferences among deciduous, conifer, and mixed stands during inter-meadow movements. Therefore, functional connectivity was shaped by hierarchical movement decisions: forest stand composition influenced meadow selection at a broad scale, but not at a fine scale, during inter-meadow travels. Like many other ecological processes (Levin 1992, 2000), functional connectivity is therefore scale dependent.

We also found that bison paths were influenced by directional persistence and by biases toward the target meadows and canopy gaps. Bison seemed to use canopy gaps as stepping stones while traveling toward the target meadow. Identification of taxis shaping inter-patch trajectories therefore can be necessary for understanding functional connectivity. Such behavioral responses to landscape features at distances farther than the adjacent cell indicate that models based on cost distance (e.g., LCP) may not properly predict trajectories in the field (Walker and Craighead 1997). Moreover, models accounting only for the influence of land cover types characterizing adjacent cells (i.e., model 4) had poor empirical support, indicating that use of the LCP method in this system would not provide the most realistic depictions of bison trajectories. Models considering movement biases only (models 1, 2, and 3) also received poor empirical support. We therefore stress the necessity of combining both determinants of movement to adequately represent inter-patch trajectories.

Inter-meadow trajectories were assessed based on continuous paths (i.e., well-defined trails). As such, the approach outlined here easily could be applied to snow or sand tracks, which previously have been used to follow animal movements (Ward and Saltz 1994, Jayne and Irscick 2000, Whittington et al. 2004, Hebblewhite et al. 2005). The implementation of our method, however, does not require continuous movement paths. Turchin (1998) indicates the sampling intervals necessary to end up with meaningful movement information. With advances in GPS technology and tracking devices, 15–30 minute relocation intervals (e.g., Rode et al. 2006) can be achieved, which might provide sufficient information for studying inter-patch trajectories using the approach outlined here.

Integration of behavioral information to evaluate landscape connectivity

Our three-step approach provides empirical definition of patch connectivity, which is an essential step for studying landscape connectivity. Graph theory has been recognized as a promising framework in which landscape connectivity can be assessed from empirical information (Andersson and Bodin 2009, Kadoya 2009). Graphs consist of nodes connected by edges, where the nodes are high-quality patches (Urban et al. 2009). Graphs provide valuable information for landscape planning concerned with ecological fluxes between patches, both at the local and landscape scale (Urban and Keitt 2001, Kadoya 2009). For example, graphs have been used to inform resource management and reserve design (e.g., Bunn et al. 2000, Fall et al. 2007). To properly evaluate connectivity at any scale and provide adequate management strategies, graphs should be adapted to the focal animal population by including as much biological information as possible (Urban and Keitt 2001). Our study proposes steps to generate probabilistic movement rules that can be used to build such a graph, thereby gaining an empirical understanding of animal spatial dynamics.

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Literature Cited


