Glass *et al. Movement Ecology* (2025) 13:45
https://doi.org/10.1186/s40462-025-00571-4

Movement Ecology

RESEARCH

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Wolverines use spatial memory to plan efficient routes through rugged terrain

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Abstract

Background To navigate, animals balance nearby perceptual cues, random search, and memory. Isolating the role of memory, however, remains difficult.

Methods Here, we use a mechanistic movement model to do so, simulating animals responding solely to local perceptual cues (i.e., lacking memory) and comparing their paths with actual routes taken. By comparing route efficiency, we evaluate whether actual routes incorporate knowledge beyond the perceptual range (i.e., spatial memory).

Results We show that wolverines (*Gulo gulo*) employ spatial memory to plan routes through a rugged, mountainous landscape. Furthermore, we find that wolverines most commonly plan routes to destinations 5.3–9.8 km ahead. We estimate that route-planning saves wolverines, on average, 19.3 kcal per 135 min of movement.

Conclusions Our findings provide a template for evaluating how free-living animals recall the world beyond their perceptual range, offer a window into the cognitive mechanics underpinning navigation for this species, and support adding wolverines to the primate-dominated list of species with complex spatial memory.

Keywords Carnivore, Circuitscape, Cognitive map, Energy landscape, Glacier National Park, *Gulo gulo*, Movement ecology, Spatial memory, Wolverine

Background

To navigate heterogenous landscapes, animals balance perceptual cues, random search, and memory of resources beyond their perceptual range [1]. Of these, the roles of perceptual cues and random search have received considerable attention, whereas attributing movement to memory remains analytically challenging [1, 2]. Nonetheless, evidence is accumulating to support memory as an important driver of movement decisions across a variety of free-living taxa. For instance, a growing body of literature supports memory's role in shaping and maintaining long-distance ungulate migration [3–5] and within home-range movements of non-human primates [6, 7].

Evidence for spatial memory among free-living animals typically stems from evaluating revisitation dynamics to valuable sites or resource patches [8–11]. For instance, wolf (*Canis lupus*) revisitation to resource patches may be influenced by knowledge of recent prey availability [8, 10], and feral hogs (*Sus scrofa*) are more likely to select recently visited habitat patches promoting foraging and/or reducing thermal exposure [9]. Focusing on such high-value sites is intuitive given their clear fitness benefits, such as increased food acquisition and reduced mortality risk. This approach, however, leaves unaddressed the possibility that animals recall and incorporate a broader range of landscape attributes into movement decisions,

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including energetic costs of competing possible routes to distant destinations.

Animals contending with a spatially variable energy landscape generally make movement decisions that reduce energy expenditure [12–15]. Such movement responses are typically evaluated using, and therefore constrained to, a traditional step selection analysis (SSA) framework, wherein energy expenditure is incorporated at the level of steps (i.e., segments connecting consecutive animal locations [16]). Most responses are therefore observed at short temporal grains, likely corresponding with animals' perceptual distance (e.g., [13]). For instance, African lions avoid steeper slopes at 5–15-min step intervals, but show no avoidance at longer (≥ 1 h) intervals [13]. Selection for energetically efficient movement paths beyond the perceptual range (i.e., incorporating spatial memory of the energy landscape), however, remains largely unaddressed.

Animals with knowledge of their distant environment (i.e., beyond perceptual range) may plan routes that reduce energy expenditure by incorporating knowledge of out-of-sight landscape features such as mountain passes, corridors of un-obstructive vegetation, or updrafts. Such route-planning behavior has been shown in chimpanzees (*Pan troglodytes*), which follow least cost paths to out-of-sight goals [6]. Since goal orientation is implicit in such behavior, the time/distance scale of efficient routes likely reflects the cognitive process by which animals select destinations, which in turn may be influenced by the spatial distribution of resources or cognitive capacity. For instance, animals inhabiting landscapes with abundant food resources may select closer destinations, and therefore plan shorter routes, than those contending with sparser resources.

The wolverine (*Gulo gulo*) is a territorial mesocarnivore occupying montane, boreal, and Arctic regions of the Northern Hemisphere [17]. In winter, the species primarily obtains food from ungulate carcasses left by other predators [18, 19], parts of which they cache for later use [20]. Such carcasses are typically sparsely distributed and, possibly because of this sparsity, wolverines maintain large territories (up to 1500 km^2 in montane regions; [18]). In mountains, wolverines avoid steep slopes and prefer valley bottoms [21], likely driven at least in part by movement energetics. This preference notwithstanding, collared wolverines are observed summiting mountain peaks and crossing high ridges [22], suggesting that movement decisions may sometimes reflect cumulative energy expenditure along distant (unperceived) paths rather than solely immediate (perceived) energetic costs.

Here, we use a mechanistic movement simulator and high-frequency movement data from free-living wolverines in a mountainous landscape to test the hypothesis that these animals use spatial memory to plan energetically efficient routes through unseen terrain. We use the term "unseen" to refer to landscape features or regions that cannot be perceived by the animal from its current location. We predict that wolverines follow lower-resistance (i.e., more efficient) routes compared with simulated wolverines responding solely to local perceptual cues (i.e., lacking memory), and that such route-planning occurs at a relatively long time/distance horizon, given the species' general reliance on sparse prey resources [18, 23].

Methods

Overview

To evaluate the role of spatial memory in wolverine movement, we compared observed movement routes to simulated "local-knowledge" (SLK) routes for the same starting and ending locations. We created SLK routes using a mechanistic movement simulator lacking spatial memory, parameterized from observed wolverine movement data using an integrated step selection analysis (iSSA) approach. SLK routes therefore represent wolverine movement solely in response to local perceptual cues, i.e., lacking spatial memory. We then compared landscape resistance along observed versus SLK routes to evaluate whether actual wolverine routes were more efficient than SLK routes, indicating use of spatial knowledge beyond perceptual range. We detail these methods below.

Study system

We collected 26,473 locations from five subadult (1–2 years) and adult (> 2 years) wolverines (1F, 4 M) in Glacier National Park (Montana, USA) between 26 March–15 April 2005, 8 January–23 March 2006, and 18 January–12 March 2007. Glacier National Park encompasses approximately 4,000 km^2 of mountainous terrain, with elevations ranging from 960 to 3,190 m. Coniferous forest dominates lower and mid elevations, transitioning to alpine tundra, meadow, and barren ground at higher elevations. The park is bisected by a single road, which is snow-covered and closed during winter when these data were collected.

We captured wolverines in baited log-box traps, anesthetized them using Medetomidine and Ketamine, and fitted them with GPS3300SL Lotek GPS collars (200 g; Lotek Wireless, Inc., Newmarket, Ontario, Canada). We programmed collars to record fixes every five minutes and used this fix rate for all analysis. Capture and handling procedures were reviewed and approved by the University of Montana Institutional Animal Care and Use Committee.

Processing and analyzing wolverine movement data

To remove erroneous fixes, we screened data following [24]. Given our focus on movement, we excluded clusters (i.e., sequences of locations separated by less than 75 m) over 20 min in duration, which we expected to generally be associated with food items and/or resting. This yielded only paths connecting clusters, within which short ($\leq$ 20 min) periods of stationary behavior could occur, which we assumed were too brief to be the object of goal-oriented movement.

To generate observed movement routes for analysis, we further segmented these paths, which could be of any duration, into set-duration "routes," ranging from 30 to 225 min at 15 min intervals (Fig. 1). Evaluating routes across this range of durations allowed us to test our prediction that route-planning occurs at longer rather than shorter time/distance horizons. We excluded routes in which (i) displacement (i.e., straight-line distance from start to end) was $<$200 m, (ii) fewer than 80% of possible steps had been recorded as successful GPS fixes, (iii) route length (i.e., sum of step lengths) was $\geq$2X displacement, indicating non-directed movement, and (iv) the route end was visible from the route start, which we determined using the viewshed function in the R package terra [25, 26]. These routes did not overlap temporally (i.e., a route only began after the previous had ended), and we evaluated all possible temporal shifts to maximize the number of routes per duration. For instance, for 30 min duration routes, we calculated the number of routes yielded when routes started 0, 5, 10, 15, 20, and 25 min past the hour, and used the shift that yielded the most routes. This process yielded 14 route sets (i.e., one for each duration between 30 and 225 min) across the five study animals, with sample sizes ranging from 648 routes at the 30 min duration to 35 routes at the 225 min duration (Fig. 1, Table S1).

In addition to set-duration routes, we expected that wolverines might exhibit route-planning behavior toward known destinations regardless of duration. To evaluate this, we extracted wolverine paths between subsequent clusters, with the end cluster having been visited previously by the same animal while wearing a collar. This yielded an additional set of 29 routes, ranging from 75 to 535 min in duration (median = 245 min) and 6.3 to 31.7 km in length (median = 13.8 km).

To characterize the influence of local perceptual cues on wolverine movement, we fit a step selection function (SSF [16]) to all data in the 30 min route set (i.e., the most inclusive set of directed movement data). We matched each observed step with five "available" steps, generated using random draws from gamma and Von Mises distributions fit to the step lengths and turning angles of the observed steps, respectively. We included a range of covariates shown to influence wolverine movement elsewhere, or that we expected might influence movement here. Specifically, we evaluated wolverine response to elevation, slope angle, a binary variable indicating whether the location fell on a ridge (hereafter "ridge"), modeled energy expenditure of the step (hereafter "energy"), distance to streams/rivers, and the land cover classes forest, shrub, grassland, barren, and road (covariate details in Appendix S1). Land cover classes were represented as separate binary variables for each class (e.g., forest/not forest), which allowed us to evaluate whether each class should be retained in the model separately, and to evaluate scale-specific selection for each class separately

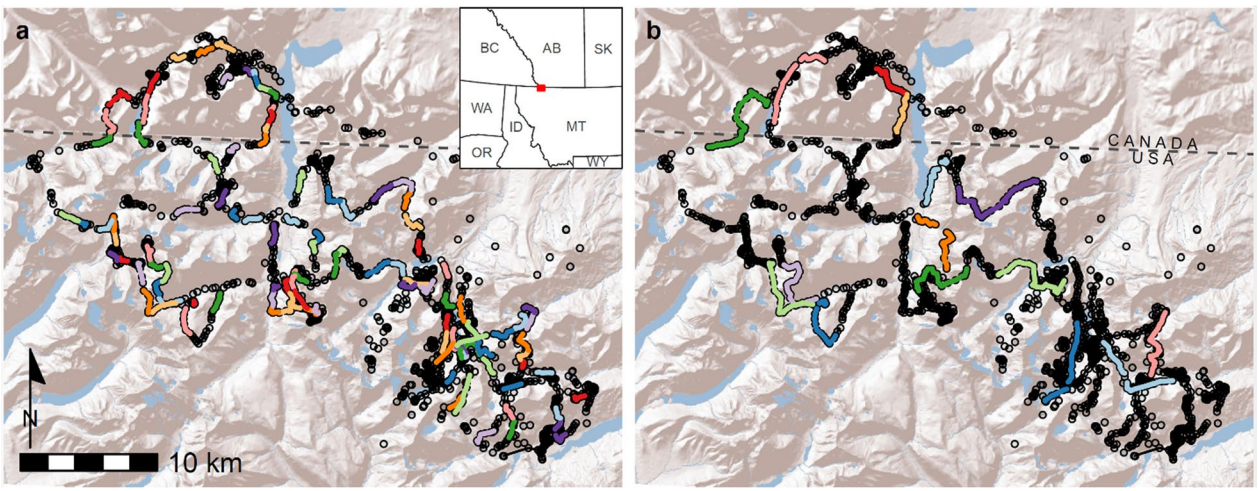

Fig. 1 Example 30-min (**a**) and 135-min (**b**) routes for a male wolverine in Glacier National Park, USA and Waterton Lakes Provincial Park, CA. Routes are differentiated by color; black paths indicate movement data shorter than the route duration and open circles indicate data excluded from the analysis

(described below). We fit models in the R package amt [27].

To determine the scale at which wolverines selected land cover classes, slope, and elevation, we calculated the majority landcover class and the mean slope and elevation within 30 to 990 m radii at 120 m increments. We then fit univariate models for each covariate-scale combination and used Akaike's Information Criterion (AIC) to determine which scale to retain for further analysis. Representing each land cover class at its appropriate spatial scale helped avoid collinearity among classes, since, if included at the same scale, each binary variable could be represented as one minus the sum of the other categories. We verified that such collinearity was not an issue using Pearson's correlation coefficient between each binary class and one minus the sum of the other classes at the selected scales. We included slope, elevation, and distance to stream/river as quadratic terms, and approximated each step's energy expenditure in Joules as

$$E = \left\{8m^{0.66} + 50[1 + \sin(2\theta - 74)]m^{0.88}\right\}d \quad (1)$$

where d is the distance traveled in meters, Θ is the slope of the step in degrees, and m is the body mass of the animal in kilograms [28, 29], which we assigned as 11 kg for all study animals (i.e., the mean weight during capture across individuals). This model of energetic cost was derived from empirical data across a variety of taxa, informed by muscle physiology mechanics [29]. We confirmed < 0.6 Pearson's correlation coefficient between any two SSF covariates.

We evaluated AIC for SSFs containing all combinations of these covariates and chose the best model as that with the lowest AIC (Table S2). We also retained the best model excluding energy for later use when evaluating movement efficiency ("Evaluating whether wolverine routes incorporate spatial memory" section). To reduce bias of parameter estimates, we included the step length, natural log of step length, and cosine of the turning angle as covariates in all candidate models [30]. This process therefore yielded a fitted SSF describing how wolverines respond to local (i.e., traversable in 5 min) perceptual cues. We used this model to generate a static habitat kernel by multiplying the selection coefficients by their respective environmental rasters (excluding energy, since rasterization depends on an animal's current location) and summing the products [31]. This habitat kernel is therefore a rasterized map with pixel values reflecting probability of use by wolverines, disregarding any influence of movement or energy [31].

Generating local-knowledge routes using mechanistic movement simulation

To simulate routes driven solely by perceptual (i.e., local) cues, we used the fitted SSF to parameterize a mechanistic movement simulator, closely following the methods of [32, 33]. The simulator incorporated the SSF-derived habitat kernel, energetic cost of movement, and movement parameters (e.g., step length, turning angle), and we used it to simulate 100 routes from the start to the end locations of each actual route (Fig. 2). To ensure that routes reached the end, we also incorporated a distribution of "deviation angles," parameterized from the empirical data, reflecting the tendency of wolverines to move toward the end location. In this way, simulated routes are intended to account for all non-memory drivers of wolverine movement in this landscape. Metrics comparing the distance and number of steps of simulated versus observed routes are in Table S3. We detail the simulator in Appendix S2.

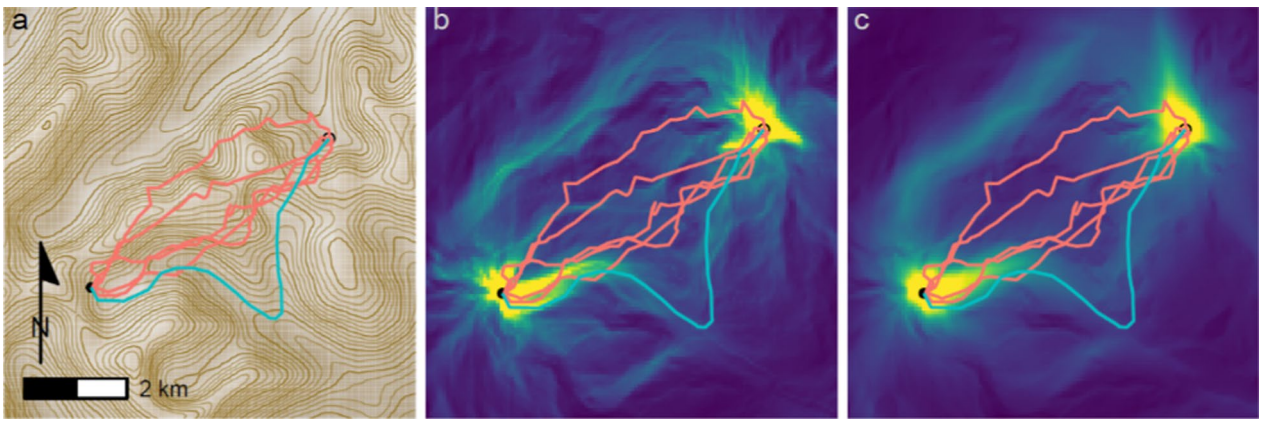

Fig. 2 Example 135 min routes of a GPS-collared wolverine (blue) and simulated local-knowledge wolverines (red), overlaid on a topographic map (**a**), energy-based Circuitscape output (**b**), and resource-based Circuitscape output (**c**) connecting the route start and end locations. In **b** and **c**, lighter colors represent areas of higher current (i.e., lower resistance)

Evaluating whether wolverine routes incorporate spatial memory

To evaluate whether wolverines incorporated knowledge beyond their perceptual range into movement decisions, we compared (1) total modeled energy expenditure and (2) efficiency of actual versus SLK routes. To determine total energy expenditure, we calculated the energy expenditure for each step using Eq. 1 and summed across steps within each route. To determine efficiency, we relied on Circuitscape (version 5.0.0, run in Julia version 1.8.5 [34]). Circuitscape treats landscape pixels as resistors, and identifies where current flows across the landscape, preferentially following areas of low resistance [34]. Cumulative flow of current can be summed for each pixel, such that sums reflect relative use by an animal avoiding high-resistance areas while moving between two nodes [34]. In this way, the cumulative flow maps produced by Circuitscape can be used to compare the efficiency of multiple alternative paths between two locations, with more efficient paths moving through pixels with higher cumulative flow. A route's Circuitscape-derived energetic efficiency is therefore inversely correlated with its total energy expenditure, and we evaluated both to make our results comparable with previous studies using similar definitions of efficiency (e.g., [35]), while also ensuring that any observed patterns were consistent across these similar but distinct metrics. We assumed that exploiting more efficient and less energetically costly routes through unseen terrain than SLK routes reflected spatial memory of that terrain.

We defined and evaluated efficiency in two ways. First, we generated a rasterized energy landscape for the study area following [28]. This relies on Eq. 1, wherein a transition matrix is calculated representing the energetic cost of moving between any two neighboring cells, and all incoming values for each cell are averaged for rasterization. Applying Circuitscape through this raster identifies the relative energetic efficiency of each landscape pixel, such that cumulatively using higher current values indicates a more efficient route (Fig. 2b).

Second, we applied Circuitscape through the inverse of the exponentiated habitat kernel generated from the best SSF that excluded energy as a covariate ("Processing and analyzing wolverine movement data" section; Fig. 2c). We used this definition of efficiency to evaluate whether wolverines incorporate other landscape attributes, such as the spatial distribution of food resources and the park road, into planning routes. We term this definition of efficiency "resource efficiency," reflecting the diversity of possible landscape drivers it represents.

We applied Circuitscape through each of these rasters separately for each route, with the route start and end as input locations (Fig. 2). We then extracted the Circuitscape current values associated with each wolverine location (simulated and real) and calculated median values for each route. We excluded route start and ends because these always had current values of 1 and inflated median values of shorter routes. We used median values rather than sums because simulated and real routes often contained different numbers of steps.

To compare observed and simulated routes, we used paired Wilcoxon signed-rank tests to account for non-normality in our data [36]. We used these tests to evaluate whether each of the response variables (resource efficiency, energy efficiency, and total energy expenditure) varied by path type (SLK versus observed) within each set of routes (i.e., the 30 min route set, 45 min route set, etc., including the route set to known destinations). Since paired Wilcoxon tests allow only one observation per sample pair, we ran each test 100 times for each route set, randomly drawing a new paired SLK route for each observed route during each iteration. We extracted estimates of the difference of medians between the two groups, along with associated 95% confidence intervals, and considered observed routes different from SLK routes if the median 95% C.I. for a given route set did not overlap zero. These models therefore address the question: are actual wolverine routes more efficient than available/simulated routes? We standardized (i.e., subtracted mean and divided by standard deviation) predictor values before fitting models to compare effect sizes across models.

Finally, we calculated Pearson's correlation coefficient between median efficiency scores for resource- and energy-based definitions of efficiency to evaluate the extent to which each represented different landscape drivers.

Quantifying energetic savings conferred by route-planning behavior

To quantify energy savings, we chose a route set at which wolverines consistently selected energetically efficient routes and calculated the median difference between the modeled energy cost incurred by the wolverine and the modeled energy cost incurred by simulated wolverines for that route. To calculate energy cost, we summed the result of Eq. 1 across all steps in each route.

Results

Local-knowledge step selection function results

The top SSF included slope, elevation, ridge, energy, streams/rivers, and the land cover classes shrub, grass, and road. Wolverines selected slope, elevation, and road at the 30 m pixel resolution but showed the strongest response to shrub and grass landcover classes when summarized within 150 m of the animal's location. Holding

all other variables constant, wolverines were 1.44 times more likely to choose pixels that were ridges than not ridges, 1.16 times more likely to select pixels coded shrubby than not shrubby, 1.49 times less likely to select pixels coded grassy than not grassy, and 4.09 times more likely to select pixels on the snow-covered and closed park road than pixels not on the road. In addition, wolverines were 1.06 times more likely to take a step if it required 1 kcal less energy. Relative selection strength (RSS [37]) for elevation increased across the gradient available to study animals (Figure S1), whereas wolverines preferred intermediate slopes (Figure S2) and areas closer to streams (Figure S3).

Comparing observed versus local-knowledge routes

Wolverines exploited more resource-efficient routes than SLK routes when navigating to destinations ranging from 30 to 180 min ahead and exploited more energetically efficient routes when navigating to destinations 30–150 min ahead (Fig. 3). Observed routes had lower total energy expenditure across all route durations we evaluated (30–225 min). Pearson's correlation coefficients between resource-efficiency and energy-efficiency of routes were high, ranging from 0.79 at the 195 min duration to 0.98 at the 30 min duration.

Median estimated differences between observed and SLK routes were highest for energy efficiency at the 105–150 min time horizon, for resource efficiency at the 105–195 min horizon, and for total energy expenditure at the 120–195 min horizon (Fig. 3; Table S4). These time horizons correspond to roughly 5.3–9.8 km traveled (Fig. 3; Table S3). For 135 min routes, falling within the peak time horizon for energetic efficiency, mean modeled energy savings of actual routes over SLK routes was 19.3 kcal (Table 1, Fig. 4). At this route duration, all study

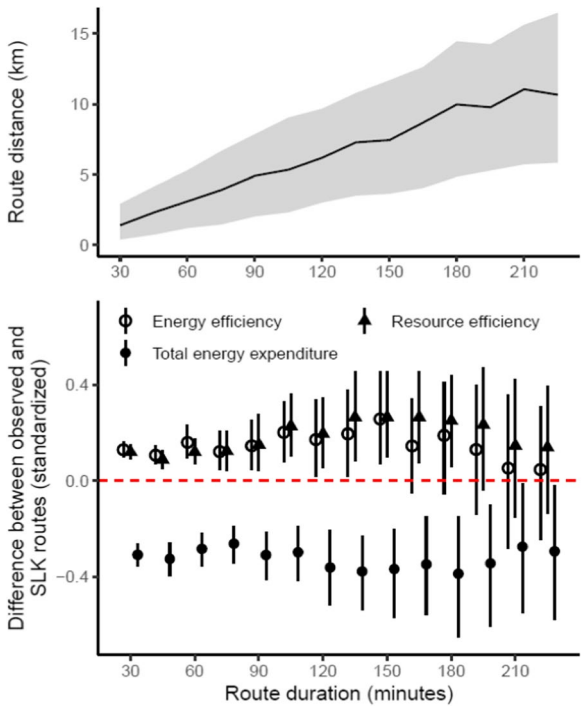

Fig. 3 Median distance traveled (top; confidence band shows 95% interquantile range) and median difference in energy efficiency, resource efficiency, and total energy expenditure between observed and simulated local knowledge (SLK) routes by route duration (bottom). Differences were evaluated using a paired Wilcoxon signed-rank test and data were standardized prior to analysis to facilitate effect size comparison across route durations. Larger absolute differences are consistent with a stronger reliance on spatial memory to plan efficient routes

Table 1 Modeled energy saved using spatial memory of unseen terrain at the 135 min route duration compared with SLK routes

Individual	Median (kcal)	95% interquantile range	Number of routes
M1	28.0	− 56.5–152.1	54
M3	17.2	− 34.6–93.6	15
M23	10.9	− 2.1–57.2	6
M19	15.0	− 14.1–59.6	3
F4	47.4	5–89.8	2
Population	19.3	− 39.1–141.3	80

Negative values indicate instances in which SLK routes used less energy than observed routes

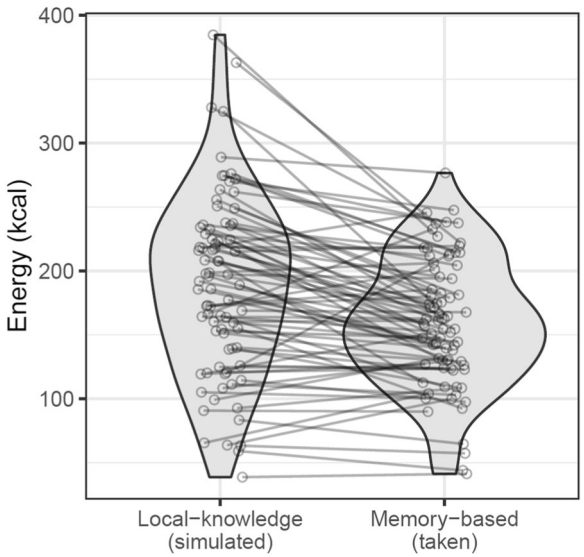

Fig. 4 Locomotion-associated energy required to traverse 135 min memory-informed routes used by wolverines (right), compared with median energy required to traverse simulated local-knowledge routes connecting the same start and end locations (left). Median energy savings is 19.3 kcal

animals saved energy over matched SLK routes, and median energy savings ranged between 10.9 and 47.4 kcal across individuals (Table 1).

Routes to previously-visited destinations had lower total energy expenditure than their SLK counterparts (median estimated difference from Wilcoxon signed rank tests performed on the standardized dataset = − 0.30, median 95% confidence interval: − 0.58 to − 0.02). We found no difference, however, in either resource efficiency (median estimated difference from Wilcoxon signed rank tests = 0.09, median 95% confidence interval: − 0.22–0.35) or energy efficiency (median estimated difference from Wilcoxon signed rank tests = − 0.01, median 95%

confidence interval: − 0.35–0.27) for these routes.

Discussion

We provide evidence that wolverines incorporate spatial memory of their unseen surroundings into route-planning decisions. Doing so enables them to plan efficient routes through distant rugged terrain, saving on average 19.3 kcal (roughly the equivalent of one third of a vole [*Microtus* spp.; [38]) per 135 min of movement. In addition, we identify 5.3–9.8 km as the predominant distance horizon at which wolverines plan such routes (i.e., the median distances traveled in 105–195 min), although route-planning was evident for destinations up to 10.7 km ahead (i.e., the median distance traveled in 225 min). We were able to arrive at these findings by isolating the drivers of movement attributable to local (i.e., perceived) cues, simulating movement solely in response to such cues, and evaluating whether paths actually taken were more efficient. We found broad support that actual wolverine paths were more efficient than those relying on local cues alone, consistent with the use of spatial memory of unseen surroundings.

Total energy expenditure generally exhibited larger differences between observed and SLK routes than did either Circuitscape-derived efficiency metric, while both efficiency metrics exhibited larger variation across route durations. This is demonstrated in Fig. 3 and in the finding that observed routes to known destinations were less energetically costly than their SLK counterparts but did not differ in either efficiency metric. We suspect that these differences derive from nuances in what each metric represents; the ability of Circuitscape current values to detect differences between routes generally relies upon a path following one or two high-current corridors, whereas comparing total energy expenditure does not. The finding that total energy expenditure was lower across all evaluated route durations (30–225 min) suggests that wolverines may incorporate spatial memory into route-planning at all durations, but the uniform pattern in elevated selection at 105–195 min durations across all metrics indicates that route-planning behavior is strongest at that time horizon.

Evaluating memory and learning in free-living animals is notoriously challenging, since infallible evidence requires perfect knowledge of an individual's past experience and potentially confounding cues [1, 2]. We suggest that accounting for local perceptual drivers of movement and thereby isolating the role of knowledge beyond the perceptual range is one method to circumvent some, though not all, such complications. We are unable to exclude, for example, the possibility that wolverines follow sequential landmarks (e.g., scent marks, terrain features) along established routes, rather than flexibly incorporating spatial memory at every movement decision [39]. For such routes to follow efficient corridors, however, would require spatial memory during their creation. Applying our method to individuals traversing novel terrain (such as dispersing subadults) would further exclude confounding explanations, since they would be expected to not move more efficiently than SLK routes.

Encoding and retrieving memories requires energy, so it is expected that memory processes conferring net fitness benefits (e.g., gaining more energy than is spent, or avoiding a previously encountered predator's den [1]) are favored through natural selection. Evaluating the balance of memory's benefits and costs, however, is challenging. By comparing the energetic cost of movement with and without spatial memory, our method offers an approach for quantifying one potentially adaptive function of spatial memory: energetic savings associated with remembering the surrounding unseen energy landscape. This provides a transferrable method for incorporating such benefits into empirical movement models, as well as a metric for comparative studies of memory across taxa or populations inhabiting different energy landscapes [40]. Since our approach relies on a unified theory of locomotion derived from other taxa, it could be extended using biologgers (e.g., tri-axial accelerometers) and respirometry to validate cost of locomotion [41]. Additional work addressing the influence of landscape features beyond slope angle (e.g., substrate hardness, fine-scale roughness, vegetative cover) on locomotion costs would help further resolve the energy savings of spatial memory [42].

To our knowledge, no previous study has evaluated the time/distance horizon on which animals plan travel routes. Such horizons could provide a novel metric for selecting taxon-specific, cognitively-informed step intervals for step selection analyses, a perennial problem in such studies [16]. We expect that this horizon is

influenced by cognitive capacity and/or the spatial distribution of resources; comparing horizons across populations encountering a gradient of resource density (e.g., prey abundance) may help disentangle the relative influence of each.

The time/distance horizon we identified (5.3–9.8 km) falls comfortably within typical territory sizes for this population (496 km^2 for males and 141 km^2 for females; [22]) and is under half of the mean daily travel distance of roughly 20 km (J. Copeland, *unpublished data*). This horizon is also consistent with our expectations for a species relying on sparse ungulate carrion at this time of year; median pairwise distance between carrion-containing sites visited by collared wolverines between January and March 2006 was 10.6 km (J. Copeland, *unpublished data*). This figure reflects sites accessed by researchers the following summer, however, which likely biases this estimate high (i.e., since not all sites were visited, and some sites may have lost evidence of carrion in the intervening months).

Our findings fit well with the Ecological Intelligence Hypothesis, which posits that environment acts as a selective pressure governing cognition [43]. Increased diversity and patchiness of food resources, for example, have been hypothesized as selective forces for more advanced spatial cognition [44], as has food caching behavior [45]. As generalist scavengers relying on caching to fuel lactation, wolverines fit these criteria [46]. Our study suggests that wolverines remember both energetic and resource-based landscape attributes when planning routes, although the collinearity of the two suggests that landscape attributes representing energetic costs (e.g., slope) may have obscured those representing food resources (e.g., landcover type) in our SSF models. Nonetheless, our study provides evidence echoing [6] that diverse facets of landscape variability, such as topography and resulting energetic costs, likely join food resource distribution in driving selection for spatial memory.

We emphasize that our findings derive from five individuals, four of whom were male, during winter only. As such, we see these results more as an intriguing springboard for future research than a conclusive investigation of the topic. These restrictions highlight ripe avenues for such future research, including differences across seasons and sexes in how spatial memory influences movement, as may be expected based on reproductive status and food availability. These limitations notwithstanding, we believe that this analysis offers a rare look into the cognitive mechanics underpinning navigation in free-living animals.

Conclusions

We provide evidence that a solitary wide-ranging carnivore, the wolverine, uses spatial memory of its home range to plan and follow energetically efficient routes to unseen destinations. In doing so, we demonstrate the utility of mechanistic movement modeling for isolating memory- versus perceptual-cue-driven movement. This approach fits well into the SSF-based framework for analyzing animal movement and can be readily adapted for any animal with high-frequency relocation data. In addition, we introduce a quantitative metric for evaluating the scale at which animals exhibit spatial memory, a topic which has received sparse attention in the literature, and offer a method for estimating locomotion-associated energetic benefit of memory. Cumulatively, our findings support adding these mammalian carnivores to the primate-dominated list of taxa exhibiting a complex spatial awareness of their unseen surroundings.

Abbreviations

AIC	Akaike's Information Criterion
RSS	Relative selection strength
SLK	Simulated local knowledge
SSF	Step-selection function

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-025-00571-4.

Additional file 1.

Additional file 2.

Acknowledgements

We are grateful to the many people who provided logistical, administrative, and fieldwork support. Steve Gniadek (Wildlife Biologist, National Park Service, retired) was particularly supportive throughout our study. Two anonymous reviewers improved this manuscript.

Author contributions

TG designed/implemented the analysis and drafted the initial manuscript. JC designed earlier versions of the analysis and oversaw data collection. LO provided analytical expertise. JW provided system-specific expertise. JS oversaw project design and implementation. All authors reviewed and edited the manuscript.

Funding

Funding was provided by Natural Resource Protection Program grant PMIS 73656, a National Park Service Challenge Cost-share Program grant, The Wilburforce Foundation Yellowstone to Yukon Science Grant Program 2004–2005, The Glacier National Park Fund, Earth Friends Wildlife Foundation, The Wolverine Foundation, USDA Forest Service Northern Region, Montana Department of Fish, Wildlife, and Parks, University of Montana, Defenders of Wildlife, Northern Rockies Conservation Cooperative, Chase Wildlife Foundation, and The Wildlife Land Trust (Humane Society of the United States). Private donations were provided by G. Kirshner, R. Bennett, D. Murray, C. Murray, G. Ohrstrom, J. Thompson, B Heinreich, A. and S. Coffey, J. and P. Case, R. and C. Atkinson, and The Glacier Park Trail Crew alumni.

Availability of data and materials

Data and code are available at https://doi.org/10.6084/m9.figshare.c.7371193. Wolverine movement data are stored on Movebank: https://www.movebank.

org/cms/webapp?gwt_fragment=page%3Dstudies%2Cpath%3Dstudy5505892931.

Declarations

Ethics approval and consent to participate
Capture and handling procedures were reviewed and approved by the University of Montana Institutional Animal Care and Use Committee.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

Received: 11 September 2024 Accepted: 1 June 2025
Published online: 21 June 2025

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