THE FORAGING AND TRAVEL PATTERNS OF WHITE-FACED SAKIS IN BROWNSBERG NATURE PARK, SURINAME: PRELIMINARY EVIDENCE FOR GOAL-DIRECTED FORAGING BEHAVIOR

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ABSTRACT

Most studies on spatial memory in primates focus on species that exploit the flesh of ripe fruits, which is the patchiest resource available to animals inhabiting tropical forests. Futhermore, these studies usually focus on primates exploiting very large home ranges. Behavioral adaptations associated with enhanced spatial memory, distance-minimization, and fine-tuned food search methods are expected to be at a premium for animals that cover a lot of ground each day exploiting clumped and ephemeral ripe fruits. The purpose of the current study is to gain insights into the foraging strategy of a seed predator exploiting a relatively small home range. While still a patchy resource, seeds are more abundant in space and time than fleshy ripe fruits. Additionally, it is assumed that animals with small home ranges can more readily encounter resources in their supplying area without having to rely upon sophisticated foraging strategies.

I investigated the modes and efficiency of travel in a group of white-faced sakis in Brownsberg Nature Park, Suriname. Using detailed maps of their daily movements, I determined that the sakis travel more quickly and more linearly to a restricted subset of food resources. Furthermore, they were able to arrive at reused feeding sites using alternate and direct pathways. Both of these behaviors are consistent with the use of spatial memory to locate resources, and, more importantly, goal-directed foraging behavior, a search technique primarily associated with ripe fruit eaters inhabiting large home ranges.

While the sakis' paths were slightly less linear than expected, linearity scores mirrored observations of goal-directed white-faced sakis studied in Venezuela. A number of behaviors and scenarios appear to lower their ability to maintain perfectly linear paths, including, their tendency to monitor the curved perimeter of their territory, their frequent participation in territorial encounters with conspecifics, their zig-zagged movements when sampling resources, and their reliance on and propensity to diverge off of established arboreal pathways to home in on particular sites. They use a small number of arboreal pathways to negotiate the numerous gaps in the canopy throughout their range and to bring them into contact with important feeding areas, overlap zones, and particular trees; however, it appears that they do have the ability to navigate solely by orienting towards certain landmarks in their range.

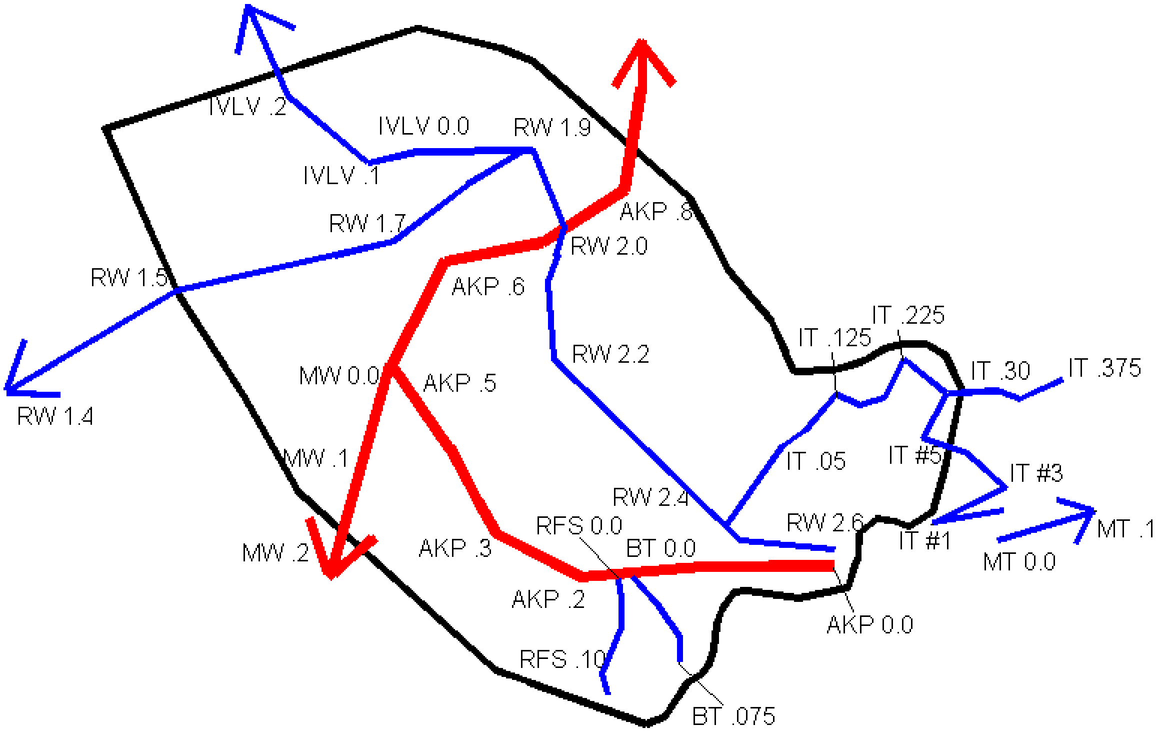
CHAPTER 1

INTRODUCTION TO THE STUDY

The aim of this study is to understand white-faced saki foraging strategies and the role that spatial memory, behavioral rules, and mental mapping play in their foraging repertoires. A large body of literature indicates that many species of primates are capable of remembering the location of resources by forming mental representations of their surroundings; primates reportedly use these mental representations to implement an efficient food search technique known as “goal-directed foraging”, whereby they travel in distance-minimizing paths to food resources when and where they are available (Milton, 1980; Garber, 1989; Garber and Dolins, 1996; Menzel, 1996, Janson 1997; Garber 2000; Janson, 2000; Bicca-Marquez and Garber, 2004).

Animals that exploit ephemeral, clumped, vital and limited, relatively predictable, and/or productive resources are those expected to employ a goal-directed foraging strategy. Since white-faced sakis are highly frugivorous primates that compete with seven other monkey species and a number of other fruit-eating vertebrates (birds, bats, non-primate mammals) for fruit resources that are limited in both space and time, there may be very precise mechanisms that the sakis use to gain access to these resources or to use them in a systematic way; i.e. they may exploit these resources in a goal-directed fashion.

Fig. 1.1 Trail system within focal group's home range. Black outline represents extent focal group's travels during study period (referred to hereafter as "home range"). Red lines represent roads, while blue lines represent trails (as is depicted, roadways are usually wider than trails). Arrows at the end of trails and roads indicate that these actually extend farther than depicted in map. Labels show trail markers (in km).



In the present study, I use detailed field data on a group of wild white-faced sakis to test hypotheses about the strategies they use to exploit resources. Specifically, I collected data on the sakis' daily paths, small and large-scale movements, feeding and sleeping site choices, and repeated use of particular trees, areas, and paths throughout their home range (Fig. 1.1). Three behavioral patterns were designated as indicators of goal-directed foraging behavior: 1) increased speed and directness to preferred feeding sites, 2) the ability to arrive at the same site using alternate, but direct, pathways, 3) and the ability to locate the nearest-neighbor sleeping site.

Additionally, I wanted to understand not only if white-faced sakis were goal-directed foragers, but also how they might utilize all of the spatial, temporal, and ecological information that goes into making goal-directed foraging choices (i.e. Do they rely on certain behavioral rules? Do they appear to exploit their range in a random or systematic manner? Do they use landmarks or arboreal pathways to find their way, or do they appear to be able to visualize spatial relationships among sites in their home range in a geocentric manner?) To these ends, I used maps of their daily paths to search for patterns and overlaps in their movements and positions on both small and large time scales.

Finally, I hoped to elucidate any differences that exist between the foraging and feeding habits of the white-faced sakis currently being observed in Brownsberg Nature Park and the white-faced sakis that have been studied extensively on the 12.8-hectare island in Guri Lake, Venezuela (Kinzey and Norconk, 1993; Cunningham, 2003; Norconk and Conklin-Brittain, 2004; Cunningham and Janson, 2007).

Beginning with Chapter 2, I lay out the theoretical framework for this study. First, I discuss the types of food search strategies expected for primary versus secondary foragers and briefly touch on the various anatomical, physiological, and behavioral adaptations known to enhance feeding and foraging efficiency (section 2.1). Next, I discuss the types of search strategies expected for animals exploiting resources with particular distribution patterns, availabilities, and degrees of predictability, and, also, how choosiness on the part of the animal weighs in (section 2.2). Finally, I discuss the type of foraging strategy we might expect from white-faced sakis considering their feeding ecology, ranging patterns, and social relations with conspecifics (section 2.3).

In Chapter 3, I discuss how spatially cognizant primates might mentally represent the locations of important sites in their environments and how they might simplify their foraging decisions by implementing behavioral rules in particular foraging contexts (section 3.1). I then discuss the particular behaviors that researchers might use to distinguish goal-directed from random or systematic search strategies (section 3.2). Chapter 3 concludes with a section laying out the specific predictions tested in this study, the unifying theme being that the sakis will exhibit a goal-directed foraging strategy: 1) the sakis will exhibit a low incidence of backtracking (subsection 3.3.1); 2) the sakis will exhibit relatively directed travel to resources and will travel more quickly and linearly to more preferred resources (subsection 3.3.2); 3) the sakis will be able to locate the same feeding site using a variety of direct pathways (subsection 3.3.3); 4) the sakis will be able to locate the closest sleeping site relative their final feeding tree each day (subsection 3.3.4); and 5) the sakis will represent the spatial relationships of features in their habitat using landmarks or topograhical mental mapping, and will not have to rely upon habitually-used pathways to find their way (subsection 3.3.5).

Chapter 4 deals with the methods used in data collection and analyses. After a brief overview of the study site (section 4.1), the climate (section 4.2), and the study group's composition, habitat, range, and inter-group interactions (section 4.3), I commence with a discussion pertaining to the methods used to collect behavioral data, mapping data (section 4.4), and feeding data (section 4.5). In the final section (4.6), I discuss modes of analysis pertinent to assessing ranging patterns and area usage (4.6.1) and the five specific predictions outlined above (4.6.2-4.6.6).

Chapter 5 involves a detailed discussion of the results, beginning with two sections discussing preliminary findings relating to the sakis' ranging patterns and area usage (section 5.1) and diet (section 5.2). Beginning with section 5.3, I discuss the results of the predictions: the results of the backtracking predictions are discussed in section 5.3, the directed travel results in section 5.4, the revisited feeding tree results in section 5.5, the nearest-neighbor sleeping site results in section 5.6, and the landmark and arboreal pathway results in section 5.7.

Due to the many phases involved in analyzing the directed travel predictions, the section exploring these results is particularly lengthy; therefore, it has been broken into eight subsections. The first subsection (5.4.1) explores how the study group's linearity in travel relates both to the expectations laid forth by this study and to travel patterns exhibited by a group of Venezuelan white-faced sakis. In subsection 5.4.2, I test the data against the null hypothesis that the sakis will exhibit equal linearity in travel to three categories of food sources that they feed upon with disparate frequencies (i.e. the three "preference" categories). In the next subsection

(5.4.3), I explore factors and scenarios expected to significantly increase or decrease linearity in travel to resources. Cases involving those factors were excluded and the original tests comparing 1) linearity in travel to all resources against stated expectations and 2) among the three feeding resource categories were rerun. These results were discussed in subsections 5.4.4 and 5.4.5, respectively. In subsection 5.4.6, I discuss the second part of the directed travel prediction; specifically, the data is tested against the null hypothesis that the sakis will travel at the same rate to all preference categories. Finally, in subsection 5.4.7, I synthesize all of the results relating to the directed travel predictions into a brief summary.

The sixth and final chapter involves an in-depth discussion of the findings of this study. Comparisons are made between the study group and groups of white-faced sakis studied in Venezuela on the basis of the following: daily path lengths and core area sizes (subsection 6.1.1), diet (section 6.2), linearity in travel to the average feeding site (subsection 6.4.1), and parameters influencing feeding preferences (6.4.2 and 6.4.3). After discussing the affects that the monitoring of range boundaries and potential feeding sources have on directness of travel (6.1.2), I discuss what the backtracking episodes explored in this study can tell us about behavioral rules, arboreal pathway use, and distance-minimization (section 6.2). In subsections 6.4.2 and 6.4.3, I take one final look at the directed travel predictions and findings. After reviewing both the methods for designating preference in the present study and the criteria used to assign preferences in similar studies, I redefine the original preference categories, compare directness in travel among the newly defined categories, and discuss the implications of all of the relevant results. In section 6.5, I discuss the contexts in which the sakis appear to use landmarks and arboreal pathways. Chapter 6 ends with a section discussing my final thoughts and conclusions (6.6).

CHAPTER 2

INTRODUCTION TO FORAGING THEORY

2.1 Original Optimal Foraging Theory and Subsequent Developments

2.1.1 Discussion

Energy obtained from foods in the form of macronutrients such as carbohydrates, lipids and proteins is vital for proper body maintenance (i.e. for regulating metabolism and basic life processes, such as respiration and digestion), as well as for growth and reproduction (pre-mating activities, egg/embryo development, lactation, parental care) (Lambert, 2007). Furthermore, energy is needed to allow animals to participate in a whole suite of normal daily activities, such as foraging, finding mates, socializing, and vigilance (Schoener, 1971). Therefore, behaviors, morphologies, and physiological processes related to the procurement of high-energy food items are expected to be under strong selective pressure (MacArthur and Pianka, 1966; Emlen, 1966; Schoener, 1971, Pyke et al., 1977; Milton, 1979; 1980; 1981). Assuming that 1) there is a range of foraging strategies that an animal could implement to meet its nutritional requirements, 2) there is a mode of transmission for these behaviors to be passed on to subsequent generations, and 3) an animal’s fitness is maximized when the net energy gains of the resources it consumes are maximized (Emlen, 1966; Schoener, 1971), natural selection should act to increase the frequency of those foraging strategies that bolster an animal’s ability to survive and reproduce (Schoener, 1971; Pyke et al, 1977).

With these assumptions in mind, a body of work began to develop in the 1960’s and 1970’s called Optimal Foraging Theory (OFT). The major players in the growth of this theory, namely MacArthur and Pianka (1966), Emlen (1966), and Schoener (1971), sought to develop models that would allow them to make predictions about how animals should procure and utilize food in order to maximize their net energy yield per unit of foraging time. Energy was deemed a sufficient and suitable fitness currency (Emlen, 1966; Schoener, 1971) because these models were developed primarily with secondary consumers in mind: animal matter typically consists of readily digestible forms of energy (with the exception of the chitin-rich exoskeleton of most arthropods) and usually contains the full complement of macronutrients (proteins, lipids, and essential amino acids) that an animal needs to maintain itself (Lambert, 1998; 2007).

With an appropriate fitness currency agreed upon, optimal foraging theory set out to explain and predict 1) the number and type of items an animal includes in its diet, 2) the number and type of patches it exploits, 3) the allocation of time to each patch, 4) and the optimal foraging patterns and travel speeds for the animal (Emlen, 1966; MacArthur & Pianka, 1966; Schoener, 1971; Krebs et al. 1974; Charnov, 1976). According to OFT, whether or not an animal decides to include any particular food item in its diet depends on the amount of energy it can obtain from that item minus the amount of energy expended in the pursuit, handling, ingestion, and, in some cases, search of it, divided by the total amount of time spent acquiring and eating that item. All potential food items are then ranked, and foods are added to the diet from highest to lowest-ranked as long as the ratio of the net energy value to the acquisition time is greater than the net rate of food intake for the diet without the item (Schoener, 1971).

Reservations about the models’ usefulness began to emerge with Pyke et al.’s

(1977) and Pyke's (1984) review of both the theories and the support for the models' associated predictions; Pyke and his contributors concluded their reviews by recognizing that the models, as they stood, were far too simplistic to be useful in most real-world foraging situations and that there was no easy way to incorporate most deviations in assumptions into the models. Specifically, as more variables are added to optimal foraging theory (the varying nutrient and chemical composition of different food types; abundance of each food type; resource renewal rates; the effects of hunger, predation risk, reproductive status, and season on a forager's strategy; etc.), situations become too cumbersome to model effectively (Pyke et al., 1977; Pyke, 1984).

However, despite it's drawbacks, the basic acknowledgement that selective processes will be influenced by both the costs (energy and time expended in food acquisition, negative effects of toxins, digestive inhibitors) and the benefits (energy, macronutrients, vitamins and minerals; enhanced knowledge of available food items in environment) of including particular food items in diets or particular food patches in foraging itineraries has been helpful in guiding thinking on optimal foraging strategies since OFT's inception (Pyke et al. 1977, Pyke, 1984; Milton, 1980; Glander, 1982; Anderson, 1983; Pochron, 2005). Milton (1980), following Schoener's (1971) original distinction, has posited that animals can manipulate this cost/benefit relationship to best suit their particular requirements and constraints by either emphasizing the numerator of the optimal foraging model's benefit/cost ratio (i.e. they can be "energy maximizers"), the denominator of the equation (i.e. they can be "time or travel minimizers"), or some combination of the two.

Somewhat concurrent with the expression of Pyke's trepidations about the efficacy of optimal foraging theory came doubts about the appropriateness of energy as the sole fitness currency for foragers that did not fit the carnivorous profile (Westoby, 1974; Freeland and Janzen, 1974). First of all, no single plant food type (whether it be young leaves, seeds, exudates, or the mesocarp of ripe fruit) contains all of the macronutrients and vitamins and minerals that an animal requires meet its nutritional needs (Garber, 1987; Lambert, 2007). Furthermore, generalist herbivores procure plant food types that can be difficult to digest and have relatively low overall nutritional value when compared to animal matter (Lambert, 1998; 2007). Therefore, Westoby (1974) proposed that most large generalist herbivores would be expected to optimize the nutrient mix, rather than the energy total, within a given bulk of food, and would be limited by digestion time rather than pursuit times. Freeland and Janzen (1974) substantiated this proposal by adding that the plant parts that herbivores feed upon generally contain some mixture of secondary metabolites that can either inhibit digestion or interfere with normal physiology. Therefore, rather than maximizing the quantity of any particular type of food (for instance, secondary consumers might want to maximize the quantity of animal matter in their diets), herbivores should be extremely selective in their choice of food types and should try to optimize the nutrient to secondary compound ratio in their diets using a variety of food types (Freeland and Janzen, 1974; Milton, 1979, 1980; Glander, 1982).

However, being selective in feeding and trying to optimize the nutrient mix would reduce the net gains acquired from food sources since these tendencies would increase the amount of time and energy devoted to procuring those items (i.e. increases in handling and digestion times, as well as search times). Consequently, if the efficiency of foraging is maximized by natural selection, herbivores might be expected to have developed morphologies and behaviors that act to minimize the costs of procuring preferred foods. While the literature abounds with evidence that some animals possess anatomical or physiological adaptations that allow them to more efficiently process or ingest certain preferred or resistant plant foods (e.g. procumbent canines for opening tough pericarps, sacculated stomachs that aid in the fermentation of structural carbohydrates, microsomal enzymatic activity and/or diverse gut flora that can help to degrade and detoxify plant toxins- Freeland and Janzen, 1974; Milton, 1979; Norconk and Kinzey, 1993; Lambert, 1998), this paper will focus on theories and evidence relating to behavioral strategies that increase foraging efficiency and decrease foraging costs.

Primates have been at the heart of many studies focusing on behavioral foraging strategies of generalist herbivores, and for good reason. While members of the primate order are not strictly herbivores, most of them obtain the majority of their nutritional requirements from plants (Lambert, 2007). In Harding's (1981) review of the diets of 131 primate species, he found that 90% of these species ate fruit, 79% ate soft foliar parts, 69% ate mature leaves, 41% ate seeds, 65% ate invertebrates, and 37% ate vertebrates. Therefore, not only is the majority of most primates' feeding time spent on resources from the first trophic level, they also may be considered generalists in the sense that they obtain foods from a large and variable array of resources (Fleagle, 1999; Lambert, 2007). Furthermore, since members of the primate order are 1) forced to procure food from tropical environments known for the widely dispersed, ephemeral, and sometimes unpredictable nature of their resources (Milton, 1979; 1981), and 2) noted for their comparatively large brain sizes and associated abilities to assimilate, retain, and integrate complex information (Napier, 1970; Clutton-Brock and Harvey, 1980), they are prime subjects for studying the ability of animals to implement behavioral strategies that allow for efficient procurement of dispersed and ephemeral foods.

Milton (1979, 1980, 1981) proposed that behavioral features for minimizing the costs of procuring preferred plant foods should be most apparent in food search activities. Primary consumers, she reasoned, do not have to be concerned with energy or time losses related to pursuing or capturing their food items, as envisioned for the predators in the original optimal foraging models. So, with respect to behavioral adaptations, herbivores could minimize costs associated with being choosy about their dietary selections simply by employing a search strategy that minimized distances traveled to resources ("travel minimization"- Milton, 1980) while increasing the probability of locating those resources. The particular search strategy that an animal uses to efficiently locate resources depends on the distribution of food items in the animal's diet (Oates, 1987; Garber 1987, 1989; Milton, 1980, 1981, 1988; Terborgh, 1983; Noser and Byrne, 2007b): 1) if resources are distributed uniformly in the environment, then the animal should strategically move back and forth in uniform swaths; 2) if resources are distributed randomly in the environment, then the animal can move randomly through their habitat since the probability of finding resources at one location would be just as good at finding resources in any other location; and 3) if resources are patchy (where "patchy" refers to situations in which areas of high food concentration are separated by areas of low food concentration, see Appendix A for glossary of key terms), the animal should travel directly those resources when and where they are available (i.e. goal-directed foraging, see Appendix A; Milton, 1980; Terborgh, 1983; Garber, 1987, 1989).

2.1.2 Summary

Generalist herbivores, and in effect most primates, must be more selective than carnivores about the items they include in their diets since 1) many plant foods contain structures and/or chemicals that inhibit digestion or interfere with normal physiology, and 2) no single plant food item contains all of the nutrients required by an animal. Therefore, most generalist herbivores would not fare well using the same foraging strategy deemed sufficient for carnivores, i.e. a foraging strategy that allows predators to move about at random through their range (even backwards movements can be effective here), consuming any prey item that it encounters as long as the net calories obtained from that item outweigh losses in energy and time spent pursuing and handling the prey.

An herbivorous diet necessarily requires a more systematic approach. Due to the varying nutritional value of different plant resources, relying on chance to encounter resources would not allow an herbivore to meet all of its nutritional requirements in a limited amount of time (e.g. during its daily foraging forays). Even if an herbivore mainly exploits resources that are distributed randomly in space and time (e.g. mature leaves), it must be more methodical and cognizant of the directions in which it chooses to search. While random movement along a basic forward trajectory would bring it into contact with many distinct randomly distributed sites, backward motion would waste time and energy as the forager would increase its chances of encountering recently exploited sites, thereby causing it to 1) revisit sites that it has already depleted or 2) consume too much of one plant species/type/phenophase with its own specific and, likely, incomplete, nutrient makeup.

If an herbivore mainly exploits items that are either uniform or clumped in their distribution, their foraging strategy would require even stricter rules and more enhanced mental capabilities. The best strategy for animals exploiting uniformly distributed food items would be to move back and forth in paths segments with equal lengths and complimentary bearings. Spatial memory is required for animals exploiting resources that are patchy in space and time as the animal would have to be able to recall when and where items were available so that it could plan direct paths to plant sources at the appropriate time in their flushing, fruiting, or flowering cycles.

2.2 Determinants of Goal-Directed Behavior: Patchiness, Predictability, and Preference

2.2.1 The Spatial Distribution of Plant Species in Tropical Forests

It is well-established fact that tropical forests exhibit a pattern of high species diversity and low species density (Milton, 1981; Garber, 1987; Oates, 1987; Terborgh, 1992; Condit et al, 2000). Oates (1987) noted that it is common to find 50-100 species per hectare in tropical rainforest environments; and Milton (1981) showed that 65% of all species occurred less than once per hectare in her analysis of roughly 60,000 m^2 of lowland tropical forest in central Panama. If an animal were to concentrate its efforts on exploiting only the nutritious fruits or exudates of a certain species, low plant densities might make those resources difficult to exploit if either the species or those particular plant parts exhibited a highly dispersed rather than clumped distribution.

Fortunately for potential consumers, most tropical plant species, while occurring at low densities overall, can be found in aggregations rather than sparsely scattered (Hubbell, 1979;

Milton, 1981; Terborgh, 1992; Condit et al., 2000). Of 1768 species assessed in six different tropical locations around the world, 1490 species (84%) showed a significantly aggregated distribution (Condit et al., 2000). Similarly, Hubbell (1979) showed that 72% of species in a Costa Rican dry tropical forest exhibited a clumped distribution, while only 28% showed a random distribution pattern (and 0% exhibited a uniform distribution).

2.2.2 Plant Parts and Patchiness

Since primates typically focus on only certain phenophases or plant parts of each species they exploit (hence categorical labels such as frugivore, folivore, gummivore, insectivore, and gramnivore/seed-predator), the varying spatial and temporal distribution of those parts would also play a role in how those animals set out to locate resources in their diet. Leaves (specifically, mature leaves) are more frequently encountered in space and time (less patchy) than virtually any other plant resource that animals exploit (Oates, 1987; Garber, 1987), and fruits are relatively scarce in comparison. Typically, plants produce more leaves annually and throughout their life cycle than flowers or fruits; furthermore, they tend to bear foliage for much longer periods than they bear reproductive parts (Oates, 1987). To emphasize the enormous contrast in temporal availability of leaves versus fruits Milton (1980, pp. 35-39) noted that mature leaves were present on trees of particular species (for twelve randomly selected species) for as many as 11.75 months per year (6.81 months per year for young leaves), while green and ripe fruits were available for only 3.67 months per year. Therefore, a primate searching for leaves, and in particular mature ones, would exert itself the least, physically and mentally, by moving through its home range in a random fashion, since this type of resource has an equal likelihood of being found in any locale at any given time.

2.2.3 Maturity Levels and Patchiness

A simple shift in focus from one maturity level to another can drastically change the distribution of the resource of interest. For instance, while the mature phase of a leaf's life cycle is considerably longer than the growth phase (Milton, 1981; Garber, 1987; Oates, 1987), the opposite holds for fruits. Ripe fruits are much more ephemeral than unripe fruits (Milton, 1981; Garber, 1987; Peres, 1993; Lambert, 2007). For instance, for an annual cycle of flowering, fruiting, and flushing on island in Lago Guri, Venezuela, Norconk (1996) found ripe fruits to be available for only 4.7 months, while unripe fruits were available for 6.6 months. Overall, then, primates searching for young leaves and/or ripe fruits (patchy resources) should travel in a more directed manner than primates searching for mature leaves, and perhaps even unripe fruits (more evenly dispersed resources).

2.2.4 Predictability in Fruiting, Flushing, and Flowering

Another very important factor determining whether or not a primate will use a goal-directed foraging strategy is the predictability in the flushing, flowering and fruiting cycles of the plant species included in that animal's diet (Garber, 1987, 1989; Pochron, 2001, 2005; Bicca-Marques & Garber, 2004). It would do the forager little good to memorize the location of individual trees of a high-quality fruit species if there was no way to gauge when during the year fruits on those trees would be available; similarly, the cognitive load involved in the processes of memorizing, integrating and recalling the location of particular feeding trees might be worthless if the ripening of fruit on one tree of a certain species told an animal nothing about the ripening pattern of conspecifics.

Fortunately for herbivores, researchers have noted relatively predictable annual peaks and valleys in the production of seasonal food items (Ausperger, 1978; Oates, 1987; Milton, 1980; 1981; Garber, 1987; 1989; de Dijn, 2006; van Schaik et al., 1993). Phenological variation corresponds to predictable fluctuations in annual rainfall, sunlight, and temperature and to the activity cycles of pollinators, dispersers and plant predators (van Schaik et al., 1993). If an animal is able to memorize and integrate information regarding the spatial distribution of preferred feeding sites in its environment, it will likely be able to rely on fairly regular and predictable temporal and ecological patterns in the plants it exploits.

2.2.5 Preference and Goal-Directed Foraging Behavior

Finally, animals are expected to be extremely goal-directed in their travels if they are heading towards resources that are highly valued or preferred (Garber, 1987; 1989; Janson, 1996; 1998; Pochron 2001; 2005; Cunningham and Janson, 2007; Janson and Byrne, 2007; Noser and Byrne, 2007a; 2007b). First and foremost, highly valued resources tend to be ones that are fairly predictable in their production schedules and those that are found in clumps (because animal can obtain relatively large food rewards by traveling to just one area). Once these criteria are met, animals tend to place higher value on 1) sources of food that make up the bulk of their diet (Garber, 1988; 1989;1993; Cunningham and Janson, 2007), 2) sources of food that are more productive (Garber, 1989; Janson, 1998; Cunningham and Janson, 2007; Janson and Byrne, 2007), 3) resources that are relatively limited in space and/or time (such as water holes or sleeping cliffs for baboons; Sigg and Stolba, 1981; Noser and Byrne, 2007 a & b), 4) food items that provide vital nutrients or minerals (Garber, 1988; Janson and Chapman, 1999; Di Fiore, 2003), 5) food items that provide large nutrient/energy rewards per unit of handling time

(MacArthur and Pianka, 1966; Schoener, 1971; Pochron, 2005), and/or 6) resources that are readily available in times of relative food scarcity (Pochron, 2001).

2.2.6 Summary of Characteristics Associated With Goal-Directed Foraging Behavior

If the plant resources available to herbivores exist on a continuum of patchiness (with mature leaves being the least patchy, followed by corms and grasses, exudates, immature leaves, flowers, unripe fruits, and finally, ripe fruits- Garber, 1987), and if the degree of patchiness, predictability, and value of resources that an animal exploits is positively correlated with the degree of linearity in travel towards those resources (Milton, 1980; Garber, 1987; 1989; Noser and Byrne, 2007b), then one would expect animals exploiting extremely patchy, predictable, and preferred resources to be goal-directed in their foraging strategies and animals exploiting less patchy, predictable, and preferred resources to exhibit more random movement. Noser and Byrne (2007b) found support for the relationship between degree of patchiness and degree of goal-directedness. In their study, chacma baboons moved faster and more linearly to food and water sources in the dry season when resources were patchier than in the wet season when resources were more evenly distributed. Furthermore, many researchers have found that primates will travel more linearly (and more quickly) towards more highly preferred resources (Menzel, 1973; Sigg and Stolba, 1981; Menzel, 1991; 1996; 1999; 2002; Garber and Dolins, 1996; Garber and Paculli, 1997; Janson, 1998; Pochron, 2001; 2005; Cunningham, 2003; Di Fiore, 2003; Janmaat et al., 2006; Cunningham and Janson, 2007; Noser & Byrne, 2007a; Valero and Byrne, 2007).

2.3 White-Faced Sakis and Expectations With Regard To Their Foraging Strategy

2.3.1 Brief Overview of Behavior and Ecology

White-faced sakis (*Pithecia pithecia* Linnaeus, 1776, type locality: French Guiana, Hershkovitz, 1987) are one of the least known New World primates. While this species is minimally sexually dimorphic in body mass (females average 1.76 kg and males average 2.38 kg, Ford and Davis, 1992), individuals are highly sexually dichromatic, with females sporting the more cryptic agouti-brown coloration and males being all black except for the stark white facial pelage (Gleason and Norconk, 1995; Norconk, 2007), .

The *Pithecia pithecia* group (including 2 subspecies) inhabits the Guiana Shield forests north of the Amazon River (Hershkovitz, 1979, 1987) and is able to exist in a variety of habitat types, including highland to lowland forests, seasonally flooded to relatively dry forests, and primary to secondary and disturbed forests (Sussman and Phillips-Conroy, 1995; Norconk et al., 1996). However, Buchanan et al. (1981) and Mittermeier and van Roosmalen (1981a) posit that sakis have a preference for high and mountain savanna forests, and possibly liane forests. Sakis occupy the lower to middle canopy levels (15-25m) and the understory (3-15m) (Mittermeier and van Roosmalen, 1981a), and will come to the ground to search for food (Thompson, personal communication), at times, for extended periods (Gleason, 1998).

While there is no doubt that group sizes are relatively small for this species, specific group size estimates have varied greatly from area to area. Some studies have produced group size averages centering around 2-3 individuals (Buchanan et al., 1981; Mittermeier and van Roosmalen, 1981b; Oliveira et al., 1985; Vié et al., 2001), leading some researchers to conclude, perhaps prematurely (Norconk, 2007), that this species is monogamous (Buchanan et al. 1981;

Robinson et al., 1987; Vié et al., 2001). However, most studies focusing on *P. pithecia* have generated larger group size estimates and group compositions comprised of more than one adult male and/or female (5-9 individuals per group for island habitats, Gleason and Norconk, 1995; Homburg 1997; Norconk, 2006; Setz and Gaspar, 1997; 4.8 ± 2.4 individuals in a study exceeding a year in a non-fragmented habitat, Lehman et al., 2001; and 4.65 ± 1.66 individuals for free-ranging sakis at Brownsberg Nature Park, Suriname, Norconk et al., 2003).

White-faced saki groups seem to occupy relatively exclusive home ranges with clearly defined boundaries (Buchanan et al., 1981; Robinson et al., 1987) and have been observed to participate in boundary advertisement behaviors (scent gland (sternal/gular/anogenital) rubbing, urine-washing, and territorial calls- Homburg, 1997; Setz and Gaspar, 1997; Gleason, 1998) and agonistic interactions, using grunts, trills, branch and body shakes, piloerection, and fast pursuits to threaten and displace extra-group members (Vi**e** et al., 2001; Norconk, 2006, 2007). Thus, they appear to be territorial in a typical primate fashion.

Estimates of home range size for white-faced sakis have varied, but overall, are small for a frugivorous primate. Home range size for groups in forest fragments (Cunningham, 2003; Oliveira et al., 1985; Norconk, 2006), for an unrestricted group in Suriname (Norconk et al., 2003) and for briefly observed and unhabituated groups (Buchanan et al., 1981) center around 10 ha. Much larger estimates, ranging from 68 to 152 ha, come from observations of a pair of relocated animals rescued from flooding and a mainland resident group with a recently relocated animal, respectively (Vié et al., 2001). White-faced sakis are reported to travel in cohesive units during their daily treks (Cunningham, 2003; Cunningham and Janson, 2007), which range from

< 1 km (Olivieira et al., 1985; Kinzey, 1997) to nearly 2 km long (Vié et al., 2001; Cunningham and Janson, 1997).

White-faced sakis have shorter days than other neotropical monkeys (9 or 10 vs. 12 hrs, Kinzey 1997; Vié et al., 2001). They are most active in the early morning and early afternoon, and typically begin to move slowly and quietly towards a sleeping site 1-1 ½ hrs before the end of their day (Olivieira et al., 1985; Vié et al., 2001). Sakis have definite preferences for particular types of sleeping sites (usually large upper canopy trees with tangles of dense foliage) and have been reported to reuse their most favored ones once every few nights or even for a few nights consecutively (Vié et al., 2001). It is not yet known whether encounters with other saki groups, general location within the home range, or proximity to feeding sites play a role in the choice of sleeping sites.

2.3.2 Sakis and Seed Predation: Costs and Benefits

The genus *Pithecia* belongs to a clade of platyrrhines known as the pitheciins that includes the larger-bodied bearded sakis (genus *Chiropotes*) and the uakaris (genus *Cacajao*). Rosenberger (1992) estimates that *Pithecia, Chiropotes*, and *Cacajao* have been adapted for a predispersal seed predator niche since the Middle Miocene. These pitheciins share a number of unique dental traits that facilitate opening and manipulating the seeds of fruits with relatively hard pericarps (i.e. they are sclerocarpic seed predators- Kinzey and Norconk, 1990, Appendix A). Dental synapomorphies include procumbent, high-crowned incisors, robust and laterally flared canines that are separated from the incisors by a diastema, and quadritubercular molars with very low cusp relief and crenulated enamel (Hershkovitz, 1985; Ayres, 1989; Kay, 1990; Kinzey, 1992; Norconk, 2007).

Despite their abundance relative to ripe fruit, seeds can be a tricky resource to exploit. Seed coats can be difficult to digest and/or penetrate as they typically contain structural carbohydrates such as cellulose or lignin and/or proteins and silica that contribute to their hardness (Lambert, 1998; Norconk et al., 1998). Furthermore, seeds, especially younger ones, can contain high levels of secondary compounds that can either impede an animal's ability to utilize proteins (e.g. tannins) or can interfere with normal physiology due to toxic qualities (e.g. alkaloids) (Lambert, 1998; Norconk et al., 1998; Norconk et al., 2002). Finally, the outer covering (pericarp) of many fruits can provide another obstacle to animals trying to extract the nutritious seeds from within: Fischer and Chapman (1993) observed that 75% of fruit genera sampled from five different localities around the world demonstrated some mechanical protection (hardness, spines, thorns, stinging hairs, etc.).

With all of these complications, one might expect that seeds have too many shortcomings to make them worth exploiting. However, seed predation is relatively common among insects, birds, and some mammals, most notably the rodents and ungulates in the neoptropics (Janzen, 1971; Norconk et al., 1998). Furthermore, 31 primate species (roughly 13% of all species in the Order Primates) include at least 20% seeds in their annual diets, either as a substantial portion of their monthly diets or on a seasonal basis (Norconk et al., in press).

Therefore, seed-eating must confer enough advantages to foragers to outweigh its drawbacks. Janzen (1971) notes that seeds are often balanced nutritionally since the plant sequesters many different nutrients to the seed compartment to provide for the seed during development. Specifically, seeds can be quite high in lipids and starches and can also be a good source of proteins and some vitamins (Lambert, 1998; 2007; Norconk and Conklin-Brittain, 2004; Norconk et al., in press). Furthermore, seeds are usually more abundant than ripe fruit pulp in both space and time (Kinzey and Norconk , 1990; Norconk et al., 1998): since the majority of frugivorous primates are soft pulp-feeders, seeds are underutilized and, therefore, more abundant throughout the forest; additionally, the temporal availability of unripe fruit (most primates exploit the young seeds of immature fruits, Kinzey and Norconk, 1993) can be 3-4 times longer than that of ripe fruit (Peres, 1993; Norconk, 1996). The dry season, a time of relative fruit scarcity for many animals, is when young seeds are most abundant (Peres, 1993). Therefore, for those animals able to exploit them, seeds can provide them with a very nutritious and relatively plentiful source of food during critical periods.

2.3.3 The Saki Diet

White-faced sakis, along with their sister taxa, *Chiropotes* and *Cacajao*, are year-round sclerocarpic seed-eaters, ingesting the seeds of mature or (more often) immature fruits, (Norconk et al., in progress). Ninety-five to ninety-nine percent of *Pithecia*'s fruit-eating time includes the ingestion of seeds alone or seeds with the mesocarp; during any month, 38-88% of their feeding time is spent exclusively on seeds (Kinzey and Norconk, 1993). Using their robust canines, they are able to open immature fruits with very hard pericarps (harder than any fruit exploited by *Ateles*, but not as hard as those taken by *Chiropotes*, Kinzey and Norconk, 1993), including fruits with wooded, bony, fibrous, thick, winged, and husked outer coverings and pods that are generally unavailable to other primate species (Norconk, 2007). They are then able to grind down the relatively soft, immature seeds within (white-faced sakis eat seeds that are harder than those eaten by *Chiropotes*, but not as hard as those swallowed by *Ateles*, Kinzey and Norconk, 1993) using their crenulated, low-cusped molars.

White-faced sakis supplement their highly frugivorous diet with young leaves (eaten daily, Kinzey and Norconk, 1993; Kinzey, 1997; Norconk and Conklin-Brittain, 2004), flowers, nectar, insects (eaten at least some every month, Kinzey and Norconk, 1993), pith, bark, and termite/wasps nests (Norconk, 2007). In the wet season, sakis increase the proportion of fruit pulp and decrease the proportion of seeds in their diet (Norconk, 1996; Oliveira et al., 2001; Norconk and Conklin-Brittain, 2004; Norconk, 2007); in the dry season, they have been reported to increase the amount of seeds they exploit (Norconk, 2007), as well as the proportion of young leaves (Oliveira et al., 2001; Cunningham and Janson, 2006) and flowers (Kinzey and Norconk, 1993; Oliveira et al., 2001; Norconk and Conklin-Brittain, 2004; Cunningham and Janson, 2006).

2.3.4 Saki Resource Selectivity

Many primates are selective about the specific resources they will exploit, whether out of necessity (i.e. during times of food scarcity or when there are many competing animals in the area vying for similar resources) or more out of preference (e.g. baboons select foods with high protein and lipid content, Whiten et al., 1991; mangabeys selectively feed on ripe fruits even during low seasonal availability, Mitani, 1989; howler monkeys prefer species from certain plant families (Moraceae, Lauraceae, Leguminosae) Estrada, 1984; many species feed selectively on young rather than mature leaves, (Clutton-Brock, 1975; Milton 1977 & 1979; Glander, 1982).

White-faced sakis are no exception. As is the case for most other primates that include leaves as an important component of their diet, they seek out the less fibrous and, in general, more protein-rich younger leaves. Furthermore, besides exploiting a part of the fruit that is much less desired among primates than the carbohydrate-rich flesh, namely seeds, white-faced sakis have even been shown to be choosy about the particular types of seeds they will ingest. Reportedly, white-faced sakis select seeds that are relatively high in lipid content (lipid content explained 50% of the variance in percent feeding time- Norconk and Conklin-Brittain, 2004; four times higher lipid intake than other primate frugivores and higher than that for their sister taxa, *Chiropotes* and *Cacajao*, Kinzey, 1997; Norconk and Conklin-Brittain, 2004) and moderately low in tannins. Unlike *Chiropotes*, *P. pithecia* will ingest seeds from ripe or nearly ripe fruit that have higher lipid contents and reduced tannins compared to their ripe counterparts, even if it means having to manipulate relatively harder seeds (Kinzey and Norconk, 1993). Finally, white-faced sakis choose a disproportionate amount of fruit parts from specific plant families, including members of Bignonaceae, Capparidaceae, Chrysobalancaceae, Connaraceae, Erythroxylaceae, Lecythidaceae, Loganiaceae, Leguminosae, and Rubiaceae (Kinzey and Norconk, 1993; Norconk, 1996; Homburg, 1997; Cunningham, 2003).

2.3.5 Expectations Based on Behavior and Feeding Ecology

The bulk of the saki diet is made of the seeds of unripe or ripe fruits and the flesh of ripe fruits, both of which are highly patchy resources in space and time. Furthermore, they exhibit strong preferences for certain foods, namely soft, lipid-rich seeds of particular plant families and younger, more easily digestible leaves. Finally, they appear to exhibit preferences for a particular type of non-food resource, namely sleeping sites. Based on theoretical models (Milton, 1980) and an abundance of evidence (Menzel, EW, 1973; Milton, 1980, 1981; Sigg & Stolba, 1981; Garber, 1987, 1988, 1989,1996; Chapman et al., 1989; Menzel, CR, 1991, 1996, 1997, 1999, 2000; Garber and Dolins, 1996; Garber and Paculli, 1997; Janson, 1998, 2006; Pochron, 2001, 2005; Menzel, CR, et al., 2002; Cunningham, 2003; Di Fiore, 2003; Janmaat et al., 2006; Cunningham and Janson, 2007; Noser & Byrne, 2007 a & b; Valero and Byrne, 2007), we expect foragers whom exploit highly patchy resources and exhibit strong preferences for certain resources to implement a goal-directed foraging strategy. Efficiently locating both preferred and patchy resources requires an ability to integrate information on the location, phenological patterns, and resource abundance of multiple sites.

CHAPTER 3

LOCATING RESOURCES

3.1 Organizing Information: Memory Potential, Rule-Based Foraging and Spatial Representations

Research on the foraging strategies of primates offers great insight into how animals integrate and organize information pertinent to the efficient location and exploitation of food patches. The amount of information alone that an animal has to mentally manipulate on any given foraging venture is daunting. For instance, it is very likely that a primate foraging party will be taking into consideration not only information relevant to obtaining a given quantity and quality of food items using the least amount of time and energy, but also factors such as predation risk at certain sites and proximity to potential mates, competing groups, and/or home range boundaries. In fact, it is probable that the choice of where to forage will be made on the basis of both short and long-term fitness goals (for example, in one day, an animal 1) will want to travel to areas that will secure enough food for it to sustain itself today, 2) may want to investigate food sites that could sustain it in the future, and 3) may want to explore other areas to secure it's chances for procreation; Pyke et al., 1977).

Primate foragers have to track resource changes in highly dynamic and fluctuating tropical environments (Milton, 1979; 1981; Garber, 2000). The areas in which they need to track these changes can be extremely large and the number of plant species for which these changes are relevant can quite numerous (primates can have diets that include resources from over 50 species, Oates, 1987; reports of over 150 species annually have been noted for some groups, Milton, 2000).

While the shear volume of information that a primate forager has to filter through to make prudent foraging decisions is astonishing, observational studies and experiments in both captive and natural settings have shown that many primate species are capable of remembering many variables related to foraging problems (Table 3.1). The neurobiology behind the retention and recollection of spatially and temporally-relevant foraging information is a whole field of study unto itself (O'Keefe and Nadel, 1978; Poucet, 1993; Jeffrey, 2003).

For the purposes of the current investigation, I will only address how foragers might mentally organize and represent relevant spatial, temporal, ecological, social information to reduce the complexity of foraging scenarios (Poucet, 1993; Menzel, 1996; Garber, 2000; Milton, 2000). Garber (2000) has postulated that foragers could reduce potential information overload by generating a set of simplifying rules or strategies applicable to the specific types of resources and situations that they encounter, i.e. they could implement "rule-guided" foraging (Menzel, 1996). These rules can guide animals through many types of foraging problems, such as where to search next, when to return to a site, and even how to organize or order successive feeding bouts throughout the day (Garber, 2000). Some rules may be useful for foragers that do not necessarily rely on spatial memory to find their resources (Table 3.2 A), while others are only useful for spatially cognizant and goal-directed foragers (Table 3.2 B).

Table 3.1 Remembering locations, amounts, and, phenologies. Proven proficiencies among various primate species in recalling the locations of various feeding sites, the quality or quantity of foods to be found there, and/or the phenological patterns of resources at particular sites. This is not meant to be an exhaustive list.

Primate Species (c = captive, w = wild)	Location	Quantity and/or quality	Phenol.	Source
Papio hamadryas <u>subspp</u>.				
hamadryas (w)	x			Sigg & Stolba, 1981
cynocepalus (w)	x	x		Noser & Byrne, 2007b
chacma (w)	x	x	x	Pochron, 2001, 2005
Pan troglodytes (w)	x			Boesch & Boesch, 1984
Pan troglodytes (c)	x			Menzel, 1999, 2002
Callicebus	x	x		Anderson, 1988
Saimiri (c)	x	x		
Ateles geoffroyi (w)	x		x	Milton, 1981b
Ateles geoffroyi (w)	x	x		Chapman et al., 1989
Saguinus mystax (w) &	x	x		Garber 1988, 1989; Garber & Dolins, 1996;
Saguinus fuscicollis (w)	x	x		Garber 1988; 1989
Macaca fuscata (w)	x		x	Menzel, 1991
Cercocebus torquatus &	x		x	Janmaat et al., 2006
Lophocebus albigena (w)	x		x	
Cebus apella (w)	x	x	x	Janson, 1998; 2007
Pithecia pithecia (w)	x	x		Cunningham & Janson, 2007
Brachyteles arachnoides (w)	x			Di Fiore & Suarez, 2007

Table 3.2 Behavioral rules and strategies requiring or not requiring spatial memory.

A. No spatial memory required.

Rule	**Meaning**	**Examples**	**Reference**
1. Travel randomly	Search randomly when resources a) are distributed randomly, b) are in ubiquitous (wet season, possibly), c) are of low quality, and/or d) when in an unfamiliar region.	c) baboons feeding on seeds on returns to nightly sleeping cliffs c) yellow baboons searching for low quality foods d) low-ranking baboons waiting for opportunity to feed in preferred trees	-Noser & Byrne, 2007a -Pochron, 2001 -Noser & Byrne, 2007b
2. Straight-line rule-of-thumb	Move in straight-line paths so as to avoid revisiting recently exploited food sites	-rats in mazes -flocks of finches	-Olton et al., 1987 -Cody, 1971
3. Sharp-turn rule-of-thumb	When I locate one food item that tends to occur in clumps, increase frequency of sharp turning and decrease speed.	-various birds, fish, insects -chacma baboons	-review of literature by Bell, 1991 -Menzel, CR,1991

B. Spatial memory required. (If the animal is also traveling directly to known resource, rule qualifies as a goal-directed foraging strategy; therefore, rules 4, 5, and 6 automatically qualify; 1, 2, and 3 would qualify if travel to respective resources were conducted in a directed manner.)

Rule	**Meaning**	**Examples**	**Reference**
1. Win-shift	1) If I just fed in that tree/area, move onto another (similar to A2), or 2) if a current feeding source is unpredictable in terms of it's schedule of rewards, don't return	1) many herbivorous foragers 2) carnivores or insectivores that find prey items in certain locales	1) Armstrong et al., 1987; Baum, 1987; Garber, 1993 2) Olton et al., 1987; Pochron, 2001
2. Win-return	1) If source known to produce food items for extended period of time, return to source until items depleted.	1) white-faced sakis returning to same fruiting trees for many days 2) nectar-feeding moustached and saddle-back tamarins	1) Cunningham, 2003; Cunningham & Janson, 2007 2) Garber, 1988; 1989; Garber & Hannon, 1993

3. Structure-guided foraging	Continue to search structures similar in appearance to structure in which food is found	- tamarins visiting trees of a particular flowering species in succession - captive long-tailed macaques searching structures similar to baited ones - wild Japanese macaques searching synchronously-fruiting akebi trees	- Garber, 1988, 1989 - Menzel, CR, 1996 - Menzel, CR, 1991
4. Nearest-neighbor	Travel directly to the closest tree of a chosen food species.	-chimpanzees -tamarins -capuchins	- Menzel, EW, 1973 - Garber, 1988; 1989 - Janson, 1998; 2007
5. Trapline	Travel directly to several trees of a given species in succession	- prosimians - New World monkeys - Old World monkeys - apes	- Sussman & Raven, 1978; Overdorff, 1993 - Terborgh, 1983; Garber, 1988, 1989 - Sigg & Stolba, 1981; Menzel, CR,1991 - Menzel, EW, 1973; Boesch & Boesch, 1984

Researchers posit two basic strategies for mentally representing the locations of important sites in one’s environment (Poucet, 1993; Benhamou, 1996; Garber, 2000), namely topographical/route-based mental mapping and Euclidean mental mapping. Euclidean mental representations of space are described as “views from above”, wherein the navigator is imagined to have a mental image of its environment that is virtually indistinguishable from a paper map (Tolman, 1948; O’Keefe and Nadel, 1978; Poucet, 1993; Benhamou, 1996; Noser and Byrne, 2007a). Therefore, this type of navigator can compute exact distances and directions from any present location to any target site in its home range, allowing it to find 1) a straight-line path between any starting location and any goal in the environment, 2) novel shortcuts, and 3) optimal detours (Muller, 1996). Topographical or route-based foragers, on the other hand, are assumed to navigate by reference to permanent landmarks in their environment (tall trees, hilltops, ridges, cliffs, forest edges, streams, roads, etc), and may habitually use particular, reliable routes to travel among those landmarks (Poucet, 1993; Shettleworth, 1998; Byrne, 2000; Garber, 2000; Di Fiore and Suarez, 2007).

Evidence for use of Euclidean-based mental maping is scant, as proving that free-ranging animals can find the shortest path between any two points in their environment and/or can use novel routes is extremely difficult (requires that the researcher has nearly flawless knowledge of the animal’s travel history and/or that the researcher can induce that animal to go where he/she wants it to go) (Janson, 2000). Even the studies that come closest to providing evidence for Euclidean-based travel (Morris, 1981; Garber, 1988; 1989; 1993; Garber and Dolins, 1996; Janson, 1996; Janson and Di Bitetti, 1997; Byrne, 2000; Menzel et al., 2002; Noser and Byrne, 2007a) fall short of meeting this goal, as each scenario could be sufficiently explained using a more parsimonious explanation (Dyer, 1991; Poucet, 1993; Benhamou, 1996; Byrne, 2000;

Noser and Byrne, 2007a; Garber, 2000). In fact, Benhamou (1996) asserts Euclidean-based navigation “has never been demonstrated nor even properly tested.” So while there is no doubt that foragers would benefit greatly if they were able to plan efficient routes using the metric properties of many locations in space at once, the jury is still out on whether any animals (even humans, Byrne, 2000) are capable of effectively and consistently using Euclidean mental maps to navigate through their environments (Poucet, 1993; Benahamou, 1996; Bennett, 1996; Byrne, 2000).

Rather than remembering the specific locations of thousands of different resources in their home ranges, route-based or topographical foragers could commit to memory a small collection of routes leading to or passing by important trees/areas (Poucet, 1993; Shettleworth, 1998; Byrne, 2000; Garber, 2000; Di Fiore and Suarez, 2007). Many primate species have been observed to find their way by means of topographical representations, whether this refers to the relatively simple, repeated use of long uninterrupted paths by howlers, spider monkeys (“arboreal pathways”, Milton, 1980; 1981b, 2000), and orangutans (“arboreal highways”, Mackinnon, 1974), or the extremely complex manipulation of numerous landmarks and intersecting routes so that multiple routes to several alternative resources become available (hamadryas baboons, Sigg and Stolba, 1981; spider monkeys and woolly monkeys, Di Fiore and Suarez, 2007; chacma baboons, Noser and Byrne, 2007a).

Since topographical/route-based travelers do not encode spatial information on the basis of actual distances and angles among features in their environments, they will likely not be able to take novel routes or shortcuts to distant sites or plan the most distance-minimizing route across a set of resources (Poucet, 1993; Cramer and Gallistel, 1997; Byrne, 2000; Garber, 2000; Janson, 2000; Menzel et al., 2002). However, depending on the number of route segments and landmarks a forager can encode, this type of navigation can potentially be a very effective and relatively undemanding means of locating, monitoring, and even maintaining food resources in one's own environment. Di Fiore and Suarez (2007) note that, over many years, primate seed dispersers that travel along habitual routes may be able to significantly affect the distribution of resources in their home range; further, they recognize that route-based navigators can avoid "cognitive overload" (Milton, 2000) by reducing the number of locations they have to memorize and by tracking the phenological status of prospective feeding trees directly (while en route to other resources along habitual routes) rather than mentally.

3.2 Proving Goal-Directed Behavior

Whether or not an animal uses behavioral rules to decide when, where, and how to locate food, or uses a topological over an Euclidean-type mental map to orient itself in space during foraging bouts, that animal is "goal-directed" if arrives at each particular resource intentionally and directly (within constraints) rather than by random search processes. Since researchers that consider spatial movement patterns agree that foragers should prefer to obtain a given quantity and quality of food items at the least possible cost in travel distance (Milton, 1979; 1980; 1981; Anderson, 1983; Stephens & Krebs, 1986; Garber, 1993; Janson, 1998; 2000), the "directed" part of "goal-directed foraging" requires that the animal move towards its goal in a distance-minimizing fashion, implying 1) straight-line (linear) travel in the absence of obstacles (steep/rough terrain, gaps in canopy, predation risk, competing groups, etc.), or at the very least, 2) the most efficient use of arboreal pathways if that animal is a route-based traveler.

This does not imply that any observation of a forager taking approximately straight-line routes between resources meets the qualifications of goal-directed foraging (Janson, 1998; 2000; Cunningham and Janson, 2007; Janson and Byrne, 2007). Cody (1971) has suggested that straight-line travel may just be a behavioral rule used to avoid recently visited areas (see Table 3.2 A2). Others have postulated that straight-line travel may just be a natural consequence of 1) following topographical features that are linear over long distances (Di Fiore and Suarez, 2007) or 2) trying to keep a foraging party together (Garber, 2000; Janson, 2000). Given that tropical forests are fairly productive environments, a primate that moves in a straight-line in any random direction is bound to reach a resource worth stopping for sooner or later (which might cause the causal observer to incorrectly infer goal-oriented behavior simply because he or she observed that straight-line travel ended in a feeding bout).

Distinguishing between chance discoveries or planned visits to sites can be a tricky business, especially when straight-line travel is involved. However, goal-directedness can be proven if it can be shown that the degree of directness towards a goal depends on the reward. The locations of clumped resources, along with productive, relatively predictable, preferred, and/or limited resources, should be worth committing to memory and traveling to directly. On the other hand, memorizing the locations of resources with unpredictable schedules, small, scattered rewards, or ubiquitous prevalence may provide little benefit to the forager; random travel or more simplified systematic search strategies are expected for locating resources of these types (Milton, 1980; 1981; Terborgh, 1983; Sigg, 1986; Garber, 1987; 1989; 2004; Oates, 1987; Janson and Di Bitetti, 1997; Janson, 1998; Pochron, 2001; 2005; Janmaat et al., 2006; Cunningham and Janson, 2007; Janson and Byrne, 2007; Noser and Byrne, 2007). Futhermore, it has been noted that even when foragers do possess knowledge concerning the locations of less valuable resources, travel to those resources tends to involve more wandering, more exploratory behavior, more sampling, and more opportunistic feeding (Garber, 1989; Pochron, 2001; Janmaat et al., 2006; Cunningham and Janson, 2007; Noser and Byrne, 2007b). Therefore, if it can be demonstrated that an animal shows "increasingly directed movement towards more valuable resources" (Janson and Byrne, 2007, pp.357), then goal-directed foraging can been inferred.

White-faced sakis have been observed consistently bypassing smaller, less productive trees in favor of more productive, more preferred sites (Cunningham, 2003; Cunningham and Janson, 2007). In order to show that the more distant, productive trees were the original goals (i.e. that the sakis were not just wandering randomly and skipping over less productive trees until they bumped into ones with larger fruit rewards), Cunningham and Janson (2007) showed that this group of sakis traveled in significantly more linear paths towards this very specific subset of resources (highly productive, previously visited trees of preferred species, *Licania discolor* or *Capparis muco*) than to the average site. It is almost impossible to imagine that any animal would be able to reach trees of such a specified nature in such linear paths over such long distances (roughly 250m for *P. pithecia*) by chance alone. Goal-directed travel must be inferred here.

Efficient use of arboreal pathways to reach important resources is also consistent with "increasingly directed movement towards more valued resources." Milton (1981) observed spider monkeys moving directly over long distances from one individual of a fruiting species to another ("traplining", see Table 3.2 B5) by means of a collection of arboreal pathways; similarly, Sigg and Stolba (1981) identified 69 "street segments" (channel-like paths at least 500m long and 150m wide) used repeatedly by hamadryas baboons in varying combinations to efficiently locate limited, and, presumably, valuable, water holes and sleeping cliffs. While habitual use of route segments might not be indicative of highly sophisticated navigational skills, if route segments are consistently used in the most efficient combinations to reach feeding trees that have been established as valuable to the forager (by virtue of being visited repeatedly and/or belonging to a commonly traplined species), then their use does signify goal-directedness (Milton, 1980; 1981; Sigg and Stolba, 1981; Janson and Byrne, 2007).

Researchers studying foraging travel patterns also believe that an increase in travel speed when approaching resources denotes goal-directed behavior. Many (Sigg and Stolba, 1981; Krebs and Davies, 1997; Janson, 1998; Pochron, 2001; 2005; Janmaat et al., 2006; Noser and Byrne, 2007) concur that increased speed is a good indicator of strength of motivation and/or an individuals expectations about resources, and Janson and Byrne (2007) go on to list this as the second of three patterns that can confirm goal-directed foraging behavior.

The final pattern identified by Janson and Byrne (2007) as being a reliable indicator of goal-directed foraging is the ability to travel directly to resources beyond the animal’s visual detection field from a number of different starting points. This capability has been shown for many primates, including white-faced sakis revisiting productive and preferred seed sources (Cunningham, 2003; Cunningham and Janson, 2007), baboons revisiting vital and limited water holes and sleeping sites (Altman and Altman, 1970; Noser and Byrne, 2007b), the famous Kanzi revisiting certain reward stations (Menzel, 2002), and saddle-back and moustached tamarins revisiting highly-ranked fruit and exudates sources (Garber, 1989).

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3.3 White-Faced Sakis and Goal-Directed Foraging: The Predictions

3.3.1 Backtracking Predictions

Prediction 1 White-faced sakis will exhibit a low incidence of backtracking, and angles of progression will not be evenly distributed across all possible values (i.e. will not be randomly distributed). Rather, angles of progression showing more forward progression should predominate.

Backtracking is not considered an efficient mode of travel for foragers exploiting sessile prey items (Garber, 1987). Futhermore, foragers that exploit spatially and temporally clumped resources are expected to move in relatively straight-line paths towards their resources, rather than relying on random wandering to encounter them (Milton, 1980; 1981; Garber 1988, 1989, 2000). White-faced sakis primarily feed on spatially and temporally patchy seed sources; therefore, they should be expected to fit the goal-directed foraging profile.

3.3.2 Directed Travel Predictions

Prediction 2 The sakis will travel more linearly and more quickly to reach more preferred items.

White-faced sakis are very selective in their choices of fruit sources; they prefer 1) highly productive fruit sources of particular taxa, 2) fruits with softer seeds, high lipid content, and moderate tannin levels, and 3) certain maturity levels of fruit from certain species (Kinzey and Norconk, 1993; Cunningham, 2003; Cunningham and Janson, 2007; Norconk et al., in press). Selective foragers are expected to incur large travel costs unless they can employ a search strategy that minimizes distances traveled while increasing their probability of locating preferred foods (Milton, 1980); the most efficient search strategy for a forager exploiting patchily-distributed resources is a goal-directed strategy. In goal-directed foraging, both directedness and speed are expected to increase when traveling to preferred food sources (Janson and Byrne, 2007).

3.3.3 Revisited Feeding Tree Predictions

Prediction 3 Revisited feeding trees will usually be of a particular species or a specific resource type (seeds or flowers or young leaves, etc.), implying that encounters with these resources are intentional. The sakis will be able to reach these sites from a variety of distant starting points or directions, and they will travel to them directly.

Primates that have located preferred, productive, and/or limited resources tend to revisit sites containing those resources until they are depleted or not economical enough to travel to anymore (Sigg and Stolba, 1981; Garber, 1989; Cunningham, 2003; Cunningham and Janson, 2007; Noser and Byrne, 2007 a & b). Cunningham and Janson (2007) showed that sites that had been visited at least once had a significantly higher probability of being selected as the next feeding source by white-faced sakis than sites that had never been visited. Revisited trees tended to have very specific characteristics, i.e. sources of fruit with the highest productivity scores and members of one of the top-ranked species in terms of feeding minutes (Cunningham, 2003). If a forager can relocate these preferred sites when coming from a variety of different starting points or directions, this signifies goal-directed behavior (Janson and Byrne, 2007).

3.3.4 Nearest-Neighbor Sleeping Site Prediction

Prediction 4 If the sakis appear to use only a limited and predictable set of trees in their range for sleeping sites, they will attempt to minimize travel distances each day by choosing the sleeping site that is closest to their last feeding tree.

White-faced sakis reportedly exhibit preferences for certain types of sleeping trees (upper canopy trees whose crowns are well-obscured by dense foliage and/or vine tangles) and have been observed to reuse favored sleeping sites on multiple occasions (Vié et al., 2001; Thompson, personal communication). Therefore, it is possible that sakis choose from a limited number of sleeping sites at the conclusion of each day’s foraging excursions**.**

If a group of animals can recall the locations of a number of available resources and if efficient travel is important to them, this group might be expected to follow a type of nearest-neighbor rule (see Table 3.2 B4), whereby they move directly to the closest available resource, whether this is a feeding or sleeping site (Garber, 1989; Garber, 2000). Baboons and spider monkeys that choose from a limited number of sleeping sites consistently select sites that are closest to their current feeding tree so as to reduce travel distances (Rasmussen, 1979; Chapman et al., 1989). Since white-faced sakis reportedly employ a goal-directed foraging strategy, whereby they travel in distance-minimizing paths to preferred feeding sources (Cunningham, 2003; Janson and Cunningham, 2007), they might also be expected to reduce travel distances when traveling to preferred sleeping sites.

3.3.5 Orientation and Navigation Predictions

Prediction 5 By overlaying all of the sakis daily routes over one another, I will be able to identify certain quadrats where sharp turning angles are frequent, indicating possible reorientation by use of landmarks. I also expect to find evidence for repeated use of certain routes, but only at or near roadways and/or trails in their range.

Being able to travel directly to specific goals and to arrive at sites from different starting locations imply impressive spatial memory skills; however, neither of these behaviors tells us how an animal mentally represents and locates its resources. While it is plausible that an animal could mentally represent its environment as a series of angles and distances among features in its environment (a Euclidean mental map), researchers have really only found definitive evidence of primates navigating and orienting themselves by use of habitual routes and salient landmarks. Since roads and clearings are common and outstanding features of the white-faced sakis' home range in Brownsberg Nature Park (see Fig. 1.1), I would expect them to be able to effectively navigate using these landmarks alone, rather than committing to memory myriad Euclidean distances and angles. However, habitual route usage may be detected in certain areas of their home range where gaps in the canopy require routing to limited, but reliable, passageways over the roads and trails.

While a positive result for any one of these predictions would not be enough to prove a goal-directed foraging strategy, cumulative positive results would definitely be incompatible with a foraging strategy based solely on random search processes.

CHAPTER 4

METHODS

4.1 Study Site

Brownsberg Nature Park (BNP) is situated in northeastern Suriname, approximately 100 km south of the country's coastline and capitol city (De Dijn, 2006; Fitzgerald et al., 2002). Suriname, as well as Guyana, French Guiana, Venezuela, northern Brazil, and southeast Columbia, are part of the northern South American land mass referred to as the Guyana Shield, formed ~ 2 billion years ago (Norconk et al., 1996; De Dijn, 2006). The rich forested areas of the Shield are supported by a lateritic-bauxite crust and are dotted with occasional outcroppings of ancient bedrock referred to as greenstone (rich in quartz and greenish in hue) (Norconk et al, 1996; De Dijn, 2006). Brownsberg Nature Park (BNP), which covers roughly12,200 ha of the Shield, straddles one such outcropping. Brownsberg's seasonal evergreen rainforest is dominated by the lateritic-bauxite tabletop plateau at its core, and by steep slopes, creek-laden valleys, and lowland forested areas as you move out towards its periphery.

Ter Steege et al. (2004) note that the northeastern portion of Suriname's modest ten-peaked mountain range, which includes Brownsberg, may be part of a specific ecosystem that occupies < .5% of Suriname's land surface. In particular, the rapidly rising and increasingly humid slopes that lead up to Brownsberg's 530m high, 1,400 ha plateau allow for a wide variety of divergent habitat zones which may serve as refuges and centers for endemism for many species. A wide assortment of forest types may be found within the borders of Brownsberg Nature Park, including high to low canopy forests, seasonally dry to seasonally flooded forests, primary to disturbed forests, and the clouded forests of the plateau to the creek-side forests of the valley regions.

The lateritic ridges and bauxite caps of the Brownsberg encourage a unique assortment of tree species, characteristic of < .5% of land surface in Suriname (ter Steege, 2004; Fitzgerald et al., 2002; De Dijn, 2006). Based on ter Steege et al.'s (2004) assessment of eight 1-ha plots in Brownsberg Nature Park, this area also has the highest floral diversity scores in all of Suriname. Six plants species are represented by over 100 individuals/ha, while most species (~ 70%) are represented by approximately 10 individuals per 1-ha plot. The families Myrtaceae, Euphorbiaceae, and Annonaceae appear to be the most abundant on the Brownsberg in terms of number of individuals per hectare, while Fabaceae, Orchidaceae, and Rubiaceae are among the most speciose in the park (ter Steege et al., 2004). Most of these families were important in the white-faced saki diet during this study.

Representatives of each of four major clades of New World primates are found in Brownsberg Nature Park (Norconk et al., 2003; Schneider, 2000). These include *Cebus apella, C. olivaceous*, and *Saimiri sciureas* of the "cebid" clade, *Saguinas midas* of the callitrichine clade, *Alouatta seniculus* and *Ateles paniscus* of the ateline clade, and *Chiropotes satanus* and *Pithecia pithecia* of the pitheciine clade. Norconk et al. (2003) noted a relatively high encounter rate for the study species (although the groups were quite skittish). In Norconk et al.'s census, white-faced saki groups were primarily encountered on the plateau. The researchers estimated an average group size of 3.7 individuals (range = 2-6, N = 10 groups) and a home range of 10.3 ha (N = 1 group).

4.2 Climate

Due to 1) the Brownsberg's proximity to the coast, 2) the eastern trade winds that cut across region, and 3) the elevation gradient of the park, the plateau is cooler and more humid than nearby locations (maximum temperature 6 degrees lower than neighboring areas of < 100 m elevation, 80% annual relative humidity reported in 1960; De Dijn, 2006). The plateau is often shrouded in a blanket of mist and fog, and some have characterized the peak as a "low elevation cloud forest" (De Dijn, 2006). The area is generally characterized as "always wet", as it lies in a "tropical wet climate zone" (no months < 60mm rainfall, annual precipitation ~ 2000mm), but De Dijn (2006) reports significant short-term interannual and seasonal variability in rainfall totals due to occasional fluctuations in the Inter-Tropical Convergent Belt. Rainfall totals and maximum and minimum temperatures were recorded at approximately 0700 hrs daily throughout the 2006 study season at the Brownsberg Weather Station located on the plateau (Table 4.1).

Inter-annual and inter-seasonal variability aside, a normal year at Brownsberg is characterized by two rainy and two dry seasons, with a shorter and a longer version of each (De Dijn, 2006). The short rainy (December-January) and short dry season (February-April) may occasionally fail or be relatively indistinct, while the long seasons are fairly reliable (long rainy: late April/May to mid-August; long dry: mid-August to November/December). Flower development peaks are seen from September to December, while fruit development peaks are most distinct from December/January to April/May.

Table 4.1 Weather Data**.** Statistics on average daily rainfall and average daily temperatures for study period, May 30-August 1, 2006. "Current" daily temperatures designate temperature readings taken between 0530 and 0700 hrs each morning. Temperatures are in degrees Celsius and rainfall totals are in millimeters (mm).

	N = # of days	**Min.**	**Max.**	**Mean**	**Std. Dev.**	**Median**	**Total for study period**
Min. Daily Temp.	60	19.50	22.00	21.10	.0759	21.00	NA
Current Temp.	59	19.50	23.50	21.82	.0861	22.00	NA
Max. Daily Temp.	60	24.00	28.00	26.62	.1039	27.00	NA
Daily Rainfall	59	.00	32.40	7.94	1.0586	4.40	484.30

4.3 Study Animals

The best habituated white-faced saki group was the focus of my study (observed since 2003, Norconk et al., 2003). During the 2006 study season, the group consisted of one adult male (AM), two sub-adult males (SAM1 & SAM2), one adult female (AF), and two juvenile males (J1, presumed son of AF and AM, and J2). Another adult female was a consistent member of this group during the previous three study seasons; it is assumed that she perished sometime after her offspring, J2, began to locomote and forage somewhat independently. The two juveniles were estimated to be approximately 6-8.5 months old (Gregory, 2006) at the onset of this study (late May). This group remained cohesive throughout the duration of this study period.

The area inhabited by the study group was mostly centralized on the top of the plateau and included part of park entrance road (AKP, MW) and many of the most frequented trails in the park (Fig. 1.1 shows relevant portion of the trail system in Brownsberg Nature Park). Their range was characterized by low topographic relief and it cross-cut two habitat zones: 1) high forest, which generally has a closed and continuous canopy at about 25-40 m, well-drained soils, and an understory dominated by smaller, slender crowned trees, and 2) savanna forest, which has a slightly lower (< 20-30 m) and more open canopy with a dense understory and rocky soils (Fitzerald et al., 2002).

The study group's home range was surrounded on all sides by neighboring white-faced saki groups (Junco's group to the south, Mazaroni Top (MT) group to the east, AKP group to the northeast, Roundwandeling (RW) group to the northwest, Mazaroni Way (MW) group to the west; all groups except Junco's were named after portions of the trails/roads that the study group shared with these groups, see Fig. 1.1 for trail/road locations).

4.4 Sampling methods

The study was conducted during the long rainy season, from late May to early August, 2006. Following a weeklong period during which I familiarized myself with the group's home range and the physical characteristics of each group member, I commenced all-day follows for a period of approximately seven weeks. Although only day off per week was planned, this usually resulted in two to three non-follow days per week due to the difficulty in relocating the sakis after a planned day off. Therefore, for the seven-week study period, the sakis were only followed for thirty out of the fifty days available to me. Furthermore, on some follow days, the sakis either could not be located until partway through the day or were lost before the end of the day; on other follow days, reduced visibility and/or fast-paced travel prevented me for collecting data for varying lengths of time, resulting in breaks in data collection partway through the day. Due to these circumstances, out of the thirty focal-follow days, only eight were "complete" (followed sakis continuously from sleeping site to sleeping site, with no breaks in between), nine were "full" (followed sakis from sleeping site to sleeping site, but there was at least one break in data collection during the day), and thirteen were “partial” (sakis not located until partway through the day and/or were lost before the end of the day).

On follow days, if possible, I met the group at approximately 0700 hrs at their previous night’s sleeping site; if their sleeping site had not been assessed on the previous day, the group’s home range was searched until the sakis were found. Behavioral data were collected using a focal animal, continuous sampling method (Altmann, 1974). Focal subjects were selected according to a fixed rotation of all adult and subadults in the group (juveniles were excluded as it was assumed that they were not yet influencing the trajectory of travel). If a focal animal was lost at any point during sampling for more than 5 minutes, the next adult or subadult spotted was the new focal animal for that day. This led to a slight bias of sampling minutes towards AM, as he was visible most of the time (usually slightly higher up in the canopy than the rest of the group, at least while resting, and stayed immobile for longer periods of time): AM accounted for 30.6% of the sampling minutes, while the other members accounted for less than 25% each (SAM1= 24.9%; SAM2 = 24.7%; AF=19.8%). Sampling ended for the day either 1) when I lost the group and was unable to relocate them, or 2) when it was apparent that the group had chosen their sleeping site for the night (I usually stayed with the group for at least 30 minutes after they entered a typical sleeping tree, i.e. until approximately 16:00-16:30).

Rigorous methodology was used to collect data pertaining to travel trajectories so that the sakis foraging strategies could be assessed with fine resolution. All feeding trees and sleeping trees, and every possible travel and resting tree entered by the focal animal were flagged. In practice, this meant that each flagged tree was roughly 5-20m away from the previously flagged tree, with notable exceptions owing to the rapidity of travel at some points during focal animal sampling. Flagging tape was retained on all trees during the entire study period so that revisited trees could be identified and arboreal pathway use could be assessed.

During the familiarization period with the group's home range, it became clear that I would not be able to use the GPS unit to acquire the positions of the group's feeding, resting, traveling, and sleeping sites, as the GPS unit only received an acceptable signal for approximately an hour or two in the afternoon. Therefore, a pedometer was used to assess inter-tree distances and a compass was used to obtain information pertinent to assessing changes in trajectory. While a pedometer is not an ideal measuring device since it does not account for vertical travel distance or slight changes in stride length, it is useful in providing a rough estimate of distance traveled.

GPS readings for the focal animals' daily start and end positions were obtained during non-follow days to serve as reference points for mapping of their travel routes. The GPS unit was also used to acquire reference points when inter-tree distances and angles could not be obtained with the pedometer and compass (i.e. when a previous focal animal was lost and a new focal animal had to be chosen), and, *ad libitum,* to obtain coordinates for frequently visited feeding trees. All GPS points and tree-to-tree distances & compass angles were entered into EasyCad Version 7 to generate daily maps of the white-faced sakis' travel routes.

Unfortunately, due to small, but cumulative, inaccuracies in pedometer readings and the regular error of the GPS unit (averaging ± 10 m), it became apparent during mapping that data points were not matching up exactly. Specifically, GPS coordinate locations for end of the day sleeping sites did not always match up with sleeping site locations obtained from cumulative pedometer and compass readings for each day (deviations between GPS locales and pedometer/compass locales for nightly sleeping sites averaged 37.6 m; see Appendix B for GPS locations of sleeping sites vs. pedometer/compass locations for the same sites). The consequences of these unavoidable sources of error were that 1) inter-tree distances were most likely slight underestimates of actual distances, which led to probable underestimates of daily path length, and 2) assessment of arboreal pathway use and landmark-based navigation were made much more difficult, though not impossible. Fortunately, since methods of obtaining inter-tree distances and angles were consistent throughout the study, inaccuracies following from these methods should not have affected assessments of backtracking, straight-line travel, or paths taken to revisited trees.

4.5 Feeding Data

All-occurrence feeding data were gathered each time a focal animal inspected or ingested food. The following data were collected for each feeding bout: 1) tree number (assigned during every feeding bout), 2) time in and out of tree for focal animal, 3) number of minutes spent ingesting or inspecting resources vs. number of minutes involved in other activities (resting, grooming, playing, etc.), 4) habit (tree vs. liana), 5) plant species, 6) plant part ingested (seeds only, mesocarp only, seeds plus mesocarp, seed coat only, exocarp only, young leaves, mature leaves, leaves- unknown maturity level, flower/flower bud, unknown), and 7) an estimate of the abundance of the food item being ingested (Zero= none, One=1-10, Two=11-100, Three=101-1000, Four>1000)..

Due to the brevity of some of the feeding bouts and the difficulty in estimating resource abundance for partially obscured trees or lianas, abundance scores could only be obtained for approximately 50% of the feeding trees used by the sakis. Species of feeding trees and lianas were identified using Fruits of the Guianan Flora (van Roosmalen, 1985), The Field Guide to the Flora of Brownsberg (STINASU, unpubl.), and also with the assistance of two botanists from the National Herbarium of Suriname in Paramaribo during a two-day visit. Fruits were never present on the trees or lianas in which the primarily item of focus for consumption was leaves. Because it is very difficult to determine the species when a leaf sample is the only plant part available, species designations could not be assigned to any leaf sources consumed during the study.

"Feeding" episodes were distinguished from "sampling" episodes during data collection. "Sampling" was defined as 1) visual, tactile, or olfactory inspection of a resource, and/or 2) ingestion of only one item if the diameter of the item was less than the feeder's gape width and only one bite if diameter of the item was larger than the feeder's gape width. By definition, sampling bouts also lasted less than one minute. "Feeding" bouts lasted longer than one minute and involved the ingestion more than one bite of a large food item or more than that one item from a smaller food source. This distinction was made in order to test the assumption that sampled items would be less valued by the sakis than food items that they spent more than one minute consuming.

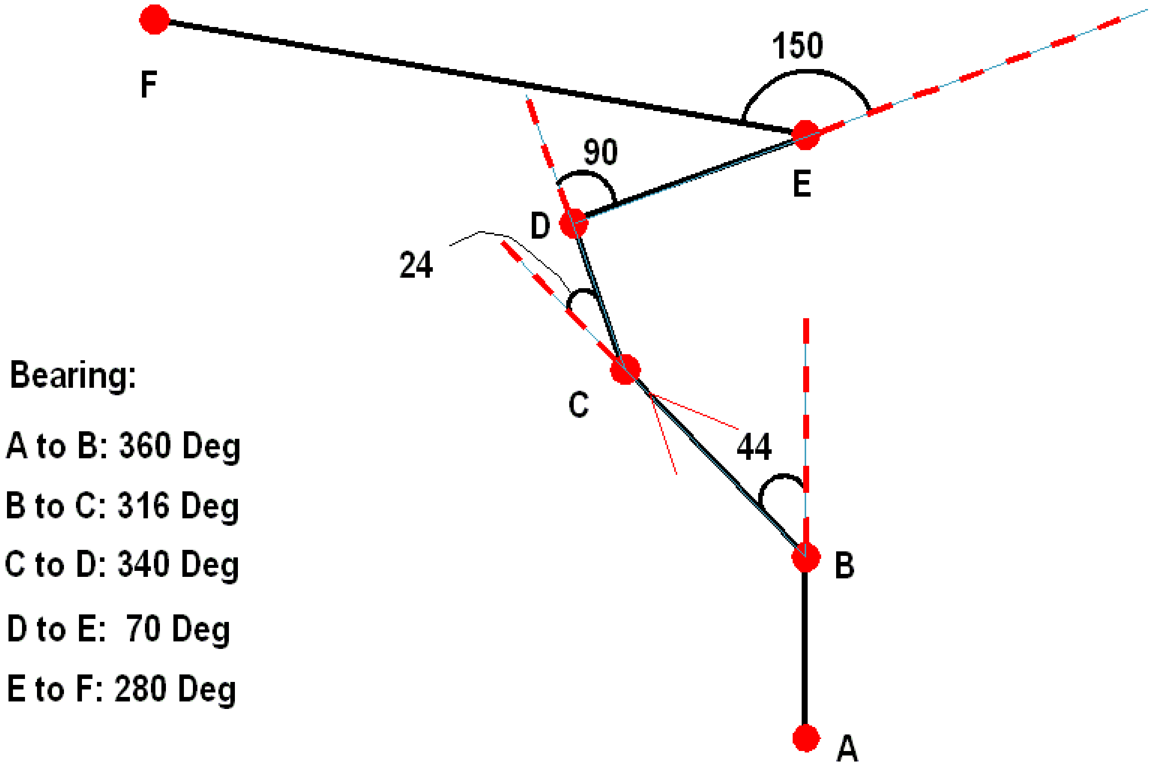
4.6 Data Analysis:

4.6.1 Ranging Patterns and Area Usage

I calculated distance traveled per day (daily path length) using 1) complete day data only, and 2) a combination of complete day data and extrapolations from partial day data. Rather than calculating an average rate of travel for the entire study period, I divided each sample day into three periods and calculated distance (in meters) traveled per minute for each. Previous studies have indicated that white-faced sakis tend to move differently at different times of the day (i.e. quickly from feeding site to feeding site in the morning, very slowly during resting and grooming periods midday, and relatively slowly between feeding sites and en route to the sleeping site in the afternoon; Vié et al., 2001; Gregory, personal communication; Thompson, personal communication). Therefore, rates of travel were calculated for Periods 1 (beginning of travels for the day until 11:00), 2 (11:01-13:00), and 3 (13:01 until sakis retire for the day) for each day of the study period.

While previous studies indicate that white-faced sakis are territorial, I use the term "home range" rather than "territory" to describe the area of land that is used by a group for a year or longer (definition adapted from Fleagle, 1999). The extent of the study group's home range was estimated by connecting the perimeter points from my mapping data with straight lines to form a polygon. The resulting boundary line was then compared to boundary line estimates from the previous study season (Thompson, personal communication) to give me a more plausible estimate of the maximum range of this group for an extended period of time. The area contained within this boundary line was then computed using EasyCAD.

Fig. 4.1 Computing angles of progression. Direction of travel indicated by arrow. Points A- F represent travel, feeding or sleeping trees. Each black line indicates the path taken, while each red dashed line shows the hypothetical straight-line path relative to the previous move. Deviations to either side of the straight line of travel are considered equivalent, and thus by convention turning angles vary from 0-180°. Compass angles or bearings for each set of points are shown to the left of the figure. Angles of progression are computed by subtracting the current bearing from the previous bearing and taking the absolute value of that number (e.g. for the angle of progression from C to D, subtract the bearing for C to D from the bearing for B to C: | 316°- 340° | = 24°). If the result is > 180°, 180° is subtracted from the result (e.g. for path C to E: | 340° - 70° | = 270°, 270° > 180°, so 270° - 180°= 90° = angle of progression from D to E).



The sakis' entire home range was distinguished from their "core area" based on intensity of usage (specifically, the core area is defined as the portion of the group's home range that is used most intensively). Areas of intense usage were identified by overlaying all daily maps on top of one another and computing the total number of data points (all flagged trees) in each of 135, 50 m by 50 m quadrats. The size of the core area was estimated using the minimum convex polygon method, whereby consecutive sets of ten observations were added (and the area within defined) until the point where continued observation produced less than a one percent increase in the total area (Odum and Kuenzler, 1955).

A commonly used index for territoriality in a species is the defensibility index (DI, Mitani and Rodman, 1979), which uses estimates of home range size and daily path length to project the likelihood of territoriality in a species. A species is presumed to be capable of effectively monitoring and defending it's home range if its mean daily path length is at least as long as the approximated diameter of their home range, assuming a roughly circular-shaped home range ($DI = DR/HR\varnothing$, where DR is the mean daily path length, $HR\varnothing = (4A/\pi)$; a $DI \geq 1.0$ is expected for territorial groups). Using estimates of the sakis' home range size and mean daily path length (from complete follow days only), I calculated the study group's DI to see how well they fit the territorial profile.

4.6.2 Backtracking Predictions

Every occasion for which there were data on the bearing from one tree to another was used in this analysis (N = 1133). Data on sequential changes in direction of movement were used to distinguish relatively straight-line travel from movements involving a lot of recrossing of paths or "backtracking". Tree-to-tree compass angles (bearings) were used to determine the angle of progression for each sequential step made by the focal animals (where a step is defined as the movement from one flagged tree to another, whether the flagged tree was a feeding, travel, resting or sleeping tree) (Fig 4.1). Deviations to either side of a straight line of travel were considered equivalent, and thus by convention, turning angles varied from 0-180°. Following from Garber (1989), angles of progression of ≤ 90° indicated forward progression, while angles of > 90° indicated backtracking.

I further divided the data into four equal angle of progression categories (1 = 0-45°, 2 = 46-90°, 3 = 91-135°, 4 = 136-180°). Using a Chi-squared test, I tested the data against the null hypothesis that the sakis' angles of progression would be evenly distributed across the four categories. Finally, the contexts of the most extreme cases of backtracking (angles of progression of > 135°) were analyzed in order to determine if there was any consistency in the when, where, or why of their backtracking episodes.

4.6.3 Directed Travel Predictions

Before commencing with the comparison of linearity and speed of travel among the three preference groups, I first compared the sakis observed travel distances to all feeding and sleeping sites to perfect straight-line travel distances. I used the Easy Cad maps to generate hypothetical straight-line distances between successively used feeding trees and sleeping sites. Directness ratios (adapted from Pochron, 2001) were then computed for each sleeping tree-to-feeding tree, feeding tree-to-sleeping tree, and feeding tree-to-feeding tree travel bout (where the directness ratio (DR) = the inter-resource straight-line distance/ the inter-resource observed distance). A DR = 1 indicates that the sakis traveled in a perfect straight line from one resource to the next, while directness ratios approaching 0 indicate a high degree of zig-zagging or wandering in between resources. All observed directness ratios (N = 246) were then compared to perfect straight-line directness ratios (DRs = 1) using a one sample t-test.

In order to evaluate the prediction that the sakis would travel more quickly and more linearly to more preferred resources, I first had to determine what criteria I would use to assign preference ranks to their food sources. Since I did not have complete data on abundance scores for individual trees, I could not evaluate preference for each feeding tree as a separate entity. Instead, high-, medium-, and low-preference food resources were identified solely on the basis of which plant parts and plant species comprised the bulk of their diet. Therefore, feeding trees belonging to same preference group were evaluated in the exact same manner, despite any differences among the individual feeding trees in their abundance scores (if they were available) or feeding bout durations.

To identify the resources that comprised the bulk of the sakis' diet, all plant species and plant parts were ranked according to the total number of feeding minutes that each contributed to the entire diet during the study period. Since there was a very substantial natural break between the top-ranked plant part (seeds alone, rest of fruit discarded = 47.7% of total feeding minutes) and the second highest ranked plant part (mesocarp and seeds eaten together = 19.82 % of total feeding minutes), identifying the most preferred plant part was relatively simple. Unfortunately, there was no such obvious break in feeding minutes for the plant species category; therefore, I included as "high-ranked" or "high-preference" only those species that 1) individually accounted for over 200 total feeding minutes and 2) were seed sources (this excluded young leaves as a high-ranked species even though 297 total feeding minutes were spent on this resource). The remaining plant species were ranked as either “medium-” or “low-” preference (“low-” preference for those species that, individually, had less than 5 feeding or sampling bouts and that, cumulatively, accounted for the bottom 10 % of total feeding minutes; everything in the middle was ranked “medium-” preference).

For the comparison of directness ratios across preference categories, I excluded all feeding bouts where the target resource was either a leaf source or resource from an unidentified species (N = 69 bouts), as there was no way to assign any meaningful ranking to sources for which the species could not be identified (i.e. some leaf species may have been highly preferred and would have yielded very high feeding minute totals, while others may not have been preferred at all, and would have yielded very low feeding minute totals; unfortunately, there was no way to determine this).

I compared directness ratios across the three preference groups by conducting three independent Mann-Whitney U tests (one comparing low-preference DRs to medium-preference DRs, one comparing low-preference DRs to high-preference DRs, and one comparing medium-preference DRs to high-preference DRs). I used the Bonferroni method account for multiplicity (using $\alpha = .05$ for the entire analysis, the adjusted significance level for each of the three Mann-Whitney tests was $.05/3 = .017$).

Judging by the somewhat erratic manner in which the sakis seemed to traveled in four contexts: 1) during ITEs, 2) near the home range boundary, 3) when they had long resting bouts before reaching resources, and 4) on their way to trees in which they only “sampled” resources, I anticipated that these cases might significantly lower DRs. On the other hand, the sakis seemed to move faster and more directly when they were 1) heading to a tree that they a) had visited previously, b) ended up sleeping in, or c) ended up resting in for a long period of time after feeding, or 2) coming from the sleeping tree first thing in the morning. Therefore, I anticipated that these occurrences might significantly boost DRs. Finally, there were instances where I lost the focal animal and had to choose another. While I had no specific prediction on how this might affect inter-resource DR's, I still investigated the possibility that it might have some sort of significant effect on directness ratios.

To examine the effects these contexts had on DRs, I conducted one sample t-tests using the nonparametric approach (Wilcoxon Signed Rank). Specifically, I tested whether or not inter-resource travel bouts involving ITE's, boundary visits, long resting bouts, etc. yielded significantly lower or higher DRs than their corresponding travel bouts in which no ITEs, boundary visits, long resting bouts, etc. occurred.

If any of the nine contexts significantly lowered or raised DRs, I excluded those cases and repeated the large sample paired t-test comparing observed directness ratios to perfect straight-line directness ratios. Similarly, I reran the Mann Whitney U tests comparing DRs across preference groups after incorporating those exclusions.

Speed has been used as a proxy for determining strength of motivation to reach a site (and, therefore, knowledge that the site exists) in many recent goal-directed studies (Pochron, 2001; 2005; Janmaat et al., 2006; Noser and Byrne, 2007b; Valero and Byrne, 2007) primarily because of Janson's (1998) observation that monkeys will significantly increase their speed once they have made visual contact with a food reward. Acknowledging this tendency, Janson (1998, 2000) has cautioned against using observations of increased speed at certain distances from a target resource as proof of memory-related knowledge of the site's existence (i.e. as proof of goal-directed travel). If a monkey is close enough to a resource to have already visually detected that resource, it will likely speed up. At this point, increased speed will tell the observer nothing about monkey's prior knowledge of the resource's location.

Detection field estimates for monkeys in tropical rainforests have varied (where a detection field is farthest point or distance at which an animal can visually detect a target tree): Terborgh (1983) estimated that the denseness of the canopy in tropical rainforests reduces the effectiveness of visual cues beyond 10-15 m; Janson and DiBitetti (1997) put the distance at ~ 50 m tropical forests; Garber (1993) set the maximum for tamarins in the dense Amazonian forest at 17.5 m. Cunningham and Janson (2007), with an estimate of 20 m for the group spread in white-faced sakis in Venezuela, determined that a detection field of 60 m was suitable for their group; however, they acknowledged that this estimate might be a little strict, so they also tested their predictions with detection fields as low as 30 m. I set detection field for the sakis in my study at 30 m, as a larger detection field would have excluded so many cases for which I could determine inter-resource distance (and speed) that I would not have had enough cases to test.

I was able to calculate the speed from the previous feeding tree to within 30 m of the target feeding tree for forty-three cases. Each of these speeds was divided by the corresponding average speed for the period of the day in which the case took place (Period 1 = start of travel until 11:00, Period 2 = 11:01 until 13:00, Period 3 = 13:01 until end of day) in order to account for differences in speed due to time of day alone or occurrences unassociated with feeding or foraging (i.e. ITEs, boundary visits, etc.) taking place within those time frames that may have boosted or lowered speeds. By factoring in these considerations upfront, I did not have to conduct two different speed analyses, as had been the case with the DR analyses (i.e. one analysis prior to considering contexts that influenced directness of travel and one analysis after factoring in these situations).

In order to test for differences in speed ratios among the three food preference categories, I conducted three Mann-Whitney U tests with a Bonferroni adjustment (using an $\alpha = .05$ for the entire experiment, the significance level for each test was $.05/3 = .017$).

4.6.4 Revisited Feeding Tree Predictions

Any feeding or sampling tree that was visited more than once was included in the following analyses. The species and the plant part eaten in each revisited tree were noted and Chi-square tests were conducted in order to evaluate whether certain species or plant parts were eaten in these trees significantly more than would be expected based solely on the proportion of feeding minutes that each contributed. The number of days that lapsed in between visits to sites was also evaluated to get an estimate of the average amount of time that sakis can remember the location and/or phenological state of the trees they feed in.

At both close range and from a distance, the routes taken to arrive at revisited sites were compared to see if the sakis were capable of taking direct paths when coming from a variety of different starting points and compass directions. Janson and Byrne (2007) cite the ability to take direct paths to distant resources from many starting locations as strong evidence of goal-directed behavior. Routes of arrival to revisited trees were evaluated at a distance of at least 100 m from the focal tree and, in some cases, up to 250 m from the focal tree. If a tree in the intervening route was recognized as one that was used on a previous occasion on the path to the focal tree, the path from that point on was evaluated to see if the exact same route was taken or if that distant tree may have just been used as an orienting landmark.

Any time that the sakis reused a feeding tree, starting points and routes to that feeding tree were evaluated in a pairwise fashion (i.e. routes assessed two days at a time, using all possible combinations of pairwise evaluation). Based on combinations of the number of visits to each of 34 sites (where the number of visits to these sites ranged from 2 to 5), assessed two at a time (i.e., if a tree was only visited twice, there was only one way to check for path reuse for those two visits, but if a tree was used 5 times, there were 10 ways to look at overlap in path usage using two days at a time), there were 69 possible combinations to evaluate.

4.6.5 Nearest-Neighbor Sleeping Site Prediction

The first part of this prediction was assessed qualitatively. In order to evaluate whether or not the sakis were being selective about the type of tree they used for sleeping, I noted the approximate tree height, crown height, crown breadth (radius) at the widest point, and density of crown foliage each time they chose a sleeping site. In order to determine if the sakis were choosing from a fairly limited number of suitable sleeping sites, I compared the total number of sites that they used during the study period to the total number of nights for which I had data on their sleeping site selection.

If I was able to conclude that the sakis were choosing from a limited and predictable number of sleeping sites, I designated all sleeping sites used during the study period as their pool of "available" sleeping sites. For each focal-follow day, daily maps were viewed to determine whether or not the sakis were choosing the closest sleeping site available to them in relation to their final feeding tree of that day. If on any occasion, the sakis did not choose the closest sleeping tree available to them after visiting their last feeding tree of the day, the location of the first feeding tree of the following day was assessed; the distance between the first feeding tree of the next day and the closer sleeping site from the night before was compared with the distance between the first feeding tree of the next day and the chosen sleeping site.

4.6.6 Orientation and Navigation Predictions

A 50 by 50m grid was overlaid on a map of the sakis' food source locations and travel routes for the entire study period. I first identified quadrats that had trees whose fruits constituted the bulk of the sakis' diet, and, therefore, may have been especially important feeding areas for the sakis. Any quadrat containing more that one tree of a fruiting species in the high-preference category was noted.

Sharp turning angles (> 90°) were identified in each of the 130 quadrats that contained data points to see if any quadrats contained substantially more sharp turns than the other quadrats. If certain quadrats were consistently the sites of large changes in trajectory, this could indicate that the sakis were using landmark(s) in/or near those quadrats to orient themselves in relation to important feeding areas. In an effort to control for misinterpretation based on quadrats that simply had more intense usage, and, therefore, a larger number of sharp turning angles, the percentage of the number of sharp turning angles to the total number of inter-tree angles in each of the quadrats was used instead of the raw counts.

If routes used on different days had one or more trees in common among them, those routes were assessed for evidence of arboreal pathway use. If the paths overlapped or were within 20 m of each other for a distance of more than 25 m, the length and width of these paths (at the widest point) were determined. The locations of these pathways in relation to trails and roads were identified in order to see if arboreal pathway use corresponded with roadway and trail crossing routes.

CHAPTER 5

RESULTS

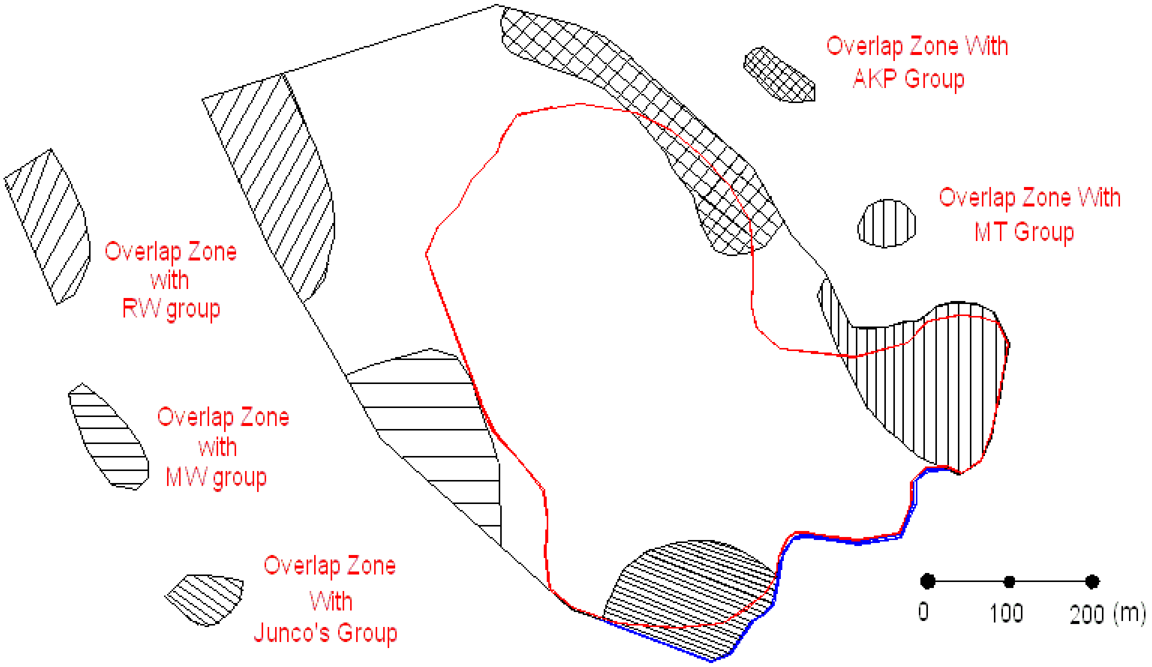
5.1 Ranging and Activity Patterns and Area Usage

According to data from the eight complete-day follows, the study group traveled an average of 587 m per day (range = 422 m – 734 m, median = 596 m). Extrapolating from partial-day data, I obtained a similar daily path length of 570 m.

Average travel speeds for the three periods of the day did not match expectations (where I expected Period 1 to exhibit the highest speed by far, Period 3 to exhibit the next highest speed, and Period 2 to exhibit the lowest speed). There was actually a trend towards slower movement as each day progressed (though not a significant trend, Kruskal Wallis H = 5.78, ns), meaning that the sakis traveled faster than expected during Period 2 and slower than expected during Periods 1 and 3 (Period 1 = from start of travel until 11:00 = 1.60 ± .612 m/min., Period 2 = 11:01- 13:00 = 1.44 ± .405 m/min., Period 3 = 13:01 until nightly sleeping tree chosen = 1.26 ± .772 m/min.).

While the sakis did cover less ground during Period 2, this was not accounted for by resting periods necessarily. Many of the extended resting bouts (≥ 30 min. in one tree) actually took place during Period 1 (N = 8 occasions, usually between 9:30 and 11:00) or Period 3 (N = 5 occasions), which led to a reduction in travel rates during those periods.

Fig. 5.1 Home range boundary, core area, and overlap zones with other white-faced saki groups during study. Home range boundary delineated by outermost line on map (area encompassed demarcates farthest extent of ranging for study group during study period). Blue line indicates an area of deforestation at the edge of the plateau. Area encompassed by red line indicates core area. Overlap zones depict areas shared with competing groups. All ITE's and Z trilling episodes occurred in overlap zones.



Furthermore, since the sakis tended to rest for extended periods of time approximately 30 min.- 1 hour before settling in to their nightly sleeping sites (N = 13 out of 23 afternoons for which there was data for this time period), this drastically lowered rates of travel in the afternoon.

The sakis longest feeding bouts usually occurred prior to 11:00, which reduced rates of travel during Period 1. Finally long periods of rain often occured in the early morning hours (N = 7 out of 26 occasions for which there was early morning data), which stalled the sakis' progress towards the first feeding trees of the day.

The most extreme perimeter points visited by the sakis during the study period were connected, resulting in a polygon with implied boundary lines. The locations of the boundary lines in my study matched up exactly with estimates of boundary line locations from the previous study season (Thompson, personal communication); therefore, I felt that I had a pretty reliable estimate of the study groups' annual home range size. The area contained within the polygon was calculated, which resulted in a home range estimate of 25.56 ha. Using the minimum convex polygon method (Odum and Kuenzler, 1955), I calculated a core area size (area of most intense usage) of 15.04 ha, which is almost half the size of the home range (Fig. 5.1).

During the seven-week study period, ITEs averaged .84 per week and separate inter-group Z trilling episodes averaged 1.5 per week. However, inter-group interactions are likely to be more frequent than these data suggest, as the sakis were only followed an average of four to five days per week (i.e. mean = 4.2 days per week, roughly 60% of each week). Extrapolating to full weeks, ITEs occured at a rate of about 1.4 days per week, and Z trilling bouts occurred at a rate of approximately 2.6 days per week. One-third of the time, ITEs occurred in the early morning (around 8:00), one-third of the time, they occurred midday (around 11:00), and one-third of the time, they occurred in the afternoon (around 13:30). Z trilling episodes usually occurred between 11-12:00 (61.5% of the time); otherwise they occurred in the late afternoon (between 13-14:00, 15.4%) or in the morning (between 8-9:00, 23.1%). Using the sakis' approximated home range area of .2556 km and their mean daily path length of .5874 for complete follow days, I obtained a DI = 1.8, which shows that this group of sakis fits the territorial profile.

I was able to five identify areas both within and beyond the sakis core area that were sites of contention between the study group and neighboring groups. These overlap zones represent areas in which all inter-group encounters (N = 6) and all Z trilling episodes (N = 11) occured. Two overlap zones were almost completely within the sakis' core area, while the three others were either completely or mostly outside of the core area (see Fig. 5.1).

Of the twenty-three different sleeping sites that were identified for the study period, 96% of them were located within the core area. Only one was located on the border or just outside of the core area (sleeping site T372, Fig. 5.2). Eight different sleeping sites were located within three of the five different overlap zones. The most frequented overlap zone in terms of sleeping sites was located in the southeastern region of their home range (shared with MT Group). Four different sleeping sites were located here, one of which was used on five different occasions (T449, see Fig. 5.2). Three different sleeping sites were located within the overlap zone shared with Junco's group, and one (T386) was within the zone shared with AKP Group. This final sleeping site was used on two different occasions by the study group.

Fig. 5.2 Sleeping sites used by sakis during the study period. Twenty-three different sleeping sites were identified. Sleeping sites are represented by triangles. Sleeping sites in red were used more than once during the study period (average number of times used = 2.6 nights, minimum = 2 nights, maximum = 5 nights); those in black were used only once. Thin black line (or blue in the southern region) represents home range boundary; red line represents core area; thick black lines indicate locations of overlap zones; yellow lines encircles sleeping sites that are tightly clustered (longest distance between any two trees in a cluster is 100 m).

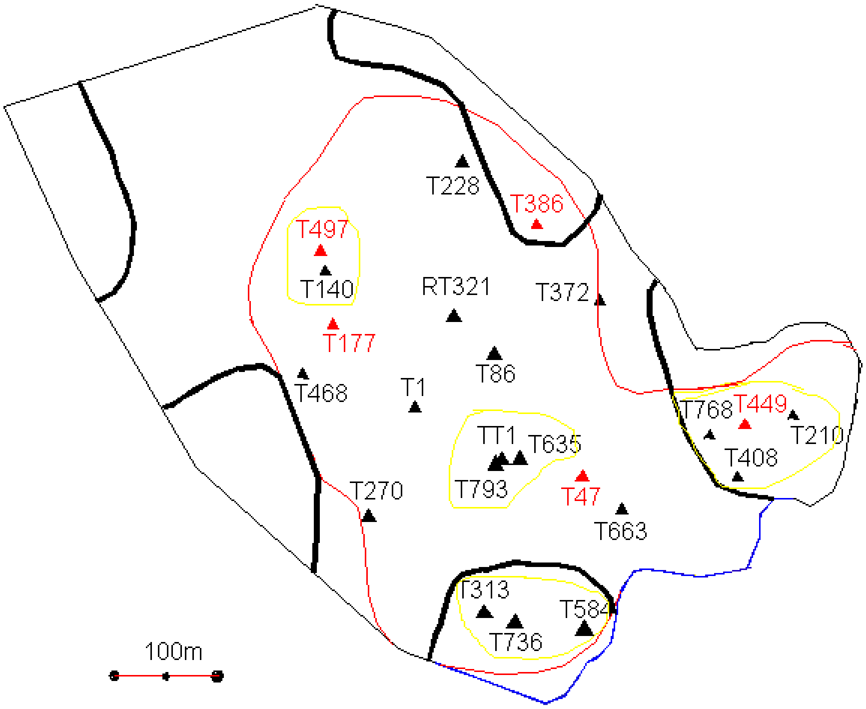


Fig. 5.3 Coverage of home range during the first nine focal-follow days of the study period. Outermost line (in black, blue) represents home range boundary. Wavy lines (shown in either black, brown, green, or orange) represent the daily routes. The beginning of each daily route is marked with a number; which specifies the study day that the route was observed. Breaks in the number sequence indicate that I was unable to locate the sakis for the day in between (i.e. I was unable to locate the sakis on study days five and seven, therefore those numbers are left out of the sequence). Closed red circles show where the sakis started their routes each day. Open circles show the continuation of a day's route after a break in data collection (sakis moving too quickly in interim to record locations). The sakis visited most of their home range during this period, with little overlap in area coverage from day to day (outer boundary line represents edge of home range). After nine days, they were again in the southern portion of there range, where they began (day #11 and day #1).

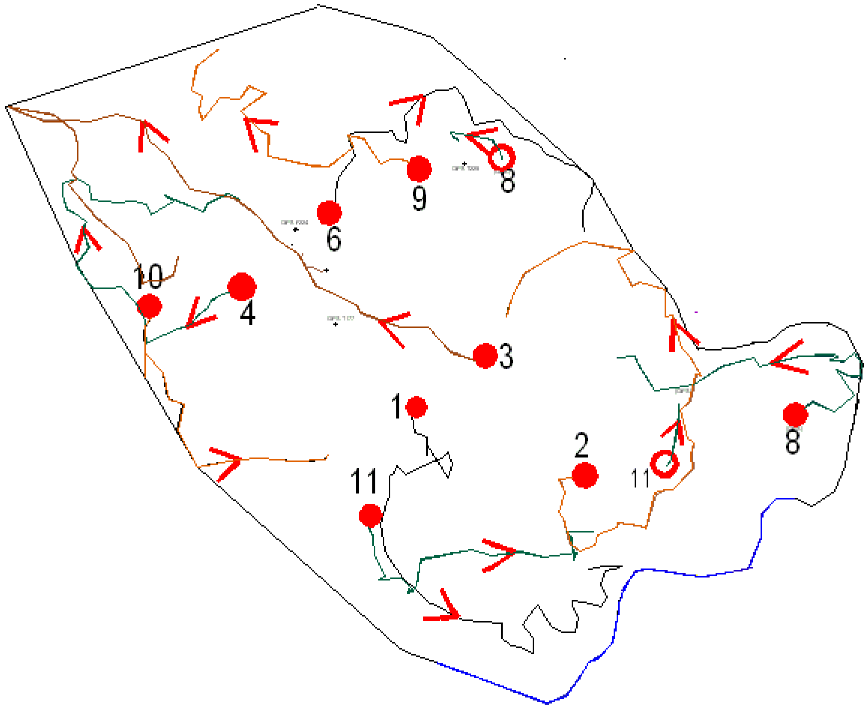
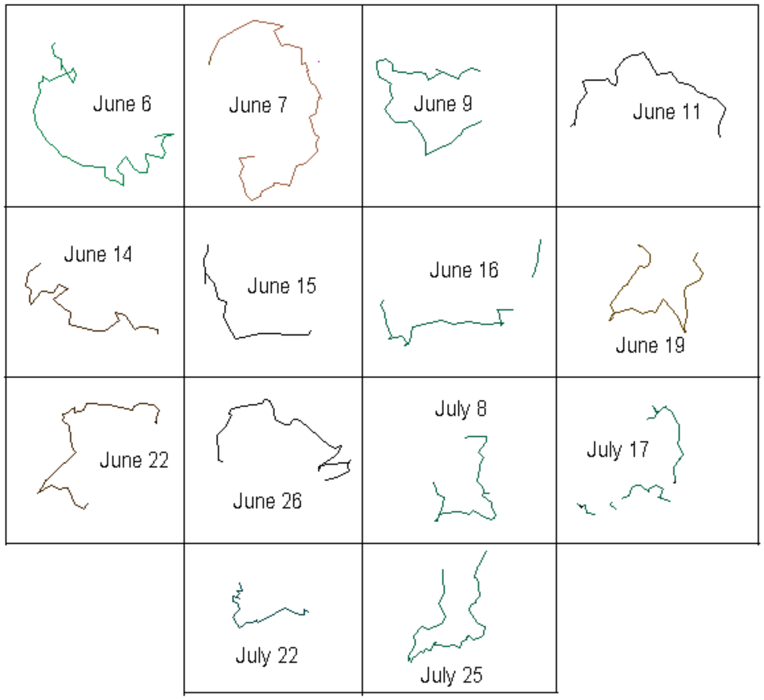


Fig. 5.4 C-shaped configurations of the many of the sakis' daily routes (53.8%). See Appendix B for routes not shown below.



The sakis cover large portions of their home range in relatively short periods of time. While they may spend the majority of their time within the core area, edges of their home range are by no means neglected. As an example, after only nine focal-follow days (the first eleven days of the study period), the sakis had visited virtually their entire home range with little overlap in coverage from day to day (see Fig. 5.3). On eight of these days, the sakis visited the edge at some point during the day (exception = study day # 11, Fig. 5.3). By the ninth focal-follow day, the sakis had returned to southern portion of their home range, at which point they repeated the cycle.

However, there were notable exceptions to this pattern corresponding to intense periods of usage of certain ephemerally present fruiting species. For instance, during the two to three-week period that *Talisia micrantha* was fruiting (species with the highest total feeding minutes for the entire study period; for more in depth information on feeding, see section 5.2), the sakis returned to one tree of this species (and, thus, to one area of their home range) roughly every 2-3 days; furthermore, they stayed in the area surrounding two other favored *Talisia* trees for two-day blocks interrupted by six-day forays to other areas. Similarly, during the time that *Bellucia grossularioides* was fruiting (another high-ranked species in terms of feeding minutes), the sakis stayed in roughly the same portion of their home range (the location of two frequently visited *Bellucia* trees) for an extended four-day period without venturing out to other areas of their home range.

For the most part, the sakis' daily paths tended to curve in on themselves rather than follow a straight-line trajectory. This resulted in C-shaped configurations for many of their daily routes (53.8%, Fig. 5.4). The majority of these daily routes (78.6%) were located on the perimeter of the sakis' home range. On the two occasions when the sakis returned to the same sleeping site that they had slept in the previous night, their routes were fairly circular (July 9 and July 12, see Appendix B). The remaining ten daily routes had either somewhat straight (June 8, June 27, June 28), winding (June 13, June 29, July 10, July 16, July 18, and July 23), or amorphous (July 11) configurations (see Appendix B). Overall, the sakis did not appear to travel in perfectly straight-line paths from a.m. to p.m. sleeping sites.

In summary, the sakis' daily path lengths are very short for a frugivorous primate, but long enough to allow them to effectively monitor and defend the edges of their home range (DI = 1.8). While the core area (15.04 ha) is the area of most intense usage for the sakis, the edges are visited regularly during daily forays (especially the eastern and southern regions of their home range) and they even house a few of the group's sleeping sites. Excepting times when favored fruit trees are producing, the sakis usually do not spend a lot of time in the same foraging area from day to day. Finally, rather than being perfect straight-lines, the sakis' daily paths tend to curve in on themselves.

5.2 The Saki Diet

Of the 1,054 individual trees that were flagged and used as data points during the study period, 33.1% were used in feeding or sampling bouts (25.6% in feeding bouts, 7.5% in sampling bouts). Forty (11.5%) of these feeding or sampling trees were used more than once during the study period (from 2-7 times each, with an average of 2.48 times each). Leaves were eaten nearly every day (7 out of 8 focal follow days for which there was complete data), but did not account for a substantial portion of the daily feeding bouts (16% of the daily feeding bouts, Table 5.1).

Table 5.1. Average number of feeding bouts, feeding minutes, species, plant parts, leaf and seed sources eaten per day. Estimates were made from complete focal-follow days only (where complete days are those in which sakis were followed from a.m. to p.m. sleeping sites and there were no breaks in data due to temporary loss of the focal animal), as well as from combined data from partial (where sakis could only be followed for part of the day) and complete focal-follow days. Median values (in parentheses) are listed for complete follow days.

	Total feeding bouts	**% bouts-leaves**	**% bouts-meso & seeds**	**% bouts-seeds only**	**# plant species**	**# plant parts**	**Total feed. min.**	**% feeding time-any seeds**	**% feeding time-only seeds**
Compl. days only (N=8)	17.38 ± 7.78 (16.50)	15.95 ± 9.08 (16.23)	63.21 ± 12.77 (62.25)	44.34 ± 22.75 (43.17)	7.63 ± 2.07 (7.50)	3.88 ± 1.13 (3.50)	138 ± 43.36 (131.0)	68.01 ± 13.37 (72.53)	41.90 ± 22.50 (39.49)
Partial and Compl. Days (N=30)	13.04 ± 6.28	17.54 ± 14.69	62.89 ± 23.07	47.47 ± 22.12	6.67 ± 2.25	3.41 ± 1.01	110.95 ± 43.45	68.47 ± 19.50	48.68 ± 21.77

Seed consumption of any type (including feeding bouts in which the mesocarp was eaten along with the seeds), was a vital part of daily feeding bouts, accounting for average of 68% of the daily feeding minutes and 63% of the daily feeding bouts (Table 5.1). Seeds only (no mesocarp) accounted for an average of 42% of daily feeding minutes and 44% of daily feeding bouts (Table 5.1). An average of 3.88 plant parts were eaten each day (out of nine possible plant part categories), and an average of 7.63 species were eaten each day. However, the number of different plant species consumed per day is an underestimate since no leaf sources could be identified to species and an average of 0.57 fruit sources per day could not be identified.

Fig. 5.5 Percentage of total feeding time devoted to each plant part category.

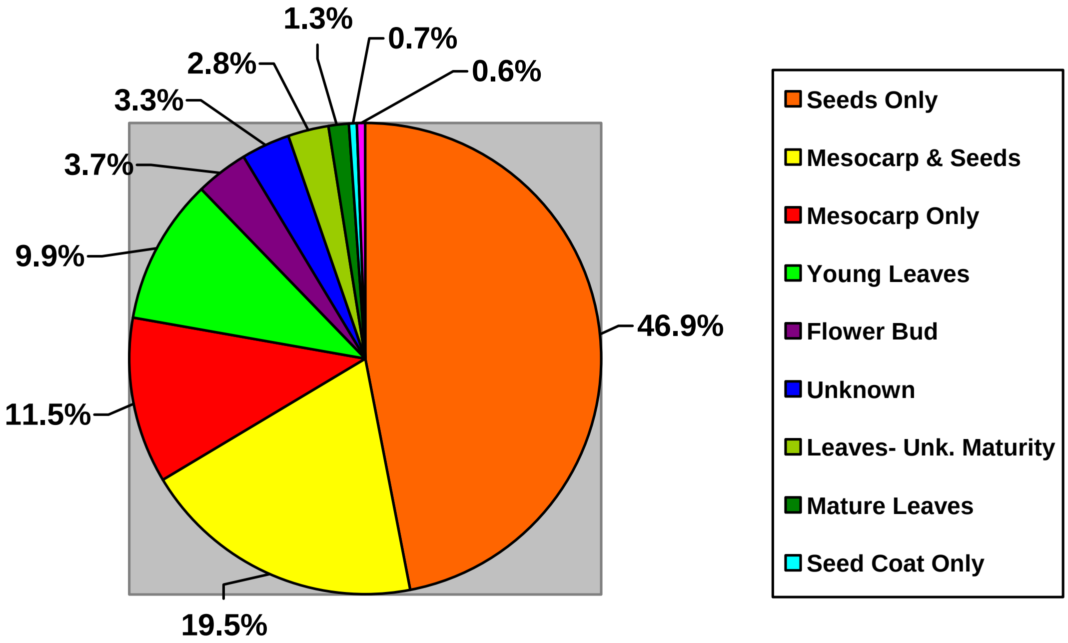


Fig 5.6 Percentage of total feeding time devoted to each plant species (for purposes of clarity, only genus names are listed here; for complete scientific names, see Table 5.2). Leaves included as genus type.

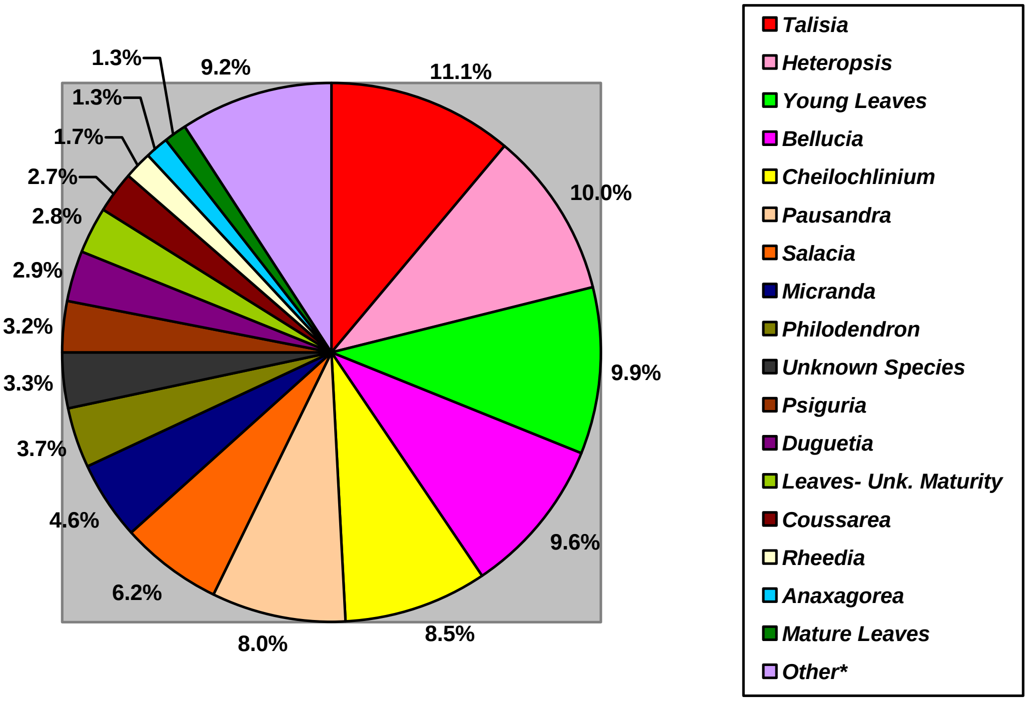


Table 5.2 Description of all plant species eaten during study.

Plant Family	Plant Species	# of Visits to Spp.	Total Feeding Minutes (%)	Plant Parts Eaten (total feeding minutes for each)	Preference Category (and rank, in terms of feeding minutes, out of 31 species)
°ANNO	*Anaxagorea dolichocarpa*	6	39 min. (1.57 %)	seeds	medium (15th)
	Cymbopetalum cf brasiliense	2	19 min. (.77 %)	seeds	low (22nd)
	Duguentia [1]*cf guianensis*	15	86 min. (3.46 %)	seeds	medium (11th)
ARAC	*Heteropsis flexuosa*	31	300 min. (12.09 %)	[2]mc and seeds (225), seeds only (75)	high (2nd)
	Monstera adansonii	1	8 min. (.32 %)	unknown	low (26th, [3]tied with 27th)
	Philodendron sp. 1	17	112 min. (4.51 %)	flower bud	medium (9th)
BIGN	*Tabebuia serratifolia*	1	11 min. (.44 %)	seeds	low (24th)
CELA	*Salacia cordata*	10	187 min. (7.53 %)	mc	medium (6th)
CECR	*Cecropia sp. 1*	1	7 min. (.28 %)	unknown	low (28th, tied with 29th)
CLUS	*Rheedia benthamiana*	6	51 min. (2.05 %)	seeds	medium (13th)
	Tovomita cf grata	1	5 min. (.20 %)	mc and seeds	low (30th)
	Tovomita cf schomburghii	3	31 min. (1.25 %)	mc and seeds (7), seeds only (17), unk. (7)	low (17th, tied with 16th)
CUCU	*Psiguria triphylla*	8	97 min. (3.91 %)	mc and seeds (80), *ec (17)	medium (10th)
EBEN	*Diospyros cayennensis*	3	32 min. (1.29 %)	mc	low (15th)
EUPH	*Micranda brownsbergensis*	15	137 min. (5.52 %)	seeds	medium (7th)
	Pausandra martinii	69	241 min. (9.71 %)	seeds	▫ high (5th), medium (8th)
FLAC	*Carpotroche surinamensis*	1	2 min. (.08 %)	mc and seeds	low (31st)
HIPP	*Cheiloclinium Cognatum*	16	254 min. (10.23 %)	seeds	high (4th)
LECY	*Lecythis*	1	21 min.	seeds	low (21st)

	Idiatimon		(.85 %)		
MELA	*Bellucia grossularioides*	17	289 min. (11.64 %)	mc and seeds	high (3rd)
MIMO	*Inga sp. 1*	4	26 min. (1.05 %)	seed coat (13), unknown (13)	medium (18th)
	Unknown sp. 1	1	13 min. (.52 %)	unknown	low (23rd)
MYRI	*Virola cf sebifera*	2	31 min. (1.25 %)	seeds	low (16th, tied with 17th)
MYRT	Unknown sp. 2	2	10 min. (.40 %)	seeds	low (25th)
RUBI	*Coussarea cf paniculata*	10	80 min. (3.22 %)	seeds	medium (12th)
SAPI	*Talisia micrantha*	15	332 min. (13.38 %)	seeds	high (1st)
SAPO	*Crysophyllum eximium*	2	8 min (.32 %)	seeds	low (27th, tied with 26th)
UNKN	Unknown sp. 3	1	7 min. (.28 %)	seed coat	low (29th, tied with 28th)
	Unknown sp. 4	2	24 min. (.97 %)	seeds	low (19th)
	Unknown sp. 5	1	22 min. (.89 %)	seeds	low (20th)
	Unknown	52	[11]297+ min.(NA)	young leaves	NA
	Unknown	5	[11]38+ min. (NA)	mature leaves	NA

[o] ANNO = Annonaceae, ARAC = Araceae, BIGN = Bignonaceae, CELA = Celatraceae, CECR = Cecropiaceae, CLUS = Clusiaceae, CUCU = Cucurbitaceae, EBEN = Ebenaceae, EUPH = Euphorbiaceae, FLAC = Flacourtiaceae, HIPP = Hippocrataceae, LECY = Lecythidaceae, MELA = Melastomataceae, MIMO = Mimosaceae, MYRI = , MYRT = Myrtaceae, RUBI = Rubiaceae, SAPI = Sapindaceae, SAPO = Sapotaceae, UNKN = Unknown family

[1] "cf " indicates less than 100% confidence in species level assignment.

[2] mc = mesocarp, *ec = exocarp

[3] Each species was given its own rank for the sake of illustrating how many individual species were identified during study even if total feeding minutes for each of two species were the same.

▫ *Pausandra martinii* trees are often found in clusters. Feeding bouts during which sakis fed in a cluster of *Pausandra* trees were given "High" preference ranks (115 total feeding minutes, 4.63%) and feeding bouts in which sakis fed on single *Pausandra* trees were given "Medium" preference ranks (126 total feeding minutes, 5.08%).

The average distance traveled between feeding trees (excluding trees in which the monkeys sampled fruit or leaves, but did not feed) was 46.6m ± 45.68 (range = 6.0 m – 454.0 m, median = 33 m). The majority of inter-feeding tree distances were under 40 m (60.9% of cases), and only 18 of 202 total cases (8.9%) were over 100 m. The average distance traveled from the last feeding tree of the day to a sleeping site was higher than the average for feeding tree-to-feeding tree distances (63.7 m ± 57.88, N = 16 cases). The average distance traveled from the sleeping site the first feeding tree of the day was the longest (73.9 m ± 57.39).

As was reported previously, seeds were the preferred plant part for the sakis; seed consumption (including feeding bouts during which the mesocarp was eaten in addition to the seeds) was responsible for 66.8% of the total feeding time for the study period (Fig. 5.5). Fruit pulp (mesocarp) was also an important resource for the sakis; the mesocarp, exclusive of any other part of the fruit, was eaten 11.5% of time.

During all feeding bouts for the entire study period, at least some part of the fruit being eaten was discarded. Usually the seeds were selectively ingested and the rest of the fruit discarded. At other times, the mesocarp was ingested and seeds and exocarp were discarded. Less frequently, only the seed coat was eaten and the rest of the fruit was discarded (*Inga sp.*1, 13 minute feeding bout; Unknown sp. 3, 7 minute feeding bout); on only one occasion, the exocarp the sole focus of a feeding bout (*Psiguria tripylla*, 17 minute feeding bout).

Flower parts were taken from only one identified plant genus (*Philodendron*); on two other occasions, flowers were taken from unidentified sources. Young leaves were definitely more preferred than mature leaves, as they accounted for approximately 71% (vs. 9%) of the total leaf-eating minutes (for 20% of the total leaf-eating minutes, maturity level could not be determined; Fig 5.5).

Twenty-seven feeding sources could be identified at least to the family level (two only to the family level, one only to the genus level, and the other 24 to the species level - Fig. 5.6 and Table 5.2). Three other species could not be identified despite the fact that there were leaf and fruit specimens available for each (labeled Unknown sp. 3-5 in Fig. 5.6 and Table 5.2). A specimen was unavailable for seventeen additional feeding sources; thus, these resources are collectively included in the “Unknown species” category in Fig. 5.6. As mentioned previously, leaf sources could not be assessed due to the difficulty in identifying plants for which there are only leaf specimens; however, leaves were still included in the breakdown of proportion of total feeding time spent on plant genera, Fig. 5.6; on the other hand, leaves were excluded from the ranking of plant species in terms of feeding minutes, Table 5.2).

Five plant species (*Talisia micrantha, Heteropsis flexuosa, Bellucia grossularioides, Cheiloclinium cognatum,* and some *Pausandra martini,* see below) were included in the “high” preference category for purposes of analyses on speed and straight-line travel to resources. These five species were responsible for 51.97% of the total feeding minutes for the entire study period. Nine plant species, contributing 36.85% of feeding minutes to the study period, were assigned to the “medium” preference group; the remaining 17 species, each accounting for less than 1.25% of the total feeding minutes and having less than five feeding bouts apiece, were assigned to the “low” preference feeding category (see Table 5.2 for specific ranks of all species in terms of total feeding minutes).

Pausandra martini feeding sources were special cases. *Pausandra* trees are small understory trees that are often found in clumps and are fairly ubiquitous in the study group's range. Feeding bouts on individual *Pausandra* trees were often short (avg. = 2.4 minutes) and relatively insignificant; however, on occasion, approximately 15-20 cumulative minutes were spent feeding on a cluster of *Pausandra* trees (where a "cluster" is defined as a group of three or more *Pausandra* trees, each less than 20 m away from the next). I felt that a cluster of *Pausandra* trees would be significantly more important to the sakis than a lone *Pausandra* tree. Since this species was right on the cusp between being ranked "high" or "medium" preference, I decided to include all *Pausandra* trees belonging to a cluster in the "high" preference category and all single *Pausandra* trees in the "medium" preference category.

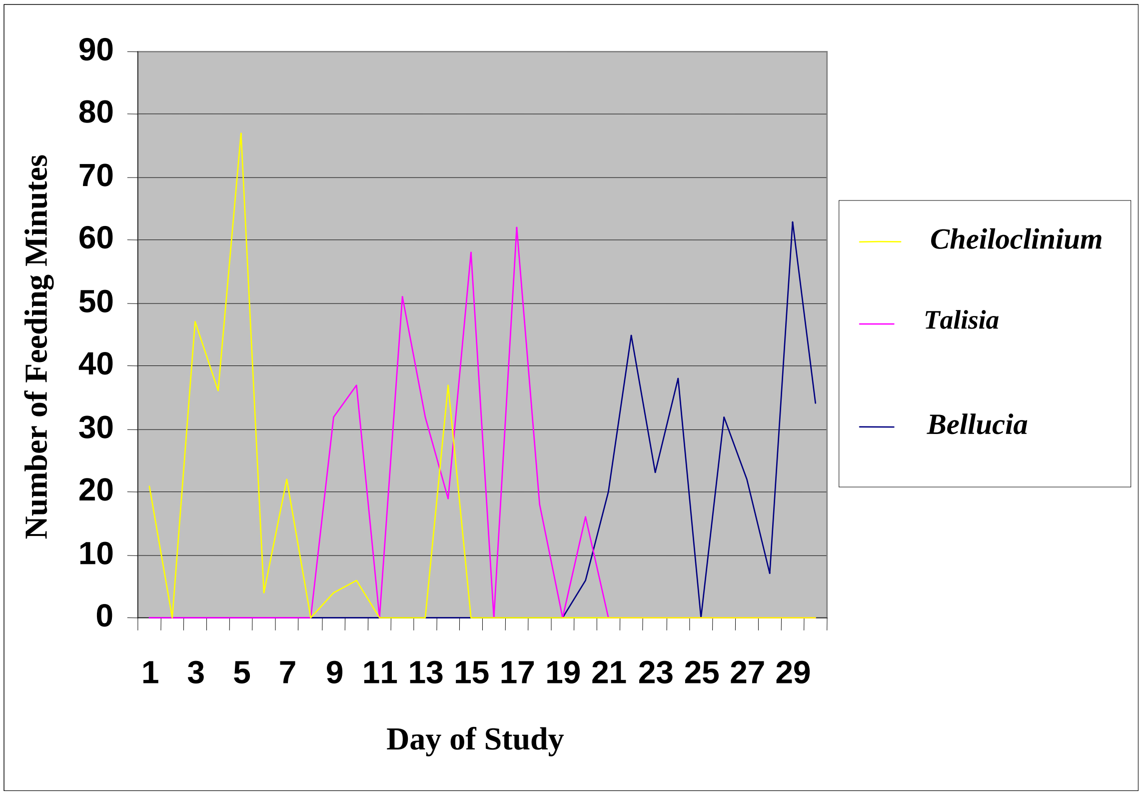
Some species were eaten on a fairly regular basis for most or all the study period (*Heteropsis flexuosa* = every day to every other day in June, roughly every 6th day in July; *Salacia cordata* = every 5-6 days during the study period; *Pausandra martini* = at least one bout nearly every day (range = 1-10 bouts per day); leaves = averaged about one bout per day). Other species were eaten very sporadically, but throughout the entire study period (range of the number of days in between feeding bouts: *Micranda brownsbergensis* = 1-8, *Philodenron* sp. = 1-12; *Psiguria triphylla* = 1-22; *Coussarea cf peniculata*= 1-14). *Duguetia cf guianensis*, *Rheedia bentamiana*, and *Anaxagorea dolichocarpa* were each eaten very sporadically for 2-4 week periods during the study. The remaining ("low" preference) species were only eaten a handful of times (1-4 feeding bouts each), sometimes with weeks in between visits.

Cheiloclinium cognatum, *Talisia micrantha*, and *Bellucia grossularioides* each stood out as a highly preferred species during separate periods of the study (see Fig. 5.7). For the first eight focal-follow days of the study, *Cheiloclinium* accounted for 29.03% of the total feeding minutes; starting on day nine, as the frequency of feeding minutes per day for *Cheiloclinium* significantly declined, *Talisia* arrived on the scene and became the predominant feeding species for the next twelve focal-follow days (accounting for 30.62% of the total feeding minutes during this period, while *Cheilochlium* only accounted for 4.44%); as the number of *Talisia* feeding minutes abruptly dropped to zero on focal-follow Day 21, *Bellucia* replaced it as the most preferred species (comprising 23.86% of the total feeding minutes for this final period).

The average length of a feeding bout during the study period was 8.59 min. ± 8.48 (range = 1.0 – 62.0 min., median = 6.0 min.; 92.3% of bouts ≤ 20.0 min.; only one bout > 60.0 min.; N = 349). *Pausandra martinii* feeding bouts were distinct from all others with respect to their brevity (average 3.49 min. ± 2.57, median = 3.0 min.; 84.1% of bouts ≤ 5.0 min.; N = 69). However, even after excluding all *Pausandra* feeding bouts and all sampling bouts, which by definition lasted less than one minute, the average length of a feeding bout only increased to 10.62 min. ± 8.82 (median = 8.0 min.; 89.5% of bouts ≤ 20.0 min.; N = 258).

In summary, the sakis were involved in an average of 17.38 feeding or sampling bouts per day. Individual feeding bouts were relatively short (nearly 90% of them shorter than 20 min, even after excluding bouts with the shortest feeding duration, i.e. *Pausandra* feeding bouts and all sampling bouts) and inter-feeding tree travel distances were usually less

Fig. 5.7 Sequential domination of feeding periods by three plant species.



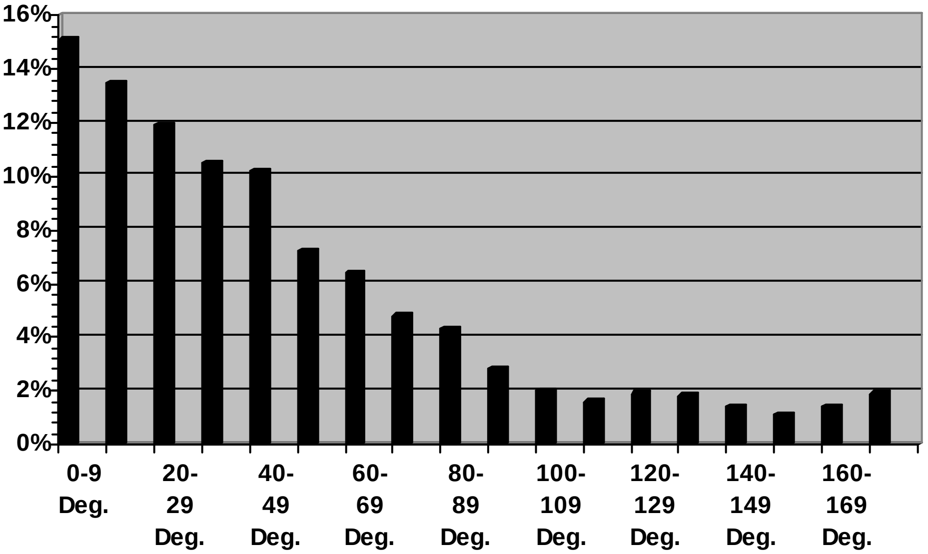
than 40 m. Their diets were fairly diverse, as they consumed a minimum of 3.88 different plant parts and, at the very least, 7.63 different species per day. While fruit pulp was consumed at least once per day and young leaves were eaten nearly every day, seeds were by far the most popular single resource consumed by the sakis during the study period (seeds, exclusive of mesocarp, accounted for 47.2% of the total feeding time). Sakis were selective during the study period, as they discarded various parts of fruits while feeding (either the mesocarp and the pericarp in favor of the seeds, the pericarp and the seeds in favor of the mesocarp, or all other parts in favor of the exocarp). A very small number of plant species (5 out of the 31 species identified) accounted for the majority of feeding minutes (nearly 52%). During three distinct periods of the study, one of these top-ranked species sequentially dominated the total number of feeding minutes.

5.3 Backtracking Predictions

Angles of progression were not evenly distributed across all angle categories (four equal angle of progression categories between 0 - 180°; Chi-Square = 753.75, p < .0005). Rather, 84% of all angles of progression were ≤ 90° (Fig. 5.8 A and B). More than half (51%) of the observed angles of progression < 40°, which indicates that the sakis gravitate towards forward progression, as opposed to backtracking (angles > 90°) or even sharp turns to the left or the right (angles between 45-90°). During each daily travel bout, the sakis tended to retain the same direction of turning, curving gradually (angles of progression < 45°) as they progressed through their route (i.e. if they began making slight turns to the left of the straight-line path early in the day, the majority of subsequent turns throughout the day

Fig. 5.8 Angles of progression in 10º categories (**A.**) and in 90º categories (**B.**). (**A.**) Shows the percentage of the total angles of progression (N = 1133) falling within each category; 51.0% of all angles are ≤ 39º and 61.3% of all angles are ≤ 49º. For both (**A.**) and (**B.**), angles of ≤ 90º indicate forward progression and angles of > 90º indicate backtracking.

A.



B.

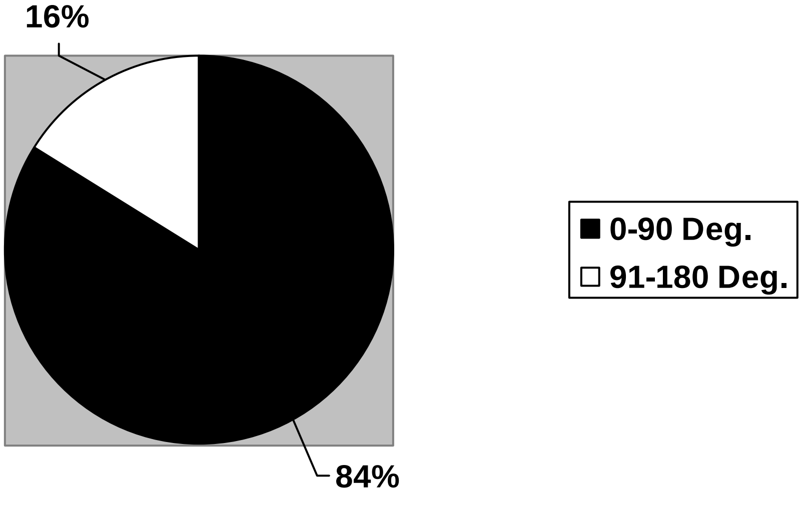
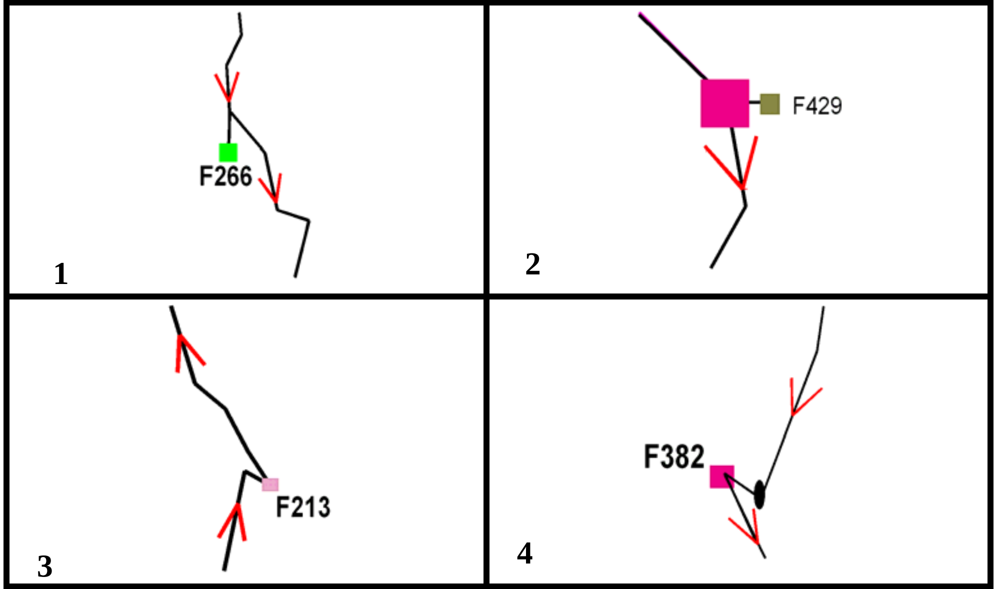
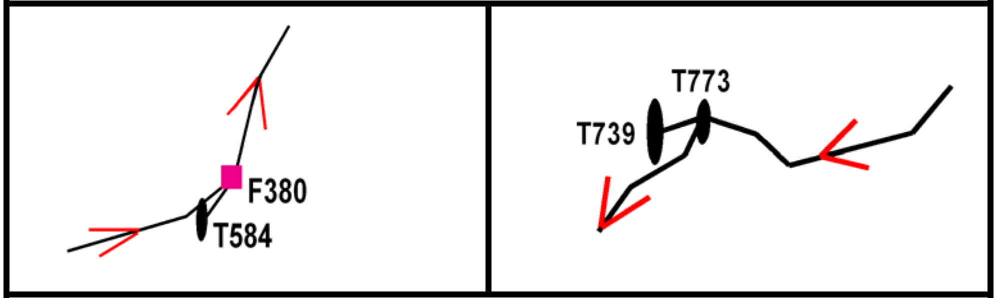


Fig. 5.9 Explanations for most extreme cases of backtracking (angles of progression > 135°, N= 75 cases). Ellipses designate resting bouts; blue lines represent forest edge; triangles represent sleeping sites. Squares represent feeding trees; color of square signifies the plant species that the sakis were feeding on- see Appendix B.1 for plant species key.

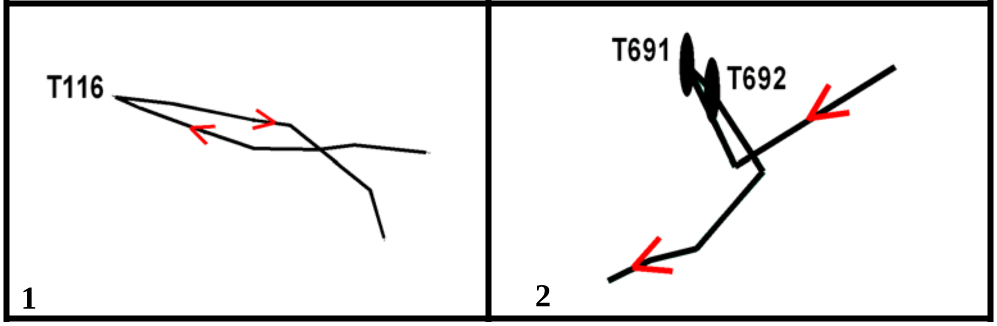
A. Diverge from established path to feed. (n = 32)



B. Diverge from established path to rest. (n = 11)

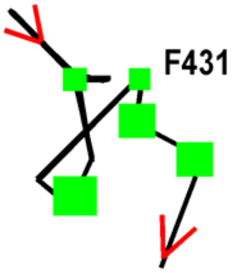


C. Movements during ITE's. **1.** Chasing and retreat. (n = 5) **2.** Erratic movements. (n = 3)



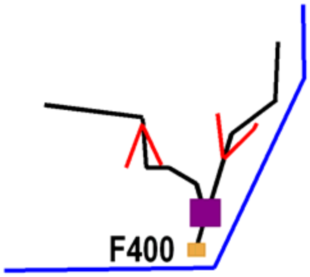
D. Feeding on clustered resources. (n = 5)

1

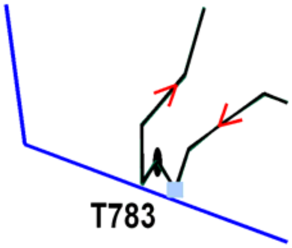


2

E. Cannot travel any further along established trajectory- have reached edge of forest. (n = 7)

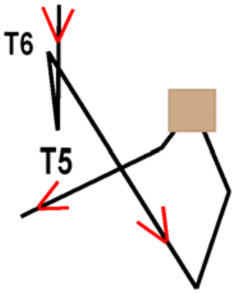


1

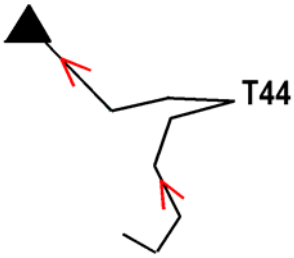


2

F. Trying to home in on a resource that they either remember is in the area or can sense otherwise (i.e. smell). (n = 3)

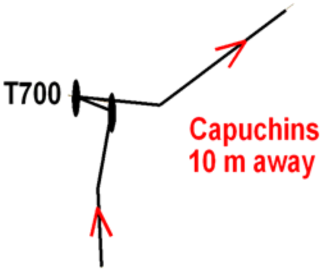


1



2

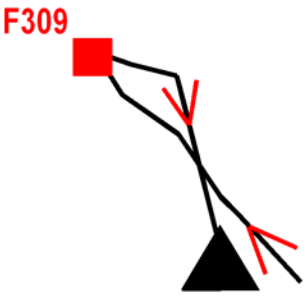
G. Other monkeys in area. (n = 1)



1

H. Last feeding bout of day before traveling to sleeping site. (n = 1)

2



were to the left; conversely, if they began making slight turns to the right of straight-line early in the day, the rest of their turns tended towards the right). This observation mirrors the previous observation that the majority of the sakis' daily paths tend to curve in on themselves (daily routes are C-shaped or circular).

When I analyzed the most extreme cases of backtracking (angles of progression > 135°, N = 75 cases), some definite trends were observed. Most cases (N = 32, 43%) conformed to the first pattern (pattern A, Fig. 5.9). In these cases, the focal animal had been traveling along an established trajectory for at least 50 m, at which point he/she abruptly diverged from the path to feed. After feeding, he/she backtracked roughly to the pre-divergence location, and then resumed travel along the same path. Overall, the sakis only traveled an average of 6.8 m off of the established path to visit these feeding trees.

The second pattern was similar to the first in that the sakis diverged off a path with an established trajectory to visit a resource; after the visit, they returned to the path, resuming roughly the same trajectory as before (N = 11 cases, see pattern B, Fig. 5.9). However, in these cases the resource was a tree that they ended up resting in for at least 20 minutes. On two of these occasions, the tree that the sakis ended up resting in was a tree that had been used previously as both a sleeping and a resting site. On five of the occasions that the sakis diverged to rest, they were resting in a tree that was within 20 m of a previous ITE location. These resting forays averaged only 9.29 m off of the established path.

Six other situations seemed to be responsible for cases of extreme backtracking. First of all, a fair amount of backtracking is involved in aggressive encounters with other saki groups (see pattern C, Fig. 5.9). During ITEs, males are often involved in chases and/or retreats, which entail long forward and backward movements, respectively, followed by travel to pre-ITE locations to rejoin the group. Even if there are no chases and/or retreats during ITEs, movements that accompany threat postures and vocalizations are characterized by short, erratic forward and backward steps, resulting in incidents of backtracking. A similar encounter that resulted in a case of backtracking occurred when a group of capuchins were heading quickly towards the study group; on this occasion the sakis abruptly moved off their path, rested in a tree for approximately 5 minutes until the capuchins passed, and then returned to approximately the same location they were at before the capuchins arrived and resumed travel along the pre-divergence path (see pattern G, Fig. 5.9).

A fair amount of backtracking also seems to be involved in occasions where the sakis are feeding on a tightly clustered group of resources, such as a patch of *Pausandra* trees (N = 4 cases, each patch contained 6-8 *Pausandra* trees) or a patch of young leaf trees (N = 1 case, patch contained 5 trees producing new leaf flushes) (see pattern D, Fig. 5.9). It seems that when distances between individual feeding trees are relatively small (as in a tight cluster of resources, where inter-tree distances were less than 20 m), the sakis do not necessarily try to visit those resources in a distance-minimizing order.

Another scenario that leads to backtracking is when the sakis reach the edge of the forest in their home range (see Fig. 5.1 for location of edge in the southern region of their range) and have no option but to turn around (N = 7 cases, see pattern E, Fig. 5.9). Janson (2000) notes that most foragers will eventually be forced by home range or territorial boundaries to make sharp turns that return them toward previously used areas.

The final two explanations were responsible for fewer incidents of backtracking (pattern F, N = 3 cases, and pattern H, N = 1 case, see Fig. 5.9), and are slightly more tenuous justifications for backtracking that the other five. On the occasion depicted in F1,

Fig. 5.9, (responsible for 2 of the 3 incidents of backtracking adhering to this pattern), the erratic movements occur within a very short distance of the *Psiguria triphylla* tree that they eventually visit; therefore, it is plausible that the sakis either 1) knew the general area that this site was in and were trying to home in on it, or 2) had no prior knowledge of the tree's existence, but began to smell its fruit around tree # T5, and subsequently began to home in on it. Similarly, the erratic movements preceding the arrival to a sleeping site (F2, Fig. 5.9) could be explained by explantation #1 above. In the final scenario (pattern H, Fig. 5.9), it appeared as if the sakis bypassed their sleeping site for the night to visit one final feeding tree, and then backtracked to reach the sleeping tree (a sleeping tree that they had used previously). Of the 75 cases of extreme backtracking, there were seven incidents that did not seem to fit any of the aforementioned patterns.

In summary, while the sakis do backtrack occasionally (only 16% of angles of progression are greater than 90°), the majority of their travel decisions are based on forward progression (51% of angles of progression involve turns off the straight-line path of less than 40°). Backtracking appears to occur the most (58.7% of extreme backtracking cases) when the sakis diverge slightly off their chosen path to visit feeding or resting sites. Obstacles in the form of competing groups (i.e. during ITEs), other species (capuchins, whom are known for their loud and destructive foraging techniques), and forest edges (in the southern part of this groups' home range) also induce episodes of backtracking (responsible for a total of 21.3% cases of extreme backtracking). Finally, movements when feeding on clustered resources (6.7% of cases) or when trying to locate particular resources (4.0% of cases) are also characterized by very sharp turning angles. Few of these episodes (with the exception of

ITE chases and retreats and homing episodes) appear to add a lot of extra distance to the sakis' daily path lengths.

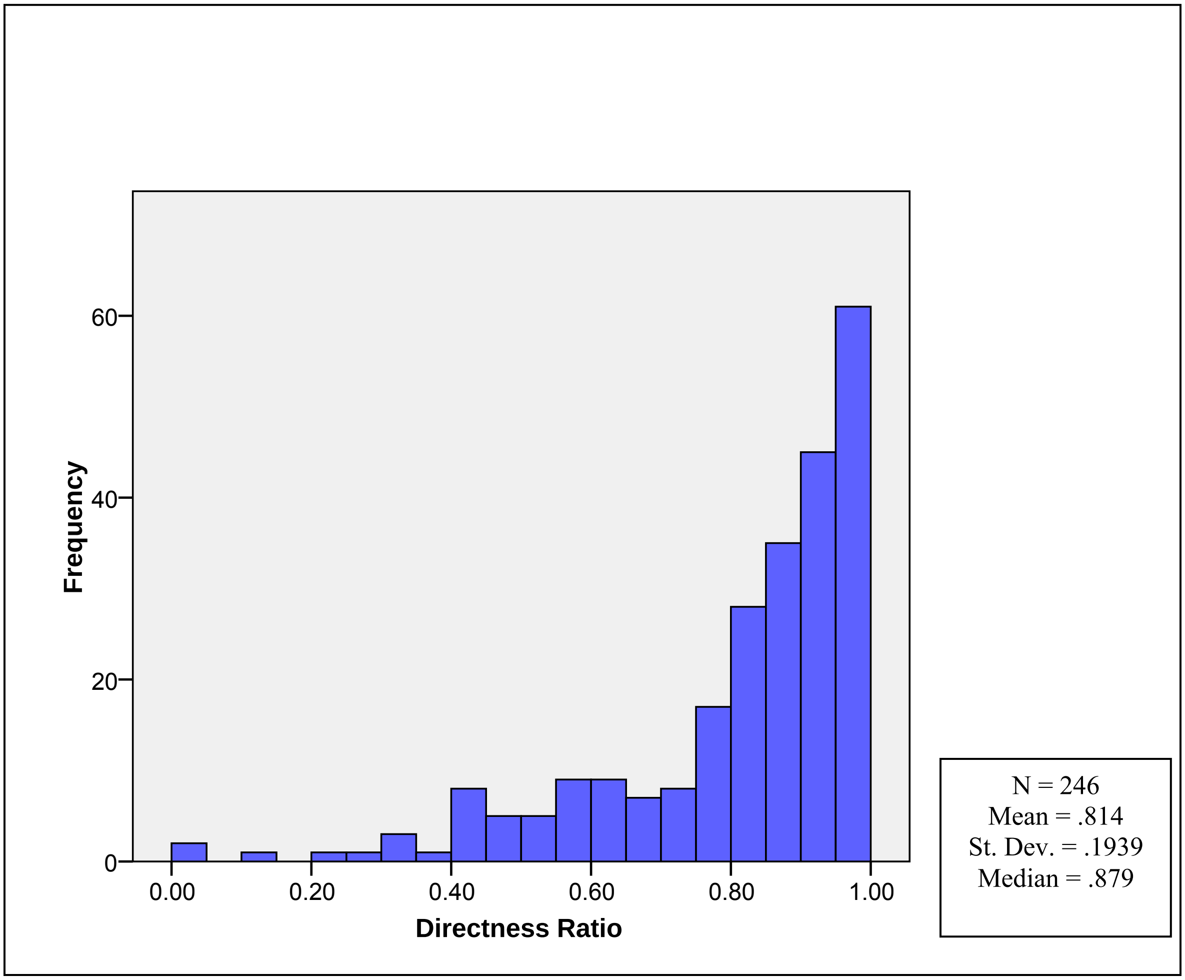
5.4 Directed Travel Predictions

5.4.1 Linearity in Travel to Feeding and Sleeping Sites, in General

In order to acquire some baseline data for the directed travel predictions, I first assessed how far off the straight-line path the sakis traveled from resource to resource (any feeding/sampling source or sleeping tree was considered a resource for this general analysis). Following the examination of trends pertaining to the general shape the sakis' daily routes (tended to be curved or C-shaped), and the observation that the sakis are inclined towards angles of progression that involve slight turning (angles between 5° and 40°), I decided to redefine straight-line travel to fit their tendencies. Accordingly, rather than testing whether observed directness ratios for the study period were significantly different from 1.0 (perfect straight-line directness ratio), I tested whether observed directness ratios were significantly different than "relatively" straight-line travel (DR = .90, meaning that if the straight-line path from one feeding tree to another was 9 m, the sakis would travel 10 m, and if the straight-line path from a sleeping tree to a feeding tree was 90 m, the sakis would travel 100 m, etc.).

According to the one sample t-test, where all observed directness ratios for the study period (N = 246) were tested against the newly-defined straight-line directness ratio (DR = .90), the sakis traveled significantly farther than the "straight-line" distance when moving

ig. 5.10 Frequency distribution of directness ratios (DR) for the entire study period.



from resource to resource (z = -6.95, p < .01). Even though only 39.8% of DRs were greater than .90, the mean DR (mean = .8141 ± .20, median = .8793; Fig. 5.10) for this study was equivalent to mean DRs for the two periods in Cunningham and Janson's (2007) study (Period 1 = .84, Period 2 = .82), which they recognized as acceptable values for proving directed travel in their group of sakis. Overall, 67.1% of all DR's were greater than .80; thus, the sakis usually only traveled 20% farther than perfect straight-line distances to reach their feeding and sleeping sites.

5.4.2 Comparisons of Directness Ratios Among High-, Medium-, and Low-Preference Foods

Directness ratios when heading to high-, medium-, and low-preference foods were compared to see if the sakis traveled more linear paths to higher vs. lower-ranked food sources. Results showed that the sakis did not travel in more straight-line paths to high- vs. medium-preference food sources (Mann-Whitney z = -.540, ns), to medium- vs. low-preference foods (Mann-Whitney z = -.377, ns), or even to high- vs. low-preference food sources (Mann-Whitney z = -.050, ns; Table 5.3 A). Interestingly, average DR values for the low-preference category were actually higher than the DRs for higher preference categories (Low: mean = .841, median = .894; Medium: mean = .818, median = .879; High: mean = .823, M = .889), which was against expectations. On the other hand, average DR values for high-preference group were slightly higher than those for the medium-preference group (though not significantly higher), which was the expected trend.

Table 5.3 Effects of main study variable (food preference group) on directness ratios (DR = straight-line distance between resources/observed distance between resources) before (**A**) and after (**B**) exclusions, using Mann-Whitney U tests with a Bonferroni adjustment ($\alpha = .05$ for entire experiment, $\alpha = .017$ for each test).

A	**Low vs. Med**		**Low vs. High**		**Med vs. High**	
Medians	.894	.879	.894	.889	.879	.889
Sample Sizes	21	81	21	73	81	73
Results	z = -.377, ns		z = -.050, ns		z = -.540, ns	
B	**Low vs. Med**		**Low vs. High**		**Med vs. High**	
Medians	.897	.875	.897	.900	.875	.900
Sample Sizes	18	64	18	49	64	49
Results	z = -.101, ns		z = -.375, ns		z = -.773, ns	

5.4.3 Factors Affecting Directness of Travel to Feeding and Sleeping Sites

Based on observations of the sakis' travel patterns in the field and on the analysis of extreme backtracking occurrences, I expected a number of contexts (nine in all) to lead to significant increases or decreases in directness ratios from "the norm" (since each scenario was responsible for such a small percentage of the observed inter-resource directness ratios (< 11% of observations in each testing situation), I defined the larger treatment groups as the "normal populations" and tested for significant departures from their respective median DR values).

Due to chases and retreats and overall erratic movements during inter-group ITEs, the sakis moved in significantly less linear paths during these incidents (Wilcoxon Signed Rank $z = 2.023$, $p < .05$; Table 5.4, test 1).

Since sampling bouts involved feeding on very small amounts of food for less than a minute, I expected that these feeding bouts would be relatively insignificant to the sakis in comparison to all other feeding episodes (i.e. sampling bouts expected to involve less preferred resources). Since animals are expected to travel more linearly to more preferred resources, I presumed that DRs for cases involving "feeding" bouts would be significantly higher than DRs for cases involving "sampling" bouts. Surprisingly, DRs for sampling bouts were actually higher than DR's for feeding bouts, though not significantly so (sampling: median = .914, feeding: median = .870; Wilcoxon Signed Rank $z = 1.232$, ns; Table 5.4, test 2).

I anticipated that if the sakis spent a fairly large amount of time (> 30 min.) resting (R), playing (P), and/or grooming (G) on their way from one sleeping/feeding tree to another that this might reduce their travel directedness. Specifically, since sakis may have certain criteria that trees have to meet before they will use them as resting sites (the sakis seem to prefer trees with a relatively open canopy for sunbathing, Norconk, personal communication), they may choose to diverge off their chosen path to search for a suitable resting site or to return to a known one that meets their criteria. These divergences would lead to increases in path length, which would lower the DRs. The Wilcoxon Signed Rank test showed that DRs were significantly lower for the 25 cases where the sakis stopped in between resources to rest ($z = 3.000$, $p < .05$; Table 5.4, test 3).

I also speculated that if the sakis rested in the feeding tree under investigation for a long period of time (more than 30 min. over the feeding duration for that tree) that this might boost the DR for that site. Once again, since the sakis seem to be choosy about the types of trees they will rest in, I assumed that a tree that was suitable enough to qualify as a resting site, as well as a feeding source, would be a highly preferred tree; therefore, travel to that site would be highly directed. However, DRs for trees that were used both as feeding and resting sites were not significantly different than DRs for trees that were used for only one activity (Wilcoxon Signed Rank $z = -1.095$, ns; Fig. 5.4, test 4).

Since Cunningham and Janson (2007) found that feeding trees that had been visited more than once by white-faced sakis were preferred over feeding trees that had either never been visited or visited only once, I expected that the same would be true for the sakis in this study. Results showed that DRs for reused feeding trees were significantly higher than DRs for first-time visits to feeding trees (Wilcoxon Signed Rank $z = -2.10$, $p < .05$; Fig. 5.4, test 5).

Table 5.4 Effects of specific contexts on directness ratios, using Wilcoxon Signed Rank tests.

(tests 1, 2 & 3)	No ITE **vs.**	ITE	Feed **vs.**	Sample	No R/G/P en route **vs.**	R/G/P en route
Medians	.886	.344	.870	.914	.889	.811
Sample Sizes	241	5	204	26	218	25
Results	z = 2.022, p < .05		z = -1.232, ns		z = 3.000, p < .05	
(tests 4, 5 & 6)	No R at target **vs.**	R at target	1st visit **vs.**	Revisit	FT as target **vs.**	SS as target
Medians	.878	.952	.892	.950	.879	.861
Sample Sizes	242	4	207	15	230	16
Results	z = -1.095, ns		z = - 2.100, p < .05		z = .569, ns	
(tests 7, 8 & 9)	FT as previous resource **vs.**	SS as previous resource	Same focal **vs.**	Switch focal	Interior **vs.**	Boundary
Medians	.878	.836	.889	.592	.887	.769
Sample Sizes	228	18	235	11	232	14
Results	z = .501, ns		z = 2.667, p < .05		z = 2.668, p < .05	

I also anticipated that since 1) sakis are fairly choosy about the type of tree they will sleep in, and 2) there are a relatively small number of sleeping site locations that they have to remember (only 23 different sleeping trees used in this seven week-long study, as opposed to 309 different feeding trees), that they would travel in a more directed manner towards sleeping sites (n = 11 cases) than they would to the average feeding tree (n = 235 cases; see Table 5.4, test 6). Contrary to expectations, the median DR for feeding trees (median = .876) was actually slightly higher than the median DR for sleeping trees (median = .861), though results were not significant (Wilcoxon Signed Rank z = .569, ns).

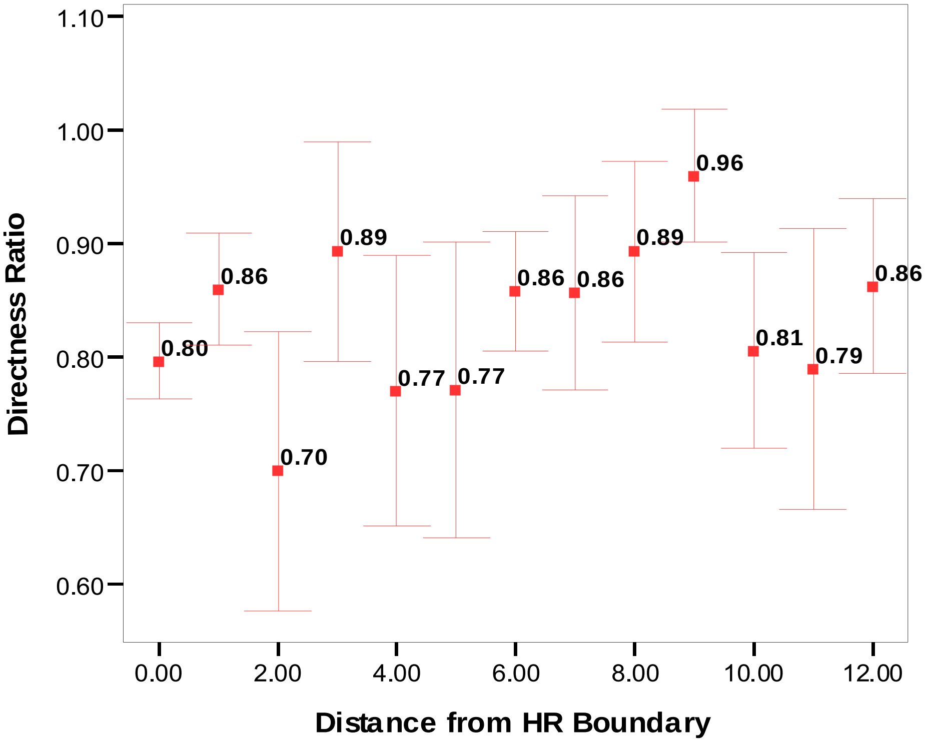
Another expectation was that after approximately 18 hours of not feeding during the night (assuming the last feeding bout for the day was at 15:00 and the first feeding bout the next day was at 8:00, which approximates nearly all observations), the sakis would be especially intent on minimizing time, distance, energy expenditure to their first feeding site (i.e. they would travel in very directed paths). Once again, though, results did not exactly match predictions: while the DRs were slightly higher for cases where the sakis were traveling from a sleeping site to the first feeding site (median = .886, n = 18 cases) than for cases where the sakis were just traveling from feeding tree-to-feeding tree or from their last feeding tree of the day to their nightly sleeping site (median = .878, n = 228 cases), values were not significantly different (Wilcoxon Signed Rank z = .501, ns; Table 5.4, test 7).

I also anticipated that uncontrollable imperfections in data collection might influence DRs. In particular, there were eleven occasions when I lost the focal animal and had to switch to another during the sakis' travels from one feeding/sleeping site to another. Foreseeing differences in directness ratios due to differences in traveling styles between the two animals and/or differences in activities proceeding the switch, I hypothesized that directness ratios obtained from cases where I had to switch the focal animal might be different than DRs obtained from cases where no changes occurred. The results showed that DRs were significantly lower for cases where I switched the focal than for cases for which there was no switch (Wilcoxon Signed Rank $z = 2.667$, $p < .05$; see Table 5.4, test 8).

Finally, I hypothesized that the sakis might move more erratically or backtrack more as they got closer to the estimated home range border, either due to encounters with competing saki groups, anxiety in anticipation of encounters, or sharp turns upon reaching the edge of their home range. While I anticipated some effect, I was uncertain as to what proximity to the border would produce an effect. Therefore, I compared distances from the border in 10 m increments up to a distance of 60 m (60 m was chosen as an appropriate maximum distance as most ITEs occurred within this distance from the border). I also hypothesized that moving towards the border would cause more trepidation (and, therefore, more erratic movements), so I distinguished between proximities when moving towards the border from proximities when moving away from the border.

According to Fig. 5.11, only distances within 40-49 m of the home range border produced drastically lower DR's. Therefore, I tested for significant differences in DRs between cases where the sakis were within 40-49 m of the border and where the sakis were at any other distance from the border, including in the interior (see Table 5.4, test 9). The sakis did have significantly less directed movements for this proximity group (40-49 m from the border) than for any other distance from the border (Wilcoxon Signed Rank $z = 2.668$, $p < .05$). Upon closer inspection, it turned out that 13 out of 14 of these boundary cases occurred

Fig. 5.11 Directness ratios by distances from the home range border. Directness ratios = straight-line inter-resource distance/observed inter-resource distance.



Integers 0-12 on the x-axis represent distances from home range (HR) border (as defined by perimeter data points collected during focal follow days, see Methods- Area Usage section).
0 means that the sakis were in the interior of their home range (> 60m from the home range border). #'s 1-6 indicate that the sakis were heading towards the HR border, and #'s 7-12 indicate that they were moving away from the HR border. 1 &12 = 50-60m from border, 2 & 11 = 40-49m from border, 3 & 10 = 30-39m, 4 & 9 = 20-29m, 5 & 8 = 10-19m, 5 & 7 = 0-9m from border.

in the southern portion of their home range near the area of deforestation at the edge of the plateau (see Fig. 5.1). Thus, it appears that DRs are really only significantly reduced within 40-49 m of the southern border, as opposed to uniformly around the border in any region of their range. Clearly, the backtracking episodes that occurred near the forest edge (identified in section 5.3; see also Fig. 5.9, pattern E) were directly responsible for the majority of these significantly lowered directness ratios.

5.4.4 Comparisons of Preference Groups After Exclusions

After excluding all cases that proved to significantly decrease or increase DRs, I reran the original tests comparing DRs among high-, medium-, and low-preference food groups Specifically, I excluded a total of 98 cases that involved 1) switching focals in between visits to resources, 2) resting in a tree for > 30 min. in between visits to resources, 3) proximities within 40-49m of the range border, 4) ITEs with other saki groups, and 5) revisits to feeding trees. Surprisingly, results for these reconfigured tests were still not significant (Mann-Whitney U, comparison of medium- to high- preference group, Mann-Whitney z = -.773, ns; comparison of low- to medium-preference group, Mann-Whitney z = -.101, ns; comparison of low- to high-preference group, z = -.375, ns; Table 5.3 B).

5.4.5 Comparison of Observed and Expected Directness Ratios After Exclusions

I also reran the one-sample t-test, employing the same exclusions, to see if the aforementioned contexts (ITEs, forest edge visits, resting > 30 min. en route to resource, switching focals, revisiting feeding trees) were the only factors causing the observed DRs to be significantly different than the expected DR value of .90. However, results still showed

Table 5.5 Comparison of speeds of arrival to high-preference vs. medium-preference vs. low-preference food categories using three Mann-Whitney U tests with a Bonferroni adjustment ($\alpha = .05$ for entire experiment, $\alpha = .017$ for each test). Arrival speeds are actually ratios (observed speed to resource/average speed for the relevant period, i.e. reported median values tell how many times faster than average speeds the sakis traveled to various resources).

	Low	**vs. Med**	**Low**	**vs. High**	**Med**	**vs. High**
Medians	.883	1.451	.883	2.050	1.451	2.050
Sample Sizes	5	18	5	20	18	20
Results	z = -.075, ns		z = -1.427, ns		z = -1.988, ns	

that the mean observed DR was significantly different than the relatively straight-line DR value of .90 (i.e. the sakis were traveling significantly farther than expected to reach feeding and sleeping sources, $z = -4.910$, $p < .01$). However, the mean and median DRs did increase from pre-exclusion values (pre-exclusion DRs: mean = .814, median = .879; post-exclusion DRs: mean = .840, median = .891).

5.4.6 Comparisons of Speed Ratios Among High-, Medium-, and Low-Preference Foods

To test whether or not the sakis traveled significantly faster to more preferred resources, I conducted three Mann-Whitney U tests that compared speed ratios (the observed speed divided by average speed for the corresponding period of the day) for approaches to high- vs. medium- vs. low-preference food sources. As was expected, the sakis traveled faster to high-preference foods than to medium- or low-preference foods (high-preference: traveled approximately 2.05 times faster than average speeds to these resources; medium-preference: traveled 1.45 times faster than average speeds to these resources; low-preference: traveled only .88 times as fast as average speeds to these resources; Table 5.5). The difference between high and medium-preference speed ratios approached significance (Mann-Whitney z = -1.988, $z_{crit} = \pm 2.394$), but the others did not (high vs. low: Mann-Whitney z = -1.427, ns; medium vs. low: Mann-Whitney z = -.075, ns).

5.4.7 Summary of Directed Travel

In conclusion, inter-resource directness ratios significantly increased when a feeding tree was being revisited, but significantly decreased in the following circumstances: 1) during ITEs, 2) when the sakis rested for longer than 30 minutes en route to the next resource, 2) when the sakis were within 40-49 m of the forest edge in the southern portion of their range, and 4) when I had switch focals in between visits to resources. Surprisingly, there were no significant differences in travel linearity between the three preference categories (high, medium, and low), either before or after I excluded cases that caused a significant increase or decrease in directness ratios. In fact, the sakis actually moved in slightly more linear paths towards low-preference food sources than either medium- or high-preference food sources. On the other hand, the results of comparisons of speed ratios among the three preference category matched expected trends, with the sakis traveling faster to more preferred food sources than to less preferred food sources. However, results approached significance only for the high- vs. medium-preference comparison. Finally, results showed that the sakis traveled significantly farther than expected when all directness ratios for the study period were compared to a fairly linear directness ratio of .90 (meaning that, on average, the sakis traveled significantly farther than 10% over straight-line distances from resource to resource).

5.5 Revisited Feeding Tree Predictions

Forty different feeding trees were used more than once during the study period. Once leaves were excluded from the analysis, a total of 34 trees were revisited. On average, each revisited tree was used 2.48 times, with a minimum of twice and maximum of seven times (seven visits to a *Bellucia* feeding site). Revisits occurred roughly every 6.95 days, with a minimum of half a day in between visits and a maximum of thirty days in between visits. The amount of time that passed in between visits to high-ranking species was less than the amount of time that passed in between visits to medium or low-ranked species (high-ranked trees = reused an average of every 5.57 days; medium-ranked trees = reused an average of every 12.0 days; low-ranked trees = reused an average of every 23.5 day).

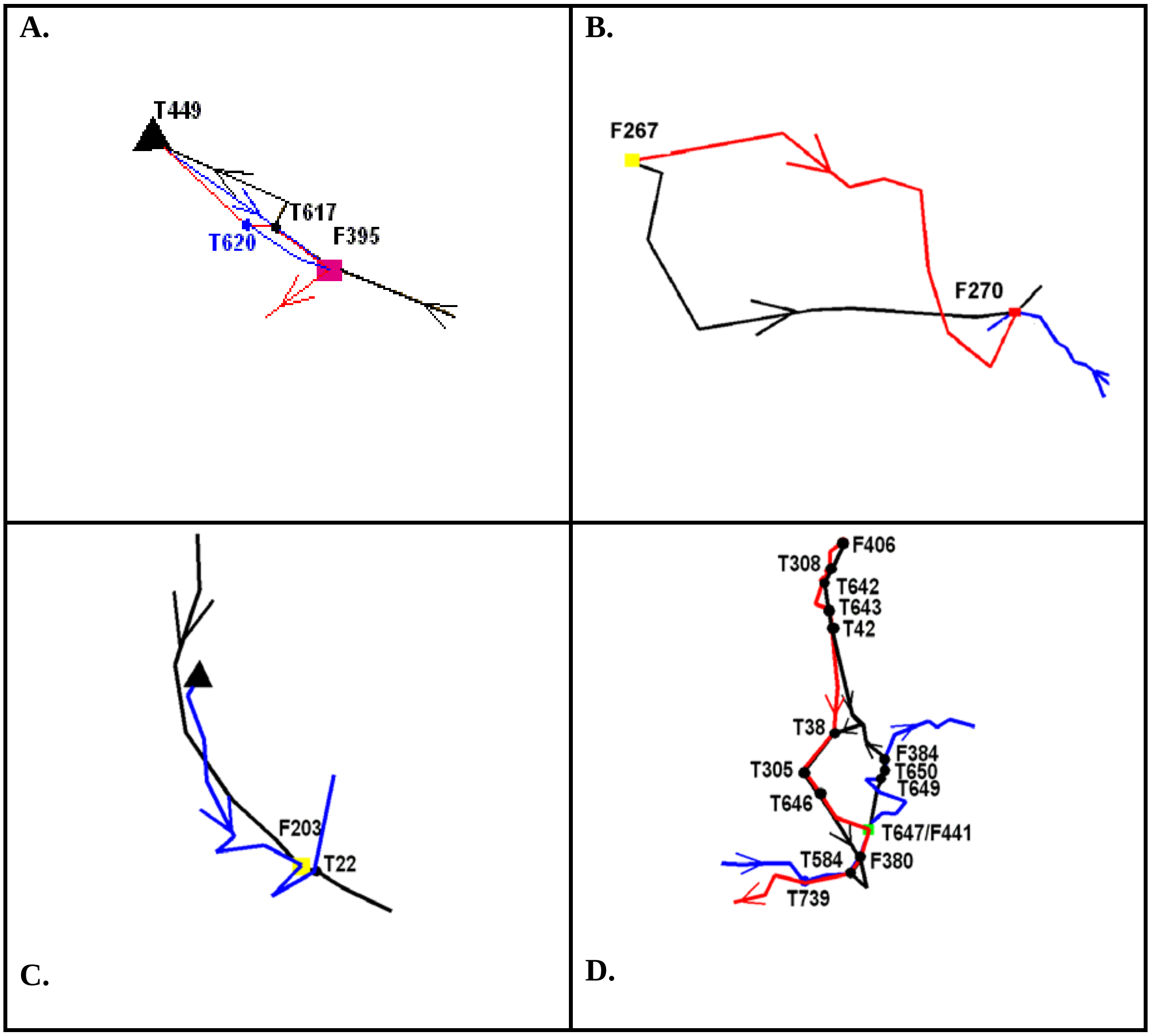
These reused trees were of 14 different identified species (out of the 31 total identified species for the study period). Of the 34 reused trees, significantly more were of a high-ranked (18/34) or a medium-ranked species (14/34), and significantly less were of a low ranked species (2/34) than was expected based on the number of plant species that comprised each of the three preference rank categories ($\chi 2 = 45.40$, $p < .0005$).

Seeds (exclusive of the mesocarp or any other part of the fruit) were the plant part of choice for these reuse episodes, comprising 71.3% of the 937 feeding minutes devoted to revisited trees. Based on a Chi-square test, where the number of observed feeding minutes for each of six plant part categories (excluding leaves once again) were compared to their expected contributions to feeding time, seeds contributed significantly more minutes than expected, while fruit pulp and flowers contributed significantly less than expected (mesocarp + seeds, exocarp, and seed coats contributed roughly the expected amount; Chi square = 154.54, $p < .05$).

In examining path use to revisited trees, I concluded that the sakis were very capable of arriving at distant feeding trees from many starting points and directions, although, on occasion, they chose to (or the terrain required) reuse roughly the same path to reach a particular feeding tree. Out of 69 occasions when the sakis could have taken the same path to arrive at a site, roughly the same path was used on only 7 (10.1%) of those occasions. Examples of sequential reuse of paths are shown in Fig. 5.12, A & D. As is depicted in Fig. 5.12 A, on the sakis' second visit to feeding tree F395, they left their sleeping site in the morning (which was 62 m away from F395), and followed roughly the same path (one travel tree in common, T617) that they used on the previous day after leaving F395; then six days later, after reusing the same sleeping site, they travel along roughly the same route used on the previous two occasions (two travel trees in common among the three days, T617 & T620) to visit F395 once more.

Another example of path reuse is shown in Fig. 5.12 D: the sakis took a roundabout route to reach F441 on the first visit; then on the third visit they followed nearly the same route (eight travel trees in common between two routes) from a point 100 m away from the target feeding tree. (On the second visit, the sakis did not use the same starting point, as in the three cases mentioned above, nor do they come from the same direction to arrive at F441. While they did pass through two trees used on the first visit to F441, these trees were very

Fig. 5.12 Examples of routes taken to feeding trees visited more than once. Black lines represent routes used on the first visits, blue lines represent routes used on 2^{nd} visits, and red lines represent routes used on the third visits. Revisited feeding tree location represented by squares. Only trees that were used on more than one occasion on the routes to the feeding trees are depicted here.



A. On the sakis' first visit to F395 (black path), they travel SE to NW through F395, then T617, and finally to SS T449. The next morning, the sakis' nearly retrace their path from the previous afternoon backwards, passing through T617 on their way to F395, and through T620 after leaving F395 (blue path). Six days later, after reusing SS T449 (62 m away from the target feeding site), they travel along roughly the same route used on the other two occasions (two travel trees in common, T617 & T620) to visit F395 once more (red path).

B. On the sakis' first visit to F270 (black path), they traveled through F267 (a straight-line distance of 162 m away from F270), taking a fairly indirect path to the target feeding site (feeding along the way). On the second visit to F270 (blue path), they came from a totally different direction to reach this feeding site. On the third visit (red path), the sakis again traveled through F267, at which point they drastically change their trajectory and eventually arrived at F270. However, between F267 and F270, totally different travel trees were used and a totally different path was taken. Therefore, at the most, F267 was just an orienting landmark for them on the first and third visit.

C. On the two visits to F203, the sakis come from nearly the same direction and their paths are fairly close to one another; however, but there are no travel trees are shared between the two paths.

D. On the sakis first visit to F441 (black path), they take a roundabout route, starting at F406 (a straight-line distance of 100 m away from F441) and heading S until they reach the southernmost point on their path, at which point they head N towards F441. On the second visit (blue path), the sakis come from a totally different distant starting point SW of this picture, passing through two points used on the first visit; however, these two points are very close to the target tree (< 25m away), and therefore do not qualify as starting points used by the sakis for purposes of finding their way to the F441. On the third visit to F441 (red path), the sakis follow nearly the same route used on their first visit (eight travel trees in common between two routes), except that the loop is not traversed on this occasion (i.e. a more direct route is taken from F406 to F441).

close to the target tree (< 25 m away), and, therefore, did not qualify as distant starting points used by the sakis for purposes of finding their way to the target tree).

In nine cases (out of 69), it is possible that the sakis reused distant travel or feeding trees as a landmarks (or orienting points) to guide them to revisited feeding trees; however, even if these faraway trees were used as guides to lead them in the right direction to a favored feeding tree, once the sakis were on the right trajectory, they did not follow that same paths used previously to reach the feeding trees. A good example of this situation is shown in Fig. 5.12 B: on the second visit to F270, the sakis again traveled through F267 (162 m away from the target feeding tree), as they had on the first visit, at which point, they drastically changed their trajectory and eventually arrived at F270; however, between F267 and F270, totally different travel trees were used and a totally different path was taken.

On one occasion (out of 69), depicted in Fig. 5.12 C, the sakis came from nearly the same direction as on the previous visit to a feeding site (F203). However, there were no travel trees in common between the two days, even though the paths were fairly close to one another at some locations and even crossed each other at one point. Therefore, while some distant landmark (other than a flagged tree from my study) may have been used to orient the sakis towards F203 on both occasions, they were still able take different routes to reach this feeding tree.

In conclusion, the sakis used similar paths, similar directions of arrival, or the same landmarks to reach favored feeding trees on only 17 out of 69 occasions (25%). However, in only seven instances can it be said definitively that they used the same starting point and roughly the same path to find their way to a target feeding tree. Conversely, on 52 of the 69 occasions (75%) for which the sakis could have used the same route to reach a target feeding tree, they came from totally different starting points and totally different directions. After excluding cases that significantly raised or lowered DRs (ITEs, forest edge cases, switching focals, cases with resting bouts en route to resources: 18 excluded cases), the median directness ratio to revisited feeding trees was .905 ($n = 34$), meaning that, on average, the sakis only traveled 9.5% farther than perfect straight-line distances to reused feeding trees. In fact, the sakis traveled in significantly straighter paths to revisited feeding sites than to all non-revisited feeding sites (Wilcoxon Signed Rank $z = -2.432$, $p < .05$). Therefore, the sakis were able to travel in fairly "directed paths to distant resources from many starting points" (Janson and Byrne, 2007), which is a finding that substantiates goal-directed foraging.

The sakis visited significantly more high and medium-ranked species and significantly more seed sources during feeding tree reuse episodes than would have been expected, implying that repeated visits to feeding trees were based on purposeful choices, not on random encounters.

5.6 Nearest-Neighbor Sleeping Site Prediction

The sakis appeared to select from a limited and predictable pool of sleeping sites. Out of 31 occasions for which sleeping tree data were available, the sakis used only 23 different sites, meaning that 5 sleeping sites were used on multiple occasions (sites reused anywhere from 2 to 5 nights, average = 2.6 nights per reused sleeping site). All of the trees chosen as sleeping sites were tall (all above 20 m), with proportionally long and narrow crowns (all crowns appeared to comprise more than half of the total tree height; all crown breadths under 5m). However, the most conspicuous features uniting all sleeping trees were dense tree foliage and the presence of at least some vine tangles.

For the most part, the sakis chose the sleeping tree that was closest to their final feeding site for the day (65% of cases, n = 23 occasions for which I could identify both the last feeding tree and the chosen sleeping site for that night). There were eight occasions when the sakis chose to travel to a sleeping tree that was farther away from their final feeding tree than an alternative sleeping site; however, in 50% of these cases, the sleeping tree that they chose was only 2-5 m farther away than the closer sleeping tree (mean = 3.25 m).

On four of the eight occasions when the sakis chose to travel to a more distant sleeping site (traveled an average of 9 m farther than if they had visited the closer SS), the chosen sleeping site was substantially closer to the first feeding tree the following morning (an average of 61.3 m closer). On another afternoon when the sakis chose a more distant sleeping site, they bypassed the closer sleeping site in the midst of an ITE in the AKP Group overlap zone.

Based upon distances to the final feeding tree of the night and the first feeding tree the following morning, on only one occasion, the sakis would have been better off in terms of distance-minimization to choose the bypassed sleeping site rather than the one they ended up at. For the final two occasions when the sakis chose to sleep in more distant trees, feeding tree data were not available for the mornings following the sleeping site choices.

In summary, the sakis did make economical decisions concerning their sleeping site choices. In 65% of cases, the sakis chose the closest sleeping site available to them after leaving their final feeding tree for the day. In an additional 17% of cases, they chose a sleeping site that was closest to the first feeding tree the following day, even though this meant that they had to travel slightly farther (mean = 9 m farther) after leaving their final feeding tree of the day in question.

5.7 Orientation and Navigation By Use of Landmarks and Arboreal Pathways

One-hundred and thirty 50 x 50 m quadrats were entered by the sakis during the study period. Just thirty-eight of these (< 30%) contained the majority of trees (95%) from the high-preference plant species category. With the exception of one quadrat, each high-ranked feeding tree quadrat was immediately adjacent to at least one other other high-ranked feeding tree quadrat. In other words, quadrats containing high-ranked feeding trees were found in clusters (called "major feeding areas"), rather than being randomly or evenly dispersed throughout the saki's home range (Fig. 5.13, major feeding area number 9 was the exception to the rule). Considering that each major feeding area was densely packed with many high-ranked feeding trees, these areas were probably very important to the sakis; subsequently, any aids that would help guide the sakis from one feeding area to the next would probably be highly valued.

Of the one-hundred and thirty quadrats entered by the sakis in their home range, 55.4% had at least one sharp turning angle (where a "sharp turning angle" is defined as one that is greater than 90°; Fig. 5.14). For fifty-eight of these cases (44.6% of all sharp turning angle quadrats examined), the percentage of sharp turning angles to the total number of turning angles in a quadrat was relatively low (between 0 and 15%- 16 quadrats, between 16% and 30%- 30 quadrats, between 31% and 45%- 12 quadrats; Fig. 5.15 A). Of the fourteen quadrats where at least 50% of all angles were greater than 90° (100%- four quadrats, between 65% and 80%- five quadrats, between 50% and 65%- five quadrats), eight (57.1%) were on the border of their home range (Fig. 5.15 A). The existence of sharp turning angles on the border of the sakis' home range can most likely be explained by the fact that these were turn-around zones for the monkeys (recall that 9.3% of backtracking episodes occurred near the forest edge in the southern portion of their home range and that directness ratios were significantly lower than average when sakis were within 40-49 m of this border). In other words, sharp turning angles on the border probably do not indicate orientation by use of landmarks in the sense that the sakis are not using range “edges” to help them find their way to major feeding areas or other important resources.

Excluding the eight border cases, six quadrats remain where more than half of all turning angles within them are greater than 90°. None of these quadrats were locations of ITEs (see Fig. 5.15 A), which has been put forth as another likely cause for location-dependent backtracking. Five of these six quadrats are located in between major feeding areas (see Fig. 5.15 A). While the existence of said landmarks is speculative, landmarks within these quadrats could have been used by the sakis as orientation tools to lead them to and from major feeding areas.

Possible routes among major feeding areas and potential landmark quadrats are explored in Fig. 5.15 B. Depending on 1) visibility of landmarks from some locations, and 2) interest on the part of the sakis in visiting intermediate feeding areas en route, several potential routes exist between each major feeding area: for instance, in moving from area A to G, the sakis could follow A→1→ 2 →3→ 4 → G, A→ 2→ 3→ 4 →G, A→ 1→ B→ 4 →G, A→ 1→ 4→G, etc.; and in moving from area C to D, the sakis could follow C→ 5 →4→ 3→ D, C→ 4 →3→ D, C →3→ D, C→ 5 →3 →D, C →5→ H →4 →3→ D, etc.. As can be seen in Fig. 5.15 B, reorienting from one landmark to the next would often involve changes in trajectory of at least 90°, which would explain the high incidence of sharp turning angles in these quadrats.

Assuming for the time being that 1) the quadrats containing the highest percentage of sharp turning angles do in fact have prominent landmarks used for orienting purposes by the sakis, and 2) the major feeding areas identified earlier are, in fact, important target sites for the sakis, the most simplistic means of travel between these landmarks quadrats and major feeding areas would be to use reliable and well-established arboreal pathways. In order to determine if any commonly used routes occurred in between landmarks and major feeding areas (as depicted in Fig. 5.15 B), I first had to assess whether or not any reused routes qualified as arboreal pathways (i.e. to qualify, paths had to be within 20 m of each other for a distance of at least 25 m for at least two study days).

In analyzing all routes with overlapping segments, I identified twenty-eight paths that were within 20 m of each other for at least 25 m (Table 5.6). However, sixteen of these were just shorter or longer versions of pathways used on other days. For instance, on both July 16th and 25th, the sakis used very similar pathways that had eleven trees in common between them; the pathways converged for a distance of 156 m and were only 12 m away from each other at the widest point (see Table 5.6, entry number four). On June 6th, the sakis traveled along a 45 m-long segment of this same pathway and on June 19th they traveled along a 123 m-long segment of this same pathway. Therefore, while the sakis only used portions of this arboreal pathway on any pair of days, they were still using the same general pathway in each instance. There are three additional pathways on which the sakis converged for various distances for at least a three-day period (see Table 5.6, entries 6-16).

Therefore, taking into consideration these convergences, the sakis really only used sixteen completely different arboreal pathways throughout the study period. When I investigated where these pathways were in relation to the landmark quadrats and major feeding areas (Fig. 5.15 A & B), 5 out of 16 (31.3%) were consistent with use of arboreal pathways for traveling among these landmarks and feeding areas. For instance, the arboreal pathway used on June 6th, June 19th, July 16th and July 25th (entry #'s 1-5 in Table 5.6) was located in between landmark # 4 and feeding area F in Fig. 5.15 B. Similarly, the arboreal pathway used on June 15th and 22nd (entry # 20 in Table 5.6) was located in between landmark #2 and feeding area D in Fig. 5.15 B. Therefore, it appears that the sakis were using these two pathways (and three others not described) as predictable routes to find their way from orienting landmarks to fairly distant feeding areas. However, the eleven remaining arboreal pathways were either located completely within major feeding areas (six cases) or between adjacent feeding areas (five cases; for instance, between feeding areas E & F or between areas F & G, see Fig. 5.15 B). While it possible that the sakis rely upon arboreal pathways to travel relatively short distances between feeding trees or between adjacent feeding areas, other evidence suggests that the sakis are at least capable of locating important sites using a variety of different routes (see Results, section 5.5).

Another possibility is that the sakis use arboreal pathways to cross the fairly ubiquitous roadways and trails that run through their home range. Considering that the roads (AKP & MW) and certain trails (BT & RFS) in this study group's home range are approximately the width of a two-lane roadway, there may only be certain trees bordering them that provide suitable enough supports for safe crossing. Of the sixteen distinct arboreal pathways identified in this study, eight of them (50%) crossed major roadways or trails in the sakis' range (Table 5.6).

In summary, a relatively small number of 50 x 50 m quadrats (38 out of 130 available quadrats in the sakis' home range) contained the majority (95%) of feeding trees from the high-preference species category. These quadrats existed in tight clusters (9 in all) and thus may have been important feeding areas for the sakis as they were comprised of relatively densely packed feeding trees that constituted the bulk of the sakis diet. Six 50 by 50 m quadrats may have housed important orienting landmarks, since 1) each of them were sites of a relatively high percentage of sharp turning angles (at least 50% of all turning angles in these quadrats were greater than 90°), and 2) other explanations for location-dependent episodes of sharp turning angles (i.e. sites of ITEs or were near the border of their home range) were excluded as possibilities for these quadrats. Hypothetically, the sakis could use arboreal pathways to travel between these landmark quadrats and the major feeding areas identified above.

Twenty-eight repeatedly used path segments (all longer than 25 m), comprising 16 different arboreal pathways, were identified for the study period. Fifty percent of these arboreal pathways crossed major roads or trails, while thirty-one percent led the sakis either from a major feeding area to a potential landmark quadrat or vice versa.

Fig. 5.13 Major feeding areas within the sakis' home range. Each 50 x 50 m quadrat containing more than one tree of a high-ranked species is depicted in black. Nine different feeding areas, each with contiguous quadrat usage, were identified.

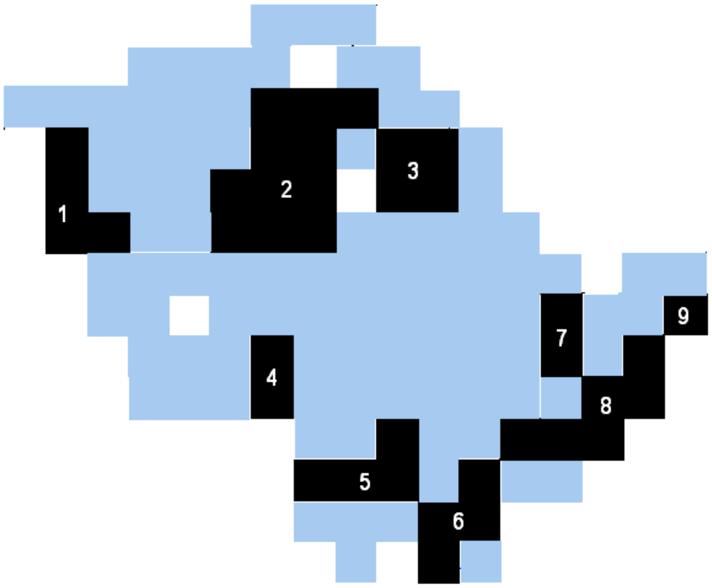


Fig. 5.14 Sharp-turning angle quadrats. The home range was broken into 135 (50 x 50 m) quadrats and the percentage of sharp-turning angles (i.e., those > 90°) compared to the total number of turning angles was computed for each. 44.6% of quadrats had no sharp-turning angles (in red), another 44.6% had a low percentage of sharp-turning angles (< 50 % of all angles in these quadrats were > 90°; in gray), and 10.8 % had a high percentage of sharp-turning angles (> 50% of all angles in these quadrats were > 90°; in blue). Yellow squares indicate that the quadrat was never entered.

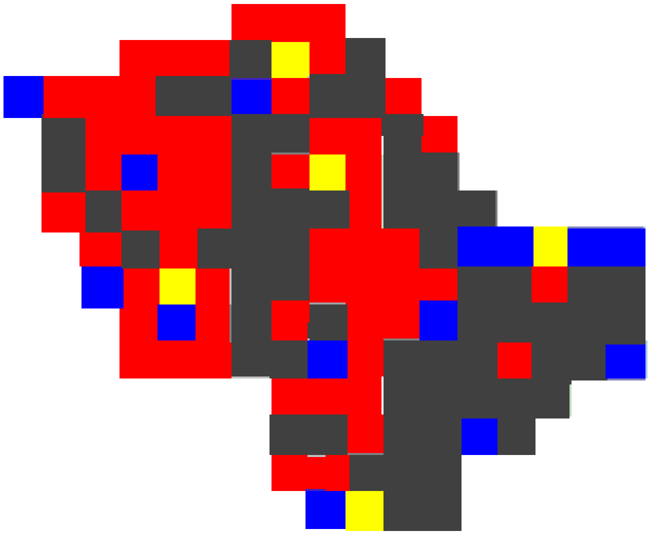
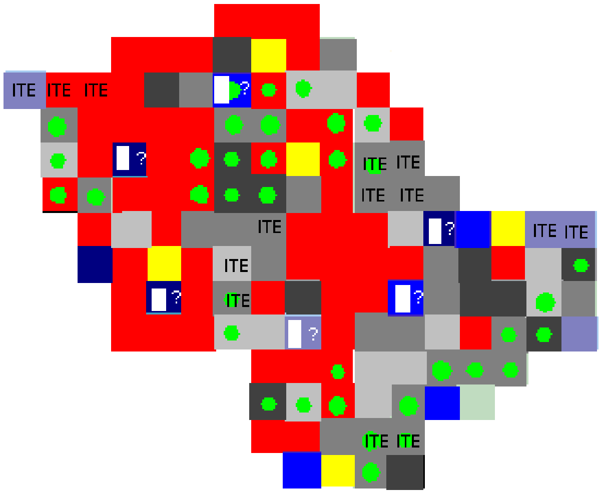


Fig. 5.15 Navigation to major feeding areas by use of landmarks. **A.** Major feeding quadrats represented by green circles. Likely location of orienting quadrats indicated by white rectangles followed by a question mark. Locations of ITEs noted. Red squares represent quadrats containing no sharp turning angles (angles > 90°). Blue squares represent quadrats where less than 50% of all angles were sharp, and gray squares represent quadrats where more than 50% of all angles were sharp. Specifically, dark blue squares indicate that 100% of all angles were sharp; medium blue squares: $80\% > x > 65\%$ of all angles were sharp; light blue: $65\% \geq x > 50\%$; dark gray: $45\% > x > 30\%$; medium gray: $30\% \geq x > 15\%$; light gray: $15\% \geq x > 0\%$. (There were no percentages between 80 and 100, or between 45 and 50). Yellow squares indicate that the quadrat was never entered. **B.** Diagram depicting possible routes to and from major feeding areas (letters A-I) by use of landmarks (numbers 1-5). Sakis could have also used sixth landmark in area B (red dot) in traveling from A to B if they wanted to visit the extreme northern edge of B rather than central or southern portions.

A.



B.

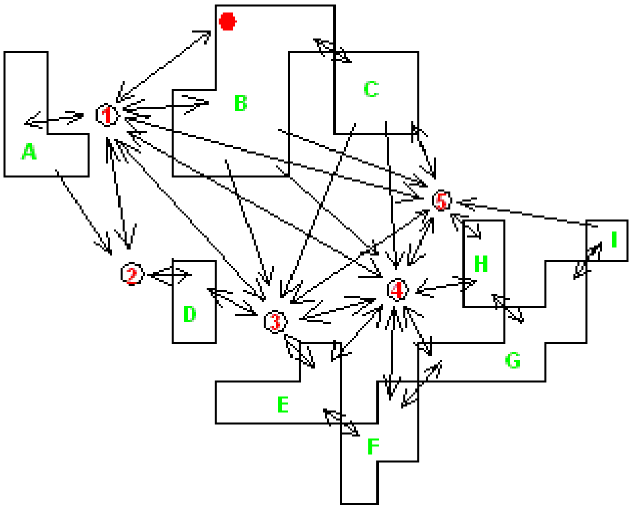


Table 5.6 Description of arboreal pathway use. Only paths over 25 m in length were analyzed. Total straight-line length and width of paths noted, as well as trees in common to pathways, and road and trail crossings intersecting or within 25 m of pathways. Feeding trees and sleeping sites in common to pathways are denoted by letters F and SS, respectively (if no letter proceeds the tree number, tree was just used for traveling or resting). Some paths converge at certain points across more than the two days noted; trees in common among those pathways are similarly identified by either boldface type, italics, underlining, or boldface parentheses.

Dates Used	Length	Width	Trees in common to pathways	Road/Trail crossings
1. 6/6 & 7/16	45 m	20 m	**38**, **42**, 43	cross AKP & BT in btwn 38 & 42
2. 6/6 & 7/25	45 m	15 m	**38**, **40, 42**	cross AKP in btwn 38 & 40, cross BT in btwn 40 & 42
3. 6/19 & 7/25	123 m	11 m	**305**, 306, **40**, **308**	cross BT in btwn 305 & 306, cross AKP in btwn 40 & 308
4. 7/16 & 7/25	156 m	12 m	F406, **308**, 642, 643, **42, 38**, **305**, 646, F441, ***F380, 584***	cross AKP in btwn 42 & 38, cross BT in btwn 38 & 305, cross BT again in btwn 646 & F441 and F380 & 584
5. 6/19 & 7/16	75 m	15 m	**305**, 281, **308**	cross BT twice in btwn 305 & 281, cross AKP in btwn 281 & 308
6. 7/11 & 7/25	35 m	15 m	*F380, 584*	cross BT in btwn F380 & 584
7. 7/23 & 7/25	48 m	16 m	739, *584, F380, F441*	cross BT 3 x's in btwn F380 & 584 (moving back & forth repeatedly)
8. 7/16 & 7/23	50 m	10 m	*584, F380, F441, F384*	cross BT in btwn F380 & 584
9. 7/11 & 7/23	215 m	30 m	*584, F380*, 597, *F384*, 598, 413, 412, 599, 601, F387, F388	cross BT in btwn 584 & F380, cross AKP in btwn 412 & 599, cross AKP in btwn F387 & F388
10. 7/11 & 7/16	50 m	8 m	*F384*	cross BT in btwn start and F384
11. 7/11 & 7/12	90 m	40 m	SS449, 617, F395, 605	cross RW in btwn F395 & 605
12. 7/11 & 7/18	65 m	8 m	SS449, 617, F395	none
13. 7/12 & 7/18	65 m	5 m	SS449, 620, 617, F395	none

14. 6/22 & 7/9	65 m	10 m	325, 326, **(**F327**)**	none (pathway 12 m east of AKP)
15. 6/22 & 7/8	40 m	20 m	**(**F327)	cross AKP in btwn path start & 327
16. 7/8 & 7/9	40 m	10 m	**(**F327**),** SS497	cross AKP in btwn 327 & SS497
17. 6/7 & 7/25	70 m	27 m	SS47	none
18. 7/22 & 7/25	76 m	20 m	730, 733, 734, F460	cross RFS in btwn 734 & F460
19. 6/21 & 7/10	62 m	15 m	F273, 313	none (pathway 2 m east of RFS)
20. 6/15 & 6/22	175 m	45 m	F267, F270	cross MW in btwn F267 & F270
21. 6/26 & 6/28	45 m	5 m	360, F310, 361, 362	none
22. 6/28 & 7/12	35 m	10 m	F332, F331, F330	none (in very tight cluster of *Paus*. trees in Rocky's garden)
23. 6/19 & 7/22	70 m	25 m	293, 299	cross RFS in btwn 293 & 299
24. 7/8 & 7/10	65 m	15 m	F375, F352	cross MW in btwn F375 & F352
25. 7/17 & 7/18	40 m	20 m	F420, 695	none
26. 7/12 & 7/23	50 m	15 m	F399, F400, 630, F331	none (in very tight cluster of *Paus*. trees in Rocky's garden)
27. 6/6 & 7/25	30 m	10 m	25, 32	None
28. 6/19 & 7/25	120 m	20 m	288, 289, 290, 292	none (pathway 25 m south of AKP crossing)

CHAPTER 6

DISCUSSION

6.1 Area Usage and Ranging Patterns

6.1.1 Comparisons of Daily Path Lengths and Core Area Size Among Saki Populations

Due to aforementioned small, but cumulative, inaccuracies in pedometer readings and the short duration of the study period (N = 30 days), approximations of daily path lengths for the study group are most likely underestimates (estimate from complete day follows = 587.4 m; estimate from entire study period = 570.0 m), as daily path lengths from long-term studies averaged 1,500 m (Norconk, 2007) and 1,772 m (Cunningham and Janson, 2007) for saki groups in Venezuela, and 1,880 m for groups in French Guiana (Vié et al., 2001). Smaller daily path lengths have been reported (300-500 m, Oliveira et al., 1985; < 1000 m, Kinzey, 1997), but these estimates are based on data from much shorter study periods.

My estimate of core area size (15.04 ha) for white-faced sakis is comparable to estimates that come from studies that also used the minimum convex polygon method to compute this figure (10.3 ha for a *P. pithecia* group in Suriname, Norconk et al., 2003 and 12.8 ha for *P. pithecia* group in Venezuela, Norconk, 2007). However, to my knowledge, no published study to date has distinguished between the area of most intense usage (core area) and the area of maximum usage (home range) for white-faced sakis; therefore, I have no point of comparison for my home range estimate of 25.15 ha. Yet, estimates of home range boundary points at trail and road crossings from a year prior to my study (Thompson, personal communication) were identical to mine; thus, I feel that I obtained a fairly strong estimate of long-term home range extent for this study group.

6.1.2 The Importance of Monitoring Range Boundaries and Potential Food Sources: Effects on Straight-Line Travel

Ranging behavior and small-scale movements can be influenced by many factors, including the distribution and abundance of food trees (Clutton-Brock, 1975; Bennet, 1986), phenology (Stanford, 1991), body size (Terborgh, 1983), group size, location of sleeping sites (Davies, 1984; Chapman, 1989), group movements on previous days (Peres, 2000; Cunningham, 2003), weather conditions, interactions between conspecific groups (Peres, 2000; Price and Piedade, 2001), and the need to monitor both the status of potential food sources and territorial boundaries (Whitten, 1982; Peres, 2000). When discussing ranging patterns and area usage, researchers often emphasize correlations between the distribution of the most eaten food sources and quadrat use (Clutton-Brock, 1975; Whitten, 1982). While the distribution of the more frequented feeding trees did match up with the areas of most intense usage (core areas) and helped explain the sakis' trajectories on many occasions, the locations of feeding sites were not the only factor influencing direction of travel from minute to minute and movements patterns on a daily scale. At times, the sakis' movements seemed to have more to do with maintenance of territorial boundaries and monitoring potential feeding sources than current feeding activities.

The monitoring and maintenance of home range boundaries constituted core daily activities for the sakis. The focal group visited the edges in at least some region of their home range once or more a day during the study period, with few exceptions (at the edge 63% of all observation days; 10-60 m from the edge the remaining 37% of observation days; see Fig. 5.3 and Appendix B for the sakis' proximity to home range boundaries each day of the study period). Further, the high frequency of ITEs and inter-group Z trilling episodes indicates that attempting to maintain an of area of exclusive use is important to the sakis (ITEs occurred approximately 1.4 days per week and inter-group Z trilling episodes occurred an additional 2.6 days per week).

Moreover, the study group spent a generous amount time in at least two areas shared with competing groups, namely the MT Group overlap zone and the overlap zone with Junco's group. In fact, these two overlap zones housed many of the feeding trees that made up the bulk of the sakis' diet (portions of major feeding areas E, F, G, H, and I were located within these zones, compare Fig. 5.1 and Fig. 5.14). In addition, 34.8% of the study group's sleeping sites were located within overlap zones and 41.9% of all of their nights were spent in these zones, which is an uncommon penchant for a territorial primate (Whitten, 1982; Day and Elwood, 1999; Peres, 2000). Positioning sleeping sites near boundaries could be very beneficial to the sakis, as this behavior would facilitate early detection of incursions by competing groups.

In addition to investing time and energy in monitoring overlap zones and in boundary contests with neighboring groups, observations also indicated that the sakis were interested in monitoring the status of potential feeding resources throughout their home range. During the study period, "sampling" occurred nearly every day (and on occasion, more than five times in a day) and the sakis tended to cover different regions of their home range every day, with few exceptions (i.e. when ephemerally present and seemingly preferred fruiting trees were producing).

If the sakis' daily routes are viewed at close range (for instance, see Appendix B.2, the path in between F207 and T47; B.6, the path in between F243 and F244; B.23, the path in between F385 and F386; B.31, the path between F406 and F380), it is obvious that some of their inter-resource paths were more zig-zagged than straight or curved to one direction or the other. If an animal was interested in tracking the status of potential feeding sites en route to known sites, it would obtain the most representative picture of the area it was traveling through by traveling back and forth in a zig-zagged pattern, which is exactly how wild chacma baboons travel during late afternoon sampling excursions (Noser and Byrne, 2007b). Therefore, zig-zagged, and thus, non-linear, movements by the study group could partially be explained by their interest in tracking the phenological status of future food sources.

However on a broader time scale (i.e. over an entire day rather than in between each feeding site throughout the day), the majority of the sakis' daily routes tended to curve in on themselves rather than zig-zag. The C-shaped configuration of their daily travel routes could be explained by their focus on monitoring home range edges. It seems reasonable that the best way to monitor a home range with a curved perimeter is to curve slightly throughout the day, thus, following the edges of the range. Conversely, a perfect straight-line bearing near a curved edge would bring an animal in close contact with this boundary only once or twice per day. In 78.6% of the instances when the sakis daily route took on a C-shaped configuration, the sakis were in fact hugging their home range edge for a substantial portion of their day.

Curvatures in daily paths when far removed from curved home range edges are harder to explain, but may have something to do with travel inertia. Travel inertia is the tendency to keep moving in the same direction or at the same velocity even when the context no longer requires it

(Janson, 2000). This tendency is posited as an explanation for consistent straight-line movements in flocks of finches (Cody, 1971). On the other hand, since individual trees of many different plant species (namely those of wind- or explosively-dispersed species) occur in aggregations (Hubbell, 1979; Milton, 1981; Terborgh, 1992; Condit et al., 2000), slight curvatures in daily paths may help the sakis locate additional sources of synchronously fruiting species once they have found one source of that species.

Overall, the sakis appear to base ranging decisions not only on immediate dietary requirements, but also on the need to uniformly monitor 1) various segments of their range boundaries in order to keep track of the activities of neighboring groups, and 2) various regions of their supplying area in order to examine the status of potential feeding sources. Both of these behaviors help to explain why sakis diverge from perfect straight-line travel when moving between feeding and sleeping sites and on the scale of an entire day.

6.2 Comparisons of the Study Group's Diet With a Venezuelan Population

The sakis consume foods from a diverse array of plant species, from a variety of developmental stages, and from all three plant phenophases (i.e. fruiting, flowering, and flushing). During the study, the sakis ate leaves (from buds to mature leaves, and only a petiole on one occasion), flowers (usually buds, on one occasion, mature), the pulp of fleshy fruits, and seeds from fruits with hard pericarps (presumably, both ripe and unripe). During the 30 days of focal-animal follows, the sakis took resources from at least 30 different plant species. Data from long-term feeding ecology studies suggest that primates may take foods from over 50 species (Oates, 1987), and even up 150 species for some populations (Milton, 1981).

When compared to the most intensively studied white-faced saki population to date (on Redonda Island in Lake Guri, Venezuela; Kinzey and Norconk, 1993; Norconk, 1996; Cunningham, 2003; Norconk and Conklin-Brittain, 2004; Cunningham and Janson, 2007), the current study group in Brownsberg Nature Park, Suriname, is similar in terms of number of feeding bouts per day, length of feeding bouts, distances traveled between successive food sources, the tendency to discard certain parts of fruits, and their preference for the fruiting phenophase of plants, namely the seeds of the those fruits. On the other hand, they diverge from the Venezuelan sakis in relation to the specific plant families and species that make up the bulk of their diets.

While the plant families Capparidaceae, Connaraceae, Chrysobalanaceae, Erythroxylaceae, Lecythidaceae, Loganiaceae, Leguminosae, and Rubiaceae dominated feeding time for the Venezuelan sakis (Cunningham, 2003; Kinzey and Norconk, 2003; Norconk, 2006; Cunningham and Janson, 2007; Homburg, 1997), the plant families Araceae, Euphorbiaceae, and Sapindaceae, took precedence during the short study period in Suriname (each of these families contributed greater than 13% to the total feeding time). In fact, only two plant families from the list above were part of the study group’s diet (Lecythidaceae and Rubiaceae), and these together contributed very little to the sakis overall diet (accounted for only 4.2% of feeding time).

The most popular genus in both Kinzey and Norconk (2003) and Cunningham’s (2003) studies, *Licania,* was noted as one of the most abundant genera on the Venezuelan island (Cunningham, 2003). This genus did not appear on the consumption list for the Brownsberg study group. Euphorbiaceae, which is one of the most abundant plant families in the Brownsberg (in terms of number of individuals per hectare, ter Steege et al., 2004) and one of the most commonly exploited families by primate seed predators (Norconk, in press), ranked second (after Araceae) for total number of feeding minutes in the current study. While it is possible that differences in the most consumed plant families for Venezuelan and Surinamese white-faced sakis reflect differences in preferences between these two populations, it is more likely that these differences simply reflect variation in type and availability of plant families in two very distant and presumably distinct habitats.

The group under investigation converges with other white-faced sakis in various aspects of feeding ecology. All observed populations of white-faced sakis prefer fruits over any other plant part available to them: 79.8% of the study group's feeding time was spent on fruits, which is very similar to figures noted by Cunningham (2003; from 63-86% of feeding time across both wet and dry seasons) and Kinzey and Norconk (2003; 85% of monthly feeding time). Specifically, white-faced sakis prefer the seeds of fruits: in this study, 84.7% of fruit-eating time included seeds eaten with or without mesocarp, and in Kinzey and Norconk's (2003) study, 95-99% of fruit-eaten time was spent on seed consumption. Exclusive seed-eating accounted for 47.7% of total feeding time in the current study and 38-88% feeding time during any month in Kinzey and Norconk's (1993) study.

Selective consumption of different fruit parts and different leaf maturity levels appears to be common in divergent populations of white-faced sakis. Norconk and Conklin-Brittain (2004) note that sakis often discard the exocarp and seed coat before ingesting seeds, and others have observed sakis discarding pulp (usually unripe), seeds, and/or the exocarp in favor of other parts of the fruit (Kinzey and Norconk, 1993; Norconk, 1996; Cunningham, 2003). Similarly, the focal group discarded the exocarp in all but one fruit-eating bout and the seeds every time that they ate *Salacia* and *Diospyros* and some of the time that they ate *Heteropsis* and *Tovomita*. While I had trouble determining whether or not the sakis were discarding seeds coats during fruit-eating bouts, I presume that they were as seed coats can present many mechanical and chemical difficulties to seed predators (Norconk and Conklin-Brittain, 2004; Norconk et al., in press). As at other sites (Kinzey and Norconk, 1993; Kinzey, 1997; Norconk and Conklin-Brittain), the sakis consumed leaves daily, and selected immature over mature ones in trees/lianas where both were available.

Finally, the number of feeding bouts per day (roughly 17.4), as well as distances traveled between feeding/sampling sites (average = 50.0 m), was comparable to figures in Cunningham's study (average # feeding bouts = 25; average distance between feeding sites = 57-63m). In the current study, the majority of feeding bouts were relatively short (48.7% bouts ≤ 5 min. and 70.8% ≤ 10 min.; however, at least once per day (and usually twice per day), the sakis fed in a single tree for at least 20 minutes (average duration of longer bouts = 28.1 min., n = 34 bouts during 21 observation days for which there was sufficient data to assess bout lengths). Similarly, Cunningham (2003) noted that the white-faced sakis occasionally had much longer feeding bouts than usual (duration of longer feeding bouts unknown, but most bouts were under 5 minutes).

Cunningham and Janson (2007) also noted that the majority of these extended feeding bouts took place in highly productive, reused feeding trees of top-ranked species (i.e. in "highly preferred" feeding trees). In the same way, 72.7% of the longer feeding bouts in the current study took place in trees of a high-ranked species (either *Talisia*, *Heteropsis*, *Bellucia*, or *Cheiloclinium*), and 58.8% took place in a revisited feeding tree. These observations lead me to suspect that revisited trees of high-ranked species that boast higher than average feeding times may actually be the most preferred sites for study group. This proposition will be explored further in section 6.4.3.

6.3 Backtracking: Insights Into Spatial Memory and Distance-Minimization

It is not surprising that the study group rarely backtracked (backtracked in only 16% of all observations), as backtracking is deemed necessary and effective only for 1) predators that track or chase mobile prey (Garber, 1987), and 2) foragers that encounter resources that are known to exist in tight clusters (Bell, 1991; Menzel, 1996). In this study, I never observed the sakis chasing or consuming insects; therefore, they would not be expected to backtrack for reason number one. The sakis only exploited one plant species whose constituents existed in tight clusters (i.e. *Pausandra* trees, inter-tree distances usually less than 20m). As expected, the sakis did tend to backtrack once they entered these clusters.

It is also not surprising that the sakis tended towards forward progression, as most goal-directed and even some non-goal directed foragers (under some circumstances) can be expected to travel in relatively straight-lines. For instance, even if a forager does not rely on spatial memory to encounter resources in its environment, straight-line travel could be used as a tool to help it avoid recently-visited sites and/or to help keep the foraging party together (Armstrong et al., 1987; Baum, 1987; Olton et al., 1987; Garber, 1993; Janson, 2000). Furthermore, straight-line travel could just be a natural consequence of following topographical features that tend to exist in straight-lines over long distances (i.e. roadways, streams, ridges, etc.; Menzel, 1996; Di Fiore and Suarez, 2007). On its own, the study group’s tendency to progress from tree to tree in relatively straight lines tells us little about how they find their resources.

Interestingly, their involvement in backtracking episodes may tell us more about their foraging strategy than will their tendency to move in relatively straight lines. To recap, in the majority of backtracking cases, the sakis had been heading in a certain identifiable direction before diverging for an ITE, a feeding tree, a resting site, or to avoid another species; once travel resumed, the sakis usually returned to their pre-divergence path. The interesting part of this behavior is not that they diverged in the first place, but that they usually went back to their former paths (see Fig. 5.9 A, B, C2, and G). If the sakis were simply following the behavioral rule, "always walk in a straight-line", you would expect them to resume their initial bearings without first making any adjustments. As can be seen in the backtracking figures listed above, the sakis did not simply start heading in the same compass direction that they had been heading in pre-divergence; rather, they fully or nearly retraced their steps to arrive back at the approximate pre-divergence location, and, only then, began traveling along the same path. This behavior implies that the sakis needed to get back to the previous path for some reason. The most likely explanation for this requirement is that the sakis navigate in relation to specific landmarks and/or routes, and if orienting routes or landmarks can no longer be seen or are seen from unfamiliar perspectives, the sakis can no longer navigate effectively.

This behavior also implies that the sakis are not capable of navigating according to a Euclidean mental map. If they knew the location of all sites from all starting points in their home range, they would not have to follow certain trajectories, paths, or landmarks to reach resources. This does not indicate that sakis do not have the capacity to locate multiple sites in their range; it only means that rather than memorizing the specific locations of thousands of individual trees, they simply remember the locations of a manageable set of landmarks and/or paths leading to those sites.

Backtracking episodes can also give us hints as to how much emphasis sakis place on distance-minimization. The sakis movements when feeding upon clustered resources (*Pausandra* trees or patches of trees that are producing new leaf flushes) were often erratic, and the sakis did not visit the individuals in these clusters in distance-minimizing sequences. However, inter-tree distances in these clusters are relatively short (< 20 m). Under conditions when the energy to be saved is so minimal, it may do an animal little good to attempt to find the most distance-minimizing route across a set of resources. In other words, there may be certain scales on which travel distances should be minimized (i.e. on large scales: over the course of an entire day; when traveling between major foraging areas; when traveling to another group's territory), and certain scales for which distance-minimization is trivial (i.e. on small scales: when traveling from tree to tree within a small food patch; when backtracking 5-10 m to get back to a known route or landmark).

6.4 Directness of Travel

6.4.1 Straight-Line Travel to the Average Feeding/Sleeping Site: Inferences

When traveling between relatively distant resources (average distance between all feeding sites and all feeding and sleeping sites = 49.65 m; range = 6- 454 m), the sakis did progress through their arboreal landscape in a distance-minimizing fashion. After factoring out the relatively infrequent scenarios (18.7% of all cases) that significantly increased or decreased straight-line travel from site to site (cases involving revisits to feeding sites, ITEs, territorial boundaries, long resting periods, and switching focals), on average (median value), the sakis traveled only 11% farther than perfect straight-line distances to reach feeding or sleeping sites. What this means in terms of actual distances is that if the straight-line distance from one feeding tree to another was 41.5 m, the sakis would travel roughly 46.6 m to get there (46.6 m = average observed travel distance between feeding trees), and if the straight-line distance from an a.m. sleeping site to the first feeding tree of the day was 65.8 m, then the sakis would travel approximately 73.9 m to get there (73.9 m = average observed travel distance between a.m. sleeping sites and the first feeding trees of the day). Considering that I could not account for all of the other natural obstacles that these arboreal primates face during their daily travels (gaps in the canopy, ill-suited supports for clinging and leaping, impractical tree-to-tree passages owing to steep terrain in some parts of range, predation risk in more exposed canopies, already occupied trees), these minor additions to perfectly straight-line distances seem extraordinarily small.

Mean directness ratios for white-faced sakis in Cunningham and Janson’s (2007) study were very similar to DRs obtained for the sakis in my study (Cunningham and Janson’s study: Period 1 = .84, Period 2 = .82; current study: before exclusions = .814, after exclusions = .840). Cunningham and Janson compared the observed DRs for every target distance to a resource to expected DRs for a random forager traveling those same distances (using a computer model developed by Janson, 1998), and concluded that the sakis were traveling in significantly straighter paths than would be expected for a forager traveling totally at random. While specific input values for DRs and distances traveled to resources would have been slightly different had I been able to run the same simulations as Cunningham and Janson, I still expect that I would have obtained very similar results considering that our average DRs were almost identical and that the average distances traveled to resources were very similar (57-63 m in their study and 49.6 m in my study). Of course, to be sure that Brownsberg sakis are traveling in significantly more linear paths than expected by chance (i.e. than expected by random foraging), tests using Janson's model and site-specific DRs and inter-resource distances will have to be conducted in the future.

6.4.2 Redefining Preference

A forager that can recall both the locations and the varying qualities of patchy resources is expected to move towards the more valuable of those resources in more linear paths than the less valuable ones (Garber, 1989; Janson, 1998; Pochron, 2005; Cunningham and Janson, 2007; Janson and Byrne, 2007; Noser and Byrne, 2007). The most valuable plant resources for primates tend to be those that are the most productive, the most predictable in their renewal schedules, the most vital (fallback foods during critical periods or foods that provide essential nutrients or minerals), the most limited, those that provide the greatest rewards per minute of preparation time, and those that are the highest-ranked in terms of feeding minutes. In the current study, I employed the supposition that the plant species with the highest number of feeding minutes were the most valuable or most preferred resources for the sakis.

Contrary to expectations, the sakis did not travel more linearly to high-ranked species than to medium or low-ranked species. There are a few plausible explanations for this result: 1) the sakis have no memory of where feeding sources are in their home range, and, therefore, travel in the same manner to every resource (in fairly linear paths, overall), 2) they know where resources are, but for the most part rank all palatable resources equally (i.e. they have no preferences), or 3) my assessment of which resources should be preferred by the sakis does not reflect their evaluation of what qualifies as preferred. Considering the following, it seems reasonable to exclude the explanation that the study group has no preferences: 1) sakis at other sites show definite preferences for certain fruit taxa, certain parts of fruits, fruits with a particular nutrient makeup, and fruit sources with relatively high productivity scores (Kinzey and Norconk, 1993; Cunningham, 2003; Norconk and Conklin-Brittain, 2004; Cunningham and Janson, 2007; Norconk, 2007); assuming that preferences for foods have a heritable component, the study group should be just as selective; 2) the study group has a tendency to revisit trees primarily of high-ranked species (i.e. they seem to show some sort of preference for these species); 3) the study group has a tendency to discard certain parts of fruits in favor of others (i.e. they seem to have a preference for certain fruit parts and/or particular maturity levels of various fruit parts); and 4) the study group shows a definite preference the less ubiquitous leaf maturity level (i.e. young leaves).

With regards to explanation number one, I have acquired evidence during the course of this study that suggests that the sakis have some idea of where certain resources are located in their range, namely revisited feeding trees and sleeping sites. Specifically, the sakis were able to travel directly to revisited feeding sites from a number of different starting points, and they were capable of locating the closest available sleeping site in relation the their last feeding tree of the day or their first feeding tree the next morning. Therefore, I do not believe that the sakis are simply unable to locate (and travel efficiently towards) favored resources in their range.

I do, however, suspect that my criteria were insufficient to wholly explain white-faced saki preferences. While I labeled any source of a species that was eaten often by the sakis as preferred (“high-preference”), other factors may have weighed in on the sakis’ perception of value. Many researchers have identified productivity as one of the most important variables in determining which specific sites will be selected as destinations by primates (Garber, 1987; 1988; 1989; Andrews, 1988; Garber and Hannon, 1993; Janson, 1998; 2007; Cunningham, 2003; Cunningham and Janson, 2007; Janson and Byrne, 2007). For example, whenever nearest-neighbor trees of particular species were bypassed by tamarins (Garber, 1988; 1989), capuchins (Janson, 1998), and white-faced sakis (Cunningham, 2003; Cunningham and Janson, 2007), these monkeys selected more distant trees that offered much higher mean food rewards than the ones they had passed. Similarly, others have found significant positive relationships between the degree of productivity of plant sources and the degree of linearity in approaches to those sources (Pochron, 2001; 2005; Noser and Byrne, 2007b).

While the six highest-ranked species in the current study were definitely of some importance to the sakis (as these species were responsible for 52% of the feeding minutes for the study period even though they were not necessarily the most prevalent species in the park, and these species were chosen significantly more for revisiting episodes than expected, $\chi2 = 45.40$, $p < .0005$), not every tree of those species may have been preferred. For instance, if certain *Talisia* trees (highest-ranked species in terms of feeding minutes) had only a few fruits on them, they probably would not have been preferred sites for the sakis, and travel to those sites most likely would have involved divergences to explore and feed at intervening sites. On the other hand, some *Talisia* trees may have been highly productive and the sakis, being highly motivated to reach them, may have traveled to these sites using time and distance-minimizing paths. Since I did not have complete data on abundance scores, I had to lump all sources that were of species that accounted for a high proportion of feeding minutes into the same preference category, despite any fruit abundance differences between those sources. In theory, then, the trees belonging to the highest ranked category in this study may have actually been a mixture of high and low preference trees for the sakis, leading to high DRs for some sites and low DRs for others (and, consequently, to unanticipated results). In summary, it is likely that while plant species designation weighed in on the sakis' perception of "value" for each food source, productivity was the formative factor determining whether or not a particular site was highly preferred.

It is also very possible that the sakis preferred some of trees that accounted for a relatively small proportion of total feeding time (i.e. trees of species in my low-ranked preference group, for instance, or "sampled" resources), and, thus, traveled to those more directly. While differences were not significant, the sakis did travel in straighter paths to low-preference trees (median DR = .897) than to either high (median DR = .889) or medium-preference trees (median DR = .871). Furthermore, they traveled in straighter paths to trees that, by definition, accounted for a very small proportion of feeding time (a sampled resource is any resource eaten for less than 1 minute; the median DR for sampled resources was .914, while the median DR for all other feeding sources was only .870).

Many researchers have highlighted the potential importance of feeding sources that animals spend relatively little time on (Freeland and Janzen, 1974; Westoby, 1974; Milton, 1979; Garber, 1988; Terborgh, 1992; Fleagle, 1999; Janson and Chapman, 1999; Di Fiore, 2003; Lambert, 2007). First of all, while fallback foods or "keystone resources" (Terborgh, 1992) may only comprise a small part of a species' annual diet, they can be vitally important during critical periods, limiting populations and exerting strong selective pressures on the morphological and behavioral aspects of an animal's feeding ecology. Therefore, fallback foods are definitely worth traveling to directly in times of relative food scarcity and are probably even worth tracking efficiently in times of relative food abundance.

Some researchers (Chapman et al., 1989; Di Fiore, 2003; Janmaat et al., 2006) have noted that rates of travel and linearity are sometimes more strongly correlated with resources that are simply being monitored for future use than foods that currently account for a large portion of the animal's diet. In other words, in some cases, sampling of potential resources may actually take precedence over current nutritional needs. As mentioned in section 6.1, the sakis did spent a substantial portion of their days sampling resources, and these sampling episodes often resulted in a zig-zagged pattern of travel to other feeding (and sleeping) sites; in this way, monitoring of potential resources did appear to take precedence over efficiency of travel to sites where more immediate nutritional needs could be met.

Finally, most primates have fairly diverse diets because no single plant item can provide them with all of the nutrients and minerals that they need. In fact, it is probable that some of the food items that are often relegated to the "other" food category in feeding budgets (owing to their small contribution to the overall diet) may contain trace minerals, vitamins, or other rare nutritional elements that the animals cannot obtain otherwise (Fleagle, 1999; Lambert, 2007). For instance, Janson and Chapman (1999) postulate that phosphorus may limit folivorous primate populations just as it limits populations of large herbivores. Therefore, some scarcely eaten items may actually be very important to animals and, therefore, more "preferred", than food items that make up the bulk of their diets.

Overall, then, it is possible that some of the low-preference or sampled resources in the current study were actually some of the most preferred items to the sakis, which is why directness ratios were so high for these rarely consumed items. Unfortunately, without more in-depth studies during which 1) chemical and nutritional analyses can be conducted on these rarely consumed items and 2) correlations between sampled items in times of relative food abundance and fallback foods in critical periods can be investigated, these possibilities will remain speculative. Therefore, from this point on, food items previously designated as "low-preference" in this study will left of the analyses.

In studies where correctly identifying an animal's preferred resources is so crucial to the interpretation of the results, exhaustive preliminary evaluations of factors influencing feeding decisions are highly advised. The following questions might help researchers accurately pinpoint an animal's preferences: Do certain resources comprise the bulk of the animal's diet simply because they are readily available in the environment? Are the nutrient and chemical compositions known for the resources that it consumes? That it discards? Can any patterns be gleaned from these considerations? Is there some common quality uniting the resources that it revisits again and again? If most feeding bouts are short and only a few are significantly longer, is there some consistent attribute connecting the resources with the longer feeding bouts? Are any of its resources both vital and limited? Are any of the trees that belong to the highest-ranked species group (ranked in terms of total feeding minutes) exceptionally productive?

6.4.3 Rate of Travel to High–Ranked, Revisited Feeding Sites

If plant species affiliation did not fully explain saki preferences, why then should rate of travel be higher for approaches to "high-preference" species than "medium-preference" species (results of this specific comparison were nearly significant, while no other comparisons among preference categories, either in the linearity or the speed analysis, approached significance)? For the speed prediction, I was assessing speed of approaches to within 30 m of the target feeding trees, meaning that I could only uses cases that had fairly high inter-resource travel lengths. Therefore, I only used a fraction of the cases from each preference group in the speed analyses that I used to evaluate directness ratios (specifically, I used only 27.4% of the high-preference cases, only 22.8% of the medium-preference cases, and only 20.8% of the low-preference cases in the speed analyses).

It turns out that 95% of the feeding sources used in the speed analysis belonged to one of the top four highest ranked species in terms of total feeding minutes, while only 79% of the feeding sources used in the DR analysis belonged to one of these species. Even more significant, it appears that 10 out of 20 (50%) of the high-preference cases that I used for the speed analysis were feeding tree reuse cases (while only 27.7% of all high-preference cases in the directness ratio analysis were reuse cases). As was determined through assessment of contexts that affected DRs, feeding trees used more than once were approached in significantly straighter paths than feeding trees that were only visited once (Wilcoxon ranked sum $z = -2.10$, $p < .05$). So, since I happened to select a subset of high-preference resources that had significantly higher DRs than the average high-preference resource, it is really no surprise that approaches to these resources were significantly faster than approaches to any other resource.

6.4.4 Newly-Defined Preference Groups and the Final Directed Travel Analyses

Overall, I suspect that most revisited feeding trees were, in fact, preferred sites for the sakis, considering that 1) visits to these types of feeding trees lasted much longer than the average feeding bout (70.8% of all feeding/sampling bouts lasted less than 10 min.; average duration of feeding bout at a reused feeding site = 19.41 min.) and 2) a significantly greater proportion of them belonged to species that comprised the bulk of the sakis diet than would have been expected by chance ($\chi 2 = 45.50$, $p < .0005$).

In particular, I believe that revisited feeding trees meeting all of the following criteria may have been the most preferred sites for the sakis: 1) those that were of top four, rather than top five, highest ranked species in terms of feeding minutes (i.e. *Talisia* trees, *Heteropsis* lianas, *Bellucia* trees, *Cheiloclinium* trees), which is a slightly more limiting criterion than was used previously; 2) those in which food was consumed during every visit, a criterion that may serve as a good proxy for the productivity of the feeding site; and 3) those for which the sakis had visited the site at least once previously, a criterion that may serve as a good proxy for the predictability of the feeding site.

I conducted one final set of analyses after 1) excluding all “low-preference” resources for reasons discussed in section 6.4.2, and 2) relegating all feeding sites previously designated as “high-preference" that did not meet the above criteria to the “medium-preference” category. Based on directional tests of hypotheses, the results showed that the sakis did, in fact, travel more linearly (Wilcoxon Signed Rank $z = -1.78$, $p < .05$; median DR to high-preference sites = .952, n = 8; median DR to medium-preference sites = .879, n = 75) and more quickly (Wilcoxon Signed Rank $z = 2.36$, $p < .05$; median speed ratio to high-preference sites = 2.985, n = 8; median speed ratio to medium-preference sites = 1.478, n = 34) to revisited feeding sites of the top four highest ranked plant species.

6.5 Arboreal Pathway Use

While sakis appear to be capable of taking alternative routes to the majority of trees that they have visited more than once, they may use arboreal pathways 1) to guide them to major feeding areas in their range, 2) to bring them into contact with many potential feeding sources for monitoring or visitation, and 3) to release them from the burden of having to continuously find new routes to traverse permanent gaps in the canopy (due to deforestation for roads and trails). It appears that the sakis were using the majority of the arboreal pathways identified in Table 5.6, at least in part, to facilitate crossing major roadways or wide trails. However, it seems curious that some of these pathways were so long (50% of paths that crossed roads or trails were 65-215 m long), considering that the gaps were only 10-15 m wide. While it would make sense to have one long continuous pathway if you had to cross multiple roads/trails in succession, this was only the situation in 33.3% of cases. On the other occasions the pathways were up to 215 m long, yet, they only intersected one major road or trail along the way. Therefore, it is likely that some of these arboreal pathways were also used for navigating among single resources or major food patches. In fact, 38.9% of pathways that crossed a major roadway or trail also connected the landmark quadrats and major feeding areas identified in Fig 5.15 B.

Many of the backtracking cases lend evidence to the notion that the sakis are using habitual routes for purposes of bringing them into contact with certain resources. In the majority of backtracking cases, the sakis appeared to diverge off of an established path to feed, rest, or threaten another saki group, and then pick back up on the same path to continue their travels. It turns out that 46% of these cases occurred along established arboreal pathways identified in section 5.7. Based on the sites that the sakis visited both during and after backtracking episodes, it appears that the sakis also use arboreal pathways to bring them into contact with single feeding sites, choice resting sites, and particular overlap zones.

6.6 The Use of Landmarks Alone to Locate Resources

On the other hand, the data suggest that the sakis can, in fact, locate a number of sites without using arboreal pathways. Recall that on 75% of all occasions, the sakis were able to arrive at reused feeding sites using novel, directed paths. This is a pretty impressive feat, as it would have required the sakis to orient from different perspectives using the same landmarks (this is assuming that they only have a limited number of prominent landmarks to choose from, as was suggested by landmark quadrat data in section 5.7). Considering that the sakis have a relatively small area to navigate through on a daily basis, they would have plenty of opportunities to memorize these views of landmarks.

On the other hand, tropical frugivores do not have nearly as many opportunities to memorize the locations of newly available feeding sites in relation to landmarks due to the ephemeral presence of most fruits (there were at least six synchronously fruiting species in this study that were only available for 2-4-week periods, including *Talisia, Bellucia, Cheiloclinium, Duguetia, Anaxagorea,* and *Rheedia*). While it is possible that the sakis would have been able to recall the exact locations of those trees from the previous fruiting season, it is somewhat unlikely. In experimental tests with white-faced sakis, Cunningham (2003) showed that their recollection of the locations of baited containers began to decline after 120 days (this is the maximum length of time they were studied, so exact limits to their memory are not known). At the very least, it is likely the sakis would have to go through a period of relearning every season to refresh their memories of exact locations of feeding sites in relation to landmarks. Unfortunately, in nature, animals often face continuously changing foraging problems and only have a few chances to perfect their responses to any given problem.

6.7 Conclusions

A number of factors prevented me from drawing more firm conclusions in this study, including, 1) the brevity of the observation period and breaks in data collection due to loss of the focal group, both of which may have prevented me from identifying all repeatedly used pathways, feeding trees, and/or sleeping sites; 2) my inability to collect abundance scores for all feeding trees visited during the study period, which may have hindered my ability to make more informed judgments concerning the sakis' true preferences; 3) imprecise methods of plotting data points, which may have weakened my capacity to identify trends and reuse of pathways when overlaying daily maps; 4) lack of assistance, which would have been useful for identifying and plotting all possible feeding sources for the sakis in their home range and for tracking changes in phenology and abundance scores for previously visited feeding sites; and, finally, 5) lack of access to Cunningham and Janson's (2007) computer models, which would have allowed me to compare the directness ratios of a hypothetical random forager to the directness ratios obtained from the study group.

While observational field studies germane to spatial memory and foraging strategies are both necessary and useful for understanding 1) how cognitive potentials are used in the wild, and 2) the selective pressures that shape foraging strategies and foraging decisions, observational studies may have to be used in conjunction with experimental field and/or captive studies if we are to fully appreciate the capabilities and methods used by primates to locate resources (for only in the latter two situations can researchers control for extraneous variables that may affect travel patterns and confound results).

However, if researchers can confidently and correctly identify 1) which foods are "available" to an animal in its natural environment, and 2) that animal's true food preferences, then they can employ one of two observational procedures that have proven useful for confirming goal-directed behavior. First of all, if a researcher knows all of the sources of food available to an animal, then the observation that that animal usually moves to the closest available resource (nearest-neighbor) is consistent with the notion that it knows where alternative resources are and purposefully chooses the closest (Garber, 1989, 2000; Janson, 1998). (Alternatively, if a researcher is confident that she has correctly identified all sources of food available to an animal, then the observation that that animal consistently bypasses the closest available resource in favor of a more distant, but more productive, resource is consistent with the notion that that animals know where all alternative resources are and intentionally chooses to travel to more productive sources of that item (Cunningham and Janson, 2007)).

Secondly, if a researcher can show 1) that an animal moves more linearly and more quickly to more preferred resources and 2) that its paths are more directed than would be expected for a forager traveling at random (which would require a computer model, along with data on the animal's detection field, a frequency distribution of observed inter-resource travel distances, and a frequency distribution of observed turning angles; see Step and Geometric Models, Janson, 1998 and Cunningham and Janson, 2007), then goal-directed travel has been demonstrated. Of course, acquiring complete information on an animal's preferences and potential food sources involves an enormous amount of work, as one would need to have 1) a complete list of all species, plant parts, and individual trees visited by the animal, 2) data on the types of items the animal selectively discards and/or consumes (and, preferably, nutritional data on each), 3) data on the availability of certain items in the environment compared to proportion of time spent on each item, and 4) detailed phenology of each food type eaten. However, if such information could be obtained for the Brownsberg sakis in the future, we would be able to achieve a much better understanding of their problem-solving skills and perceptual abilities in a natural setting; and combined with the following conclusions, we would be able to explain their foraging strategies with confidence:

- Sakis appear to consider both 1) the benefits and 2) the costs of including particular food items in their diet, and they attempt to optimize the benefit/cost ratio during foraging bouts. With reference to 1), they appear to optimize the nutrient mix of foods included in their diet, as they include an average of 6.7 plant species and 3.4 plant parts in their diets each day. Furthermore, they are selective about the types, maturity levels, species, and nutrient compositions (Norconk and Conklin-Brittain, 2004) of plant parts they will ingest. With reference to 2), other studies have shown that sakis avoid fruits with high tannin levels and the digestive inhibitors found in seed coats (Kinzey and Norconk, 1993; Norconk and Conklin-Brittain). The sakis also try to minimize travel costs by moving in relatively straight lines to all resources.
- The sakis exploit resources that are patchy in both 1) space and 2) time. With reference to 1), their most favored plant part, fruits, exist in aggregations in the crowns of trees, and

each fruiting tree is dispersed from all others, except in the case of *Pausandra martini*. With reference to 2), fruits, as well as the seeds of fruits, are only available for short periods of time throughout the year.

- The sakis appear to prefer feeding sites that 1) they have visited at least once (possibly a good predictor for them, as, after each visit, they will be better able to assess what they can expect on subsequent visits in terms of availability, productivity, and phenophase), 2) facilitate multiple feeding bouts (presumably productive trees), 3) are producing seeds, and 4) are of a species which comprises the bulk of their diet. They travel to these preferred sites more directly and more quickly than to other sites, which provides evidence for goal-directed foraging behavior.
- The sakis prefer sleeping trees that are tall and camouflaged, and will even sleep in areas of their home range that are shared with competing groups. They attempt to minimize travel distances by choosing sleeping sites that are either closest to their last feeding tree of the day or closest to their first feeding tree the next morning. In choosing the closest sleeping site available to them, it shows that they 1) know the locations of multiple sites relative to their current and projected positions, 2) can accurately gauge the distances between those sites, and 3) can make the most economical decision when faced with multiple alternatives.
- The sakis exhibit tendencies for forward progression and relatively straight-line travel.
- The paths that the sakis choose to take throughout the day appear to be a compromise between the need to monitor potential resources and the movements of competing groups (two behaviors which may secure food sources for them in the future) and the need to

fulfill current nutritional needs. They choose to monitor home range edges and potential feeding sources at the expense of traveling slightly longer distances to feeding and sleeping sites.

- The sakis appear to use arboreal pathways not only to cross permanent gaps in the canopy, but also to lead them to major feeding areas, single feeding sites, single resting sites, and boundary edges in their range. They appear be able to use landmarks alone to travel to feeding sites that they have visited on previous occasions.
- Finally, three lines of evidence suggest that the sakis can recall the locations and qualities of some resources in their environment, and, further, that they employ a goal-directed foraging strategy in some circumstances. 1) They are able to reach distant feeding sources from a variety of different starting points, and they travel to these sources directly. 2) They travel significantly more quickly and more linearly to more preferred feeding sites (i.e. revisited feeding sites of high-ranking plant species). 3) Out of all of the sleeping sites available to them, they are able to locate the closest relative to their last feeding site of the day.

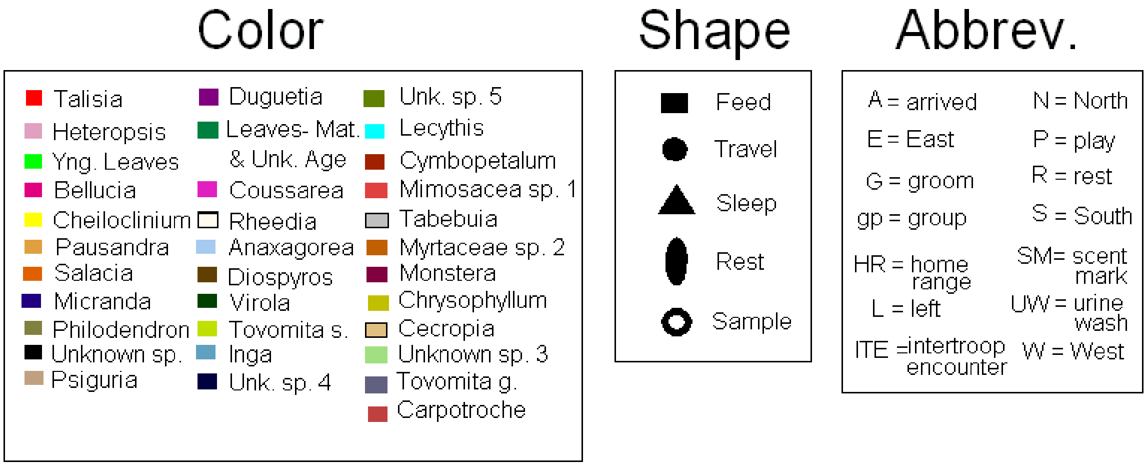
Appendix A. Glossary of Key Terms

Arboreal pathway	Frequently used route used to get from one area of the home range to another; for the purposes of this study, repeatedly used routes must be overlapping or within 20 m of each other for at least 25 m to qualify as arboreal pathways.
Directed travel	Travel characterized by (approximately) linear forward progression and/or quick movements.
Euclidean map	Mentally representing features of one's environment as either a set of specific locations in a coordinate system or as a series of angles and distances among those features. Allows direct movement between any pair of points.
Intertroop Encounter (ITE)	Aggressive encounters between groups of the same species. Encounters characterized by loud vocalizations, branch/body shakes, piloerection, chasing and retreating, and otherwise erratic Movements. Visual contact between the two groups must be made (implying relatively close proximity) in order for the incident to qualify as an ITE (contrast with "Z trilling").
Goal-directed Foraging	Foraging characterized by purposeful movement towards predetermined feeding sites using directed travel.(Contrast with "random foraging".)

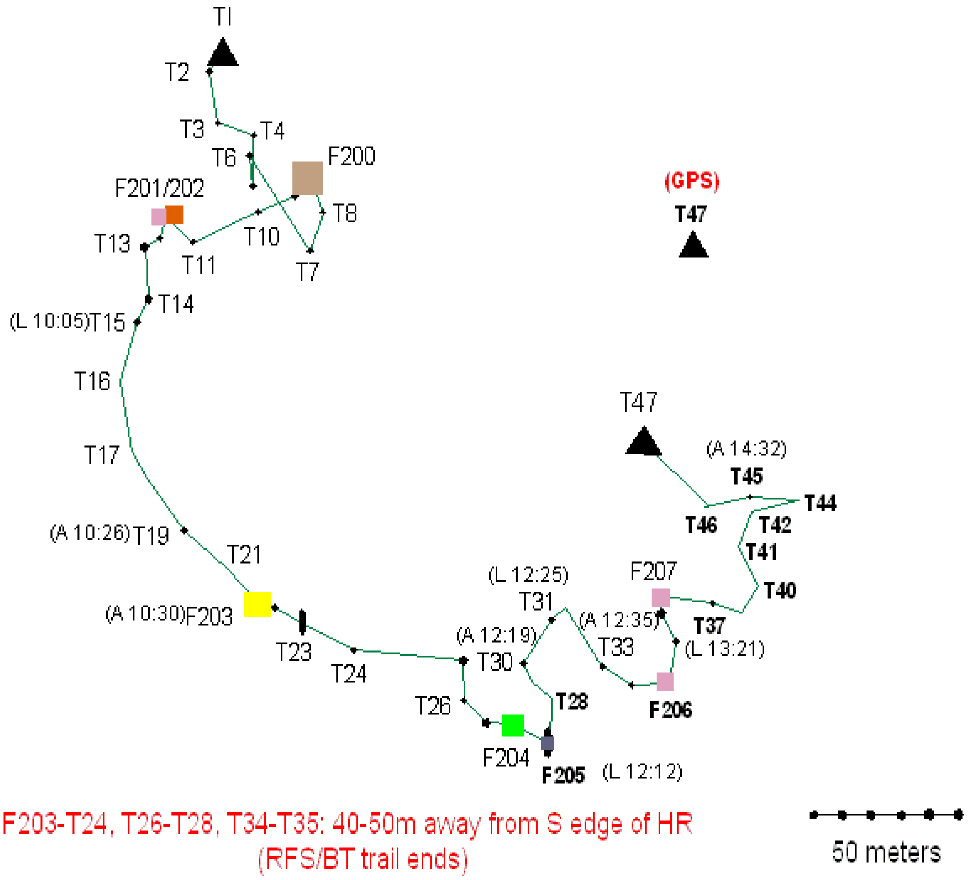
Mental Map	A means of mentally representing the spatial layout or spatial relationships of features in one’s environment.
Overlap Zone	Shared area among two groups. Groups are presumed to be competing for sole access to area, as areas always sites of ITE’s and/or Z trilling.
Patch	A discrete feeding site, usually separated from other such sites by at least one tree crown. Patches are generally single tree crowns; more rarely, patches are a closely-spaced cluster of same-species trees or lianas that span several tree crowns.
Patchy	(Spatial or temporal) distribution pattern wherein areas of high concentration of certain species or resource types are separated by areas of low concentration of those items; dispersed clumps of resources vs. randomly- or uniformly-spaced resources.
Random Foraging	Foraging characterized by random wandering through habitat; angles of progression are chosen randomly; resources encountered by chance.
Rule-Guided Foraging	“Applying or generalizing a set of preexisting expectations learned in one foraging context to other foraging contexts.” (Garber, 2000, pp. 270)
Sclerocarpic Harvesting	“The preparation and ingestion of fruit with a hard pericarp.” (Kinzey and Norconk, 1993).
Topographical/	Mentally representing space either by memorizing a set of landmarks

Route-Based Map	that one can use to orient self and/or by memorizing a sequence of landmarks to follow along known routes. (Does not require that animal uses habitual routes, only orienting landmarks.)
Traplining	Feeding pattern in which several trees of a single species or single resource type are visited in succession
Z trilling	Aggressive type of saki vocalization, usually occuring in overlap zones, and made in response to or in anticipation of contact (visual or auditory) with a competing group. Can occur beyond or within visual contact.

Appendix B.1. Legend and Saki Daily Routes.

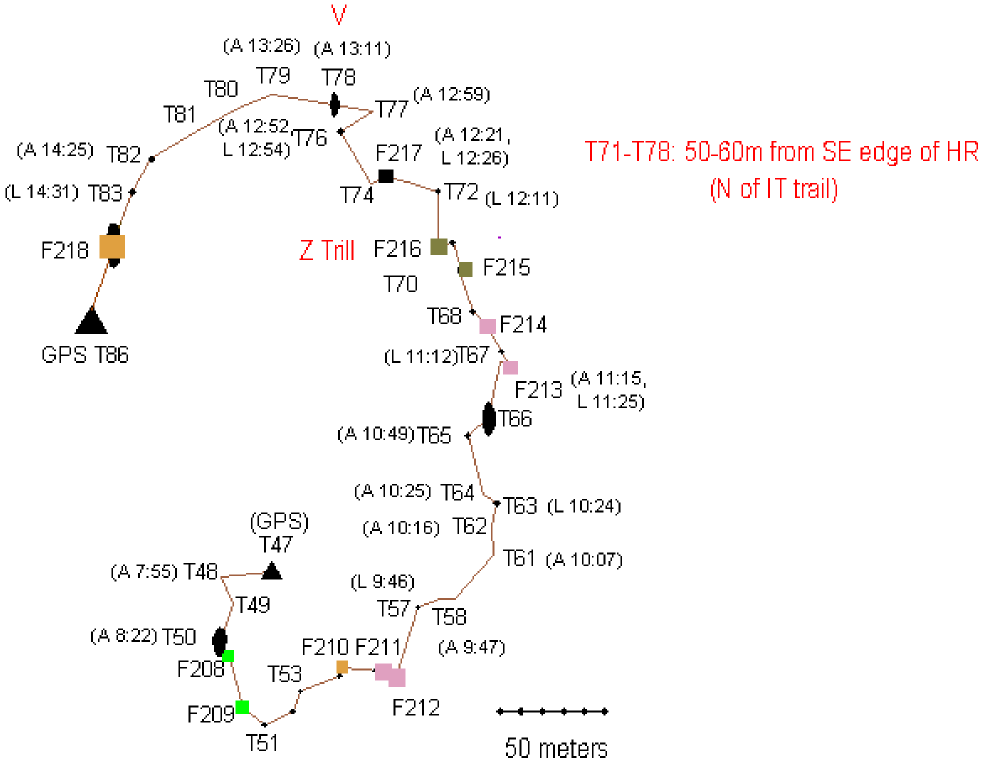


Appendix B.2. Route for June 6. Focal Animals: SAM1 (T1-T33), AM (T34-T47).

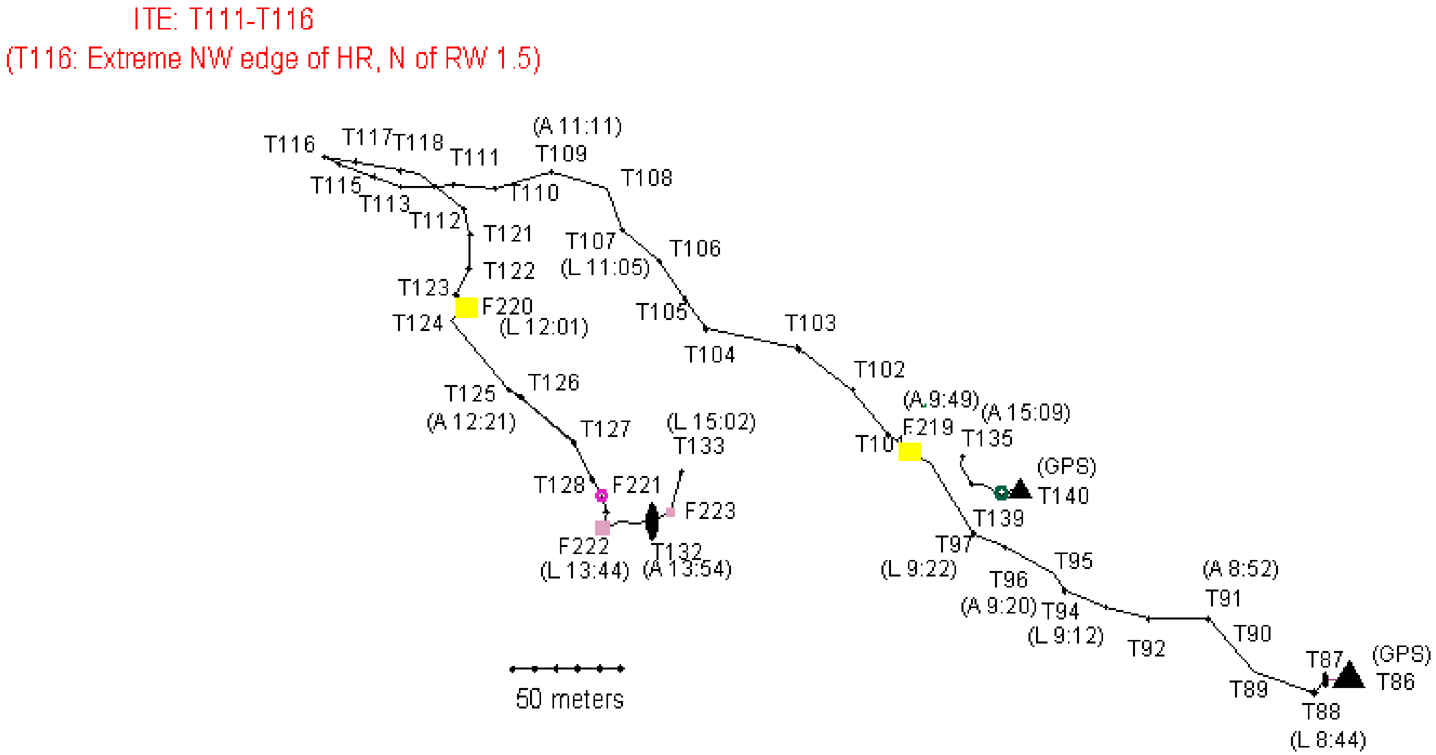


F203-T24, T26-T28, T34-T35: 40-50m away from S edge of HR
(RFS/BT trail ends)

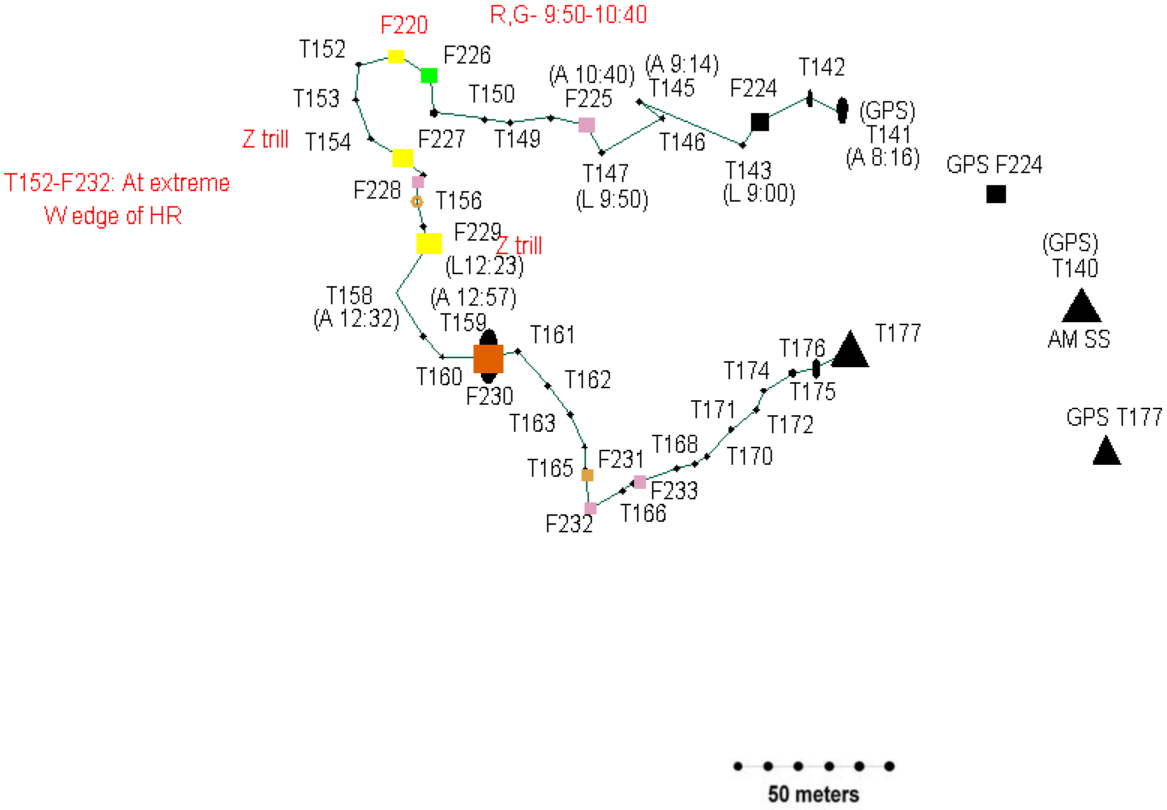
Appendix B.3. Route for June 7. Focal Animal: AM.



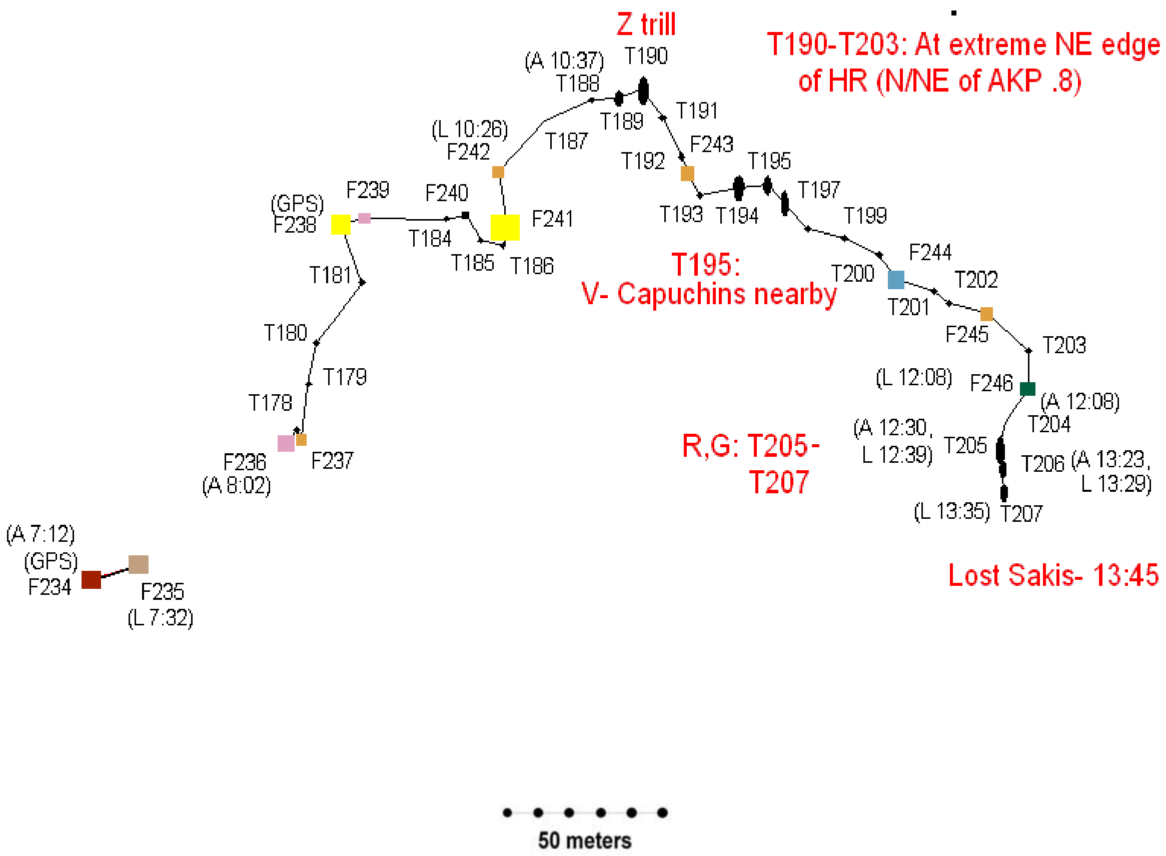
Appendix B.4. Route for June 8. Focal Animals: SAM1 (T86-T97), AM (T100-T109 & T128-T140), SAM2 (T110-T127).



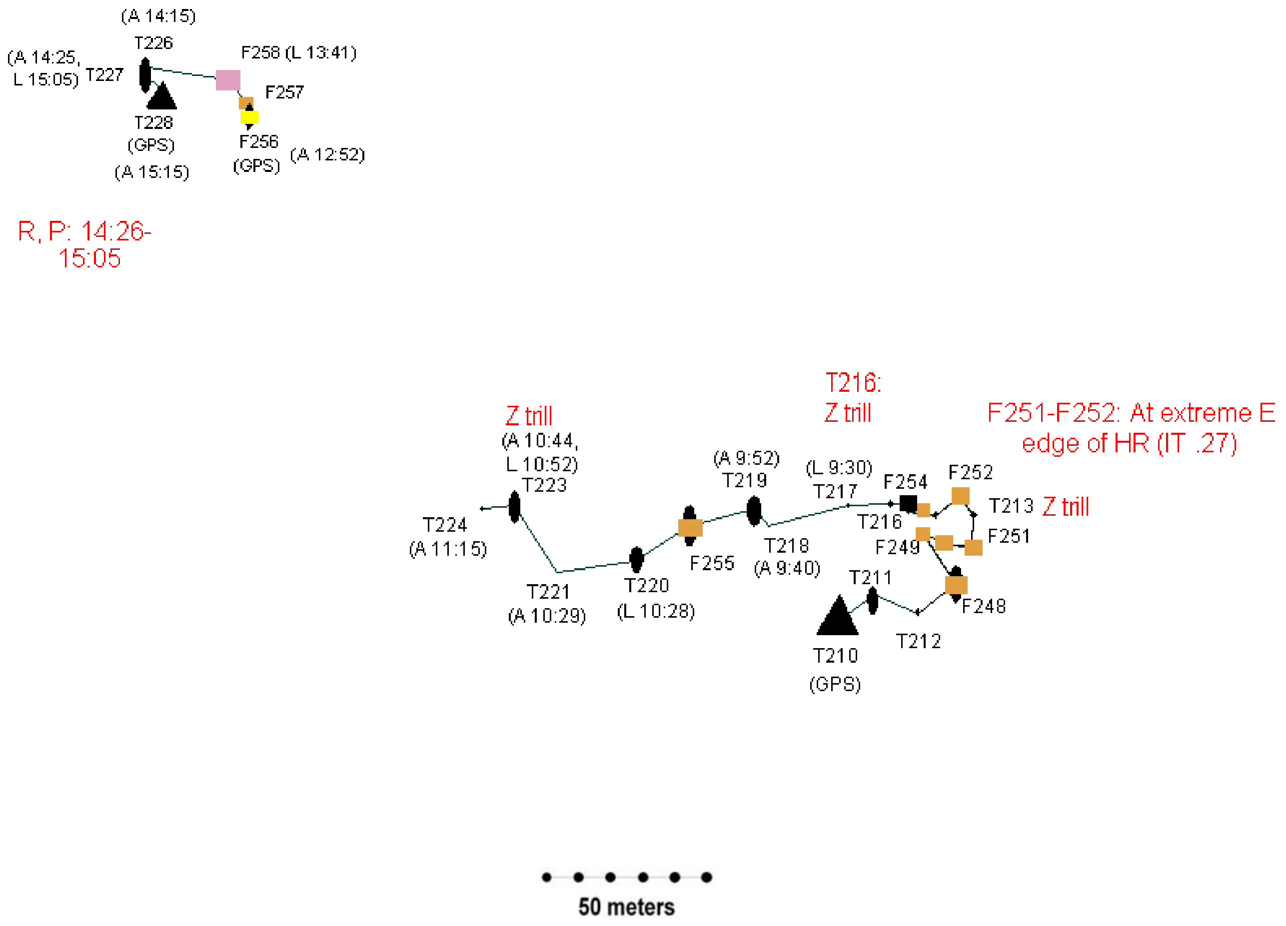
Appendix B.5. Route for June 9. Focal Animal: AF.



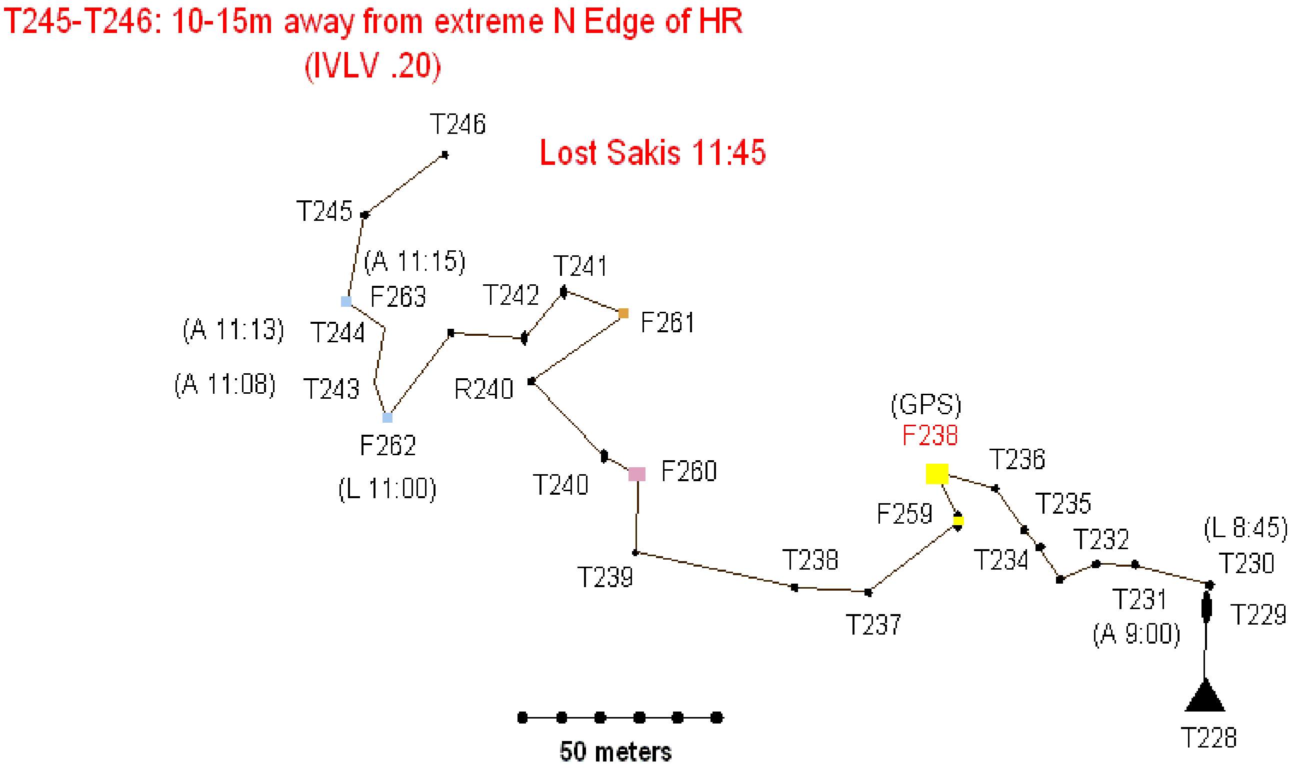
Appendix B.6. Route for June 11. Focal Animals: SAM1 (F234-F235), AF (F236-T207).



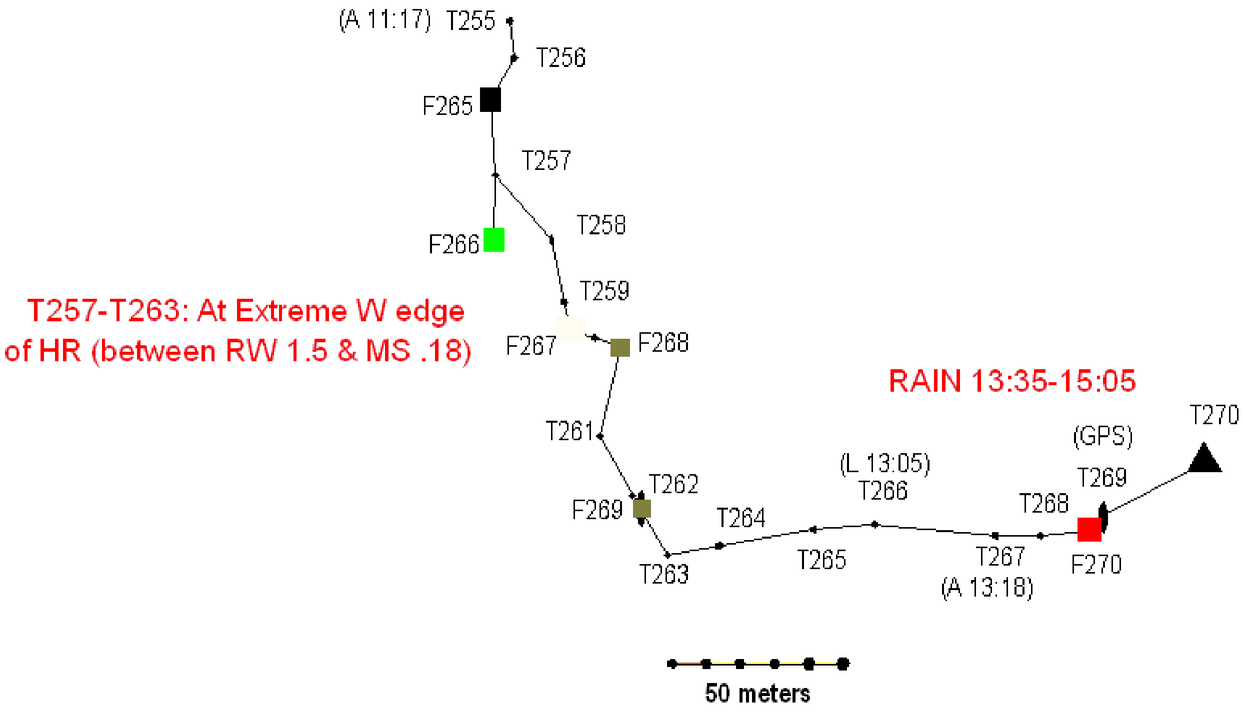
Appendix B.7. Route for June 13. Focal Animal: SAM1.



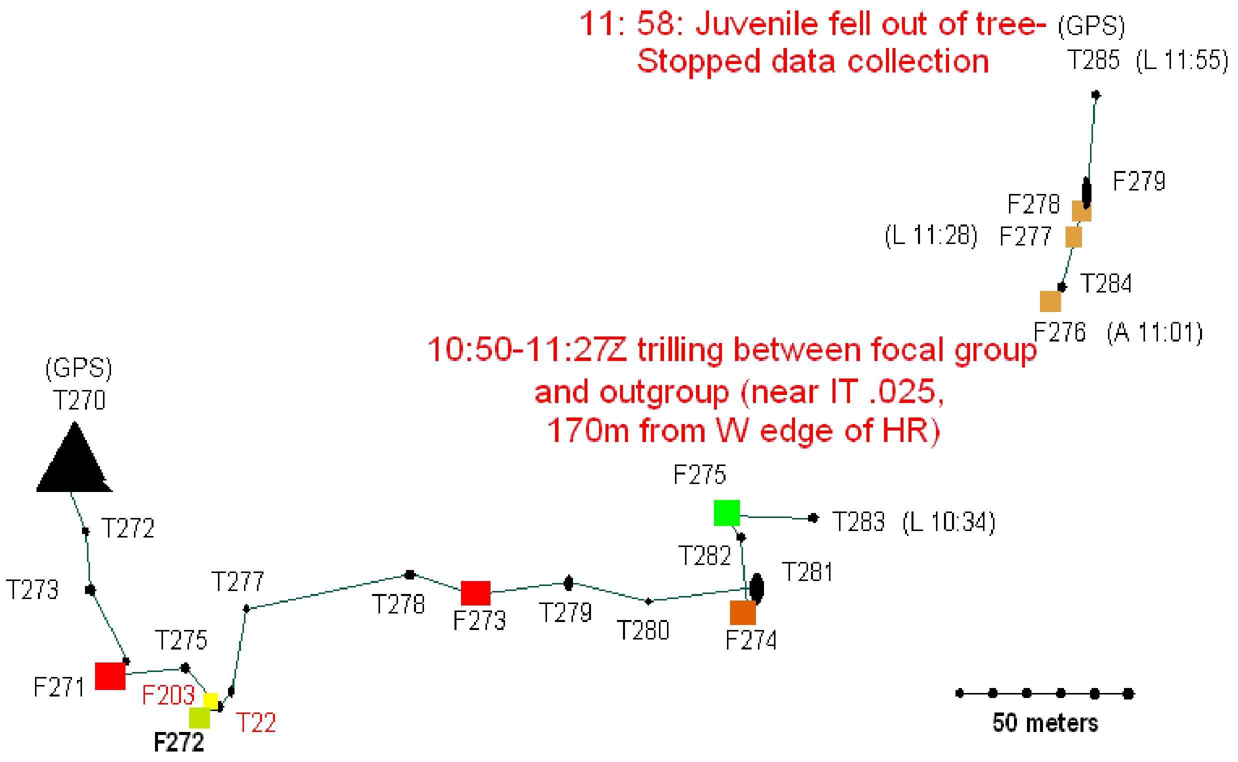
Appendix B.8. Route for June 14. Focal Animals: SAM2 (T228-T239), AF (F260-T246).



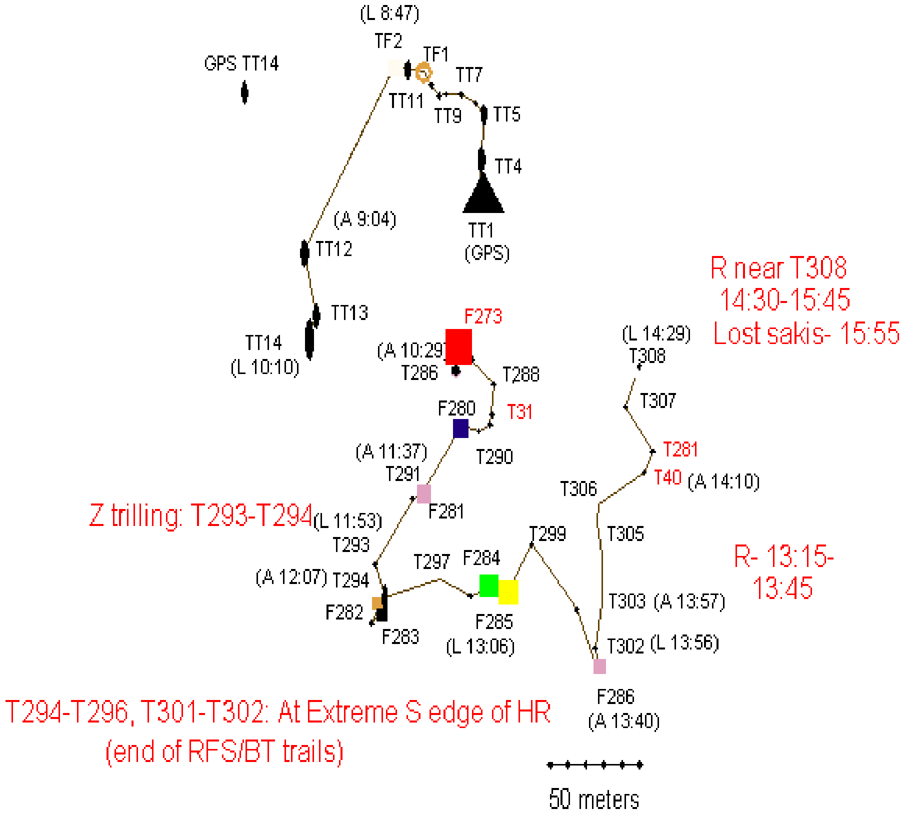
Appendix B.9. Route for June 15. Focal Animals: F (T247-T254), S (T255-T270). Could not map T247-T254 (didn't obtain GPS point by which to reference route).



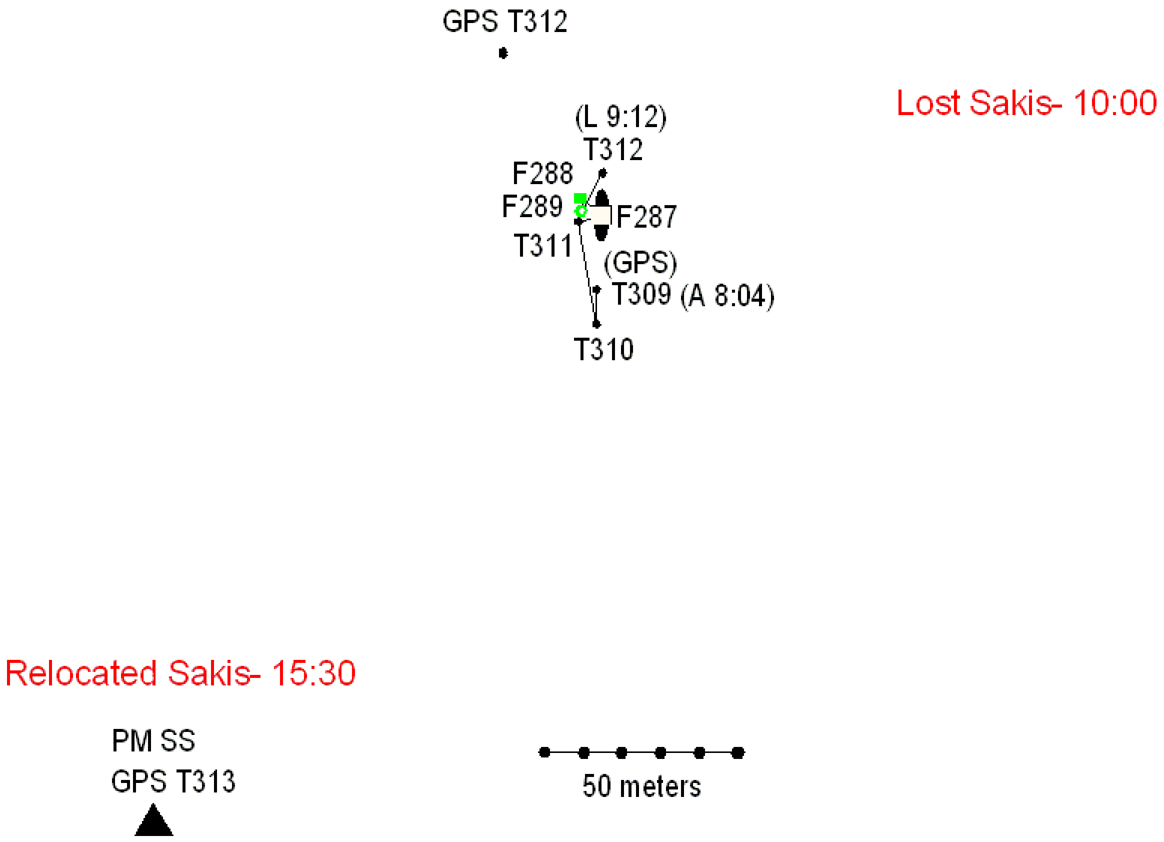
Appendix B.10. Route for June 16. Focal Animal: AM.



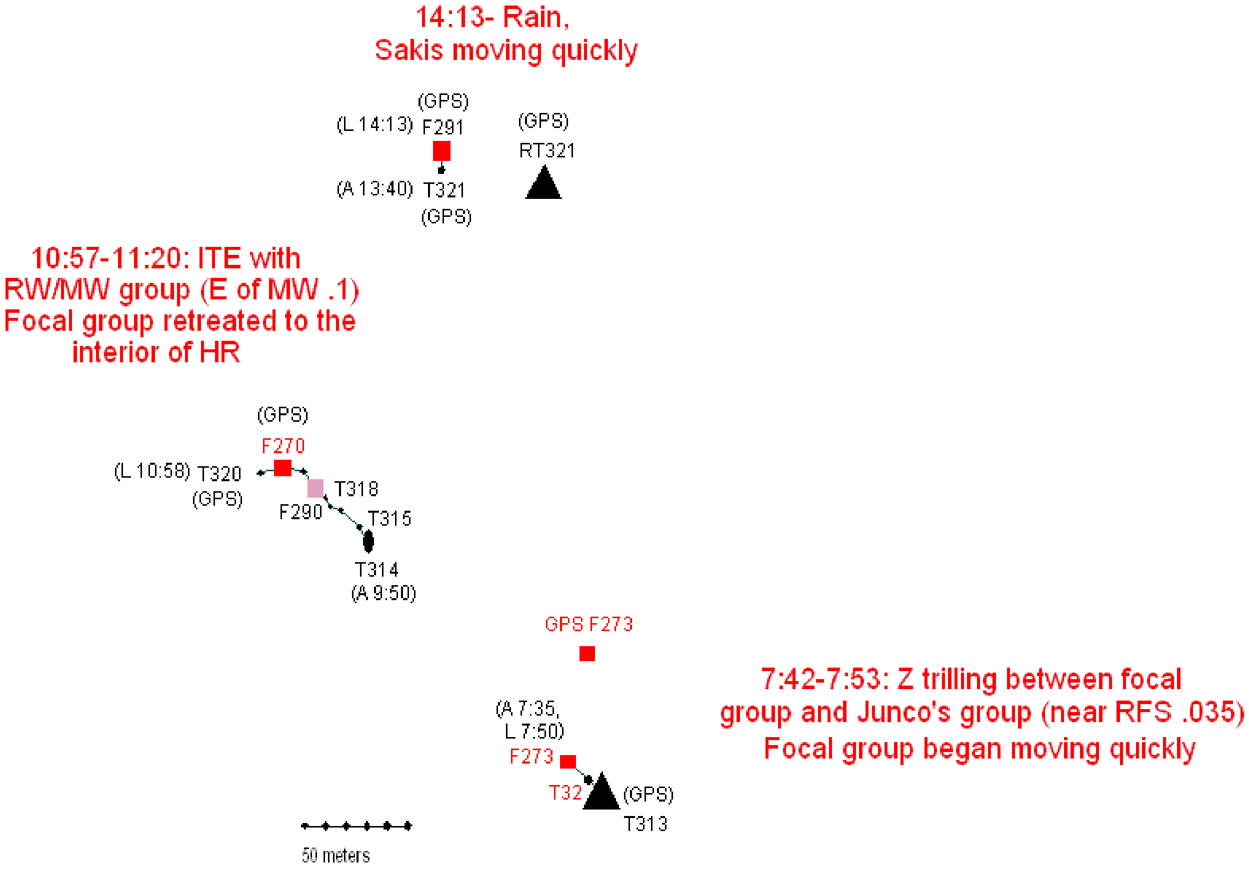
Appendix B.11. Route for June 19. Focal Animals: SAM1 (TT1-TT14), AM (T286-T308).



Appendix B.12. Route for June 20. Focal Animal: SAM2.



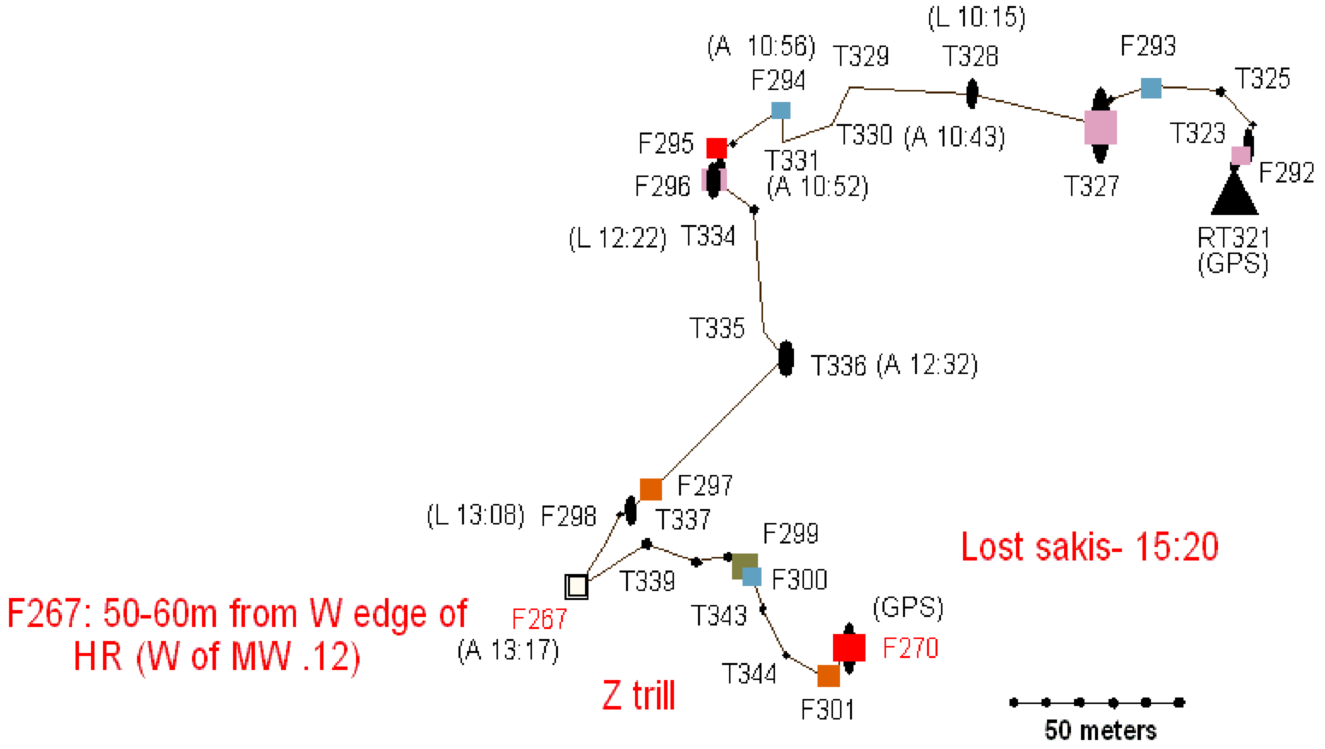
Appendix B.13. Route for June 21. Focal Animal: SAM1.


14:13- Rain,
Sakis moving quickly

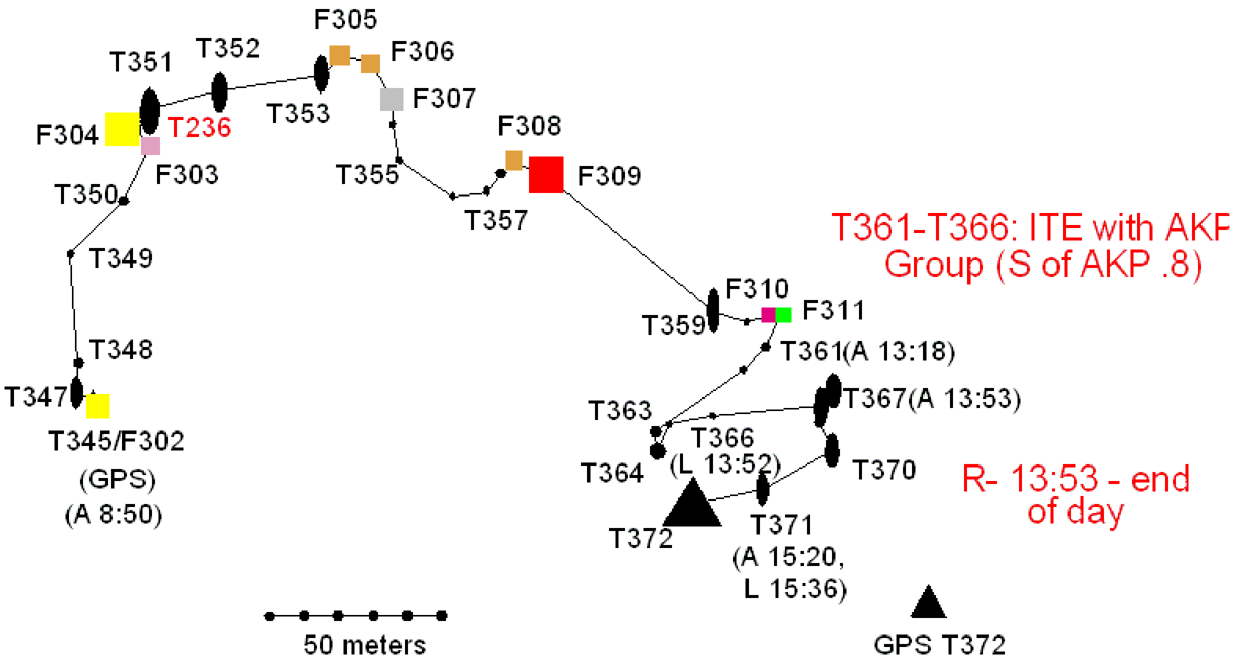
10:57-11:20: ITE with
RW/MW group (E of MW .1)
Focal group retreated to the
interior of HR

7:42-7:53: Z trilling between focal
group and Junco's group (near RFS .035)
Focal group began moving quickly

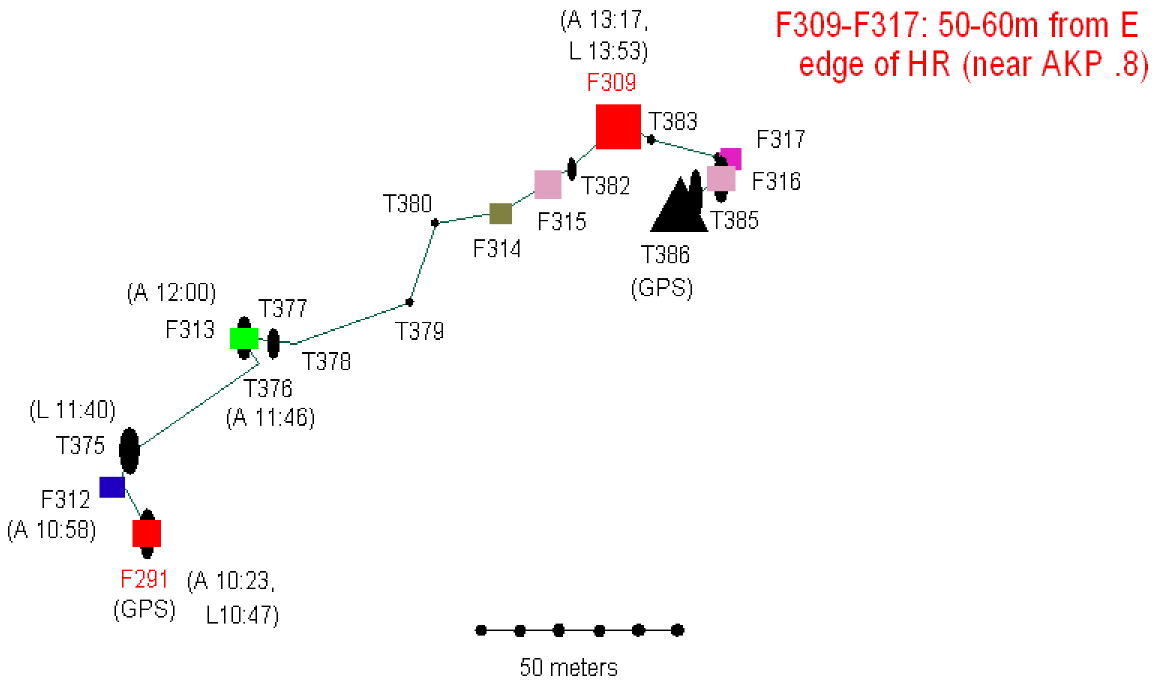
Appendix B.14. Route for June 22. Focal Animal: AM.



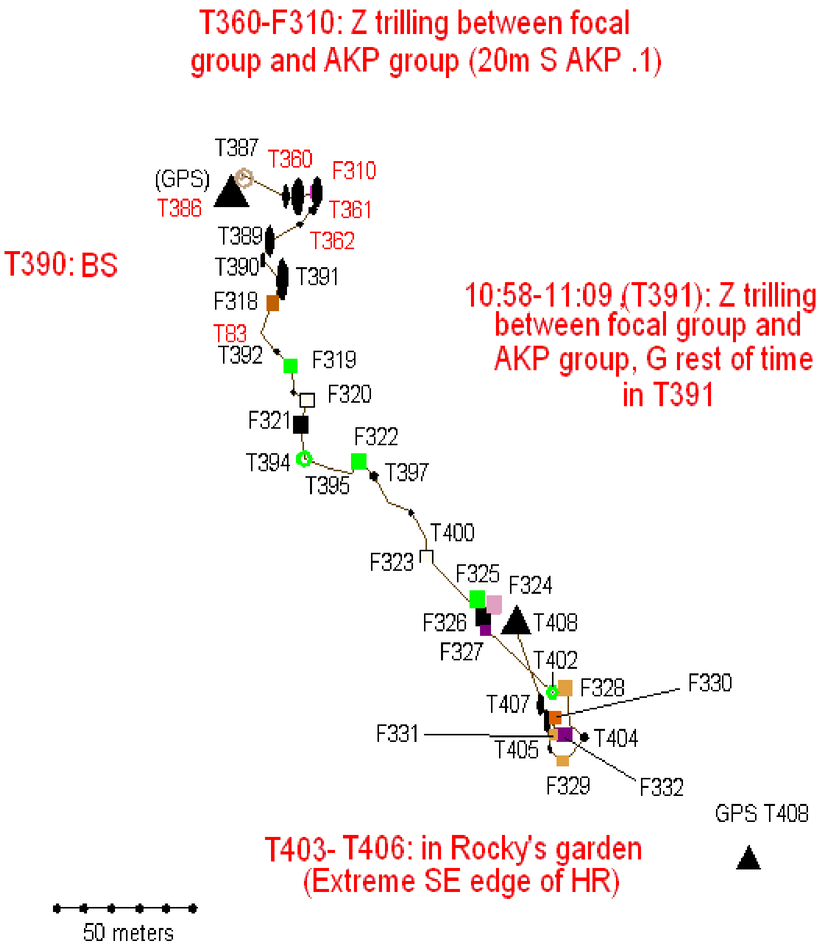
Appendix B.15. Route for June 26. Focal Animal: AM.



Appendix B.16. Route for June 27. Focal Animals: AM (F291-T376 & T384-T386), AF (F313-F309).



Appendix B.17. Route for June 28. Focal Animals: SAM1 (T386-F326), SAM2 (F327-T408).



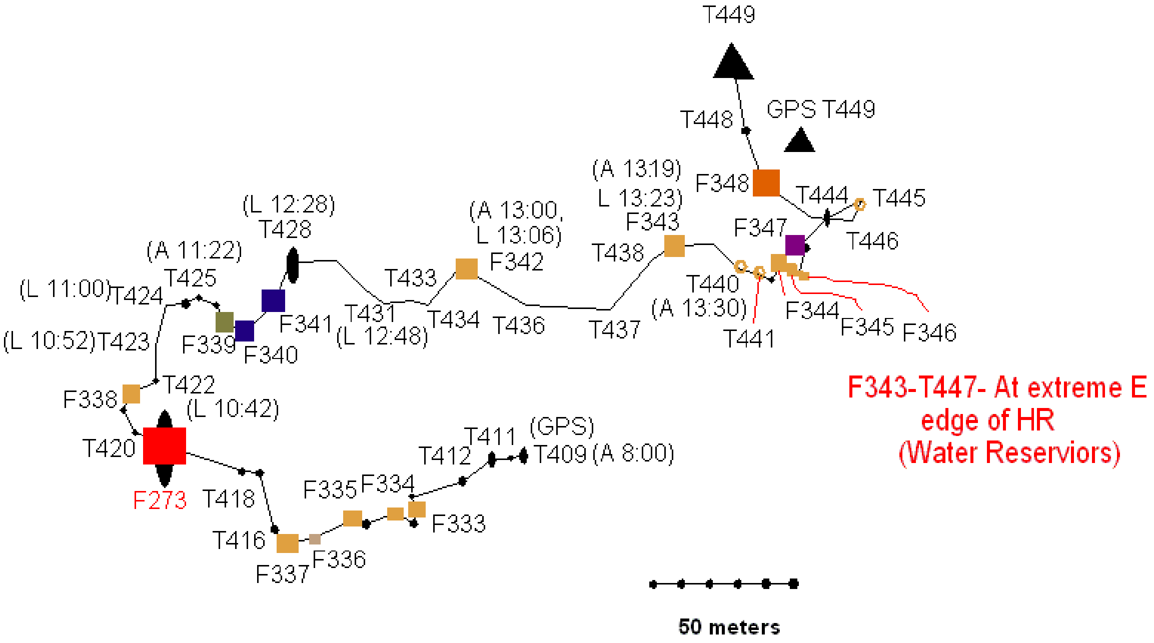
T360-F310: Z trilling between focal group and AKP group (20m S AKP .1)

T390: BS

10:58-11:09 (T391): Z trilling between focal group and AKP group, G rest of time in T391

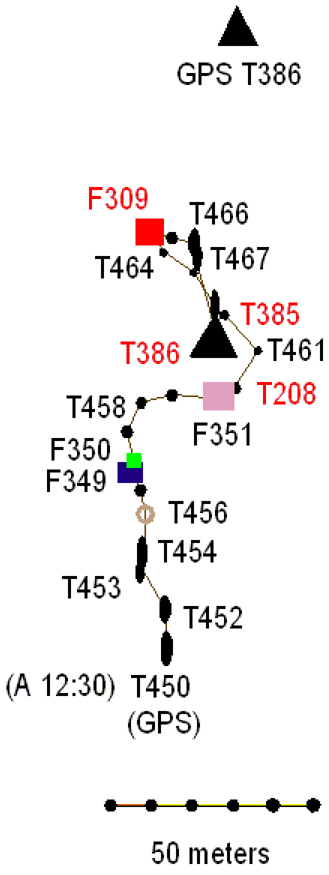
T403- T406: in Rocky's garden (Extreme SE edge of HR)

Appendix B.18. Route for June 29. Focal Animal: AF.

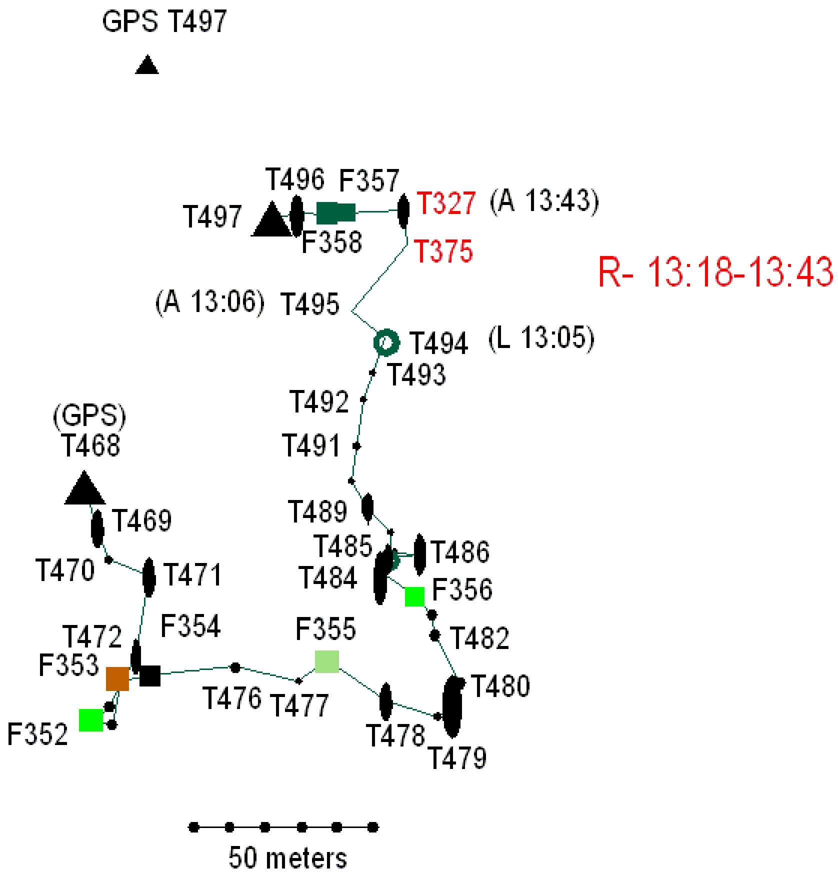


F343-T447- At extreme E edge of HR (Water Reserviors)

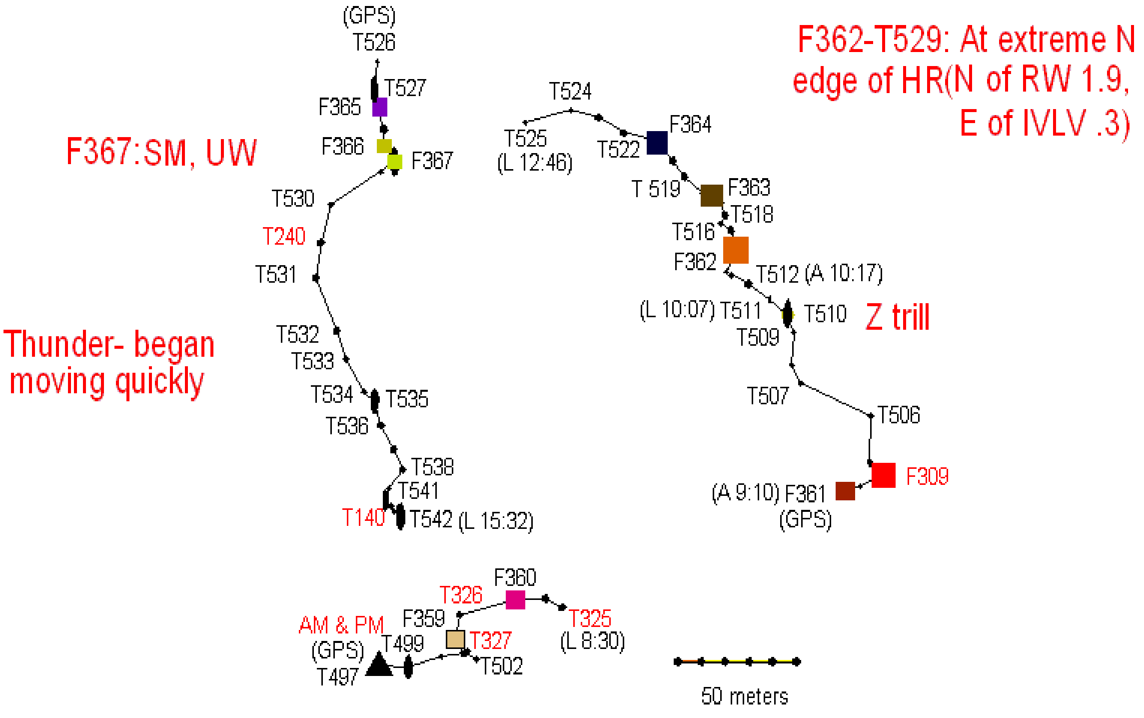
Appendix B.19. Route for July 3. Focal Animal: AM.



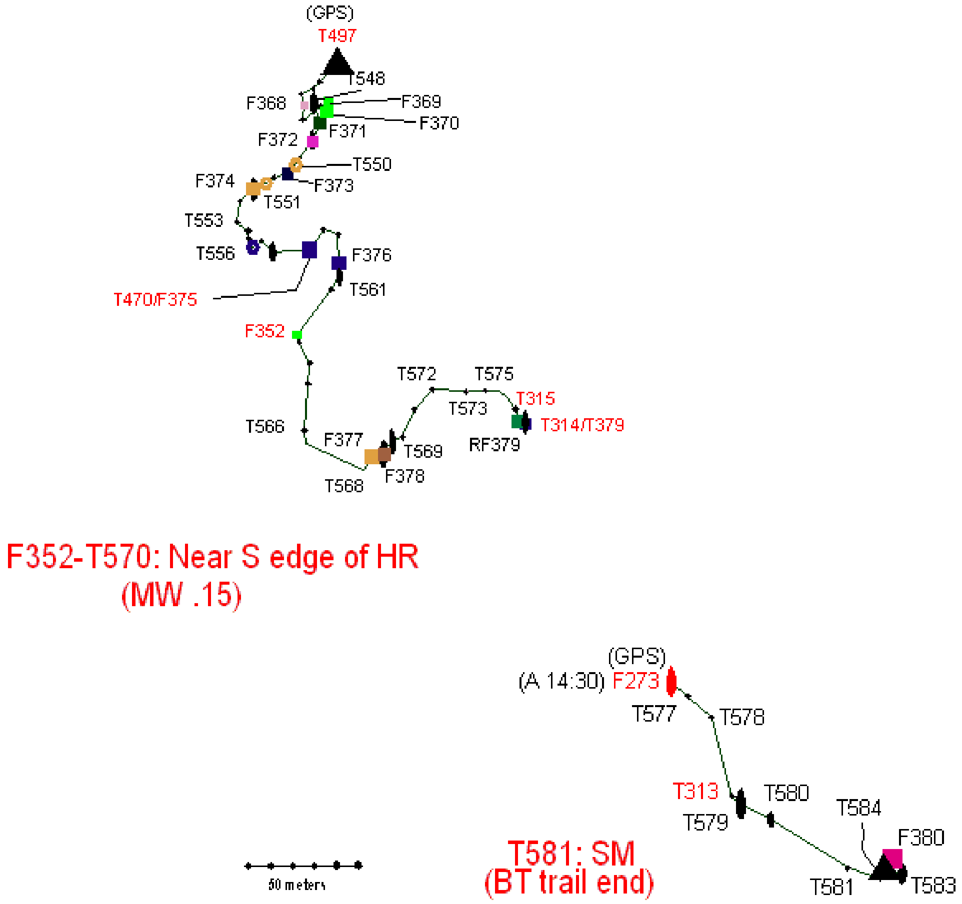
Appendix B.20. Route for July 8. Focal Animal: AM.



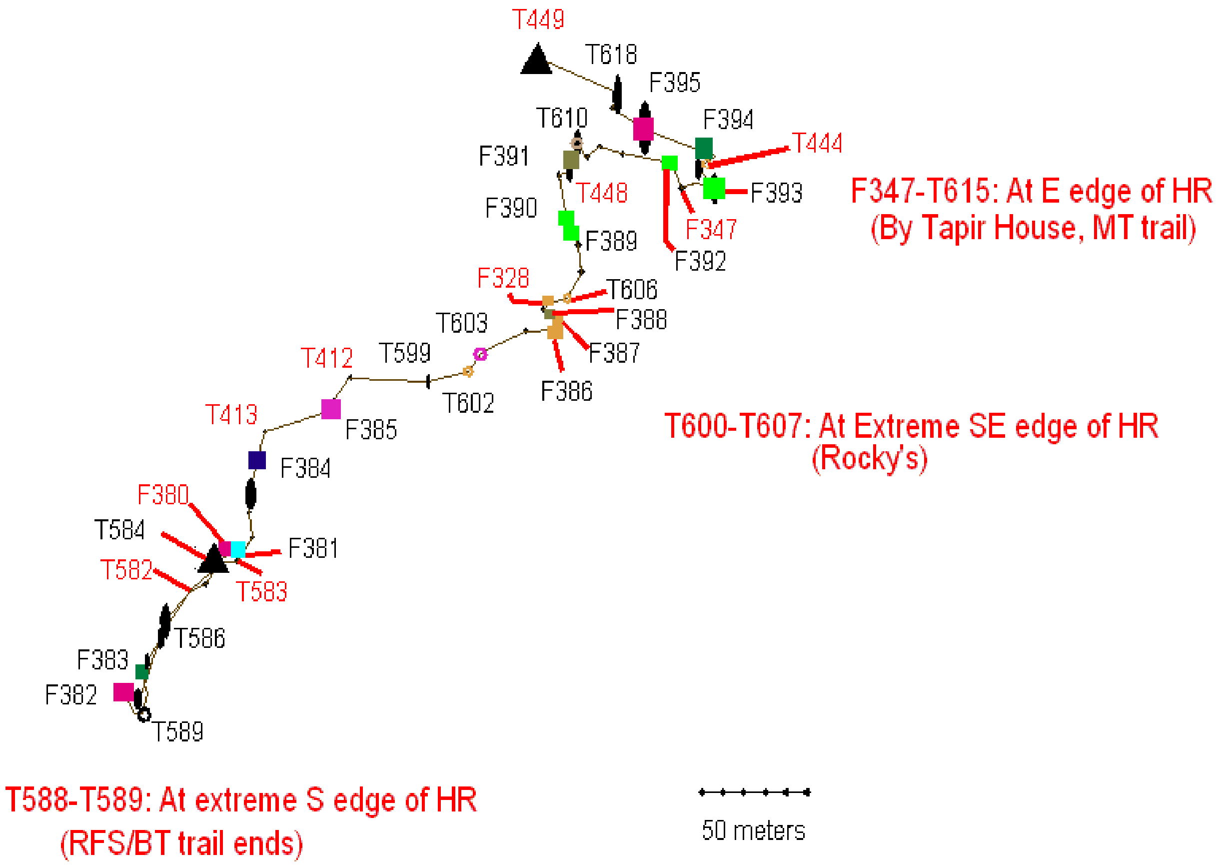
Appendix B.21. Route for July 9. Focal Animals: SAM2 (T497-T325), AM (F363-T525), SAM1 (T526-T497).



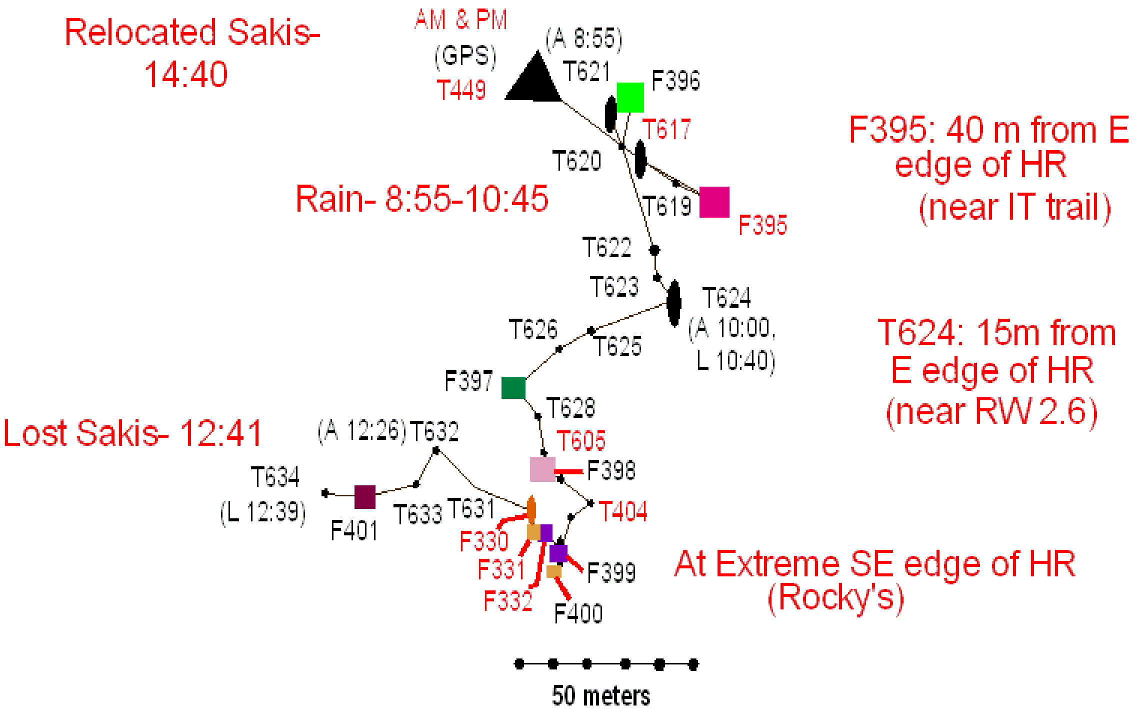
Appendix B.22. Route for July 10. Focal Animals: SAM2 (T497-F371 & F374-T560), SAM1 (F372-T551 & F376-T584).



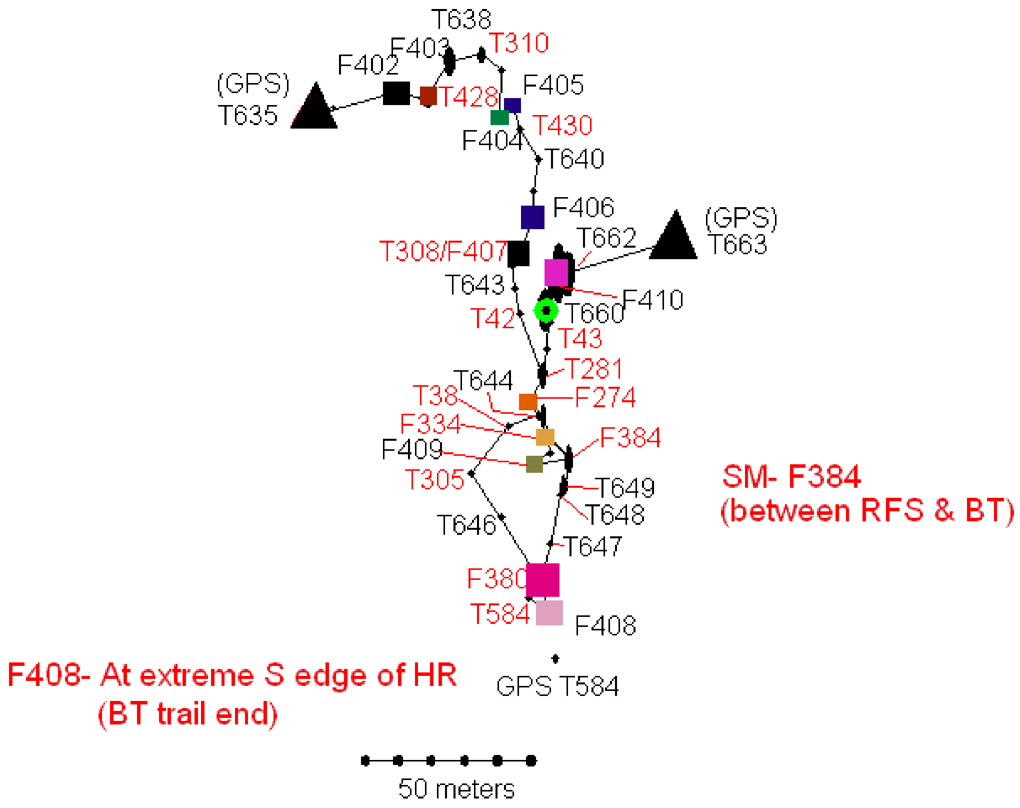
Appendix B.23. Route for July 11. Focal Animal: SAM2.



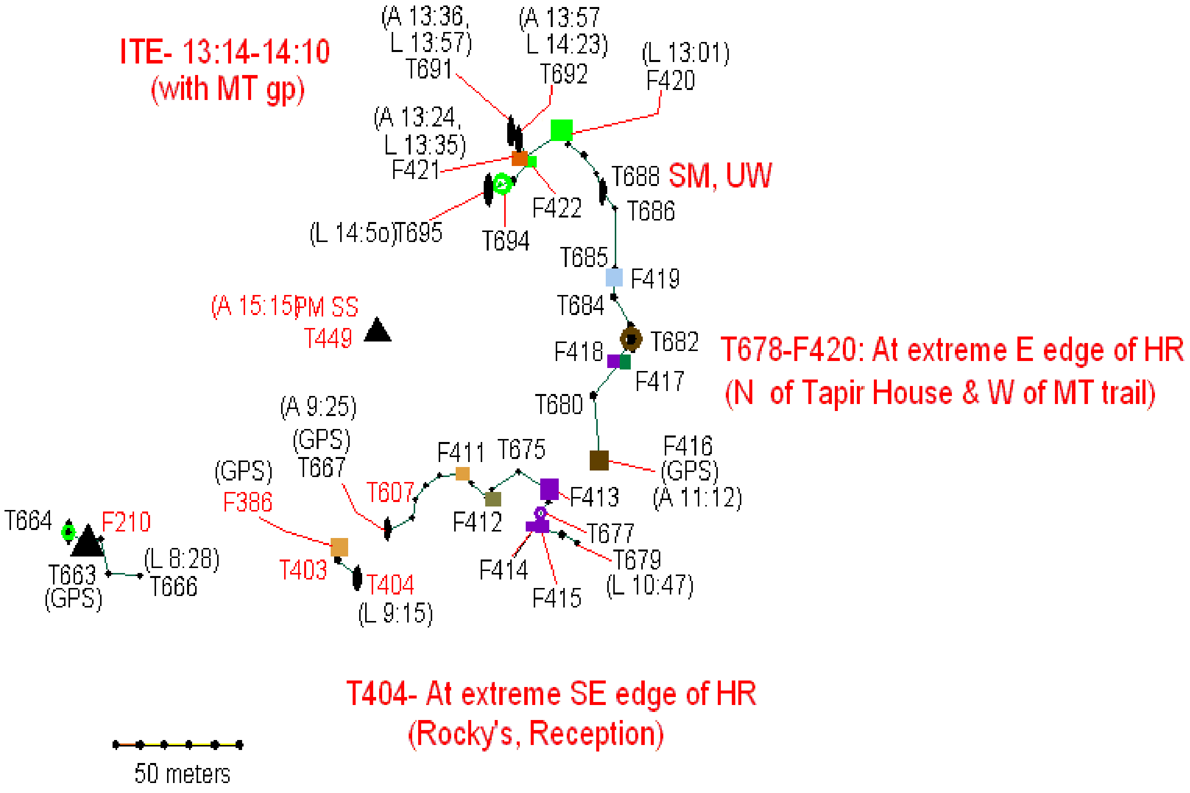
Appendix B.24. Route for July 12. Focal Animal: SAM2.



Appendix B.25. Route for July 16. Focal Animals: SAM2 (T635-F409), AM (T652-T663).



Appendix B.26. Route for July 17. Focal Animals: SAM1 (T663-T666), AF (F386-T679), AM (F416-T449).

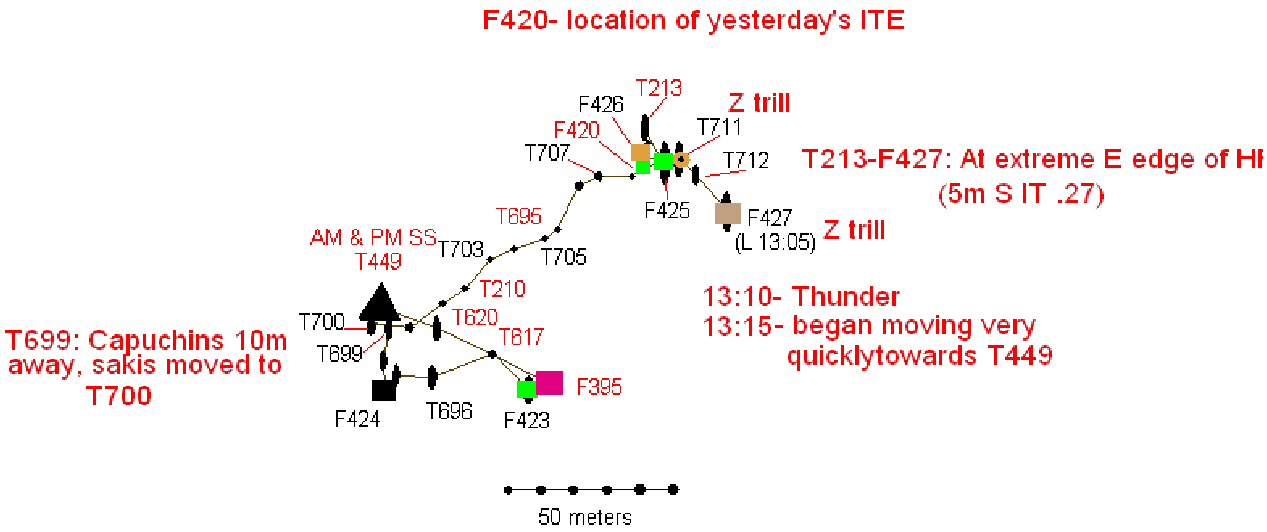


ITE- 13:14-14:10
(with MT gp)

T678-F420: At extreme E edge of HR
(N of Tapir House & W of MT trail)

T404- At extreme SE edge of HR
(Rocky's, Reception)

Appendix B.27. Route for July 18. Focal Animals: SAM1 (T449-F425), AF (T213-T449).



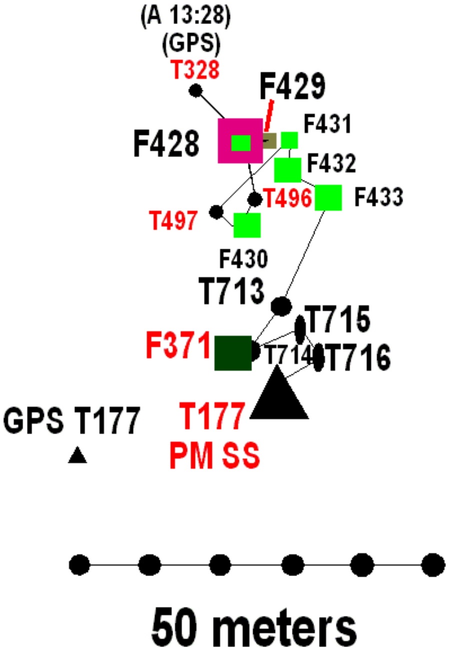
F420- location of yesterday's ITE

T213-F427: At extreme E edge of H
(5m S IT .27)

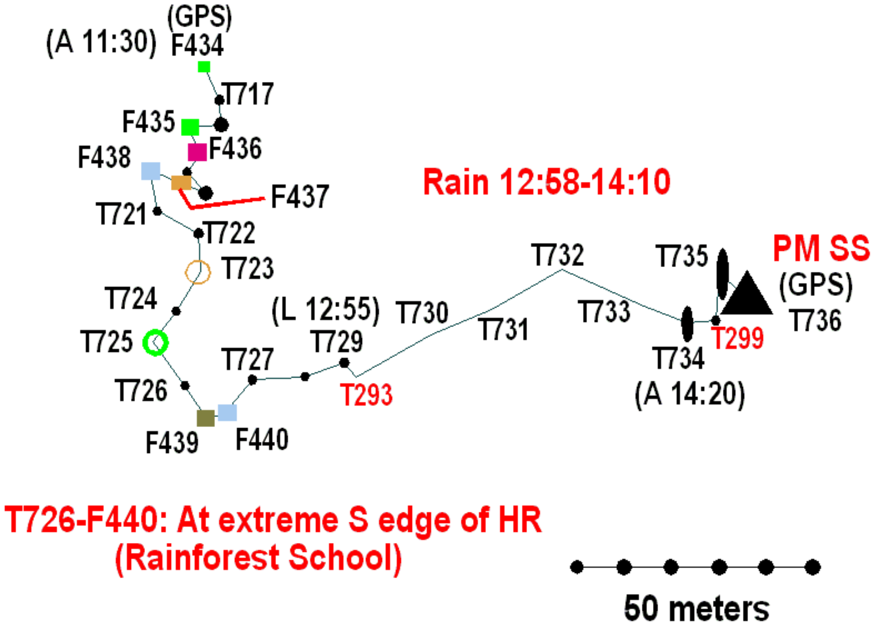
13:10- Thunder
13:15- began moving very quicklytowards T449

T699: Capuchins 10m away, sakis moved to T700

Appendix B.28. Route for July 21. Focal Animal: SAM1.

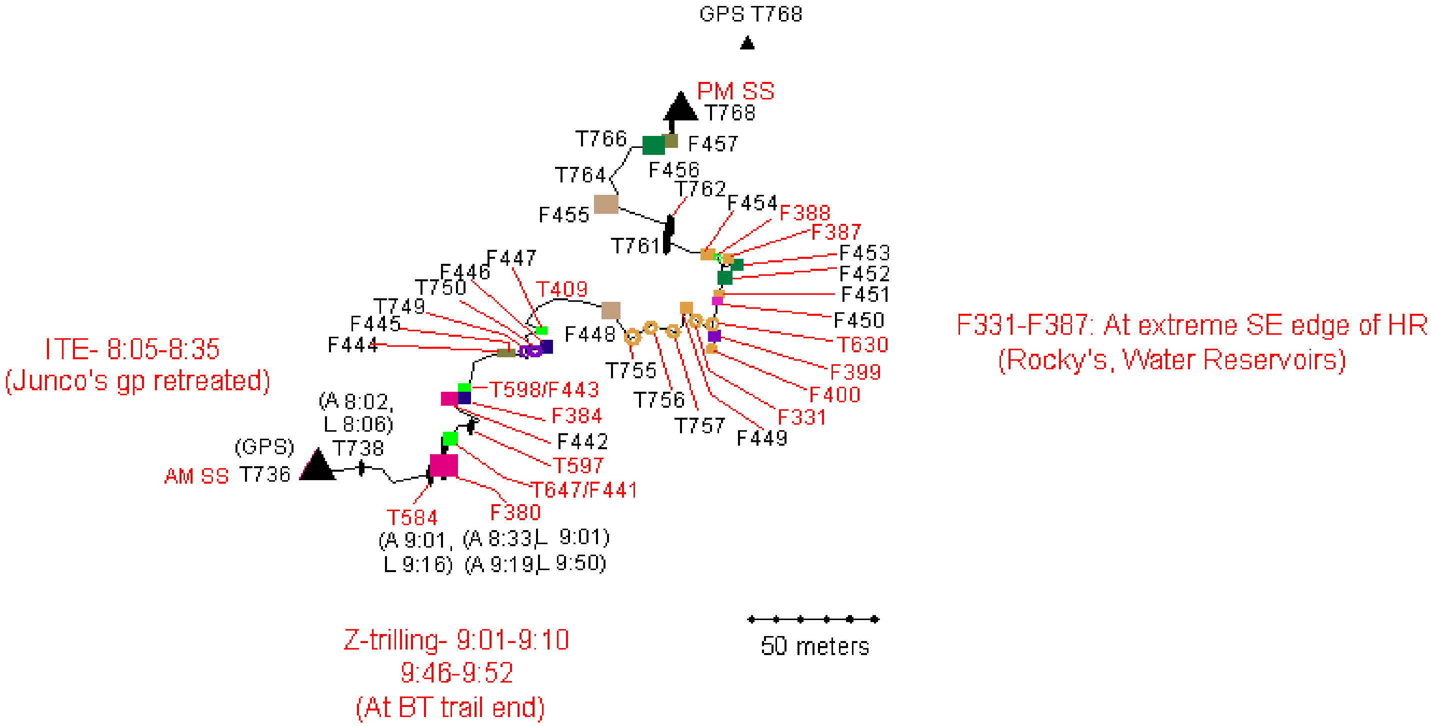


Appendix B.29. Route for July 22. Focal Animal: AF.

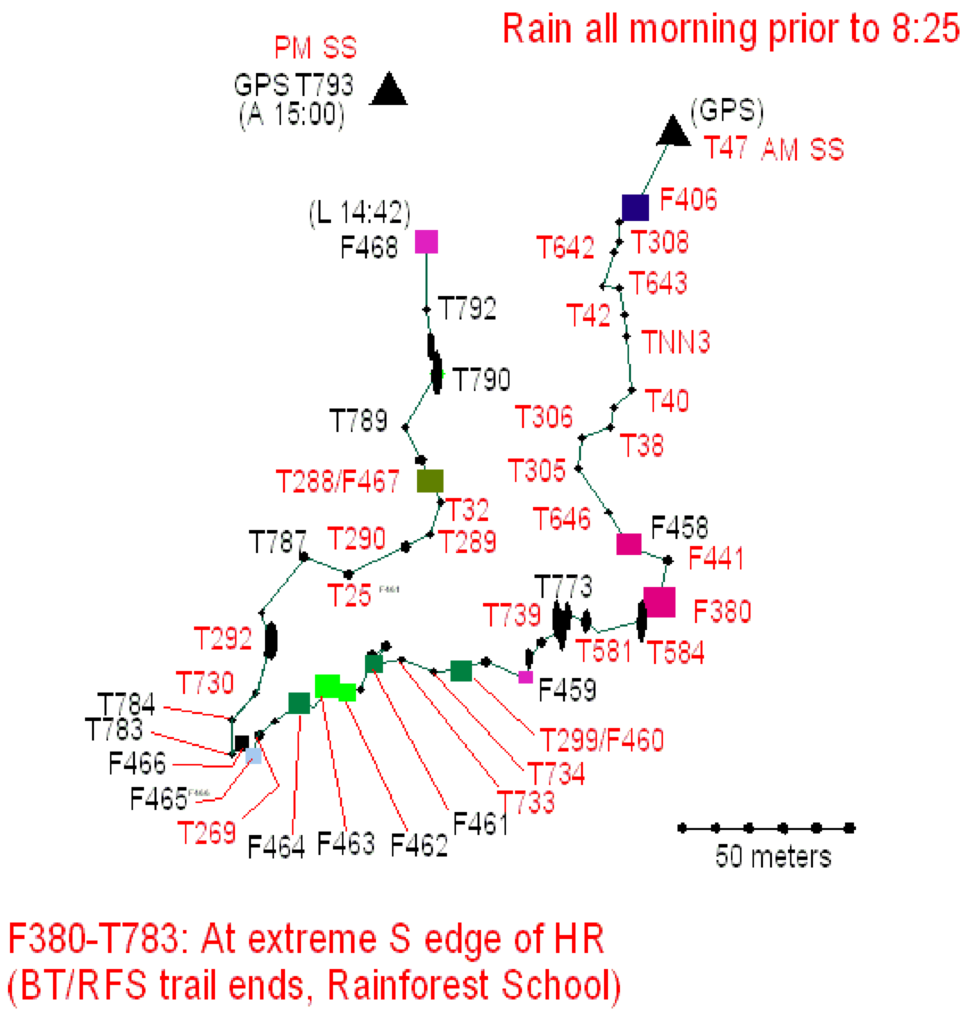


T726-F440: At extreme S edge of HR
(Rainforest School)

Appendix B.30. Route for July 23. Focal Animals: AF (T736-F447), SAM2 (T412-T768).



Appendix B.31. Route for July 25. Focal Animals: SAM1 (T47-T776), SAM2 (F459-T792), AF (F468-T793).



Rain all morning prior to 8:25

F380-T783: At extreme S edge of HR
(BT/RFS trail ends, Rainforest School)

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