SPATIAL COGNITION, MOVEMENT, AND USE OF SPACE IN BEARDED CAPUCHIN MONKEYS

by

ALLISON MARIE HOWARD

(Under the Direction of Dorothy Fragaszy and Marguerite Madden)

ABSTRACT

The spatial cognition and movement ecology of an animal cannot be completely understood without knowledge of the landscape context within which the animal lives. This dissertation investigated the influence of landscape features on the spatial cognition, movement, and use of space of bearded capuchin monkeys (*Sapajus libidinosus*) ranging in Northeast Brazil. Two key landscape features influencing the use of space of these monkeys were identified: proximity to areas of human influence and proximity to steep ridges. Higher values of green vegetation were also identified as a landscape feature associated with the use of stone tools. The identification of landscape features associated with the presence of bearded capuchin monkeys has implications for conservation efforts for this unique population. Movement of bearded capuchin monkeys was investigated through three movement models which incorporated landscape variables to varying degrees. The minimum resistance path model moved so as to incur the absolute least cumulative resistance for each segment of travel. The landscape perceiving model moved through areas of low resistance by moving in the direction of the travel goal through neighboring pixels of least resistance. A straight line path model was also developed to
test the tendency of bearded capuchins to travel linearly. The straight line path model resembled actual travel in its resistance values but not in its linearity, as the monkeys did not move in straight line paths. The minimum resistance and landscape perceiving models had lower cumulative resistance values than actual travel. A novel method of manipulating the monkeys’ travel paths experimentally was also tested in which the monkeys were called to a provisioning site using an auditory cue and their movement patterns were observed. For experimentally manipulated travel goals, the monkeys travel more linearly and incur higher landscape resistance when compared to natural travel paths. Without the consideration of landscape variables, the movement of bearded capuchin monkeys may have been considered inefficient, but their movements appear to be related to the landscape features of the environment in which they move. These results indicate the importance of the consideration of landscape factors for the study of nonhuman primate spatial cognition in natural environments.

INDEX WORDS: Bearded capuchin monkeys, *Sapajus libidinosus*, spatial cognition, movement ecology, use of space, home range
SPATIAL COGNITION, MOVEMENT, AND USE OF SPACE IN BEARDED
CAPUCHIN MONKEYS

by

ALLISON MARIE HOWARD

BA, Appalachian State University, 2003
BS, Appalachian State University, 2003
MS, University of Georgia, 2010

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial
Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2014
SPATIAL COGNITION, MOVEMENT, AND USE OF SPACE IN BEARDED CAPUCHIN MONKEYS

by

ALLISON MARIE HOWARD

Major Professors:  Dorothy Fragaszy
                   Marguerite Madden

Committee:        Irwin Bernstein
                   Nathan Nibbelink

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
May 2014
DEDICATION

“Many a trip continues long after movement in time and space have ceased.”

John Steinbeck

Dedicated to Sergio Bernardes
ACKNOWLEDGEMENTS

This work was supported by the American Society of Primatologists, the Graduate School of the University of Georgia, the UGA Latin American and Caribbean Studies Institute, and ERDAS/DigitalGlobe.

I would like to thank my advisors, Dr. Dorothy Fragaszy and Dr. Marguerite Madden for their continued support and guidance throughout this process. It has been an honor to work under the direction of these two talented women. Their leadership and suggestions have greatly improved the quality of this work and I am thankful for the influence of their diverse skill sets. I thank Dr. Dorothy Fragaszy specifically for her keen eye in editing and for helping to guide the foundational theories underpinning my understanding of primate behavior. I am especially grateful for her invitation to visit the Boa Vista field station for the first time in 2009, changing me forever. To Dr. Marguerite Madden, I am endlessly grateful for the opportunity to join the Center for Geospatial Research. My work at the Center has changed my perspective on the spatial world, on computer programming, and on geospatial technologies. Your support and enthusiasm has carried me through the most difficult times in my career as a graduate student.

I would also like to thank my committee members, Dr. Irwin Bernstein and Dr. Nathan Nibbelink for their helpful suggestions and comments throughout the development of this dissertation. I am grateful for the time they took in reading my work and in helping to guide my understanding of primate behavior and spatial ecology. Their
expertise and thoughtful input has helped me greatly through this process. I also thank Dr. Janet Frick, and Dr. Tommy Jordan for their advice, guidance, and friendship throughout my graduate career.

Thank you to all my incredible research assistants and mentees that I have worked with over the years: Marjolein De Nijs Bik, Michelle Vogel, Josh Lukemire, Natalie Schwob, and Leigh Anna Young. You have all been great friends and collaborators to me and you have supported this process either directly through data collection and analysis or through helping train me to become a better mentor. Working with you all has given my graduate career special meaning, and I am extremely grateful for your many contributions. I extend a very special thank you to my dearest friend, Leigh Anna Young. She not only made the collection of data for this dissertation possible, but became a friend and a confidante in the process. She has my deepest respect and gratitude.

I hardly know where to begin in thanking my family. To my mother, Pat Howard, I am grateful for the example she has set for me as a hardworking wife and mother. You are my guiding light in life, Mom. To my father, Steve Howard, I am grateful for the instilling my curiosity and interest in science. This whole journey began because you encouraged me, Dad. To my brother, Zachary Howard, thank you for always being yourself and for pushing me to do the same.

There are not words enough to describe how grateful I am to Sergio Bernardes for all that he is and all that he has done to help me through this process. He is my devoted life partner and my most dependable collaborator. He believed in me when I could not believe in myself and supported me in every way. I could not have asked for a more patient sounding board or a more enthusiastic cheerleader.
TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS ...........................................................................................................................................v

LIST OF TABLES ....................................................................................................................................................ix

LIST OF FIGURES ..................................................................................................................................................x

CHAPTER

1 INTRODUCTION AND LITERATURE REVIEW ....................................................... 1

   SPATIAL COGNITION IN NONHUMAN PRIMATES ................................ 1

   EFFICIENCY AND SPATIAL COGNITION .................................................... 2

   A LANDSCAPE PERSPECTIVE ON NONHUMAN PRIMATE

   SPATIAL COGNITION .................................................................................. 4

   REFERENCES ........................................................................................................... 8

2 ENVIRONMENTAL FEATURES AND USE OF SPACE BY BEARDED

   CAPUCHIN MONKEYS .................................................................................. 11

   INTRODUCTION ................................................................................................. 13

   METHOD ........................................................................................................... 15

   RESULTS ......................................................................................................... 33

   DISCUSSION .................................................................................................... 49

   REFERENCES .................................................................................................... 53
3 MOVEMENT EFFICIENCY IN BEARDED CAPUCHIN MONKEYS:
CONCLUSIONS FROM NATURAL ROUTE OBSERVATIONS AND
FIELD EXPERIMENTS

INTRODUCTION

METHOD

RESULTS

DISCUSSION

REFERENCES

4 GENERAL DISCUSSION

SUMMARY OF FINDINGS

THE CALLBACK METHOD FOR FIELD EXPERIMENTS

FUTURE DIRECTIONS

REFERENCES

APPENDICES

A NETLOGO CODE FOR LANDSCAPE PERCEIVING MODEL

B MONKEY LANDSCAPE PERCEIVING MODEL ODD

DESCRIPTION

viii
LIST OF TABLES

Table 2.1: Land Cover/Land Use Classes from Visual Interpretation of WorldView-2 image ........................................................................................................................................ 24

Table 2.2: Model Evaluation Parameters for Candidate MaxEnt Models .................. 39

Table 2.3: Permutation Importance of Variables across the Candidate MaxEnt Models ........................................................................................................................................ 41

Table 2.4: Mean Values of Landscape Variables at Observation Points and across the Area of Interest and Degrees of Freedom and T-values from a Welch’s two-sample t-test ........................................................................................................................................ 46

Table 3.1: RMSE and Normalized RMSE of the Models of Capuchin Monkey Travel across Segmentation Methods ........................................................................................................................................ 86

Table 3.2: Models of Capuchin Travel Compared with Actual Travel Segmented by Stop Points and Change Points ........................................................................................................................................ 89

Table 3.3: Parameters of the Actual and Modeled Travel Paths in Experimental Trials ........................................................................................................................................ 103

Table 3.4: Models of Capuchin Travel Compared with Actual Travel in Experimental Trials ........................................................................................................................................ 103

Table 3.5: Models of Capuchin Travel Compared with Actual Travel in Natural Observations and in the Experimental Trials ........................................................................................................................................ 108
LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Map of Brazil showing the location of Piauí state and our study site</td>
<td>16</td>
</tr>
<tr>
<td>2.2</td>
<td>Screen shot from the Avenza PDF Maps application depicting the pан-sharpened satellite image and an observation point</td>
<td>19</td>
</tr>
<tr>
<td>2.3</td>
<td>Example of GPS error under conditions of signal obstruction</td>
<td>19</td>
</tr>
<tr>
<td>2.4</td>
<td>WorldView-2 satellite image scene with area of interest outlined in red</td>
<td>22</td>
</tr>
<tr>
<td>2.5</td>
<td>Visual interpretation and classification of the land cover/land use in the area of interest</td>
<td>23</td>
</tr>
<tr>
<td>2.6</td>
<td>Random Points Visited for Field Validation in Area of Interest</td>
<td>28</td>
</tr>
<tr>
<td>2.7</td>
<td>WorldView-2 satellite image scene with large area of interest outlined in red and small area of interest outlined in yellow</td>
<td>31</td>
</tr>
<tr>
<td>2.8</td>
<td>Polygons showing use of space by our study group</td>
<td>34</td>
</tr>
<tr>
<td>2.9</td>
<td>End member bands resulting from the SMA with lighter shades representing higher percentages of each respective end member in the pixel: green vegetation, dark, and bare soil</td>
<td>36</td>
</tr>
<tr>
<td>2.10</td>
<td>NDVI image with lighter shades representing higher index values and greater radiation from green vegetation</td>
<td>37</td>
</tr>
<tr>
<td>2.11</td>
<td>A three-dimensional representation of the digital elevation model generated through Automated Terrain Extraction</td>
<td>38</td>
</tr>
</tbody>
</table>
Figure 2.12: (A) Final MaxEnt habitat model with warmer colors representing areas of lower habitat suitability for bearded capuchin monkeys and cooler colors representing higher suitability; (B) All observation points shown as black dots...

Figure 2.13: Histograms showing the distribution of (A) Land Cover/Land Use, (B) Elevation, (C) NDVI, (D) Distance to Areas of Human Influence, (E) Distance to Steep Ridges, (F) Distance to Roads, (G) Percent Shadow, (H) Percent Bare Soil, and (I) Percent Green Vegetation...

Figure 3.1: Map of Brazil showing the location of Piauí state and our study site...

Figure 3.2: Numbers of Change Points as found by the Change Point Test under q = 1 through q = 10...

Figure 3.3: Change Points Detected in the May 16 path with q = 5, q = 6, q = 9, and q = 10...

Figure 3.4: Change Points (green) detected for Naturally Observed Travel on May 21, June 13, and July 17 (q = 5; p < 0.01), stop points (red), and points designated as both stop and change points...

Figure 3.5: Provisional MaxEnt model of capuchin habitat used to select appropriate locations for experimental trials...

Figure 3.6: Distribution of Elapsed Time at Observation Points...

Figure 3.7: Boxplots of mean resistance, resistance per meter, total resistance, and sinuosity of the models of capuchin travel and actual naturally occurring travel paths...

Figure 3.8: Actual and modeled paths and observation points for May 16, 2013...
Figure 3.9: Actual and modeled paths and observation points for May 21, 2013 ........ 94

Figure 3.10: Actual and modeled paths and observation points for June 13, 2013 ....... 95

Figure 3.11: Actual and modeled paths and observation points for July 11, 2013 ....... 96

Figure 3.12: Boxplot of the Percent Ranks of Mean Corridor Resistance Values for the
Stop and Change Points Segments of Capuchin actual travel ...................... 98

Figure 3.13: Actual path from July 17, 2013 with corridor resistance values overlaid on
WorldView-2 satellite imagery................................................................. 99

Figure 3.14: Modeled and actual paths from the experimental trial on July 19; Red
triangle indicates location from which photo (B) was taken; Blue triangle
indicates location from which photo (C) was taken........................................ 105

Figure 3.15: Experimental Trial, July 13 .................................................... 106
CHAPTER 1
INTRODUCTION AND LITERATURE REVIEW

Spatial Cognition in Nonhuman Primates

Finding resources, mates, and shelter are challenges that mobile animals face in natural environments. These challenges are resolved in diverse ways across the animal kingdom with some nonhuman animals exhibiting specialized behavioral and physiological adaptations for solving spatial problems. For example, desert ants (Cataglyphis noda) foraging in nearly featureless landscapes return directly to their nests via straight line travel after foraging in long, meandering, outbound paths by integrating the distance and direction they’ve traveled to calculate a return route (Buehlmann, Hansson, & Knaden, 2012). Clark’s Nutcrackers (Nucifraga columbiana) demonstrate exceptional spatial memory, caching and retrieving between 22,000 and 33,000 seeds each year in thousands of cache sites (Vander Wall & Balda, 1977). Whooping cranes (Grus americana) migrate long distances using routes and overwintering sites that are learned socially from conspecifics or from ultralight escorts (Mueller, O’Hara, Converse, Urbanek, & Fagan, 2013).

Nonhuman primates exhibit complex behaviors of movement relative to their environment that may have a foundation in their spatial cognition. Compared to other mammals, primates have relatively large brains (Jerison, 1973). Structural differences such as prefrontal cortex size (Dunbar, 1992) and the brain : body size relationship
(Clutton-Brock & Harvey, 1980) have been associated with the unique cognitive abilities of the clade. In particular, brain differences have been associated with innovation and sociality in nonhuman primates (Dunbar, 1998; Reader & Laland, 2002). What is unclear is whether these exceptionalities translate to a set of unique or advanced cognitive skills in the spatial domain. It has been hypothesized that foraging requirements exerted a critical selective pressure for the evolution of cognitive abilities in nonhuman primates (Milton, 1981; Woerden & Willems, 2012). Considering their unique problem solving and social skills, primates may have also evolved unique cognitive skills that enhance their ability to solve spatial problems. Animals ranging in natural environments confront a variety of spatial challenges such as finding resources and returning to them, localizing oneself in the environment, representing and remembering information regarding the quantity and quality of ephemeral resource sites, and applying temporal information to estimate a resource’s present quantity and quality based on past observation. Of particular interest in the field of spatial cognition is whether nonhuman primates plan their travel routes and to what extent they remember the locations of out of sight resources (Garber & Dolins, 2014).

**Efficiency and Spatial Cognition**

An animal’s efficiency in its movements or spatial choices is the parameter by which we determine whether its actions were adaptive. Many studies have investigated the efficiency of movement or spatial choices in humans and nonhuman animals in laboratory and natural settings. For example, the traveling salesman problem is a mathematical construct based on the concept of spatial efficiency in which one must
choose an efficient path through a series of destinations and then return to the start point, as a traveling salesman might choose his movement sequence through multiple cities and return home at the end of the day. The traveling salesman problem has been presented to humans and nonhuman animals in laboratory settings and there is evidence that nonhuman primates use spatial decision making strategies that reduce (although perhaps do not minimize) the cumulative distance traveled between a series of destinations (Howard & Fragaszy, 2014; MacDonald & Wilkie, 1990; Menzel, 1973). Tamarin monkeys (Saguinus mystax and S. fuscollis) show evidence of foraging efficiency by traplining, or making foraging decisions which seem to be largely based on minimizing the distance traveled from one resource patch to the next (Garber, 1988). Also, nonhuman primates ranging in natural environments have been observed to use linear travel segments between foraging sites (Janson, 1998, 2007; Normand & Boesch, 2009; Noser & Byrne, 2007; Presotto & Izar, 2010), and have demonstrated a preference for the nearest feeding site (Janson, 1998). There is evidence that some species of nonhuman primates use Euclidean cognitive maps in natural environments to help them relocate known resources efficiently (Normand & Boesch, 2009; Presotto & Izar, 2010). A Euclidean cognitive map is a mental representation of the environment that includes two metric categories of spatial data, distance and direction, and would allow an animal to compute novel and efficient routes (Shettleworth, 2010). For a variety of reasons, demonstrating that an animal is indeed implementing a cognitive strategy that incorporates metric spatial data (i.e., direction, distance) and can calculate a novel shortcut is particularly challenging (Bennett, 1996), yet identifying primate species that
use this strategy to increase movement efficiency continues to be a priority for studies of nonhuman primate cognition (Garber & Dolins, 2014).

No matter the mechanism of spatial orientation and locating resources in one’s environment, movement efficiency is an important indicator of adaptive spatial decision making. The previous studies on nonhuman primate spatial cognition have by and large identified movement efficiency as straight line movement, that is, movement minimizing travel distance. It is possible, however, that preferred routes may be nonlinear if they reduce the energetic costs of travel or the probability of predation or if they increase the animal’s likelihood of finding food resources (Janson & Byrne, 2007). I propose that in order to understand the movement efficiency and spatial cognition of nonhuman primates, we may need to consider the habitat preferences of these animals and the spatial dynamics of the landscapes in which they move. For example, spider monkeys (Ateles belzebuth) and woolly monkeys (Lagothrix poeppigii) in Amazonian Ecuador were shown to use a network of familiar routes that coincided with ridge tops, a strategy the authors hypothesize to be related to the energetic efficiency of their movement (Di Fiore & Suarez, 2007). To what extent do other heterogeneous landscapes impact the movement decisions of nonhuman primates and should we consider these landscape impacts in our evaluation of movement efficiency?

A Landscape Perspective on Nonhuman Primate Spatial Cognition

Previous work on nonhuman primate spatial cognition has discounted the influence of landscape features through the use of laboratory controls (e.g., Beran & Beran, 2005; Hoffman & Beran, 2006; MacDonald, 1994; Potì, 2000; Potì, Bartolommei,
& Saporiti, 2005), the selection of study areas in which topographic variation is minimal (Janson, 2012), or the omission of landscape variables from analyses (Normand & Boesch, 2009). Other work on primate spatial cognition has taken landscape variables into account by considering the line of sight to specific topographic features when analyzing the goal-directed nature of travel (Presotto & Izar, 2010), using elevation maps to visually evaluate the spatial relationships between repeated travel routes and ridges (Di Fiore & Suarez, 2007), and evaluating the concordance of resource sites with locations at which nonhuman primates changed the direction of their movement (Asensio & Brockelman, 2011; Byrne, Noser, Bates, & Jupp, 2009; Joly & Zimmermann, 2011). This dissertation will present a novel perspective for analyses of spatial cognition in nonhuman primates in which the influence of landscape features on spatial cognition is not merely controlled for, but, rather, investigated directly and comprehensively.

Chapter 2 of this dissertation describes the development of a species distribution model using Maximum Entropy habitat modeling techniques over a large scale of space encompassing just the home range of one group of bearded capuchin monkeys (*Sapajus libidinosus*). Although species distribution models are normally used to estimate the geographic distributions of entire species or populations (Elith & Leathwick, 2009), this study utilizes this technique to estimate the suitability of landscape features and microhabitats for a single group of bearded capuchins over the study period. This method is used to describe the use of space by bearded capuchin monkeys and also to estimate the habitat suitability of areas near their home range where they were not observed during the study period. Our research on the capuchins’ use of space is important for understanding
their spatial decision making and cognition, but also for conservation efforts attempting
to better estimate how current and future habitat changes may affect this species.

In Chapter 3 I used geospatial techniques to develop a series of models against
which to compare the observed movement patterns of bearded capuchin monkeys,
considering questions of efficiency of movement in nonhuman primates. I tested methods
of segmenting the monkeys’ travel for analysis by their directional change points (Byrne
et al., 2009), by temporal stop points where the monkeys stopped for extended periods of
time, or by both stop and change points. Three models of movement between those stop
and/or change points were tested in Chapter 3: the straight line path model, the landscape
perceiving model, and the minimum resistance path model. These three models vary in
the degree to which landscape determines the modeled monkeys’ spatial decisions, and a
layer of resistance to movement was used to estimate these landscape effects. The
landscape resistance layer used was developed from the Maximum Entropy species
distribution model described in Chapter 2. The straight line path model does not consider
landscape at all (aside from Euclidean distance between points). The landscape
perceiving path model considers the landscape features immediately surrounding the
monkey but does not consider any landscape features further afield. The minimum
resistance path model considers the entire landscape between the beginning and end of
each travel segment, and plans the path of absolute least resistance considering landscape
features and Euclidean distance.

Chapter 3 also presents the results from an experimental manipulation of the
capuchins’ travel goals. The monkeys in this study were trained to associate an auditory
cue with the distribution of food by the human experimenters. Their travel decisions
under the conditions of a manipulated travel goal are evaluated using the movement models described above. Experiment sites were chosen to highlight the spatial decision making strategies of bearded capuchin monkeys and the impact of landscape across microhabitats with very high resistance values.

This dissertation presents novel analyses of the use of space, spatial decision making, and efficiency of movement in nonhuman primates. The studies in this dissertation investigate the influence of landscape features on spatial cognition through a series of models of their habitat preferences and their movement patterns. We evaluate how these animals use the space and landscape features of their home range, how their movement can be divided into segments for analysis, and how landscape and movement interact. Of particular importance is the introduction of landscape perspectives to the concept of movement efficiency in nonhuman primates. The three movement models tested in this dissertation incorporate landscape and travel distance in varying degrees of complexity. Similar techniques could be applied to test the degree to which landscape features impact the movement decisions of any mobile animal. This research has important implications for understanding the spatial cognition of nonhuman primates and other animals, since efficiency lies at the core of evaluating movement decisions that may result from a variety of cognitive mapping or spatial representation strategies.
REFERENCES


CHAPTER 2

ENVIRONMENTAL FEATURES AND USE OF SPACE BY BEARDED CAPUCHIN MONKEYS

Howard, A. M., Nibbelink, N., Bernardes, S., Madden, M., Fragaszy, D.M., to be submitted to Animal Conservation
Abstract

An animal’s use of space can be defined in a variety of ways which incorporate increasing levels of complexity and biologically relevant variables. This study examines the use of space of a group of bearded capuchin monkeys (*Sapajus libidinosus*), a species unique in their use of stone tools to extract encapsulated foods. Our definition of use of space incorporates data on the frequency and density of observations of the study animal in their home range, data on the landscape features through which these animals move, and data on the behavior of these monkeys observed through focal animal follows. We define important landscape variables associated with the monkeys’ behavior, especially the use of stone tools. Maximum Entropy habitat modeling is used to define the landscape characteristics associated with the monkeys’ use of space. The variables evaluated in model building include normalized difference vegetation index, distance to roads, distance to areas of human influence (e.g., agriculture and residential areas), distance to steep ridges, elevation, land cover/land use class, and fractional cover values of green vegetation, bare soil, and shadow (from Spectral Mixture Analysis). Distance to areas of human influence and distance to steep ridges were the variables most closely associated with capuchin use of space. Stone tool use behavior occurred in areas of lower elevation and higher percentage of green vegetation relative to other behavior. These results may assist in decision making regarding the conservation of this unique stone tool use behavior of the species, especially relevant due to the recent expansion and intensification of industrial agriculture in the region.

*Keywords:* Species distribution model, Capuchin monkeys, *Sapajus libidinosus*, use of space, conservation
Introduction

Understanding the space used by an animal improves our knowledge of the animal’s behavior and ecology. Knowledge of use of space by animal populations of interest due to their threatened or endangered status, unique behaviors, or economic importance, for example, may also aid in conservation efforts for that species, giving decision makers important information regarding the animal of interest. Thus, defining a population’s use of space is an important goal for biologists and conservationists alike.

The most common method of defining and describing the space used by an animal is its home range. Home range was originally defined by Burt (1943) as the area used by the animal during normal activities. Related to the notion of a home range is the utilization distribution, an area with defined probabilities for finding an animal in a given location within an area of interest (Kernohan, Gitzen & Millspaugh, 2001). Species distribution models similarly generate models of habitat suitability by combining point observations of animal locations with data on the landscape in which these animals are located (Elith & Leathwick, 2009). Species distribution models generate a more complete picture of use of space through their incorporation of landscape data.

To better understand the use of space of an animal of interest, we must incorporate information regarding the environmental features of the landscape upon which the animal moves, as well as behavioral data regarding how the animal utilizes specific areas of the landscape. Data and analysis tools needed to acquire and compile this information include remotely sensed imagery from spaceborne, airborne, or ground-based sensors, geo-located tracking data usually in the form of GPS ground coordinates and field based observations of animal behavior as individuals and/or groups move within
their home range. Imagery of high resolution (i.e., pixel sizes on the order of 1 x 1 m or smaller) are excellent sources of information about the environmental features of the landscape where an animal lives. Regular and systematic field observations of animal behavior tied to GPS locations can be incorporated in a geodatabase that integrates high temporal resolution observations of the animal’s behavior with the image-based landscape context within which the animal moves. This rich database can then be used to model, assess, and understand an animal’s use of space.

Maximum entropy (MaxEnt) is a spatial distribution modeling technique that estimates the suitability of a habitat for a study animal based on presence-only observations and environmental information (Phillips & Dudík, 2008). Through direct observation and following of a study animal, we can gain information regarding not only their use of space, but also the behaviors associated with that space. This method of defining use of space, including both environmental and behavioral descriptors, better represents the biologically relevant aspects of our study subjects’ home ranges and movement patterns during our period of observation than methods which define use of space on the basis of spatial metrics or landscape analyses alone.

Capuchin monkeys are unique in that they are the only nonhuman primates in the New World known to use stone tools. The bearded capuchin monkeys of northeastern Brazil have gained particular attention due to their proficient use of stone tools to crack open the hard casings of various species of ground palms (Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004). Tool use is generally of interest to biologists and psychologists alike (Fragaszy, Pickering, Liu, & Izar, 2010), and stone tool use in nonhuman primates is especially interesting due to its resemblance to the stone tool use
behavior of early hominids (e.g., Susman, 1994). The area inhabited by the bearded capuchin monkeys in northeastern Brazil is an area of extensive recent agricultural expansion and intensification (Barretto, Berndes, Sparovek, & Wirsenius, 2013). These agricultural activities have recently arrived very close to the area of our field laboratory in Piauí state, Brazil. We are interested in better understanding how our study species uses space and landscape features for its various activities, including stone tool use. Specifically, we are interested in identifying the primary landscape characteristics of the home range of our study group. We also wish to investigate whether there are interactions between specific landscape variables and specific behavioral patterns of our study group. This study may assist decision makers and scientists interested in preserving the unique stone tool use behavior exhibited by this species by presenting a more complete picture of how these animals use space and the space in which they use tools.

Method

Subjects and Study Area

The subjects of this study were a group of bearded capuchin monkeys (*Sapajus libidinosus*) in a wooded savanna habitat in northeastern Brazil (Piauí state) (Figure 2.1). The topography of the study area is a flat plain punctuated by steep vertical ridges 20 to 165 meters in height. The climate of the study area is seasonally dry during the period of April to September, with 230 mm mean precipitation during the dry season (Visalberghi et al., 2009). Historically, agriculture in the study area has been limited to small, subsistence farms, but recent research has demonstrated a dramatic increase in industrial
agriculture in the region generally (Barretto et al., 2013) and in the area inhabited by these monkeys specifically over the past 26 years (Remillard et al., 2014).

Fig 2.1 (A) Map of Brazil showing the location of Piauí state and our study site; (B) Photograph showing the landscape of the region

**Behavioral and Positional Data Collection**

Observations of the monkeys’ naturally occurring routes were conducted during the months of May, June, and July of 2013 (n = 27 days; n = 8,611 points). Following the recommendation of Isbell et al. (1999), daily data collection consisted of following a single focal animal in the monkey group, recording its location and activity. For each complete day of data collection, the focal individual was chosen at random among all (n=8) adult monkeys in the study group. The capuchin monkeys in this study were habituated to human presence and their behavior was not apparently altered by being followed by a human observer.
The observer recorded geographic coordinates of the focal individual’s location for approximately 9.5 hours each day 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). The image on the tablet computer resulted from the fusion of panchromatic and multispectral bands from WorldView-2, a process which adds high spatial resolution detail from the panchromatic image to the multispectral image of lower spatial resolution. The Gram-Schmidt Spectral Sharpening method (Brower & Laben, 2000), a module of the ENVI image processing software, was used to sharpen the multispectral bands, while co-registering (i.e., overlaying) the result with the high spatial resolution panchromatic band. Due to the lack of atmospheric data and reliable atmospheric models for the area of study, atmospheric correction of the WorldView-2 image was performed using the Quick Atmospheric Correction algorithm implemented by the ENVI image processing software (Bernstein et al., 2005). This method provides an adequate approximation of physically-based atmospheric corrections with multiple cover types and dark pixels (Bernstein et al., 2005).

The tablet computer technique for positional observation gave the observer greater control in recording the position of the focal monkey than use of a handheld GPS unit alone. Figure 2.2 shows an image depicting the screen of the tablet computer, the pan-sharpened image, and a GPS point. Observable discrepancies (greater than approximately 10 m) between the monkey’s location and the coordinates reported by the GPS receiver were corrected manually through visual interpretation during behavioral
observations. For example, Figure 2.3 depicts a difference of approximately 10.5 m between the recorded GPS coordinate (blue dot) and the actual location of the GPS receiver within an open-air research building. These discrepancies were most often apparently caused by proximity to steep ridges that interfered with satellite reception. The high-resolution satellite image also guaranteed the retrieval of more accurate locations when the observer was at a distance from the focal monkey, a task usually performed in the field by estimating the distance and direction between the focal animal and the observer and entering these estimates into the handheld GPS. In contrast to GPS collaring or handheld GPS techniques, the GPS-enabled tablet computer with satellite imagery provided maximal spatial and temporal resolution of location recordings with minimal invasiveness for the focal animals.
Fig 2.2 Screen shot from the Avenza PDF Maps application depicting the pan-sharpened satellite image and an observation point

Fig 2.3 Example of GPS error under conditions of signal obstruction. (A) Screenshot from Avenza PDF Maps showing the coordinates indicated by the GPS signal (blue dot). (B) Photograph showing the actual location of the tablet at the time the screenshot was acquired (10.5 m distance between actual location and GPS coordinate location).
Location of the focal animal was recorded semi-continuously. That is, as movement is a continuous spatiotemporal phenomenon, the focal individual’s movement behavior was recorded 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. In practice, this meant that each time the focal individual changed its location or its activity, this change in state was recorded by the observer. At each point observation, the monkey’s location and its behavior were recorded and the points were time stamped. Behavior was recorded as one of the following categories: stationary (animal sits, stands, or lies down), foraging (animal ingests or processes food items), locomoting (animal walks, leaps, or climbs), social interaction (animal is involved in interaction with another individual), or self care (animal grooms self). If foraging and locomotion happened simultaneously, the behavior was recorded as foraging and the animal’s new location was recorded. If social interaction and another behavior occurred simultaneously (e.g., social interaction and self care), both behaviors were noted. For the purposes of the categorical behavioral analyses, locomotion and foraging took precedence over social behavior. The other behavioral categories were considered secondary to social behavior. No other behavioral categories occurred simultaneously during the data collection period.

A minimum bounding geometry polygon was generated surrounding all observation points for our study group to identify the area encompassed by capuchin activity. A kernel density estimation measuring the intensity of observations within the capuchin’s visited range, or their utilization distribution, was calculated using ArcGIS.
software, and isopleths of 50%, 90%, and 95% were generated using the R statistical package. These isopleths are polygons that represent statistical probabilities of the animals’ use of the enveloped space, with 95% representing the animals’ home range (Gitzen, Millspaugh, & Kernohan, 2006). While the 50% kernel density isopleth is typically considered the animals’ core area, our method of collecting data in this study (i.e., recording a data point each time the animal moved instead of on a temporal interval) does not produce point clusters in areas where animals spend extended periods of time, the traditional definition of core area, but rather in locations where the animals move frequently.

Landscape Analysis

Visual interpretation

An atmospherically corrected subset of a multispectral WorldView-2 satellite image (2 meter spatial resolution) of the study area was visually interpreted to identify features and land cover elements relevant to the movement of capuchin monkeys. The subset of the image was created by clipping an area of interest that encompassed the space used by the capuchin monkeys and extended to areas of intermittent use (as described by the field guides following these monkeys for multiple seasons) (Figure 2.4).
Fig 2.4 WorldView-2 satellite image scene with area of interest outlined in red. All point observations of our study group are shown as blue dots within the area of interest.

The land cover elements in the area of interest were identified and digitized as vectors in ArcGIS 10.1 by visually interpreting the satellite image at a scale of 1:8000. Elements were classified on the basis of tone, texture, shape and pattern, as well as from familiarity with the area of study (Figure 2.5). The image was hierarchically classified as recommended by Anderson (1976), but all specific classes were customized for this study. The land cover classes identified were fluvial vegetation (dense and less dense), ridges (steep vertical ridges and their borders), grassland vegetation, wooded savanna, bare soil, human influence (roads, residential and agricultural areas), and wetlands (Table 2.1).
Fig 2.5 Visual interpretation and classification of the land cover/land use in the area of interest
### Table 2.1

*Land Cover/Land Use Classes from Visual Interpretation of WorldView-2 Image*

<table>
<thead>
<tr>
<th>Level 1 Class</th>
<th>Level 2 Class</th>
<th>Level 3 Class</th>
<th>Description of Level 3 Class</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Vegetation</td>
<td>11. Wetland</td>
<td>111. Wetland</td>
<td>Land areas seasonally saturated with water</td>
</tr>
<tr>
<td>1. Vegetation</td>
<td>12. Fluvial</td>
<td>121. Dense fluvial vegetation</td>
<td>Areas proximal to streambeds; Forested area with dense vegetation cover; trees, shrubs, grasses, and ground palms</td>
</tr>
<tr>
<td>1. Vegetation</td>
<td>12. Fluvial</td>
<td>122. Less dense fluvial vegetation</td>
<td>Areas proximal to seasonal streambeds; Forested area with tall tree cover; grasses and ground palms understory</td>
</tr>
<tr>
<td>1. Vegetation</td>
<td>13. Savanna</td>
<td>131. Wooded Savanna</td>
<td>Grassland with trees 5-10 m in height, understory shrubs, grasses, and ground palms</td>
</tr>
<tr>
<td>1. Vegetation</td>
<td>13. Savanna</td>
<td>132. Grassland</td>
<td>Grassland with shrubs less than 5 m in height, understory of grasses and ground palms</td>
</tr>
<tr>
<td>2. Geomorphological features</td>
<td>21. Bare soil</td>
<td>211. Bare soil</td>
<td>Areas of exposed soil or rock with little vegetation (e.g., sparse grasses and shrubs &lt; 5 m) or no vegetation</td>
</tr>
<tr>
<td>2. Geomorphological features</td>
<td>22. Ridges</td>
<td>221. Steep ridge</td>
<td>Steep ridges composed of sedimentary rock; Rising vertically from the grassland plains; 20-100 m tall</td>
</tr>
<tr>
<td>2. Geomorphological features</td>
<td>22. Ridges</td>
<td>222. Steep ridge borders</td>
<td>Borders surrounding vertical ridges covered by regolith, or loose soil and rock, and dense scrubby and thorny vegetation</td>
</tr>
<tr>
<td>3. Developed</td>
<td>31. Human activity</td>
<td>311. Human influence</td>
<td>Areas of human activity including residential areas, active, and inactive agricultural fields, and areas cleared for human recreation (e.g., soccer fields)</td>
</tr>
<tr>
<td>3. Developed</td>
<td>31. Human activity</td>
<td>312. Roads</td>
<td>Dirt roads for car or motorcycle transportation; 3-5 m in width</td>
</tr>
</tbody>
</table>
**Spectral Mixture Analysis.**

Spectral Mixture Analysis (SMA) is an image classification method that estimates the percentages of landscape elements within a pixel, considering that most pixels are actually composed of more than one type of land cover. Pixels containing only one land cover element are pure pixels, and SMA extracts the percentage values of each identified land cover element from the pixels of the image through a comparison with their spectral signature to the spectral signatures of identified pure pixels. The identification of pure pixels required by the Spectral Mixing Analysis followed the methods presented by Small (2004) and incorporated an analysis of the WorldView-2 image mixing space. Pure pixel selection also involved cascaded principal component analysis of geometrically and atmospherically corrected images, resulting in the generation of Minimum-Noise-Fraction (MNF, Green, Berman, Switzer, & Craig, 1988) images. Pixel Purity Index (PPI, Chaudhry, Wu, Liu, Chang & Plaza, 2006) images were generated and used with MNF results as input to ENVI's n-dimensional visualizer, for pure pixel selection. Pure pixels were identified for green vegetation, soil and shadow. Images representing fractional coverage for each of these landscape descriptors were generated using the linear spectral unmixing function of ENVI. The quality of the resulting images was analyzed based on the Root Mean Square Error (RMSE) band. The pure pixel values for each endmember are multiplied by the proportions of that endmember in the pixel in question, and this value should sum to the total reflectance value for each pixel. The difference between the modeled values and actual pixel reflectance value is the basis for the output RMSE band.
Normalized Difference Vegetation Index.

After converting to radiance values and performing the QUAC atmospheric correction on the WorldView-2 multispectral image, a Normalized Difference Vegetation Index (NDVI) was computed using the band math function of ENVI Image Analysis Software. NDVI is an index calculated from the light reflected by vegetation to remote sensors developed by Rouse and colleagues (1974). The index is used to assess remote sensing imagery for the presence or absence and intensity of green vegetation. NDVI is calculated as a ratio of the near-infrared radiation minus the red visible spectrum radiation, divided by the near-infrared radiation plus the red visible spectrum radiation. In the absence of green vegetation, NDVI values will be close to zero, while values close to one indicate dense green vegetation. This index and other similar vegetation indices have been used to study seasonal changes in the vegetation of this region (Ferreira & Huete, 2004). In the present study, NDVI, like the spectral mixing analysis end member percent green vegetation, represented the presence of green vegetation in the area of interest.

Digital Elevation Model.

A WorldView-2 Ortho-Ready stereo pair of satellite images (2 meter spatial resolution) was used to create a digital elevation model (DEM) of the study area. These images facilitate DEM creation since they are area based and geo-referenced to the Universal Transverse Mercator projection, Zone 23 S, and to a constant base elevation. ERDAS LPS software was used for automatic terrain extraction. Automatic Tie Points between the two images in the stereo pair were generated based on the rational polynomial coefficient model file from the stereo pair, a mathematical model associating
the pixels of the imagery with ground coordinates. This process followed the methodology recommended by DigitalGlobe for their WorldView-2 product.

Field validation.

Results of landscape analyses were verified in the field by navigating to the random sample of points within the monkeys’ area of use (30 points). This random sample of 30 points was selected from a larger random sample that was geographically distributed throughout the area of interest (Figure 2.6). The 30 points visited were all points from the larger sample which fell within or nearby to the monkeys’ home range. The ground truth procedure consisted of visiting the random selection of points and recording land cover/land use class, height and identities of predominant vegetation (understory and canopy), and distances to prominent physiographic and land cover features (e.g., steep ridges, roads) from each point. The land cover/land use class observed in the field was recorded and compared to the results of landscape analyses. If the recorded class differed from the results of visual interpretation, the visual interpretation was changed to reflect the actual class observed in the field. The accuracy measures calculated from the ground truth procedure were not altered, however. In addition to the random sample of 30 points visited, an opportunistic sample of 27 points was also taken while following the capuchin monkeys. Opportunistic sampling consisted of recording the land cover class at the point where the focal monkey was being observed. Cohen’s Kappa Statistic for reliability was calculated comparing the land cover/land use class recorded in the field (random and opportunistic sample) to the land
cover/land use class from visual interpretation. The Kappa statistic calculates validity of one’s samples by including the chance of a sample being correct just by random chance.

**Fig 2.6** Random Points Visited for Field Validation in Area of Interest

**Maximum Entropy Habitat Modeling**

**MaxEnt Model Creation.**

The species-distribution modeling program MaxEnt (version 3.3.1) (Philips et al., 2009) was used to generate a predictive model of capuchin monkey use of space for the focal group of monkeys over the study area using presence-only observation points, environmental layers, and a random selection of background points distributed over the study area. A random selection of 20% of the observations points were set aside from model building for testing the models. A total of 8,611 observation points were recorded for the study group during their natural daily ranging activities. These points included observations of focal individuals and group points when the focal individual was out of
sight. This meant that for the complete initial run of the model, 1,722 presence points were used for model testing, while the remaining 6,889 points were used for model building. Environmental layers included in initial model testing were land cover/land use class (from visual interpretation and supervised classification), elevation, NDVI values, fractional cover from Spectral Mixture Analysis (percent bare soil, shadow, and green vegetation), distance to steep ridges, distance to roads, and distance to areas of human influence (i.e., residential areas, farms). MaxEnt software generated a random selection of 10,000 background points over the area of interest to inform the model of variation in the environmental variables across the modeled space. The final model output was logistic, representing suitability of a given pixel in the modeled space (Phillips & Dudík, 2008).

**MaxEnt Model Selection.**

Models were built and tested using a random test percentage of 20% of the observation points. A receiver operating curve was generated for the training and the test data during this process. This graph plots the model’s false positives on the x-axis and true positives on the y-axis, and, as a result, the area under the curve (AUC) of this plot is a measure of model fit with a random model having an AUC value of 0.5 and a perfect model having an AUC value of 1. To analyze the tradeoff between model fit and parsimony, the Akaike Information Criterion (AIC\textsubscript{c}) was calculated for the models with varying numbers of predictor variables. AIC\textsubscript{c} differs from the standard AIC in that it includes a correction for sample size. Raw model output, instead of the logistic output
used for model interpretation, is used to calculate the AIC<sub>c</sub> value. In a set of models to be compared, the model with the lowest AIC<sub>c</sub> value is preferred.

Model selection followed the methods outlined by Hickey et al. (2013) which deal with concerns regarding species distribution modeling using MaxEnt that included issues of sampling bias and analysis of the modeled relationships (Yackulic et al., 2013). An all-inclusive initial model was built for the previously described area of interest (area = 24 square km) using landscape variables of biological importance to our study group.

To deal with potential issues caused by the spatial clustering of observation points (Phillips et al., 2009), a smaller area of interest (area = 5.936 square km) was defined in the model building process to avoid problems that may be caused by the clumping of the observation points in the animals’ home range relative to the larger area of interest (Figure 2.7). While the larger area of interest appropriately characterized the larger potential home range of these monkeys and neighboring groups in response to seasonality, the smaller area of interest was important for characterizing the capuchins’ actual movements and use of space during our study period. In addition, the complete set of presence points was divided into subsets of points that were no closer than 30, 25, 20, and 10, and 5 meters from one another, and models using these levels of spatial separation were tested iteratively. This process generated a progressively more selective set of observation points for the model building and model testing process.
Fig 2.7 WorldView-2 satellite image scene with large area of interest outlined in red and small area of interest outlined in yellow. Point observations are shown as blue dots.

Pearson’s correlation of landscape variables was calculated using ENMTools software. To avoid over fitting the model, highly correlated landscape variables ($r > 0.5$) were removed from model building. The permutation importance and gain of each variable was compared, and the variable that contributed most to model fit was retained. Gain is a measure of goodness of fit related to deviance which starts at zero and increases asymptotically during the model run. As the model runs, the gain of each variable contributing to model fit increases as its model coefficient changes to represent the modeled system better, and those gains are used to calculate percent contribution to the final model once the model run is complete. Permutation importance is a measure of
variable performance generated by randomly permuting the values of that variable among the training points and measuring their contribution to the model by measuring the degree to which this process reduces AUC. A jackknife analysis was conducted in which one of the landscape predictor variables was eliminated and the others left in place, and then a model was generated using only the eliminated predictor variable. This process was repeated for each of the predictor variables in the model. Training (using training data) and test (using data reserved for model testing) AUC and gain were calculated for each of the models in the jackknife analysis, and for each variable individually.

**Landscape and Behavioral Analyses**

The landscape variables across the smaller area of interest (6 sq. km) were compared using paired two sample t-tests and a Chi-square goodness of fit analysis. In order to analyze the relationships between behavior and landscape, nonparametric and parametric analyses were conducted on the landscape variables and categorical measures of behavior observed in the field. Nonparametric analyses of variance were conducted on the non-normally distributed landscape variables. When significant relationships between the behavior and landscape variables emerged, *post hoc* analyses were used to determine which behaviors showed significant differences in the landscape variable of interest. Chi-square goodness of fit analyses were conducted on the categorical landscape variable land cover/land use class. The relationships between nut cracking behavior and the landscape variables were also investigated using these methods.
Results

Behavioral and Positional Data

The geographic coordinates and behaviors of individual capuchin monkeys were recorded 8,504 times over 24 complete days. The mean point-to-point time interval between observation points was 00:01:20 ($\sigma = 00:04:16$). The mean distance between observation points was 5.75 m ($\sigma = 19.17$ m). When point intervals where the focal individual went out of sight were excluded, the mean time between point observations was 00:01:06 ($\sigma = 00:02:59$) and the mean distance between point observations was 4.91 m ($\sigma = 6.04$ m). The mean daily path length for individuals in our study group was 2017.36 m ($\sigma = 616.99$ m). The mean straight-line distance from the first observation point of the day to the last was 507.31 m ($\sigma = 366.60$ m). The mean sinuosity for individual travel over the entire daily path (actual distance traveled divided by minimum possible distance) was 7.27 ($\sigma = 7.01$).

The capuchin monkeys in our study group spent most of their time foraging (49.88%; 77 h 31 min), followed by time spent locomoting (28.84%; 44 h 49 min), time spent stationary (15.77%; 24 h 30 min), time spent in social interactions (3.99%; 6 h 11 min), and time spent in self care (1.53%; 2 h 22 min). Since the interest of this study was in capuchin movement patterns and use of space, locomotor behavior was prioritized over the other behavioral categories. This may have given an artificially high measure of locomotor behavior in relation to the other categories, since locomotion often occurred concurrently with foraging.

The minimum bounding polygon surrounding all points of observation for our study group was 2.92 square-kilometers in area. The 95% isopleth generated from the
kernel density estimation (typically considered home range) had an area of 1.6 square-kilometers, the 90% isopleth had an area of 1.24 square-kilometers, and the 50% isopleth had an area of 0.29 square-kilometers (Figure 2.8). The 50% contour polygons occupy 1.21% of the 24 square-kilometer area of interest, while the 95% contour polygons occupy 6.67% of this area of interest.

**Fig 2.8** Polygons showing use of space by our study group. Blue points indicate all point observations acquired during our period of study. The outer black polygon indicates the minimum bounding geometry of all observation points. Red polygons indicate the 50% isopleth; green polygons indicate the 90% isopleth and blue polygons indicate the 95% isopleth. Isopleths were generated from a kernel density estimation, which is overlaid on the image. Areas of greater image transparency indicate lower kernel density, while areas of less image transparency indicate higher kernel density.
Results of Landscape Analyses

Visual interpretation was validated in the field through opportunistic and random sampling. The samples were correct 76.79% of the time, with agreement expected by chance 14.19% of the time. The Kappa statistic of field validation data to visual interpretation class was 0.729 ($\sigma_p = 0.066$).

The spectral unmixing analysis resulted in three end member images with values of each image representing percent green vegetation, percent bare soil, and percent shadow respectively (Figure 2.9). The SMA end member images aligned with the panchromatic WorldView-2 satellite image and with the landscape observed in the field. The results of the SMA were found to be of sufficient accuracy for use in the habitat modeling. Of pixels in the spectral unmixing error band, 95% of them had an RMSE of less than 6.5%. At the level of 99.9% of pixels, the RMSE of the spectral unmixing result was less than 11.14%.
Fig 2.9 End member bands resulting from the SMA with lighter shades representing higher percentages of each respective end member in the pixel: green vegetation, shadow, and bare soil.

The NDVI generated from the WorldView-2 satellite image had values ranging from -1.21 to 1 (mean = 0.29; σ = 0.15), with the highest NDVI values representing dense green vegetation in areas of dense fluvial vegetation near seasonal wetlands (Figure 2.10).
Fig 2.10 NDVI image with lighter shades representing higher index values and greater radiation from green vegetation

The Automatic Terrain Extraction process completed in ERDAS LPS software generated a DEM with elevation ranging between 362.7 m and 540.6 m (mean = 396 m, \(\sigma = 25.5\) m). Steep ridges in the monkeys’ home range showed elevations between approximately 400 and 540 m. Figure 2.11 shows a three-dimensional representation of the digital elevation model in the monkeys’ home range.
MaxEnt Habitat Modeling Results

Maximum Entropy habitat model selection began using all observation points, the larger potential area of interest (AOI), and all landscape variables. This complete model had a test AUC value of 0.771 (σ = 0.005), and a test gain of 0.580. This model ranked the distance variables as the most important contributors to model fit with distance to human influence having a permutation importance of 29.8, distance to roads 26.8, and distance to steep ridges 21.5.

To counteract the potentially problematic effects of clumping, models were developed within the smaller area of interest. In addition, subsets of the complete point data set with a minimum of 5, 10, 20, 25 and 30 meters between each point were created for model testing. For the complete model including all landscape variables, model AUC
reached an optimal level at 10 and 25 meters of minimum distance between points, with those two models producing very similar measures of model fit and permutation importance of the landscape variables (Table 2.2). Compared to the fit of the small area of interest model with no minimum distance between occurrence points (AUC = 0.73; σ = 0.006), the reduced models were better fits of the data set.

<table>
<thead>
<tr>
<th>Model Evaluation Parameters for Candidate MaxEnt Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test AUC</td>
</tr>
<tr>
<td>Complete model; large AOI; all points</td>
</tr>
<tr>
<td>Complete model; small AOI; all points</td>
</tr>
<tr>
<td>Complete model; small AOI, 10 m</td>
</tr>
<tr>
<td>Complete model; small AOI, 25 m</td>
</tr>
<tr>
<td>No veg, no soil; small AOI; 10 m</td>
</tr>
<tr>
<td>No veg, no soil; small AOI; 25 m</td>
</tr>
</tbody>
</table>

NDVI and percent green vegetation were strongly correlated (Pearson’s r = 0.6532), and since percent green vegetation generally contributed less to model fit across the models (lower permutation importance; Table 2.3), it was removed. Percent bare soil and percent green vegetation were also strongly correlated (Pearson’s r = -0.6252), but since percent bare soil generally contributed little to the model fit, it was removed.
Jackknife analyses also showed percent bare soil and percent green vegetation to have consistently lower training gain values across all possible models.

The reduced 10 meter minimum distance and 25 meter minimum distance models (percent green vegetation and percent bare soil omitted) were compared. In terms of how individual variables contributed to the model fit, they both were highly similar with almost the same rank order of variable permutation importance (Table 2.3). The differences between rank order occurred between the distance to steep ridges and elevation variables, with the 10 m minimum distance model ranking elevation as more important while the 25 m minimum distance model ranked distance to steep ridges as more important, and also between the variables distance to roads and NDVI. The 10 m minimum distance model ranked NDVI as slightly higher in permutation importance while the 25 m minimum distance model ranked distance to roads as higher in importance to model fit.

Due to the similarity of the models, the 25 m minimum distance reduced model (omitting percent green vegetation and percent bare soil) was selected on the basis of (1) objectively reducing the degree of point clumping to the maximum degree possible and (2) the lower AICc value of this model. Thus, the finalized model was the 25 meter minimum distance model in the small area of interest constructed with the following variables (in order of permutation importance): distance to areas of human influence, distance to steep ridges, elevation, distance to roads, NDVI, land cover/land use class, and percent shadow. Distance to areas of human influence, distance to steep ridges, and elevation were the variables that contributed the most to the fit of the model. The mean
logistic output value of the final model at the observation points, a value that estimates habitat suitability for the study species, was 0.55 (σ = 0.18) (Figure 2.12).

Table 2.3
Permutation Importance of Variables across the Candidate MaxEnt Models

<table>
<thead>
<tr>
<th></th>
<th>Permutation Importance of Landscape Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Complete model; large AOI</td>
</tr>
<tr>
<td>Distance to human influence</td>
<td>29.8</td>
</tr>
<tr>
<td>Distance to steep ridges Elevation</td>
<td>21.5</td>
</tr>
<tr>
<td>Distance to roads</td>
<td>12</td>
</tr>
<tr>
<td>Elevation</td>
<td>26.8</td>
</tr>
<tr>
<td>NDVI</td>
<td>3.9</td>
</tr>
<tr>
<td>Land cover/use class</td>
<td>1.6</td>
</tr>
<tr>
<td>Percent shadow</td>
<td>2.5</td>
</tr>
<tr>
<td>Percent green vegetation</td>
<td>1.5</td>
</tr>
<tr>
<td>Percent bare soil</td>
<td>0.1</td>
</tr>
</tbody>
</table>
**Fig 2.12** (A) Final MaxEnt habitat model with warmer colors representing areas of lower habitat suitability for bearded capuchin monkeys and cooler colors representing higher suitability; (B) All observation points shown as black dots. White dots represent the subset of points used to construct the final model (minimum 25 m distance between points).

**Landscape and Behavior**

The mean values of the continuous landscape variables (i.e., percent dark pixel, distance to human influence, distance to steep ridges, elevation, NDVI, percent bare soil, percent green vegetation) at the points where the monkeys were observed were all significantly different from the mean values of the same landscape variables across the small area of interest (Welch’s two-sample t-test; Table 2.4). The pixels containing the observation points for the monkey group had a lower percentage of bare soil, a lower percentage of shadow, and a higher percentage of green vegetation when compared to the
area of interest (Figure 2.13 – G, H, I). NDVI values were also significantly higher in areas where the monkeys were observed than in the rest of the area of interest (Figure 2.13 – C). The monkeys in this study were, on average, found closer to areas of human influence and closer to roads than all other points in the small area of interest (Figure 2.13 – D, F). The monkeys were found on average farther from steep ridges than the other points in the area of interest (Figure 2.13 - E). The elevation of the observation points was also significantly lower than that of the small area of interest (Figure 2.13 - B). Three land cover classes dominated the points at which the monkeys were observed: dense fluvial vegetation (2), less dense fluvial vegetation (3), and wooded savanna (4), while the area of interest was overwhelmingly dominated by the wooded savanna class (Figure 2.13 - A). The land cover in the area of interest was significantly different from the land cover at the points where the monkeys were observed ($\chi^2 = 10,797.315; \text{df} = 9; p < 0.0001$).
Fig 2.13 Histograms showing the distribution of (A) Land Cover/Land Use, (B) Elevation, (C) NDVI, (D) Distance to Areas of Human Influence, (E) Distance to Steep Ridges, (F) Distance to Roads, (G) Percent Shadow, (H) Percent Bare Soil, and (I) Percent Green Vegetation. Histograms numbered as 1 show the distribution of these variables across the area of interest and histograms numbered as 2 show the distribution of the variables at the observation points.
Prior to analyzing the relationship between landscape variables and behavioral categories using an analysis of variance procedure, a Kolmogorov-Smirnov test of normality was performed to determine whether the continuous landscape variables fit a normal distribution. This normality test was chosen since it performs well with very large sample sizes, such as is the case for the large number of observation points in this study. The following variables were found not to have a normal distribution: distance to steep ridges ($D = 0.0998; p < 2.2e-16$), distance to areas of human influence ($D = 0.2272, p < 2.2e-16$), distance to roads ($D = 0.1608, p < 2.2e-16$), NDVI ($D = 0.055, p < 2.2e-16$), elevation ($D = 0.1404, p < 2.2e-16$), percent shadow ($D = 0.0747, p < 2.2e-16$), and percent green vegetation ($D = 0.0648, p < 2.2e-16$). Percent bare soil was found to have a
normal distribution (D = 0.0141, p = 0.06901). For the non-normally distributed variables, a nonparametric Kruskal-Wallis one-way analysis of variance test was performed to examine the relationship between the variable and behavioral categories. The null hypothesis, that there was no relationship between behavioral category (i.e., foraging, locomoting, stationary, social, and self care) and distance from roads was supported (Kruskal-Wallis $\chi^2 = 2.1553$, df = 4, p = 0.7072). The null hypothesis was rejected and a relationship between behavioral category and landscape was supported for the following landscape variables: distance from areas of human influence (Kruskal-Wallis $\chi^2 = 32.7195$, df = 4, p = 1.363e-06), distance from steep ridges (Kruskal-Wallis $\chi^2 = 16.7043$, df = 4, p = 0.002206), elevation (Kruskal-Wallis $\chi^2 = 31.4838$, df = 4, p = 2.439e-06), NDVI (Kruskal-Wallis $\chi^2 = 17.9467$, df = 4, p = 0.001264), and percent green vegetation (Kruskal-Wallis $\chi^2 = 11.1942$, df = 4, p = 0.02447). No significant relationship between percent bare soil and behavioral category was found using a parametric one-way ANOVA test (F = 0.093; p = 0.985).

Pairwise comparison t-tests were performed post hoc on the landscape variables shown to have a significant relationship with behavior. A Bonferroni correction method was used to counteract the effect of multiple comparisons. Using this method, no significant difference was found between any of the behavioral categories for distance from steep ridges (all categories p $\geq$ 0.09) or percent green vegetation (all categories p $\geq$ 0.32). Significant differences were found in the elevations at which self care behaviors were performed compared to all other behavioral categories (vs foraging: p = 0.00010; vs locomoting p = 0.00138; vs social p = 0.03610; and vs stationary p = 0.00012). Self care occurred on average at lower elevations compared to the other behavioral categories.
\( \bar{x}_{\text{Foraging}} = 373.7487 \text{ m}; \bar{x}_{\text{Locomoting}} = 373.2744 \text{ m}; \bar{x}_{\text{Self Care}} = 370.6 \text{ m}; \bar{x}_{\text{Social}} = 373.5483 \text{ m}; \bar{x}_{\text{Stationary}} = 373.9243 \text{ m}. \) A significant difference was found in the NDVI values at which foraging behaviors were performed compared to locomotion \((p = 0.013)\).

Comparing foraging to locomotion, foraging occurred, on average, in areas of higher NDVI values than did locomotion \((\bar{x}_{\text{Foraging}} = 0.4446706; \bar{x}_{\text{Locomoting}} = 0.4316824\)).

Significant differences were found in the distances from human influence at which self care behaviors occurred compared to foraging and locomotion \((\text{vs foraging: } p = 0.00061; \text{ vs locomoting } p = 0.00798)\) and in the distances from human influence at which monkeys were stationary compared to foraging, locomoting, and self care \((\text{vs foraging: } p = 0.00315; \text{ vs locomoting } p = 1.5e^{-06}; \text{ vs self care } p = 2.9e^{-07})\). Self care behaviors occurred, on average, closer to areas of human influence than foraging and locomotion \((\bar{x}_{\text{Foraging}} = 97.42685 \text{ m}; \bar{x}_{\text{Locomoting}} = 92 \text{ m}; \bar{x}_{\text{Self Care}} = 84.309 \text{ m}).\) Remaining stationary occurred, on average, farther from areas of human influence than foraging, locomoting, and self care \((\bar{x}_{\text{Stationary}} = 124.153 \text{ m}).\)

A significant relationship was found between elevation and nut cracking behavior, with lower average elevations where monkeys were observed to crack nuts \((\text{Kruskal-Wallis } \chi^2 = 18.0004, \text{ df } = 1, p = 2.209e^{-05})\). A significant relationship was also found between NDVI and nut cracking behavior, with higher average NDVI values where monkeys were observed to crack nuts \((\text{Kruskal-Wallis } \chi^2 = 6.487, \text{ df } = 1, p = 0.01087)\). A significant relationship was also found between percent green vegetation and nut cracking behavior, with higher average percent green vegetation values where monkeys were observed to crack nuts \((\text{Kruskal-Wallis } \chi^2 = 5.5145, \text{ df } = 1, p = 0.01886)\). No significant relationships between percent shadow \((\text{Kruskal-Wallis } \chi^2 = 3.6169, \text{ df } = 1, p = \)
distance from areas of human influence (Kruskal-Wallis $\chi^2 = 1.8251$, df = 1, p = 0.1767), or distance from roads (Kruskal-Wallis $\chi^2 = 0.4293$, df = 1, p = 0.5123) and nut cracking behavior were found using a nonparametric Kruskal-Wallis one-way analysis of variance test. No significant relationship between percent bare soil and nut cracking behavior was found using a parametric one-way ANOVA test ($F = 0.003; p = 0.956$).

**Discussion**

Our MaxEnt model demonstrated that the most important landscape characteristics for generating a model of capuchin use of space were distance to areas of human influence (e.g., agriculture, residential areas) and distance to steep ridges, with elevation and distance to roads also of high importance for our study animals. These results are important since the rapid increase in large-plot agricultural use (involving clear-cutting and conversion to monoculture) of the area near our study site and other similar areas in the region may have dramatic effects on the habitat choices of the bearded capuchin monkeys in the near future. Compared to the small area of interest in which our study group was observed, the points at which the monkeys were observed during our study period had lower percentages of bare soil, lower percentages of shadow, and higher percentages of green vegetation. The observation points also were closer to areas of human influence and steep ridges than the rest of the area of interest, and had a lower elevation. Fluvial vegetation and wooded savanna were the land cover classes that were most common at observation points.

The significantly higher NDVI values observed in locations where the monkeys were foraging compared to locomoting may result from the higher abundance of food
resources in locations with more green vegetation. Although self care behaviors were on average recorded at lower elevations compared to the other behavioral categories, this result may represent an artifact of distance between the human observer and the focal animal. At greater distances, self care behaviors become more difficult to detect and the animal may incorrectly be coded as stationary or as some other behavioral category. Self care behaviors also usually occurred closer to areas of human influence than foraging and locomotion while stationarity was more common farther from areas of human influence. The reasons for these differences are not clear, although there may be a relationship between avoidance of open areas typical near human influence and choosing a location to stop and rest. These relationships are not conclusive, however, and their nature should be further investigated in future work.

The unique nut cracking behavior of bearded capuchin monkeys was the aspect of this study group that initially drew researchers to habituate and follow these animals. Previous work has demonstrated that vegetation and terrain are important predictors in finding anvil sites of the bearded capuchin monkeys at our study site (Hinely, 2006). Our study supported this previous finding by demonstrating that not only are anvil sites associated with lower elevations and higher values of green vegetation, but also that using two measures of green vegetation from high spatial resolution satellite imagery, the behavior of nut cracking is significantly associated with green vegetation. The distinction is important since anvil sites may represent locations of prior stone tool use but behavioral measures recorded during this study period indicate present day nut cracking behavior.
This study presents information regarding the use of space of bearded capuchin monkeys. The home range of these animals is relatively small with an area of 1.6 square kilometers. However, compared to the rest of the region, the habitats chosen by these animals show a distinct set of landscape characteristics. These landscape characteristics are similar to the landscape characteristics of areas of industrial agricultural development and expansion, and the conservation of this species and their unique tool use behavior may depend on the protection of habitats vulnerable to development. In our evaluation of the potential impacts of expanding human influence, we draw a distinction between the small subsistence farming in and around the home range of these monkeys and the large plots of industrial farms that are becoming ever more common in the region (Barretto et al., 2013). The former category of agriculture has been present in this area for multiple generations of capuchins with apparently minimal impact on the local nonhuman primate populations (Fragaszy et al., 2004). These small farms often occupy a fraction of the area covered by industrial agricultural plots (Ratter, Ribeiro, & Bridgewater, 1997) and land use practices in our area of study involve periods of nonuse during the dry season, a factor that may have been related to our study group’s proximity to these areas during our study period. In addition, the subsistence farming style does not necessitate the clear cutting of large land areas, and native species of plants have many uses (e.g., building materials, seasonal fruits, fiber, etc.) (Ratter et al., 1997). For these reasons, we believe that these two types of agriculture are likely to differ in their impacts on bearded capuchin monkeys and their unique tool use behavior. While these monkeys were found closer to human influence than other points in our area of interest, these areas of human influence differ dramatically from the potential future land use types caused by an
insurgence of industrial agriculture. Industrial agriculture in this region appears to occur frequently in open areas of low relief (Brannstrom et al., 2008), and these practices coincide with our study group’s preferences for the land cover/land use class wooded savanna, as well as their preference for areas of low elevation.

Incorporating landscape and behavioral data into our characterization of the group’s use of space makes this analysis more meaningful than defining home range by density of spatial use alone or by generating a model of habitat suitability in the area of study based on landscape characteristics without the incorporation of behavioral data. The results of this study may help us to better conserve areas of importance to this unique species through improved understanding of their use of space.
References


CHAPTER 3

MOVEMENT EFFICIENCY IN BEARDED CAPUCHIN MONKEYS:
CONCLUSIONS FROM NATURAL ROUTE OBSERVATIONS AND FIELD EXPERIMENTS

Howard, A.M., Nibbelink, N., Young, L. A., Bernstein, I., Madden, M., Fragaszy, D.M.,
to be submitted to Movement Ecology
Abstract

This study presents a comparison of three models of animal movement and a novel call back method to test the impact of landscape features on the movement decisions of bearded capuchin monkeys (Sapajus libidinosus). We analyzed four days of travel and tested three methods of segmenting the monkeys’ paths for analysis: by temporal stop points, by directional change points, or by both stop points and change points. Dividing routes by stop and change points was most effective in replicating the movement patterns. In modeling the monkeys’ movement, we generated a surface of resistance to movement by calculating the inverse of a MaxEnt habitat suitability model of our study group’s use of space over the study period. The movements and spatial decisions of the monkeys were modeled using a straight line path model which connected the start and end points of each segment as a straight line, a minimum resistance model which connected the start and end points through the path of least resistance, and a landscape perceiving path model, which connected the start and end points by moving a simulated monkey toward the goal using the pixels of least resistance in its immediate surroundings. The travel of capuchin monkeys resembled straight line travel in resistance values (mean resistance, NRMSE = 5.49%), but their movement was not linear. We conclude that capuchin monkeys move in zones of low resistance but do not conform to minimum resistance patterns. A field experiment demonstrated that when travel goals were manipulated by the researchers, the monkeys increased the linearity of their movements and resistances they incurred in travel also increased. These results indicate that for a limited, high quality resource, capuchin monkeys in our study group are more sensitive to movement linearity. This raises the question of whether their natural
movements would vary in linearity with varying resource quantity or quality. We present the advantages and challenges of the call back method of experimental analysis of animal movement and we conclude that future analyses of movement efficiency should include some consideration of the landscape context in which movement occurs.

Keywords: Spatial cognition, efficiency, spatial decision making, Euclidean cognitive map, animal movement, field experiment, capuchin monkey, *Sapajus libidinosus*
Introduction

The localization and exploitation of resources are essential to the survival of mobile animals. These activities may present substantial cognitive challenges for nonhuman primates ranging in natural environments (Clutton-Brock & Harvey, 1980). It has been suggested that selection pressure imposed by foraging requirements was critical in the selection of greater cognitive ability for nonhuman primates (Milton, 1981, 1988). However, the mechanisms by which nonhuman primates remember and revisit the locations of out of sight 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 behavioral ecology of these animals. Two models of spatial cognition have dominated the study of nonhuman primate behavior, 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, 2007b; Valero & Byrne, 2007). These models differ in 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 include, however, metric information regarding the distances and directions between mapped points. Topological maps may reflect limitations on movement imposed by the environment, such as habitat connectivity or energetic demand of moving over landscapes (Di Fiore & Suarez, 2007). 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.

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 traveling between two points in the environment (Di Fiore & Suarez, 2007). Certainly then, it would be useful for understanding primate spatial cognition to operationally define travel efficiency in a way that reflects the ecological variables to which these animals are sensitive when choosing their paths.

The challenges of defining the relevant currency of movement efficiency have long belabored studies of optimal foraging (Nest & Moore, 2012; Pierce & Ollason, 1987; Pyke, Pulliam, & Charnov, 1977). Movement efficiency continues to be relevant to the field of ecology today as it relates to the role of foraging decisions in adaptation and competition. Defining movement efficiency is also relevant to the field of animal cognition, as it guides our evaluation of animals’ knowledge of their environment.

Since a straight line is the shortest distance between two points, we might expect that efficient movement choices would consist largely of straight line travel. Indeed, a large number of studies have based their evaluations of animals’ spatial knowledge on the
degree to which an animal’s path was linear or sinuous (Cunningham & Janson, 2007; Janson, 1998; Noser & Byrne, 2007a; Pochron, 2001; Presotto & Izar, 2010; Valero & Byrne, 2007). However, landscape features are likely to impact the costs of travel chosen by animals (Janson & Byrne, 2007). Therefore, it seems that animals traveling in heterogeneous environments may be sensitive to the effects of landscape. The impact of these landscape variables may be that travel in a straight line is not the most efficient in terms of energy expenditure, predator avoidance, or maximizing use of preferred habitats. The studies investigating the paths of nonhuman primates in natural environments have typically not taken into account the landscape features underlying these paths. 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 in 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). This study will model efficient movement choices using a landscape and Euclidean distance based currencies.
Another challenge in evaluating the efficiency of a path is how to best to divide the path into segments for analysis. After all, considering energetic cost alone, the least energetically costly movement strategy would be to remain stationary. However, we know that in order to find resources or mates, or to evade predators, movement is necessary for most animals. Paths may be analyzed in their entirety, such as from the beginning to the end of each day. However, some animals return to the same sleeping sites night after night, while other animals reuse a limited number of sleeping sites in their home range. In these cases, had the sleeping site been the travel goal of the animal (the location to which it would attempt to achieve maximal travel efficiency), we would not predict much movement at all on the part of the study animal. Instead, it is assumed that intermediate locations comprise goals for the traveling animal and that these locations may provide food resources, water, or protection from the elements and/or predators for the traveling animal. The challenge then is to define what locations are travel goals for a moving animal among all the locations they visit. In studying goal-directed behavior and the efficiency of movement of animals, the location where an animal arrived cannot be considered to have been its a priori goal just because it arrived there. Thus, identifying an animal’s goal prior to its arrival presents a challenge.

Travel goals have been defined as locations in which animals feed (e.g., Janson & Di Bitetti, 1997; Normand & Boesch, 2009), assuming that when resources are clumped, travel is directed toward these sites. Other studies have used locations at which animals stop for a period of time to define travel goals (Bates & Byrne, 2009; Valero & Byrne, 2007). More recently, points of directional change have been incorporated as a method of evaluating goal-directed travel (Asensio & Brockelman, 2011; Byrne et al., 2009; De...
Raad, 2012; Joly & Zimmermann, 2011). These methods attempt to define the travel goals of naturally moving animals post hoc, using heuristics that serve as a proxy.

One method of dealing with the challenge of determining an animal’s travel goals a priori is through implementing experimental techniques in the field to manipulate its goals. 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) moved toward feeding platforms using straight line travel from farther distances than predicted by any random models of search. These results suggest use of memory of the location of platforms in the monkeys’ spatial decisions. 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 (to both nearby and far feeding platforms in sequence) in their decisions to travel to the farther platform.

Our study aimed to evaluate the nature of goal-directed travel and spatial decision making in bearded capuchin monkeys. We developed and, through comparisons to actual movement observations, tested a series of models of route choice which vary in the extent to which landscape variables determine their structure. Comparable to the linearity-based evaluations of Euclidean cognitive maps that have dominated the primate literature, we tested a minimum resistance path model. This model considers landscape resistance as well as distance, and plans the ideal path based on comprehensive spatial knowledge of the landscape between the animal and its goal. We also tested 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, this study focuses on refining the way in which we evaluate movement efficiency and the role of landscape and linearity in travel choices. We also evaluate methods for dividing the movement of capuchin monkeys into segments for analysis. Temporal and spatial methods of segmenting travel are tested for each of the models of capuchin monkey movement. These methodological reconsiderations allow for more in-depth analyses of the relationship between landscape and cognitive mapping in previously studied species, especially those ranging in heterogeneous environments.

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.
Method

Movement Observations

The subjects of this study were a group of bearded capuchin monkeys (*Sapajus libidinosus*) in northeastern Brazil (Piauí state) (Figure 3.1). Observations of the monkeys’ naturally occurring routes were conducted during the months of May, June, and July of 2013 (n = 27 days; n = 8,611 points). Data collection consisted of following a single focal animal in the monkey group and recording its location and activity. For each complete day of data collection, the focal individual was chosen at random among all (n=8) adult monkeys in the study group. The capuchin monkeys in this study were habituated to human presence and their behavior was not apparently altered by our presence. The human observer recorded geographic coordinates of the focal individual’s location for approximately 9.5 hours each day 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 semi-continuously, 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. Compared to the technique of using a handheld GPS unit and estimating distance and direction between the observer and the focal individual, this method allowed for more controlled location observations when the observer was at a distance from the focal monkey. Coordinates recorded using the tablet computer were
uploaded and converted from CSV to shapefiles in ArcGIS software (version 10.1) using the World Geodetic System 1984 datum and the Universal Transverse Mercator projection, Zone 23 S.

Fig 3.1 Map of Brazil showing the location of Piauí state and our study site

**Segmentation of Movement**

We previously demonstrated that dawn-to-dusk analyses of the paths of bearded capuchin monkeys in this study site are not effective in describing the full extent of the variability in their travel (Howard, Bernardes, & Presotto, 2011). This is because the monkeys in our study site frequently return to the same or nearby sleeping sites at the end of each day, thus analyses of their travel from start to finish alone does not fully describe the complexity of their spatial choices. For the purposes of our analyses, the travel paths analyzed in this study were divided into smaller units of travel using both spatial and temporal methods. The monkeys’ travel was segmented using both spatial and temporal methods. We used the Change Point Test (Byrne et al., 2009) to evaluate the focal individual’s travel for points of directional change. This test evaluates path vectors prior
to and following the point in question to determine whether there was a significant change in direction, and evaluates travel within a specified backward-looking window of points (q). The value of q specifies the sensitivity/power of the test, and we followed the methods recommended by Byrne and colleagues (2009) for selecting an appropriate value of 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. We chose an alpha level of 0.01 due to the dense spatial nature of our observation points and the need to differentiate noise from actual change points. Also, Byrne et al. (2009) point out that due to the multiple comparisons nature of the change point test, higher degrees of selectivity may be appropriate. Comparing q = 1 through q = 10 for each path, we chose q = 5 as this value maximized the number of change points detected for each day’s path while also failing to “look around the corner” and overshoot the change point as higher values of q have the tendency to do (Byrne et al., 2009). The path of May 16 showed a different pattern of response to the Change Point Test than the other three days we examined (Figure 3.2). This date showed the largest number of change points at q = 9 (Change Points = 12) and a lower number of change points at q = 5 (Change Points = 8). For consistency of treatment across the daily paths, it was important to use the same q value for all paths analyzed. Examining the spatial distribution of change points detected for May 16 with q = 5, q = 6, q = 9, and q = 10 (the values of q detecting the highest number of change points), it was apparent that the test was relatively robust to these values of q (Figure 3.3), and that consistency of treatment across the routes to be analyzed should be prioritized. Therefore, the change points detected for q = 5 were used for all 4 days of
travel analyzed in this study. The change points for the other dates at q = 5 are depicted in Figure 3.4.

**Fig 3.2** Numbers of Change Points as found by the Change Point Test under q = 1 through q = 10
Fig 3.3 Change Points Detected in the May 16 path with $q = 5$, $q = 6$, $q = 9$, and $q = 10$. 
In addition to analyzing spatial segments of the capuchins’ travel paths, we analyzed the temporal segments of their travel, dividing paths into segments at points where the focal animal stopped for long periods of time. 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 four minutes or longer (Valero & Byrne, 2007),
ten minutes or longer (Presotto & Izar, 2010), or twenty minutes or longer (Bates & Byrne, 2009). We chose the criterion for defining a stop point as a function of the distribution of elapsed times the study group spent in any given location.

For the four days of travel examined more closely in this study, the paths were segmented in three different ways: by stop points alone, by change points alone, and by change points and stop points together. If two consecutive stop points or change points fell within 5 meters of each other, the second point was deleted and segments were calculated only to the first of the two adjacent points. This process was executed for stop points alone, change points alone, and for stop points and change points together.

**Modeling Travel Paths**

We compared actual monkey travel to a series of models representing possible strategies for movement: a straight-line path model, a minimum resistance path model, and the landscape perceiving path model. The models were compared using the three methods of segmenting travel routes, such that for each model, three variants existed: the change points variant, the stop points variant, and the change and stop points variant.

A MaxEnt model of the use of space of bearded capuchin monkeys in our study group was calculated using points where the monkeys were observed to travel as well as the following landscape variables: 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) (See Chapter 2). MaxEnt model values in their logistic form represent the suitability of the habitat for the study animal (Phillips & Dudík, 2008). Therefore, we
used the inverse of these values (= logistic model output/1) as a layer of landscape resistance to capuchin monkey movement. In this way, the landscape preferences of the capuchin monkeys in this study were represented continuously across their home range and the resistance to movement was not determined subjectively, but rather through a mathematical representation of the preferences of our study animal during the period of observation. This method addresses recently published concerns with generating path models based on resistance layers constructed from expert opinion (Sawyer, Epps, & Brashares, 2011). The inverse MaxEnt resistance layer served as the input to the models of capuchin monkey route choice. Through this method areas of steep ridges, bare soil, and wetland areas with standing water were shown to be areas of very high resistance to capuchin movement (See Figure 2.12).

Three models of capuchin route choice were developed to test the extent to which capuchin monkeys use landscape features to decide on their paths between points in their environment. The methods for modeling capuchin movement generated paths of differing geometry types. In order to maintain consistency in the spatial resolution of our modeling and to compare the model results across categories, all models were submitted to a series of conversions prior to comparing their parameters. Points were converted to polylines, which were then converted to rasters, and then back to points again. This resulted in every pixel underlying the capuchins’ path 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 that the model in question yielded.
The straight-line model consisted of straight lines connecting the beginning and end points of each segment. These straight-line paths were generated in ArcGIS first as polylines, then converted to rasters, and then converted from rasters to points. Resistance values from the inverse MaxEnt resistance layer were extracted to the points that made up the straight line path, and mean resistance values, total cumulative resistance values, and resistance per meter values were calculated for each straight line path segment. The sinuosity (a ratio of the modeled distance to the straight line distance) of the straight line model was inherently 1 for every segment.

For both the start and end points of every travel segment, Cost Distance rasters were calculated using ArcGIS 10.1. The Cost Distance Tool in ArcGIS determines the least accumulated travel resistance possible between all pixels in an image and the source (i.e., the pixel containing the start or end point of the segment). The resistance values calculated by the Cost Distance Tool are based on distance between the pixel and the source (via the least resistance series of pixels in between) as well as the values of the pixels of a resistance layer, which, in this study, resulted from a quantitative estimate of our study group’s use of space and preferences regarding landscape features. ESRI (2012) describes the generation of the cost distance raster as an iterative process beginning with the cells closest to the pixels of interest and continuing outward. ArcGIS software was used to calculate a minimum cumulative resistance path between the start and end points of each segment for each of the four days. This minimum cumulative resistance path, using the inverse MaxEnt model as its input, is the path by which the traveling animal would maximize its use of spaces containing desirable landscape features while traveling between the start and end points of that segment. If we consider
that 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 traveling animal to minimize its use of undesirable habitats and maximize its use of desirable spaces between these two points. The minimum cumulative resistance path minimizes cumulative travel resistance by considering every possible sequence of pixels in the environment through which movement is possible, and choosing the sequence of pixels that results in least cumulative resistance.

The landscape perceiving model of travel was developed using the NetLogo modeling environment (version 5.0.4), a program for simulating natural and social phenomena. A modeled 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 is available in Appendix A and the ODD (Overview, Design Concepts, and Details) description of the model recommended by Grimm et al. (2010) is available in Appendix B. The cost-distance surface across which the modeled monkey moved was derived from the previously described ArcGIS cost distance analysis, and the values of this image are a result of combining resistance and distance for each cell in the environment relative to a given destination. The cost-distance surface used in each model run is specific to the location of the monkey’s goal for that travel segment. The modeled monkey in the landscape perceiving model was programmed to travel from its current pixel to the neighboring pixel of minimum cost distance (considering its eight neighbors). It repeated this process until arriving at the location of the goal. The path resulting from this program was exported to a CSV file and the coordinates of the path were converted to a point shapefile in ArcGIS software. The point shapefile was converted to polyline,
the polyline was converted to raster, and the raster was converted to a point shapefile in order to capture every cell in which the model predicted travel to occur and to insure consistency of comparison across the different movement models. Resistance values were extracted to the points and mean and cumulative resistances were calculated for each travel segment, as well as resistance per meter. In contrast to the minimum resistance path model, the landscape perceiving model considers only the environment immediately surrounding the monkey for each movement step.

The landscape perceiving model of monkey travel was tested using independent reimplementation of submodels as recommended by Railsback and Grimm (2012). Using this method, code was written such that the possible pixel values from which the monkey could choose and its subsequent choice were written to an output text file. The chosen pixel value was verified from the text file to be the lowest of the eight neighbors and it was also verified that the monkey considered the eight pixels nearest to it when choosing where to move. This verification was conducted across multiple locations in the NetLogo modeling environment, in varying scenarios of cost, distance, and locations of the monkey and the goal. Initial independent reimplementation revealed that in a turtle context (i.e., in the context of sending commands to the mobile agent or “turtle”, in this case the monkey), considering a radius of cells around the monkey resulted in $4 \times radius$ number of neighboring cells (a Von Neumann neighborhood) to be considered in each choice. Subsequent model corrections used the “neighbor” command of NetLogo, verified to consider the eight cells closest to the monkey itself. The commands, annotations, and comments used to reimplement and test the model are included in the model’s code in Appendix A.
Once cost-distance rasters had been calculated for the both the beginning and the end points of each segment, these rasters were combined using corridor analysis in ArcGIS. The Corridor tool generates a raster in which the pixel values represent the sum of the resistances for two input rasters (i.e., the cost-distance raster from the beginning and the cost-distance raster from the end of each segment). The sum of the two rasters identifies for each pixel the least possible cumulative resistance that could have been incurred to travel between the beginning and end of each analyzed segment using a path that included that particular pixel. Pixels far from both the beginning and end points of each segment generally have high cumulative resistance values since traveling from the segment’s start to the segment’s end by way of that distant pixel would usually incur more cumulative resistance than traveling between those two points by way of pixels near the start and/or end points. The function of the corridor image was to compare the resistance values of the minimum cumulative resistance path to the resistance values of other possible paths through the landscape. In this way, we could better understand how the minimum resistance path ranks compared to other possible low resistance paths between the start and end points of the segment.

Using the corridor image for each travel segment, a percentile was calculated for the cumulative resistance values of the monkeys’ actual paths and of their modeled paths (i.e., the minimum resistance path, the straight line path, and the landscape perceiving path). Comparing the resistance values of these paths to the resistance values of the pixels of the entire resistance raster (6 square km) 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 kilometers 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. These buffers were used to clip the corridor image, and the size of the buffer was specific to the travel segment being analyzed. All the segment points were buffered by a distance equal to the actual distance traveled 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 traveled, the percent rank of the mean corridor value was calculated 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 Watts, Model # PMP53IN) and played on repeat. The advertised projection range of this device is up to one mile, 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, during which approximately 500 g of diced bananas were scattered over an area of approximately 100 square meters by a human experimenter. Prior to test,
the monkeys in the study group were trained to associate the auditory cue with the dispersal of diced bananas in ten training sessions. These training sessions occurred in an outdoor laboratory area, 30 meters in diameter, in which the animals have 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 contains natural and man-made anvil stones and lies adjacent to a vertical ridge 415 meters in height. The training sessions occurred when the majority of the group was present in the outdoor laboratory area. Training sessions resulted in some, but not all, members of the group receiving diced bananas. The alpha male, alpha female, and juveniles appeared to retrieve the largest proportion of the provisioned food with notable other adult individuals (male and female) competing for food as well. Contest competition was 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 naturally. A human observer followed a focal individual away from the outdoor laboratory and, upon traveling 100 to 200 meters from the outdoor laboratory, the observer communicated with the experimenter at the laboratory using handheld 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 consistently follow. Other group members, although they moved toward the auditory cue, did so at a speed that allowed the human observer to consistently record their location and update it as the individual moved. Trials were terminated when the focal individual had arrived at the site of the auditory cue, or after a minimum period of ten minutes in which the focal individual had not moved toward the auditory cue.

After succeeding in 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 as on the results of a preliminary model of our study group’s movement preferences. Using the methods presented in chapter 2 of this dissertation, a provisional version of a MaxEnt model of capuchin habitat preferences was used to generate a resistance surface for their movement (Figure 3.5). This resistance surface was used in the field for choosing areas to conduct the experiment outside of the outdoor laboratory. We chose to conduct these trials in locations where the animals would pass near a natural barrier to movement (i.e., an area 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 experimenter 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.
**Fig 3.5** Provisional MaxEnt model of capuchin habitat used to select appropriate locations for experimental trials. Warm colors represent areas of higher resistance and lower MaxEnt habitat suitability. Cooler colors represent lower resistance and higher MaxEnt habitat suitability.

From the 12 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: the straight line path model, the minimum resistance travel model, and the landscape perceiving model of travel. 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.
Results

Movement Observations

Of all the naturally occurring daily paths we observed, 15% (4 days) were set aside for in-depth analysis and modeling of capuchin spatial decision making. In selecting the routes to be analyzed, we prioritized days in which the focal animal went out of sight for the least amount of time. These days coincided with days in 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 analyzed the path of a former alpha male, Mansinho, on May 16, 2013 and May 21, 2013. We analyzed the path of the contemporaneous alpha male, Jatoba, on two dates, June 13 and July 17, 2013. These observation dates had the following total times that the focal individual was out of sight of the human observer: May 16, 0 minutes; May 21, 9 minutes; June 13, 17 minutes; and July 17, 15 minutes.

Segmentation of Movement

In order to analyze how landscape features impact capuchin monkeys’ movements toward a goal, we needed to first settle on one method of segmenting their observed movements into logical sections. The two methods of dividing their travel gave three options for segmentation: by stop points alone, by change points alone, or by both stop and change points together. Segmentation of the routes by all three methods for each of the four days analyzed in this study resulted in 147 natural path segments to be analyzed. 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. Stop and change
points were combined and when those points fell within 5 meters of one another, only the first point was used, resulting in an average of 17.25 change and stop points per day. For the four days analyzed, change points and stop points fell within 5 meters of one another 21 times and 3 points were classified as both stop points and change points. Larger numbers of points by which to divide travel into segments resulted in longer overall travel distance for each model. Therefore, the stop point plus change point method of path segmentation resulted in the longest average modeled path lengths. Both the points where the monkey changed its direction significantly and the points where it stopped for an extended period of time may have been travel goals for the monkey. We defined stop points as pauses longer than the 99th percentile in duration (≥ 8.01 min) since the distribution of times elapsed at a single location demonstrated an apparent natural break at the 99th percentile (Figure 3.6). The mean elapsed time at a single location was 0.97 minutes (SD = 1.90 min).
Examining the modeling results for the three segmentation methods, we compared the actual travel to modeled travel. The mean and cumulative resistances of each path segment (modeled and actual) were calculated by averaging or summing the resistance values of the pixels through which the path passed. Resistance per meter was also calculated by summing the resistance values of the paths’ pixels and dividing this value by the length of the segment. The root mean square error (RMSE) of the path models was calculated for mean and cumulative resistance, as well as for resistance per meter and sinuosity (Table 3.1). Normalized RMSE (NRMSE) of each parameter was also calculated by dividing the RMSE by the observed range of the parameter (NRMSE =

**Fig 3.6.** Distribution of Elapsed Time at Observation Points; Vertical line indicates the 99\textsuperscript{th} percentile of elapsed time (8.01 min)
RMSE/(\text{max}_{\text{obs}} - \text{min}_{\text{obs}})). NRMSE is frequently expressed as a percentage and allows for comparison between parameters using different scales. Comparing the modeled routes visually, the stop points plus change points segmentation method and the change points only segmentation method performed better than the stop points alone method. Considering NRMSE, the stop points plus change points segmentation method resulted in a higher error in five of the nine parameter cases and a lower error in four of the nine parameter cases. Looking at the straight line model alone, the model with the least error for both methods, the change points plus stop points resulted in less error. Considering that both places where the monkeys changed direction and places where they stop seem to be plausible goal sites, we determined that the change points and the stop points segmentation method was the most descriptive for our analyses.
When the monkeys’ travel was segmented by both stop points and change points, no model fit the actual travel patterns completely. However, 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, \( t(68) = 0.1848, p = 0.8539 \). Significant differences did exist in mean resistance between actual travel and the minimum resistance path model, \( t(68) = 5.6416, p = 3.553 \times 10^{-7} \), 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) = 3.148, p = 0.002441, 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: the minimum resistance model, t(68) = 5.1737, p = 2.203 x 10^{-6}, the landscape perceiving model, t(68) = 4.8343, p = 7.971 x 10^{-6}, and the straight line model of travel, t(68) = 3.3699, p = 0.001243. Actual travel had higher cumulative resistance values than all models. There were also significant differences in the sinuosity of actual travel when compared to all travel models: the minimum resistance model, t(68) = 6.1413, p = 4.808 x 10^{-8}, the landscape perceiving model, t(68) = 4.1659, p = 8.953 x 10^{-5}, and the straight line model of travel, t(68) = 8.5438, p = 2.258 x 10^{-12}. Actual travel was less linear than any of the models of travel. Finally, the resistance per meter was significantly different comparing actual travel to all models of travel, the minimum resistance model, t(68) = 8.377, p = 4.531 x 10-12, the landscape perceiving model, t(68) = 3.7378, p = 0.0003827, and the straight line model of travel, t(68) = -5.5544, p = 5.013 x 10^{-7}. The minimum resistance and landscape perceiving models of travel had significantly lower resistance per meter than actual travel. The resistance per meter of the straight line model of travel was significantly higher than actual travel, however.

Travel segmented by change points alone and by stop points alone showed a similar pattern to that of the stop points/change points segmentation method. That is, the mean resistance of straight line travel was similar to the mean resistance of the actual observed natural travel for these other segmentation methods. There was no significant difference between the mean resistance of the straight line model of travel and the actual
travel for either the change points segmentation method, $t(57) = 0.4845, p = 0.6299$, or the stop points segmentation method, $t(19) = -1.4625, p = 0.16$.

Comparing not just the models’ central tendencies, but their distribution of errors in comparison to actual travel, RMSE was calculated for each of the parameters of travel for each model using the stop points and change points segmentation method (Table 3.2). For capuchin travel segmented by both stop points and change points, the RMSE and NRMSE of the parameters total cumulative resistance, mean resistance, and resistance per meter 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. Figure 3.7 shows boxplots of the distribution of the various model parameters and the same parameters for actual capuchin monkey travel.
Table 3.2

*Models of Capuchin Travel Compared with Actual Travel Segmented by Stop Points and Change Points*

<table>
<thead>
<tr>
<th>Models</th>
<th>Total Cumulative Resistance</th>
<th>Mean Resistance</th>
<th>Resistance per Meter</th>
<th>Sinuosity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>RMSE</td>
<td>NRMSE</td>
<td>Mean</td>
</tr>
<tr>
<td>Actual</td>
<td>142.81</td>
<td>N/A</td>
<td>N/A</td>
<td>2.39</td>
</tr>
<tr>
<td>Min. Res. Land.</td>
<td>74.45</td>
<td>128.63</td>
<td>11.61%</td>
<td>2.01</td>
</tr>
<tr>
<td>Perc Straight Line</td>
<td>98.44</td>
<td>87.74</td>
<td>7.92%</td>
<td>2.20</td>
</tr>
<tr>
<td></td>
<td>116.11</td>
<td>70.60</td>
<td>6.37%</td>
<td>2.38</td>
</tr>
</tbody>
</table>
Considering total cumulative resistance per segment, mean resistance (per pixel visited), and resistance per meter, the resistance incurred by the monkeys’ actual travel was closest to that of traveling 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 (Figure 3.7). 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 of travel.

Kolmogorov-Smirnov tests of goodness of fit of model parameters to the parameters of actual travel were conducted for mean resistance, total cumulative resistance, resistance per meter, and linearity for the stop and change points segments. Significant differences were found between actual travel and the minimum resistance paths for total cumulative resistance ($d = 0.3188; p = 0.001675$), mean resistance ($d = 0.2754; p = 0.01038$), resistance per meter ($d = 0.4638, p = 4.514 \times 10^{-7}$) and sinuosity ($d = 0.5942, p = 5.255 \times 10^{-11}$). For the landscape perceiving model and the straight line path model, significant differences from actual travel were detected in the distributions of resistance per meter (landscape perceiving: $d = 0.2609, p = 0.01791$; straight line: $d = 0.2609, p = 0.01791$) and linearity (landscape perceiving: $d = 0.4203, p = 7.614 \times 10^{-6}$; straight line: $d = 1, p < 2.2 \times 10^{-16}$). No significant differences were detected, however, between actual travel and the landscape perceiving model or between actual travel and
the straight line path model for mean resistance (landscape perceiving: $d = 0.1449, p = 0.4662$; straight line: $d = 0.0725, p = 0.9942$).

If we segment travel less frequently, the deviation from the straight line model becomes even more apparent. The RMSE of the mean resistance, total cumulative

Fig 3.7 Boxplots of mean resistance, resistance per meter, total resistance, and sinuosity of the models of capuchin travel and actual naturally occurring travel paths.
resistance, and resistance per meter of the straight line paths segmented by stop points alone is higher than the RMSE of those parameters for travel segmented by stop and change points (See Table 3.1). Segmenting the paths by the change points alone results in RMSE values similar, although lower, than those of the paths segmented by both stop points and change points. The straight line paths segmented by stop points alone also lie spatially distant from the actual paths.

Figures 3.8 through 3.11 show the actual and modeled travel paths for the four days of travel analyzed in this study. Points at which the monkeys were observed are shown in dark red and a corresponding line of actual travel is also shown in dark red. The models shown in the maps are those generated by dividing travel by stop and change points. All models of travel lie in relative close proximity to the actual travel paths. The minimum resistance paths and landscape resistance paths appear visually similar in many places and their mean and total resistance values and resistance per meter values are similar. The straight line model paths are the most visually dissimilar from the actual paths and from the other models of travel. For June 13 in particular (Figure 3.10), all the modeled paths lie very close to one another in space.
Fig 3.8 Actual and modeled paths and observation points for May 16, 2013
Fig 3.9 Actual and modeled paths and observation points for May 21, 2013
Fig 3.10 Actual and modeled paths and observation points for June 13, 2013
Fig 3.11 Actual and modeled paths and observation points for July 17, 2013
Comparing the monkeys’ actual paths to not only the minimum resistance path but to other possible paths through the environment, we see that the actual paths are of low resistance. A portion of the corridor layer for each segment was clipped from the larger corridor image file (6 square km). The corridor layer itself consists of pixel values representing the minimum possible resistance incurred passing through the pixel in question while traveling 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 m to 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. The mean of the actual path’s corridor resistance values was calculated and this was compared to the distribution of values of the corridor clip. An inclusive percent rank of the segment’s mean corridor resistance values was calculated for each segment. The inclusive percent rank is the relative rank of a given value within a dataset, 0 and 1 inclusive, expressed as a percentage value. For example, in a dataset of three values: 4, 6, and 8, the value 4 has a percent rank of 0, 6 of 0.5, and 8 of 1. For the four days of capuchin travel analyzed in this study and segmented by the stop points and change points, the monkeys’ actual travel paths had a mean percent rank of 0.0324, or 3.24%. This meant that, on average, 96.76% of pixels had a higher travel resistance than the ones visited by the monkeys. The percent rank of the observed travel segments ranged between 0.301 and 0.0009. Figure 3.12
shows a boxplot of the distribution of percent ranks of corridor resistances for all the observed segments of capuchin monkey travel.

Figure 3.12 Boxplot of the percent ranks of mean corridor resistance values for the stop and change points segments of capuchin actual travel.

Figure 3.13 shows the actual path from July 17 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 and below of corridor resistance values, the image also depicts the minimum resistance path, or the lowest possible corridor resistance, as the 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.

**Fig 3.13** Actual path from July 17, 2013 with corridor resistance values overlaid on WorldView-2 satellite imagery; Corridor resistance values range from the minimum resistance path (black line) to slightly higher resistances (green) to the tenth percentile of possible path resistances (red-orange).

**Experimental Analysis of Route Choice**

The responses of our study group to the novel auditory stimulus in this 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 indicated that
there exists some upper limit to the influence this stimulus has on changing the travel
goal of the study group, and that calls are not effective if the stimulus is initiated too far
from the monkey group or if the individual is 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.

In some trials, the focal individual moved in the direction of the auditory cue, but
ultimately resumed movement in their original direction, rejoining their 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 traveling 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 center of the outdoor laboratory). In this example, the monkey did not
move toward the auditory cue and continued to forage in the same location beside a low
ranking adult female while other members of the group moved toward 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 (common name: jatobá de
porco) 150 m from the outdoor laboratory. While most of the group moved to the outdoor
laboratory in response to the auditory cue, the focal individual did not change its location.
The first attempt at conducting a trial outside the outdoor laboratory was unsuccessful. This trial was conducted when the monkey group was traveling east along the southern border of a wetland area. The experimenter was placed on the northern border, 203 m from the location of the group and the auditory cue was initiated. Prior to this attempt, the animals had not experienced the auditory cue in any other location in their home range outside of the outdoor laboratory. After the call was initiated, the group crossed over the wetland at a fence line where the ground was dry. After having crossed over, the group did not move west in the direction of the auditory cue, but continued moving east. The focal individual, an adult female, moved west toward the auditory cue to a minimum of 130 m from the location of the experimenter, and then continued moving east, rejoining the group. After this failed trial, a training session was conducted from the middle of the group in an area outside of the outdoor laboratory. Future trials outside the outdoor laboratory were successful in calling the monkeys to the auditory cue.

The movement of the monkeys in the experiments was compared to the models of capuchin travel: the minimum resistance model, the landscape perceiving model, and the straight-line path model. The movement parameters for each experiment and the models of movement are shown in Table 3.3. Instead of segmenting the paths of the monkeys by change points or stop points, 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. 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 are high for the resistance related parameters of travel, ranging from 28.56 to 34.08 percent error in those models. In contrast, the NRMSE values of the straight-line path model are low, with values ranging from 1.14 to 4.83 percent error for the resistance-related parameters of travel (Table 3.4). The sinuosity of travel ranges from below 7 percent error (NRMSE = 6.80) for the minimum resistance model to under 1 percent error for the straight line path model (NRMSE = 0.62) (Table 3.4).

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 (1.21) ranked between the mean sinuosity of the minimum resistance model paths (1.14) and the sinuosity of the landscape perceiving model paths (1.22). This is in contrast with the actual path sinuosity of the naturally occurring travel of capuchin monkeys (average across all segmentation methods, 1.40) which was higher than the mean sinuosity of both the minimum resistance and landscape perceiving models of travel (1.09 and 1.16, respectively). 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 a mean length of 160.26 m (SD = 224.53 m) while experimental trials had a mean length of 111.27 m (SD = 71.59 m). The mean sinuosity of natural travel segments equal to or shorter than 111.27 was 1.29.
Table 3.3

Parameters of the Actual and Modeled Travel Paths in Experimental Trials

<table>
<thead>
<tr>
<th>Date</th>
<th>Actual Path</th>
<th>Minimum Resistance Path</th>
<th>Straight Line Path</th>
<th>Landscape Perceiving Path</th>
</tr>
</thead>
<tbody>
<tr>
<td>7/1/13</td>
<td>1.66</td>
<td>112.5</td>
<td>0.84</td>
<td>1.19</td>
</tr>
<tr>
<td></td>
<td>7/3/13</td>
<td>207.4</td>
<td>3</td>
<td>0.89</td>
</tr>
<tr>
<td>7/19/13</td>
<td>36.86</td>
<td>663.4</td>
<td>19.25</td>
<td>1.09</td>
</tr>
<tr>
<td>7/22/13</td>
<td>2.24</td>
<td>111.2</td>
<td>1.36</td>
<td>1.16</td>
</tr>
<tr>
<td>7/24/13</td>
<td>2.23</td>
<td>111.2</td>
<td>1.27</td>
<td>1.18</td>
</tr>
<tr>
<td>7/25/13</td>
<td>2.54</td>
<td>78.70</td>
<td>1.50</td>
<td>1.07</td>
</tr>
</tbody>
</table>

Note: July 19, July 24, and July 25 indicate experiments that occurred outside the outdoor laboratory, in other areas of the monkeys’ home range. Mean Resis., RPM, and Sin. are abbreviations for resistance, resistance per meter, and sinuosity, respectively.

Table 3.4

Models of Capuchin Travel Compared with Actual Travel in Experimental Trials

<table>
<thead>
<tr>
<th>Model</th>
<th>Total Cumulative Resistance</th>
<th>Mean Resistance</th>
<th>Resistance per Meter</th>
<th>Sinuosity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>RMSE</td>
<td>NRMSE</td>
<td>Mean</td>
</tr>
<tr>
<td>Actual</td>
<td>223.89</td>
<td>N/A</td>
<td>N/A</td>
<td>7.88</td>
</tr>
<tr>
<td>Minimum Resistance Path</td>
<td>106.21</td>
<td>199.04</td>
<td>34.04%</td>
<td>2.94</td>
</tr>
<tr>
<td>Landscape Perceiving Path</td>
<td>138.69</td>
<td>167.03</td>
<td>28.56%</td>
<td>3.64</td>
</tr>
<tr>
<td>Straight Line Path</td>
<td>210.44</td>
<td>28.24</td>
<td>4.83%</td>
<td>7.41</td>
</tr>
</tbody>
</table>

103
The experiment from July 19 was a particularly interesting example of path choice (Figure 3.14). This trial occurred outside the outdoor laboratory, across a clearing in the far eastern portion of the monkeys’ home range. The mean resistance value of actual travel was 36.86, over four times the mean resistance values of the minimum resistance model path (8.61) or the landscape perceiving model path (11.25). However, the mean resistance of actual travel was similar to that of the straight line path model (33.29) and the length of the actual path was 34.37 meters compared to the straight line length of 31.58 m, a difference of less than 3 meters. In this trial, the focal monkey traversed an area of very high resistance using nearly linear paths to reach the provisioned food. This example is interesting since the minimum resistance model and landscape perceiving model both resulted in paths that were far from linear, with sinuosities of 1.54 and 1.67, respectively. Due to the proximity of the experiment start point to the goal, visibility of the experimenter with the megaphone may have played a role in the linear nature of the travel of the monkey in this trial. Figure 3.14 shows the view from the perspective of the location of the monkey (in the tree) at the location of the red triangle, and then the view of the monkey from its location at the blue triangle.

Overall, the experimental trials are more linear on average than the natural segments of travel. One trial, July 13, was less linear than the others, with a sinuosity of 1.40 (Figure 3.15). The focal monkey in this trial was an adult female monkey who traveled from the start point to the outdoor laboratory where the food was being provisioned with a path with a sinuosity of 1.21. After arriving at the border of the outdoor laboratory, she moved away from the lab and then approached the area again with a less direct path. She arrived after the alpha male and female of the group, and she
did not immediately or directly approach the provisioned food but instead moved around the border of outdoor laboratory area before entering to forage.

**Fig 3.14** (A) Modeled and actual paths from the experimental trial on July 19; Red triangle indicates location from which photo (B) was taken; Blue triangle indicates location from which photo (C) was taken.
Fig 3.15 Experimental Trial, July 13; Red and orange points indicate observation points prior to playing the auditory cue. The first yellow point is the time at which the auditory cue began. Yellow and green points indicate observation points after/during the auditory cue. The red circle indicates the area of the outdoor laboratory and the inset map shows the path around the border of the outdoor laboratory.
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 traveled in a straight line toward the goal. Alternately, 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). In 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 3.5 for comparisons of all parameters from the natural travel to the experimental trials. The movement of the monkeys in the experimental trials thus decreased in sinuosity and increased in resistance compared to naturally occurring travel.
Table 3.5
Models of Capuchin Travel Compared with Actual Travel in Natural Observations and in the Experimental Trials

<table>
<thead>
<tr>
<th></th>
<th>Total Resistance</th>
<th>Mean Resistance</th>
<th>Resistance per Meter</th>
<th>Sinuosity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RMSE NRMSE</td>
<td>RMSE NRMSE</td>
<td>RMSE NRMSE</td>
<td>RMSE NRMSE</td>
</tr>
<tr>
<td>Natural Travel</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minimum Resistance</td>
<td>128.63 11.61</td>
<td>0.66 13.59</td>
<td>0.48 17.16</td>
<td>0.55 24.45%</td>
</tr>
<tr>
<td>Landscape Perceiving</td>
<td>87.74 7.92</td>
<td>0.52 10.68</td>
<td>0.43 15.23</td>
<td>0.51 22.85%</td>
</tr>
<tr>
<td>Straight Line</td>
<td>70.60 6.37</td>
<td>0.27 5.49</td>
<td>0.33 11.63</td>
<td>0.59 25.99%</td>
</tr>
<tr>
<td>Experimental Trials</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minimum Resistance</td>
<td>199.04 34.03</td>
<td>11.54 32.77</td>
<td>6.27 34.08</td>
<td>0.23 68.48%</td>
</tr>
<tr>
<td>Landscape Perceiving</td>
<td>167.03 28.56</td>
<td>10.45 29.70</td>
<td>5.86 31.86</td>
<td>0.27 81.83%</td>
</tr>
<tr>
<td>Straight Line</td>
<td>28.24 4.83</td>
<td>1.47 4.17</td>
<td>0.22 1.88</td>
<td>0.21 63.15%</td>
</tr>
</tbody>
</table>

Compared to the percent ranks of natural travel (mean percentile = 3.24), the experimental trials had a higher average corridor resistance (mean percentile = 12.45). The percent ranks of the corridor resistances of the experimental trials ranged from the 0.7 percentile to the 65.9 percentile while the percent 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**

**Path Segmentation**

We tested three methods for segmenting the travel of bearded capuchin monkeys into smaller sections for analysis. The stop points segmentation method, a method
commonly used to study movement patterns in nonhuman primates (Bates & Byrne, 2009; Presotto & Izar, 2010; Valero & Byrne, 2007), failed to divide the travel of the monkeys into a sufficient number of segments for any model of travel to be effective in predicting their actual movements. With a less selective criterion for identifying stop points (e.g., 90th or 95th percentile of elapsed time at a stop), the larger number of segmentation points may have resulted in larger numbers of segments that would more closely approximate the travel patterns of these monkeys. However, it is worth noting that our stop point threshold of 8.01 minutes is lower than some other published criteria for temporal segmentation of routes in capuchin monkeys (*Sapajus nigritus*) (10 minutes; Presotto & Izar, 2010) and chimpanzees (*Pan troglodytes*) (20 minutes; Bates & Byrne, 2009).

The change points method of segmenting routes was effective in isolating locations of directional change for our study group. For the four days of travel analyzed, three days converged on a q value of 5 which yielded the largest number of change points per route without overshooting the path’s apparent changes in direction. The fourth route resulted in larger numbers of change points with q = 6, q = 9 and q = 10. However, these additional change points were nearby to those found by q = 5 and did not appear to add substantial additional information about the monkeys’ directional changes for this route.

Combining both change points and stop points for route segmentation resulted in modeled paths that more closely resembled actual travel when compared to the stop points segmentation method alone. Comparing the stop points and change points segmentation method to the change points method alone, both segmentation types resulted in models that performed similarly. We ultimately selected the change points and
stop points method of segmentation as the most effective segmentation method. This method resulted in lower RMSE values for the resistance per meter and mean resistance parameters, two measures that would be less affected by the overall length of the path segment and would more closely reflect the resistances of individual movement choices of our study animals.

**Results of Movement Models**

The movement patterns of bearded capuchin monkeys do seem to be attendant to the landscape resistances incurred as they move through their environment. The monkeys travel in a zone of low cost in their paths from the start to the end of each travel segment. However, the resistances incurred by their travel are not so exceptionally low that a model predicting 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 is very similar to actual travel. Some differences between the straight line travel model and actual travel are apparent in the resistance per meter parameter with straight line travel having slightly higher resistance per meter. This means that while straight line travel has central tendencies of resistance that are similar to actual travel, actual travel is in fact lower in resistance than this model and actual travel has longer travel distances per segment. Importantly, actual travel does not resemble straight line travel in the very parameter that is used to define this model: sinuosity. On average, actual travel has a 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 alternatively could suggest an alternate 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 model paths. In these environments, straight line travel may be an effective strategy for efficient travel for the moving animal. Further testing is necessary to determine the extent to which the predictions of movement and the movements themselves vary when landscape variables are included in other types of habitats and whether the movement of nonhuman primates in those habitats is shaped by their landscape.

**Experimental Analysis of Capuchin Movement**

When 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. It is worth noting that, on average, the experimental trials were shorter in distance 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. While the monkeys are sensitive to the resistances of their landscape, these resistances do not determine their movement patterns entirely. This result may lend support for the idea that the study group, when ranging naturally, is not traveling in a goal-directed way. When a goal was introduced to the study group, their travel patterns were changed and ceased to resemble their natural travel paths. Alternatively, the monkeys may still have travel goals in natural conditions, although those natural goals may be different in distance, quality, or quantity from the experimental goals, resulting in different behavior. The experimental trials presented the
monkey group with a resource completely unlike any other resource encountered by our study group during the study period. This resource was clumped, high in caloric value, and limited in quantity. Future studies should investigate the effect of resource abundance or quality on the movement patterns of bearded capuchin monkeys by training the group on distinctive calls representing varying provisioning regimes. In addition, in this study, the experimental trials were conducted in areas of moderately high resistance. Future experiments should test the movement of capuchin monkeys across areas of higher resistance like wetlands or steep ridges by carefully selecting an optimal distance from which to call the group and by spacing human observers between the group and the provisioning site to facilitate observation of their movements across areas of impassable terrain (i.e., steep ridges).

The movement decisions of the monkeys in the experimental trials appeared to have been impacted by the social rank of the moving individual. Lower ranking individuals were observed declining to visit the provisioning site. The entire group was also observed to ignore the auditory cue when they were widely dispersed or when higher ranking individuals were moving away from the call. The social dynamics of response to the provisioned food item and auditory cue are interesting avenues for future research.

**Advantages and Challenges of the Callback Technique**

The novel technique tested in this study, the callback method, has both advantages and disadvantages for the experimental analysis of movement decisions of animals. The method allows researchers to control the travel goals of animals moving in natural environments. This circumvents the substantive challenge (Janson & Byrne, 2007) of
identifying an animal’s travel goal post hoc and allows researchers to definitively state the goal of a moving animal prior to its arrival in a location of interest. Researchers may manipulate the location of the goal, its distance and direction from the moving group, and the quantity and quality of the provisioned resource in order to tease apart the complex relationships between space, resources, and cognition. These advantages come with a complex set of challenges to the researcher working in the field. First, the impacts of provisioning and training the animals on an auditory cue must be considered. In the case of our study group, the animals were accustomed to sporadic provisioning of water and food prior to the beginning of this study. Thus, we concluded that the introduction of a small quantity (~ 500 g) of provisioned food would have minimal effects on the natural behavior of the group. In addition, the animals in our study group live in an area that is sparsely populated by humans. Nonhuman primates living in closer proximity to human populations may suffer ill effects should they be trained to pursue food following the auditory cue of a cell phone ring tone.

Trial and error was necessary in order to understand the degree of control the experimental manipulation could have over the movement of our study group in natural environments. Training the monkey group to recognize the auditory cue and associate it with the provisioned food was straightforward and acquisition occurred quickly. Reinforcement following long periods of absence likely facilitated the continued use of the cue over the study period. It was also important to train the monkeys to associate the cue with provisioning in a novel experimental context, outside the outdoor laboratory. The megaphone became a conditioned stimulus with which the monkeys associated the provisioned food. Therefore, it had to be kept hidden as we followed the monkeys during
their natural movements in order to avoid influencing their movement prior to the onset of a trial.

Logistically, the callback method presents some additional challenges. When callbacks are not carried out in an outdoor laboratory environment, experimenters must improvise goal locations on the fly as well as locations from which to call the focal monkey. This process occurs while the monkey group continues to move naturally through its home range. The process of selecting locations for trials requires the researchers to estimate where the group is likely to go naturally and what foods they may find naturally between their present location and their possible future location when the trial is projected to begin. Field estimations of interesting experimental scenarios are inherently rough, and do not allow for precise site selections that would maximize the differences between alternate hypothetical routes. In addition, the use of a high value provisioned resource results in competition for food such that the resulting movement patterns may be different from natural movement. Subjects may increase the speed with which they move through the landscape to such a degree that following the focal animal becomes impossible. We recommend the use of a team of observers interspersed between the focal monkey and the travel goal that can record the location of the focal monkey as it moves, especially when the travel goal places areas of high resistance between the monkey and the goal. This is important since the concept of landscape resistance impacts both human and nonhuman primates in their travel.
Conclusions

The results of this study call in to 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.
References


Understanding animal behavior requires that we consider its spatial context. The importance of spatial context has long been evident to geographers and spatial ecologists. Tobler’s first law of geography states that “Everything is related to everything else, but near things are more related than distant things” (Tobler, 1979). However, few studies of animal cognition have considered the role of space and landscapes in evaluating behavior. For animals ranging in natural environments, once cannot isolate the animal’s movement decisions from its landscape setting. Bennett (1996) emphasizes the importance of landscape features that function as landmarks or beacons for animal navigation. According to his evaluation, care must be taken in ascribing a complex spatial orientation mechanism such as a Euclidean cognitive map to an animal ranging in natural environments since the animal may be making use of a perception-based orientation strategy rather than a memory- or cognition-based strategy. Just because we, as human observers, do not detect a perceptual cue does not mean no cue is guiding the animal’s navigation. This warning could be extended to include the consideration of the impacts of landscape features in our evaluation of the movements of nonhuman animals. Not only may landscape features serve as landmarks or beacons, but they may also serve to guide or manipulate animal movements such that travel patterns carry artifacts of the landscape
where they occur. In order to understand animal behavior, especially animal movement, we must consider its spatial context.

Summary of Findings

The studies in this dissertation describe our findings on the use of space and movement decisions of bearded capuchin monkeys. Understanding an animal’s use of space is important for conservation efforts, especially in areas of rapid habitat change like the cerrado of northeastern Brazil. The movement decisions of these animals are critical for understanding how they navigate in their environment. We present novel methods for investigating the efficiency of capuchin monkey movement decisions and a novel experimental method for manipulating travel goals in natural environments.

Use of Space

Chapter 2 of this dissertation details the use of space of our study group by combining data on the area used by the monkeys with data on the landscape of those spaces and data on their behavior. We saw that the monkeys tend to use areas of high percent green vegetation, low percent bare soil, and spaces near areas of human influence (i.e., residential areas and subsistence farming). The monkeys also tend to use areas of low elevation, but stay close to the steep ridges that are interspersed throughout their home range. Behaviorally, the monkeys tended to forage in greener spaces than the spaces in which they were seen to locomote. Also, the unique stone tool use behavior exhibited by our study group was significantly associated with areas of green vegetation. The results of Chapter 2 demonstrate that the monkeys of our study group use similar spaces to those in the region that are currently being converted to industrial monoculture:
areas of low relief and areas of wooded savanna vegetation. The unique stone tool use behavior of these monkeys is at risk of encroachment from the rapidly expanding industrial agriculture of the region (Barretto et al., 2013). Understanding the spaces used by our study species may allow for conservation efforts directed at spaces with landscape features that these animals prefer.

**Spatial Decisions and Movement Efficiency**

Chapter 3 of this dissertation investigates the impacts of landscape features on the spatial decisions of bearded capuchin monkeys. We tested stop points and change points as methods for dividing their daily paths into segments for analysis and conclude that a combination of the spatial and temporal methods best represented the actual travel of our study group. Importantly, the movements of bearded capuchin monkeys in Chapter 3 appear to be impacted by the landscape features in their home range. In terms of movement sinuosity, natural movements of focal monkeys are better described by a minimum resistance path model and a landscape perceiving model of capuchin movement than by straight line travel. In terms of resistance, the straight line path model was most similar to that of the capuchin’s actual movement patterns. These results indicate that the monkeys in our study group travel in a zone of low resistance relative to nearby areas where they could have traveled but did not. The monkeys in this study avoid areas of high landscape resistance such as steep ridges, wetland areas with standing water, and areas of bare soil with sparse vegetation. This pattern of movement was predicted by the landscape resistance layer developed in Chapter 2 and used in Chapter 3 as the basis for the minimum resistance and landscape perceiving path models.
The results of Chapter 3 suggest that incorporating the effects of landscape in our analyses of nonhuman primate spatial cognition may allow us to better understand nonlinear movement patterns. These movement patterns and their relationship to the landscape may reflect knowledge of the locations of out of sight landscape features, including resources, and this knowledge may prove to be topological or metric (i.e., distance and direction) in nature. Since the investigation of the effects of landscape features has been limited in past studies, this is an interesting avenue for future research.

Chapter 3 also presents results from the experimental manipulation of the travel goals of our study group. Our callback technique was pioneered to investigate how bearded capuchin monkeys make movement decisions in areas of very high landscape resistance. We found that movement in these experimental trials was more linear and higher in landscape resistance than the natural movements of the study group. The limited quantity and high quality of the provisioned resource likely contributed to the linear, high resistance nature of the capuchins’ movements in the experiment. A more linear route may have been more advantageous to the traveling monkeys in these trials since there was intense competition for the resource.

The results of Chapter 3 call into question the goal-directed nature of the movement of our study group during natural travel. We saw that in conditions of extreme resource quality and quantity (i.e., during the experiment), the monkeys move in a linear way. During natural travel, however, their movements are less linear. We hypothesize two possible explanations for these results. The monkeys may be exploiting resources opportunistically during natural travel without a definitive travel goal that directs their spatial decisions. A contrasting explanation may be that these results indicate an alternate
modality of goal-directed travel in natural movements compared to experimental trial movements. In this case, natural travel would consist of movement directed toward a goal, but moderated by the landscape features between the monkeys’ location and its goal.

**The Callback Method for Field Experiments**

The callback method tested in Chapter 3 of this dissertation has both advantages and disadvantages for the experimental analysis of movement decisions of animals. The method allows researchers control over the travel goals of animals and avoids the *post hoc* definition of travel goals. Distance, direction, quality and quantity can be easily manipulated for travel goals. The impacts of provisioning and training and the potential interactions between the study animal and human populations must be considered prior to using this technique, however.

The training portion of the callback method was straightforward and acquisition occurred quickly. Reinforcement without testing following long periods of absence of the study animal ensures that the animals will remember the auditory cue and move toward the provisioned location. Training in all experimental contexts (e.g., spatial, temporal, social) is also likely to facilitate the use of this method. Tools used in calling the animals to a provisioned location (e.g., sound amplifiers) may become associated with the experiment, and measures must be taken to avoid alerting the animal to the beginning of a trial before its onset.

The greatest challenge in using the callback method is in choosing experimental sites while animals are on the move. Experience with the animals’ daily movement
patterns will facilitate use of this method and allow researchers to more easily plan a trial based on expectations of the destination of the group at any given time. Moving through areas of high resistance for the study animal often means moving through areas of high resistance for the human observer as well. Logging the focal individual’s movements remotely or by use of multiple human observers may facilitate this challenge.

**Future Directions**

The results of the studies presented in this dissertation highlight the importance of incorporating landscape variables in the study of animal behavior in natural environments. We have shown that our study group demonstrates movement patterns and patterns of use of space that are impacted by landscape variables. Further investigation is needed to understand what this impact of landscape variables means in terms of these monkeys’ cognitive mapping strategy or the content of their spatial memory. I would like to extend my experimental analyses of these monkeys’ movement patterns into areas of more extreme resistance gradients (i.e., very high resistance spaces surrounded by areas of very low resistance), and into areas where Euclidean cognitive mapping would predict one movement pattern, while the use of a topological, habitual route network would predict a different pattern (i.e., habitually used zones of travel opposing a low resistance path to a provisioned goal). In this way, the experimental callback method could be used to test these alternate theories of cognitive mapping in nonhuman primates.

Another interesting avenue for future research is to extend the use of auditory cues to train the monkeys on a series of calls signifying the provisioning of resources of varying quantities and qualities. I hypothesize that an auditory cue signifying the
presence of a dispersed, moderate value food item would prompt movement patterns similar to those of natural travel. This result would indicate that natural travel and travel in the experimental trials exist on a continuum and that movement responses of the monkeys are proportionate to some motivational feature of the available resource.

Many previous studies have investigated the cognitive mapping strategies of nonhuman primates using measures of the linearity of their travel paths (e.g., De Raad, 2012; Di Fiore & Suarez, 2007; Normand & Boesch, 2009; Noser & Byrne, 2007a, 2007b; Noser & Byrne, 2010; Presotto & Izar, 2010). More research is needed to understand the impact of landscape features on the choices of the animals in these studies. Especially in heterogeneous landscapes, nonlinear movement may not indicate lack of knowledge regarding the locations of resources.
References


APPENDIX A

NETLOGO CODE FOR LANDSCAPE PERCEIVING MODEL

breed [monkey]
breed[goal]

extensions [ gis]
globals[
]
patches-

own [ 
cost
used?
goal-distance
cost-distance
costdist
]
turtles-

own [ start-patch ]

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

;KNOWN BUGS
;; Model does not STOP automatically when the monkey reaches the goal. Must be stopped manually.
;; Perception slider is not currently functioning due to a change in the decision criteria (only looks at 8 neighbors). Perception slider may be re-implemented in patch context (as a move procedure).

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
to setup
ca

;setting up patches with cost.asc layer to fill variable "cost"
let cost-
dataset gis:load-
dataset "cost.asc"
let costdist-
dataset gis:load-
dataset "data/asc_cd/expjul25_e_cd.asc"
gis:apply-raster costdist-
dataset costdist
gis:apply-raster cost-
dataset cost
gis:set-
world-envelope (gis:envelope-
union-of (gis:envelope-
of cost-
dataset))
let min-cost gis:minimum-
of cost-
dataset
let max-cost gis:max-
imum-of cost-
dataset
let min-costdist gis:minimum-
of costdist-
dataset
let max-costdist gis:max-
imum-of costdist-
dataset
resize-world min-pxc-
max-pxc min-pyc max-pyc
ask patches [  
  ifelse cost-distance-display = true  
  [  
    if (costdist <= 0) or (costdist >= 0) ;setting color for patches based on cost distance raster  
      [set pcolor scale-color black costdist min-costdist max-costdist]  
    ]  
  ]  

[  
  if (cost <= 0) or (cost >= 0) ;setting color for patches based on cost raster  
  [set pcolor scale-color black cost min-cost 14]  
  ifelse cost > 14  
  [set pcolor red]  
  [set pcolor scale-color black cost min-cost 14]  
  ]  
]  

create-monkey 1  
[  
  set size 25  
  ifelse monkey-netlogocoordinates = true  
  ;;;;; Input the xy position of the monkey in NetLogo world coordinates  
  [setxy (x-input-monkey) (y-input-monkey)]  
  ;;;;; Input the xy position of the monkey in UTM coordinates  
  [setxy ((x-input-monkey - 452400) / 2) ((y-input-monkey - 8931234) / 2)]  
  set start-patch patch-here  
  set shape "face happy"  
  set color blue  
  ;set pen-size 1  
  pen-down  
]  
reset-ticks  
create-goal 1  
[  
  ifelse goal-NetLogoCoordinates = true  
}
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to go
avoid

;;;; procedure to check values of neighbors and verify that the monkey is moving to the neighboring cell of lowest costdistance

file-open "testmay16stop_0_1.txt"

ask monkey [ ; test procedure continued
 ; ask neighbors [file-type (word costdist ",")]

;;;; test procedure from in-radius - showed that in-radius command in turtle context was not looking at all neighbors (actually a Von Neumann neighborhood)
 ; ask patches in-radius perception-radius [file-type (word costdist ",")]

move-to patch-here ;; moves the monkey to the center of the patch
face turtle 1 ;; makes the monkey face the goal

;;;; Early version of the model had cost distance conceptualized as cost divided by distance which resulted in the monkey being stuck in some cells or moving to areas of very low cost and not being drawn to the goal. This problem was temporarily corrected by moving the monkey forward (toward the goal) by one cell ;; every other step. Ultimately, this procedure was determined to not accurately represent the desired movement hypothesis, and the costdistance raster from
;; ArcGIS was implemented as the input (resistance layer).
; ifelse used? = true
; [fd 1
 ;  move-to patch-here
 ; ]
 ; [

;; Move by radius distance (set by slider) at a time (now obsolete). The neighbor function in turtle context looks only at a Von Neumann neighborhood.
; move-to min-one-of patches in-radius perception-radius [costdist]

move-to min-one-of neighbors [costdist] ;; Moves the monkey one set of neighbors (8 pixels around the monkey) at a time
move-to patch-here ;; moves the monkey to the center of the patch
set used? true ;; Sets the patch the monkey is on as used

;; test procedure continued
; file-print costdist

; From every other step forward procedure (end of the ifelse procedure).
; ]

graphiphy ;; create graphs and outputs

];
tick

;; continued procedure to check values of neighbors and verify that the monkey is moving to the neighboring cell of lowest costdistance
;if ticks > 15
 ; [
 ; file-close
 ; stop
 ; ]
end

;';;;;;;;;;;;;;; This determines the distance of every patch from the goal's location (now obsolete).
;to patchdistance
;set goal-distance (distancexy ((x-input-monkey - 452400) / 2) ((y-input-monkey - 8931234) / 2))

;end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

;;;;;;;;;;;;;;;;;;;;;; This is the resistance surface upon which the monkeys move uphill. It combines distance from the goal with cost (now obsolete).

;to costdist1
; if (goal-distance > 0)
; [set cost-distance ( cost * (goal-distance))]
;end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to avoid ;; Keeps monkey from getting stuck repeating the same cells over and over again. Monkey must move to a cell it has not visited before. Obsolete now that the costdist1 raster has been implemented.

ask patches [if used? = true [set cost-distance 9999999]
] end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to graphiphy ;; Plots accumulated cost and creates output of accumulated cost. Also creates csv file with cost and xy coordinate of the monkey as it moves.

let accumulated-cost sum [cost] of patches with [used? = true]
plot accumulated-cost
let mean-cost mean [cost] of patches with [used? = true]

let xxx ((pxcor * 2) + 452400)
let yyy ((pycor * 2) + 8931234)
let xxxyyy (word xxx " " yyy)
output-print xxxyyy
;output-print word "Accumulated Cost: " accumulated-cost
;output-print word "X Coordinate " pxcor
;output-print word "Y Coordinate "pycor
;output-print word "Cost " cost
;output-print word "Mean cost " mean-cost
if write-csv = true
[export-output (word "/data/output/" output-label ".csv")]] ;; Creates a csv file including the segment name from the input box on the interface.

end
move procedure (adapted from Railsback & Grimm butterfly model; now obsolete)
;to move

; face turtle 1
; forward 1

;if else random-float 1 < q
;[uphill cost]
;[move-to one-of neighbors]

;if goal-distance = 0 and used? = false
;[goal-distance] of max-one-of neighbors [goal-distance]
;[stop]

;let accumulated-cost sum [cost] of patches with [used? = true]
;set used? true
;plot accumulated-cost
;output-print word "Accumulated Cost:" accumulated-cost

;end

;let mean-distance mean [distance start-patch] of turtles
;report patches-visited / mean-distance
APPENDIX B
MONKEY LANDSCAPE PERCEIVING MODEL ODD DESCRIPTION

This file describes the model of Howard (2014) developed in NetLogo 5.0.4.

**Purpose**

The model was designed to test the movement decisions of capuchin monkeys living in Northeastern Brazil. This model represents movement decisions based on landscape resistance when the monkey is sensitive to the resistance of its immediate surroundings, but is drawn in the direction of a goal.

**Entities, State Variables, and Scales**

The model has three kinds of entities: monkeys, goals and square patches of land. The patches make up a square grid landscape of $1929 \times 773$ patches, and each patch has the state variables: cost and costdist. One monkey and one goal entity are generated in the setup of this model. Monkeys and goals are characterized by the patch they are on. Each patch represents a $2 \times 2$ meter patch of land located in northeastern Brazil. The approximate length of one time step in the simulation is between twenty seconds and 1 minute, based on the mean travel speed of capuchin monkeys observed in the field (Howard 2014). Simulations should be stopped when the monkey reaches the goal.

**Process Overview and Scheduling**

There is only one process in the model: movement of the monkey. On each time step, the monkey moves once.

**Design Concepts**

The basic principle addressed by this model is the concept of movement within areas of low landscape resistance. The movement behavior of the monkey is not emergent or adaptive, but rather it is determined by the rules of the model which are based on hypotheses regarding capuchin movement decisions. This hypothesis is that monkeys may make their spatial decisions based on the landscape of their immediate surroundings, rather than on the basis of a complete knowledge of the landscape between their present location and the goal. This hypothesis is modeled through a rule that the monkey will move to the neighboring cell of the lowest cost distance considering all eight of its
neighbors. Objectives and prediction are not explicitly considered and the model does not incorporate learning.

Sensing is incorporated by the monkey which identifies which of the surrounding patches has the lowest costdist value.

The model does not include interaction between monkeys. Only one foraging monkey is modeled.

This model does not include stochasticity. All the movement choices, start locations and goal locations are determined by the inputs to the model.

To allow observation of the monkey’s movement, a CSV file is written with the X Y coordinates of the monkey at each time step. Accumulated cost is visualized on the interface allowing us to observe how the monkey accumulates cost as it moves through the landscape.

Initialization

The cost of the landscape is initialized at model setup. Two kinds of landscape cost can be shown depending on the setup of the model: (1) the landscape cost irrespective of the goal location, imported from an ascii file representing landscape cost and (2) the cost distance raster, imported from an ascii file specific to each goal location. The monkey is placed in a start location based on actual observations of capuchin movements and the goal is placed in a location based on the place to which capuchins were observed to move. A switch allows the monkey and goal locations to be input in the NetLogo world coordinates.

Input Data

The landscape is constant, so the model has no input data.

Submodels

The go submodel defines how monkeys move to neighboring cells of the lowest cost. The monkeys are asked to move to the neighboring cell with the minimum value for the variable costdist. If two neighboring cells have equal costdist, the monkey chooses randomly between the two. The neighboring cells are defined as the eight cells immediately surrounding the monkey’s current patch.

Credits And References