FROM MAZE TO MAPS: GEOSPATIAL TECHNOLOGIES AND THE PATTERN OF NAVIGATION IN WILD ANIMALS

by

ANDRÉA PRESOTTO

(Under the Direction of Marguerite Madden)

ABSTRACT

The assessment of spatial navigation in wild animals was challenging before recent advances in Geotechnologies. From the experimental studies in mazes to the Global Positioning System (GPS) and the Geographic Information System (GIS) capabilities, many new perspectives on how wild animals move through their environment have emerged. To date, it is widely accepted that nonhuman animals efficiently travel their home range to locate resources according to the environmental pressures they face. This dissertation investigated the patterns of navigation in two mammals with high levels of cognition. The bearded capuchin monkeys live in the Brazilian savanna, in northeastern Brazil, and the African elephants live in the African savanna, in northeastern South Africa. The bearded capuchins were followed by researchers on foot and tracked with a GPS hand-held device for 200 days, while the African elephants were fitted with GPS-enabled collars that recorded coordinates for 600 days. The GIS-based method used to investigate the patterns of navigation across taxa was adjusted only to accommodate the distance animals move, the types of resources they use, and the extent of their natural habitat. The hypotheses tested were as follows: Both species living in a savanna landscape use a sequence of landmarks to navigate, a mechanism consistent with the use of route-based network.
Alternatively, the visual access to large parts of their home range would allow the animals to use new paths, decreasing the travel distance toward resources, consistent with cognitive maps. While bearded capuchin monkeys’ patterns of navigation support the hypothesis of the route network, the analysis of African elephant movement suggest they combine both systems: the route network in unfamiliar areas, and a system analogous to cognitive maps in familiar areas.

INDEX WORDS: GIS-based method to animal navigation, African elephants, bearded capuchin monkeys, patterns of navigation, animal behavior
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“Do not go where the path may lead, go instead where there is no path and leave a trail”
Ralph Waldo Emerson

To Gordon Martin

AND

To all the animals who find themselves lost
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CHAPTER 1
INTRODUCTION

Spatial analyses of navigation in nonhuman animals and accurate assessment of their movements were challenging before recent advances in technology. Researchers have advanced from decades of observing animal behavior, to conducting experiments aimed at testing theories of why animals move the way they do. Scientists today draw from a number of disciplines to fully understand animal navigation including geographic technologies of geographic information systems (GIS), Global Positioning Systems (GPS) and geospatial analysis. Knowledge of the biology of animals is needed to fully understand their physiological requirements and their use of habitat. In addition, brain development and the psychological capacity of animals to sense their environment, remember the landmarks of their surroundings and mentally map the resources of their habitat known as spatial cognition is critical for studying mechanisms of animal navigation.

Tolman (1948) was the first to show that rats navigating in mazes were able to use an internal representation of their environment, which he termed “cognitive maps”. Tolman used mazes with diverse configurations and experimentally analyzed how the rats increased their ability to reach their goals. He attributed the rats’ the ability to short the mazes’ routes. Tolman’s cognitive map hypothesis encountered resistance by the scientific community because the attribution of high levels of cognition in nonhuman animals (Thinus-Blanc, 1996, Jeffery et al, no date).

Thirty years later, O’Keefe and Nadel (1978) showed “cognitive maps” were guided by a specific part of the brain, called the hippocampus, where the brain stores certain cells named
“place cells”. The place cells are responsible for guiding the decision making process behind navigation in animals, firing if the animals are in specific locations, such as familiar areas of navigation (Boccara et al., 2010; Jeffery, 2015).

There is now a large body of literature about animal navigation with varying results about the different types of mechanisms of navigation animals use to find their way. It is widely accepted that nonhuman animals efficiently travel within their home range to find resources (Brooks, Bonyongo, & Harris, 2008; Dyer, 1996; Wystrach & Graham, 2012). Recent discoveries mapping the brain of mammals show that group of cells contribute to the navigational system animals use (Boccara et al., 2010; Jeffery, 2015). With the new technologies, smaller parts of the hippocampus can be mapped, and provide further understanding about the function of place cells. For instance, these cells collectively form a “multitude of spatial maps individualized to the variety of environments that animal has experienced” (Boccara et al. 2010, p. 987). The spatial cells previously believed to be only in the hippocampus now seemed to be found in a structure called Medial Entorhinal Cortex or MEC. MEC is an interface between the presubiculum, hippocampus and neocortex (Boccara et al., 2010; Poucet et al., 2014), with a key cell of spatial representation called grid cells.

It is noteworthy that experimental psychological studies show the linkage between specific cells firing at specific locations the animals are using and that clear patterns of navigation are found. However, what happens in the brain of wild animals when they navigate and the environmental conditions under which their brain cells are more or less active is still unknown since natural landscapes are filled with prominent features that may lead the animal movement (Cheng et al., 2013). The role and map of these spatial cells across taxa is also poorly understood. Further evidence suggest that the cognitive ability to find places and reach goals in
the wild can be contingent on the development of the animal related to the landscape they learned (Shettleworth, 1999) an assumption that is supported by new studies of brain cells (Tan et al. 2015). Currently, the question of how animals process environmental information according to diverse ecological demands they face in the wild is still open for debate (Shettleworth, 1999).

Animal cognitive theories suggest that species are able to internally represent space using either the less demanding mechanism, topologic map (Poucet, 1993) or the more demanding mechanism, Euclidean map. In a topologic system the organism locates an object with reference to its own body (Potì, 2000), including eye, head and body coordinates (Iachini & Ruggiero, 2006; McNamara & Shelton, 2003). If an animal uses a Euclidean system, the location and orientation of the organism are centered on the objects or features of the surrounding environment (Iachini & Ruggiero, 2006). In this Euclidean model, organisms locate an object with reference to other objects (Potì, 2000) such as the direction of gravity, the Sun’s azimuth, and the Earth’s magnetic field (McNamara, Rump, & Werner, 2003). However, the overall questions remain the same: whether or not non-human animals have prior knowledge of their destination and whether they able to maintain a “mental” representation of previously navigated geographic spaces.

Insects are one of the most studied taxa, showing efficiency in their navigation to find food and return to the nest (Wystrach & Graham, 2012). The central-place foraging insects use a form of topologic system known as path integration to keep track of their position in relation to the nest while foraging. The insects then return to the nest in a straight line. Migratory birds achieve directional orientation using sun, star, and magnetic compasses. A recent study of turtles
equipped with GPS show that individuals go to the ocean surface to find landmarks when navigating (Lohmann, Luschi, & Hays, 2008).

The use of geotechnologies on animal navigation, including the increased accuracy and precision of GPS, and availability of spatial analysis capabilities in GIS, significantly improved the knowledge about how animals navigate in their habitat (Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2015). These innovative perspectives allow quantification of descriptive data, storage, and systematic order of data collection (Hughes, 2003; Longley, Goodchild, Maguire, & Rhind, 2001). The data standardization improvements in GPS receivers contributed to solving the problem of poor signal reception in remote, wild landscapes (Bohrer, Beck, Ngene, Skidmore, & Douglas-Hamilton, 2014; Phillips, Elvey, & Abercrombie, 1998; Robbins & McNeilage, 2003). Recent proliferation of satellite and airborne remote sensing programs to image the “earth’s resources” has created a rich database of multi-scale imagery documenting habitat conditions over time. Consequently, spatial analysis based on GPS, GIS and remote sensing techniques offers opportunities to advance the methodologies used to study wild animal navigation (Bohrer et al., 2014). The combination of GPS and GIS visual maps allow researchers to better understand the navigational characteristics of wild animals. These advances in technology also provide insight to aspects about the mechanism of orientation that may underlie animal navigation patterns.

In this study, I consider animal movement across the landscape through which they travel as a form of habitat adaptation (Shettleworth, 1999). In other words, the environment is learned (Mackintosh, 1983) and animals may use topologic or Euclidean systems according to the type of features offered by their environment. An open-canopy habitat, such as a savanna, allows higher visibility of prominent landmarks like hills and trees. In this sense, animals may
memorize the landmarks and use them as cues to find resources (Garber, 2000). The mechanism of using sequential landmarks to memorize location is consistent with a route network system (Poucet, 1993). Route network is a topologic system and has been reported for many species living in similar environments (DiFiore & Suarez, 2007). Characteristics of the route network system are the use of repeated paths (segments of individual routes) and the use of repeated routes (length of the daily travel navigation) to reach resources. In a route network system animals reuse common paths to reach resources in their home range, they also use the intersections of the paths and routes as locations where they change directions or decide the next travel path (Di Fiore & Suarez, 2007; Erhart & Overdorff, 2008; Garber, 2000; MacKinnon, 1974; Milton, 2000; Noser & Byrne, 2007; Sigg & Stolba, 1981). This spatial representation allows individuals to construct novel routes through the combination of paths (Poucet, 1993). Animals also travel using the route-based network, keeping visual access to the route system or the landmarks associated to the routes and resources (Garber, 2000). This type of navigation may be considered a default mechanism for many animals since they can find resources around the route network year-around (Chapter 2).

On the other hand, a dense-forested habitat may demand a more precise internal representation of resource distribution, especially in times of scarcity when the cost of navigation is high. Knowing where out-of-sight resources are saves energy in the navigation process, but requires better cognitive ability (Presotto & Izar, 2010). Animals that keep the mental representation of their home range use a system consistent with the cognitive maps usually reported to the following primates: humans (Haun, Rapold, Call, Janzen, & Levinson, 2006), chimpanzees (Normand, Ban, & Boesch, 2009), and black capuchins (Presotto & Izar, 2010).
Geotechnologies and Animal Navigation

The development of geotechnologies and their availability to the public was a revolution for animal navigation and movement studies (Brooks et al., 2008; Lötter et al., 2009; Pinto & Keitt, 2009). Collecting animal data in a naturalistic fashion is still difficult and requires effort to further the analysis provided by the geotechnologies. The introduction of remote sensing technique to the field of animal navigation is in its early stages. Remote sensing has been used in a wide range of environmental studies (Gillespie, 2001; Kerr & Ostrovsky, 2003), offering the potential to investigate important aspects of the geographical factors related to animal home range. The American Association for the Advancement of Science (AAAS) defines geospatial technologies as “the technologies relating to the collection of processing of data that is associated with location”. The three geotechnologies referred by AAAS are the Global Positioning System, Geographic Information Systems, and remote sensing, the three I have used to amplify the research methods applied in wild primates and more recently to African elephants.

The Primates

Primates are considered good systems to study because they are capable of high levels of cognition and are phylogenetically closer to humans. They use tools; have intense social interaction, good memory, and knowledge of their space (D. Fragaszy, Izar, Visalberghi, Ottoni, & De Oliveira, 2004; Milton, 2000; Visalberghi et al., 2007). These characteristics have previously only been attributed to humans. Studies with primates have emphasized the use of route network system in different species. In certain habitats, primates have high visual access to their surroundings, which may facilitate the use of route network system (Di Fiore & Suarez,
2007; Normand et al., 2009; Noser & Byrne, 2007). For instance, when baboons (*P. anubis*) leave a habitual route they are able to reach their source using a novel path if they can still see a prominent landmark but if they cannot see the landmark they return to the habitual route to reach their goal (Noser & Byrne, 2007). Here we suggest that species living in open environments, like savannas, with food availability year-around would maintain the use of route network because the route system is visually accessed from different locations inside the animal home range. If food is available around the route network system it would be costly and unnecessary to maintain a detailed mental representation of the entire home range. Chapter 1 shows a study conducted with the bearded capuchin monkey living in the Brazilian savanna (Figure 1.1). Bearded capuchins are well known for their tool use behavior (Ottoni & Izar, 2008), the only monkey capable to use tools (D. Fragaszy et al., 2004; D. M. Fragaszy, Visalberghi, & Fedigan, 2004).

![Figure 1.1. Fazenda Boa Vista, the study area of the bearded capuchin monkeys](image-url)
Primates are common subjects to be followed by foot from dawn to dusk. Yet, other animal species live in geographic locations that are not feasible to follow by foot. This is one of the reasons wild primates have been subjects of long-term cognitive studies, while other species, sharing similar capabilities lack long-term cognitive studies in the wild (Nissani, 2004). However, with the increased use of GPS collars, the continuity of data collection (consecutive days), and the new capabilities of GIS and Remote Sensing, it is possible now to conduct preliminary investigation about the mechanism of orientation using existing data.

The African Elephants

Chapter 2 shows comparative data analysis about the navigation of African elephants \textit{(Loxodonta africana)} living in the southern portion of Kruger National Park (KNP), Skukuza in South Africa (Figure 2). I adjusted the GIS method applied to primates to accommodate the specie-specific characteristics of African elephants, such as distances from each paths and distance of visibility. African elephants are also considered ideal species to be studied since they use larger areas to travel, have impressive memory (Nissani, 2004), and more knowledge about their behavior is urgently demanded in certain areas (Blake et al., 2008; Douglas-Hamilton, 1998).
Figure 1.2. Skukuza, the study area of the African elephants

The Elephantidae family originated in the Miocene and includes modern Asian Elephants (genus *Elephas*) and African elephants (genus *Loxodonta*) (Rohland et al., 2010). Elephants have high cognitive abilities and share similarities with humans. They are born with a brain that is 35% the size of their adult brain. The postnatal growth suggests that they are one of the most “intelligent” mammals. The brain of an elephant is the largest brain of all land mammals (Rensch, 1957). But elephants are large animals and the comparison with the size of their brain with other species is not a fair one. The structure of an elephant brain is not similar to the human structure, but their brain is highly convoluted, which is a potential indication of higher intelligence and learning capacities (Alexander, 2000). They are able to individually recognize
their relatives among a hundred individuals (Byrne, Bates, & Moss, 2009). Experiments conducted to access elephants’ memory suggest that once elephants learn tasks their improvement is high, and it has been shown that even eight years later they are able to perform the tasks to the same extent (Markowitz, 1982). They are also proficient tool users (Chevalier-Skolnikoff & Liska, 1993; Shoshani, Kupsky, & Marchant, 2006), and are included in a small group of animals that are able to make tools for problem solving (Byrne et al., 2009).

In the wild, African elephants are matrilineal relatives and form a family unit that normally travels, forages, and socializes together, using the strategy of fission-fusion navigation (Moss and Lee, 2011). That is individual elephants split themselves in smaller groups to travel and re-join the larger group after a certain period of time. This fission-fusion strategy is used because it allows animals to access and share resources more efficiently when traveling in smaller groups during times of food scarcity (Lehmann, Korstjens, & Dunbar, 2007). The elephants use a variety of sounds to communicate. They have the ability to communicate with closer individuals, but also to use infrasound for long-distance communication. Family units are able to coordinate their movement using infrasound contact (Sukumar, 2003). While the sound communication plays a role in movement, it may not determine the spatial levels of cognition elephants use to find their way.

Spatial cognition or mechanism of orientation studies with African elephants are not conclusive, in part due to the lack of studies in this area and no sufficient results to conclude how elephants define their system of navigation (Byrne et al., 2009). Previous studies tracking elephants with GPS collars showed that they travel an average of 10.3 km per day in Nairobi. This study was conducted with one male, traveling long distances looking for females. This male traveled in a more linear way, reaching 15 kilometers in 24 hours. This study confirmed that GPS
radio tracking was feasible to be used in large animals (Douglas-Hamilton, 1998). Blake et al. (2001) used GPS collars in African forest elephants to test GPS’s reception in dense forest. More recently Boettiger et al. (2011) focused on the landscape of the elephants in Samburu and Buffalo Springs National Reserves (Kenya) suggested that auto-correlation models using elephants GPS data and landscape features help to analyze movements of elephants. In this study the authors highlighted the importance of areas with higher NDVI (or healthy vegetation) chosen by elephants. Still, the authors did not have conclusive results about the patterns of navigation related to the cognitive ability of African elephants (Boettiger et al., 2011). The literature suggests that assumptions about wild elephants’ spatial ability to navigate are still unclear. Thus, African elephants, living in the wild savanna are ideal subjects to study their spatial pattern of navigation. In order to understand the convergence between primates, in this case the capuchins, and the African elephants about their patterns of navigation I used the same method of analysis.

Although it is important to use similar methods to investigate convergence across taxa, the method needs adaptation according to the specie-specific behavior. The method applied in this study takes advantage of the capabilities of the technology, including data visualization to construe the analysis about animal behavior in navigation. My Chapter 3 describes, in detail, the methods that can be used to investigate wild animals’ patterns of navigation using existing data.

**Objectives and Hypotheses**

The general objective of this study is to improve our understanding of the convergence in the spatial cognition and navigational systems use among different animal taxa, including understanding what capabilities humans share with other species.
Chapter 2

Objectives

a) Investigate if bearded capuchin monkeys living in open savanna habitat use the route network system of navigation,

b) Assess what types of landscape features offered by the habitat can lead the capuchins to use the route network system, or alternatively a different system of navigation.

Hypothesis:

Because fruit availability is high and spatio-temporally predictable along with a landscape with prominent landmarks in northeastern Brazil, we expected that route-based network system may be sufficient to locate resources within the home range of our study group.

Prediction:

If our hypothesis is correct, a) bearded capuchins would heavily repeat their paths independently of the food source, b) used paths would be highly intersected forming a network, c) locations of intersections and consumed resources would be in close proximity with the route network system. In addition, we analyzed if the intersections of routes were used as nodes, or locations were animals change direction, and if the subsequent movement is visually associated with landmarks and/or resources.

Chapter 3

Objectives:

a) Investigate if our individual African elephants leaving in an open savanna share similarities in their patterns of navigation when compared with other species living in analogous habitat,
b) Compare intra-individual and inter-individual patterns of navigation in the savanna of Kruger National Park, using existing GPS data.

**Hypothesis:**

Savannas promote the use of route network system. The use of route network is not considered the lack of cognitive ability to locate resources. However, the characteristics of open savanna offer opportunities for animals to visually access and memorize important locations.

**Prediction:**

If the animals learn to use and encode routes and paths that offer resources they would memorize these resources and would more frequently repeat routes (entire day of navigation) and paths (segment of routes) rather than the use different ones. Alternatively, if the openness and visual access of the environment does not determine the use of route network system, especially because of seasonal lack of resources, animals would have to maintain an internal representation of their home range, using a system consistent with cognitive maps.

**Chapter 4**

**Objectives:**

a) Document the method used to compare the patterns of navigation across taxa, using mammals with high levels of cognition: primates and elephants.

b) Use existing GPS data, GIS-based method, and Remote Sensing to investigate the pattern of navigation of wild animals using existing data.

This dissertation will conclude with a final Chapter 5 that summarizes the findings and contributions of these studies. I will add concluding remarks and suggestions for future research.
References


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CHAPTER 2

BEARDED CAPUCHINS (SAPAJUS LIBIDINOSUS) USE A ROUTE-BASED SYSTEM TO NAVIGATE THE BRAZILIAN CERRADO-CAATINGA ECOTONE

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Abstract

Many studies indicate that wild primates use route-based network on a topological system to navigate, while few of them find evidence for the use of a Euclidean system, or cognitive maps. A route network can be an efficient pattern of navigation when resources are predictable and associate with landmarks. Alternatively, a Euclidean system may be effective when resources are unpredictable and out-of-sight. We tested the prediction that bearded capuchin monkeys in a savanna landscape, with prominent landmarks and abundant and predictable plant food sources will use a route network to navigate. We investigated the spatial navigation of wild bearded capuchins (*Sapajus libidinosus*) in the *Cerrado-Caatinga* ecotone of Fazenda Boa Vista, Gilbués, Brazil. We analyzed 200 daily routes of one wild capuchin group during four consecutive years of study. Results show that the group traveled by re-uses paths to visit resources that in their majority were located within 100 meters of their route network; the intersections of routes were associated with prominent landmarks; and bearded capuchins exploit repeated diverse path to arrive at familiar food sources. Differences in social organization, diet, culture, and habitat with black capuchins (*Sapajus nigritus*) suggest that related congeners display varied navigation patterns in different environments. We suggest that route network is default navigation pattern in diverse environments. The remaining question is what environment circumstances promote the use of presumably more cognitive demanding Euclidean system.

Keywords: Bearded capuchin monkeys, route-based network, food availability, landmarks, *Sapajus libidinosus*
**Introduction**

Different species successfully move through space relying on different navigational systems and the type of spatial information they are able to access, such as memory of routes and landmarks (Byrne, 2000; Suarez, 2014). An animal can maintain spatial information about the position of resources, the direction and distance to itself, calculating the most efficient travel routes through stored spatial information about geometric relationships among features in their environment, using what is reported as Euclidean system of navigation (Dyer, 1996; Gallistel, 1990; Wang & Spelke, 2002).

Alternatively, a variety of animal taxa navigates efficiently by encoding a set of learned and interconnected sequences of landmarks that function as beacons to nearby resources, using what is called a route-based network navigation system (Garber, 2000; Poucet, 1993). The route-based network is characterized by the repetition of travel paths following a sequence of landmarks. When navigating through their home range animals combine many paths linked by points of intersections, which are suggested to be locations where animals reorient themselves to follow the next path (DiFiore & Suarez, 2007; Garber, 2000).

Wild primates are generally considered good examples of animals that navigate based on Euclidean systems, due to their alleged capacity of traveling directly to food sources within their typical large home ranges. In other words, primates can efficiently revisit important resources (R. Byrne, 2000; Milton, 2000; Valero & Byrne, 2007). Nevertheless, the evidence suggests that many primate species navigate in a pattern consistent with a route-based network (DiFiore & Suarez, 2007; Erhart & Overdorff, 2008; MacKinnon, 1974; Noser & Byrne, 2010; Noser & Byrne, 2007; Porter & Garber, 2013; Sigg & Stolba, 1981). In addition, primates, as has been described for other taxa (Sprague-Dawley rats, (Margules & Gallistel, 1988); *Odontomahus*...
hastatus, (Rodrigues & Oliveira, 2014); Long Evans rats, Rattus norvegicus, (Shettleworth & Sutton, 2005); Hymenopterans, (Wehner, 1992); golden hamsters, Mesocricetus auratus (Etienne, Teroni, Hurni, & Portenier, 1990), may rely flexibly on route-based network or Euclidean navigation systems depending on what environmental features are more efficient or beneficial (Presotto & Izar, 2010).

For taxa inhabiting a wide range of habitats, such as the Neotropical genus Sapajus (formerly the robust species of Cebus; see Lynch-Alfaro et al., 2012), this view predicts intrataxa variation in navigational strategies, in accord with local habitat conditions. Studies on spatial cognition in Sapajus indicated that black capuchin monkeys (S. nigritus) inhabiting an area of montane Atlantic Forest in Brazil (PECB) relied on both route-based network and Euclidean strategies, depending on food distribution and availability. In PECB, fruit availability is low and spatiotemporally unpredictable (Izar, 2004; Izar et al., 2012). In this context when monkeys were mainly feeding on uniformly distributed foods, they navigated through repeated paths, in a pattern consistent with a route-based network system. When rich fruit sources became available they repeatedly revisited fruit trees using different direct paths, even in the absence of associated visible landmarks that could function as beacons, in a pattern consistent with a Euclidean system (Presotto & Izar, 2010).

In this report, we examine the pattern of navigation of bearded capuchin monkeys (Sapajus libidinosus). We studied a group of wild bearded capuchins living in an area within the Cerrado-Caatinga ecotone (Fazenda Boa Vista, FBV). At FBV there is no seasonality in fruit availability (Izar et al., 2012). Moreover, predictability of fruit resources is higher than in PECB. In PECB, during 2002, 2006, 2007 and 2008, from the 90 species of fruits eaten by black capuchins, 5.5% (N= 6) produce fruit at five-year intervals, and only 3.4% (N=4) occurred
annually. The fruiting period at PECB is short for most plant species (range 1 to 3 months) (Izar et al., unpublished data). In FBV, during the period encompassed by this study, 51 plant species considered as patchy food sources were included in the *S. libidinosus*’ diet. Among them, 25.5% (N=13) were eaten every year, including three species of palms that bear coconuts all year around; 21.5% were eaten in three of the four years, and 33.3% were eaten in two years (Verderane & Mendonça-Furtado unpublished data). Fruit trees are important resources for bearded capuchin monkeys at FBV (Verderane, Izar, Visalberghi, & Fragaszy, 2013). However, in addition to the fruit trees, bearded capuchins travel to a type of feeding location that most monkey species do not, anvil sites, where the monkeys crack palm nuts using stones as hammers (D. Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004b). Although capuchins do not use nuts and other encased seeds as their primary food source, spending on average just 2% of their foraging and feeding time cracking nuts, they perform the activity routinely throughout the year (Spagnoletti et al., 2012). In addition, *S. libidinosus* face smaller intervals of fructification and higher amount of available fruit year around, which sharply differ from those of *S. nigritus* that rely on unpredictable resources, and higher intervals of fructification (Izar et al., 2012).

Because fruit availability is high and spatio-temporally predictable along with a landscape with prominent landmarks in FBV, we expected that route-based network system may be sufficient to locate resources within the home range of our study group. If our hypothesis was correct, a) bearded capuchins would heavily repeat their paths independently of the food source, b) used paths would be intersected forming a network of routes, c) locations of intersection and consumed resources would be in close proximity with the route network system. In addition, we analyzed if the route intersections were locations were animals change direction, and if the subsequent movement is visually associated with landmarks and/or resources.
Methods

Study Area

This study was conducted at Fazenda Boa Vista, (hereafter FBV) in Gilbués, Piauí, Brazil (9° 39’S 36”, 45° 25’ 10”W). FBV is a privately owned land in the *Cerrado-Caatinga* ecotone (Oliveira & Marquis, 2002) at approximately 420 meters (m) above sea level (Figure 2.1). The ecotone *Cerrado-Caatinga* presents a heterogeneous canopy cover, divided in five different physiognomic or vegetation structures (Vourlitis & Rocha, 2011): *cerradão*, *cerrado sensu strictu*, *campo cerrado*, *campo sujo* and *campo limpo*. The altitude of the trees varies among the five physiognomies with the lowest tree heights averaging 4 m in *Campo Cerrado* and the greatest tree heights averaging 20 m in the *Cerradão* (Vourlitis & Rocha, 2011). This region around FBV is a plain with low-nutrient sandy soils punctuated by sandstone ridges, pinnacles, and mesas, composed of sedimentary rock rising steeply to 20-100 m above the plain (Visalberghi et al., 2007). The sandstone cliffs and plateaus are heavily eroded and there are ephemeral watercourses during the wet season (southern summer - approximately October to April). Annual rainfall at FBV averaged 1290 millimeters (mm) per year (25 mm in the dry season and 1266 mm in the wet season, from 2006 to 2008). The annual mean daily maximum temperature was 32.8°C; the annual mean daily minimum temperature was 21.5°C (Spagnoletti et al., 2012).
Figure 2.1. Topographic map of Fazenda Boa Vista (FBV). Contour lines derived from Aster Satellite Image (30 m x 30 m). Counter lines interval of 10 meters. ZA’s home range (grey).

Subjects

We studied one wild, non-provisioned group of *S. libidinosus* (Zangado, hereafter ZA) composed of up to 17 individuals: two adult males, two sub-adult males, three adult females, one sub-adult female, four juveniles, and five infants.

Geographic Position and Behavioral Data

Data were collected during four consecutive years, from May 2006 to December 2009. During two periods of study the group was followed from dawn to dusk, 4 to 10 days per month, by MPV and NS (from May 2006 to April 2008), and by LCB and OM-F (from October 2008 to
December 2009), with the aid of one trained field assistant. Data were separated into two periods because different GPS technologies were used in the field, which did not affect the results and navigation patterns (see details below). The two periods of data collection of the ZA group generated 200 daily routes (set of navigated paths for one day) in which the observers had the monkeys in view over at least 6 hours from 5:30 am to 6:30 pm.

We followed the group by foot and collected geographic coordinates from the estimated center of the group. The group was observed traveling linearly and spreading, and the overall group spread was lower than 50 m: “the group was generally cohesive and observations were conducted at close distance (1-10 m) from the animals most of the time” (Izar et al. 2012; p. 4). When the group was lost before 6:30 pm, then the last geographic coordinate location was our last coordinate recorded. From May 2006 to April 2008, geographic coordinates were collected using an Etrex GPS (Garmin) at 20-minute intervals. Satellite signals were always received by our GPS with ≤ 10 m accuracy. In the second period, from September 2008 to December 2009, we used the Garmin GPS MAP 60 CSx and geographic coordinates were collected at 5-minute intervals with 3 to 5 m accuracy. We reduced the GPS data collection intervals from 20 to 5 minutes to match the procedures applied by Presotto & Izar (2010) in the Atlantic Forest. Additionally, GPS locations of fruit trees were collected when the group stopped to feed for at least five minutes during all the 200 days.

In this study, to analyze route-based network we considered paths, daily routes, landmarks, stopping points and nodes, as defined in Figure 2.2. From sequential geographic coordinate locations we derived the paths traveled by the monkeys. We did not take into account the width of the paths and did not assume its width, since our objective was to measure the length of the paths. We used the sequence of paths to derive the routes navigated by bearded
capuchins. We compared the data from the two periods to confirm its consistency. Paths were traced and analyzed using ArcGIS 10.x.

Method Adaptation and Data Validation

At FBV, capuchins travel along and over steep ridges. Whenever possible in the first study period, observers climbed the ridges and collected geographic coordinate points close to the animals (less than five meters). In the second period, observers used an optical range finder to project the coordinate’s distance from the observers’ position on the flat land. Then, we projected the range finder distance for each path where the animals crossed the ridges. We superimposed these paths on those generated by the observers collecting data with the animals crossing the hills. Paths from the second period matched the paths from the first period. Paths
from the first study period (black), and the second study period (grey) formed intersections in the same locations (Figure 2.3). These intersections generated by combining all the paths were considered the nodes of our analysis. We used ArcGIS 10 to superimpose the 200 days data set.

![Figure 2.3](image)

**Figure 2.3.** FBV located in the South of Piauí State. The total routes created from the two periods of data collection 2006-2007 (black) and 2008-2009 (grey) with the 19 nodes (black circles) occurring in the same location during both periods

**Identifying Paths as Habitual-Traveled Routes**

To investigate whether ZA group navigated using a route-based network we adopted the method used by Presotto & Izar (2010), devised by Di Fiore & Suarez (2007). Using ArcGIS 10, paths were separated in layers and were plotted together by days, months and years. We built layers for each month and visually compared the layers for each month with each other month through four years. For example, the paths of April and May were plotted together, then another layer was created and the common paths for April-May were traced on the new layers. Superposition of georeferenced layers in the map allowed us to identify all paths repeated within a distance of 50 m, the assumed visual detection range of an individual bearded capuchin
monkey in a forest (Janson & Di Bitetti, 1997). In the Cerrado-Caatinga ecotone, the visual
detection is probably higher, but we used the 50 m previously applied in forests. Same paths
farther than 50 m from each other were not used in this analysis. We then created the route
network (Presotto & Izar, 2010) by connecting all paths repeated at least four times (Figure 2).

Identifying Nodes and Change Direction

Following the procedures set by Di Fiore and Suarez (2007) we overlapped the paths,
which in turn became the route network connected by intersections. For each visited resources
(food trees and anvil sites) we traced back the last intersection (nodes) the animals went across
and verify the changes in angles. We verified the change in direction from the intersection to the
next resource. After passing the intersection, the following path was coded as: same cardinal
direction or change in cardinal direction (North, South, East and West). We displayed the routes
in ArcGIS 10.x, and then we created a vector line to the internal angle of the navigated path.
Each angle of 60 degrees or higher was classified as one change in cardinal direction; angles
smaller than 60 degrees were classified as no change in direction. The 60 degrees change
direction is a conservative value. Angles of 45 degrees could be a threshold, but studies with
human subject’s memory of turns show that memory improves near right-angle connections
(Hillier, 2012; Sadalla & Montello, 1989).

Classification of Paths and Routes to Specific Resources as ‘Same’ or ‘Different’

Following the procedure used by Presotto & Izar (2010), we classified all the paths
traveled by the animals from the last stop point (see Figure 2.2) to the next feeding tree, as
‘different’ or ‘same’. To classify the routes we visually assessed and classified all the routes as
‘different’ when the entire daily route to reach repeated resources was different than any other route to reach the repeated resource and as ‘same’ route when the entire daily route was exactly the same at least one other day to reach the repeated resource. We superimposed the 200 routes in pairs using ArcGIS 10. Same route criteria include routes displaced less than 50 m from each other. Paths were differentiated in the same way. If the animals approached repeated trees using a reverse entire route or path (i.e. the same route in the opposite direction) it was considered as ‘same’ route or path. We expected the paths to be repeated more often than the routes, illustrating the flexibility of reaching available resources by repeating paths, rather than the entire daily route, resulting in a system previously identified as route-based network (Poucet, 1993).

**Classification of Paths from the Intersections to Resources**

To evaluate the hypothesis that bearded capuchins could use the intersections as nodes to plan their next goal, we classified all the paths traveled by the animals after they crossed the nodes to the next feeding tree, as ‘different’, when the path to reach repeated resources was different than any other to reach the same resource or ‘same’, path when the path was exactly the same as on at least one other day. We tested whether the proportion of the repeated visits bearded capuchins used to reach food source was statistically equal to 75%, testing the results previously reported for *Lagotrix* that navigated within habitual routes in over 75% of the locations (Di Fiore & Suarez, 2007). We used a binominal test to verify this hypothesis (two tailed). Statistical analyses were performed using STATA 10.0.
Location of Food Sources with Respect to Route Network

Repeated paths were used to identify the route-based network. The entire data set of routes was designated as route-based network. Following Presotto & Izar (2010), using the Proximity Analysis Tool in ArcGIS 10, we conducted buffer analysis to estimate the proportion of (a) total geographic coordinate points, (b) feeding trees, (c) sleeping sites, and (d) anvil sites (stones used as anvils to crack open nuts (Verderane et al., 2013) used by the animals that fell within zones that were 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 150, 200, 250, 300, 350, 400, 450, 500, and more than 500 m around the route-based network. The buffer analysis tool was used to create bands of predetermined distances around the route-based network. We tested whether the distribution of points that fell in each distance band around the route-based network differed between the two conditions (repeated food source or not) using chi-square test.

Visual Access to Landmarks and Resources

We tested the monkey’s visual access to used resources and landmarks (above defined) associated with the location of each node. We classified the following as landmarks: topographical features such as cliffs and hilltops, rivers and riparian vegetation (taller trees ≥ 10 m). When the monkeys crossed the node, we analyzed the visibility of the next immediate resource (fruit source, anvil sites, and sleeping sites), and its association with the landmarks. We investigated whether resources and landmarks were visible to the monkeys from the last crossed node using the “line-of-sight” 3D analyst tool in ArcGIS 10.1. As previously applied by Presotto & Izar (2010), the “line-of-sight” tool functions by considering the terrain features (digital elevation model, including trees height), measuring the visibility of each two chosen locations. It creates a graphic indicating what parts of the terrain were visible from the starting point over the
extension of the path to the resource. Therefore, after crossing the nodes, we accounted for the proportion of time the monkeys changed directions, associated with: a) visible resources, b) visible landmarks, and c) when both, resources and landmarks were visible or invisible at the same time.

This research complied with protocols approved by the Animal Research Ethics Committee of Institute of Psychology of University of São Paulo, Brazilian legal requirements, and the principles for the American Society of Primatologists for the ethical treatment of primates.

**Results**

During the 200 days for which we analyzed travel, the ZA group navigated on average 1445 m per day through a route network summing 16 kilometers (km) total. We identified 170 paths repeated between four up to twenty times during the study period. The repeated paths were on average 613 m in length (Sd: 242 m; range: 287 to 1056 m). The monkeys visited 925 fruit sources during the study period. We identified 19 intersections crossed at least four times, acting as nodes along the route network. During the 200 days, the ZA group crossed the 19 intersections 316 times (in some cases more than once a day). When crossing the intersections in 60% (N=188) the monkeys changed travel direction, while in 40% (N=128) they continued traveling in the same direction. Only in the 188 times the ZA group changed direction after passing the intersection. The line-of-sight analysis showed that capuchins, after passing the intersection to navigate to the next food source, could visually access the landmark associated with resources in 100% of the cases, while the immediate visited resources *per se* was visible in 53% of the cases.
In the 128 times they continued traveling in the same direction after crossing an intersection, the capuchins were not able to see the next goal (food source and anvil sites), nor the proximate landmark (Figure 2.4).

![Image of line-of-sight measured from intersections towards resources and prominent landmarks (digital elevation model). The black segments of the line-of-sight show the invisible access, while the white segments show visibility from the determined location to the landmark of resource.]

Figure 2.4. Example of line-of-sight measured from the intersections ♠ toward to resources ▲ and the prominent landmarks (digital elevation model). The black segments of the line-of-sight show the invisible access, while the white segments show visibility from the determined location to the landmark of resource.

Seventy-four percent of the 8,904 geographic locations indicating the monkeys’ position fell within 50 m of the route-based network. Eighty-one percent of fruit trees on which they fed were located within 50 m from the habitual route system, 80% of their sleeping sites were within 50 m from the habitual routes, and 73% of the anvil sites locations were within 50 m from the habitual routes (Figure 2.5). The repeated paths occurred nearby the watercourse, and in the
transition of the slope between the hills and plain, with the longest repeated path occurring in the plain.

![Graph showing cumulative proportion of location across distance bands]

**Figure 2.5.** Cumulative proportion of: coordinate points, feeding trees, sleeping trees, and anvil sites used by bearded capuchins, falling within distance bands around habitual route network

**Repetition of Paths**

When approaching a feeding tree after the previous stop location the animals followed the same path used to visit resources 489 times (83% of our sample, N=589) and a different path 100 times (17%). The proportion of same path .83 was higher than the expected (0.70, p = 0.000) when applying the 70% proportion used for analyzing *lagothrix, atelis* and *nigritus* (DiFiore & Suarez, 2007; Presotto & Izar, 2010). To reach a food source, in 66% of the cases the capuchins traveled by different daily routes (N=181), and in 34% they traveled using the same route (34%). The ZA group proportional travels by different routes .70 was higher than expected .70, p = 0.000.
Using the same procedure we found that after passing an intersection, bearded capuchins traveled to a visited feeding tree using a different path from the previous visit in 109 times out of 192 (57%) and the same path in 43% of the times. Using the assumed 0.70, to visit a feeding tree the proportion of different path was higher than expected, \( p = 0.000 \).

**Discussion**

Confirming our hypothesis, the navigation pattern found for *S. libidinosus* at FBV, includes repeated paths, intersection used as nodes, and landmarks associated with resources along the route network, similarly to the navigational characteristics found in many other primate species in the natural settings (DiFiore & Suarez, 2007; Garber, 2000; Garber & Jelinek, 2006; Milton, 2000; Noser & Byrne, 2007). Bearded capuchin monkeys living in *Cerrado-Caatinga* navigate in a pattern consistent with the route-based network system. We found little or no evidence suggesting the use of a Euclidean travel pattern. They more frequently repeated paths than entire daily routes, constructing different daily routes by combining habitual paths. Nodes are locations where *S. libidinosus* change direction when landmark is used as cues to find resources (Garber, 2000).

Similarly to *Lagotrix* and *Ateles* in the forested environment (Yasuni’s National Park, Ecuador, Di Fiore & Suarez, 2007), bearded capuchins also show a high degree of permanency across multiple years of study, using high proportion (80%) of their resources within 50 m of their route network, in a different fashion found for *S. nigritus* in the Atlantic Forest, that use high proportion (80%) of resources felling around 300 m of their habitual routes (Presotto & Izar, 2010). In our study site bearded capuchins rarely leave the route network system.
The assumption that bearded capuchins, as seed dispersers, could shape the fruit source distribution re-enforcing ecological niches goes against what one of us (Verderane et al., 2013) has shown that the food distribution does not limit the use of the route network system because the plant species consumed by ZA group were available at the same time period in their route network system and in areas they did not visit in FBV. Alternatively, the use of route network system could minimize energetic costs of locomotion in a well-established home range, avoiding risks, and intergroup competition (Verderane et al., 2013).

By constantly repeating paths *S. libidinosus* has flexibility to create different entire routes. Intriguingly, when visiting the subsequent resource immediately after crossing a node, bearded capuchins use more often different than same paths. The ability to combine paths in different route configuration, especially after crossing nodes, suggests that bearded capuchins are able to maintain a spatial knowledge of the location of the nodes in the route network system (Poucet, 1993), using the nodes as point of decision. If the bearded capuchins plan their entire day of navigation, similar to what is suggested to spider monkeys and baboons (Suarez, 2014; Noser & Byrne, 2007), by combining paths and forming different route they have the possibility to diminish the distance between actual locations to the next goal, shortcutting their travel distance.

FBV presents many prominent geographical features (hills, streams, cliffs, and differences in canopy), an ideal landscape to use landmarks. The use of landmarks for orientation has been suggested for many other species (Garber, 1989; MacKinnon, 1974; Sigg & Stolba, 1981; Vlasak, 2006). In the bearded capuchins case, the most traveled paths at FBV occurred closer to the rivers (watercourses), in the transition of the slope of the hills, and among the tallest trees in the area. The topography has been suggested to play a role in navigation in other species.
Here different that was suggested for chimpanzees in forests, that they have easy access to landmarks (Normand & Boesch, 2009), we believe that the geographical features of savanna environment facilitate the use of landmarks, while forests limited the use of prominent features as landmarks.

The bearded capuchin monkeys’ navigational system at FBV is distinctive from the black capuchins’ navigational system in the Atlantic Forest. The monkeys at FBV travel only a third of the distance of the Atlantic Forest capuchins where deviations of up to 1500 m from habitual routes occur (Presotto & Izar, 2010). In addition, black capuchin monkeys used the same paths in only 15% of the recorded geographic locations. Yet, when they reused the same sleeping sites they traveled by different paths 100% of the time to reach it, similar to chimpanzees in the Taï Forest, which also do not typically use the same path to revisit resources (Normand & Boesch, 2009).

*S. libidinosus* and *S. nigritus* are congeners that are thought to have diverged around 400,000 years ago (Lynch Alfaro et al., 2012). Their genus, *Sapajus*, inhabits a range of ecosystems and landscapes, and is notable for the breadth of foods eaten, diversity of foraging techniques, variation in social systems, and diversity in use of terrestrial and arboreal resources across the range of habitats where it is found (D. M. Fragaszy et al., 2004; Izar et al., 2012; Wright et al., 2009). *S. libidinosus* is well known for its tool use ability, whereas *S. nigritus* do not use tools in the forest, although studies in captive or semi-captive conditions do not present species differences for tool use (Freitas & Bicca-Marques, 2009; Ottoni & Izar, 2008). This study has shown another dimension of behavioral diversity in the genus: the spatial orientation system used in navigation. We do not think that the differences we have found reflect a fundamental difference between the species in spatial cognitive processes. Instead, we think
differences in social cohesion (Izar et al., 2012), and navigation patterns reflect flexible accommodation to local circumstances. In our view, a population’s spatial orientation system reflects experience with particular landscapes and resource regimens in time and space, coupled with locomotor preferences.

Conclusions

The comparison with the two species of *Sapajus* shows that the food distribution and availability show flexibility in the genus system of orientation. Thus, we believe our subjects adjust their system according to the food distribution and availability (Presotto & Izar, 2010). Some support for this hypothesis is provided by experimental evidence from captive bearded capuchins (*Sapajus* spp.) that learned to use a different navigational scheme with practice. Fragaszy et al. (2009) showed that captive capuchin monkeys initially try to solve two-dimensional mazes by moving a cursor directly toward the goal, but Pan et al. (2011) showed that with extended practice, bearded capuchins use a more playful strategy to solve the same kind of mazes, looking ahead to see if an alley continues. Future comparative studies may show to what extent landscape differences predict variations in spatial navigational systems.

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References


CHAPTER 3

AFRICAN ELEPHANT PATTERNS OF NAVIGATION: GPS AND GIS SPATIAL ANALYSIS IN KRUGER NATIONAL PARK, SOUTH AFRICA

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Abstract

The question of how animals successfully move through space is debated in the animal navigation literature. Animals visit and re-visit important resources by using specific mechanisms of navigation. While a route-based navigation system allows animals to travel efficiently by using a set of interconnected, learned travel routes, a cognitive mapping system allows animals to calculate efficient and use novel routes through stored spatial information about geometric relationships among features in their environment. The two mechanisms allow animals to re-visit locations and habitat conditions may play a role in determining which mechanism is optimized. Route-based navigation tends to be used by animals when prominent landmarks occur in plain view, while in dense forests animals may need to maintain an internal representation to reach their goals. The later and more costly and demanding mechanism, require animals to form a representation of their habitat. African elephants are long-lived, highly-social and large-brained animals, making them an interesting species for studying modes of navigation.

We expected African elephants to repeat paths more often than create new ones, in a pattern consistent with the use of route-based system find in animals living in open savannas. Utilizing a geographic information system, we analyzed approximately 600 daily routes from four GPS collared female elephants living in the savanna of Kruger National Park, South Africa. Conversely and expected, geospatial analysis revealed that our female elephants in this study used novel paths to reach resources more often than they used repeated paths, suggesting the use of a system analogous to cognitive mapping. These findings contribute to improve the understanding of elephants’ navigation related to the habitat they life, and the convergence in spatial cognition between elephants and other species.

Keywords: African elephants, patterns of navigation, cognitive maps, route-based network
Introduction

The ability of animals to re-visit the location of resources in the wild is important to efficiently forage though the landscape, especially in times of scarcity. Wild animals visit resources by following certain patterns of navigation, which can differ over time period and habitat characteristics (Charnov, 1976). For example, species navigating within larger home ranges encode different types of spatial information in order to find resources such as food, water and shelter. To do so, animals need to be able to leave a resource site and efficiently travel to the next. Yet, the spatial knowledge of species that travel large home ranges is not well-known (Polansky, Kilian, & Wittemyer, 2015), especially when they re-visit resources over time.

The time-place learning ability is essential for animals to revisit locations and associate them with resources in time and space (Zhang, Schwarz, Pahl, Zhu, & Tautz, 2006). Time-place is the ability to learn spatiotemporal characteristics of biologically significant events (Gallistel, 1990), such as food location, predators, and mates. The advantages to learn spatiotemporal variability of resources in the wild is the possibility to maximize the time spending in looking for them.

Deibel et al. (2014) showed that when rewards are displaced at different locations at different times of the day, rats learned when to travel to the rewarded locations. Desert ants (Cataglyphis) are able to travel large distances from their nest and efficiently returning to the nest (Wehner, Michel, & Antonsen, 1996). They navigate along their routes using their visual system, as opposed to ants that rely on pheromones exuded along routes, such as Melophorus bagoti (Kohler & Wehner, 2005). In addition, many species use more than one type of spatial information to navigate, which helps them to avoid errors. For example, social insects that return to their nests such as ants and rats memorize the landmarks around the nest even though they may remember the routes (Wang & Spelke, 2002). Ants are considered very efficient foragers
when they combine two systems, pheromone and visual cues. However, when the systems are in conflict the visual cues are dominant (Harrison, Fewell, Stiller, & Breed, 1989; Klotz, 1987; Kohler & Wehner, 2005). An interesting find is that when ants are placed along their route, they are able to find their way to locate their goals starting from different points (Mangan & Webb, 2012). Ants have been experimentally determined to constantly update their route memories, when traveling through unfamiliar areas for the first time. They learn the paths and store this spatial information with knowledge of previously navigated routes, and use the new routes when it is necessary (Wystrach & Graham, 2012). The information is visually acquired and the ants retain it for their entire lifetime (Kohler & Wehner, 2005; Mangan & Webb, 2012). Honeybees (Apis) also rely on optical information to calculate distances, find direction and consequently navigate to their resources (Wehner, 1992).

Among the mammals, primates optimize energy according to food quality, distribution, and availability (Milton, 2000). They are efficient in navigation due to their high levels of cognition and memory of food locations (Chapman & Chapman, 2000; DiFiore & Suarez, 2007; Presotto & Izar, 2010; Robinson, 1986). However, the decision making process when animals travel to determined locations, and which spatial information is associated with the location of their goals is unclear.

African elephants are ideal subjects to investigate spatial pattern of navigation over time periods. They occupy large home ranges and use a variety of plants as food sources within their habitat (Smit, Grant, & Whyte, 2007). Likewise, water sources also affect the navigation of elephant family units, which may be influenced by distance from water bodies and rivers (Chamaillé-Jammes, Mtare, Makuwe, & Fritz, 2013; Polansky et al., 2015). They also use the strategy of “fission-fusion”, a social system where species living in groups (Filippo Aureli et al.,
2008) split off and change their group size to create subgroups (i.e., fission) when food or water are scarce and fuse into larger groups when resources are plentiful (Kummer, 2006; Moss & Lee, 2011; Wittemyer, Douglas-Hamilton, & Getz, 2005). The strategy of fission into smaller groups, for elephants, may happen more often during the dry season when competition for resources increase (Chapman & L. Chapman, 2000; Terborgh, 1984).

African elephants move in small, gender and age-influenced social units, and they are able to perform long-distance vocal-communication (McComb, Moss, Sayialel, & Baker, 2000), which may facilitate travel decisions. Female elephants and their sub-adult young live separately from mature bulls, although their ranges may overlap (Douglas-Hamilton, Krink, & Vollrath, 2005). The location of elephant bulls is influenced by the location of the female groups, especially if there is an individual in estrus. Female groups live in a multi-level social structure (Archie, Moss, & Alberts, 2006) subdivided into: a) the mother-calf units; b) core groups: mother-calf units combined together (breeding or family groups), c) bond-groups: formed by core groups with high indices of association and elaborate greeting displays, and d) clans – all elephants in a region, whether bond groups or not. The structure of elephant society, in turn, affects their distribution. While some families travel to unfamiliar areas when looking for resources, others stay within their clan familiar areas. The African elephants present fidelity to their home range. For instance, temporally defined home ranges occur in Amboseli National Park, where the elephant families are using the same home range for over 34 years (Moss & Lee, 2011). The analysis about navigation in wild animals, including African elephants has been improved with the use of Global Position System (GPS), including studies highlighting social relationships of captive individuals, showing elephants’ activity budgets by tracking their position in an enclosed environment (Hacker, Horback, & Miller, 2015). Seven female African
elephants traveled on average 0.41 km/h during the daylight (Leighty et al., 2009), while six others traveled an average of 0.36 km/h in a 24-h period (Horback, Miller, Andrews, Kuczaj, & Anderson, 2012). Comparative studies of animals in captivity and in the wild are very important to understanding species-specific patterns of navigation and habitat usage. Yet, results are not clear about the features of the mechanisms of navigation such as: route and path repetition, route network system, or different paths usage (i.e., cognitive mapping) elephants use to find repeated resources.

Using Geographic Information Systems (GIS) we now can verify the efficiency of animal movements and the patterns of navigation they use in the wild, such as home range usage and walking distance within defined time periods (Boettiger et al., 2011), including other factors that may affect navigation. For wild African elephants, the travel rates may vary according to environmental differences, seasonality, resources distribution, and weather factors (Guy, 1976; Viljoen, 1989).

In this study, we first explore the data with descriptive statistics of four females African elephants’ navigation. We assess the individual differences of activity, step length (distance navigated by hour), and the total distance navigated per day. Additionally, we measure the distances individual females keep from the touristic location, roads, and water bodies during the study period. We hypothesized that the African elephants use the route network system of navigation. African elephants living in open savanna, would use a route network as reported for other species living in similar environment (Noser & Byrne, 2007; Chapter 2). Therefore, as evidence of route-based network navigation the elephants would: a) repeat routes and paths more often than using novel ones when re-visiting resources; and b) use intersections of routes and paths as locations where they take decision to the next movement. Alternatively, because African
elephants are considered a species with high level of cognition, they may use a more sophisticated system of orientation cognitive maps or even combine more than one system to find resources in the wild. We also statistically analyzed external variables that may affect elephant daily navigation and the activity of the females, such as temperature, time, rainy and non-rainy days, by using a general linear mixed model.

**Methods**

**Study Area**

Our study area is the southern portion of Kruger National Park (KNP), known as the Skukuza region along the northeastern border of South Africa (Figure 3.1). The KNP is the flagship conservation unit of South Africa, occupying an area of 19,485 square kilometers. The elevation of the Park extends from 200 meters (m) to 840 m, with rich drainage and savanna physiognomies. The average annual precipitation in the area ranges from 401 millimeters (mm) to 600 mm and the minimum and maximum precipitation is uncertain, varying yearly. The dry season typically occurs from October to March, and the wet season from middle October to February). To define our area of interest within the KNP boundaries we used the Minimum convex polygons (MCPs) determined by connecting the peripheral points of our female subjects travel locations as recorded by GPS during the study period.
Figure 3.1. Kruger National Park location, the vegetation prevalence, and our study area, defined by the minimum convex polygons (MCP) determined by connecting the all the peripheral points of our female locations as recorded by GPS during the study period.
Field Data Collection from GPS-Collars

Data were derived from four females African elephants (*Loxodonta africana*) inhabiting the area of interest at Skukuza, KNP. The females were deployed with GPS collars as part of a study conducted in the late 1990s on the effects of contraceptives on elephant social behavior (Fayrer-Hosken et al., 1997). The collars recorded geographic locations at one-hour intervals over a five-month period (October 1998 to February 1999) during the transition from dry to wet season. The original data collection produced 600 daily routes, continuously for 150 days for each individual. These data were collected from four females within the same clam [named and numbered Annabelle (3A), Tara (43), Frieda (45), and Anna (4A)], in order to observe their movements during the use of contraceptives (Barber & Fayrer-Hosken, 2000; Fayrer-Hosken et al., 1997). Our subjects were of reproductive age, and were deployed with GPS collars produced by Lotek Fish and Wildlife monitoring systems (for effectiveness of the Lotek collars in elephants see Douglas-Hamilton, 1996). Collected data of individual ID, positional coordinates; positional accuracy, time and ambient temperature (Table 1) were stored cumulatively in a dedicated bank of nonvolatile random access memory (RAM) within the GPS units and downloaded upon retrieval of the GPS collars at the end of the study.

Table 3.1. Data attributes from the GPS (differential) collars - LOTEK Wireless Fish and Wildlife Monitoring

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lon</td>
<td>longitude in milliseconds (West is negative)</td>
</tr>
<tr>
<td>Lat</td>
<td>latitude in milliseconds (North is positive)</td>
</tr>
<tr>
<td>Time</td>
<td>seconds since midnight, 1/1/1970</td>
</tr>
</tbody>
</table>
The GPS data set for each elephant was collected from an hour intervals for the 24 h period (from 00:00 to 23:00). As reported by Douglas-Hamilton (1998), since the activity collected by the collar represent levels that do not change gradually, an hourly temporal resolution was considered adequate for this study. The activity provided by Lotek (1998) collars is an activity count sensor, which has an arbitrary scale from 0-255 units (Moen, Pastor, & Cohen, 2001). In other words, when an animal is sleeping or resting, its activity should be very close to zero, whereas active behaviors of walking, eating, and running produce relatively high levels of activity captured by change in position over hours (Gervasi, Brunberg, Swenson, & Bowman, 2006). The arbitrary values of activity have been classified for different animals, according to the observed behavior. For elephants we categorize the activity variables as: from 0 to 100, as stationary; from 100 to 150 as foraging, and as 150 to 255 as movement.
collect the data was given to Dr. Richard Fayrer-Hosken by SANParks. The project was funded by the U.S. Fish and Wildlife and was conducted following the protocols of KNP.

**Geospatial Analysis of Navigation**

The descriptive statistics for individual females were calculated using the total locations per female: Anabelle (N=1653); Tara (N=2137); Frieda (N=1874); and Anna (N=2104). We show the mean values for activity, temperature, and the daily navigated distances for each month. All the geographic coordinates were continuously recorded by GPS collars from September 29\(^{th}\) 1998 to February 10\(^{th}\), 1999. We used for this analysis data from four complete months (October, November, December and January). We show the monthly distances the female elephants were from touristic locations, roads and water bodies and made comparisons for each female elephant using Kruskal-Wallis rank test.

**Defining Resources: Forest and Water Identification**

In this study we extracted information about resources distribution (tree patches and water sources) from 1998 at KNP by remote sensing analysis. Remotely sensed satellite imagery has been used to predict the presence of wild animals based on the distribution of resources (Boettiger et al., 2011; Rouget, Cowling, Pressey, & Richardson, 2003). In KNP, the patches of tall trees and water are important resources for elephants (Codron et al., 2006). Some of the trees used by elephants are marula (*Sclerocarya birrea*) and knob-thorn acacia (*Senegalia nigrescens*), and some riparian wetland tree species in KNP include jackal-berry (*Diospyros mespiliformis*), and in the north, Baobab (*Adansonia digitata*). These trees are large in size and located either singularly or in patches within uplands and riparian areas. To classify the tree
patches and water resources we used satellite images acquired in October, 5\(^{th}\) 1998 for our area of interest. We used a publicly available Landsat 5 (30 x 30 m resolution) satellite image of the south portion of Kruger National Park, and the Digital Elevation Model (DEM, ASTER 30 x 30 m resolution). We classified the Landsat 5 image from 1998 to extract the landscape information at the same time of our elephant GPS collar data collection (Scene ID = LT51680771998278JSA00, acquired on 05-10-98). Imagery (path 168, row 77) were acquired from the United States Geological Survey (USGS), Earth Explorer, and GLOVIS databases. Areas with dense vegetation as indicated by higher Normalized Difference Vegetation Index (NDVI) values are considered to have greater forage abundance and/or quality within African forests (Boettiger et al., 2011). Thus, we also computed NDVI values in our classification using ERDAS Imagine image processing software. Water bodies were provided by the KNP GIS center as a vector data layer.

**Classification Method**

The Landsat 5 bands and NDVI were used in a pixel-based classification in order to identify five categories of land cover: grassland, mixed vegetation, woodland or forest, bare soil, and water (Table 3.2).

**Table 3.2. Land Cover classes and features**

<table>
<thead>
<tr>
<th>Class</th>
<th>Land Cover Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>Identified by lower and taller grass</td>
</tr>
<tr>
<td>Mixed Vegetation</td>
<td>Identified shrubs and sparse trees smaller than 10 m</td>
</tr>
<tr>
<td>Forest</td>
<td>Identified by tree density and with trees taller or equal 10 m</td>
</tr>
</tbody>
</table>
Bare soil  Identified by absence of foliage
Water  Consists of perennial rivers, streams, and lakes

The pixel-based classification was performed using ArcGIS10.x and employed a standard supervised classification using the maximum likelihood algorithm. This method required the selection of training areas representative of each land cover class, which were selected from multiple areas of the image. We selected 10 training samples for each class, generating a total of 50 samples (besides shadow and clouds). The signature (or spectral mean) of the training samples was then used to assign classes to the remaining pixels. The Landsat bands were cropped to our area of interest using the Spatial Analyst, Extract by Mask tool (ArcMap 10.1). As re-visited areas of resources, we used only patches of forest and water. Every time our females re-visited a patchily distributed forested area and water we classified the path they took as “different” or “same” (see method below).

Validation of Image Classification

To validate the Landsat image classification we generated random points in the classified Landsat image (using ArcGIS), and then used the confusion matrix or error matrix, which compares the category-by-category basis between the reference data (in this case, high-resolution images and Google Earth) and our results of the supervised classification (Lillesand et al., 2014). From the error matrix we calculated the overall accuracy (total number of correct classified pixel by the total number of reference pixels), the producer’s accuracy (dividing the number of correctly classified pixel in each category by the number of test set pixels used for that category), and the user’s accuracy (dividing the number of the correctly classified pixels in each category
by the total number of pixels that were classified in that category). We then applied the Kappa (or KHAT) statistic that measures the difference between the actual agreement between reference data and the classified data (Lillesand et al., 2014), defined as:

\[
k = \frac{\text{observed accuracy} - \text{chance agreement}}{1 - \text{chance agreement}}
\]

**Daily Routes and Paths**

The data set were separated by day for each individual female. From the daily sequence of geographic coordinates we created the entire daily routes, and consequently paths (segments of routes). For each route we calculated the daily length, the straight-line vector (straight line from the first to the last recorded location of the day), and calculated the ratio between the traveled length and the straight-line. The ratio between the traveled daily route and the straight-line vector was given a value between 0 and 1, and if the result is close to 1, the animals moved more directly along the daily route and did not fully explore the area during that given day, while a ratio closer to 0 indicated the area was explored more during that day. We tested whether the dependent variables of daily distances and activity were correlated with weather variables. We used daily rain amounts in millimeters per day, binary rain (1) and non-rain (0), daily minimum and maximum temperature. We also tested the correlation of the ratio between females’ daily travel and the straight-line distance from the first to the last locations of the day and the rain binary variable and total daily rain. The correlation shows if rainy days affect the exploration of the area. We presented individual differences in activity according to changes in temperature, rain and time of the day.
Do Female African Elephants Use Different or Same Paths to Re-visit Resources?

To investigate if the females re-visit resources using “different” or “same” paths, we: a) displayed the routes day-by-day, b) identified the first visit when the individual was in the water or patchily distribute forest, and c) identified the second visit, d) and classified repeated location, successively for all the other repetitions. We visually assessed the repeated locations of the resources. To avoid using subsequent days as repeated, we for example, visually classify October 3rd as first visit, then October 5th as repeated, and exclude October 4th, and 6th, and successively to the entire data set (Figure 3.2). We classified if the animals reached the repeated locations by using “different” or “same” path. To compare the proportion of “different” and “same” paths our individuals used to re-visit resources, we applied a binomial test using the proportion of .70, already showed to be significant for the movement of other animals (DiFiore & Suarez, 2007; Presotto & Izar, 2010).
Figure 3.2. Forest class used to identify repeated locations. Arrows show the direction the elephants navigated toward to repeated resources.

Do African Elephants Use a Route Network?

In order to compare spatial navigation of African elephants with other species, we replicated a methodology used to study other species (Chapter 2) living in diverse landscapes (Presotto & Izar, 2010, Chapter 2). Thus, to analyze interspecies navigation we used the same method already applied in primate species. Our method consists of building daily routes as layers for each monthly data set and comparing layers between pairs of days and months. For example, the October routes were compared during the month, and then plotted with November routes. When the animals use the same route or path during both months, another layer was created and the common routes for October and November were traced. When all repeated paths for each
month were plotted, and we found two or more repeated paths we created the route network system. Superposition of all repeated paths (using ArcGIS 10.1) derived from the females’ daily routes allowed us to visually identify them, and then we created the route network system by connecting all paths that were repeated at least two times during the period of data collection (Figure 3.3). The route network was super-imposed on all the actual repeated locations. Using the Proximity Analysis Tool in ArcGIS 10.1, we then conducted buffer analyses to estimate the proportion of the total elephant positions each individual location fall within 500, 1000, 1500, 2000, 2500, 3000, 3500, 4000, 5000 and more than 5000 meter zones around the habitual route network. The buffer analysis tool creates a zone of predetermined distance around the habitual routes and then creates a list of all coordinate points that are located within the zone (Figure 3.4). We then tested whether the proportion of the same routes and different routes present statistically significant results (binomial test). We used the buffer analysis to show how far the total locations of our females were from the roads (human influenced areas), using the same above mentioned pre-determined distances.
Figure 3.3. a) Repeated paths used by all females; b) the connection of the repeated paths forming a route network system
Figure 3.4. Female locations around the buffer band of 500 meters in the North and the South of their home range

Distances from Touristic Locations, Roads and Water Bodies

We run the buffers around the roads. We used the total data set (N=7708) and show the proportion of locations falling within 500, 1000, 1500, 2000, 2500, 3000, 3500, 4000, 5000 and more than 5000 meter zones to observe if our females varies their distance across the study period. The touristic activity may affect the presence of the females on the road.

Female Activity

To test if our variables can predict the activity of the females during our study period we used a generalized linear mixed model (GLMM) testing the behavioral variable “activity”. As
fixed variables we used: temperature, rain, class, and time. We set the individuals and months as random variables.

**Alternative Patterns of Navigation**

While analyzing the “different” and “same” paths the female elephants use to reach repeated resources locations, we noticed an intriguing pattern of navigation. While some animals use the same routes and paths in parallel, the female elephants revisit certain locations by re-use a small length of an already used route. They also re-visit the locations by crossing a portion of the previously used routes (Figure 3.5). We then re-analyzed the “different” and “same” category for paths by creating four categories (1. *Different-crossing*, 2. *Different-non-crossing*, 3. *Same-crossing*, and 4. *Same-non-crossing*) and used chi-square to test if they were significantly different. We tested the hypothesis that female elephants use a higher proportion of different routes when they cross the previously used routes more often than when they use the same route. If this is the case, the *Different-crossing* category would be statistically significant higher than expected by chance.
Figure 3.5. Annabelle crossing routes, a) shows the first day observation: route first time observed in October 3rd, re-visited and crossed area, using different path and route to get there second time on October 19th, re-visited and crossed area, using different path and route to get there third on October 20th, idem on October 21th, and idem on October 30th.
Are the Crossing Locations Randomly Distributed?

We created a layer with the locations crossed by the female elephants, and we run the cluster analysis of the crossing points using the Cluster and Outlier Analysis tool in ArcGIS 10.2. This analysis identifies statistically significant spatial clusters of the plotted geographic locations. The tool uses the Moran’s I value, a z-score, and a p-value. The z-value and the p-values represent the statistical significance of the index values. Statistical significance is set at the 95% confidence level.

Results

The Landsat image classification presented an overall accuracy of 66%. Table 3.3 shows the results of the classification data and the reference data (High-resolution image and Google Earth) as well as the producer’s accuracy and the user’s accuracy. The kappa statistic showed that 52% of our classification was satisfactory.

Table 3.3. Error matrix presenting the results of the classification, the producer’s and user’s accuracy
<table>
<thead>
<tr>
<th></th>
<th>Producer's Accuracy</th>
<th>User's Accuracy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BS</td>
<td>BS</td>
</tr>
<tr>
<td></td>
<td>2/3</td>
<td>2/3</td>
</tr>
<tr>
<td></td>
<td>67%</td>
<td>67%</td>
</tr>
<tr>
<td></td>
<td>Shadow</td>
<td>Shadow</td>
</tr>
<tr>
<td></td>
<td>3/5</td>
<td>3/3</td>
</tr>
<tr>
<td></td>
<td>60%</td>
<td>100%</td>
</tr>
<tr>
<td></td>
<td>Grass</td>
<td>Grass</td>
</tr>
<tr>
<td></td>
<td>34/47</td>
<td>34/45</td>
</tr>
<tr>
<td></td>
<td>72%</td>
<td>76%</td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td>Mixed</td>
</tr>
<tr>
<td></td>
<td>9/12</td>
<td>9/26</td>
</tr>
<tr>
<td></td>
<td>75%</td>
<td>35%</td>
</tr>
<tr>
<td></td>
<td>Forest</td>
<td>Forest</td>
</tr>
<tr>
<td></td>
<td>18/31</td>
<td>18/24</td>
</tr>
<tr>
<td></td>
<td>58%</td>
<td>75%</td>
</tr>
<tr>
<td></td>
<td>Water</td>
<td>Water</td>
</tr>
<tr>
<td></td>
<td>0/0</td>
<td>0/3</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Cloud</td>
<td>Cloud</td>
</tr>
<tr>
<td></td>
<td>3/6</td>
<td>3/0</td>
</tr>
<tr>
<td></td>
<td>50%</td>
<td>0</td>
</tr>
</tbody>
</table>

From September 1998 to February 1999 the savanna in northeastern South Africa presents a transition from dry to wet season (Figure 3.6), with minimum average temperature of 13°C and maximum of 33°C.

**Figure 3.6.** Average minimum and maximum temperatures and rain in milliliters during the study period. Data provided by South Africa Weather Service

Monthly descriptive statistic shows inter individuals mean values of step length (distance traveled by hour, Table 3.4), and activity (Table 3.5). We also shows the average distances navigated by day for each female (Table 3.6), and the differences in distance the individuals keep from touristic locations, roads and water bodies.
Weather Affecting Female Elephants Distance of Navigation

Correlation of ratio and rain showed that the rain (rainy days vs. non rainy days) has an effect on linearity of the daily route females navigate, rho: .149, p=0.001 at 99% confidence level. As expected, the females explore smaller areas in days with rain.

Table 3.4. Average of the Step Length navigate by hour navigated Step Length during the study period in meters

<table>
<thead>
<tr>
<th></th>
<th>October</th>
<th>November</th>
<th>December</th>
<th>January</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anabelle</td>
<td>426</td>
<td>502</td>
<td>614</td>
<td>612</td>
</tr>
<tr>
<td>Frieda</td>
<td>277</td>
<td>424</td>
<td>636</td>
<td>796</td>
</tr>
<tr>
<td>Tara</td>
<td>389</td>
<td>437</td>
<td>532</td>
<td>423</td>
</tr>
<tr>
<td>Anna</td>
<td>465</td>
<td>487</td>
<td>896</td>
<td>796</td>
</tr>
</tbody>
</table>

As expected, the step lengths shows monthly inter individual differences. Anabelle, Anna and Frieda increased the distance they navigated by hour from October to January. Tara only significantly increased her hourly distance of navigation during December. December presented the highest amount of rain. This may suggest that once the rain increases the quality of the vegetation may increase too, giving the animals more opportunity to range.

Table 3.5. Average Activity (0 – 255) during the study period

<table>
<thead>
<tr>
<th></th>
<th>October</th>
<th>November</th>
<th>December</th>
<th>January</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anabelle</td>
<td>168</td>
<td>145</td>
<td>133</td>
<td>190</td>
</tr>
<tr>
<td>Frieda</td>
<td>182</td>
<td>179</td>
<td>155</td>
<td>107</td>
</tr>
<tr>
<td>Tara</td>
<td>65</td>
<td>87</td>
<td>65</td>
<td>49</td>
</tr>
<tr>
<td>Anna</td>
<td>206</td>
<td>207</td>
<td>192</td>
<td>107</td>
</tr>
</tbody>
</table>

The activity also varies among the individuals, with Tara being the less activity individual during the study period. Tara was a younger female, Anabelle’s daughter. They did not leave the area of Skukuza. Tara and Anabelle traveled around Skukuza for the entire period. Yet, Tara activity confirmed the smaller distance she navigated during the study when compared
to the other females. However, the results were not significant (Appendix 3, graphics activity by
time). Calculating all the distance traveled by day during the studied period the mean value of
the females travel are presented on Table 3.6.

Table 3.6. Average daily navigation distance in meters for the total study period

<table>
<thead>
<tr>
<th>Daily Navigation (m)</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annabelle (N=107)</td>
<td>7400</td>
</tr>
<tr>
<td>Frieda (N=115)</td>
<td>7480</td>
</tr>
<tr>
<td>Tara (N=131)</td>
<td>7112</td>
</tr>
<tr>
<td>Anna (N=131)</td>
<td>9559</td>
</tr>
</tbody>
</table>

The averages daily distance varies inter individuals. Anna was the individual that present
the larger travel distance during the study period; she was also the female that traveled to the
north part of the home range.

Inter-individual Distance Differences From Touristic Locations, Roads and Water Bodies

There is an inter-individual difference between the distances the females keep from three
main locations inside of the KNP: touristic locations, roads, and water bodies (Table 3.7).
Graphics to illustrate the differences are on Appendix 1.

There are inter-individual differences from the distance the females keep from human-
influenced locations, such as touristic locations and roads. Some individuals are easier to be
habituated to humans, while others do not. From 5 to 6 am the animals seem to avoid the roads,
but during the rest of the day the elephant locations showed indifference to being near or
crossing the roads. This provides preliminary evidence that human-elephant interactions might
affect the behavior of the elephants. Based on our results, elephants appear to avoid the roads,
with only 20% of the total locations falling at 500 m from the roads (Figure 3.7). Yet, when
compared females present statistical significant differences for the distance they keep from the all the three locations.

![Figure 3.7](image)

**Figure 3.7.** The buffers around the roads show that the elephants do not use the roads intensively. Only 20% of their locations are around 300 m from the roads; the rest of the collected locations were farther from the roads

**Table 3.7.** Differences in distance the females keep from the resources during the study period

<table>
<thead>
<tr>
<th></th>
<th>Touristic Locations</th>
<th>Roads</th>
<th>Water Bodies</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>October</strong></td>
<td>H=357.497, 3 d.f., P =0.0001</td>
<td>H=295.784, 3 d.f., P =0.0001</td>
<td>H=95.599, 3 d.f., P =0.0001</td>
</tr>
<tr>
<td><strong>November</strong></td>
<td>H=24.704, 3 d.f., P =0.0001</td>
<td>H=21.217, 3 d.f., P =0.0001</td>
<td>H=267.175, 3 d.f., P =0.0001</td>
</tr>
<tr>
<td><strong>December</strong></td>
<td>H=466.373, 3 d.f., P =0.0001</td>
<td>H=357.683, 3 d.f., P =0.0001</td>
<td>H=91.969, 3 d.f., P =0.0001</td>
</tr>
<tr>
<td><strong>January</strong></td>
<td>H=165.924, 3 d.f., P =0.0001</td>
<td>H=366.763, 3 d.f., P =0.0001</td>
<td>H=52.476, 3 d.f., P =0.0001</td>
</tr>
</tbody>
</table>

**Generalized Linear Mixed Model (GLMM)**

The generalized linear mixed model results show that time and temperature are significant predictors of the females’ activities (Figure 3.8). As fixed coefficient the time shows statistical significance for morning, afternoon and night, but temperature (Table 3.8) affects activity only during the night time (22 pm to 5 am), with time affecting activities along the day.
Figure 3.8. Time was categorized as: 1. from 22 pm to 5 am; 2. from 5 am to 10 pm; 3. from 10 to 13 pm; 4. from 13 to 17 pm, and 5. from 17 to 22 pm

Table 3.8. Results of the Fixed Coefficients variables time and temperature (range from 12.5 to 34.5 C)

<table>
<thead>
<tr>
<th>Model Term</th>
<th>Coefficient</th>
<th>Std. Error</th>
<th>t</th>
<th>Sig.</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>151.729</td>
<td>26.4953</td>
<td>5.727</td>
<td>.000</td>
<td>99.791</td>
<td>203.667</td>
</tr>
<tr>
<td>22 pm to 5 am=1</td>
<td>-64.507</td>
<td>2.8905</td>
<td>-22.317</td>
<td>.000</td>
<td>-70.173</td>
<td>-58.841</td>
</tr>
<tr>
<td>5 am to 10 am=2</td>
<td>6.854</td>
<td>2.9817</td>
<td>2.299</td>
<td>.022</td>
<td>1.009</td>
<td>12.699</td>
</tr>
<tr>
<td>10 am to 13 pm =3</td>
<td>7.812</td>
<td>3.7133</td>
<td>2.104</td>
<td>.035</td>
<td>.533</td>
<td>15.091</td>
</tr>
<tr>
<td>13 to 17 pm=4</td>
<td>9.709</td>
<td>3.2668</td>
<td>2.972</td>
<td>.003</td>
<td>3.305</td>
<td>16.113</td>
</tr>
<tr>
<td>17 to 22 pm=5</td>
<td>-.205</td>
<td>.1372</td>
<td>-1.491</td>
<td>.136</td>
<td>-.474</td>
<td>.064</td>
</tr>
<tr>
<td>Temperatur [=1]</td>
<td>.831</td>
<td>.1599</td>
<td>5.196</td>
<td>.000</td>
<td>.517</td>
<td>1.144</td>
</tr>
<tr>
<td>Temperatur*[=2]</td>
<td>-.291</td>
<td>.1599</td>
<td>-1.817</td>
<td>.069</td>
<td>-.604</td>
<td>.023</td>
</tr>
<tr>
<td>Temperatur*[=3]</td>
<td>-.343</td>
<td>.1903</td>
<td>-1.803</td>
<td>.071</td>
<td>-.716</td>
<td>.030</td>
</tr>
<tr>
<td>Temperatur*[=4]</td>
<td>-.246</td>
<td>.1651</td>
<td>-1.490</td>
<td>.136</td>
<td>-.570</td>
<td>.078</td>
</tr>
</tbody>
</table>

a

b
**Route-based Network**

The binomial test applied to each female elephant, shows Anabelle’s paths to re-visit patches of trees and water did not show a significant difference between using “different” or “same” paths to reach repeated locations (.70, p= 365). Annabelle was the only female that presented a non-significant difference using the proportion of .70. The binomial test using the same proportion of .70, shows statistically significant differences for Frieda (p=0.004), Tara (p=000), and Anna (p=000). Tara, Frieda and Anna use different paths to re-visit resources proportionally higher than expected. The crossing location analysis shows, as expected, that when the females use different paths, they more often cross previously used ones. The high significant clustered locations are 32% of all (N=866) crossed locations (Figure 3.9).

We found an intra-individual difference in Annas’ patterns of navigation. The highest number of repeated paths occurred in the north part of the females’ home range. Anna, the individual that travels to the North presented the use of same routes higher than the expected when compared with the other individuals. Anna also use the Different-crossing category higher than the expected, similar to all the other females. Anna navigational behavior changes when she moves to the north. Most of the crossed locations occur when the females use the fission-fusion strategy, in the North area. As expected the Different-crossing category was significant higher than expected by change (Figure 3.10).
Figure 3.9. The map represents the results of Cluster Analysis from all the locations that were crossed by the four female elephants. Black dots are the high clustered crossing locations, and the red dots are the low clustered crossing locations.
Chi-square results for the four tested categories representing the pattern of navigation. The category *Different-routes-and-crossing* was higher than expected by change for all individuals.

<table>
<thead>
<tr>
<th></th>
<th>Observed N</th>
<th>Expected N</th>
<th>Residual</th>
<th></th>
<th>Observed N</th>
<th>Expected N</th>
<th>Residual</th>
</tr>
</thead>
<tbody>
<tr>
<td>Different-Crossing</td>
<td>35</td>
<td>32</td>
<td>3</td>
<td>Different-Crossing</td>
<td>66</td>
<td>42.5</td>
<td>23.5</td>
</tr>
<tr>
<td>Different-Non-Crossing</td>
<td>40</td>
<td>32</td>
<td>8</td>
<td>Different-Non-Crossing</td>
<td>37</td>
<td>42.5</td>
<td>-5.5</td>
</tr>
<tr>
<td>Same-Crossing</td>
<td>17</td>
<td>32</td>
<td>-15</td>
<td>Same-Crossing</td>
<td>42</td>
<td>42.5</td>
<td>-0.5</td>
</tr>
<tr>
<td>Same-Non-Crossing</td>
<td>36</td>
<td>32</td>
<td>4</td>
<td>Same-Non-Crossing</td>
<td>25</td>
<td>42.5</td>
<td>-17.5</td>
</tr>
<tr>
<td>Total</td>
<td>128</td>
<td>Total</td>
<td></td>
<td></td>
<td>170</td>
<td>Total</td>
<td></td>
</tr>
</tbody>
</table>

**Figure 3.10.** Chi-square results for the four tested categories representing the pattern of navigation. The category *Different-routes-and-crossing* was higher than expected by change for all individuals.

**How Far Do the Female Elephants Travel from the Route Network?**

One of our four females traveled to the north section of the study area as part of their home range, suggesting the use of fission-fusion strategy to access resources in an area around 40 kilometers away from the clam’s familiar area, in the south. Because the clam lived in Skukuza at the time of the data collection and was selected in this area, their familiar area of navigation is presumed to be in the Skukuza region, since elephants present site fidelity (Moss & Lee, 2011). Here we presented how far the females navigated from their route network system, including in this analysis the data we separated for Anna: South and North navigation, since she was the one who traveled away from the herd, and then we measure the distance from the route network system for these two locations (Figure 3.11).
Eighty per cent of Frieda’s total locations fall around 4000 m from her most used areas. Tara’s total locations show that she found 90% of her resources around 2200 m from the route network, as well as Annabelle (2300 m). However, in this analysis, Anna presents intra individual difference in her total used locations. When she travels in the south 90% of her total locations are at 3000 m, whereas when she travels to north, 60% of her locations are in less than 1000 m showing statistically significant differences in how far she travels from the most repeated areas she uses ($Z = -2.666$, $p = .008$).
Discussion

Our descriptive and quantitative results using descriptive statistics show inter-individual differences in their patterns of navigation, such as the distance navigated by day, and the daily activity. The activity varies among individuals. Tara presented the shortest distance navigated by hour, during all months, and consequently the slower values of activity. Our generalized linear mixed models show that temperature and time of the day plays a role in the activity of the females. Temperature and time seems affecting the individuals may be responsible for monthly differences in activities. Elephants may just travel to water at certain times of the day, and their presence/absence from road areas may be explained by the need to find water rather than by avoidance of roads per se. Yet, the females present individual differences in the distances they keep from human influenced areas. When the park opens and closes it is evident that they avoid the roads, but during the day, while traveling to find resources is necessary, the animals cross the roads in their home range.

Geospatial analyses of hourly movement data for four individuals over five months did not support the hypothesis that female African elephants travel using the route network system. They navigate more often using “different” paths rather than the “same” to reach repeated resources. Our data show that when individuals travel far from their familiar area they use the same path above than the expected. Yet, the female that traveled far from the familiar area was observed crossing the routes in a large proportion than when she uses her familiar areas, along with find resources closer to the route network. We find intra-individual (Anna) changes in navigation when the family unit uses fission-fusion strategy. To date, it is already known that the acquired spatial information changes the way the cells in the brain fire when animals are in familiar or unfamiliar areas, according to the type of environment the animal visits and learn
(Boccara et al., 2010). Therefore, the differences we see when one of the female elephant traveled may be related to these physically process, supported by research with other mammals (Boccara et al., 2010). Anna presents the same pattern of navigation of other individuals when navigating in the clam’s area. Additionally, Anna did not travel farther from the route network she established in the north, using 60% of the resources in less than 1000 m from the most used routes.

The pattern our subjects use to navigate in their familiar area is different than the route network system (Chapter 2). In a route network system the animals travel most of the time in parallel repeated paths and use determined intersections as nodes (intersections of routes) or decision locations to combine paths after crossing the nodes (Poucet, 1993). They then create new routes configurations by combining different paths. The female elephants use a system of crossing previously used routes. They do use small paths of the previous route. They also can navigate far from the route network system when they are in familiar areas. Navigating closer to the route network system is a strategy used by many primate species in the wild (orangutans, *Pongo pygmaeus*, (MacKinnon, 1974); howler monkeys, *Alouatta palliate*, (Milton, 2000); baboons, *Papio hamadryas*, (Sigg & Stolba, 1981); *Papio anubis*, (Byrne, 2000; Noser & Byrne, 2007); spider monkeys, *Ateles belzebuth*, wooly monkeys, *Lagotrichs poeppigii*, (DiFiore & Suarez, 2007); and lemurs, *Propithecus diadema edwardsi, Eulemur fulvus rufus*, (Erhart & Overdorff, 2008). A small number of species (humans, *Homo sapiens*, (Haun, Rapold, Call, Janzen, & Levinson, 2006); chimpanzees, *Pan troglodytes*, (Normand, Ban, & Boesch, 2009); and black capuchin monkeys, *Sapajus nigratus*, (Presotto & Izar, 2010) use a more costly mechanism of navigation by keeping an internal representation of their home range (Shettleworth, 1998). Our data show that African elephants are able to combine the two patterns
of navigation. When they travel in familiar areas, their pattern of navigation is consistent with the cognitive maps as humans, chimpanzees, and black capuchins; but when they are learning or visiting new areas they use a less demanding system of memorizing specific routes (Poucet, 1993).

In general, our females return to previously used routes by navigating a path of the route and crossing specific points. Our subjects can return to their repeated locations from any location of their home range, using different paths and routes, just as C. velox ants, living in the desert. When C. velox is displaced at any point of any route they are familiar with, they are able to return to the nest, suggesting that ants use visual cues to reach their routes (Margan & Webb, 2012). Cataglyphis when trained and displaced in any point of their known routes, they can return to the hive, acquiring and using multiple visual route memories. Thus, the visual spatial information, once acquired it is kept by ants by their lifetime (Sommer, von Beeren, & Wehner, 2008). The extreme good learning and memory has been suggest for elephants by researchers (Alexander, 2000), and the fact that they are reported to use the same home range for 34 years (Moss & Lee, 2011) support the hypothesis of site fidelity during their live time.

There are many other questions that we still do not know about our females, for example, a how their interaction occurred before the fission-fusion? Does the network of interactions (social network analysis for small number of individuals) show the level of interaction among the females? Does this level is a predictor of decision about who should fission from the herd?

Conclusions

This study concluded that African elephants showed a particular way to find their resources. They present strong evidence that they use more than one mechanism of orientation.
They navigate more often using “different” paths rather than the “same” to reach repeated resources, an evidence of mental representation. Yet, the female that traveled far from the familiar area navigated using a system closer to the route-based network. These findings are in accord to the new studies about the different brain cells process when animals are in familiar or unfamiliar areas. Our subjects can return to their repeated locations from any location of their home range, using different paths and routes, just as C. velox ants, living in the desert, showing that phylogenetically proximity may not be important to determine efficiency in navigation, but the environmental features can play a superior role in the animals’ internal representation of space.

**Acknowledgements**

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CHAPTER 4
GIS AND REMOTE SENSING TO EVALUATE ANIMAL NAVIGATION USING EXISTING DATA

Presotto A, Izar P, Madden M.

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Abstract

Recent developments in Geotechnologies play an important role in animal ecology and behavioral studies. The significant improvement in analytical power of Global Positioning Systems (GPS) and Geographic Information System (GIS) has furthered the discussion of patterns of navigation of wild animals over the past two decades. Tracking animals with GPS started during the 1990s’ and has facilitated the development of new animal research designs supported by the generation of large amounts of data not possible before. Along with GPS data acquisition, the GIS further allowed analytical capabilities in data visualization, contributing to re-evaluate existing data. Considering the differences in technologies and the re-use of existing data, here we argue that there is a substantial advantage to investigate the daily vector of navigation when one wants to understand why wild animals follow different pattern of navigation. We used 2D and 3D representations to explore existing GPS data sets in order to demonstrate our method to compare similarities in the patterns of orientation between two mammals: capuchin monkeys and African elephants.

Keywords: Global Position System (GPS), Geographic Information System (GIS), Remote Sensing, Animal Navigation, Vector data, Spatial Analysis, Data Visualization
Introduction

Recent developments in Geotechnologies play an increasingly important role in animal ecology and behavioral studies (Brooks, Bonyongo, & Harris, 2008). From paper and pencil maps to experimental studies with rats and mazes, the significant improvement in analytical power of Global Positioning Systems (GPS) and Geographic Information System (GIS) has furthered the discussion of patterns of navigation of wild animals over the past two decades.

The first improvement in geotechnologies to overcome the limitations when studying wild animal navigation was the GPS (Kie et al., 2010). Tracking animals with GPS started during the 1990s’ and has facilitated the development of new animal research designs (Rodgers, 2001), supported by the generation of large amounts of data not possible before. The ability to associate the animal to its geographic location was a breakthrough to understanding the ecological aspects of space usage and home range of different species (Blake, Douglas-Hamilton, & Karesh, 2001; Bohrer, Beck, Ngene, Skidmore, & Douglas-Hamilton, 2014; Cagnacci, Boitani, Powell, & Boyce, 2010; Casaer, Hermy, Coppin, & Verhagen, 1999; Rodgers, 2001; Sibbald & Gordon, 2001; Weimerskirch et al., 2002). Along with GPS data acquisition, the GIS further allowed for large data storage, spatial and temporal measurements, increased analytical capabilities, and data visualization (C. S. Smith, Howes, Price, & McAlpine, 2007). GIS capabilities visually communicate field data measurements better, which can now contribute to the re-evaluation of existing data (MacEachren et al., 2004). Past methods using Euclidean geometry were subject to inaccuracy due to the absence of systematic data or data protocol to support spatial statistical analysis in animal navigation. However, with GPS and GIS improvements the variables affecting wild animal navigation can now be quantified in a more precise way (e.g. Normand, Ban, & Boesch, 2009; Presotto & Izar, 2010).
While spatial statistical analysis supports important mathematical understanding, the Geovisualization is a process to build behavioral suggestions based on visual methods to support a wide array of geospatial data applications (MacEachren et al., 2004). One of the biggest differences in studies of wild animal navigation is how GPS data is collected. GPS Collars continuously provide 24 hours location-records, while the GPS units that are human dependent data collection occur continuously for 12 hours a day (Blake et al., 2001; DiFiore & Suarez, 2007; Douglas-Hamilton, 1998; Presotto, 2009). Therefore, it is important to have a clear objective and knowledge about the species and the type of environment (Tomkiewicz, Fuller, Kie, & Bates, 2010) when choosing a GPS device. For some species and habitat, following animals by foot is not possible. Here battery powered pre-programmed GPS collars have proven most effective, allowing real-time geolocation of wildlife during sampling. Battery powered collars allow the researcher to decide the balance between the level of data resolution and sampling limitations of the batteries in the collar. Higher resolution data results in more finely detailed analysis but for a shorter overall sampling time. Lower data resolution has more gaps but resulting in a less detailed but broader analysis capability over a greater sampling time. This spectrum allows sampling to be adjusted to gain the appropriate data for more in depth analysis tailored to the study design. One caveat is some species do not accept the collars or are able to remove them. When the only option is to sample the animals by foot because of field conditions, data maintaining a systematic order becomes very important.

With GPS data and GIS capabilities, analysis can be automated, currently very popular in modeling animal movement (Cagnacci, Boitani, Powell, & Boyce, 2010; Cushman, 2010; Löttker et al., 2009; Pinto & Keitt, 2009; Tomkiewicz, Fuller, Kie, & Bates, 2010). One of the most functional association between GPS and GIS is the ability to combine these technology to
reconstruct existing data, usually formatted in long or abstract tables, into highly detailed and organized yet more readily understood visual format.

**Data Set and Analysis**

The first step is to look the data acquisition, the type of GPS and the identification of inaccuracies to the daily vector analysis. In the rain forest, for example, past GPS technologies were not able to acquire large numbers of satellites, increasing errors rapidly, reducing both the arrangement of the data (Markham & Altmann, 2008; Phillips, Elvey, & Abercrombie, 1998), and the amount of geographic coordinates collected. Some GPS required the researcher to stand still for up to many minutes while acquiring satellites and some species move faster than the satellite acquisition. The researcher then had to choose between losing the geographic coordinate or the subjects themselves. In the dense rain forest vegetation, GPS signal reception was not always adequate, and the use of larger more precise GPS units were not practical to carry when following animals on foot through thick vegetation. Studies conducted in the open areas of savanna, received superior GPS reception. We previously conducted a study with three different hand-held GPS units in the rain forest (Figure 4.1) demonstrating the lack of capacity some technologies presented in maintain the systematization of the data, meaning that some GPS did not acquired geographic coordinates in some locations.

We followed black capuchin monkeys, on foot, collecting GPS data daily (Izar, 2004; Presotto, 2009). Using GIS we compared the GPS’s reliability in collecting geographic coordinates in the Atlantic rain forest. Following black capuchin monkeys, we measured the distances between two successive points collected for the 105 whole days. We collected 31 days in 2002 using the Garmin Etrex, which received signal depending on the topography and the
density of the canopy, with no systematic data; 16 whole days in 2006 using the Garmin Etrex Vista, slightly better, acquiring geographic coordinates around each 100 m, still terrain dependable. Finally, we collected 58 days in 2007 using the Garmin Map 60 CsX, with geographic location marked every 5 minute intervals. All the GPS units were able to receive geographic coordinates at least in certain locations inside the dense Atlantic rain forest. However, comparing the GPS devices, we found statistically significant differences ($H (2) = 79.359, p=0.001$) for the distances the technologies were able to acquire geographic coordinates while following the animals. This problem is consistent with GPS collars on animals under dense vegetation.

![Figure 4.1](image)

**Figure 4.1:** Differences in distances measured between each two successive points per day using Etrex (1- 2002), Etrex Vista (2- 2006), and MAP 60 CSx (3- 2007)

We also calculated the variables from the capuchin group movement with the three data sets. We evaluated: a) size of the area explored daily, b) width of the area, c) length of day travel, d) straight line vector between the first coordinate of the day (where the group woke up), to the
last point of the day, the sleeping sites (first point of next day), and e) ratio between the straight line and the length of the way. All measurements were made using ArcGIS 10.x (scale 1:5,000).

We found statistically significant differences for four of the five tested variables (Table 4.1).

Table 4.1. Significant differences of variables measuring with three different GPS-technologies, except the ratio.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Test results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size of the daily explored area</td>
<td>(H (2) = 24.459, p=0.001)</td>
</tr>
<tr>
<td>Width of the area</td>
<td>(H (2) = 52.507, p=0.000)</td>
</tr>
<tr>
<td>Length of day travel</td>
<td>(H (2) = 31.783, p=0.000)</td>
</tr>
<tr>
<td>Resultant vector</td>
<td>(H (2) = 22.771, p=0.000)</td>
</tr>
<tr>
<td>Ratio between the length-day/resultant</td>
<td>(H (2) = 1.028, p=0.598)</td>
</tr>
</tbody>
</table>

These comparisons show two important facts: a) that the older technologies can affect the data when compared with the new technologies in habitats with dense vegetation and with abrupt changes in topography, and b) analyze the daily vector with caution if daily behavior or navigation is being studied. Yet, past technologies used in savannas with sparse vegetation, the topography did not invalidate the data when compared to newer GPS technologies (Chapter 2, Figure 2.3).

Considering the differences in technologies, here we argue that there is a substantial advantage to investigate the daily vector of navigation when one wants to understand why wild animals follow different pattern of navigation in the wild. We used 2D and 3D representations to explore existing GPS data sets in order to demonstrate the method we used to compare similarities in the patterns of orientation between two mammals: capuchin monkeys and African elephants.
Method

Building Daily Routes

We construct daily routes (total distance traveled per day) based on connecting the sequential geographic coordinates points from each day (Figure 4.2a). We identify locations where the animals stop for a predetermined time period for each activity, such as feeding, resting, or for social activities. For capuchins we used 10 minutes as a stopping point (Figure 4.2b). The last point of the day is the sleeping tree or sleeping site. We use the daily routes in the analyses below, also dividing them into paths (segment of the routes) to perform more detailed analysis (Figure 4.2c).
Figure 4.2. Sequence used to build routes: a) daily sequence of the geographic coordinates, b) stopping points visited during the day, and c) shows the daily route, stopping points, sleeping sites, vector between the length travel per day and the last geographic coordinate of the day, with the paths of the routes.

**Linearity and velocity**

To calculate the velocity of navigation, the distance between two successive stopping points, or where the animals stopped for 10 minutes or more were measured and included in the GIS visualization. For those points, we combined the behavioral information with the daily navigation in ArcGIS. Thus, we used the five-minutes interval scans to calculate the total time animals stopped in each location. These point-locations are measured from the first stopping
point in the route to the next stopping point in the route, which in turn form a path from stopping one to stopping point two (Figure 4.2c). For example, the first point is the beginning of the movement when the group woke up and the first stopped point is the point where animals stayed 10 minutes or more. For this path we calculated the velocity of navigation \((V=d/t; \text{velocity} = \text{distance/time})\).

If geographic locations are collected every 30 minutes two successive points in the same location could be considered a stopping point, since it spans a one-hour period of non-significant movement. Here it is important to know the species-specific behavior. We classify the travel paths in each daily route according to the location of the animals. If the animals stopped in patchily distributed vegetation (food source) or water sources, the travel path is a “Goal Travel”. Goals are subdivided in “New Goals” (first time observed by the researcher) and “Repeated Goals” (starting at the second time the animal visits the location). If the animals stop in locations that are not resource locations, the travel path is “Non Goal Travel”. We then calculate the length of each path by summing the distance between every two stopping point. A path can be more than two consecutive points, according to the resource location on the route. We simply calculate the Geometry in ArcGIS. Then we calculate travel velocity (meters/hour) for every travel path as the length of the path divided by the time the animals spent to travel that path. For every Goal Travel Path, we measure the distance traveled by the animals from the starting point until reaching the goal (Figure 4.3).

Assuming that an animal heads in a straight line for an object in plain view (Dyer 1998), every time the animals travel along a linear path ending at a resource patch representing food or water, we measured the length of this linear path of foraging behavior. We analyzed the linearity of every path calculating the ratio between the actual distance traveled by animals between two
stop points and the vector length of a straight line between those points (Figure 4.3). We calculated the ratio between the length of the path travel distance and the vector straight line from the start to the last stopping point. A linear ratio of 1.0 means that the animals took the shortest possible path to a target, whereas a ratio of 1.3 means they traveled 30 per cent more than necessary to reach that point. We also verify whether travel velocity differs between types of paths as a function of differences in distance traveled to each type of resource. We compare the length of “Goal Paths” versus “Non Goal Paths”, comparing the whole sample of paths as independent samples.

Figure 4.3. Daily route showing the paths: Goal-Travel-Path and Non-Goal-Travel Path. Data collected at five-minute intervals
We then test the hypothesis that travel velocity in paths ending at repeated feeding sources would differ whether the animals are following the “same path” (Figure 4.4) as the previous visit or a “different path” (Figure 4.5), and whether there are geographic features that could be used as prominent landmarks associated with the goal (e.g. Presotto & Izar, 2010). Additionally, we display the entire routes and analyze them using the same criteria used to classify the paths. We test whether the proportion of the “same" routes and “different” routes present statistically significant results (binomial test). We used the same procedures to investigate the repetition of the paths. We always test the hypothesis that the animals remember the amount of food they encountered on a given feeding location using a correlation test between velocities in repeated feeding Goal Paths and first visit Goal Paths. For these all the statistical tests significance levels are set to p<0.05.

Figure 4.4. Capuchins visit a repeated location using different routes, and same path to reach repeated food source.
Figure 4.5. Capuchins visit a repeated location using different routes and different paths to reach repeated food source.

**Habitual Route Network Analysis**

The habitual route network analysis is a GIS-based method used to compare patterns of navigation across species. We adjusted the method from DiFiore & Suarez (2007), and applied it to two species of wild capuchin monkeys in two diverse Brazilian landscapes: Atlantic rain forest (Presotto & Izar, 2010) and Savanna (Chapter 2), and African elephants in the savanna of South Africa (Chapter 3). To investigate convergence across taxa it is important to use comparable methods. Our method consists of building daily routes as layers for each monthly data set and
comparing layers between pairs of days and months (Figure 4.6a). For example, April and May routes are plotted together, and then for both months, another layer is created and the common routes for April and May are created (Figure 4.6b). All pairs of months and all months are combined (Figure 4.6c). We then superimpose the georeferenced layers on the animal’s home range and visually identify all repeated paths that fall within 50 meters from each other, the assumed distance that a capuchin can see inside the dense forest (Janson & Di Bitteti, 1997). However, it is necessary to have a preliminary knowledge about the visual acuity of the study subject to identify the distance they are able to see in a particular landscape. We then create a habitual route by following two criteria: (1) by connecting all paths repeated at least four times, and (2) by connecting all paths repeated at least two times during the study period. For some species the criteria may be more or less conservative. The number of times the animal uses the same path may help to define the best criteria, if the animal excessively repeats the same path (20 times, Chapter 2) over the study period, the two times criteria may not be necessary. The habitual route network is super-imposed on all the actual daily locations used by the animals.

Prior to data collection, the appropriate balance of sampling interval, data resolution, battery life, and total sample duration must be determined and is based on the study species. There is a trade-off because higher sampling frequency, which can be taken by the second (Strandburg-Peshkin, et al. 2015), produces higher data resolution but shorter sampling duration due to battery life. Lower sampling frequency gives the ability to sample longer, but results in lower resolution data and data gaps, however may be appropriate in some cases such as long term home range uses where it is not necessary to log every movement.
How Far Animals Travel from the Habitual Routes

We use the Analysis Tool - Proximity in ArcGIS 10.x to conduct the buffer analyses. The buffer analysis tool creates a zone of predetermined distance around the habitual routes and then creates a list of all coordinate points that are located within the zone (Figure 4.7). We then calculate the proportion of the a) total geographic coordinates of the animal locations, b) location of each food sources used by the animals, and c) location of any sleeping sites that falls within a pre-determined distance, based on the literature about the species, or field observation. For example, we can use locations that fall within: 50, 100, 200, 300, 400, 500, 600, 700, 900, 1000, 1500, 2000, and 2500-meter zones around the route network or habitual routes. We tested these distances for capuchins. However, for African elephants, based on their daily distance
navigation, the bands around their locations were established as: 500, 1000, 1500, 2000, 2500, 3000, 4000, 5000, and greater than 5000 m.

![Image](image_url)

**Figure 4.7.** a) Complete route network, b) buffer around the food sources, and c) buffers around the sleeping sites

**Analyzing Existing Data from GPS-collars Using Remote Sensing**

Habitual Route Network analysis has performed successfully using both new and existing data. To conduct the buffer analysis, we used the total locations traveled by the animals. However, for the first time, to our knowledge, we used remote sensing to overcome the lack of habitat information to apply this method. Remote sensing is proving to be an important tool for data analysis. Though a relatively new technology, it has the potential to make significant contributions to the study of animal navigation and spatial analysis.
Land Cover classification shows the physiographical features of the environment at the time the data was collected (Kerr & Ostrovsky, 2003). Remote sensing is widely used to support studies with endangered species (Gillespie, 2001). For existing GPS data remote sensing is becoming essential to understand the spatio-temporal changes in the species habitat. It is a way to identify resource distribution of an area at the time the animal data were collected.

To perform analysis of linearity and velocity using existing data with no full time behavioral observation there is a need to identify the resources the animals were using at the time of the data collection. We used remote sensing to extract the landscape information in the savanna of South Africa to classify the visits and re-visits elephants did to certain potential resource locations. We used existing data from five females of African elephants with GPS collars living in the same clam. GPS collar data were collected from October of 1998 to February of 1999 in the area of Skukuza in the Kruger National Park, South Africa (Figure 4.8).
Figure 4.8. Study area to investigate the use of Remote Sensing, Skukuza, Kruger National Park, South Africa
Here we consider the general report that resources uses for foraging are one of the primary factors that drive the animal movement (Boettiger et al., 2011). With this premise, we first classified the land cover, focusing on the vegetation structure of the home range of our elephants, using publicly available Landsat 5 (30 m x 30 m, Scene ID = LT51680771998278JSA00, acquired on 05-10-98) satellite image from the same period of the GPS collar data collection. We combined the image with the Digital Elevation Model (DEMs) constructed from stereopairs of ASTER satellite imagery, and the Normalized Different Vegetation Index (NDVI) model to classify the Land Cover of the study area. The NDVI values range from 0 (low) to 1 (high). Areas with higher NDVI values have greater forage abundance and/or quality when used in African forests (Boettiger et al. 2011). Thus, we used the NDVI model to improve the vegetation classes. We characterize different types of vegetation within the sample areas over the range of African elephants (Figure 4.9a). We used ERDAS Imagine to create the NDVI. We used ArcGIS 10.x to classify the Landsat image. We conducted the supervised classification using samples collected in 2014, and data from earlier old satellite images. The supervised classification consist in find representative training areas as samples, and then the pixel in the image data set is assigned to the land cover class created during the training samples. The result is a raster image representing the grounded land cover (Lillesand, Kiefer, & Chipman, 2014).

To validate the classification of earlier imagery we used Google Earth or high-resolution imagery of the area (usually higher resolution than the classified image). Google Earth incorporates high-resolution images and its own language, Keyhole Markup Language (KML) to facilitate the overlay of GIS data on a variety of imagery types (Ballagh et al., 2011; Chien &
Tan, 2011; T. M. Smith & Lakshmanan, 2011; Turk, Hawkins, Richardson, & Surratt, 2011; Wu, He, & Gong, 2010).

**Figure 4.9.** a) Land Cover classification over the home range of the female African elephants, b) patchily distributed resources, woodland and water

After classifying the vegetation structure, we attributed numbers to each class. Then we displayed all the elephant locations and using the ArcGIS Spatial Analyst tool, we extracted the numerical values of the classes. Each location was assigned a value. Even though we classified the entire home range to investigate the linearity and speed, we used the woodland/forest and water as Goal Travel Path, and the rest of the classes as Non Goal Travel Paths (Figure 4.9b). To
create a generalized linear mixed model (GLMM) we used the patchily distributed resources, woodland/forest, and water, and assigned them as 1, and the rest of the classes as 0.

Discussion

Previous calculations using different technologies show that past analysis can now be re-evaluated using new GIS capabilities, maintaining the idea that linearity and speed may differ according to the technology. Straight lines produced by lower sampling frequency can miss micro movements off a linear path which would give the illusion of a slower or faster traveling speed. Questions related to size of home range, daily movements, traveled distance, linearity to reach goals were complex to measure with lack of accuracy in data field collection. Regardless, such questions are extremely necessary to understand the species movement in their habitat.

The representation of daily routes associated with behavioral data is rich in details since we know the locations and the activity the animals are performing in time-space. It is time consuming compared with analysis using modeling, or spatial analysis performed with GIS. However, it gives us the statistical power to discern patterns of navigation that the automatic process does not allow. When we overlay existing data using day-by-day over the land cover classification we have the flexibility to investigate the time animals spend in each resource class. This allows the access to analyze linearity and velocity and compare the results with the theories of how animals navigate toward Goal or Non Goal locations (Brooks et al., 2008).

An important consideration about linearity is that animals “balance” costs and gains, increasing linearity of navigation to reach their goals (Pochron, 2001). Therefore, knowing
the potential goal-locations is important if one cannot follow the animal. The stopping points are necessary to understand repeated resources, and classify the same and different routes and paths, which results implicate in animals levels of cognition. Without the classification of the vegetation structure and the class values given to the locations it would not be possible to assume linearity and velocity toward to resources in existing data.

As much as we agree with the aspect that even when the data collection is not enough to show environmental or assuming behavioral details, basic information can be important to build databases (Hugues, 2003), find preliminary results, and provide additional information, maintaining a standardized data set to future time-space analysis.

Statistical analysis is extremely important to confirm our hypotheses, but visual observation of the navigated routes based on GPS data collection was the first to demand the need to calculate measurements and statistically test them. We used data visualization to classify the way animals use and re-use their routes and paths. Our method is a time-consuming but allows leveraging of data resources to meet scientific needs, and to develop visual methods in the GIS tools to support an array of behavioral activities using geospatial data applications (MacEachren et al., 2004).

**Conclusions**

We always represent our data in the highest of details possible to elucidate new thoughts. However, to understand animals’ pattern of navigation we suggest that the technology should consider the topography of the study area and the biology of the subject in order to overcome lack of behavioral data, if the case. The capability of the GIS to represent the data gives us the
ability to identify concepts of route and path travel which the geospatial referencing (Lorenz, 2008, MacEachren et al., 2004) in order to be more realistic.

Acknowledgements

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References


CHAPTER 5

CONCLUSIONS

The method used in this dissertation to investigate the patterns of wild animal navigation illustrates the daily routes and paths analyses satisfactorily represent species-specific patterns. Statistical analysis would be incomplete without the support of visual observation to classify the use and re-use of routes and paths of wild animals.

Currently, there has been research linking the brain with how animals learn and maintain spatial representation by analyzing rats navigating in laboratory conditions (Cheng, Huttenlocher, & Newcombe, 2013; Kathryn J Jeffery, Anderson, Hayman, & Chakraborty; Poucet et al., 2014; Boccara et al., 2010; Kate J. Jeffery, 2015).

The pattern of navigation found for *S. libidinosus* at FBV confirmed the hypothesis that they use a system of navigation consistent with route-based network. They used repeated paths, intersections as nodes, landmarks associated with resources along the route network, similar to the system found for other primate species (DiFiore & Suarez, 2007; P. Garber, 2000; P. A. Garber & Jelinek, 2006; Milton, 2000). Bearded capuchins at FBV more frequently repeated paths than entire daily routes; they constructed different daily routes by combining familiar paths, finding 80% of the resources the use within 50 meters of their route network system. The use of route network system appears to minimize energy costs of locomotion in a well-established home range, avoids risks and intergroup competition (Verderane, Izar, Visalberghi, & Fragaszy, 2013). Yet, the ability to combine paths in different route configurations after node crossings, suggests that bearded capuchins are able to maintain geo-spatial knowledge of the
nodes in the route network system (Poucet, 1993) and use them as a point of directional decision making. The open savanna may give the capuchins visual access to many prominent features in the terrain that could be used as landmarks (P. A. Garber, 1989; MacKinnon, 1974; Sigg & Stolba, 1981; Vlasak, 2006). FBV presents many prominent geographical features (hills, streams, cliffs, valleys, and differences in canopy density and height), a rich landscape for animals to use landmarks (Visalberghi et al., 2007). Even though visibility is high in the capuchin’s habitat they did not leave their route network area during the study period. This may be related to food distribution and availability (Izar et al., 2012). Since bearded capuchins have food sources year-round and their habitat is rich in prominent landmarks, maintaining a “mental” representation larger than their route network system would be unnecessary energy expenditure. One hypothesis proposes in rats the brain remembers specific objects and shapes and accommodate these memories in the same spatio-temporal index (Gallistel & Matzel, 2013). The idea of storing space-time in the same index may explain the use of sequence of landmarks in a route-network configuration because the route system is perceived as places that offer resources during certain time, and therefore maintaining this information the animals can also maintain for decades the same home range (Gallistel & Matzel, 2013). In my view, a population’s spatial orientation system reflects experience with particular landscapes and resource availability in time and space.

In the same methodological fashion, our data on African elephants rejected the hypothesis that they use the route network system of orientation. African elephants navigated by different routes most of the time when going to repeated resources. We found that when individuals travel far (fission-fusion strategy, up to 35 kilometers in our data) from their familiar area, they adjust for the unfamiliarity of the area by crossing routes more often than when they do not leave the familiar areas. This system is controversy to the route network system (Chapter
2). In a route network system, most of the time animals travel on parallel routes and paths, using specific locations to form intersections and use these intersections as nodes (Poucet, 1993). The female elephants use a system of revisiting and crossing previously used routes. However, their crossing locations reached more than 800 points in five months which may not be suitable to be used with the same purpose as the nodes are, meaning that these may not be used as points of decision-making. Additionally, our females navigated far from their habitual paths (or the paths they repeat the most) when they are in familiar areas, in the south of the home range, Skukuza. But when one of the females traveled far from the familiar area (Anna) was observed crossing routes more often proportionally than when in the familiar area, showing intra-individual changes in navigation when the family unit use fission-fusion strategy.

To date, it is already known that the acquired spatial information present different patterns of firing cells in the brain when animals are in familiar or unfamiliar areas, and in accord to the type of environment the animals visit and learn (Boccara et al., 2010). Therefore, Anna’s navigational differences may be related to these recent discoveries. Anna presented the same pattern of navigation as the other females in their familiar areas, but changed her strategy when she visited an unfamiliar area. She then used a large number of repeated paths, and when she used different paths she crossed previously used routes proportionally in a larger amount than when traveling in the south, sometimes more than once a day. Additionally, Anna did not travel farther from the habitual routes she established in the unfamiliar area, using 60% of the resources within 1000 meters from them.

Our African elephant data demonstrates that females can revisit locations from any other location in their home range by using different paths and routes, just as *C. velox* ants, living in the desert. When *C. velox* is displaced at any point of any route they are familiar with, they are
able to use visual cues to reach a familiar route and return to the nest (Mangan & Webb, 2012), acquiring and using multiple visual route memories. Thus, the visual spatial information, once acquired it is kept by ants by their lifetime (Sommer, von Beeren, & Wehner, 2008).

Insects are particularly good in navigation, and many experiments have shown that they are efficient throughout their life (Wystrach & Graham, 2012). Their small life spans, facilitates to understand their spatial learning throughout their lifetime. Wild mammals do not offer the same opportunity in some areas. However, through the body of knowledge from insects and other experimental studies it is possible to infer that wild elephants would use their extremely good learning and memory capabilities to find their way around (Alexander, 2000). The spatial memory in African Elephants can be related to the fact that they have site fidelity probably for long periods of their life, as reported by Moss & Lee (2011) in Amboseli, Kenya, where elephants use the same home range for up to 34 years.

Here our results show African elephants are able to combine the two discussed navigational mechanisms: the topological maps and the cognitive maps. When they use their familiar areas, their pattern of navigation is consistent with the cognitive maps as humans, chimpanzees, and black capuchins, meaning that they maintain a representation of resources and can travel to them from any point of their home range; and when they are learning or visiting new areas they use a less demanding system by memorizing specific routes which is less costly while avoiding unnecessary risks.

Brain studies on rats provide a possible explanation. A subset of cells called place cells fire when the animal is in certain locations, and only if the animal is at that specific location (Boccara et al., 2010). By knowing that small mammals brain cells can distinguish specific spaces in their environment we can suggest that our subjects are able to use or utilize a different
form of navigation according to their location, supporting that the behavior could be guided by convergence with other species.

Advances in technology now allow us to examine how animals navigate in their environment like never before. There are so many intriguing questions about navigation in the wild as well as means to investigate them. What is the role of the visual system in navigation? Does the openness of the landscape or the density of the forest affect the visual cognition of wild animals and consequently contribute to the use of one mechanism or the other? How do African elephants decide which family unit would use the fission-fusion strategy? Is the age of the individuals affecting the family unit that travels farther? These are questions for long term studies that direct observation of individuals as well as the group (dependent on species and the question asked) along with the appropriate technology are essential to understanding their ontogenetic changes through time and space.
References


APPENDICES

Appendix 1. Graphic with distance of individual differences from touristic locations, roads and water bodies at Kruger National Park, Skukuza, South Africa
Appendix 2. GLMM test results

Case Processing Summary

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Model Summary

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Information criteria are based on the \(-2\) log likelihood (67991.201) and are used to compare models. Models with smaller information criterion values fit better.

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Covariance Parameters Summary

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<td>Common Subjects</td>
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Common subjects are based on the subject specifications for the residual and random effects and are used to chunk the data for better performance.

a. This is the number of columns per common subject.

Residual Effect

<table>
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<tr>
<th>Residual Effect</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>Z</th>
<th>Sig.</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
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</tr>
</tbody>
</table>

Covariance Structure: Scaled Identity
Subject Specification: (None)

Random Effect

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<th>Estimate</th>
<th>Std. Error</th>
<th>Z</th>
<th>Sig.</th>
<th>95% Confidence Interval</th>
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<td>4.931</td>
<td>1.22</td>
<td>.222</td>
<td>1.211</td>
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<td>Var(month)</td>
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<td>.251</td>
<td>1.545</td>
<td>.122</td>
<td>1.09</td>
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<tr>
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<td>1.219</td>
<td>.223</td>
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Covariance Structure: Variance components
Subject Specification: (None)
Generalized Linear Mixed Model

Warnings

Estimated means are not available with the multinomial distribution.

Case Processing Summary

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Classification

Overall Percent Correct = 72.4% a

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a. Target: Act_2

Fixed Effects a

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Probability distribution: Multinomial
Link function: Generalized logit
a. Target: Act_2
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<th>Coefficient</th>
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<th>t</th>
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<th>Exp(Coefficient)</th>
<th>Lower</th>
<th>Upper</th>
<th>95% Confidence Interval for Exp(Coefficient)</th>
<th>Exp(Coefficient)</th>
<th>Lower</th>
<th>Upper</th>
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Probability distribution: Multinomial
Link function: Generalized logit
a. Target: Act_2
b. This coefficient is set to zero because it is redundant.
### Random Effect Covariance

#### Random Effect Block 1

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<th>Ind=Anna</th>
<th>Ind=Frieda</th>
<th>Ind=Tara</th>
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</tbody>
</table>

---

**Fixed Coefficients**

- **Intercept**: 1.00
- **Month**:
  - December 1998: 0.00
  - February 1999: 0.00
  - January 1999: 0.00
  - October 1998: 0.00
  - September 1998: 0.00

---

**Coefficient Estimates**

- **Random Effect Block**
  - **Ind=Anabelle**: 6.021
  - **Ind=Anna**: 6.021
  - **Ind=Frieda**: 6.021
  - **Ind=Tara**: 6.021
<table>
<thead>
<tr>
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</table>

Covariance Structure: Variance components
Subject Specification: (None)

Covariance Parameters

### Covariance Parameters Summary

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<thead>
<tr>
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<th>Residual Effect 0</th>
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</table>

Common subjects are based on the subject specifications for the residual and random effects and are used to chunk the data for better performance.

a. This is the number of columns per common subject.

### Residual Effect

<table>
<thead>
<tr>
<th>Residual Effect</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>Z</th>
<th>Sig.</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variance</td>
<td>1.000</td>
<td>.</td>
<td>.</td>
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</tbody>
</table>

Covariance Structure: Scaled Identity
Subject Specification: (None)

### Random Effect

<table>
<thead>
<tr>
<th>Act_2</th>
<th>Random Effect</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>Z</th>
<th>Sig.</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>.00</td>
<td>Var(Ind)</td>
<td>6.021</td>
<td>4.927</td>
<td>1.222</td>
<td>.222</td>
<td>1.211 - 29.942</td>
</tr>
<tr>
<td></td>
<td>Var(month)</td>
<td>.389</td>
<td>.252</td>
<td>1.545</td>
<td>.122</td>
<td>.110 - 1.384</td>
</tr>
<tr>
<td>1.00</td>
<td>Var(Ind)</td>
<td>2.700</td>
<td>2.215</td>
<td>1.219</td>
<td>.223</td>
<td>.541 - 13.483</td>
</tr>
<tr>
<td></td>
<td>Var(month)</td>
<td>.233</td>
<td>.157</td>
<td>1.485</td>
<td>.138</td>
<td>.062 - .873</td>
</tr>
</tbody>
</table>

Covariance Structure: Variance components
Subject Specification: (None)
Appendix 3. Individual female activity by time (5 months)

Anabelle

Tara
Frieda

Anna