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LETTER

A memory-based foraging tactic reveals an adaptive mechanism for restricted space use

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Abstract

The restricted area of space used by most mobile animals is thought to result from fitness-rewarding decisions derived from gaining information about the environment. Yet, assessments of how animals deal with uncertainty using memory have been largely theoretical, and an empirically derived mechanism explaining restricted space use in animals is still lacking. Using a patch-to-patch movement analysis, we investigated predictions of how free-ranging bison (*Bison bison*) living in a meadow-forest matrix use memory to reduce uncertainty in energy intake rate. Results indicate that bison remembered pertinent information about location and quality of meadows, and they used this information to selectively move to meadows of higher profitability. Moreover, bison chose profitable meadows they had previously visited, and this choice was stronger after visiting a relatively poor quality meadow. Our work demonstrates a link between memory, energy gains and restricted space use while establishing a fitness-based integration of movement, cognitive and spatial ecology.

Keywords

Bison bison, cognitive map, connectivity, home range, intake rate, past experience, patch selection, reference point, site fidelity, spatial memory.

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INTRODUCTION

Despite the movement capabilities of most animals, many use only a restricted portion of the landscape they inhabit. The adaptive value of such site fidelity and home range behaviour largely rests in the advantages of gaining information about the environment (Börger *et al.* 2008; Piper 2011). For an animal that encounters new information or is faced with options of known and unknown quality, it should be evolutionarily advantageous to track information such as patch quality and location and to employ behaviours that use this information to improve foraging efficiency (Real 1991; Dall *et al.* 2005). Because memory allows for the retention of information, identifying how free-ranging animals use memory to make beneficial foraging decisions is fundamental for understanding the evolution of resource selection and for a general theory of animal space use (Gautestad & Mysterud 2005; Spencer 2012). Yet, assessments of how animals deal with environmental uncertainty through memory have been largely theoretical or laboratory based (Bailey *et al.* 1996; Sulikowski & Burke 2011; Spencer 2012; Fagan *et al.* 2013), and a robust mechanism for explaining restricted space use in free-ranging animals is still lacking (Börger *et al.* 2008).

While classic foraging models assume that animals are omniscient (Stephens & Krebs 1986), foragers realistically possess incomplete environmental information and they must rely on past experience to make decisions (Pyke 1984). Theoretical work on animal behaviour offers a conceptual basis of how an animal might learn about and optimally exploit its environment. For example, McNamara & Houston (1985) developed a framework for a naïve forager to estimate the long-term intake rate of food (i.e. a reference point), which provides the animal with a threshold to know when to stop exploiting a patch. Furthermore, Bayesian decision theory has been linked to animal behaviour to demonstrate that animals can combine previous experience with present information to estimate environmental states such as the expected intake rate of food within their current patch (McNamara *et al.* 2006).

Herein, we consider the question of how animals decide which patch to visit next (Pyke 1984). Foragers commonly must choose among previously visited and unknown patches in a network of potential patches. To begin resolving the problem, foragers could bias their movements towards previously visited patches (Gautestad & Mysterud 2005; Wolf *et al.* 2009), particularly if they tend to leave patches before experiencing a decrease in food intake rate (Fortin *et al.* 2004). This situation may arise, for example, when animals elude predators by frequently moving among patches (Mitchell & Lima 2002). Natural selection, in this case, should favour the development of spatial memory (i.e. the encoding of spatial relationships; Benhamou 1997; Gautestad 2011) so foragers can efficiently return to previously visited patches where they know they can find food (i.e. a familiarity hypothesis; Piper 2011; Wolf *et al.* 2009). Indeed, this movement bias towards previously visited sites has been shown in free-ranging elk (*Cervus elaphus*) in Canada (Dalziel *et al.* 2008; Wolf *et al.* 2009).

A forager's incomplete information also poses challenges when coping with environmental heterogeneity and stochasticity. In this context, foragers may increase fitness pay-off by tracking the quality of previously visited patches (e.g. Lihoreau *et al.* 2011) using attribute memory (i.e. the encoding of feature characteristics; Fagan *et al.* 2013). Tracking patch quality should provide foragers with an expectation of nearby patch quality, similar to using spatial autocorrelation to establish a reference point for deciding whether or not to forage in a given patch and when to leave it (McNamara & Houston 1985; Fortin 2003). Furthermore, combining spatial and attribute memory would allow individuals to choose previously visited patches that were also of high quality, further increasing foraging efficiency (Avgar *et al.* 2013). For example, simulated foragers can maximise food intake rate by biasing their movements towards the location of high-quality patches that were previously visited (Nabe-Nielsen *et al.* 2013). Accordingly, in a two-phase laboratory foraging trial, rufous hummingbirds (*Selasphorus rufus*) were able to return to high-quality artificial flowers while avoiding poor quality flowers (Hurly 1996).

Although the use of environmental information can improve the success of foraging decisions, animals are also faced with physiological costs when transferring this information to memory (Dall *et al.* 2005; Fagan *et al.* 2013). In heterogeneous landscapes with attributes that are constantly changing, foragers have likely adapted to remember only the most pertinent information gathered while foraging (Real 1991; Spencer 2012). For example, in artificially constructed environments, food patch selection by least chipmunks (*Tamias minimus*) was based on recent information trends when information was fresh, and on patch averages as information became outdated (Devenport & Devenport 1994). Identifying how free-ranging animals perceive the value of information is therefore essential to understanding how a forager might use memory to make fitness-rewarding decisions in the wild (Dall *et al.* 2005).

Our objective was to investigate how spatial and attribute memory is used by wild animals to increase foraging efficiency during patch selection. We examined four predictions. First, we predicted that foragers using spatial memory would choose patches they have previously visited more often than at random given abiotic landscape characteristics (e.g. size, connectivity) of nearby patches (P1; Gautestad & Mysterud 2005). Second, we predicted that foragers using spatial and attribute memory would be able to choose relatively high-quality patches based only on expectations from past foraging experience (P2; Bailey *et al.* 1996). Finally, we predicted that foragers using both types of memory would more strongly choose previously visited patches if the quality of their current patch (i.e. an indicator of local patch quality) is worse than their average past experience (P3; Spencer 2012), or if previously visited patches are also of relatively high quality (P4; Nabe-Nielsen *et al.* 2013). We examined the empirical support of these predictions by parameterising several patch selection models using relocation data from free-ranging plains bison (*Bison bison bison*) living in a meadow-forest matrix (Table 1). For all variables derived from past experience, we used a time-weighted devaluation function (McNamara & Houston 1985) to simultaneously consider the rate of memory decay and how far into the past bison perceive relevant information. We parameterised models based on season, with the expectation that long-term past experience is more valuable during dormancy periods when heterogeneity in vegetation quality is lower (Devenport & Devenport 1994; Avgar *et al.* 2013). Unlike other empirical memory-based habitat selection models where fitness was not explicitly incorporated (e.g. Wolf *et al.* 2009), we specified meadow quality using a fitness-based foraging currency: expected intake rate of digestible energy. Bison in our study area maximise their short-term intake rate of digestible energy while foraging in meadows (Fortin *et al.* 2002). Based on this currency, we make inference on the adaptive value of using information from past experience to more efficiently forage, which ultimately provides an evolutionary link between the cognitive abilities of animals, their movement decisions under uncertainty, and their spatial distribution.

METHODS

Study area

Free-ranging plains bison inhabit the south-western corner (*ca.* 1000 km^2) of Prince Albert National Park (PANP), Canada. PANP (53°44′ N, 106°39′ W) is located within the mixed-wood boreal forest, and has a cool subhumid continental climate. PANP is characterised by long cold winters (January daily mean −19 °C) and short warm summers (July daily mean +16 °C), with the majority of the annual precipitation (*ca.* 250 mm of 450 mm) falling as rain between June and September. The bison range inside PANP comprised a matrix of three land cover types: forest (85%), meadow (10%) and water (5%). Meadows are classified by a variety of graminoids, sedges and rushes (Fortin *et al.* 2002). Forests are a

Table 1 Candidate models investigating how memory is used by female plains bison during meadow selection in Prince Albert National Park, Canada, 2005–2013

No.	Patch selection model	Predictions supported
1	*Dist* + *LogArea* + *LogBC*	Null
2	*Dist* + *LogArea* + *LogBC* + *PrevVis*	P1
3	*Dist* + *LogArea* + *LogBC* + *ExpProfit*	P2
4	*Dist* + *LogArea* + *LogBC* + *PrevVis* + *ExpProfit*	P1, P2
5	*Dist* + *LogArea* + *LogBC* + *PrevVis* + *ExpProfit* + *PrevVis* × *RelRefPoint*	P1, P2, P3
6	*Dist* + *LogArea* + *LogBC* + *PrevVis* + *ExpProfit* + *PrevVis* × *ExpProfit*	P1, P2, P4

Models were developed to investigate four predictions concerning the use of spatial and attribute memory. First, foragers using spatial memory should chose patches they have previously visited more often than at random given abiotic landscape characteristics of nearby patches (P1). Second, foragers using spatial and attribute memory should chose relatively high-quality patches based only on expectations from past foraging experience (P2). Finally, foragers using both types of memory should more strongly chose previously visited patches if the quality of their current patch (i.e. an indicator of local patch quality) is worse than their average past experience (P3), or if previously visited patches are also of relatively high quality (P4).

mix of deciduous [dominated by trembling aspen (*Populus tremuloides*)] and conifer [dominated by black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*)] trees. During the study, minimum counts of the population ranged between 134 and 389 individuals. Other large mammals in the study area include elk, white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*) and grey wolves (*Canis lupus*).

Capture and collaring

All analyses were based on relocation data collected every 3 h from radio-collared female bison between 2005 and 2013. We captured and fit Global Positioning System (GPS) collars (4400M, Lotek Engineering, Newmarket, Ontario, Canada, and TGW 4780-3, Telonics, Mesa, Arizona, USA) on adult (> 3 years old) females using a helicopter in winter. Because we make inference on past experience, we only used data from individuals monitored for > 6 months. Individual bison used in our study ($n = 33$) were monitored for a mean of 777 (SD = 511) days. Differences in period lengths were due to animal mortality, collar malfunctions, or battery exhaustion.

Patch selection modelling framework

We developed patch selection models using an individual-based patch-to-patch movement framework (i.e. a step selection function; Fortin *et al.* 2005) with movement data from inside the boundaries of PANP (Dancose *et al.* 2011). To render GPS location data to such a framework, we first identified whether each bison location was inside or outside a meadow. We then simplified the data, and identified every incidence when an individual departed a meadow (i.e. the source meadow) and then entered a different meadow (i.e. target meadow), hereafter referred to as patch-to-patch movement. This patch-to-patch movement did not have to be two consecutive locations, i.e. the animal could have spent time (> 3 h) in the forest before entering the target meadow. For each patch-to-patch movement, we generated a sample of 20 possible meadows that the animal could have chosen from the source meadow, which were then compared to the observed target meadow. We selected these meadows by first identifying the realised distances between the source and target meadows from our data, and fit a linear spline function with 10 knots to this distribution (i.e. the so-called resource-independent movement kernel; see Figure S1). Using the density distribution of the spline function as weights, we selected 20 random meadows within a buffer of 6 km (accounting for > 95% of patch-to-patch distances) of each source meadow (Forester *et al.* 2009).

Meadow delineation and profitability

To identify meadows and quantify mean profitability, we used a land cover classification derived from a SPOT5 multispectral image (taken in August 2008; 10-m resolution; Dancose *et al.* 2011). We defined meadows as open areas > 0.04 ha, with a classification accuracy of 89% (Dancose *et al.* 2011). Also using the multispectral image, we established a relationship between total aboveground dry biomass and the normalised difference vegetation index (NDVI) of pixels, using the equation: total dry biomass = 1.55 × NDVI − 0.77 ($R^2 = 0.47$, Dancose *et al.* 2011). Using this relationship, we calculated mean biomass for each meadow ($n = 9015$) within the study area.

Dancose *et al.* (2011) found a quadratic relationship between meadow use by bison and mean dry plant biomass in meadows, consistent with the forage maturation hypothesis (Fryxell 1991). From field-based vegetation sampling in meadows, we developed an index of mean profitability derived from dry plant biomass and expected energy intake rate. First, we calculated the local maximum of the quadratic relationship between relative meadow use and mean plant biomass (0.549 kg per m^2) while taking into account meadow area, and distance between source and target meadows (see 'model parameterisation and selection' section for details). Using this maximum, we calculated a biomass index as

$$b = 0.549 - |mean\ dry\ plant\ biomass - 0.549| \tag{1}$$

where larger values of b correspond to intermediate plant biomass and small values of b correspond to high and low plant biomass in meadows. Second, we calculated the expected mean forage intake rate of digestible energy (kJ per min) for 21 meadows sampled in summer 1998 following the methods of Fortin *et al.* (2002), and confirmed that our biomass index predicted this rate ($R^2 = 0.31$, $F_{1\ 21} = 9.55$, $P = 0.005$). Hereafter, we use the term meadow profitability when referring to the biomass index of meadows.

Abiotic meadow characteristics

Without using memory, animals may return to certain patches more often than others simply due to their size and spatial location within the patch network. We therefore calculated the log of the area (*LogArea*) of each meadow, and for each patch-to-patch movement, the distance between the source and target meadows (*Dist*; Dancose *et al.* 2011). We also calculated betweenness centrality (Rayfield *et al.* 2011) of each meadow as an index of connectivity. Betweenness centrality is the proportion of pairwise shortest paths that pass through a given patch, i.e. an index capable of highlighting patches that are important movement pathways in the landscape (Rayfield *et al.* 2011). We calculated betweenness centrality using a minimum planar graph (MPG) because it assumes that movements among patches proceed in a stepping-stone fashion (Fall *et al.* 2007), similar to the behaviour of many terrestrial mammals (Courbin *et al.* 2014), including bison (Dancose *et al.* 2011). Links in our MPG were based on the minimum distance between the edges of two given meadows.

Because of the large number of meadows within our study area, we were unable to create a MPG for the entire study area simultaneously. Thus, using a moving window approach, we divided the study area into 16 sections (i.e. windows). Windows overlapped each other by 4 km, minimising biases from edge effects. For each meadow in its respective window (i.e. meadows ≥ 4 km from the edge of the window), we calculated the log of betweenness centrality (*LogBC*). We calculated the MPG using the grainscape package, and calculated betweenness centrality using the igraph package in program R 2.15.2 (R Core Team 2013).

Quantifying past experience

We quantified memory decay and the relevance of information to bison using a flexible devaluation function of time modified from McNamara & Houston (1985):

$$w(k, t) = \frac{1}{1 + k \times t} \tag{2}$$

where $w(k,\ t)$ is the weight of a past event in memory, based on the devaluation (or memory decay) factor k, and time since the event happened t (in h). The larger the k, the faster the devaluation and the more weight is attributed to most recent experience.

For each patch-to-patch movement, we first identified all previously visited meadows. We then calculated each previously visited meadow's weight in memory (*PrevVis*) using $k_{PrevVis}$ in eqn 2. Meadows not previously visited were assigned a value of zero. Similarly, we calculated reference points of past experience (*RefPoint* and *RelRefPoint*) based on:

$$\text{Reference point} = \left(\sum_{m=1}^{n} w(k, t) \times b_m\right) \times \left(\sum_{m=1}^{n} w(k, t)\right)^{-1} \tag{3}$$

where b_m is the biomass index (i.e. expected meadow profitability) of each meadow m visited t h into the past, n is number of meadows visited since 24 h after the individual was collared and $w(k,\ t)$ is the devaluation function of memory using $k_{Refpoint}$ or $k_{RelRefPoint}$ in eqn 2. For *RefPoint*, we identified $t = 0$ as the last GPS location in the source meadow. For *RelRefPoint*, we identified $t = 0$ as location prior to entering the source meadow, then subtracted the source meadow profitability from this reference point value.

Following the landscape grazing distribution model developed for large herbivores by Bailey *et al.* (1996), we calculated the expected profitability (*ExpProfit*) of each target meadow as:

$$ExpProfit = RefPoint + (TargetProfit - RefPoint) \times w(k, t) \tag{4}$$

where *TargetProfit* is the profitability of the target meadow and $w(k,\ t)$ is the weight of this value in memory using $k_{ProfitPrevVis}$. If the target meadow was not previously visited, $w(k,\ t)$ was set to zero, and the meadow's expected profitability was given the individual's current reference point. After all variables were calculated, we removed the first 3 months of data for each individual prior to analysis to reduce false negatives for previously visited meadows, and to keep reference point calculations from being truncated when individuals were within the first months of monitoring.

Model parameterisation and selection

We compared observed target meadows from patch-to-patch movements (n = 10 248 in summer; n = 9655 in winter) to available target meadows using conditional logistic regression for summer (weeks 18–33) and winter (weeks 45–52 and 1–17), separately. We removed weeks 34–44 because > 5% of weekly bison locations were outside PANP where vegetation quality is unknown. In the analysis, a stratum included the observed target meadow and its associated 20 available target meadows. Because of temporal autocorrelation (thus potential pseudoreplication) within an individual's patch-to-patch movements, we calculated robust SE and 95% confidence intervals of parameters using generalised estimating equations (GEE; Craiu *et al.* 2008). All strata for a given individual within a given year were assigned a unique cluster (i.e. a total of 85 clusters) in the GEE analysis. Model parameters were estimated using maximum likelihood in the survival package in R (see Fortin *et al.* 2005; Forester *et al.* 2009 for implementation details and code). We verified that variance inflation factors for each variable were < 3.

We assessed the level of relative empirical support received for each of the six models (Table 1) for summer and winter using the quasi-likelihood under independence criterion (QIC). QIC accounts for non-independence between subsequent observations within a cluster (Craiu *et al.* 2008). For models with memory-based variables, we identified the devaluation factors and memory decay rates (k) for each variable (i.e. $k_{PrevVis}$, $k_{ProfitPrevVis}$, $k_{Refpoint}$, $k_{RelRefPoint}$) with an optimisation routine based on lowest QIC of the model in question. We used the algorithm developed by Byrd *et al.* (1995), because it allows the specification of upper and lower bounds to the parameter of interest (i.e. k, which lies between 0 and 1). We validated the seasonal model with the most empirical support using cross validation, following the framework developed by Fortin *et al.* (2009) for step selection functions.

Determining whether returning to a patch is beneficial

To test whether returning to previously visited meadows was beneficial, we developed a separate model and analysed only the patch-to-patch movements where bison chose a previously visited meadow. We again used conditional logistic regression, specifying strata and clusters, and calculating robust standard errors as explained in the 'Model parameterisation and selection' section. We parameterised one model with summer and winter data that included distance (*Dist*), area (*LogArea*), betweenness centrality (*LogBC*) and target meadow profitability (*TargetProfit*). A positive coefficient for target meadow profitability, while taking into account area, distance and connectivity, would suggest that returning to a previously visited location provided a higher expected energy intake rate given the available options.

RESULTS

Meadow selection by bison was influenced by information gained from their past experience in winter and summer (see Table S2). The top-ranking model (Model 5; QIC weight > 0.99 for both winter and summer; Table S2) included terms for how expected meadow profitability and previous foraging experience affected which meadow would be chosen next. Furthermore, bison chose meadows that were larger and closer than other available target meadows in both seasons

Table 2 Parameter estimates (β) of the summer and winter patch-to-patch movement models receiving the most empirical support

	Summer		Winter	
Variable	β	*SE*	β	*SE*
Dist	−0.153*	0.014	−0.661*	0.033
LogArea	0.693*	0.013	0.765*	0.015
LogBC	0.007	0.004	−0.005	0.005
PrevVis	1.284*	0.037	0.822*	0.037
ExpProfit	−1.948*	0.465	2.282*	0.303
PrevVis × *RelRefPoint*	0.183	0.294	0.896*	0.451

*Denotes when the 95% CI of β did not overlap zero.

Models were parameterised using conditional logistic regression, and provided inference on how memory is used during meadow selection by female plains bison (n = 33) in Prince Albert National Park, Canada, 2005–2013.

(Table 2). We did not detect an effect of connectivity on meadow selection, as the 95% confidence intervals of coefficients for betweenness centrality in all models overlapped zero. The top-ranking model was robust to cross-validation in summer (observed r_s = 0.97, range 0.91–0.99; random r_s = 0.05, range −0.52 to 0.69) and winter (observed r_s = 0.95, range 0.88–0.98; random r_s = 0.01, range −0.49 to 0.65).

In both seasons, bison restricted their use of the study area by choosing previously visited meadows in the majority of their patch-to-patch movements (77.2% in summer, 57.7% in winter; supporting P1). During winter, bison chose meadows with a higher expected profitability given their current knowledge of potential target meadows and selection for previously visited meadows was even stronger after visiting a source meadow with a lower mean profitability than recent foraging experience (supporting P2 and P3; Fig. 1). During summer, bison chose meadows of lower profitability than that of their past experience (Table 2). We did not detect a multiplicative increase in preference for choosing previously visited meadows that also had high profitability (P4; Table S2).

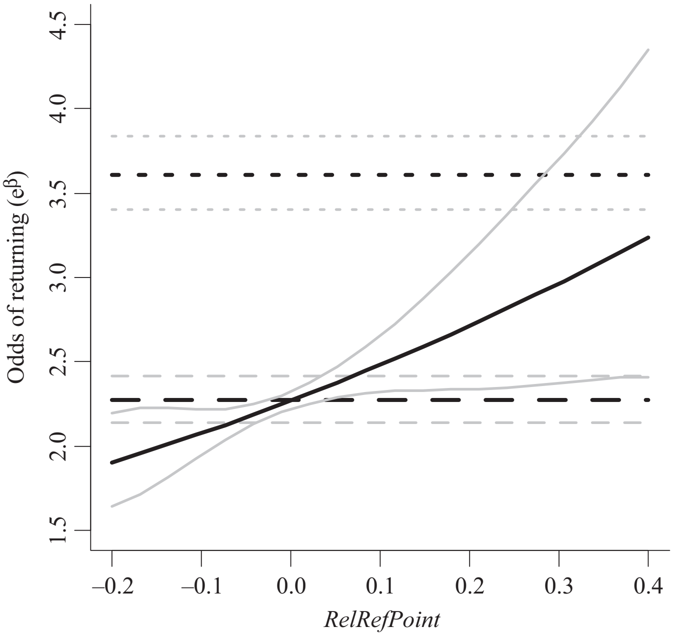

Figure 1 Relative odds (with 90% confidence intervals) of returning to previously visited meadows by female plains bison (n = 33) in Prince Albert National Park, Canada, 2005–2013. Parameter estimates (β) were based on the seasonal patch-to-patch movement model with the most empirical support during summer (dotted lines), and with (solid lines) and without (dashed lines) the influence of the relative reference point (*RelRefPoint*) during winter. *RelRefPoint* was calculated during winter as the reference point of past experience (excluding the source meadow) minus source meadow profitability.

Memory decay of the location of previously visited meadows was low in both seasons ($k_{PrevVis}$ = 0.0000001 for summer and winter), indicating that bison chose recently visited meadows as strongly as meadows visited farther into the past (Fig. 2). Memory decay of the profitability of previously visited sites was low during winter ($k_{ProfitPrevVis}$ = 0.0000001), but relatively high during summer ($k_{ProfitPrevVis}$ = 0.004), indicating that information about meadow quality is more important over time during winter than in summer. Meadow profitability information used for estimating expected quality of nearby meadows was based on relatively short-term information in the winter ($k_{RefPoint}$ = 0.0007) and long-term information in the summer ($k_{RefPoint}$ = 0.000001). Finally, the temporal value of recent foraging experience, used for deciding whether or not to return after visiting a given source meadow in winter ($k_{RelRefPoint}$ = 0.008), was based on a reference point of meadow profitability determined from the preceding 27 days of foraging (i.e. given an approximate threshold of how many hours into the past previous events were weighted > 0.2; Fig. 2).

When bison chose a previously visited meadow, this decision led to the use of a meadow with higher profitability ($\bar{X} \pm$ SE; $\beta_{TargetProfit}$ = 2.657 ± 0.140) than expected given available options, indicating that returning was beneficial. Meadows previously visited were also closer (β_{Dist} = −0.306 ± 0.009), larger ($\beta_{LogArea}$ = 1.169 ± 0.009) and less connected (β_{LogBC} = −0.019 ± 0.005) than available options.

DISCUSSION

Our illustration of how animals use past experience to improve foraging efficiency during patch selection reveals a novel link between the use of memory and the maximisation of energy gains. Bison chose which meadow to visit next based on information derived from their past experience. As predicted, bison chose meadows that were previously visited and had a higher expected profitability than that observed during their recent foraging experience during winter. In addition during winter, if a bison encountered a meadow with a lower profitability than its recent foraging experience (i.e. indicating that it entered a relatively poor quality area), the probability of returning to a previously visited meadow on its subsequent move was higher. This behavioural tactic is one of the first empirically supported mechanisms for explaining restricted space use in mobile animals (Börger *et al.* 2008), and supports the predictions of theoretically derived memory-based movement models that result in restricted space use (Gautestad & Mysterud 2005; Spencer 2012). Moreover, the

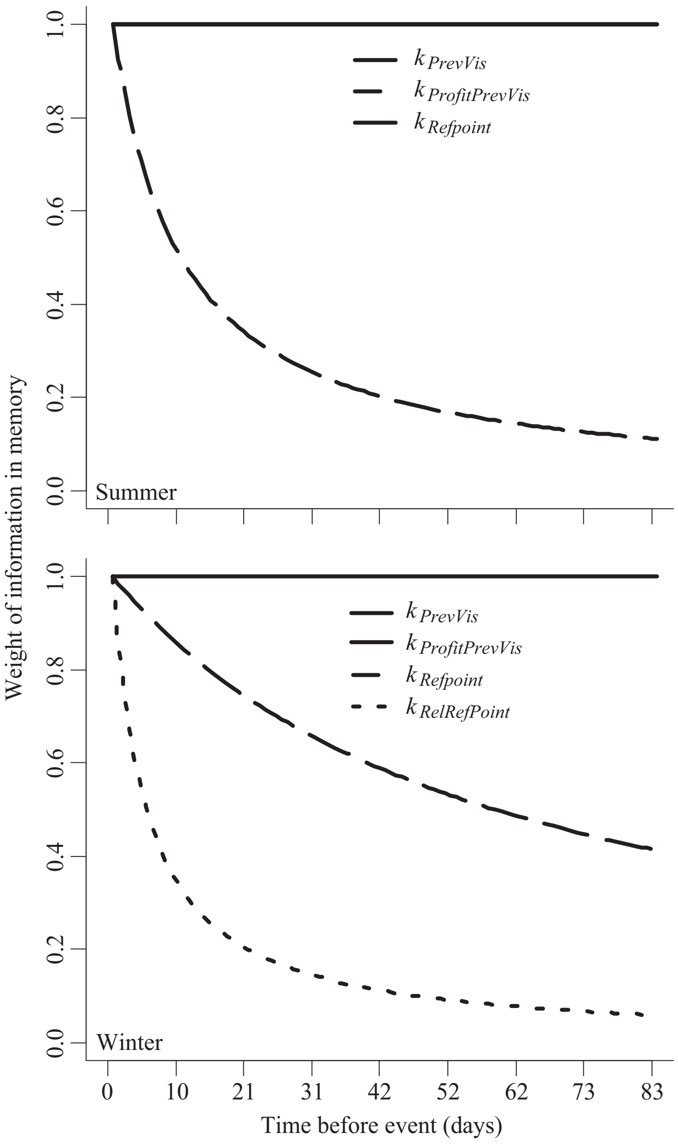

Figure 2 Information devaluation and memory decay for the location of previously visited meadows ($k_{PrevVis}$), the profitability of previously visited meadows ($k_{ProfitPrevVis}$), tracking quality of recently visited meadows including source meadow ($k_{RefPoint}$) and tracking quality of previously visited meadows excluding source meadow ($k_{RelRefPoint}$) derived from the seasonal patch-to-patch movement models with the most empirical support. Models were parameterised with movement data from female plains bison in Prince Albert National Park, Canada 2005–2013.

behaviours we observed have adaptive value since returning to previously visited meadows provided bison with opportunities to increase their energy intake rate. Our findings provide unique support that free-ranging bison use both spatial and attribute memory to make beneficial foraging decisions that result in restricted space use.

Few studies have incorporated memory-based parameters into movement and habitat selection models of wild animals (Fagan *et al.* 2013). Our work demonstrates how large ungulates use past experience by extending the analysis of Wolf *et al.* (2009) in three ways. First, similar to the majority of resource selection models, Wolf *et al.* (2009) derived their variables based on the assumption that animals know the vegetation biomass and land cover type of all sites available to them. In contrast, consistent with the theoretical framework of Bailey *et al.* (1996), our analysis assumed that the only information bison had for choosing their subsequent meadow was based on their previous experience. For example, if bison had previously visited a meadow, we assumed that they knew its quality (although we also assumed that this knowledge decayed over time). If they had not previously visited a meadow, we assumed that they anticipated that its value was similar to their recent foraging experience (i.e. their reference point). Second, because we related mean plant biomass estimates with field-based estimates of intake rate of digestible energy, we were able to infer why bison remembered past experience and to what extent their decisions were beneficial. Perhaps quantifying vegetation intake rate could have explained the puzzling result that elk selected for and returned to sites with relatively high cured forb biomass (Wolf *et al.* 2009). Finally, Wolf *et al.* (2009) used a *post hoc* analysis to examine how selection for previously visited sites was influenced by time since the previous visit. We employed a more quantitative and mechanistic approach that included a time devaluation function for memory-based variables, where we could simultaneously identify memory decay and the temporal scale of relevant information for bison.

Our work contributes to the growing understanding of how free-ranging large herbivores use memory to make beneficial foraging decisions at different scales. At the feeding station scale, for example, bison have been shown to track the past 2 m^2 of food quality information, using it to decide how much effort should be spent digging to access vegetation covered by snow (Fortin 2003). At the annual home range scale, caribou (*Rangifer tarandus*) show high site fidelity by returning to similar areas from the prior year (Faille *et al.* 2010). However, between these scales evidence of memory capabilities comes largely from experimental studies on domestic livestock. For example, cattle can remember both the location and quality of food sites (Bailey *et al.* 1989), and using this information results in relatively higher intake rates of food (Laca 1998). Our results suggest similar patterns. To increase their opportunities for a relatively high forage intake rate, we showed that bison tracked and used past meadow profitability estimates at different time scales in winter, and could orient their movements towards memorised locations visited months in the past (Fig. 2). Thus, our empirical study is one of the first to show that a free-ranging large ungulate uses both spatial and attribute memory in foraging decisions made at the patch scale. We do recognise that bison are gregarious (i.e. group fusions and fissions occur on a daily basis; Fortin *et al.* 2009), so inferred memory capabilities of individuals could also be affected by the cognitive abilities of other group members (Codling *et al.* 2007).

Although memory decay for tracking past experience should vary according to the temporal variability of the environment (e.g. across growing and dormancy periods throughout the year; McNamara & Houston 1985), we found that bison made little use of the reference point of past profitability to efficiently forage during summer. Bison chose meadows with a lower profitability than their reference point in summer

(Table 2). This finding is likely due to the fact that meadow choice during this season is influenced by other factors than just expected food profitability. For example, bison avoid foraging in deep water (Fortin & Fortin 2009), and they need dry areas to rest in summer. Thus, although profitable vegetation is abundant in relatively wet meadows, bison may only rarely visit them in summer. Only after the water has frozen and the vegetation becomes accessible will bison begin to use these profitable areas (Fortin *et al.* 2009). Indeed, bison choose meadows with an overall lower expected profitability in summer than in winter (Dancose *et al.* 2011).

It has been hypothesised that memory of patch locations is more resistant to memory decay (i.e. remains relevant for longer periods of time) than information about those locations (Nadel 1991; Spencer 2012). Our results support this hypothesis. We found low memory decay for choosing previously visited meadows, and relatively high memory decay for tracking meadow profitability (Fig. 2). Transferring information to memory is a neurological process that is influenced by redundancy of information as well as reorganisation and consolidation of systems within the brain (reviewed in Frankland & Bontempi 2005). In most cases, the spatial location of patches does not change, particularly at short time scales similar to the length of this study, and a high rate of return to some patches can increase the richness and accuracy of the cognitive map (Spencer 2012). An accurate cognitive map is indeed essential for the development of restricted space use patterns (Gautestad & Mysterud 2005; Gautestad 2011). For instance, long-term memory of the location of previously visited sites (i.e. high temporal predictability of resources) plays an important role in the development of both home range and migratory behaviour (Mueller & Fagan 2008), as individuals have the capability to return to locations not visited for months or even years. In these cases, other devaluation functions of information (discussed in Dunlap & Stephens 2012) could be useful to explain the temporal gradient of information used by animals. Whereas our devaluation function identifies a point along a gradient between short term and a mean of all past experience, a function that identified, for example, how information memorised during one season may not be relevant again until the next year, could clarify what information is relevant to a forager.

Our findings also have conservation implications. Predicting the state of ecosystems, including species distributions, is an increasingly critical mandate for ecologists (Coreau *et al.* 2009), and incorporating parameters such as returning to previously visited sites is thought to improve distribution predictions of home-ranging species (Gautestad & Mysterud 2005; Börger *et al.* 2008). Not only does our framework advance the application of modelling tools for applied ecologists making such predictions, but we provide empirical evidence that memory-based behaviour is essential to understanding patch selection. For example, our findings support the theoretically derived memory-based movement models of Van Moorter *et al.* (2009), Boyer & Walsh (2010), Spencer (2012) and Nabe-Nielsen *et al.* (2013), which all predict increased foraging efficiency compared to a forager without memory, and in most cases, an emergent restricted space use pattern.

The space used by an individual animal can be thought of as an accumulation of foraging decisions satisfying a fitness-driven need for efficient consumption of resources (Mitchell & Powell 2004). By linking patch selection decisions of bison to the energy gains expected within meadows, we show that memory plays an important role in reducing uncertainty during decision making. The resulting increase in foraging efficiency is likely the fitness reward that maintains the use of memory within this species. Moreover, bison chose previously visited meadows in the majority of their patch-to-patch movements. In winter, this preference was particularly apparent after visiting a poor quality meadow relative to recent experience, which provides a clear mechanism explaining the emergence of home range patterns from unrestricted movement (Börger *et al.* 2008; Spencer 2012). Our work advances distribution modelling techniques for home-ranging species while contributing to the unification of movement, cognitive and spatial ecology.

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AUTHOR CONTRIBUTIONS

DF and JMM developed the original idea. DF secured funding and provided the data. JAM conducted all analyses. JAM wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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