



## Landscape influences on the natural and artificially manipulated movements of bearded capuchin monkeys



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Cognitive mechanisms underlying the choice of movement patterns between resource sites for nonhuman primates are not well understood. Specifically, the influence of landscape features on decision making and spatial memory of naturally ranging animals has not been explicitly investigated. We evaluated three models of bearded capuchin monkey, *Sapajus libidinosus*, movement decisions that incorporated varying degrees of landscape and memory influences, and we conducted a field experiment using a novel call-back technique to test these influences. The movements and spatial decisions of the monkeys were modelled between temporal stop points and spatial change points during natural travel using straight-line path, a minimum-resistance path and landscape-perceiving path models. For these movement models, resistance was calculated as the inverse of habitat suitability, a surface based on the natural movement patterns of the study group. Of the three models, natural travel most closely resembled the straight-line path model in its landscape resistance, but not in its geometry. This result indicates that while the monkeys travel in zones of low resistance, they do not minimize distance or landscape resistance between travel nodes. When monkeys were called to an artificial resource site using the call-back experiment, their travel was more linear and higher in landscape resistance. The limited quantity and high quality of the food resource in the artificial resource sites may have influenced the nature of the monkeys' travel in these experiments. We present the advantages and challenges of the call-back method of experimental analysis of animal movement and we conclude that future analyses of spatial cognition should include consideration of landscape context.

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The mechanisms by which nonhuman primates remember and revisit the locations of visibly hidden resources are not well understood (Janson & Byrne, 2007). More specifically, the question of what cognitive mechanisms underlie the choice of movement patterns between resource sites for nonhuman primates is still unanswered (Garber & Dolins, 2014).

This study examines the spatial decisions of nonhuman primates as they relate to the spatial cognition and behavioural ecology of these animals. Two models of spatial cognition have dominated the study of nonhuman primate behaviour, Euclidean

cognitive maps and topological maps, and substantial debate exists concerning the relative validity of the two (Bennett, 1996; De Raad, 2012; Normand & Boesch, 2009; Noser & Byrne, 2007a; Valero & Byrne, 2007). These models differ in terms of the knowledge they hypothesize that animals possess. Topological maps hypothesize that animals know the actions they need to take in order to arrive at a location of interest. They do not, however, include metric information regarding the distances and directions between mapped points. Euclidean cognitive maps consist of metric information on the distances and direction between locations in the landscape. Euclidean maps are hypothesized to permit efficient movement patterns between important resource sites. This metric knowledge is also hypothesized to make it possible for animals to take efficient shortcuts between points via previously unused paths.

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These two central hypotheses in the field of primate spatial cognition, the topological map and the Euclidean cognitive map, both rely upon the idea of movement efficiency. An animal that has metric knowledge of the distances and directions between locations in the landscape is expected to choose its movements efficiently based on this knowledge. Likewise, animals using a topological map are expected to repeat travel segments again and again, and these segments may have developed because they are the most efficient way of travelling between two points in the environment (Di Fiore & Suarez, 2007). Certainly then, it would be useful for understanding primate spatial cognition to define travel efficiency operationally in a way that reflects the ecological variables to which these animals are sensitive when choosing their paths.

Since travel distance is related to energy expenditure and travel time, we might expect that a relevant measure of travel efficiency would be distance, and that efficient travel choices would incorporate a distance-minimizing strategy. Indeed, many studies have based their evaluations of animals' spatial knowledge on the degree to which an animal's path is linear or sinuous (Cunningham & Janson, 2007; Janson, 1998; Noser & Byrne, 2007b; Pochron, 2001; Presotto & Izar, 2010; Valero & Byrne, 2007). In addition, nonhuman primates have been reported to travel in linear segments between resource sites, leading researchers to believe they might possess spatial knowledge of the locations of important places in their home range (Di Fiore & Suarez, 2007; Janson, 1998; Noser & Byrne, 2007a; Pochron, 2001).

However, in a heterogeneous landscape, topographic features are likely to impact the costs of travel chosen by animals (Janson & Byrne, 2007), and we might expect animals to be sensitive to the landscape effects of their travel choices. Landscape variables may mean that travel in a straight line is not the most efficient in terms of energy expenditure, predator avoidance or maximizing use of preferred habitats. Thus, a measure of travel efficiency that takes landscape features into account may be crucial to the interpretation and prediction of travel of animals in heterogeneous landscapes. Many studies investigating the paths of nonhuman primates in natural environments have not taken into account landscape features underlying these paths (but see Sprague, 2000, for an analysis of topographic effects on macaque travel).

Not only is it unclear to what extent landscape features play a role in the spatial decision making of nonhuman primates, we also do not know the extent to which landscape features are incorporated into an animal's spatial memory of its home range. Studies of spatial memory in nonhuman primates living in natural environments have largely been limited to memory for resource sites (e.g. Janson, 1998, 2007; Joly & Zimmermann, 2011) and memory for landscapes has been ignored. To what extent do the landscape features beyond an animal's immediate surroundings factor into their spatial decision making? Do only the landscape features immediately surrounding the animal impact its decisions, or do landscape features further afield also have an impact? Previous implementations of Euclidean cognitive mapping models have presumed that, should an animal possess metric knowledge of the location of a travel goal, they will minimize Euclidean travel distance to arrive at the goal (e.g. Bonnell et al., 2013). In the present study, we modelled efficient movement choices using landscape- and distance-based currencies.

Our study aimed to evaluate the extent to which landscape variables influence the spatial decisions of bearded capuchin monkeys, *Sapajus libidinosus*, in a heterogeneous landscape. We developed and, through comparisons to actual movement observations, tested a series of models of route choice that varied in the extent to which landscape variables determined their structure. We tested a minimum-resistance path model, which considers

landscape resistance as well as distance, and executes an ideal path based on comprehensive spatial knowledge of the landscape between the animal and its goal. We also developed a landscape-perceiving model, which presumes that the animal is drawn in the direction of the goal but does not use comprehensive knowledge of the landscape features beyond its immediate surroundings to make its movement decisions. Finally, we tested a straight-line path model, evaluating the resistances and distances of straight-line travel. Our evaluation of the landscape's impacts on capuchins' travel choices does not distinguish between the Euclidean cognitive map and a habitual route network indicating use of a topological map. Indeed, efficient travel choices incorporating landscape features may be indicative of either cognitive strategy. Instead, we focus on refining the manner in which movement efficiency is evaluated and the role of landscape and linearity in travel choices.

Field experiments afford researchers greater control and ecological validity than observation or laboratory experimentation alone (Janson, 2012). Janson (1998) showed that capuchin monkeys, *Sapajus nigritus* (formerly *Cebus apella*) move towards feeding platforms using straight-line travel from farther distances than predicted by any random models of search. Janson (2007) also used field experiments to demonstrate that these monkeys prefer nearby resources over resources farther away and that they appear to consider their entire foraging path in their decisions to travel to the farther platform. To understand how goal-directed travel is impacted by landscape variables, we conducted experiments in which we manipulated the travel goals of our study group by training them to respond to an auditory cue signifying the presence of a high-value provisioned food item. Comparing the natural movement patterns of capuchin monkeys to their movement patterns during the experimental trials allowed us to evaluate the impact of landscape variables on spatial decisions when the travel goal was a high-value, low-abundance ephemeral resource.

## METHODS

### *Movement Observations*

The subjects of this study were a group of bearded capuchin monkeys in northeastern Brazil (Piauí state). Observations of the monkeys' naturally occurring routes were conducted during the months of May, June and July of 2013 ( $N = 27$  days;  $N = 8611$  points). Data collection consisted of following a randomly chosen, adult focal animal in the group ( $N = 8$  adults) and recording its location and activity for approximately 9.5 h each day. The capuchin monkeys in this study were habituated to human presence and their behaviour was not apparently altered by our presence. Geographical coordinates of the focal individual's location were recorded using a first-generation iPad © tablet computer with GPS (model MC497LL), Avenza PDF Maps application and a GeoPDF of a pan-sharpened WorldView-2 satellite image (50 cm spatial resolution) of the study area loaded to the application (image acquired September 2011) (DigitalGlobe, 2011). Location of the focal animal was recorded semicontinuously as a set of points with the maximum possible spatial and temporal resolution, limited by the spatial resolution of the satellite image (50 cm pixels) and the response time of the human observer. Each time the focal individual changed its location or its activity, this change in state was recorded by the observer. This technique allows the observer to record changes in location at a minimum spatial resolution several times more coarse than the spatial resolution of the satellite image (due to the number of pixels required for landscape feature detection in the field), and at a temporal resolution of approximately 20 s per observation. In practice, the mean point-to-point

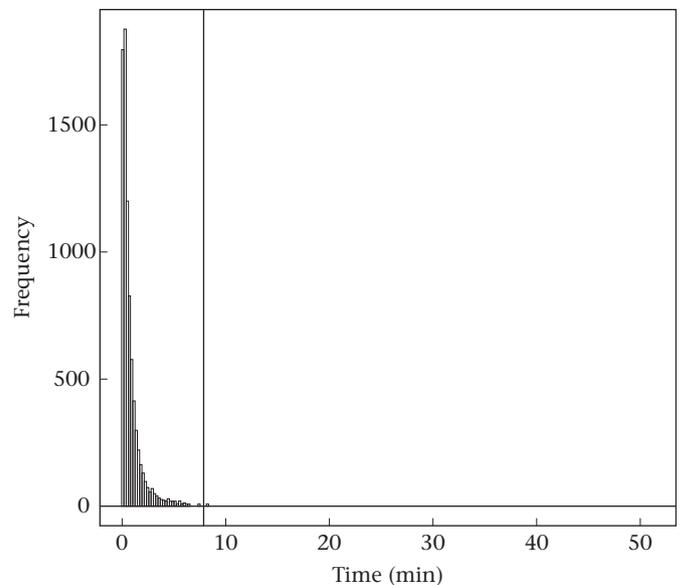
time interval between observation points was 80 s ( $\sigma = 256$  s). The mean distance between observation points was 5.8 m ( $\sigma = 19.2$  m). When we excluded point intervals where the focal individual went out of sight, the mean time between point observations was 66 s ( $\sigma = 179$  s) and the mean distance between point observations was 4.9 m ( $\sigma = 6.0$  m). Capuchin monkeys in our study site move through the tree canopy along discontinuous branches as well as on the ground (Biondi, Wright, Frigaszy, & Izar, 2011). Compared to the technique of using a hand-held GPS unit and estimating distance and direction between the observer and the focal individual, this method allowed for more controlled observations of location when the observer was at a distance from the focal monkey. To measure the inherent spatial accuracy of the iPad GPS device, 21 landmarks visible on the satellite image were selected and visited by experimenters, and the distance between the GPS reported location and the landmark on the image was recorded. The average  $\pm$  SD error of GPS device was  $11.71 \pm 6.33$  m (range 1.35–29.70 m). This accuracy is similar to that of GPS hand units commonly used in field research (e.g. Garmin eTrex<sup>®</sup>, positional accuracy within 15 m, 95% of the time (Garmin International, n.d.)).

Of all the naturally occurring daily paths we observed, 15% (4 days) were set aside for in-depth analysis and modelling of capuchin spatial decision making. These 4 days were excluded from the construction of the habitat suitability and resistance model described below.

#### Segmentation of Movement

We assumed that the movement paths of focal animals in this study consisted of a number of intermediate goals between the start and end of each day, since spatial analyses of movement from the start and end points do not adequately represent movement complexity (Howard, Bernardes, & Presotto, 2011). We therefore conducted movement analysis between travel nodes, defined both temporally and spatially, since locations where animals change direction or stop to forage may be considered travel goals (Janson & Byrne, 2007). This division of paths into segments is a common technique (e.g. Di Fiore & Suarez, 2007; Janson, 2007; Normand & Boesch, 2009), however, we acknowledge that measures of sinusosity and resistance reported here are only valid per segment, not for daily paths. We used the change point test (Byrne, Noser, Bates, & Jupp, 2009) to evaluate the focal individual's travel for points of directional change within a specified backward-looking window ( $q$ ). We ran variants of the test for  $q = 1$  through  $q = 10$  for the four naturally observed paths evaluated in this study using an alpha level of  $P < 0.01$  and chose  $q = 5$  since this value maximized the number of change points detected for each day's path while also failing to 'overshoot the change point' (Byrne et al., 2009).

In addition to analysing spatial segments of the capuchins' travel paths, we analysed the temporal segments of their travel. The amount of elapsed time that focal individuals spent at each point was calculated for all 27 observation days in this study. Previous studies have divided travel by temporal criteria, defining stop points as locations where the animals remained for 4 min or longer (spider monkeys, *Ateles geoffroyi yucatanensis*: Valero & Byrne, 2007), 10 min or longer (black capuchin monkeys, *Sapajus nigritus*: Presotto & Izar, 2010), or 20 min or longer (chimpanzees, *Pan troglodytes schweinfurthii*: Bates & Byrne, 2009). We chose the criterion for defining a stop point as a function of the distribution of elapsed times that the study group spent in any given location, using the 99th percentile of all elapsed times spent in a single location (Fig. 1). The mean  $\pm$  SD elapsed time at a single location was  $0.97 \pm 1.90$  min. The spatial distribution of stop points and change points along the four daily paths analysed in this study are shown in Fig. 2.

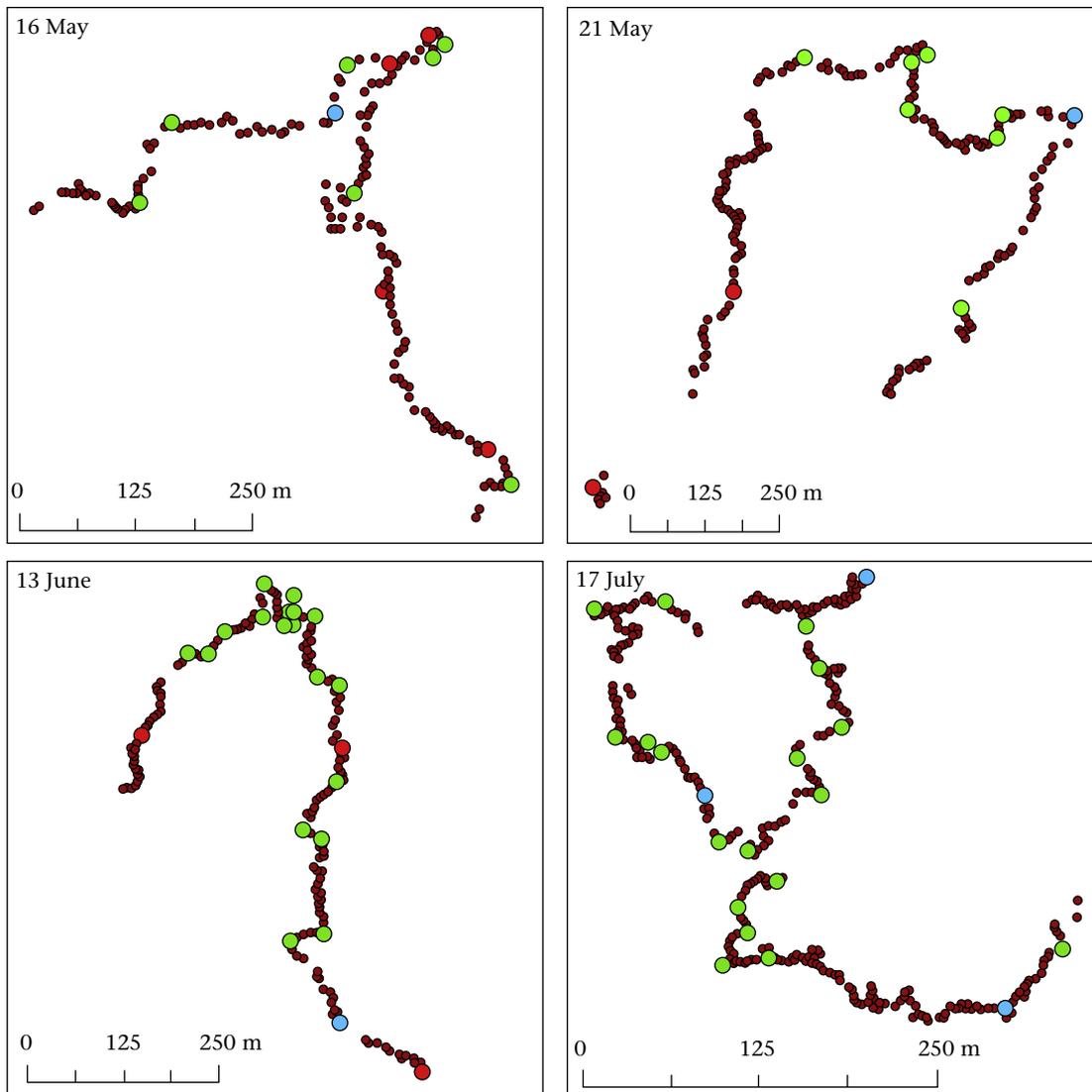


**Figure 1.** Distribution of elapsed time at observation points; vertical line indicates the 99th percentile of elapsed time (8.01 min).

#### Habitat Suitability and Resistance Model

To model the monkeys' movement in response to landscape features, we interpreted the landscape of their home range from satellite imagery and joined these data with point data on the monkeys' patterns of movement. From the point data and environmental layers, we generated a model in MaxEnt, a software package that utilizes the concept of maximum entropy to generate logistic values representing habitat suitability (Phillips & Dudík, 2008). In short, MaxEnt estimates the probability distribution of suitability over the landscape as constrained by its environmental features. The model in this study extrapolates habitat suitability for movement over the extent of the modelled space, not just to the locations where monkeys were observed to move. Here the modelled space was a bounding rectangle around the movement observation points, such that the suitability model represented habitat suitability within the monkeys' home range. Inherently, modelling within the monkeys' home range means that the results of this particular model should not immediately be extrapolated outside of our study area, and are most applicable to the familiar area of the monkeys' home range. However, the model does not represent visited areas as more suitable than areas of the same landscape characteristics that we did not observe the monkeys to visit. In this way, the model does not represent landscape familiarity, but rather suitability. To demonstrate this, we tested two variants of the final MaxEnt model: a model excluding points found in locations of intense movement activity (the 50% isopleth from a kernel density estimation) and a model created from points exclusively found within those intense movement locations. These two models were not found to differ significantly from one another using a measure of niche similarity ( $I = 0.85$ ), which ranges from 0, where niches show no overlap, to 1, where niches are identical in their suitability (Warren, Glor, & Turelli, 2010). This result indicates that our MaxEnt model represents niche suitability consistently throughout the monkeys' home range, not as a function of intensity of use or familiarity.

From the 8611 observation points obtained from focal animal follows, 20% were set aside for model testing. We used the corrected Akaike's information criterion (AICc) and the area under the curve (AUC) to evaluate model fit. Model testing used the method of



**Figure 2.** Change points (green) detected for naturally observed travel on 16 May, 21 May, 13 June and 17 July ( $q = 5$ ), stop points (red), and points designated as both stop and change points (blue). Gaps in the movement paths indicate periods of rapid movement in which observations were more difficult to obtain.

reducing environmental covariates by excluding correlated covariates as well as excluding covariates that contributed little to model fit (see Howard et al., 2012). Environmental covariates of the final model were distance to steep ridges, distance to roads, distance to areas of human influence, land cover class, elevation, normalized difference vegetation index, and fractional cover of shadow (i.e. areas near steep ridges or in dense vegetation cover; for further information on the derivation of these landscape data, see Howard, 2014). The final model also used a subset of the original observation points with a minimum distance of 25 m between points, which functioned to remove clusters of observation points (for further details regarding model specification and the selection of a minimum distance between points, see [Supplementary Material](#)). We used the inverse of these values ( $=1/\text{logistic model output}$ ) as a layer of landscape resistance to movement. In this way, the landscape preferences of the capuchin monkeys in this study were represented continuously across their home range. This resistance surface represents the aversion the monkeys demonstrated to moving through a particular pixel based on its landscape features alone. The resistance may be based on a number of biological factors relevant to the lives of the monkeys. For example,

moving across steep ridges may represent a prohibitive physiological cost, or, in some extreme cases, movement may be a physical impossibility. However, resistance also captures more subtle aversions to movement through habitats that may be based on exposure to predation risk or low resource densities. Importantly, this technique determines resistance to movement through a mathematical representation of the preferences of our study animal during the period of observation, rather than through subjective estimates of suitability. This method addresses recently published concerns with generating path models based on resistance layers constructed from expert opinion (Sawyer, Epps, & Brashares, 2011). The inverse of the final MaxEnt model represented areas of steep ridges, bare soil and wetland areas with standing water as highly resistant to capuchin movement.

#### *Movement Models*

We developed three models of capuchin route choice to test the extent to which capuchin monkeys use landscape features and memory in their movement decisions: the straight-line path model, the minimum-resistance path model and the landscape-

perceiving path model. In the models incorporating landscape (minimum-resistance path model and landscape-perceiving path model), the basis for the incorporation of landscape features was the MaxEnt model described above. The spatial resolution of this model was a 2 m pixel, and landscape features smaller than this resolution were not differentiated by our models.

The straight-line path model consisted of straight lines connecting the beginning and end points of each segment and draped over the landscape features. These straight-line paths were generated in ArcGIS first as polylines, then converted to raster, and finally converted from raster to points. We extracted resistance values from the inverse MaxEnt resistance layer to the points that made up the straight-line path, and calculated mean resistance values, total cumulative resistance values and resistance per metre (resistance/m) values for each straight-line path segment. The sinuosity (a ratio of the modelled distance to the straight-line distance) of the straight-line path model was inherently 1 for every straight-line segment. An animal whose path resembles the straight-line path model uses a distance-minimizing strategy and a spatial memory of the location of the goal. It does not consider landscape features in its immediate surroundings, nor does it use spatial memory of landscape features to choose a path.

The minimum-resistance path model is the path of least landscape resistance between the start and end points of each observed travel segment. This model was generated using the Cost Distance Tool in ArcGIS 10.1 and functions by assigning cost values to pixels based on a user-defined cost layer (in this case, the inverse habitat suitability model) and iteratively connecting the start point to subsequently more distant pixels via the least cost sequence of connecting pixels. The final cost raster represents the cost of the pixel and its distance from the start point via a least cost set of connecting pixels. The formula used by ArcGIS to calculate the relationship between cost and distance for two adjacent pixels is:

$$a1 = \frac{(\text{cost1} + \text{cost2})}{2}$$

where  $a1$  represents the total cost to travel between pixel 1 and cell 2,  $\text{cost1}$  represents the cost value of pixel 1, and  $\text{cost2}$  represents the cost value of pixel 2. In the case of two diagonally connected pixels, ArcGIS accounts for the larger distance ( $\sqrt{2}$ ) between them to calculate the relationship between cost and distance as follows:

$$a1 = \frac{1.4142 (\text{cost1} + \text{cost2})}{2}$$

The minimum cumulative resistance path was calculated between the start and end points of each segment for each of the 4 days. In terms of behaviour, the minimum cumulative resistance path is the path by which the travelling animal would maximize its use of spaces containing suitable landscape features while travelling between the start and end points of that segment. This movement model requires spatial memory of the distance and direction of the goal location as well as spatial memory for the landscape features of the animal's home range. An animal whose path resembles the minimum-resistance path model uses a distance-minimizing and landscape-maximizing strategy and spatial memory of the location of the goal and the location of landscape features in making its spatial decisions. If the start point of the segment marks a change in the animal's travel goal and the end point of the segment marks its new putative goal, then we may expect a travelling animal to minimize its use of undesirable habitats and maximize its use of desirable spaces between these two points if it has complete memory of the landscape features of its home range and knowledge of the distance and direction to its goal location.

The landscape-perceiving model of travel was developed using the NetLogo modelling environment (v.5.0.4), a program for simulating natural and social phenomena. This model was tested using independent reimplementations of submodels as recommended by [Railsback and Grimm \(2012\)](#). A modelled monkey was programmed to travel between user-defined start and end points across a cost–distance surface specific to the location of its goal. The code for this model and a description of the model recommended by [Grimm et al. \(2010\)](#) are included as [Supplementary Material](#). The cost–distance surface across which the modelled monkey moved was derived from the previously described ArcGIS cost–distance analysis. The cost–distance surface used in each model run was specific to the location of the monkey's goal for that travel segment. The modelled monkey travelled from its current pixel to the neighbouring pixel of minimum cost distance (considering its eight neighbours), repeating this process until arriving at the location of the goal. In contrast to the minimum-resistance path model, the landscape-perceiving model considered only the environment immediately surrounding the monkey for each movement step. An animal whose path resembles the landscape-perceiving model uses a distance-minimizing and landscape-maximizing strategy and spatial memory of the location of the goal in making its spatial decisions. This animal does not use spatial memory of landscape features in making spatial decisions, although landscape features in its immediate surroundings influence its movement patterns.

#### *Comparing Movement Models and Actual Travel*

The three methods for modelling capuchin movement generated paths of differing geometry types in the geographical information systems software packages in which they were developed. To maintain consistency in the spatial resolution of our modelling and to compare the resistances of model results across categories, all models were submitted to a series of conversions prior to comparing their resistance parameters. Points were converted to the polyline file type, which was then converted to raster format, and then back to points again. This resulted in every pixel underlying the capuchins' paths being sampled at an equal rate, and no model of equal metric length would have a much larger number of samples (i.e. pixels) than any other model. Model outputs ranged from point to polyline to raster. The geometry conversion of each model proceeded along the same sequence, beginning with the first geometry type yielded by the model. The sinuosity of paths was calculated at the stage of the polyline geometry.

Cost–distance rasters with origins at the beginning and end of each path segment were combined using corridor analysis in ArcGIS. This sum of the cost–distance rasters identifies the least possible cumulative cost for a path travelling (independent of travel direction) between two cells that intersects the cell in question ([ESRI, 2013](#)). Pixels far from both the beginning and end points of each segment generally have high cumulative resistance values since travelling from the segment's start to the segment's end by way of that distant pixel would usually impose more cumulative resistance than travelling between those two points by way of pixels near the start and/or end points. The corridor raster also identifies areas of particularly high environmental resistance based on the landscape features of the pixel. The function of the corridor image was to compare the resistance values of the monkeys' actual travel to other low-resistance paths between the start and end points of each segment. Using the corridor image for each travel segment, we calculated a percentile for the cumulative resistance values of the monkeys' actual paths and of their modelled paths (i.e. the minimum-resistance path, the straight-line path and the landscape-perceiving path). This percentile is a measure of how

closely the monkeys follow their own habitat preferences in each pixel of the modelled and actual paths. Comparing the resistance values of these paths to the resistance values of the pixels of the entire resistance raster (6 km<sup>2</sup>) would have skewed our analysis of the monkeys' choices as having been in the most efficient percentile of possible resistance values compared to other pixels of the image. While this comparison may be accurate, it is a logical fallacy to compare actual travel segments to theoretical travel segments between points A and B, which would include pixels that lie kilometres away from either A or B. To avoid this problem, buffers were generated around each travel segment within which the resistance values of the pixels were compared. All the segment points were buffered by a distance equal to the actual distance travelled by the monkeys in the segment in question, and the buffers around each point were merged into a single polygon for each travel segment. The cumulative resistance values of each pixel in the corridor clip were rank ordered. For the segments of travel in which the monkeys actually travelled, we calculated the percentage rank of the mean corridor value from the distribution of possible values within the corridor clip.

#### *Experimental Analysis of Route Choice*

For the experimental analysis of capuchin monkey route choice, the monkeys in our study group were trained on a unique auditory cue indicating that a rare, high-value food item (i.e. diced bananas) would be distributed near the source of the auditory cue. The auditory cue consisted of an iPhone © “Marimba” ring tone amplified using a megaphone (Pyle Pro ©, 50 W, model PMP531N) and played on repeat. The advertised projection range of this device is up to 1 mile (1.6 km), and the ring tone was confirmed in the field to be audible up to at least 600 m, despite geomorphological barriers of the landscape (e.g. steep ridges). The ring tone was played for the duration of each testing session (i.e. from the initiation of the session until the focal animal retrieved the food), during which approximately 500 g of diced bananas were scattered over an area of approximately 100 m<sup>2</sup> by a human experimenter. Food dispersal began at the precise moment the tone was played. Prior to test, the monkeys in the study group were trained to associate the auditory cue with the dispersal of diced bananas in 10 training sessions. These training sessions occurred in an outdoor laboratory area, 30 m in diameter, in which the animals had been previously provisioned with nuts, corn, fruits and water. During the dry season, this outdoor laboratory is frequently visited by the study group, from approximately once daily to once weekly. It lies adjacent to a vertical ridge 415 m tall. The training sessions occurred when the majority of the group was present in the outdoor laboratory area. The tone was played from the centre of the outdoor laboratory and the food was distributed from the same location as it was in testing. The tone and food distribution continued until there was no food remaining. Training sessions (and subsequent experimental trials) resulted in some, but not all, members of the group receiving diced bananas. The alpha male, the alpha female and juveniles appeared to retrieve the largest proportion of the provisioned food with certain other adult individuals (male and female) competing for food as well. Contest and scramble competition were evident as the food was dispersed evenly although over a space small enough that some individuals displaced others from small patches of the provisioned food. Refresher training sessions were also conducted on four occasions when the group had not visited the outdoor laboratory for three or more consecutive days and testing was planned for the following day.

Initially, testing sessions were carried out near the outdoor laboratory immediately after the group left the area of their own volition. In these trials, an experimenter stayed in the outdoor

laboratory area as the study group left the area. A human observer followed a focal individual away from the outdoor laboratory and, upon travelling 100–200 m from the outdoor laboratory, the observer communicated with the experimenter at the laboratory using hand-held, two-way radios. The experimenter then initiated playback of the auditory cue. Distribution of diced bananas began when the first monkey of the group arrived in view of the laboratory area. During the playback of the auditory cue, the observer followed the focal individual's movements. In early testing trials, the alpha male was chosen as the focal individual to be observed. Experience showed that, in experiments near the outdoor laboratory, the speed with which this male moved through the forest to reach the auditory cue was too fast for a human observer to follow consistently. Other group members, although they moved towards the auditory cue, did so at a speed that allowed the human observer to record their location consistently and update it as the individual moved. Trials were terminated when the focal individual arrived at the site of the auditory cue, or after a minimum period of 10 min in which the focal individual did not move towards the auditory cue.

After calling the animals back to the outdoor laboratory in early experimental trials, testing was extended to other areas of the monkeys' home range. The sites for these trials were chosen in the field based on the location of the monkey group and the direction of their movement as well natural barriers to movement (i.e. areas of high resistance). In practice, travel through areas of naturally high resistance was easiest to observe and record when the high resistance values were related to open areas with little vegetation. In real time, as the monkeys continued to move naturally, we chose an area in which the experimenter would be stationed with the megaphone, waiting for communication from the observer. The observer followed a focal individual and communicated with the experimenter when the focal individual arrived in a predetermined area from which the experiment should begin. These start points were chosen because the experimenters estimated them to be pivotal points from which the animals might change direction when hearing the auditory cue, but also points from which the experimenter's location would still be invisible to the focal individual. This was important since it was essential to capture the moment at which the monkeys' travel direction was manipulated by our auditory stimulus, and not potentially miss the moment at which the monkeys' travel goal changed due to perceiving the visual cue of the experimenter holding the megaphone. However, we chose locations for the human experimenters to stand where their presence would be easily detected by the monkeys once they had moved in the direction of the auditory cue. This was important since the animals were timid to move into high-resistance spaces (i.e. open areas with little vegetation) until they saw the provisioned food being distributed.

From the experimental trials conducted, we chose six trials in which the auditory cue resulted in the movement of the focal animal to the site of the provisioned food and the observer was able to follow the focal monkey to the provisioned food without losing sight of the animal. The actual travel of the focal monkey was compared to the three theoretical models of capuchin travel previously described. We also compared the monkeys' travel paths in these experiments to the sinuosity and resistance of naturally occurring travel paths chosen by the monkey group outside of the experimental context. Instead of segmenting the paths of the monkeys by change points and stop points for analysis, the travel was segmented by the beginning and end of each trial. For each model, the start point was taken as the location of the focal monkey at the time when the auditory cue began. The end point of the segment was taken as the location where the focal monkey began foraging on the provisioned food.

## Analysis

In both the naturally occurring routes and the routes taken during the experiment, we calculated the mean and cumulative resistances of each path segment (modelled and actual) by averaging or summing the resistance values of the pixels through which each path passed. We also calculated resistance/m by summing the resistance values of the paths' pixels and dividing this value by the length of the segment. Mean resistance differs from resistance/m since the mean is based on pixels while resistance/m is based on distance. Pixels measure 2 m across and 2.83 m diagonally. We then calculated the normalized root mean square error (NRMSE) between the actual and modelled path segments ( $N = 68$ ) for the mean and cumulative resistance, resistance/m and sinuosity. NRMSE was computed by dividing the root mean square error by the observed range of the parameter ( $\text{NRMSE} = \text{RMSE}/(\text{max}_{\text{obs}} - \text{min}_{\text{obs}})$ ) for each path segment (Table 1). NRMSE is frequently expressed as a percentage and allows for comparison between parameters using different scales.

## RESULTS

### Natural Movement Observations

In selecting the four routes to be analysed, we prioritized days in which the focal animal went out of sight for the least amount of time. These days coincided with days on which the focal individual was an adult male member of the group that tended to remain central in relation to the rest of the group members. We analysed the path of a former alpha male, Mansinho, on 16 May 2013 and 21 May 2013 and the path of the contemporaneous alpha male, Jatoba, on two dates, 13 June and 17 July 2013. These observation dates had the following total times that the focal individual was out of sight of the human observer: 16 May, 0 min; 21 May, 9 min; 13 June, 17 min; and 17 July, 15 min.

For each daily path, change points were more frequent than stop points with an average of 14.5 change points per day and an average of 5 stop points per day. When a stop point and a change point fell within 5 m of one another, only the first point was used, resulting in an average of 17.25 change and stop points per day. For the 4 days analysed, change points and stop points fell within 5 m of one another 21 times, and three points were classified as both stop points and change points.

### Comparing Movement Models and Actual Travel

No model fit the actual travel patterns in geometry and resistance-related measures. The straight-line travel model was similar in its mean resistance to that of actual monkey travel, while other parameters of straight-line travel differed from that of actual travel. There was no significant statistical difference between the mean resistance of actual travel and the mean resistance of the straight-line model of travel ( $t_{68} = 0.18$ ,  $P = 0.85$ ). Significant differences did exist in mean resistance between actual travel and the

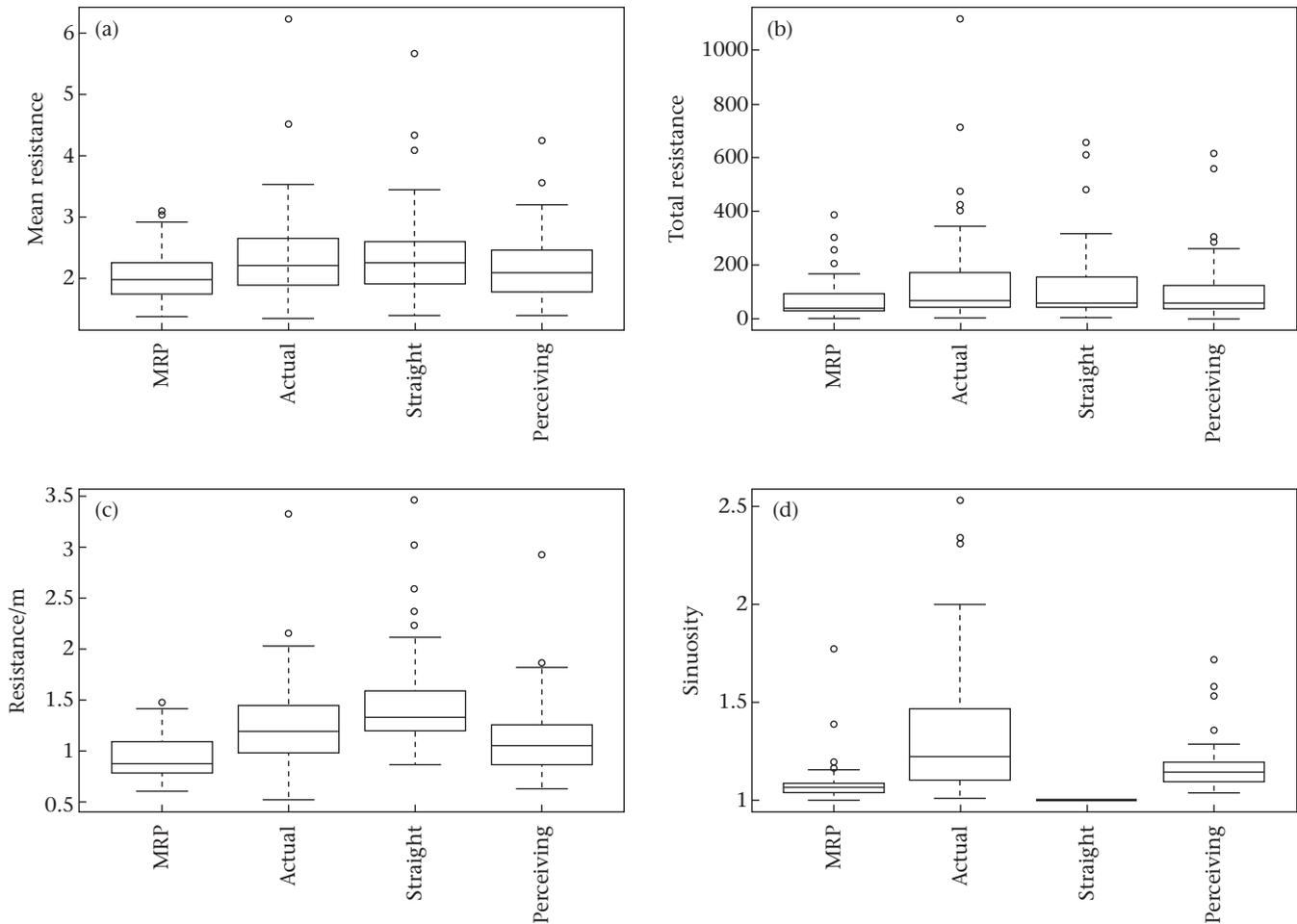
minimum-resistance path model ( $t_{68} = 5.64$ ,  $P = 3.56 \times 10^{-7}$ ), with actual travel segments having higher mean resistances. There were also significant differences between the mean resistance of actual travel and the landscape-perceiving model ( $t_{68} = 3.15$ ,  $P = 0.0024$ ), with actual travel segments having higher mean resistances. There were significant differences for the cumulative resistance totals of the travel segments between actual travel and all the travel models (minimum-resistance model:  $t_{68} = 5.17$ ,  $P = 2.20 \times 10^{-6}$ ; landscape-perceiving model:  $t_{68} = 4.83$ ,  $P = 7.97 \times 10^{-6}$ ; straight-line model:  $t_{68} = 3.37$ ,  $P = 0.0012$ ). Actual travel had higher cumulative resistance values than all the models. There were also significant differences in the sinuosity of actual travel when compared to all travel models (minimum-resistance model:  $t_{68} = 6.14$ ,  $P = 4.81 \times 10^{-8}$ ; landscape-perceiving model:  $t_{68} = 4.17$ ,  $P = 8.95 \times 10^{-5}$ ; straight-line model:  $t_{68} = 8.54$ ,  $P = 2.26 \times 10^{-12}$ ). Actual travel was less linear than any of the models of travel. Finally, resistance/m differed significantly when comparing actual travel to all models of travel (minimum-resistance model:  $t_{68} = 8.38$ ,  $P = 4.53 \times 10^{-12}$ ; landscape-perceiving model:  $t_{68} = 3.74$ ,  $P = 0.00038$ ; straight-line model:  $t_{68} = -5.55$ ,  $P = 5.01 \times 10^{-7}$ ). The minimum-resistance and landscape-perceiving models of travel had significantly lower resistance/m than actual travel. The resistance/m of the straight-line model of travel was significantly higher than actual travel, however.

To compare not just central tendencies of the model path parameters (i.e. total cumulative resistance, mean resistance, resistance/m and sinuosity), but also the distribution of their deviations from actual travel, we calculated NRMSE for each of the parameters of travel for each model using the stop points and change points segmentation method (Table 1). This measure shows how the models differed from actual travel choices in the quantitative model parameters. For example, in the case of mean resistance, how did the landscape resistance of model paths deviate from that of actual travel? Were they higher or lower in resistance than the monkeys' actual travel paths? For capuchin travel segments, the NRMSE of the parameters total cumulative resistance, mean resistance and resistance/m were lowest for the straight-line model of travel. This indicates that the resistance values associated with the straight-line model of travel were similar to the resistance values of the capuchins' actual travel. Fig. 3 shows box plots of the distribution of the various model parameters and the same parameters for actual capuchin monkey travel. We conducted Kolmogorov–Smirnov tests of goodness of fit of model parameters to the parameters of actual travel for mean resistance, total cumulative resistance, resistance/m and sinuosity for the path segments. Significant differences were found between actual travel and the minimum-resistance paths for total cumulative resistance ( $d = 0.32$ ,  $P = 0.0017$ ), mean resistance ( $d = 0.28$ ,  $P = 0.010$ ), resistance/m ( $d = 0.46$ ,  $P = 4.51 \times 10^{-7}$ ) and sinuosity ( $d = 0.59$ ,  $P = 5.26 \times 10^{-11}$ ). For the landscape-perceiving model and the straight-line path model, significant differences from actual travel were detected in the distributions of resistance/m (landscape-perceiving:  $d = 0.26$ ,  $P = 0.018$ ; straight-line:  $d = 0.26$ ,  $P = 0.018$ ) and sinuosity (landscape-perceiving:  $d = 0.42$ ,  $P = 7.61 \times 10^{-6}$ ;

**Table 1**  
Models of capuchin travel compared with actual travel, segmented by stop points and change points

Models	Total cumulative resistance			Mean resistance			Resistance/m			Sinuosity		
	Mean	SD	NRMSE	Mean	SD	NRMSE	Mean	SD	NRMSE	Mean	SD	NRMSE
Actual	142.81	176.40	N/A	2.39	0.77	N/A	1.27	0.42	N/A	1.34	0.34	N/A
Min. Resis.	74.45	69.88	11.61%	2.01	0.40	13.59%	0.93	0.21	17.16%	1.08	0.10	24.45%
Perceiving	98.44	109.28	7.92%	2.20	0.53	10.68%	1.10	0.36	15.23%	1.16	0.12	22.85%
Straight	116.11	126.35	6.37%	2.38	0.70	5.49%	1.46	0.47	11.63%	1	0	25.99%

NRMSE: normalized root mean square error; Min. Resis.: minimum-resistance model; Perceiving: landscape-perceiving model; Straight: straight-line model.

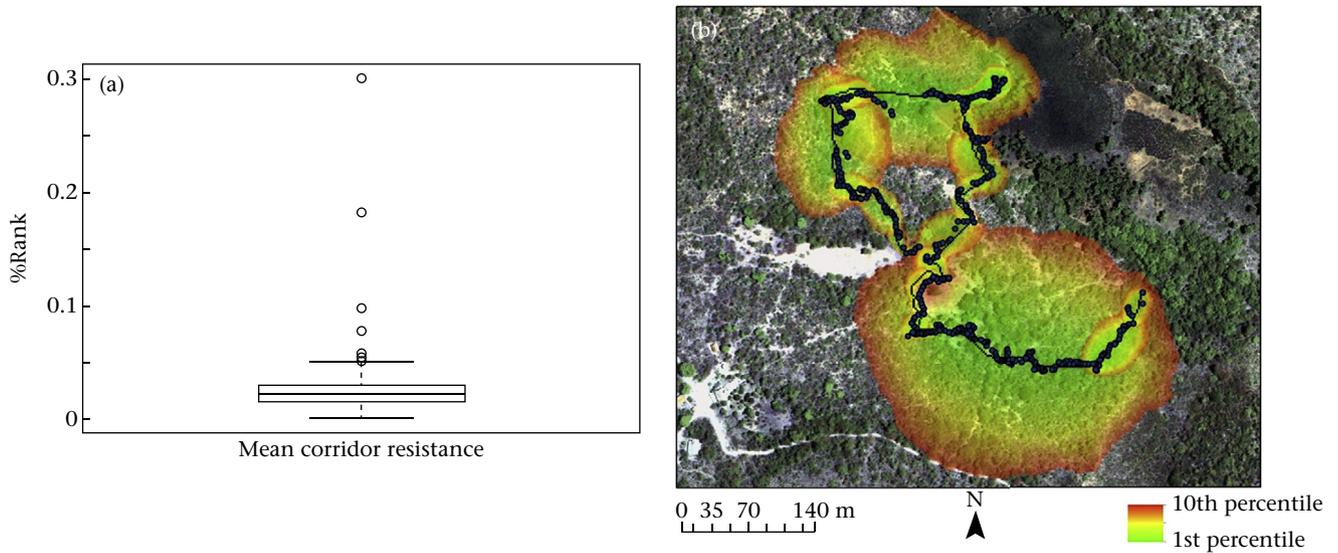


**Figure 3.** Box plots of (a) mean resistance, (b) total resistance, (c) resistance/m and (d) sinuosity (actual path length (m)/straight-line path length (m)) of the models of capuchin travel and actual naturally occurring travel paths. Box plots show 25% and 75% quartiles (boxes), medians (horizontal lines), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles). MRP: minimum-resistance path; Actual: actual path; Straight: straight-line path; Perceiving: landscape-perceiving path.

straight-line:  $d = 1$ ,  $P < 2.2 \times 10^{-16}$ ). No significant differences were detected, however, for mean resistance between actual travel and the landscape-perceiving model ( $d = 0.15$ ,  $P = 0.46$ ), or between actual travel and the straight-line path model ( $d = 0.073$ ,  $P = 0.99$ ). KMZ files of the actual and modelled travel paths for the 4 days of travel (16 May, 21 May, 13 June, 17 July) analysed in this study are available in the [Supplementary Material](#).

Comparing the monkeys' actual paths to the minimum-resistance path and to other possible paths through the environment, we see that the actual paths were of low resistance. A portion of the corridor layer for each segment was clipped from the larger corridor image file (6 km<sup>2</sup>). The corridor layer itself consists of pixel values representing the minimum possible resistance incurred passing through the pixel in question while travelling from the beginning to the end of the segment. The size of each corridor clip corresponded to a buffer with a radius the length of the actual travel segment (10.32–1427.33 m). Thus, the corridor clip represents a selection of possible pixels through which the monkey may have chosen to travel when moving between the segment's start and end points. The actual path of the monkey was associated with the corridor layer's values, such that each point of the path was given a resistance value related to travel between the segment's start and end points. We calculated the mean of the actual path's corridor resistance values and compared it to the distribution of values of the corridor clip. We then calculated an inclusive percentage rank of the segment's mean corridor resistance values for

each segment. The inclusive percentage rank is the relative rank of a given value within a data set, 0 and 1 inclusive, expressed as a percentage value. For example, in a data set of three values, 4, 6 and 8, the value 4 has a percentage rank of 0, 6 has a rank of 0.5, and 8 has a rank of 1. For the 4 days of capuchin travel analysed in this study, the monkeys' actual travel path segments had a mean percentage rank of 0.0326 (or a mean  $\pm$  SD of  $3.26 \pm 4.12\%$ ). This meant that, on average, 96.76% of pixels had a higher travel resistance than the ones visited by the monkeys. The mean percentage rank of the straight-line path model was  $2.98 \pm 4.59\%$ . We conducted Welch two-sample  $t$  tests to compare percentage ranks of the landscape-perceiving model and the actual path as well as the straight-line path model and the actual path. There was a significant difference between the perceiving model (mean  $\pm$  SD =  $2.02 \pm 2.70\%$ ) and the actual paths (mean  $\pm$  SD =  $3.26 \pm 4.12\%$ ) ( $t_{117,13} = -2.09$ ,  $P = 0.03$ ). There was no significant difference between the straight-line model (mean  $\pm$  SD =  $2.98 \pm 4.59\%$ ) and the actual paths (mean  $\pm$  SD =  $3.26 \pm 4.12\%$ ) ( $t_{134,56} = -0.37$ ,  $P = 0.71$ ). The points of the minimum-resistance path model inherently had the lowest resistance values among all the pixels in the image, and thus their mean percentage rank was 0%. We conducted a one-sample  $t$  test to evaluate the difference between the actual path and a mean percentage rank of zero, as in the minimum-resistance path model. There was a significant difference between the percentage rank of the minimum-resistance path model and the actual path (mean  $\pm$  SD =  $3.26 \pm 4.12\%$ ;  $t_{68} = 6.6$ ,  $P < 0.001$ ). [Fig. 4a](#) shows a



**Figure 4.** (a) Box plot of the percentage ranks of mean corridor resistance values for the stop and change points segments of capuchin actual travel. Box plot shows 25% and 75% quartiles (box), median (horizontal line), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles). (b) Actual path from 17 July 2013 with corridor resistance values overlaid on WorldView-2 satellite imagery (DigitalGlobe); corridor resistance values range from the minimum-resistance path (black line) to slightly higher resistances (green) to the 10th percentile of possible path resistances (red-orange).

box plot of the distribution of percentage ranks of corridor resistances for all the observed segments of capuchin monkey travel.

Fig. 4b shows the actual path from 17 July over the corridor resistance surfaces for each of the path segments (by stops and change points). The corridor resistances are represented as a gradient from green to red with green representing lower percentiles of corridor resistance and orange/red representing values up to the 10th percentile of corridor resistance. Corridor resistance values higher than the 10th percentile are not shown in the image. In addition to the 10th percentile values of corridor resistance and those below it, the image also depicts the minimum-resistance path, or the lowest possible corridor resistance, as black pixels. Some corridors are wider than others, indicating an interaction between the length of the travel segment and the low resistance values of the landscape surrounding the start and end points of the travel segment.

**Experiment Results**

We compared the movement of the monkeys in the experiments to the same three models of capuchin travel described in the analysis of naturally occurring routes for six trials in which the focal animal reached the food reward. The movement parameters for each experiment and the models of movement are shown in Table 2. Comparing the sinuosity of the actual travel in the

experiments to the models of travel, some surprising patterns emerge. The NRMSE values of the minimum-resistance path model and landscape-perceiving model were high for the resistance-related parameters of travel, ranging from 28.56% to 34.08% error. In contrast, the NRMSE values of the straight-line path model were low for the resistance-related parameters of travel, with values ranging from 1.14% to 4.83% error (Table 3). The sinuosity of travel ranged from below 7% error (NRMSE = 6.80) for the minimum-resistance model to under 1% error for the straight-line path model (NRMSE = 0.62; Table 3).

The movements of the monkeys in the experiments were, on average, more linear than their naturally occurring travel. The mean sinuosity of the monkeys' actual paths in the experiments (mean ± SD = 1.21 ± 0.14) ranked between the mean sinuosity of the minimum-resistance model paths (mean ± SD = 1.14 ± 0.19) and the sinuosity of the landscape-perceiving model paths (mean ± SD = 1.22 ± 0.23). This is in contrast to the actual path sinuosity of the naturally occurring travel of capuchin monkeys (mean ± SD = 1.34 ± 0.34), which was higher than the mean sinuosity of both the minimum-resistance (mean ± SD = 1.09 ± 0.10) and landscape-perceiving (1.16 ± 0.12) models of travel. Thus, while the models predicted higher sinuosity of the resistance minimizing paths in the experiments compared to natural travel, the monkeys were observed to decrease the sinuosity of their travel in the experimental conditions. Natural travel segments had

**Table 2**  
Parameters of the actual and modelled travel paths in experimental trials

Date	Actual path				Minimum-resistance path				Straight-line path				Landscape-perceiving path			
	Mean Resis.	Total Resis.	RPM	Sin.	Mean Resis.	Total Resis.	RPM	Sin.	Mean Resis.	Total Resis.	RPM	Sin.	Mean Resis.	Total Resis.	RPM	Sin.
1 July	1.66	112.56	0.84	1.19	1.54	91.02	0.74	1.04	1.77	120.28	1.06	1	1.87	104.50	0.83	1.06
13 July	1.79	207.43	0.89	1.40	1.62	135.90	0.74	1.11	2.09	186.34	1.12	1	1.93	162.05	0.86	1.14
19 July <sup>a</sup>	36.86	663.45	19.25	1.09	8.61	189.42	3.90	1.54	33.29	599.24	18.98	1	11.25	258.80	4.90	1.67
22 July	2.24	169.92	1.36	1.16	1.94	98.99	0.86	1.07	2.45	178.94	1.66	1	2.33	170.08	1.45	1.09
24 July <sup>a</sup>	2.23	111.25	1.27	1.18	1.93	71.40	0.89	1.08	2.43	104.39	1.41	1	2.10	77.68	0.91	1.15
25 July <sup>a</sup>	2.54	78.70	1.50	1.07	2.02	50.55	1.00	1.03	2.45	73.43	1.50	1	2.36	59.02	0.98	1.23

Resis.: resistance; RPM: resistance/m; Sin.: sinuosity.

<sup>a</sup> Experiments occurred in areas of the monkeys' home range away from the outdoor laboratory.

**Table 3**  
Models of capuchin travel compared with actual travel in experimental trials

Model	Total cumulative resistance		Mean resistance		Resistance/m		Sinuosity	
	Mean	NRMSE	Mean	NRMSE	Mean	NRMSE	Mean	NRMSE
Actual	223.89	N/A	7.88	N/A	4.18	N/A	1.18	N/A
Minimum-resistance path	106.21	34.04%	2.94	32.77%	1.35	34.08%	1.15	68.48%
Landscape-perceiving path	138.69	28.56%	3.64	29.70%	1.65	31.86%	1.23	81.83%
Straight-line path	210.44	4.83%	7.41	4.17%	4.29	1.14%	1	63.15%

NRMSE: normalized root mean square error.

a mean  $\pm$  SD length of  $160.26 \pm 224.53$  m, while experimental trials had a mean length of  $111.27 \pm 71.59$  m. The mean sinuosity of natural travel segments that were equal to or shorter than 111.27 was 1.29.

The sound of the auditory cue, especially in the trials outside the outdoor laboratory, functioned as a beacon drawing the monkeys to the site of the food, a site heretofore unknown to the group. They did not rely on memory to arrive at the site of the experiment, since it was unknown. Instead, they followed the sound and travelled in a straight line towards the goal. Alternatively, we might have expected them to use the path of least resistance as they perceived it from their start location (i.e. the landscape-perceiving model). By increasing their linearity, the monkeys decreased the degree to which the landscape-perceiving model fit actual travel (NRMSE of total cumulative resistance, natural travel, landscape-perceiving model = 7.92%; NRMSE of total cumulative resistance, experimental trials, landscape-perceiving model = 28.56%). The increase in error was even larger for the minimum-resistance path model (NRMSE total cumulative resistance, natural paths, minimum-resistance path = 11.61%; NRMSE total cumulative resistance, experimental trials, minimum-resistance path = 34.04%). See Table 3 for comparisons of all parameters for natural travel and experimental trials. The movement of the monkeys in the experimental trials thus decreased in sinuosity and increased in resistance compared to naturally occurring travel.

Compared to the percentage ranks of natural travel (mean percentile =  $3.24 \pm 4.12\%$ ), the experimental trials had a higher average corridor resistance (mean percentile =  $12.45 \pm 14.20\%$ ). The percentage ranks of the corridor resistances of the experimental trials ranged from the 0.7 percentile to the 65.9 percentile while the percentage ranks of natural travel ranged from the 0.09 percentile to the 30.1 percentile. These higher corridor ranks are indicative of use of higher resistance habitats for travel during the experimental trials than during natural movement conditions.

## DISCUSSION

Bearded capuchin monkeys do seem to be attentive to the landscape resistances incurred as they move through their environment. The monkeys travelled in a zone of low resistance in their paths from the start to the end of each travel segment. They also avoided areas of highest landscape resistance entirely as they moved through the landscape (i.e. open areas void of vegetation, the steepest sections of ridges, wetland areas with open water). However, the resistances incurred during their travel were not so exceptionally low that a model assuming comprehensive knowledge of the landscape between their location and a goal would predict their movements. In mean resistance and total resistance per segment, the straight-line travel model was very similar to actual travel. Some differences between the straight-line travel model and actual travel emerged in the resistance/m parameter, with straight-line travel having slightly higher resistance/m. This difference signifies that, while straight-line travel has central tendencies of resistance that are similar to actual travel, actual travel is

slightly lower in resistance/m than this model. The similarities in total resistance per segment result from actual travel having longer travel distances per segment. That resistance/m is a bit more sensitive to distance than mean resistance, which counts resistance by the pixel, accounts for the differences in these two parameter results.

Considering total cumulative resistance per segment, mean resistance (per pixel visited) and resistance/m, the resistance incurred by the monkeys' actual travel was closest to that of travelling in a straight line. However, while the resistance values of actual travel were similar to that of straight-line travel, the travel was not actually linear. This suggests that straight-line travel and actual travel both lie in a zone of low resistance, resulting in their similar resistance-related values, but that they are otherwise different with respect to their spatial patterns. Actual travel also had a wider range of sinuosity than any of the models of travel. In terms of sinuosity, the defining parameter for a model built as a straight line, actual travel differs the most from the straight-line path model of travel and the least from the landscape-perceiving model. Compared with other studies indicating straight-line travel in nonhuman primates (chimpanzees, *Pan troglodytes schweinfurthii*: linearity = 0.939 (sinuosity 1.06): Bates & Byrne, 2009; *Pan troglodytes verus*: linearity = 0.962 (sinuosity = 1.04): Normand & Boesch, 2009; baboons, *Papio ursinus*: linearity 'on route' = 0.959 (sinuosity = 1.04): Rahel Noser & Byrne, 2010), our monkeys' movements were not linear. Capuchin travel segments had a mean sinuosity of 1.34, with a 26% NRMSE compared to the straight-line travel model. We conclude that neither straight-line travel nor resistance-based travel models describe the movement patterns of bearded capuchin monkeys in natural environments completely. However, the error of resistance-based models was lower than that of the straight-line travel model. This result suggests that the capuchin monkeys in this study attended to landscape resistance when making spatial decisions about movement.

The finding that actual travel of bearded capuchin monkeys does not conform to a straight-line model of travel across multiple methods of path segmentation may raise questions about the goal-directed nature of their movement patterns. These results may indicate lack of goal-directed travel on the part of the capuchin monkeys in our study group. Perhaps failure to travel in a linear way is indicative of opportunistic exploitation of densely distributed resources in the monkeys' home range, without a particular goal location directing movement. The results could also suggest an alternative definition of efficiency of movement in nonhuman animals. The travel of bearded capuchin monkeys in this study was better explained by parameters related to the landscape resistance of their paths than by the parameter of sinuosity alone. We therefore believe that, in testing hypotheses of cognitive mapping or spatial memory, the use of resistance-related models of knowledgeable travel would be more informative than the use of linearity- or velocity-related parameters alone.

The monkeys in this study range in a highly heterogeneous landscape with steep ridges, wetlands and patches of bare soil that punctuate their home range with patches of extremely high

resistance. These patches likely serve as barriers to the monkeys' travel, and circumventing these high-resistance patches is a movement strategy that this group demonstrates. It is possible that more homogeneous landscapes may not require movement strategies that take into account the landscape variables of the animals' home range. This would result in minimum-resistance path models and landscape-perceiving path models that yield nearly straight-line paths. In these environments, straight-line travel may be an effective strategy for efficient travel. Further testing is necessary to determine the extent to which the predictions of movement and the movements themselves vary in other types of habitats when landscape variables are included and to determine whether the movement of nonhuman primates in those habitats is shaped by the landscape.

In the experimental trials, monkeys were presented with a high-value, ephemeral resource for which they needed to compete. The monkeys increased the linearity of their travel irrespective of the resistance of the landscape between them and their goal in these trials. Note that, on average, the distances travelled during the experimental trials were shorter than the segments of natural travel, and that distance to the goal may have impacted the linearity of the monkeys' movements. Natural travel segments equal to or shorter than the experimental mean were higher in sinuosity than the experimental trials, however. The variation from average of these measures may indicate that the differences we observed were not significant. Yet, our observations in all the experimental trials (including trials in which we lost the focal monkey in route to the provisioning site, which were excluded from our analysis) indicated that the monkeys were travelling very linearly and at a high rate of speed when approaching the site. These fast, linear movements often made the task of following the focal monkey very difficult, because of the irregular terrain in which the human observer was moving.

While the monkeys are sensitive to the resistances of their landscape, these resistances do not determine their movement patterns entirely. While travelling in natural conditions, the monkeys' goals differ in distance, quality and quantity from the experimental goals. The experimental goals were clumped, high in caloric value, and limited in quantity. Future studies could investigate the effect of resource abundance or quality on the movement patterns of bearded capuchin monkeys using calls that represent varying provisioning regimes. In this study, the experimental trials were conducted in areas of moderately high resistance. Future experiments could test the movement of capuchin monkeys across areas of higher resistance by spacing human observers between the group and the provisioning site to facilitate observation of their movements across areas of impassable terrain.

In some trials, the focal individual moved in the direction of the auditory cue, but ultimately resumed movement in its original direction, rejoining its fellow group members. Focal individuals were observed contact calling in the direction of the remainder of the group while frequently looking back in the direction of the auditory cue on two occasions in which the auditory cue did not result in the group travelling to the location of the auditory cue. During these trials, it appeared that some social variable, such as maintenance of group cohesion, played a role in the individual's decision not to pursue the provisioned food. On another occasion, the focal individual (a low-ranking adult male) failed to respond to the auditory cue despite being within range of the cue (130 m from the centre of the outdoor laboratory). In this example, the monkey did not move towards the auditory cue and continued to forage in the same location beside a low-ranking adult female while other members of the group moved towards the auditory cue. Another individual that failed to respond to the auditory cue on one occasion was an adult female that, between the time of the observers' communication with the experimenter and initiation of the auditory cue, began foraging

on a fruit tree 150 m from the outdoor laboratory. While most of the group moved to the outdoor laboratory in response to the auditory cue in this trial, the focal individual did not change its location.

The responses of our study group to the novel auditory stimulus in the experiment indicated that they did associate the call with distribution of food, and that this food was sufficiently motivating for some members of the monkey group to change their travel goal and move to the location of the call. Our observations also indicate an upper limit to the influence of the novel auditory stimulus on changing the travel goal of the study group, and that calls were not effective if the stimulus was initiated too far from the monkey group or if the individual was not sufficiently motivated by the food, for example. Possible reasons for insufficient motivation to respond to the cue include low probability that an individual can compete to obtain food, or the availability of a naturally occurring food resource at an individual's current location.

Previous research has largely ignored the impact of landscape features on the movement decisions of nonhuman primates. The models presented here consider each monkey's movement decisions in relation to goal locations but also in relation to the features of the landscape. However, the social dynamics of the group also likely impact the natural and experimentally manipulated movement decisions of capuchin monkeys. Future research should examine the resistance surfaces of individuals of different age/sex classes in comparison to one another to identify any age/sex class-specific responses to landscape. Since individuals likely affect one another's movement decisions dynamically, these models must consider the movement decisions of the group as a whole at each movement step.

The results of this study call into question the use of sinuosity as the primary indicator of travel efficiency. Travel efficiency relates to the spatial cognition of nonhuman primates, as it indicates goal-directed movements. We suggest that future studies indicating the goal-directed travel of nonhuman primates should take some measures to account for the effects of landscape variation on the travel of the study animal since large variations in landscape resistance may cause efficient, nonlinear travel to appear to be an inefficient method of arriving at a goal. These movements may be incorrectly described as not goal directed, or controlled by some random process, rather than as an indicator of spatial knowledge of the landscape.

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## Supplementary Material

Supplementary Material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2015.05.003>.

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