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Energy benefits and emergent space use patterns of an empirically parameterized model of memory-based patch selection

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(Abstract)

Many species frequently return to previously visited foraging sites. This bias towards familiar areas suggests that remembering information from past experience is beneficial. Such a memory-based foraging strategy has also been hypothesized to give rise to restricted space use (i.e. a home range). Nonetheless, the benefits of empirically derived memory-based foraging tactics and the extent to which they give rise to restricted space use patterns are still relatively unknown. Using a combination of stochastic agent-based simulations and deterministic integro-difference equations, we developed an adaptive link (based on energy gains as a foraging currency) between memory-based patch selection and its resulting spatial distribution. We used a memory-based foraging model developed and parameterized with patch selection data of free-ranging bison *Bison bison* in Prince Albert National Park, Canada. Relative to random use of food patches, simulated foragers using both spatial and attribute memory are more efficient, particularly in landscapes with clumped resources. However, a certain amount of random patch use is necessary to avoid frequent returns to relatively poor-quality patches, or avoid being caught in a relatively poor quality area of the landscape. Notably, in landscapes with clumped resources, simulated foragers that kept a reference point of the quality of recently visited patches, and returned to previously visited patches when local patch quality was poorer than the reference point, experienced higher energy gains compared to random patch use. Furthermore, the model of memory-based foraging resulted in restricted space use in simulated landscapes and replicated the restricted space use observed in free-ranging bison reasonably well. Our work demonstrates the adaptive value of spatial and attribute memory in heterogeneous landscapes, and how home ranges can be a byproduct of non-omniscient foragers using past experience to minimize temporal variation in energy gains.

Introduction

During patch selection, animals that are omniscient and know the location and profitability (i.e., digestible energy / handling time) of all foraging options would be expected to only forage in the best patch until the rate of energy gain decreases below the average energy gain of all foraging options (Charnov 1976). If those best patches are randomly distributed in the landscape, omniscient foragers should gradually drift away from their starting point because there is no systematic mechanism to bring them back to a particular location. The same outcome would result from foragers that are completely naïve to heterogeneity in energy gain and travel completely at random among food patches (Codling et al. 2008). In reality, animals are not omniscient and must gain information about their environment to deal with spatio-temporal heterogeneity in resource availability (Dall et al. 2005). The information gained while foraging still leaves animals with incomplete knowledge, which can result in strong differences in the food choices and spatial dynamics between non-omniscient and omniscient foragers. In addition, many species frequently return to previously visited patches (i.e., site fidelity; Piper 2011), resulting in space use patterns such as home ranges (Van Moorter et al. 2009). Home range behavior is among the most basic patterns observed in animals (Börger et al. 2008), and it influences many ecological processes including population regulation and biological transport of resources (Fagan et al. 2007, Wang and Grimm 2007). The disconnect between observed animal distributions and predictions of foraging models that assume omniscience or naivety, underscores the need to improve the understanding of how animals use their past experience during patch selection.

We contribute to this gap in knowledge by quantifying the energy benefits and emergent space use properties of the memory-based patch selection model developed and parameterized by Merkle et al. (2014) for free-ranging bison (*Bison bison*) in Prince

Albert National Park, Canada. The model has three main components, where animals employing it use spatial and attribute memory to choose food patches based on 1) whether or not they have previously visited them, 2) their reference point of patch profitability derived from recent foraging experience, and 3) their memory of the profitability of each previously visited patch (Merkle et al. 2014). The motivation for developing the model was based on the fact that theoretical developments of animal memory as a mechanism resulting in home range formation have assumed that foragers significantly deplete resources within patches during a visit (Nabe-Nielsen et al. 2013, Riotte-Lambert et al. 2015, Spencer 2012, Van Moorter et al. 2009). This assumption logically leads to the hypothesis that animals have a working memory, used to avoid recently depleted patches, and a reference memory, used to store preferences for certain feeding areas (Van Moorter et al. 2009). Many animals, however, are routinely on the move (Boinski and Garber 2000) and do not forage in a patch long enough to experience a decrease in intake rate (e.g., Fortin et al. 2009, Illius et al. 2002). In these cases, animals leave patches sooner than expected by energy maximization principles to sample and gather information about adjacent patches (Lima 1985) or to avoid predators (Mitchell and Lima 2002). Natural selection should thus favor individuals that have developed spatial memory so they can efficiently return to previously visited patches where they know food is still available (component 1 of the model). Component 1 is based on the hypothesis that animals develop a cognitive map of locations they have visited and bias their movements towards them (Benhamou 1997, Spencer 2012). This tactic differs from memory enhancement models, where selection for a site increases with the number of repeated uses of that site (Tan et al. 2001), and models where previously visited sites are chosen at random from all visited sites (Gautestad and Mysterud 2005). Component 1 does though incorporate memory decay for remembering previously visited sites (McNamara and Houston 1985, Merkle et al. 2014, Tan et al. 2002).

To further utilize past experience to their benefit, animals could also develop a system of attribute memory – the encoding of resource attributes without a spatial association (Fagan et al. 2013). Individuals in this case could keep a running mean of the quality of recently visited patches, which would provide a reference point to evaluate local resource quality (Fortin 2002, Fortin 2003), and a guide for when to return to previously visited sites within the individual’s cognitive map (component 2 of the model; Merkle et al. 2014). This foraging tactic is similar to Bayesian foraging where, at each time step, an animal can update its expected distribution of available site qualities by combining past and current information (Cheng et al. 2007). Individuals could also combine spatial and attribute memory so that they have a cognitive map of the distribution of patch quality (Avgar et al. 2013, Fagan et al. 2013, Nabe-Nielsen et al. 2013). Animals could then bias their movements towards patches that they know, from past experience, are of higher quality than their current reference point and avoid ones that are of lower quality (component 3 of the model; Bailey et al. 1996). Overall, in comparison to a forager selecting patches at random, combining spatial and attribute memory should provide animals with the information to maximize energy gains while resulting in restricted space use patterns (Boyer and Walsh 2010, Dalziel et al. 2008, Van Moorter et al. 2009).

Despite recent developments in memory-based foraging models (Fagan et al. 2013, Riotte-Lambert et al. 2015), including numerous hypotheses for how animals integrate past experience into their behavioral decisions (e.g., Avgar et al. 2013, Folse et al. 1989, Gautestad and Mysterud 2005, Van Moorter et al. 2009), there is a lack of demonstrations of: a) the benefits of empirically derived memory-based foraging models; b) the extent to which memory-based foraging models give rise to restricted space use patterns, and c) whether or not predicted space use patterns derived from fine-scale memory-based foraging models fit empirical space use patterns of wild animals (but see Boyer and Walsh 2010). As Merkle et al. (2014) did not examine emergent predictions of their memory-based patch selection model, we first employed an agent-based simulation approach to investigate the energy benefits of the model by monitoring the cumulative expected energy intake rate per distance traveled that simulated agents experience while foraging. Second, we employed an integro-difference equation approach (Potts et al. 2014) to examine the extent to which our memory-based movement model gives rise to restricted space use. Finally, to verify that predictions of the model have successfully captured key aspects of the empirical space use dynamics of bison, we again employed the integro-difference equation to test whether model predictions match movement trajectories of bison in their natural habitat over the course of a year. Because energy gains should be strongly linked to fitness, a fundamental premise of optimal foraging theory (Stephens and Krebs 1986), our analysis informs why memory-based foraging behavior might have evolved, and how such behavior can translate into restricted space use distributions.

Methods

Simulation approaches

We used an agent-based simulation and an integro-difference equation approach, respectively, to examine the energy benefits and restricted space use properties of memory-based movement. Both approaches rely on the same movement kernel (Fig. 1), but use it differently. A movement kernel is a probability distribution specifying the probability of moving to location x (a potential target patch) given being previously at location y (a given source patch; Fig. 1). At every iteration of an agent-based simulation, a target patch is selected by an agent based on a probability proportional to the movement kernel, and the agent then moves to that patch. The agent-based simulation approach results in a movement trajectory of a single animal over time. By contrast, for the integro-difference equation approach, the movement kernel is converted into a *master equation* (ME; Van Kampen 1992), enabling quantitative investigation of how space use patterns emerge from the underlying movement process (Potts et al. 2014). Instead of simulating individuals, as in the agent-based approach, the ME gives the probability density of a population at some time $t + \Delta t$ as a function of both the probability density at time *t*, and the movement kernel. Denoting the probability that the population is in patch x at time *t* by $u(\mathrm{x},t)$, the ME is

$$u(\mathrm{x}, t + \Delta t) = \sum_{y \epsilon \Omega} f(\mathrm{x}|\mathrm{y}, \varepsilon, \boldsymbol{\gamma}, \boldsymbol{\beta}) u(\mathrm{y}, t) \quad (1)$$

where $f(\mathrm{x}|\mathrm{y}, \varepsilon, \boldsymbol{\gamma}, \boldsymbol{\beta})$ is the movement kernel, and Ω is the set of all patches in the landscape. Note that the general form of an integro-difference equation has an integral expression on the right-hand side, whereas in eq. 1 there is a sum. The reason for this, in our case, is that the spatial domain is a discrete set of patches, and an integral over a discrete domain is defined to be a sum over that domain. The main advantage of using a ME (i.e., integro-difference equation) over stochastic, agent-based simulations comes when calculating the utilization distribution over time, u(x,t). The ME allows for such a calculation in a single, deterministic numerical simulation, whereas it would take a very large number of agent-based stochastic simulations to obtain an accurate estimate of u(x,t) (see Potts et al. [2014] for more details on its use with SSFs).

For both approaches, the movement kernel is calculated as

$$f(\mathrm{x}|\mathrm{y}, \varepsilon, \boldsymbol{\gamma}, \boldsymbol{\beta}) = K^{-1} \Phi(\mathrm{x}|\mathrm{y}, \boldsymbol{\gamma}) W(\mathrm{x}, \mathrm{y}, \varepsilon, \boldsymbol{\beta}). \quad (2)$$

where $\Phi(\mathrm{x}|\mathrm{y}, \boldsymbol{\gamma})$ is a step length distribution, $W(\mathrm{x},\mathrm{y},\varepsilon,\boldsymbol{\beta})$ is a Step Selection Function (SSF; Fortin et al. 2005) denoting the effect of the environment on the animal's movement, and *K* is a normalizing constant ensuring $f(\mathrm{x}|\mathrm{y},\varepsilon,\boldsymbol{\gamma},\boldsymbol{\beta})$ integrates to 1 with respect to x (Fig. 1). Eq. 2's formulation assumes a uniform turning angle distribution. The symbol ε denotes the information that the animal has about its environment, $\boldsymbol{\gamma}$ is a vector of parameters for the step length distribution, and $\boldsymbol{\beta}$ is a vector of coefficients denoting the strength that each of the pertinent environmental covariates has on the animal movement.

In the present study, $\Phi(\mathrm{x}|\mathrm{y}, \boldsymbol{\gamma})$ is a Weibull distribution

$$\Phi(\mathrm{x}|\mathrm{y}, \boldsymbol{\gamma}) = \frac{\kappa}{\lambda}\left(\frac{dist}{\lambda}\right)^{\kappa-1} e^{-\left(\frac{dist}{\lambda}\right)^{\kappa}}, \quad (3)$$

where $\boldsymbol{\gamma} = (\kappa,\lambda)$, κ is the shape parameter, λ is the scale parameter, and *dist* is the distance between x and y. The SSF is

$$W(\mathrm{x},\mathrm{y},\varepsilon,\boldsymbol{\beta}) = \exp(\boldsymbol{\beta}\cdot\mathbf{Z}), \quad (4)$$

where $\mathbf{Z} = \mathbf{Z}(\mathrm{x},\mathrm{y},\varepsilon)$ and $\boldsymbol{\beta}\cdot\mathbf{Z}$ is the scalar product of $\boldsymbol{\beta}$ and $\mathbf{Z}$. Each of the entries in the vector $\mathbf{Z}$ can be derived from knowledge of x, y and ε, but we drop the explicit dependence of $\mathbf{Z}$ on these parameters for notational convenience. Details of $\boldsymbol{\beta}$ and $\mathbf{Z}$ are explained below.

The memory-based patch selection model

The memory-based foraging model developed by Merkle et al. (2014) is a statistical model taking the form of a SSF (Fortin et al. 2005) of patch-to-patch movements, where at each discrete time step, an animal chooses among available target patches based on a set of environmental parameters. The model is comprised of three main components (i.e., parameters). First, animals choose patches they have previously visited more often than random (*PrevVis*). *PrevVis* is an indicator of whether or not an individual has previously visited a given patch. Second, animals are more likely to choose previously visited patches if the profitability of their current patch (i.e., an indicator of local patch quality) is lower than their recent past experience (*PrevVis* × *RelRefPoint*). *RelRefPoint* is calculated as the reference point (i.e., mean profitability of previously visited patches multiplied by a memory decay function of time) minus the profitability of the currently occupied patch. Third, individuals choose patches with a relatively high profitability given what they know about their options (*ExpProfit*).

ExpProfit or expected profitability is calculated for a given patch based on whether or not the animal has previously visited it. If the patch has not been previously visited, the patch's *ExpProfit* is the animal's reference point. If the patch has been previously visited, the patch's *ExpProft* is the actual profitability of the patch multiplied by a memory decay function which tends towards the animal's reference point over time (Bailey et al. 1996). The memory decay function in all components is calculated as $1/(1+k \times t)$, where k is the devaluation or memory decay factor and t is time in hours since the event happened. See Merkle et al. (2014) for further details on how the variables were calculated. Altogether, the vector of parameters of the memory-based foraging tactic is $\mathbf{Z} = (Dist, Area, PrevVis, PrevVis \times RelRefPoint, ExpProfit)$. Here, *Dist* is the distance between x and y, and *Area* is the area of a potential target patch. The other entries of **Z** – *PrevVis*, *RelRefPoint*, and *ExpProfit* – are related to memory and explained above. The vector $\boldsymbol{\beta} = (\beta_{Dist}, \beta_{Area}, \beta_{PrevVis}, \beta_{Prevvis \times RelRefPoint}, \beta_{ExpProfit})$ is a vector of coefficients representing the strength of influence given by each variable in **Z**.

Energy benefits of memory-based patch selection

Simulated landscapes – Because the energy benefits of memory are expected to be highest among landscapes with intermediate spatial complexity (Fagan et al. 2013), we simulated four different landscapes with the same randomly located patches, but with varying degrees of the observed spatial autocorrelation in patch profitability found in Prince Albert National Park. We simulated one landscape with no spatial autocorrelation, one with the observed autocorrelation, and two landscapes with relatively high (i.e., five and ten times more than observed) autocorrelation (see Appendix A for details). These simulations provided landscapes with a resource gradient from approximately random to highly clumped (Fig. 2).

Parameter values and starting locations – To examine the energy benefits of memory-based foraging, we monitored the energy gains that simulated agents experienced across

20 different scenarios. The scenarios included all combinations of the four simulated landscapes, and five different sets of parameters values (i.e., strength of movement bias with respect to each memory component) governing the influence that memory-based foraging behavior has over random movement. Using the observed parameter values (i.e., $\boldsymbol{\beta} = [-0.661, 0, 0.822, 0.896, 2.282]$) for bison during winter as a baseline (Merkle et al. 2014), we increased the relative odds (exponent of the $\boldsymbol{\beta}$s) of choosing patches with parameters $\beta_{PrevVis}$, $\beta_{Prevvis \times RelRefPoint}$, and $\beta_{ExpProfit}$ by factors of 3, 6, 9, and 12 times. For example, to increase the relative odds by a factor of 3, we calculated each new β_i as $\ln(\exp(\beta_i) \times 3)$, where i = *PrevVis, Prevvis*×*RelRefPoint,* or *ExpProfit*.

We only used parameter values from winter because i) winter was the season when all components were supported by empirical movement, and ii) we did not want to add temporal variation in patch selection because of its potential to muddle our inference on energy benefits and space use over time. Our specified variation in parameter values allowed us to assess the relationship between random movement and the strength of memory-based movement bias with respect to energy gains (Boyer and Walsh 2010). We did not assess the effect of patch area (i.e., β for *LogArea* was always specified as 0), as we were interested in the rate of energy gain within patches only.

To examine the energy benefits of spatial and attribute memory separately, we examined three models (two additional models) representing the effect of each of the three components of the memory-based foraging model: agents equipped with the ability to remember (1) patch location only ("Loc": *PrevVis*), (2) patch location and a running mean of previous experience ("Loc + RP": *PrevVis* and *PrevVis* × *RelRefPoint*), and (3) patch location and quality along with a running mean of past experience (i.e., the full memory-based foraging model; "Loc + RP + Qual": *PrevVis* and *PrevVis* × *RelRefPoint* and *ExpProfit*). For each scenario, we specified parameter values of $\boldsymbol{\beta} = [-0.661, 0, 2.61, 2.68, 4.07]$ for $\mathbf{Z}$ = [*Dist*, *Area*, *PrevVis*, *ExpProfit* ×

RelRefPoint, *ExpProfit*] (i.e., six times the size of the exponent of the observed parameter values). These parameter values were found to produce the highest cumulative expected energy intake rate per distance traveled over time (see Results). The two additional models were simulated over all four landscapes (adding eight additional scenarios, totaling 28).

For all simulations, we specified the Weibull shape and scale parameters as κ = 1.12 and λ = 1.41, respectively (see Appendix B for details), representing estimates of the observed annual distribution of step lengths of patch-to-patch movements (n = 19,903) for bison (Merkle et al. 2014). For all simulations, we used devaluation factors (i.e., parameter of the weighting function of past experience) for memory-based variables reported in Merkle et al. (2014). Briefly, the devaluation factors for remembering the location of sites were near 0, meaning that once a patch is visited, its location is not forgotten. Devaluation factors for remembering patch profitability were higher, suggesting that there is memory decay, and patch information becomes forgotten or valueless over time (see Merkle et al. 2014 for details).

To emulate the movement of bison within their natural habitat, we assumed that the agents within our simulation represent a single group. Given our knowledge of population size (mean 420; Merkle et al. 2015) and winter group size (mean = 16; Fortin et al. 2009) within the year that patch depletion was estimated (i.e., 2007), we simultaneously monitored 26 agents (420/16 ≈ 26) in each simulation, with each agent representing a group. Starting locations of the 26 agents in each simulation were chosen by randomly placing each agent in a patch that was < 2 km from the center of the landscape and had an expected intake rate that was greater than the landscape mean. We chose to start individuals in patches that had a greater than average profitability to reflect that, i) during a reintroduction effort, individuals would likely be released in patches that were better than average, and ii) when bison are young, they learn about their landscape by following their mother, which is assumed to use patches with a profitability that is equal to or higher than average because she has successfully raised a calf. Finally, we verified that random variation in the specified patch profitability in the simulated landscapes would not influence comparisons across the landscapes. The mean profitability of all patches < 2 km from the center of each simulated landscape was < 2.2 units (< 10% of 1 SD) away from the observed mean of 699.8 kJ/min.

We started simulations on the first day of the growing season (which lasts 156 steps from May through August), and monitored agents for a total of 28 months (1,092 steps), with the time-step length $\Delta t = 18.8$ h (representing the mean of the observed distribution of residency times plus inter-patch travel time for bison). As in Van Moorter et al. (2009), we specified the first 156 steps as an initial transition or learning phase, and removed it from further analyses. For each of the 28 different scenarios for simulation, we ran 100 replicates (i.e., 100 different populations), providing 2,600 individual trajectories used for further analyses. Although resource depletion by bison is minimal in our study system (Merkle et al. 2015), we still incorporated a decrease in patch profitability after an agent moves through a patch during our simulations. Further, during the growing season, we also incorporated regrowth in vegetation during the growing season (see Appendix C for details).

Analysis of energy intake rate – To estimate the energy benefits of the memory-based foraging model, we calculated the sum of the gross energy gains consumed (in kJ of digestible energy obtained per min) while taking into account travel time based on distance (in km) from the previous patch at each time step (sensu Mitchell and Powell 2004). Bison travel between feeding stations within a patch at a mean speed of approximately 23.9 m/min (Fortin et al. 2002); thus, it takes bison approximately 41.9 min to travel one km. Bison spend a mean of 642 min/day foraging (Hudson and Frank 1987), which we translated to spending 502 minutes foraging at each time step Δt. Thus, our index (*E*) of the cumulative expected energy intake rate per distance traveled (*Dist*) was calculated as

$$E = \sum_{t=1}^{936} \frac{p(\mathrm{x}, t) \times 502}{Dist \times 41.9} \ (7)$$

where $p(\mathrm{x}, t)$ is the profitability of patch x at time *t*. To be conservative in assessing differences in the cumulative resources consumed among the different scenarios, we calculated population level 95% CIs (i.e., $1.96 \times \sqrt{\sigma^2/100}$). We considered the energy benefits between two scenarios to be different if the 95% CI did not overlap.

Finally, to establish a point for comparison, we also simulated a random and informed forager in each of the four landscapes. The random forager chose patches based on a probability proportional to the step length distribution $\Phi(\mathrm{x}|\mathrm{y},\boldsymbol{\gamma})$. The informed forager knew the location and profitability of all patches in the landscape and chose patches based on a probability proportional to the ratio of expected profitability of each patch divided by distance, multiplied by the step length distribution $\Phi(\mathrm{x}|\mathrm{y},\boldsymbol{\gamma})$. For these two foragers, we also monitored *E*, as explained in the previous paragraph.

Emergent space use properties of memory-based patch selection

Because the integro-difference equation approach (i.e., the ME) deals with probabilities, and not individual locations, some modifications needed to be made in the calculation of patch depletion and regrowth, as well as the incorporation of memory into the movement kernel (details of the modifications can be found in Appendix D).

Parameters and starting locations of the ME – All parameters for the 28 scenarios for the ME were the same as the agent-based simulation. However, because the ME determines space use at the population level, we modified how starting locations were specified. For each of the four landscapes, we started the ME as if the populations were equally distributed among all the patches that were both < 2km from the center and had greater than the mean profitability of the landscape. With this specification, we were able to eliminate any potential bias associated with starting locations. As with the agent-based simulation, we specified a learning phase of 156 steps. After this period, we restarted the ME at the same starting locations, and monitored for a total of 936 additional steps.

Analysis of space use – We examined the resulting space use distribution of the ME in two ways. First, we monitored mean squared displacement (MSD) of the cumulative utilization distribution over time, using the mean of the starting locations as the initial location. Such a cumulative MSD is comparable to calculating the total area covered over time, as was executed in Van Moorter et al. (2009). Second, to compare the relative stability of the utilization distribution over time (i.e., development of a home range), we calculated the predicted utilization distribution of the ME for each of the two years after the learning phase. We calculated the distribution by summing the $u(\mathrm{x},t)$ for each patch over the course of the year in question. Using the resulting distributions at each patch location as weights, we then estimated a kernel density using a 200 m grid and a fixed bandwidth matrix of 1 km for easting and northing. We calculated the overlap between the utilization distribution of the two years using the volume of overlap statistic of the 95% utilization distribution (Fieberg and Kochanny 2005). As a comparison, we also calculated the volume of overlap between the distribution of bison over consecutive years (see below for how the bison data were prepared for calculating kernel density estimates).

Space use of observed and simulated bison in empirical landscape

To verify that predictions of the memory-based foraging model have successfully captured key empirical space use dynamics of bison, we used the integro-difference equation approach to assess whether changes in the ME over time were similar to actual movement and space use data of bison from inside the boundaries of Prince Albert National Park. Between 2005 and 2013, we monitored the movements of adult (> 2 years old) female bison using GPS collars (CanadaGPS collar 4400M, Lotek Engineering, Newmarket, Ontario; Telonics Argos [TGW-4780H], Telonics, Mesa, Arizona, USA). Locations of bison were taken every three hours. For the analysis, we used data from 25 bison that were collared for full consecutive years (April to March), resulting in a total of 41 bison-years (i.e., some bison were collared for two years). We then adapted the data into a patch-to-patch framework so that trajectories could be compared to simulations. To do so, for each individual we identified the locations that represented the last GPS location that was taken within a meadow, before a subsequent location was collected in another meadow (i.e., a patch-to-patch movement).

For comparison, we used the integro-difference equation approach to simulate matched 41 trajectories. In this case, we considered the ME to represent the movement kernel of an individual. We monitored changes in the ME for one year (i.e., 468 steps), based on starting locations derived from the first meadow visited in April by the collared bison in each bison-year. We chose starting locations in April because this month represents a period when bison are in transition between their large winter range to their smaller summer range. As with above, we specified the vegetation growing season as the months May to August. We parameterized the ME using the seasonal coefficients β and devaluation factors *k* reported in Merkle et al. (2014). These parameters include selection for relatively large meadows (See both Merkle et al. 2014 and Dancose et al. 2011), which likely explains why the ME in this case predicts much less diffusive space use than the ME parameterized in our simulated landscapes. All other parameters (e.g., step length distribution) were specified as reported in the "Parameter values and starting locations" sections.

Using the coordinates of the initial meadows as starting points, we calculated MSD of the ME at each time step. We then calculated the predicted utilization distribution of each simulated individual over the entire monitoring period by summing the $u(\mathrm{x},t)$ for each meadow over the course of the year, then averaging these distributions across each meadow for each of the 41 simulated trajectories. Using the resulting distributions at each meadow location as weights, we then estimated a kernel density using a 200 m grid and a fixed bandwidth matrix of 1 km. To assess restricted space use predictions, we first compared MSD between observed trajectories and the ME over time, with the expectation that 95% CIs of estimates would overlap over time. We then calculated the overlap between the utilization distribution of the observed bison-years and the ME (Fieberg and Kochanny 2005). We report: i) the probability that theoretical individuals from the ME can be found in the utilization distribution of the GPS collared bison, and ii) the volume of intersection between the two distributions. All analyses were conducted in R, version 3.1.0 (R Core Team 2014).

Results

Energy benefits of memory-based patch selection

The combined memory-based foraging model included agents equipped with the ability to remember (while taking into account memory decay) 1) patch location, 2) a running mean of previous experience, and 3) patch quality (Loc + RP + Qual). Relative to the random forager, simulated agents using this foraging behavior experienced an approximately 8% higher cumulative expected energy intake rate per distance traveled (E) over the two years of simulation (Fig. 3, left panel). As expected, energy benefits of the memory-based foraging model were influenced by the spatial autocorrelation in patch quality. As landscapes became more clumped in their distribution of patch profitability, memory allowed agents to choose patches which led to higher energy gains (Fig. 3, left panel). For all landscapes, E peaked near parameter values that were six times larger than the exponent of the observed memory-based parameters. In other words, some amount of random movement was beneficial for the simulated foragers (Fig. 3, left panel).

Relative to the random forager, agents that remembered patch locations and biased their movements towards previously visited sites (Loc) experienced an approximately 3% increase in *E*. Keeping a running mean of the intake rate experienced in previously visited patches, and using it to return when past experience was better than local profitability (Loc + RP), was only beneficial in landscapes with relatively high spatial autocorrelation in patch profitability. In these cases, *E* was approximately 1% higher than for agents with only a bias towards previously visited patches. *E* was greatest for agents that remembered both patch location and quality, and biased choices towards patches that have a greater expected profitability than recent past experience (Loc + RP + Qual). These agents experienced a 5% increase in *E* compared to agents able to remember only patch locations and a reference point. Again, the increase in *E* was more pronounced in landscapes with relatively high spatial autocorrelation in patch profitability (Fig. 3, right panel). Although there are benefits to using spatial and attribute memory over random movement, the energy benefits of these abilities do not approach that of the informed forager. In comparison to agents equipped with the complete memory-based foraging model, informed agents experienced nearly twice the *E* during the simulation (Fig. 3).

Emergent space use properties of memory-based patch selection

A gradient of weak to strong population-level restricted space use patterns were observed in our simulations using the integro-difference equation approach, where the underlying movement process was parameterized by all three components of the memory-based patch selection model (Fig. 4b). These findings were consistent across landscapes of varying spatial autocorrelation in patch profitability. Simulations with parameter values of the complete memory-based patch selection model that were similar to observed parameters provided the least restricted space use and strongest diffusive space use patterns, where the final MSD was 7% smaller than the random forager

(Appendix E). Increasing the size of the parameter values (i.e., decreasing the influence of random movement over memory-based foraging behavior) resulted in the least diffusive space use patterns with a MSD that was up to 85% smaller than the random forager (Appendix E; Fig. 4b). In comparison to changing the strength of movement bias with respect to memory, the spatial autocorrelation of patch profitability within simulated landscapes had less effect on overall MSD. Differences in the ending MSD among landscapes were always < 5% of the differences among parameter values (Appendix E).

The cumulative MSD was higher for random foragers than for simulated animals that used any of the three memory-based foraging model components (Fig. 4). Notably, in all landscapes, the full memory-based foraging model (Loc + RP + Qual) resulted in a slightly larger spatial distribution than a tactic with only a bias towards previously visited sites (Loc; Fig. 4). However, adding the reference point as a guide for determining when to return to previously visited sites (Loc + RP) resulted in a significant decrease (> 40% decrease across landscapes) in the ending MSD and diffusive space use patterns compared to a tactic with only a bias towards previously visited sites (Loc; Fig. 4).

The stability of the total utilization distribution between years one and two of the simulations varied with the strength of parameter values, and to a lesser extent, the spatial autocorrelation of quality within simulated landscapes. In contrast to the random forager (i.e., volume of intersection ≈ 0.59), the stability of the utilization distribution between year one and two was strongest for populations with the largest parameter values (e.g., least amount of random patch use) in highly clumped and random landscapes (volume of intersection ≈ 0.81). Populations with smaller parameter values in any landscape were only slightly more stable (volume of intersection ≈ 0.61) than the random forager (Appendix F). For reference, the volume of overlap (i.e., stability) between years one and two of monitoring for 15 individual bison was on average 0.68 (SE = 0.05).

Space use of observed and simulated bison in empirical landscape

Space use derived from the integro-difference equation approach using the memory-based foraging model predicted the empirical space use of bison within Prince Albert National Park reasonably well (Fig. 5). The 95% CI of MSD over the course of a single year for both observed individuals and the simulated ME generally overlapped (Fig. 5a). For the UD, the probability that simulated individuals from the ME were found in the utilization distribution of the observed bison was 0.78. The volume of intersection between the two UDs was 0.60. In general the ME predicted the core area of the bison population in Prince Albert National Park well, but predicted a wider peripheral population range than actually observed (Fig. 5b, c).

Discussion

Recent reviews have suggested that mechanistic processes for how home range patterns emerge are lacking (Börger et al. 2008, Potts and Lewis 2014, Spencer 2012). In response to such suggestions, numerous studies on the use of memory by foragers have emerged (Avgar et al. 2013, Boyer and Walsh 2010, Folse et al. 1989, Nabe-Nielsen et al. 2013, Riotte-Lambert et al. 2015, Van Moorter et al. 2009). Nonetheless, few studies have tested predictions regarding energy benefits and emergent space use patterns of memory using an empirically derived memory-based foraging model (e.g., Nabe-Nielsen et al. 2013). Here we evaluated such predictions using a memory-based movement model where animals use spatial and attribute memory to choose food patches based on three components: 1) whether or not they have previously visited them, 2) their reference point of patch profitability derived from recent foraging experience, and 3) their memory of the profitability of each previously visited patch. Using an agent-based simulation approach, we first demonstrate that in comparison to choosing patches at random, memory-based foraging decisions have adaptive value by increasing feeding efficiency. Second, we use an integro-difference equation approach to show that the use of memory by foragers leads to restrictions in population-level spatial distribution. Finally, the emergent space use properties of the memory-based patch selection model are realistic when simulating bison distribution in their natural habitat; the space use of simulated individuals fit the observed trajectories of free-ranging bison reasonably well.

Because the strength of site fidelity increases with an increase in the strength of movement with respect to previously visited sites, energy intake rate will be lower for animals with poor knowledge of the most profitable patch locations in the foraging area. Even if an animal has perfect memory of where it has been foraging, this information may not be useful if relatively high quality patches have never been visited. Thus, the animal could not learn anything new if it did not occasionally employ a random search pattern or visit a new site. For example, animals that employ an extensive search mode after encountering a relatively poor quality site compared to recent past experience will increase overall foraging efficiency (Fortin 2002). Such patch sampling behavior provides information about whether or not certain areas might be richer, and thus worth exploiting (Lima 1985). Without this ability, our simulations demonstrate how cumulative expected energy intake rate per distance traveled will saturate (or even decline) with a decrease in the probability of choosing a random patch (i.e., increasing the movement bias relative to memory). Indeed, frequently moving into unknown patches (e.g., exploratory behavior, experimental forays) affords fitness advantages, including enhancing an animal’s capacity to quickly adapt to changing environments (Lefebvre et al. 2004). Other theoretical models predict similar patterns (Boyer and Walsh 2010, Nabe-Nielsen et al. 2013), where incorporating intermediate levels of both random movement and memory-based navigation proves most efficient for foragers.

Whereas their models are based on the rate of switching between memory-based and random search movements, the patch selection model presented here combines the two, with the size of the parameter guiding the strength of memory-based versus random patch use.

We employed stochastic, agent-based simulations and a deterministic numerical approach (i.e., integro-difference equation) to determine energy benefits and emergent space use patterns, respectively. The agent-based simulation approach was beneficial for monitoring intake rate of simulated agents. Yet, for determining population-level space use patterns, an agent-based simulation framework can be influenced by the number of stochastic realizations employed. Further, predictions using this framework need greater technical analysis to verify that they are robust to stochastic fluctuations and generally require significant computational power (Potts et al. 2014). Thus, we formulated a ME allowing for the emergent space use properties to be solved deterministically (Potts et al. 2014). Such a generalization of the commonly-used SSF (Fortin et al. 2005), allows for inference of all possible outcomes of the animals' behavior (at the population-level) in a single equation (Moorcroft and Barnett 2008). The integro-difference equation approach provides a stepping-stone between individual-based models and mathematically tractable mean-field models, such as those exemplified by Moorcroft and Lewis (2006). By translating what an animal might remember from many previous time steps into a single equation defined across the entire landscape (following Potts et al. 2014), the model described here provides robust predictions of how memory-based individual-level foraging behavior results in population-level spatial distribution.

Classic random walk models do not predict restricted space use patterns (Börger et al. 2008), and up until recently, space use predictions resembling a home range have only been produced in territorial species and central place foragers, or by defining landscape boundaries (Briscoe et al. 2002, Moorcroft and Lewis 2006, Potts and Lewis

2014, Stamps and Krishnan 1999). Recent advances by, for example, Van Moorter et al. (2009) and others who have adapted Van Moorter et al.'s model (Nabe-Nielsen et al. 2013, Riotte-Lambert et al. 2015), have used a memory-based foraging model to clearly demonstrate restricted space use patterns in non-territorial or central place foragers, and without defining boundaries. Here, we demonstrate similar patterns of restricted space use based on our memory-based patch selection model. However, our model differs from others (e.g., Nabe-Nielsen et al. 2013, Riotte-Lambert et al. 2015, Van Moorter et al. 2009), because we do not assume that animals significantly depress expected profitability at each visit. Further, in contrast to Tan et al.'s (2002) model with memory enhancement and decay of previously visited sites, our model predicts a constant home range core that does not drift away from its starting location over time.

In support of previous predictions (Bailey et al. 1996, Stamps and Krishnan 1999), the ability of foragers to remember the location and the profitability of previously visited patches led to the highest energy gains of all memory-based foraging components we examined. Yet, this full memory-based model did not lead to the smallest possible space use distribution. Instead, similar to a Bayesian forager (Cheng et al. 2007), foragers that use a reference point to inform when they have entered a poor quality area, and thus when to return to a previously visited site, had the smallest space use distribution of all memory-based foraging components we examined. In addition, such a tactic led to higher cumulative expected energy intake rate per distance traveled in spatially autocorrelated landscapes compared to foragers that could only remember the location of previously visited sites. As previously hypothesized (Merkle et al. 2014, Spencer 2012), if an animal moves towards the edge of a clump of high-quality patches, it can "turn-around" and remain within its clump after visiting a patch that seems to be of rather poor-quality. Such a decision will reduce the temporal variation in energy gains, which is a fundamental objective of risk-sensitive foragers (McNamara and Houston 1992).

In the simulated landscapes, observed parameter values of the memory components were not strong enough to detect large reductions in diffusion and MSD (only a 7% decrease in MSD) over time compared to random foragers. Further, based on energy gains of agents in our simulations, we would expect parameter values of memory based foraging to be six times higher than observed in bison. We propose two reasons for why observed behavior was more similar to choosing patches at random than expected given the results of our simulations. First, prior to parameterizing the memory-based patch selection model, Merkle et al. (2014) removed the first three months of movement data to reduce false negatives for selecting previously visited meadows. However, since there was little to no memory decay detected for remembering previously visited meadows in bison, there were likely a significant number times when bison chose previously visited meadows that were classified as not previously visited, particularly within the first year of monitoring. Such false negatives in identifying previously visited meadows likely biased *PrevVis* (or selection for previously visited patches) toward zero, resulting in MSD that was more similar to a random forager than expected. Second, variation in intake rate of digestible energy in our observed and simulated landscapes ranged from 600-800 kJ/min. Thus, making a foraging error and choosing the worst patch over the best patch only led to a maximum 25% decrease in intake rate for that animal. If making a patch selection error led to an expected intake rate of 0 kJ/min, we would expect adaptive evolution to result in a stronger influence of memory-based behavior than we observed. Nonetheless, our results reiterate how difficult it is to extract true memory processes from empirical movement patterns of free-ranging animals, and we suggest that our methodological advancements and simulation results be the focal contribution of this study.

There are clear differences between the expected spatial dynamics of foragers with memory capabilities and omniscient and randomly traveling foragers; the use of memory of past experiences is more likely to result in restricted space use, as commonly observed among mobile animals. Explicit illustrations of emergent home range patterns derived from empirically established movement data are particularly scarce (but see Nabe-Nielsen et al. 2013). In a step towards bridging this gap, our results demonstrate how memory-based foraging is beneficial and will result in restricted space use dynamics (Nabe-Nielsen et al. 2013, Van Moorter et al. 2009). Based on our simulations, the memory-based patch selection model developed in Merkle et al. (2014) makes two general predictions that are robust across foraging and spatial ecology disciplines. First, although it is beneficial for animals to have excellent memory, it is adaptive to occasionally employ random movement so as to "discover" better food patches or "sample" others to verify that current knowledge is still good (Boyer and Walsh 2010). Secondly, animals that employ such a memory-based foraging tactic will portray space use patterns that resemble a home range (Van Moorter et al. 2009). Our work therefore provides a detailed understanding of why memory-based foraging behavior may have evolved and how these processes give rise to restricted space use and home range patterns.

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Figure Legends

Figure 1. Flow chart depicting how various aspects of the memory-based movement model fit together into either an agent-based simulation or a master equation of space use (eq. 1). For each arrow, the quantity at the tail of the arrow feeds into the quantity at the head of the arrow. Where applicable, numbers in brackets refer to pertinent equations from the text and in Appendices C and D.

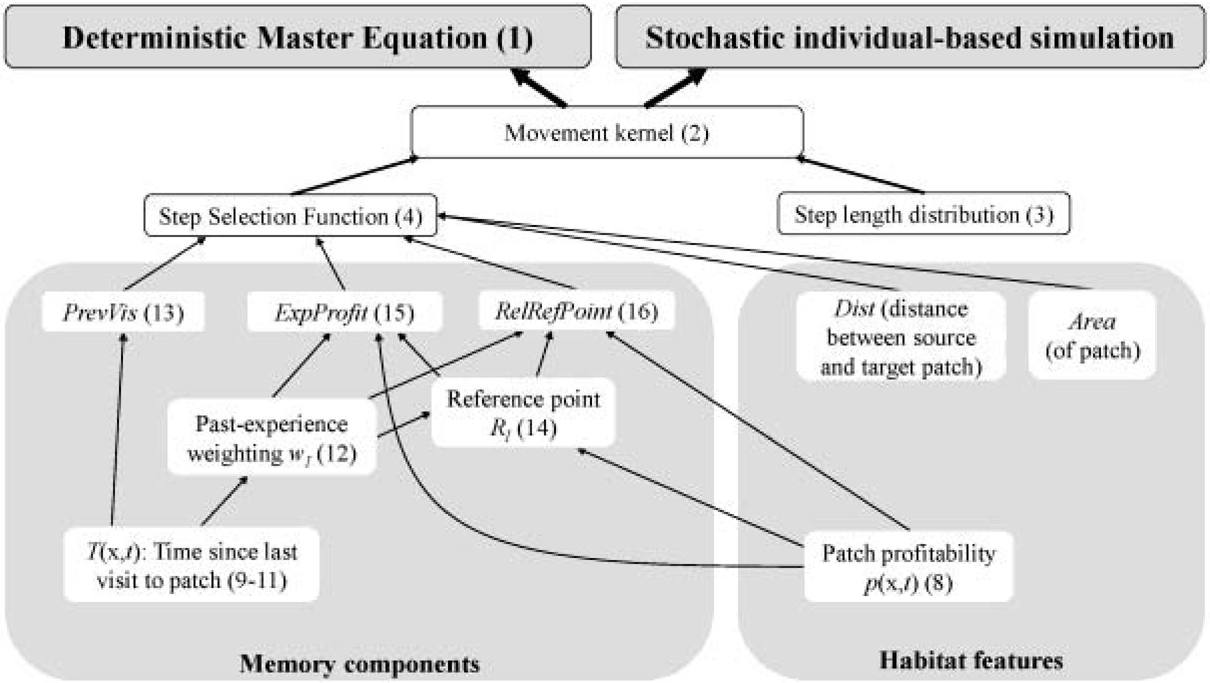

Figure 2. Simulated landscapes with varying levels of spatial autocorrelation in the expected profitability (kJ of digestible energy / min) of patches. Patches within each landscape have a mean expected profitability of 699.8 (SD = 22.0). Landscape configurations include completely random (a), the observed spatial covariance structure of patch profitability within the bison range of Prince Albert National Park (Canada; b), and five (c) and ten (d) times the spatial autocorrelation as the observed. Simulated landscapes were based on a random generate of a Gaussian stationary isotropic covariance model. For visual clarity, we only show the inner section of each landscape, consisting of a 20 km radius.

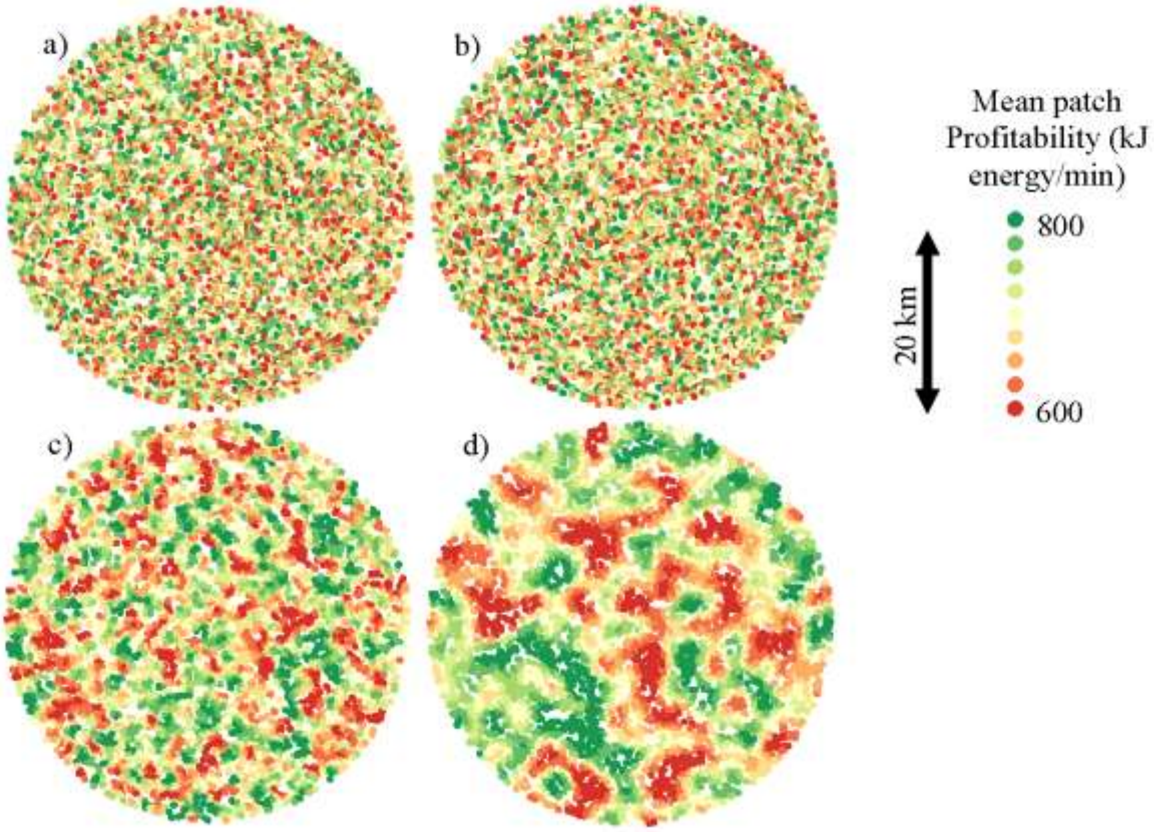

Figure 3. The energy benefits of using memory during patch selection in four landscapes with varying spatial autocorrelation in patch profitability (from random [a] to highly clumped [d]; see Fig. 2). Points represent a mean (vertical lines represent population-level 95% CI) of the cumulative expected energy intake rate per distance traveled at each step (*E*). Agents foraged for 936 steps (approx. two years) with varying influence (from the observed odds [exponent of β] to 12 times the observed odds) that all components of the memory-based foraging model have over random movement (left panel), and different components of memory-based foraging model employed separately (with a × 6 influence of memory on movement; right panel). Types of memory components include: 1) a bias towards previously visited patches (i.e., Loc), 2) using a reference point to determine local patch quality (Loc + RP), and 3) the ability to remember profitability of previously visited patches (Loc + RP + Qual). For comparison, we include an agent choosing patches at random (“Rand”), and an informed forager with perfect knowledge of patch profitability and travel costs (“Informed”).

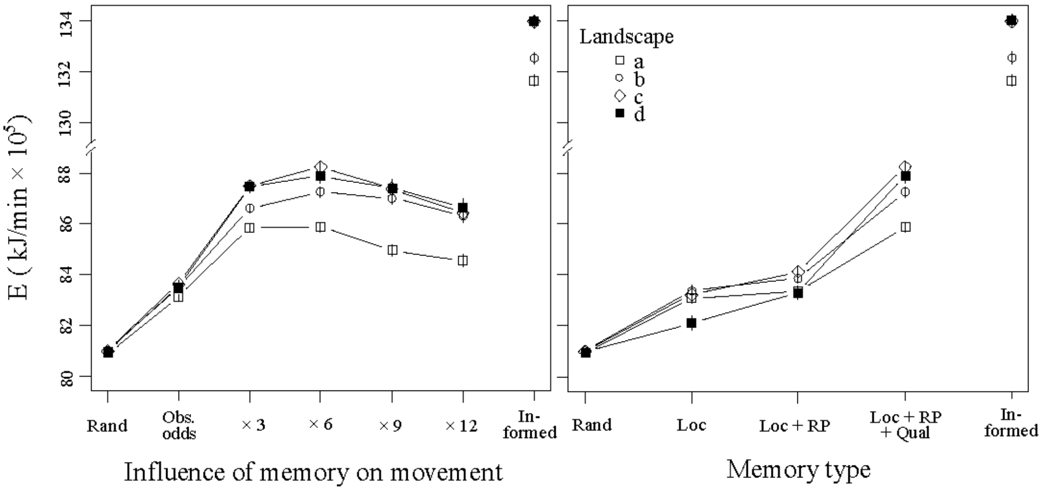

Figure 4. Mean squared displacement of the cumulative utilization distribution of simulated populations over time (two years, 936 steps) across the three memory-based patch selection components (a), and varying influence (from the observed odds [exponent of β] to 12 times the observed odds of wild bison) that the memory-based behavioral model employed simultaneously has over random movement (b), as well as the total utilization distribution (c, d) of two of the memory-based patch selection components estimated using an integro-difference equation approach. Types of components include: 1) a bias towards previously visited patches (i.e., Loc), 2) using a reference point to determine local patch quality (Loc + RP), and 3) the ability to remember profitability of previously visited patches (Loc + RP + Qual). For illustrative purposes, we report results from the master equation that was monitored in the clumped simulated landscape (landscape d). Black lines represents mean squared displacement of an agent choosing patches at random. Yellow and green in b and c represent areas of relatively high use.

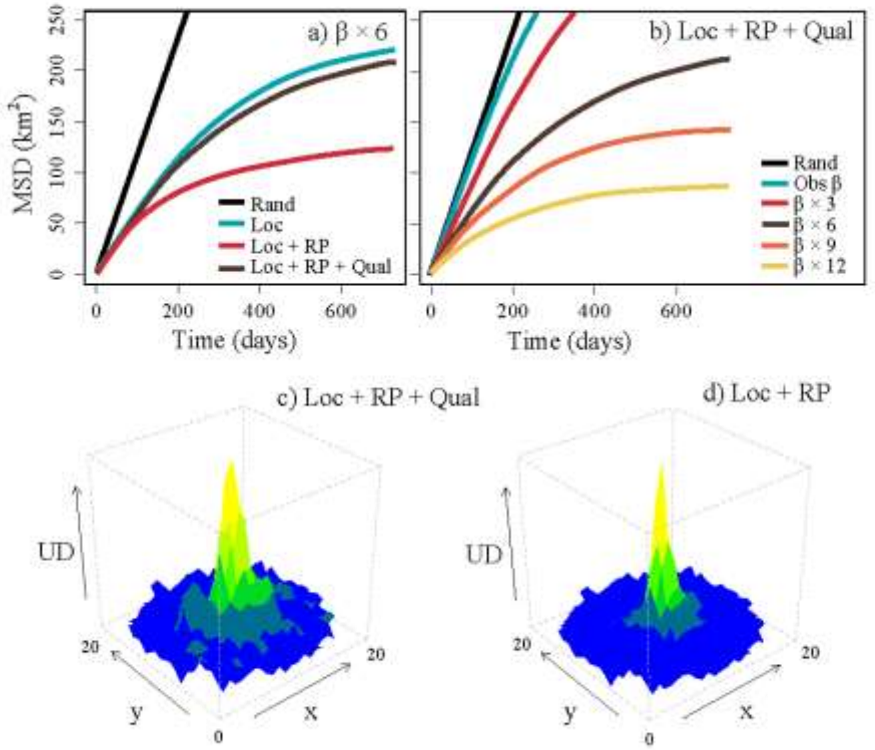

Figure 5. Mean squared displacement (with 95% CI in gray) of the cumulative utilization distribution (a) and total utilization distribution (b, c) of observed bison movements in Prince Albert National Park (Canada; area of approx. 1,000 km^2) and simulated individuals using the integro-difference equation approach parameterized with the full memory-based foraging model in the same landscape. Information based on monitoring and simulations over the course of one year. Yellow and green represents areas of relatively high use.