LETTER

Spatial memory shapes migration and its benefits: evidence from a large herbivore

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Abstract

From fine-scale foraging to broad-scale migration, animal movement is shaped by the distribution of resources. There is mounting evidence, however, that learning and memory also guide movement. Although migratory mammals commonly track resource waves, how resource tracking and memory guide long-distance migration has not been reconciled. We examined these hypotheses using movement data from four populations of migratory mule deer ($n = 91$). Spatial memory had an extraordinary influence on migration, affecting movement 2–28 times more strongly than tracking spring green-up or autumn snow depth. Importantly, with only an ability to track resources, simulated deer were unable to recreate empirical migratory routes. In contrast, simulated deer with memory of empirical routes used those routes and obtained higher foraging benefits. For migratory terrestrial mammals, spatial memory provides knowledge of where seasonal ranges and migratory routes exist, whereas resource tracking determines when to beneficially move within those areas.

Keywords

Cognitive ecology, habitat selection, migration, movement ecology, mule deer, *Odocoileus hemionus*, past experience, spatial memory, step selection function.

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INTRODUCTION

Developments in niche (Grinnell 1917; Chase & Leibold 2003) and foraging (Emlen 1966; MacArthur & Pianka 1966; Stephens & Krebs 1986) theory have together led to a general understanding that behaviour, movement and distribution of animals can be understood and predicted through variation in environmental characteristics (e.g. topography, temperature, habitat quality). For instance, models of optimal diet, prey selection, patch choice and residency time are all derived from the distributions of available food and prey items, habitat patches and habitat quality (Pyke 1984; Stephens & Krebs 1986). Yet, there is mounting evidence that many animals use another, intrinsic mechanism – learning and memory – to navigate and choose habitat. Indeed, several studies have shown that past experience of animals is critical to predicting movement and space use (Börger *et al.* 2008; Fagan *et al.* 2013; Merkle *et al.* 2014). Recent research also has revealed that some animals tend to return to areas previously used even after taking into account the profitability of an area (Wolf *et al.* 2009; Merkle *et al.* 2014); and in some instances, such fidelity can cause individuals to return to areas even if they are less profitable or incur fitness costs

(Merkle *et al.* 2015; Sigaud *et al.* 2017). The growing realisation that learning and memory play an important role in movement and habitat selection of animals has brought into question how both memory and environmental variability shape animal ecology (Bracis & Mueller 2017; Abrahms *et al.* 2019).

Migration in terrestrial mammals is a fascinating navigational feat prompted by various cues in the environment. Yet, it is still unclear whether spatial memory is fundamental to its occurrence (Avgar *et al.* 2013). For mammals, the only evidence of memory-based migration has come from zebra (Bracis & Mueller 2017) and blue whales (Abrahms *et al.* 2019). Most studies suggest that migratory behaviour could simply emerge from tracking resource waves across large landscapes, where individuals follow cues within their perceptual range that change predictably along seasonal gradients (Avgar *et al.* 2013; Lendrum *et al.* 2013; Armstrong *et al.* 2016; Monteith *et al.* 2018). For example, mammals such as Mexican long-nosed bats (Moreno-Valdez *et al.* 2000) and West Indian manatees (Deutsch *et al.* 2003) appear to track waves of food or thermal conditions during migration. Also, movements of migratory ungulates are timed to coincide with the flush of high-quality vegetation in spring that

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occurs along elevational and latitudinal gradients (Merkle *et al.* 2016; Aikens *et al.* 2017). Herbivores that track green waves of forage (i.e. green-wave surfing; Bischof *et al.* 2012) maximise their exposure to plants at intermediate phenological states when they are most profitable (Bischof *et al.* 2012) resulting in fitness benefits (Middleton *et al.* 2018). Small movements to optimise resource acquisition may therefore be the mechanism that scales up to create mammalian migration.

Nonetheless, many mammals migrate distances that greatly exceed their perceptual range (Teitelbaum *et al.* 2015) – suggesting that spatial memory also may be necessary to guide such movements (Fagan *et al.* 2013). Indeed, the ability to learn from past experience is a pervasive adaptive trait in many mammals (Papini 2002); and consistent with theory (Spencer 2012), many mobile animals use spatial memory of their environment so that they can move efficiently and maximise resource gain (Fagan *et al.* 2013). Although memory has been predicted to facilitate mammalian migration (Berbert & Fagan 2012), and there is some initial evidence that it does (Bracis & Mueller 2017; Sawyer *et al.* 2019), it is still unclear whether tracking resource waves alone can generate the long-distance migrations evident in some terrestrial herbivores, or whether spatial memory is necessary to navigate during such journeys.

Here, we evaluated the underlying basis of movement and habitat selection during migration to assess the mechanistic role of spatial memory and tracking local resources (including green-wave surfing during spring and tracking snow depth during autumn) in shaping long-distance mammalian migrations. We used detailed GPS-collar data from 91 migratory mule deer (*Odocoileus hemionus*) monitored for 2–3 consecutive years from four distinct wintering populations across the Mountain West (USA; Fig. 1). Mule deer represent an ideal study taxa because timing of their spring migration is closely matched with the timing of spring green-up (Aikens *et al.* 2017), and their autumn migration is prompted by winter weather (Monteith *et al.* 2011). We isolated spring and autumn migratory movements from the data and fit movement models to individuals in each of the four populations separately. We then used simulation to identify whether spatial memory or green-wave surfing was capable of recovering long-distance migratory routes during spring, while quantifying the foraging benefits in terms of matching movements
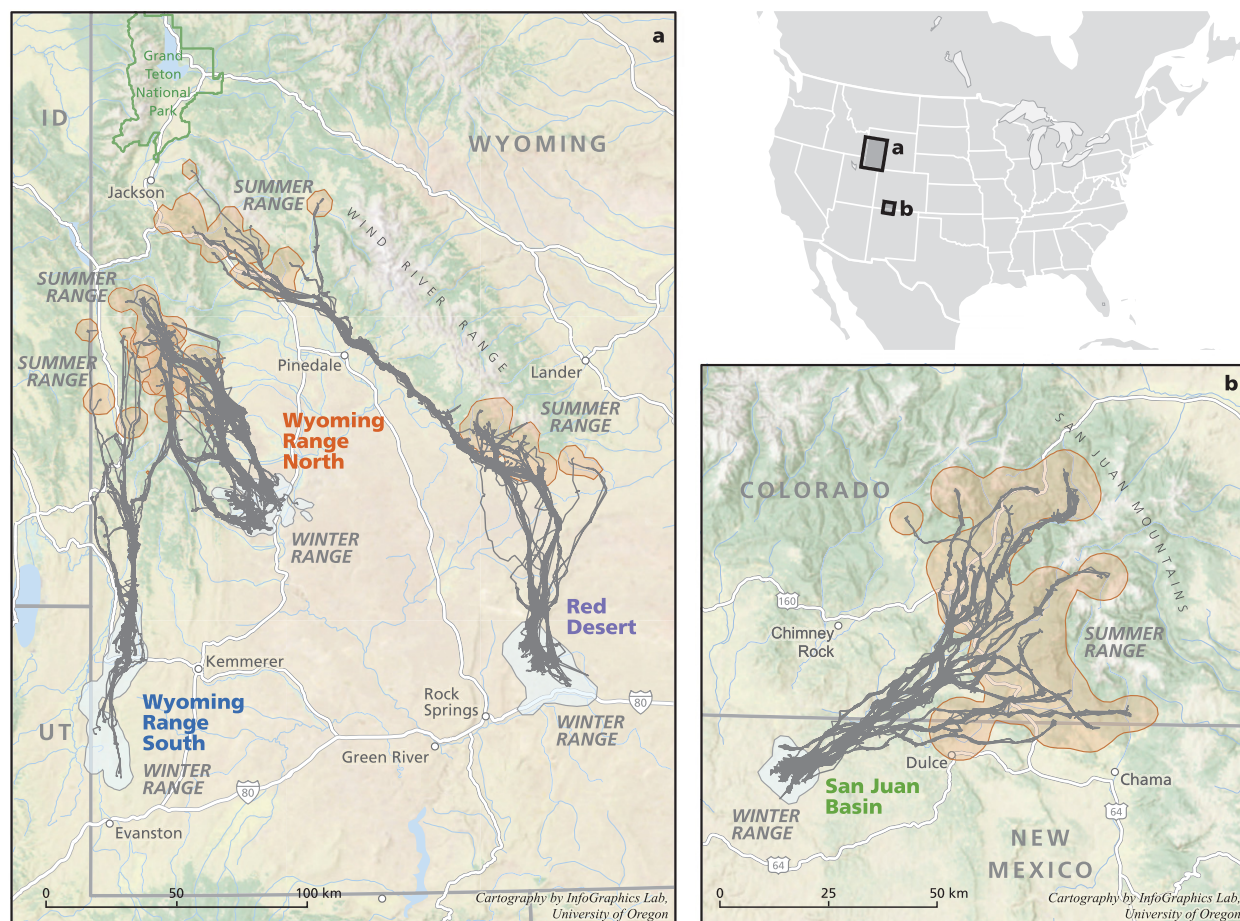
Figure 1 Map of migratory routes (black lines) between winter and summer ranges from four populations of mule deer marked in distinct winter ranges in the intermountain west, USA. Migration distances ranged from 20 to 250 km (Fig. S1).

with peaks in forage quality of each strategy. Our work has implications for how individuals integrate memory and resource tracking to migrate and acquire resources across large landscapes, and importantly, highlighting the role of memory in such feats.

METHODS

Study area

We used GPS locations of mule deer that winter in four distinct areas in western Wyoming and northern New Mexico (San Juan Basin, Red Desert, Wyoming Range South and Wyoming Range North; see Fig. 1). All four are semi-arid mountainous regions with elevations ranging from approximately 1500 to 4000 m with mean annual precipitation ranging from 10 to 150 cm across elevations (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu). Further details of the study areas can be found in Aikens *et al* (2017) and Sawyer *et al.* (2016, 2019).

Animal capture and GPS-collar data

We used GPS-collar data from female mule deer monitored for 2–3 years and migrated > 20 km from their winter to summer range. This resulted in sample sizes of $n = 28$ in the San Juan Basin, $n = 19$ in the Red Desert, $n = 24$ in Wyoming Range North and $n = 20$ Wyoming Range South populations. Animals were captured during February 2012 in the San Juan population, March 2013 in the Wyoming Range, and March 2011 and 2015 in the Red Desert. After removing the first year of monitoring (i.e. the first year was used to represent spatial memory for each animal), our analysis was based on a total of 144 animal-years. Fix rates of GPS collars ranged from every 2–5 h.

Modelling migratory movements

We used Step Selection Functions (SSF; Fortin *et al.* 2005) to examine whether deer make movement decisions during migration through the use of spatial memory or by tracking local resources. We first identified the GPS locations representing spring and autumn migration within a given year using plots of net squared displacement over time (Bunnefeld *et al.* 2011; Aikens *et al.* 2017). Consecutive GPS locations within these migratory trajectories were considered steps. To reduce the influence of resting site selection and better focus on the movement and foraging behaviour, we only included steps > 30 m in length in the analysis. We verified that this choice in a cut-off did not affect our results by also parameterising models with steps > 100 m in length. Besides a few small changes to coefficient estimates, results were not different. For each step, we identified the source and target points, and drew 10 potential target points originating from the known source point by sampling from the individuals' step and turning angle distribution simultaneously (Fortin *et al.* 2005). These 10 potential target points were identified as available and compared with the used target step.

Explanatory variables

For each used and available step, we extracted variables that related to resources (i.e. landscape variables, green waves of forage, snow depth) and spatial memory (i.e. knowledge of a previously used location). For variables related to resources, we developed a base resource model for each population that included the landscape factors of elevation, slope, aspect, terrain position index, percent tree cover, distance to roads, and an index of overall productivity or biomass of an area. We obtained a grid of elevation from the U.S. Geological Survey National Elevation Dataset (30 m resolution). From the elevation grid, we calculated slope (degrees), aspect (ranging from −1 as southerly aspects with early green-up to 1 as northerly aspects with late green-up) and terrain position index (ranging from −50 as valley bottoms to 50 as ridgetops, calculated as the difference between the elevation of a cell and the mean elevation of its nearest 80 surrounding cells). We used the 2011 National Land Cover Database (30 m resolution) to obtain estimates of percent canopy cover. We calculated distance to any road including highways and off-road trails (30 m resolution) using data obtained from the U.S. Department of Commerce, Bureau of the Census. We calculated overall productivity or biomass of a habitat patch (250 m resolution) each year of the study as the annual integrated Normalized Difference Vegetation Index (NDVI; Pettorelli *et al.* 2005). We calculated integrated NDVI following the cleaning, smoothing and fitting methods for NDVI data in Bischof *et al.* (2012) and Merkle *et al.* (2016).

In addition to the base resource model of landscape variables in spring, we calculated the Instantaneous Rate of Green-up (IRG). The IRG indexes peak green-up, that is, the phenological stage at which vegetation is at intermediate growth biomass, which indexes the phenological state offering the highest quality forage to deer (Hebblewhite *et al.* 2008; Bischof *et al.* 2012; Aikens *et al.* 2017). Following the methods of Bischof *et al.* (2012) and Merkle *et al.* (2016), we calculated IRG as the first derivative of the spring portion of the fitted NDVI time series in each grid cell. We then scaled those values between 0 and 1, where 1 represents habitat patches at peak in forage quality and values near 0 represent when habitat patches are before or after peak in forage quality. We used IRG to represent green waves of forage to which large herbivores commonly synchronise their migratory movements in spring (Merkle *et al.* 2016; Aikens *et al.* 2017). In addition to the base resource model of landscape variables in autumn, we extracted snow depth of each used and available step from the Snow Data Assimilation System (SNODAS; https://nsidc.org/data/g02158; 1 km, daily resolution).

For each individual, we calculated two variables that represent how movements during migration may be affected by spatial memory of the location of the migratory route and summer range of the previous year. For years two, and sometimes three when data were available, we calculated for each used and available step in spring and autumn (1) the distance from the spring or autumn migratory route of the previous year; and (2) an index of whether the animal was moving towards or away from the centroid of the summer or winter range of the previous year respectively. We verified that our

results were not influenced by only using the previous year of data to quantify memory. To do so, we calculated the minimum distance to any previous route of the same season (i.e. referencing the total known experience of each animal) instead of distance from the previous route only. We refit all models with this variable and while they indeed had more empirical support (ΔQIC > 2) in 3 of the 4 populations, there were no significant differences in the estimated beta coefficients. Because of this, and because we wanted to keep our sample balanced (i.e. all steps were assessed with respect to only 1 year of past experience), we defined memory as experience from only the previous year. We identified migratory routes by interpolating linearly between successive GPS locations during migration, and identified the centroid of the summer and winter ranges as the mean of the x and y coordinates while an animal was on its summer or winter range. We calculated our index of direction towards or away from the centroid of the summer or winter range of the previous year as the cosine of the discrepancy between the compass bearing from the source point to the summer or winter range centroid and the bearing of each target point. The index ranged from 1 to −1, where 1 is representative of a target step moving directly towards the summer or winter range of the previous year and −1 moving in the opposite direction.

Data analysis and model selection
Before analysis, we scaled and centred all variables separately for each population and each season, so that we could compare effect sizes of variables within populations (Schielzeth 2010). Then for each of the four populations, we parameterised five models for spring and autumn, separately. First, we parameterised the base resource model, which included only landscape variables. Second, we examined relative empirical support for adding IRG to the base resource model in spring (i.e. a green-wave surfing model) because deer follow IRG during spring migration (Merkle *et al.* 2016; Aikens *et al.* 2017), and for adding snow depth to the base resource model in autumn (i.e. snow depth model) because deer are prompted to migrate by inclement weather in autumn (Monteith *et al.* 2011). Finally, we added the two variables representing spatial memory one at a time and together to the green-wave surfing or snow depth models. We fit models using conditional logistic regression, with each stratum identified as a used point and its paired 10 available target points. We calculated robust SE and 95% CI of parameters using generalised estimating equations, because of temporal autocorrelation and a lack of independence within individual movements (Craiu *et al.* 2008). All strata for a given individual and year were assigned a unique cluster. To reduce the bias in estimated coefficients, we included distance (in km) between the source and target points as a covariate (Forester *et al.* 2009). We assessed the level of relative empirical support received for each model by calculating the Quasi-likelihood under independence criterion (QIC), which accounts for non-independence among observations within a cluster (Craiu *et al.* 2008). There was no collinearity among variables within fitted SSFs – Pearson correlations coefficients were < 0.42 and variance inflation factors were < 2.

Simulating migratory movements

As a landscape-level test of the extent to which spatial memory or tracking local resources shapes movement decisions, we used simulation to identify which of these mechanisms were capable of recovering spring migratory routes of the longest distance migrants in each population, and which mechanisms provided better foraging benefits in terms of exposure to forage patches at peak green-up. Using an agent-based simulation approach, we simulated four populations of mule deer (n = 1000 in each population) in the observed spring landscape of each mule deer population with evidence of green-wave surfing (Figs 1 and S1), and a movement tactic parameterised by different combinations of resource characteristics, green-wave surfing (i.e. IRG) and spatial memory.

Our agent-based simulation followed the methods of Merkle *et al.* (2017), where at every iteration of the simulation, a target location was selected by a deer based on a probability proportional to the product of the probability distribution of the observed step length distribution (i.e. the resource-independent movement kernel) and a parameterised SSF (which provides information on how an animal chooses habitat based on local resource availability, IRG and spatial memory). The resource-independent movement kernel was specified as a Weibull distribution, with estimated parameters of shape = 0.74 and scale = 0.62 based on the distribution of observed step lengths (in km) during spring migration. We simulated four populations where deer chose steps based on a probability proportional to the resource-independent movement kernel multiplied by fitted SSFs that included (1) landscape variables only, (2) landscape and green-wave surfing variables, (3) memory variables only and (4) landscape, green-wave surfing, and memory variables.

Each iteration of the simulation represented a step of 3 h. We implemented simulations for the number of days IRG was available (buffered by 2 weeks) in a representative year for each population. For example, in the Red Desert study area, green-up was available for 117 days starting on 26 February in the spring of 2012. Each simulated deer was given a starting location randomly chosen from the first GPS location during migration for the eight longest distance migrants in each population. For each simulated deer with spatial memory, we assigned a randomly selected empirical summer range and migratory route. Parameters for the SSF were based on the fitted SSF (fitted using unscaled variables) for each population respectively.

We assessed whether spatial memory or tracking local resources were capable of recovering the observed long-distance migratory routes of each herd using two metrics. First, we calculated and mapped a kernel density (or utilisation distribution) of the distribution of locations derived from the 1000 deer of each of the four simulated populations. Second, we identified the locations of the last 30 days (i.e. *c.* final 25%) of each simulated population, and calculated their mean distance to the nearest observed summer range (similar to the methods of Bracis & Mueller 2017).

We then assessed whether spatial memory or green-wave surfing provided better foraging benefits in terms of two metrics of exposure to forage patches at peak green-up. First, we

calculated days-from-peak IRG, which is a metric of how well-simulated individuals matched their movements to peak green-up (sensu Aikens *et al.* 2017). For each simulated population, we calculated the mean of the absolute difference between the dates that simulated deer occupied grid cells and the Julian date that IRG peaked in those same grid cells. Here, small values represent a match between the timing of movement and peaks in forage quality, whereas large values represent a mismatch (Aikens *et al.* 2017). Second, we calculated an index (termed 'productivity-scaled green-up') of the foraging benefits obtained. For each simulated population, we calculated the mean of each visited location's IRG value (which is scaled between 0 and 1) multiplied by its integrated NDVI value. Here, large values represent increased energy gain during migration.

RESULTS

During spring migration, mule deer across the four populations generally chose movements that led them to more open and productive areas on southerly aspects of ridges that were farther from roads (Fig. 2). The influence of elevation and slope, however, was variable across populations. After taking into account the influence of these landscape variables, deer from three of the four populations (all but San Juan) surfed green waves of high-quality forage in spring. Deer in general chose movements that led them to areas with higher IRG than available (Fig. 2; Table S1). Overall, there was a detectable influence of green-wave surfing on migratory movements of deer. During autumn migration, mule deer across the four populations generally chose movements that led them to steeper slopes at locally higher elevations. Responses to all the other landscape variables were either insignificant or differed among populations. Only one population of deer (Wyoming Range North) clearly avoided locally deep snow during autumn migration (Fig. 2).

Migratory movements of deer during spring and autumn were driven strongly by spatial memory of previous migratory routes and seasonal ranges, as evidenced by empirical support for inclusion of variables representing spatial memory of past migratory routes and seasonal ranges in the movement model (ΔQIC > 161 for all populations and seasons; Table S1). Moreover, the effect size of variables representing spatial memory was always the largest of any other landscape or resource tracking variable. Compared with any other significant variable for each population, the effect size of spatial memory was 2 to 28 times higher during spring and 2 to 14 times higher during autumn (Fig. 2). Thus, spatial memory played a stronger role than tracking local resources in the migratory movements of deer.
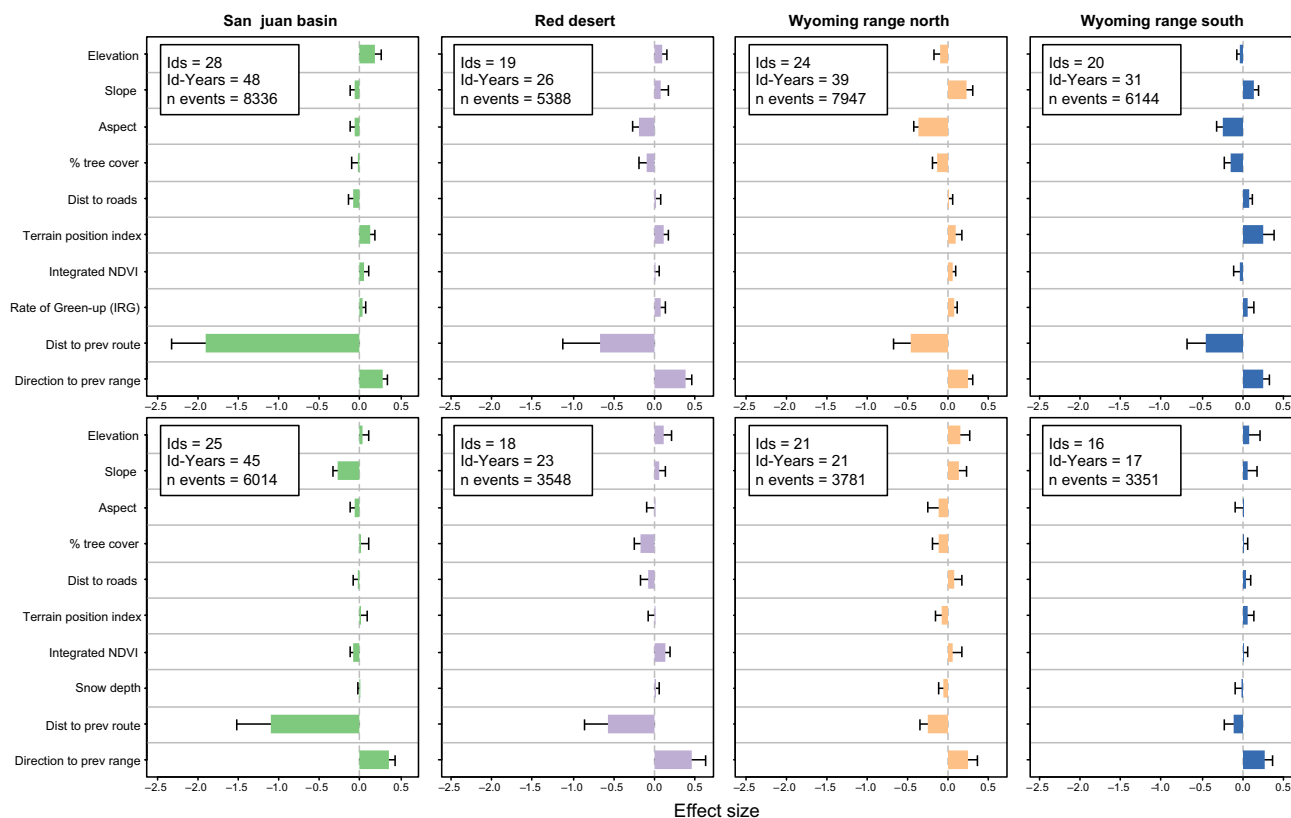
Figure 2 Predicted relative influence (i.e. effect size) of landscape variables, Instantaneous Rate of Green-up (IRG), snow depth and spatial memory on mule deer movements during spring (top panel) and autumn (bottom panel) migration 2012–2016 across four populations from distinct winter ranges of the intermountain west, USA. Parameter estimates were from Step Selection Functions that compared observed steps (i.e. sequential GPS locations) with 10 potential steps chosen based on the observed distributions of step lengths and turning angles. Sample sizes for Ids (number of unique individuals), id-Yrs (number of unique migration sequences) and n events (number of actual observed movement steps) included in each analysis.

Allowing simulated deer to select migratory movements based on tracking local resources alone failed to recover the observed migration trajectories during spring, even after thousands of simulations (Figs 3, S2, and S3). Results were consistent across the three populations that surfed the green wave, and thus for illustrative purposes we report the simulation results from the Red Desert population only. But see Figs S2 and S3 for results from Wyoming Range North and South.

When compared with a simulated individual moving based on landscape variables, simulated deer that surfed green waves of forage and selected landscape features as the observed deer did, finished their migration only 1 km closer to observed summer ranges. These distances were still, on average, at least 150 km from observed summer ranges (Fig. 3e). By contrast, when simulated deer also were given spatial memory of their past summer ranges and migratory routes, they charted
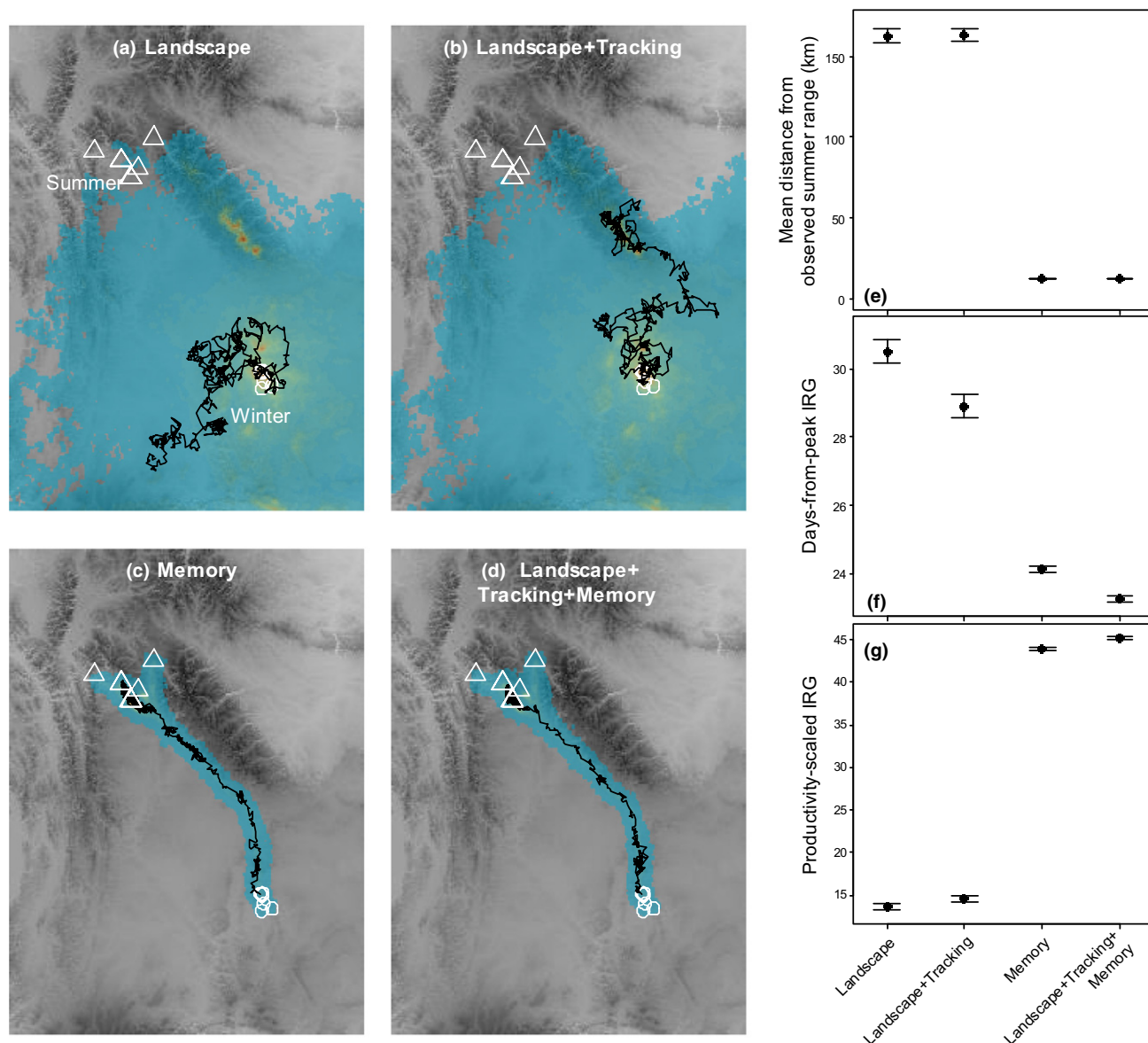
Figure 3 Utilisation distributions calculated from the 1000 simulated migration trajectories initiated at observed winter ranges (white circles) during spring. Red to blue coloration represents a gradient from high to low use. Black lines represent a single representative simulated individual. White triangles represent observed summer ranges. Simulated individuals chose steps based on a probability proportional to the observed step length distribution multiplied by a fitted Step Selection Function that included landscape attributes (a), and landscape attributes and green-wave surfing (b), spatial memory of an observed migratory route and summer range (c), and landscape attributes, green-wave surfing and spatial memory of an observed migratory route and summer range (d). For each of the four simulations, we calculated the mean distance that the final 25% of each simulated migration trajectory was from an observed summer range (e), the average days from the date of peak Instantaneous Rate of Green-up (IRG) at each pixel visited during the simulation (f), and the average productivity-scaled green-up (i.e. the IRG value obtained at each step of the simulation multiplied by the integrated Normalized Difference Vegetation Index value; (g) Black lines represent the 95% CIs of the means across simulated individuals. The step length distribution, parameters for the Step Selection Function and the starting points were derived from empirical spring migration data ($n = 8$) of mule deer migrating >175 km in the Red Desert population of western Wyoming (USA).

migratory routes that approached the observed summer ranges (i.e. < 13 km from observed summer ranges) and clearly followed the general path of the empirical migratory route (Fig. 3e).

Based on our simulations, both spatial memory and tracking local resources were key to the foraging benefits of migration (Fig. 3). Compared with simulated deer moving based on landscape variables, including green-wave surfing led to a 6% increase in productivity-scaled green-up (a measure of experienced IRG multiplied by integrated NDVI) and a 5% decrease in the mean number of days a simulated individual occupied a given site from the date that the same site peaked in IRG. Integrating spatial memory into migration, and therefore exploiting the entire observed migratory route (up to 250 km) led to a 230% increase in productivity-scaled IRG and a 24% decrease in mean days from peak green-up (Fig. 3f and g) compared with simulated deer moving based on landscape variables.

DISCUSSION

Our results indicate that the migrations of a large terrestrial mammal arise predominately from spatial memory of past experiences, and to a lesser extent from behavioural decisions at the local scale that optimise resource use (e.g. green-wave surfing). This result was robust to replication across multiple populations of mule deer inhabiting a wide geographical gradient. Moreover, we demonstrate the adaptive benefits of the use of spatial memory. Simulated deer with spatial memory improved their access to high-quality forage during spring migration compared with animals equipped with only an ability to track local resources. Therefore, empirical migratory routes – which likely were derived from generations of exploration, learning and cultural transmission (Jesmer *et al.* 2018) – are optimised for green-wave surfing and represent routes not readily discoverable within a single generation.

For migration in terrestrial mammals, to our knowledge, only a single theoretical foraging model has demonstrated that memory should underlie the emergence of migratory behaviour (Berbert & Fagan 2012), and only a single empirical study has demonstrated how migration is driven in part by memory of long-term averages of past vegetative resources (Bracis & Mueller 2017). Although our findings are in congruence with Bracis & Mueller (2017), our results suggest an even stronger influence of memory on terrestrial mammal migration. Without spatial memory, our simulated deer did not navigate to empirical summer ranges, whereas many simulated zebra (*Equus burchelli*) were able to arrive at their migratory endpoint without memory and only an ability to perceive local resources (Bracis & Mueller 2017). Neither Berbert & Fagan (2012) nor Bracis & Mueller (2017) assessed the foraging benefits of memory-based migration. Doing so here allowed us to quantify the adaptive value of memory use (Merkle *et al.* 2017). Further, both studies assume rather complicated memory capabilities in animals. In the model developed by Berbert & Fagan (2012), individual animals are assumed to have a working memory to repel them from recently visited patches and a reference memory of high-quality patches visited in the past. Bracis & Mueller (2017) assume

that zebra in Botswana can remember the spatial distribution of long-term averages of vegetation patterns across a rather large landscape. Such complicated cognitive abilities may not be necessary to give rise to migratory movements because the ability to remember previously visited locations and a simple reference point of recent past experience can produce other non-random space use patterns such as home ranges (Spencer 2012; Merkle *et al.* 2017). Here we demonstrate that spatial memory along with resource tracking can reproduce empirical migratory routes of mule deer that migrate nearly 500 km round-trip.

Our results have strong implications for the fields of landscape and movement ecology, where processes occurring at fine-scale are thought to scale-up to form landscape-level patterns (Morales & Ellner 2002). The use of spatial memory, and the passing of information through social learning (Sigaud *et al.* 2017; Jesmer *et al.* 2018), reveals that scaling-up only from an extrinsic, spatial (and short-term temporal) perspective can be misleading because the patterns we see are a function of generations of experience. Relatedly, the classic definition of habitat is based on static, environmental characteristics of a location such as vegetation or cover type (Hall *et al.* 1997; Morris 2003). Based on our results and other studies documenting the influence of past experience on animal movement (Fagan *et al.* 2013), it is becoming clear that the habitat concept should be re-conceptualised as an interaction among extrinsic environmental characteristics, and the knowledge an animal possesses of a place (Merkle *et al.* 2015), including when it is available or advantageous to use that place (Armstrong *et al.* 2016; Monteith *et al.* 2018). Without embracing such a comprehensive framework, terms such as migration habitat can be misleading.

There is ample evidence that terrestrial mammals are capable of developing a spatial representation of their landscape within their brains (O'keefe & Nadel 1978; Fagan *et al.* 2013); however, the cognitive state of an animal is always unknowable, and thus has been generally ignored in studies that model movement and habitat selection. Although it is possible to quantify resource preferences when spatial memory is ignored, our ability to predict the spatial distribution of animals becomes limited (Fig. 3). For instance, translocated bighorn sheep (*Ovis canadensis*) do not fully exploit the available resources within their novel environments until decades of learning have occurred following initial release (Jesmer *et al.* 2018). Without an understanding of the information that is known and remembered by these translocated individuals, predicting their space use after reintroduction, or even decades after reintroduction, can be difficult. One way to overcome this difficulty is to bridge the fields of cognitive ecology and movement ecology. Cognitive ecology draws upon knowledge of cognitive architecture (a field developed mainly in human subjects) and applies it to behavioural ecology (Real 1993; Healy & Braithwaite 2000). Although cognition was included into the original development of the movement ecology framework (Nathan *et al.* 2008), and memory has been integrated into models of animal movement (Fagan *et al.* 2013), a complete incorporation of the cognitive mechanisms underlying animal behaviour has yet to emerge.

Our results have important implications for conservation, particularly in the light of the documented loss of terrestrial mammalian migrations worldwide (Wilcove & Wikelski 2008; Harris et al. 2009). First, when migratory populations are lost (Wilcove & Wikelski 2008), pockets of potential habitat will likely be left unoccupied because of the lost memory of viable migratory routes (Sawyer et al. 2019). Restoration of migration in those locations via colonisation or reintroduction likely will take decades if not longer, especially if migratory behaviour is culturally transmitted across generations (Jesmer et al. 2018). Second, offsite restoration or mitigation will be unsuccessful if restored habitats are not 'discovered' or integrated into the past experience of individuals (Merkle et al. 2015). Finally, because migration is primarily guided by spatial memory and only to a lesser extent by habitat or environmental variables, it will be difficult to predict migratory routes in areas without movement data. Overall, practitioners must consider cognitive components of animal behaviour when assessing and predicting how animals will respond, through movement, to a given management or conservation action.

In conclusion, we provide strong evidence that learning and spatial memory can be viewed as the template for adaptive migration in a large terrestrial mammal. Such memory provides a spatial representation of an individual's seasonal ranges and migratory routes that can span > 200 km, and ultimately provides fitness benefits in terms of tracking resource waves that propagate across broad landscapes. Tracking local resource gradients, however, is perhaps best thought of as an adaptive mechanism for individuals to determine when to move within known areas of the landscape. Supporting the hypothesis that the evolution of spatial memory led to relatively rapid species diversification (Ginsburg & Jablonka 2010), our work suggests that the migratory movements of terrestrial mammals we see today may not have been possible without the cognitive capacity for spatial memory and the retention of individuals with memory of those routes.

AUTHORSHIP

JAM and MJK conceived the original idea. JAM conducted the analysis and wrote the first draft of the manuscript. All authors helped refine the idea, collect data, and write the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.