Report

Current Biology

Chimpanzees Use Least-Cost Routes to Out-of-Sight Goals

Highlights

- Application of least-cost analysis to chimpanzee travel in a montane environment
- First example of chimpanzees taking least-cost routes to out-of-sight goals
- Suggests chimpanzees use spatial knowledge of their landscape to optimize travel
- Landscape complexity may play a role in shaping cognition

Authors

Samantha J. Green, Bryan J. Boruff,
Tyler R. Bonnell, Cyril C. Grueter

Correspondence

samantha.green@research.uwa.edu.au

In Brief

Green et al. provide the first evidence that chimpanzees are able to walk least-cost routes in a variable energy landscape. Least-cost modeling predicted the costs and sinuosity of chimpanzee paths better than local knowledge and straight-line null models. Results suggest chimpanzees use spatial knowledge of their landscape to optimize travel.

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Chimpanzees Use Least-Cost Routes to Out-of-Sight Goals

Samantha J. Green,[1,2,7,*] Bryan J. Boruff,[3] Tyler R. Bonnell,[4] and Cyril C. Grueter[1,2,5,6]

[1]School of Human Sciences, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia
[2]UWA Africa Research & Engagement Centre, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia
[3]School of Agriculture and Environment, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia
[4]Department of Psychology, University of Lethbridge, 4401 University Drive, Alberta T1K 3M4, Canada
[5]Centre for Evolutionary Biology, School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia
[6]International Centre of Biodiversity and Primate Conservation, Dali University, 2 Hongsheng Road, Dali, Yunnan 671003, China
[7]Lead Contact
*Correspondence: samantha.green@research.uwa.edu.au

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SUMMARY

While the ability of naturally ranging animals to recall the location of food resources and use straight-line routes between them has been demonstrated in several studies [1, 2], it is not known whether animals can use knowledge of their landscape to walk least-cost routes [3]. This ability is likely to be particularly important for animals living in highly variable energy landscapes, where movement costs are exacerbated [4, 5]. Here, we used least-cost modeling, which determines the most efficient route assuming full knowledge of the environment, to investigate whether chimpanzees (*Pan troglodytes*) living in a rugged, montane environment walk least-cost routes to out-of-sight goals. We compared the "costs" and geometry of observed movements with predicted least-cost routes and local knowledge (agent-based) and straight-line null models. The least-cost model performed better than the local knowledge and straight-line models across all parameters, and linear mixed modeling showed a strong relationship between the cost of observed chimpanzee travel and least-cost routes. Our study provides the first example of the ability to take least-cost routes to out-of-sight goals by chimpanzees and suggests they have spatial memory of their home range landscape. This ability may be a key trait that has enabled chimpanzees to maintain their energy balance in a low-resource environment. Our findings provide a further example of how the advanced cognitive complexity of hominins may have facilitated their adaptation to a variety of environmental conditions and lead us to hypothesize that landscape complexity may play a role in shaping cognition.

RESULTS

Physical features of the landscape, such as steep slopes or dense vegetation, can significantly increase energy expenditure during foraging, [6] and recent studies have shown that animals will alter their ranging patterns in response to landscape features [3, 7–10]. This landscape driven variation in movement costs is termed the "energy landscape," [4, 5] and it follows that animals living in more variable energy landscapes would gain fitness benefits from remembering the physical landscape of their natural environment and using this knowledge to walk energy-minimizing routes. By using chimpanzee ranging data collected in Nyungwe National Park, Rwanda (Figure 1) and a least-cost model that incorporates direction of travel (anisotropic), we were able to investigate whether chimpanzees use efficient foraging routes in a variable energy landscape.

To test for evidence that chimpanzees use energetically efficient routes to goals outside the line of sight (out of sight), we used change points to define movement segments [11] and used a subset of these movement segments, together with the available laboratory measurements of chimpanzee energy expenditure, to define movement "costs." We then compared the costs and geometry of observed movements (minimum segment length: 150 m) with predicted least-cost paths (LCPs) and two null models. One null model assumes chimpanzees use knowledge of the landscape within their visual detection (30 m) when choosing travel routes (the local knowledge model), and the other assumes chimpanzees do not incorporate the landscape in travel decisions (the straight-line model).

The least-cost model was a better predictor of actual chimpanzee travel than the local knowledge and straight-line model across all measures and for all parameters. The relationship between actual travel costs and the local knowledge model is analyzed separately, as for 89 of the 167 segments, chimpanzees/agents did not reach the end point following the local knowledge rule.

The normalized root mean square errors (NRMSEs) of cumulative and per m costs were lowest for the least-cost model, with the straight-line model overestimating both cumulative and per m travel costs (Table 1). The NRMSE between least-cost and actual cumulative costs was less than 5%, indicating that chimpanzee path segments are similar in "cost" to the LCP.

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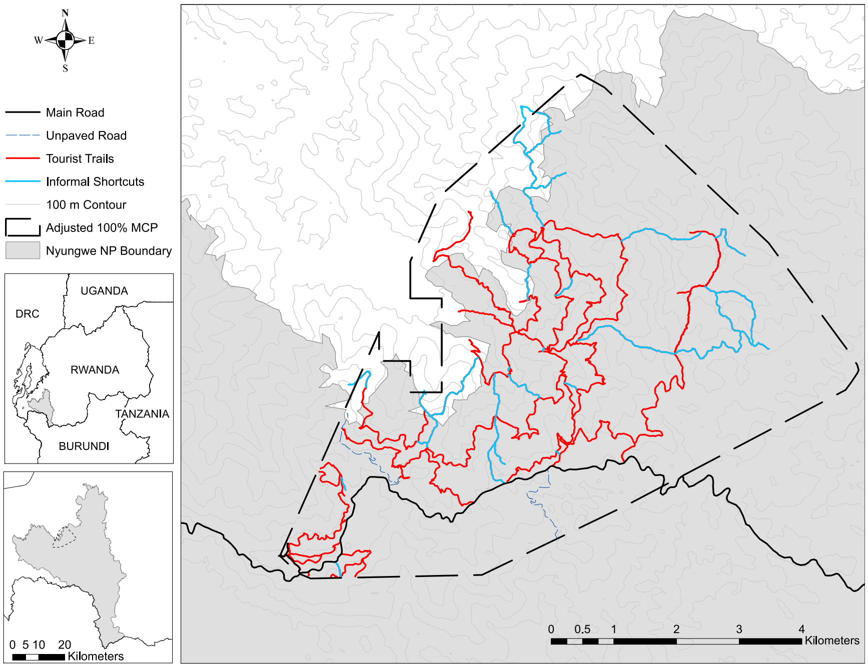

Figure 1. Location of the Study Area in Nyungwe National Park, Rwanda

Nyungwe is montane forest in south-west Rwanda that supports a community of chimpanzees that range to the highest known altitudinal limit of their species distribution. The study community's home range (Adjusted 100% MCP) has a highly variable energy landscape, consisting of rugged terrain, dense ground cover, and a network of human-made trails.

Multicollinearity (VIF > 10) was detected in the cumulative cost linear mixed effects model (LMM), and cumulative costs were therefore excluded from further analysis. However, the cost per m LMM yielded a VIF of 2.99, which is below recommended cut-offs [12, 13]. The full LMM with the least-cost and straight-line costs as predictor variables and actual costs per m as the response, was significantly different from the null model containing only the intercept and the random effect (chi square = 100.84, df = 3, p = < 0.001). The final model revealed a significant effect of both the least-cost and straight-line models on actual cost per m (Table 2), but separate models revealed that the least-cost model explained 91% of the variation in actual costs (estimate = 0.71, standard error = 0.02, r^2 = 0.91, p = < 0.001), while the straight-line model only explained 66% of the variation (estimate = 0.60, standard error = 0.3, r^2 = 0.66, p = < 0.001).

These results held true for distant goals (>1 km in length). The NRMSE between actual and least-cost cumulative costs remained less than 5%, and the NRMSE between per m costs remained less than 10%, while the NRSME between actual and straight-line costs more than doubled for both cumulative and per m costs (Table 1). The LMM showed that the least-cost model was still a strong predictor of actual per m costs for long segments (estimate = 0.31, standard error = 0.02, r^2 = 0.88, p = < 0.001).

The least-cost model is also a better predictor of actual travel sinuosity and length than the straight-line model (Table S1), with chimpanzees taking longer, more sinuous paths that incorporate trails and/or avoid steep inclines (e.g., Figure 2).

For 89 of the 167 segments, agents did not reach the end point following the local knowledge rule. For the 78 segments where the agent did reach the endpoint in at least one simulation, the probability was low, with only 7 segments having a >50% probability of reaching the end point (Figure S1). Of these 78 segments, only three had at least one simulation where the agent was able to reach the end point with a cumulative cost greater than or equal to that of the chimpanzees (Figure S2).

The LMM with the least-cost and lowest cost local knowledge paths as the predictor variables and actual costs as the response variable, yielded VIFs below the recommended cut offs for both cumulative and per m costs. The full model was significantly different from the null model for cumulative (chi sq = 204.69, df = 3, p = < 0.001) and per m costs (chi sq = 197.24, df = 3, p = < 0.001). The final model revealed a significant effect of the least-cost, but not the local knowledge model on actual cumulative costs (Table S2) and actual costs per m (Table S3).

DISCUSSION

The least-cost model predicted the costs and sinuosity of chimpanzee paths better than the local knowledge, and straight-line model and linear mixed modeling showed a strong relationship between the costs of chimpanzee travel and the modeled least-cost routes. These results cannot be explained by use of visual or olfactory cues, as agent-based modeling showed that chimpanzees/agents rarely reached the "goal" when navigating using local knowledge of the landscape only. For those segments where agents were able to reach the goal, the local knowledge model was a poor predictor of actual travel costs compared to the least-cost model.

While the travel costs do not represent metabolic rates, the available laboratory data on chimpanzee energetics was used to inform vertical factor calculations and the cost surface was calibrated to a subset of chimpanzee pathway data, which recent reviews have recommended as the most ecological meaningful technique [14, 15]. Outputs not based on modeled costs (path segment sinuosity and length) also showed better agreement with the least-cost than the local knowledge and straight-line models. As the model employed assumes complete knowledge of the landscape [15], our results provide strong evidence that chimpanzees walk least-cost routes to out-of-sight goals, suggesting that Nyungwe chimpanzees use spatial knowledge of their home range landscape to optimize travel. Chimpanzees demonstrated remarkable spatial accuracy in taking least-cost routes, even for long (>1 km) path segments when

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Table 1. Costs of Chimpanzee Path Segments Compared to Least-Cost and Straight-Line Models

	Cumulative cost			Cost per m		
Model	Mean	SD	NRMSE	Mean	SD	NRMSE
All segments (n = 167)						
Actual	954	705	NA	1.80	0.75	NA
LCP	902	676	3%	1.72	0.71	6%
Straight	1,150	1,024	10%	2.23	0.83	17%
Segments > 1 km (n = 27)						
Actual	2,079	884	NA	1.37	0.33	NA
LCP	1,967	869	4%	1.35	0.31	8%
Straight	2,757	1,386	28%	2.23	0.58	57%

SD, standard deviation; NRMSE, normalized root mean square error; actual, actual path, LCP, least-cost path; straight, straight-line path.

Table 2. Results of the LMM with Actual Costs per m as the Response Variable and Least-Cost and Straight-Line Cost per m as the Predictor Variables (n = 167)

Predictor Variable	Estimate	Std. Error	*t*	95% CI	*P*
Intercept	1.79	0.02			
LCP	0.65	0.03	22.07	0.02, 0.14	<0.001
Straight	0.08	0.03	2.67	0.59, 0.71	0.008

LCP, least-cost path; straight, straight-line path

the number of potential alternative routes increases considerably. These results differ to previous studies, which found no relationship between predicted least-cost and actual travel routes in non-human primates [3, 16]. However, these findings may be due to the use of unrealistic isotropic models [15] and lack of model calibration to pathway data [14] and not a reflection of the animals' cognitive abilities.

Inferring spatial knowledge in naturally ranging animals that travel in relatively linear segments is difficult, as straight-line movement can be associated with a number of foraging processes that are not goal-orientated [1]. Thus, a number of onerous measurements are required to infer cognitive processes [1], such as recording all alternative food resources bypassed [17, 18] and identifying which of those resources are more valuable, which can be extremely difficult in itself [19]. Our work suggests that LCP modeling can offer an alternative approach to infer cognitive abilities in wild animals that are known to modulate their movements in response to energy landscapes.

Advances in hand-held Global Positioning Systems (GPS) allowing more accurate collection of movement data in rugged environments and increasingly sophisticated modeling tools that can incorporate landscape features into measures of movement efficiency have opened opportunities for analysis of animal memory of landscape and route choice [20, 21]. The ability to choose least-cost routes to out-of-sight goals is expected to be most beneficial to animals that (A) live in highly variable energy landscapes, as the potential savings in movement costs are greater, and (B) rely on resources that are (based on [22]) (1) stationary, and therefore predictable in space as opposed to mobile prey, (2) patchily distributed, making random search a less efficient strategy, and (3) lower in density, resulting in increased travel distances between patches and thus increased movement costs.

Ecological models, by their nature, represent a simplified version of the natural environment and are therefore limited in their ability to capture the full complexity of interactions between landscape features and animal movement. Our model was able to predict the travel costs of chimpanzees within a 3% error. However, analyzing where the model did not fit well can yield important insights into other key drivers of animal movement [5, 23]. Some inconsistencies could be explained by the lack of detailed super and substrate information, which resulted in landscape features that facilitate chimpanzee movement (e.g., exposed rocks, vines that allowed chimpanzees to climb up or down steep cliff faces and fallen logs that enable stream crossings) being omitted from the cost surface. The importance of compact substrate and reduced superstrate was demonstrated by one occasion when the focal chimpanzee deviated 75 m from the predicted least-cost route to travel along an area at the altitudinal limit of their home-range with exposed rocks and sparse ground cover. Additionally, the digital elevation model (DEM) used was coarser in resolution than other model elements (e.g., trails). This sometimes resulted in the least-cost model underestimating actual travel costs. More detailed elevation, super, and substrate layers could be obtained using high resolution imagery collected using new satellite constellations (Planet Labs) or surveys flown by manned and unmanned aerial vehicles (UAVs). Landscape features could be extracted with the aid of LiDAR classification software to produce high resolution cost surfaces (see [24] for an example). With fine-scale remote sensing technologies becoming increasingly more affordable, this offers an exciting area for future research.

To maximize collection of travel path data, we limited our analysis to male chimpanzees. However, using least-cost routes may be more beneficial to anestrous females who bear the additional energetic costs of gestation, lactation, and travel with dependent offspring. Application of least-cost modeling to anestrous female chimpanzees in future research is recommended to test for sex differences in ranging response to the energy landscape.

Our study also assumes that chimpanzees move to a goal of optimizing energy balance, but as our cost surface does not represent metabolic rates, alternative drivers like time [25] cannot be excluded. Future studies could rule out alternative drivers of route choice by constructing cost-space maps for subjects where the functional relationship between movement costs and terrain is well understood [4, 5] or, where ethically justifiable, use animal-attached accelerometers to measure energy expenditure across defined landscape features (e.g., [4]).

To our knowledge, this study provides the first example of chimpanzees' ability to walk least-cost routes to out-of-sight goals, suggesting they have spatial knowledge of their home range landscape. As chimpanzees exhibit a relatively inefficient form of terrestrial locomotion (knuckle walking [26]) and expend more energy traveling up slopes than on level ground [27, 28], the ability to use least-cost routes may be a key trait that has allowed Nyungwe chimpanzees to survive in a low-resource, montane environment. Our study provides a further example of how the advanced mental complexity of hominins may have facilitated their adaptation to a variety of environmental conditions.

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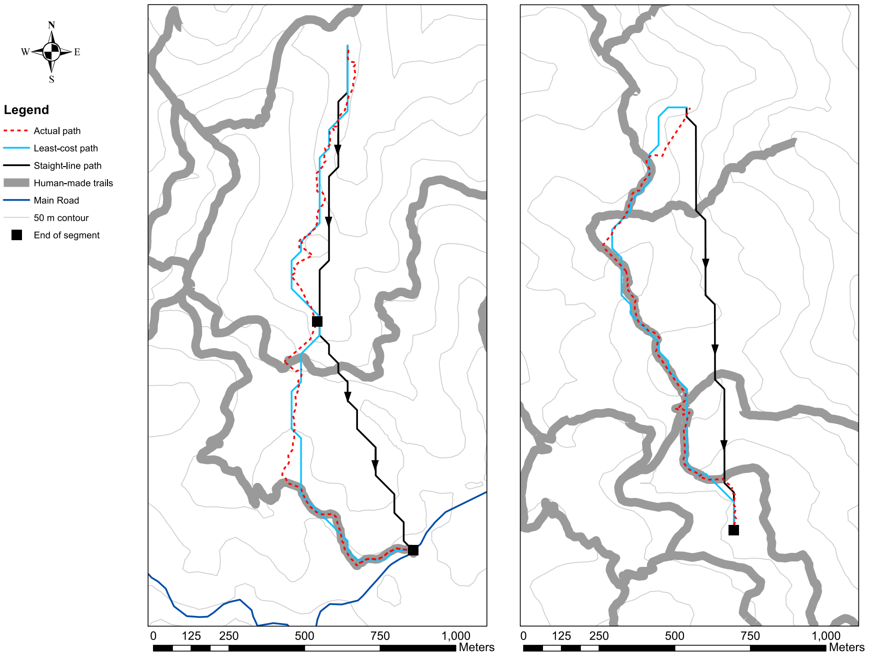

Figure 2. Modeled and Actual Path Segments on 9 April 2017 (Left) and 27 November 2017 (Right)

See Tables S1–S3 for summary statistics.

Recent research has renewed interest in the role ecological variation plays in shaping cognitive abilities [29, 30]. The “ecological intelligence” or “harsh environment” hypothesis argues that environments with resources that are low in abundance, sparsely distributed and ephemeral, favor the development of mental abilities that facilitate efficient foraging [22, 31–33]. There is growing evidence to support this from comparative studies of primates (review in [29]), birds [34–37], bats, and rodents (review in [38]). However, a recent study highlighted the need for a clearer definition of what constitutes environmental “harshness” [39]. Based on the results of this study, we propose that environmental harshness could be expanded beyond the spatio-temporal complexity of food resources to include landscape complexity. Studies in relatively homogeneous landscapes suggest that chimpanzees consider the Euclidean distances between potential food trees when deciding where to forage [17]. Chimpanzees in highly variable energy landscapes may face the additional cognitive load of recalling the landscape between themselves and potential food trees and comparing the least-cost routes between them. Future research on the cognitive abilities used by chimpanzees and other large-brained animals to navigate a variety of landscapes is required to shed light on the role energy landscapes play in shaping animal cognition.

While there is growing evidence that naturally ranging animals are able to remember the location, type, and seasonality of food resources and choose distance-minimizing routes between them [2, 20, 40], their ability to walk efficient foraging routes in heterogenous landscapes is not well understood. By using anisotropic least-cost modeling, we provide the first evidence that chimpanzees are able to walk least-cost routes, suggesting that they have spatial knowledge of their physical landscape. This ability may be key to chimpanzee survival in low-resource, montane environments and may have been shaped by the “harshness” of their energy landscape. Application of least-cost modeling in cognitive studies of other naturally ranging animals in a variety of landscapes would shed light on this.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2020.08.076.

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AUTHOR CONTRIBUTIONS

S.J.G. collected and analyzed data; T.R.B. conducted the agent-based modeling; and S.J.G., B.J.B., and C.C.G. wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
Chimpanzee, *Pan troglodytes*	Wild	N/A
Deposited Data		
Raw data	This paper	https://doi:10.5061/dryad.wdbrv15m7
Software and Algorithms		
R	[39]	https://www.r-project.org
Local knowledge model R code	This paper	https://github.com/tbonne/least_cost_movement_ABM

RESOURCE AVAILABILITY

Lead contact and materials availability

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Samantha Green (samantha.green@research.uwa.edu.au). This study did not generate new or unique materials.

Materials availability

This study did not generate new unique reagents.

Data and code availability

The R-code used in this study is available from: https://github.com/tbonne/least_cost_movement_ABM. Original data have been deposited to Dryad: https://doi.org/10.5061/dryad.wdbrv15m7.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Chimpanzees (*Pan troglodytes*) have been the subject of more spatial cognition studies than any other non-human primate [41], but as most field studies have been undertaken in relatively homogeneous environments [42], their ability to incorporate spatial knowledge of the landscape into their route choice has not been tested. Chimpanzees rely on food resources that are characterized by high spatio-temporal complexity [43] and thus travel relatively long daily distances, expending more energy on terrestrial locomotion than any other activity [44, 45]. A recent study in Nyungwe National Park, Rwanda showed that chimpanzee ranging patterns can be influenced by their terrain [46], making them perfect study subjects.

Nyungwe is a low-productivity montane forest [47] in south-west Rwanda (Figure 1). Across locations where chimpanzees have been studied, Nyungwe has one of the most variable energy landscapes, consisting of rugged terrain, dense ground cover and a network of human-made trails that chimpanzees preferentially use for travel (Figure 1, [46]). It protects 1,020 km^2 of forest and is estimated to contain 380 chimpanzees [48]. The study community range, to our knowledge, to the highest altitudinal limit of their species distribution [2,951 m ASL, [46]] and consisted of 67 members by the end of the study: 14 adult and 4 sub-adult males, 18 adult and 7 sub-adult females, 12 juveniles and 12 infants [49].

METHOD DETAILS

Movement observations

Data were collected between November 2016 and December 2017 in Nyungwe National Park, Rwanda (Figure 1). Male chimpanzees are usually more terrestrial [50–54] and travel longer distances per day [50, 55–57] and between food patches [54] than anestrous females. As it also took longer to identify all female chimpanzees in the community, only male chimpanzees were sampled to maximize path segment data (n = 14 individuals). Focal follows [58] were undertaken for as long as possible, ideally from nest to nest, on approximately ten days per month. When the focal chimpanzee was traveling, his location was recorded at 5 m intervals with a hand-held Garmin GPSMAP 64 device, with GLONASS receiver. The GPS accuracy was checked continuously and was within 3–6 m throughout most of the Mayebe home range, but could increase to 20 m in some valleys. Party size and composition was recorded every 15 min, with any individuals within 50 m of each other considered to be a part of the same party (following [59]).

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Least-cost analysis

Our hypothesis, that chimpanzees in Nyungwe take least-cost routes to out-of-sight goals, was tested using an anisotropic LCP model that assumes full knowledge of the environment [15]. The model calculates the least-cost route between two locations as a function of distance and the ‘cost’ of moving across the landscape. Low costs are assigned to features that facilitate movement and high costs to features that impede movement, such as slope, vegetation cover or human disturbance [14]. Least-cost analysis is increasingly employed to model animal movement for landscape connectivity studies; however, recent reviews found that few studies use empirical data to assign landscape costs or assess model accuracy [14, 60]. Most studies also employ isotropic models which are often not realistic [15], particularly in rugged environments where the cost to travel upslope is greater than downslope for many species [28].

We employed the ArcGIS Path Distance Tool which incorporates anisotropy by modifying the cost distance function with a user defined vertical factor. Path Distance calculates the cost of travel between two perpendicularly adjacent cells (*a* and *b*) using the following formula:

$$a1 = \frac{(cost\ surface(a)\ +\ cost\ surface(b))}{2} * surface\ distance(ab) * vertical\ factor(ab)$$

Where

$a1 = cost\ assigned\ to\ travel\ from\ cell\ a\ to\ cell\ b$

$cost\ surface(a) = the\ cost\ to\ travel\ through\ cell\ a$

$cost\ surface(b) = the\ cost\ to\ travel\ through\ cell\ b$

$surface\ distance(ab) = the\ surface\ distance\ between\ cells\ a\ and\ b\ calculated\ from\ a\ digital\ elevation\ model$

$vertical\ factor(ab) = accounts\ for\ the\ vertical\ cost\ of\ travel\ from\ cell\ a\ to\ b,\ calculated\ from\ a\ user\ specified\ relationship\ between\ the\ vertical\ relative\ moving\ angle\ and\ the\ vertical\ factor$

For diagonally connected cells, the larger distance (√2) between cells *a* and *b* is accounted for as follows:

$$a1 = \frac{(cost\ surface(a)\ +\ cost\ surface(b))}{2} * \sqrt{2} * surface\ distrance(ab) * vertical\ factor(ab)$$

Least-cost model inputs

Shepard et al. (2013) [5] identify three landscape factors that influence costs of transport for terrestrial animals: topographic variation, and super and substrate penetrability. Substrate is defined as “the medium over or on which an animal moves” ([5] p. 299), and superstrate as “any material against which an animal must push to move” ([5] p. 300). Landscape features that had the potential to influence chimpanzee travel in our study area were: slope, trails (reduced superstrate, compact substrate and gently sloping topography), ridges (reduced superstrate) and streams (costly substrate).

A 30 m x 30 m resolution Shuttle Radar Topography Mission (SRTM, available from the US Geological Survey’s EROS Data Center) DEM covering the study area was used to calculate a GIS slope layer. Human-made trails were mapped by walking all trails within the Mayebe chimpanzees home range, taking GPS readings every 5 m. This included both tourist trails and informal shortcuts. Established chimpanzee trails were mapped whenever chimpanzees were observed traveling along them. These are trails that were narrower than 1 m, had level substrate that cut into steep slopes, were free from superstrate up to approximately 1 m (sometimes forming a tunnel through vine thickets), and where bark had been worn off any dead logs or living vines that lay on the trail, suggesting regular use by chimpanzees [46]. These human and established trails were imported into ArcGIS and converted to a raster corresponding to the 30 m x 30 m SRTM DEM.

The ArcGIS 10.6 Hydrology Toolset was used to extract stream and ridge lines from 30 m x 30 m SRTM DEM. Extracted stream and ridge lines were visually inspected using Google Earth and any lines that had not been extracted using automated techniques were manually digitized on screen as described by Gregory et al. [61]. Both stream and ridge lines were converted to a raster corresponding to the 30 m x 30 m SRTM DEM.

Path segmentation

To create daily travel paths, any location points that were less than 30 m apart were discarded to align with the DEM resolution and each consecutive waypoint was then joined with a straight-line segment in ArcMap 10.6 (n = 106 days). Chimpanzees traveled along a valley with poor signal on one occasion. This path was reconstructed manually in ArcMap based on field notes. When chimpanzees crossed valleys with poor signal, they did so perpendicularly. In these cases, we linearly extrapolated from the preceding and subsequent location points.

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The paths were then divided into segments for analyses using a change point test (CPT) developed by Byrne et al. [11] to detect significant changes in terrestrial travel direction.While it is difficult to know the goal of naturally ranging animals [62], several studies have shown that changes in travel direction can identify the location of important food resources and other biologically important activities [19, 63–65]. We considered a spatial criterion to be more appropriate than a temporal criterion (used by Valero and Byrne [66] and Bates and Byrne [57]) as a defined ‘stop time’ would not capture some important determinants of chimpanzee travel routes such as changes in direction after hearing a pant-hoot (fusion) or reaching a tree that bore no ripe fruits (fruit monitoring).

Variants of the CPT were run from $q = 1$ through $q = 10$ for 10% of the daily travel paths using an alpha level of $p < 0.05$ with $q = 5$ chosen as the most representative since this value maximized the number of change points detected for each day’s path while also failing to ‘overshoot the change point’ [11]. After running the CPT on all paths, the behavior associated with each change point was recorded. Change points that were associated with any behavior other than ‘traveling’ and did not occur on a human-made or established trail, were used to divide paths into segments. Since the CPT would sometimes identify a change point one to two steps away from what could be considered the intuitive change point [11], the behavior associated with the two location points immediately before and after the detected change point were checked before dividing segments. Any segments less than 150 m were excluded from analysis as movements to out-of-sight resources was the focus of the study. This resulted in a total of 217 segments.

Movement costs

Fifty segments were set aside for model testing. While it is not possible to isolate the influence of each landscape factor on travel in observational studies, segments chosen for model testing contained travel both off and on trails and incorporated a range of landscape characteristics from flat to rugged terrain. As there is a paucity of research examining the role of landscape characteristics on energy expenditure of primates, landscape factors were examined in turn to develop a cost surface incorporating topography as well as trails, ridges and streams.

Vertical factor

To date, the best available information on chimpanzee energetics is Taylor et al.’s [27] measurements of energy use of a chimpanzee running on a treadmill with a +15 degree, and −15 degree incline. The chimpanzee used up to 1.75 times more energy on a +15 degree incline and as little as 0.64 times less energy on a −15 degree incline compared to a level surface. As our study area has slopes up to 58 degrees we extrapolated our data based on the trends shown for other quadrupeds [28]. As the true function of energy expenditure to slope is not known, we assume a linear function extrapolated for slope ranging from 0 to +58 degrees with values held constant for negative slopes. These values were converted to a Vertical Factor Table for input to the Path Distance tool (Table S4).

As measured movement costs for chimpanzees are only available for three gradients, a model developed for humans was also tested as recommended by Lempidakis et al. [23]. Tobler’s empirically derived Hiking Function [67] was used to convert slope to velocity (as a proxy for cost) using the following equation:

$$V = 6e^{(-3.5|G+0.05|)}$$

Where
V = *Velocity*
G = *Slope*
e = *Euler's number*

Vertical Factors calculated using this formula [68] were used to calculate Path Distance. Tobler’s hiking function and the extrapolated chimpanzee model were tested against segments that did not contain any trail travel. The extrapolated chimpanzee model visually approximated the actual path well, while the Tobler’s hiking function overestimated the sinuosity of most segments. Tobler’s hiking function was thus omitted from further model testing.

Cost surface

Of the remaining landscape features, human-made trails were expected to have the greatest influence on chimpanzee travel patterns. Cost values were iteratively tested for on versus off-trail travel on all test segments that included some trail travel. Relative to the fixed cost of 1, we tested off-trail cell costs from 2 to 10 using 1 increment intervals. As all path segments were influenced by topography, the segments were tested with and without the chimpanzee Vertical Factors identified previously (Table S4). An off-trail cost value of 2 with chimpanzee Vertical Factors included was the most accurate in predicting the locations where chimpanzees would enter and exit human-made trails.

As the model did not provide a good visual fit for all segments, the cost surface was further refined by including established trails. All cells that contained a human-made trail or established trail were given a value of 1 and all others a value of 2. The majority of segments showed improved visual representation with the addition of established trail costs.

Adding cost values for ridges and streams did not improve the visual fit for any of the test segments and were therefore excluded from further analysis.

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Final least-cost model inputs

The inputs to the Path Distance tool included: a cost surface raster consisting of a 30 × 30 m grid with all human-made and established trail cells representing a cost of 1 and all others a cost of 2; the 30 × 30 m SRTM DEM Surface Raster and the extrapolated chimpanzee Vertical Factor Table (Table S4).

Least-cost model accuracy

The Path Distance model was then run for each test segment. The output cost distance and backlink rasters (which specifies the neighbor that is the next cell on the LCP), were then used in the ArcGIS Cost Path tool and the cumulative cost for each segment was extracted.

To calculate the cumulative cost of travel on the actual segments, each polyline segment was converted to a 30 m x 30 m raster, and the SRTM DEM cells that corresponded to these rasters were extracted. This was input as a Surface Raster in the Path Distance tool and the same process was followed.

To assess the accuracy of the LCP model in predicting chimpanzee travel costs, the NRMSE between the cumulative cost of the actual and modeled LCP segments was calculated by dividing the root mean square error by the range of actual path costs ($\max_{obs} - \min_{obs}$). The LCP achieved a NRMSE of within 3% (n = 50).

Comparing actual travel to the least-cost model

To test whether chimpanzees use LCPs when traveling in their environment, the costs of actual travel were compared with predicted LCPs and two null models for all remaining segments (n = 167). One null model assumes chimpanzees use knowledge of the landscape within their visual detection when choosing travel routes (the local knowledge model) and the other assumes chimpanzees do not incorporate the landscape in travel decisions (the straight-line model).

Straight-line model

To calculate the cumulative cost of linear travel, straight polylines were created between the start and end of each segment in ArcGIS. The polylines were then converted to 30 m x 30 m rasters, and the SRTM DEM cells that corresponded to these rasters were extracted. This was input as a Surface Raster in the Path Distance tool and the same process was followed.

Local knowledge model

To calculate the costs of travel routes that incorporate only local knowledge of the energy landscape, an agent-based model was created the gDistance package [69] in R version 1.2-2 [70]. As the visual detection distance of landscape features (trails and slope) for humans in the study site was usually less than the resolution of the DEM (30 m), an agent was programmed to move to a local cell based on the relative costs of the neighboring 8 cells, i.e., the agent compared all neighboring cells and chose a cell based on a weighted probability of the costs. This step length also aligns with the mean estimated olfactory detection distance for chimpanzees (37 m, [71]). Following this rule, the agent tends to make the least-cost local choice.

Cost of travel between two neighboring cells was calculated using the same model inputs and equation as the least-cost model. As the gDistance package uses conductance rather than costs, the costs were then inverted using the following equation:

$$\textit{conductance assigned to travel from cell a to cell b} = \frac{1}{\textit{cost assigned to travel from cell a to cell b}}$$

To assess comparability of the ArcGIS Path Distance tool and R agent-based model, LCPs were calculated in R for all segments (n = 167). The LCP lengths and costs calculated in R were strongly correlated with those calculated by the Path Distance tool ($r^2 = 0.99$ for both length and cost).

For each segment start point, 100 simulations were run to extract the probability that agents considering only the landscape within visual and olfactory detection reach the segment end point (Figure S1). Each simulation was run for a maximum of 122 steps (equivalent to the maximum segment length). An agent was considered to have reached the end point when it arrived within its detection distance (i.e., a neighboring cell, Table S5). For agents that did reach the end point, the cumulative costs and distance was extracted. The code for this model is is available from GitHub: https://github.com/tbonne/least_cost_movement_ABM.

QUANTIFICATION AND STATISTICAL ANALYSIS

The per m costs of actual and modeled paths were calculated by dividing the cumulative costs by segment length. To compare the geometry of actual and modeled paths, the sinuosity of each segment was calculated by dividing the least-cost and actual distance by the straight-line distance.

For 89 of the 167 segments, agents did not reach the end point following the local knowledge rule. The relationship between actual travel costs and the local knowledge model is therefore analyzed separately to the straight-line and least-cost models.

Least-cost and straight-line models

The NRMSE was calculated following Howard et al. [3] to measure how accurately each model predicted actual travel costs and sinuosity. The strength of the relationship between actual travel costs and the least-cost and straight-line models was examined using a LMM and identity link function. Actual cost was modeled as the dependent variable and fixed effects were the least-cost and straight-line costs. To account for certain individuals having a disproportionate effect on the dependent variable, the identity of the focal chimpanzee was included as a random effect. To examine potential collinearity among the two independent variables, we determined variance inflation factors (VIFs) applied to a standard linear model without the random effects. To avoid inflating Type 1 error rates we included the random slopes for the effects of least-cost costs on actual costs to vary between levels of individual ID [72, 73].

The assumptions of normally distributed and homogeneous residuals were checked by visually inspecting the distribution of the residuals and plotting the residuals against fitted values [12]. To achieve comparable estimates and increase the likelihood of model convergence, all covariates were z-transformed to a mean of zero and a standard deviation of one before fitting the model [74]. To establish the significance of the combined set of predictor variables, we ran a likelihood ratio test comparing the full model with a respective null model containing only the intercept and random effect [75, 76]. Coefficients of determination were calculated following Nakagawa and Schielzeth [77] and Johnson [78]. Model stability was checked by excluding data points one by one and comparing the estimates derived with those obtained for the full model, which indicated no influential cases.

To test if results changed when the number of alternative route choices increases, the same analyses were run for long segments (>1 km) only (n = 27).

Local knowledge model

Where agents were able to reach segment endpoints following the local knowledge rule, the replicate with the lowest cost path was extracted (n = 78 segments, Figure S2). The strength of the relationship between actual travel costs and the costs of the lowest cost, local knowledge paths the least-cost paths was examined using the same analyses described above.