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FORAGING RESPONSES TO NUTRITIONAL PRESSURES IN TWO SPECIES OF CERCOPITHECINES: *Macaca mulatta* AND *Papio ursinus*

by

GRETCHEN A. CLYMER

Under the Direction of Frank L'Engle Willliams

ABSTRACT

Papio ursinus are dietary generalists that exploit a diverse repertoire of food resources. This study explored the foraging strategies of a group of *Papio ursinus* and the foraging differences between subgroups classified by age and sex. Food resource preference, nutritional properties of food resources, and nutritional demands were examined to test the hypotheses that the foraging strategies exhibited by the subgroups would differ and that food selection is driven by nutritional demands. Adult females and juveniles were found to seek out food resources higher in proteins, while adult males were found to prefer food resources higher in carbohydrates. The findings support the alternative hypotheses and suggest that nutritional pressures are the best predictor of foraging optimization. A pilot study, involving the observation of a provisioned group of *Macaca mulatta,* that proved elemental to the formulation of the research design employed in the study of *Papio ursinus*, is also described.

INDEX WORDS: *Papio ursinus*, *Macaca mulatta,* chacma baboons, rhesus macaques, foraging, diet, dietary choice, nutrition, cercopithecines, optimal foraging strategy

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GRETCHEN A. CLYMER

A Thesis Submitted In Partial Fulfillment of the Requirements for the Degree of

Master of Arts

in the College of Arts and Sciences

Georgia State University

2006

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2006

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by

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May 2006

DEDICATION

To my grandmother, Catherine Clymer, as well as Kris and Euki, for always believing in me and inspiring me to be more than I ever thought was possible.

Thank you for all of your love and support.

ACKNOWLEDGEMENTS

Thank you to the members of my committee: Dr. McCombie, Dr. Petrulis, and Dr. Williams for all of their advice and help throughout this process. I would like to express my gratitude to Dr. Sue Howell and Mr. Justin Buchman for facilitating research access to Morgan Island and Table Mountain National Park. Without the constant support and encouragement of my mother, father, Katie, Andrew, and Elizabeth this would not have been possible. Thank you to my grandfather, William Carr, for his positivity and prayers throughout the years, and also to all of my wonderful friends who have been nothing but the best! For all of his amazing patience, proof-reading skills, and confidence, I am truly indebted to Kristopher Bash. And finally, thank you to all of the primates that I have met along the way for making me realize how satisfying and fulfilling this journey truly has been!

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CHAPTER 1: INTRODUCTION

Primates face constant challenges when engaging in foraging behaviors, and they must be able to make crucial choices about what food resources to exploit, how to most efficiently process food items, and when to choose one resource over another (Post, 1984). Foraging is broadly defined (Cant and Temerin, 1984) as the "location, acquisition, and assimilation of food," but many factors and pressures affect the outcome of foraging behavior in non-human primates, particularly: what foods should be eaten or avoided, the length of time spent feeding on certain foods, and what food patches will produce optimal foraging and nutritional results (Post, 1984). Most foraging behaviors are learned behaviors (Rapaport, 1999) – selectivity and discrimination in foraging are learned from conspecifics.

Cercopithecines, particularly *Macaca mulatta* and *Papio ursinus*, are highly adaptable and plastic in their foraging behaviors and could be considered the quintessential models for generalist foraging strategies, which allow them to exploit more habitats and resources than other niche-specialized primate species. *M. mulatta* is omnivorous, consuming a variety of fruits, seeds, leaves, gums, grass, clover, roots, bark and small invertebrates (Southwick, 1965; Lindburg, 1971). *M. mulatta* has been documented to eat over 92 different species of plants, but have a tendency to be more frugivorous if resources are available (Lindburg, 1971). *Papio* is also typically described as a generalist omnivore, subsisting on large quantities of grass, seeds, leaves, invertebrate and vertebrate prey, and occasional fruits (Hill, 1966; Kummer, 1968; Altmann and Altmann, 1970; Ransom, 1981).

Key aspects of *Macaca* and *Papio*'s adaptable foraging strategies are the inclusion of a wide variety of food sources and the ability to make pertinent choices about which exploitable food resource best address the specific and immediate nutritional needs with the optimal return on energy expenditure. Seasonal availability of food resources (e.g. flowers and fruits) and exposure to novel food items augment the dietary repertoires of both species and can increase the complexity of foraging choices. While all macaque (*Macaca*) and baboon (*Papio*) group members may employ similar foraging strategies, there are distinct nutritional demands that may affect subgroups (e.g., adult male, adult female, and juveniles) differentially. Nutritional pressures on subgroups of individuals result from ontogenetic, social and reproductive pressures and must be properly addressed to insure the viability and success of the population. These pressures, when most ideally addressed, would demand a particular balance of nutritional input, such as carbohydrates, proteins, fat, and trace minerals (Milton, 1984).

The most nutritionally demanding time periods of a primate's life history occur during the growth and development stage for juveniles and also during gestational and lactational periods for mature females (Lee, 1996; Power, 1999). Adult males must also intake enough calories to maintain strength for mating, dominance and vigilance behaviors. Therefore, the nutritional demands of each subgroup will be somewhat unique, such that the nutritional requirements of a juvenile at the height of the ontogenetic process are dissimilar from that of a fully matured adult. Likewise, the nutritional demands of a lactating or pregnant female differ from the nutritional demands of a male.

1.1: Research Goals and Design

A preliminary and exploratory pilot study was conducted on the *M. mulatta* of Morgan Island. The purpose of this phase of study was threefold: (1) to explore the ways in which the provisioned (and non-indigenous) subjects may exploit additional resources for supplementary nutrition, (2) to gain experience in the specific area of observing and recording the dietary behaviors of a cercopithecine population, and (3) to test different methods of data collection to ascertain the effectiveness of the methods for future studies. The knowledge gained from this specific study was then applied to the second and primary phase of the research, the observation of *P. ursinus* of the Cape region of South Africa.

Given the vast array of food resources that *P. ursinus* is known to exploit and the large quantity of those resources that may be available at any given time, it is likely that some factor or combination of factors is driving the foraging strategy employed by individuals of the species. The analysis of the observations resultant from the exploratory study of *M. mulatta* on Morgan Island seemed to reveal that a dominant motivational factor in supplementary foraging strategy was the mitigation of specific nutritional requirements that were not satisfied in the provisioned diet. The study of *P. ursinus* was designed to both describe the exhibited foraging strategies and to test if nutritional pressures were the primary motivational factor in the exhibited foraging strategies, as opposed to social pressures, immediacy of availability, or individual preferences. For this purpose, the research questions were identified:

- What differences in food resource exploitation or foraging strategies between subgroups (adult male, adult female, juvenile male, juvenile female) can be observed?
- If differences are found between the age and sex classifications, do these differences represent a foraging response to the distinct nutritional pressures that the subgroup would be subject to?

The types of food resources consumed by a wild population of *P. ursinus* at the Cape Peninsula, South Africa were examined to reveal how the subjects were optimizing their dietary choices. Ethological observations were used as a means to document foraging strategy and dietary choices, and differences in herbaceous material exploitation between subclasses were statistically analyzed. Concurrently, the potential nutritional benefits of categories of food resources were assessed to determine basic nutritional composition through subsequent plant identification.

If the dietary preferences and behavioral patterns differ between the subgroups and the nutritional properties of the subgroups' preferred food resources correspond to the most demanding nutritional pressure facing the subgroup, it can be postulated that the individuals are specifically seeking out those resources that most effectively meet their nutritional requirements. Conversely, if these differences are not demonstrated, or if the preferred food resources do not appear to address the most pressing nutritional demands of the exhibiting individuals, it can be surmised that other pressures (such as immediacy of availability or further social pressures) are prioritized over optimal nutritional benefits. This research was conducted to ascertain if adult males, adult females, and juveniles differed in their food preferences and rate of consumption due to the differing energetic

and nutritional demands needed for these physiological processes. The alternative hypotheses were:

- Adult female and juvenile dietary intake would diverge from that of adult males.
- Subgroups (e.g., adult males, adult females, and juveniles) will seek out food resources that most adequately optimize dietary levels needed for separate ontogenetic and reproductive nutritional pressures.

Prior dietary research on *Papio* has focused predominantly on describing foraging strategies (Wasburn, and DeVore, 1961; DeVore and Hall, 1965; Hall and DeVore, 1965; Altmann and Altmann, 1970, Altmann, 1974; Hamilton, et al., 1978; Daegling and Grine, 1999) and optimization (Hill and Dunbar, 2002) on a population or species level. However, differences in dietary optimization and the nutritional pressures affecting subgroups, stratified on the basis of maturity and sex, within a population have not been studied. By analyzing the potential differences amongst these subgroups, this research was conducted to augment the body of knowledge of foraging behaviors exhibited in *Papio ursinus.*

CHAPTER 2: LITERATURE REVIEW

Scientific study is a cumulative process, with the foundations for research built from those studies that have come before. Therefore, an understanding of the studies and findings relevant to *Macaca* and *Papio*, and their dietary choices, provides the basis of knowledge from which these research questions are explored. Taxonomical classification is largely determined by morphological characteristics, many of which are the selected evolutionary result of successful dietary adaptations, and thus, an overview of the taxonomical classification of *P. ursinus* and *M. mulatta* describes the evolutionary foundation that may have shaped extant dietary behaviors. No single and ultimate factor likely determines the dietary choices of a primate. The physiological characteristics of the species are fundamental to the appropriation of a foraging strategy, as physiology largely determines both what nutritional intake is optimal and what food resources the animal is able to exploit. The ecology of the habitat of *P. ursinus* and *M. mulatta* dictates those food resources that are available for exploitation, while the social organization of the species may play a further role in the shaping of an animals foraging strategy. In this regard, the application of theoretical models proves to be a useful method for research design by providing a framework of categorization and understanding – built from prior study – by which the researcher may approach complex topics, such as dietary preference and organization around resources.

2.1: Historical Perspective of Dietary Research

Research previously conducted on primate diets has often been directed toward classifying the subject primates into dietary categories, such as frugivores, folivores, gumnivores, insectivores, and mixed-object and hard-object feeders. Additionally, researchers have sought to identify the specific types of herbaceous materials that are consumed by various species (Milton, 1984; Richard, et al., 1989; Strier, 1992), the manipulation levels and anatomical structures that are involved in consumption (Temerin, et al., 1984; Milton, 1984; Kay, 1984), metabolic requirements and nutrients needed for sustainability (Milton, 1984; Post, 1984), and how all of these variables relate to primate social organization (Altmann, 1974; Wrangham, 1980; Rodman, 1998).

Primates, in general, can be classified into broad dietary groups based on the predominance of certain food types incorporated into their dietary repertoires. Plant material is typically divided into the subcategories of leaves, fruits, flowers, and seeds. (DeVore and Hall, 1965; Southwick et al., 1965; Strier, 1992) Overall intake of categorically defined food types is then analyzed to yield a baseline percentage for food consumption (Strier, 1992), which can then be used to make a generalization about dietary preferences. For example, *Callithrix flaviceps* (Buffy-headed marmoset), and all marmoset species to a certain extent, are classified as gumnivores owing to the 65.8% of their diet that is composed of exudates and gums (Ferrari, 1988). *Macaca nemestrina* (Pig-tailed macaque) is considered to be strongly frugivorous based on the 73.8% of fruits and seeds in its diet (Richard, et al., 1989), while *Gorilla gorilla beringei* (Mountain gorilla) is highly folivorous, consuming 85.8% plant materials, including leaves, shoots and stems (Fossey and Harcourt, 1977). It should be noted that while some

primates may dietarily specialize on one major group of plant material, all primates must choose foods from more than one category to get the required levels of nutrients and energy (Milton, 1984).

In Northern India, Southwick, et al., (1965), observed *M. mulatta* populations eating the leaves and fruits from *Ficus religiosa, Ficus bengalensis, Bauhinia variegata, Melia azadirachta,* and *Tamarindus indica*. *M. mulatta* populations in India are often provisioned at temples and roadsides, creating an inclination for artificial food resources that results in frequent crop raiding (Southwick, et al., 1965; Roonwal and Mohnot, 1977). Although *M. mulatta* are very geographically widespread and prolific, there has not been a wealth of dietary information available for indigenous populations, as most *Macaca* dietary studies have focused on other species within the genus, such as *M. sylvanus* (Menard, 2002), *M. nigra* (O'Brien and Kinnaird, 1997) and *M. fuscata* (Otani and Shibata, 2000; Otani, 2001).

DeVore and Hall (1965) were the first to document the diet of *P. ursinus* in the Cape region. It was noted that noted that *P. ursinus*' diet was extremely variable and eclectic, with a total of 94 different herbaceous materials being consumed. Key foods consumed were divided into the subcategories of leaves, seeds, flowers, and bulbs/tubers, and included: the leaves of *Tetraria*, *Leucospermum conocarpum,* and *Leucadendron*; seeds from *Acacia* and *Metalasia muricata* plants; flowers from *Carpobrotus edulis*, *Cullumia squarrosa*, and *Protea lepidocarpodendron*; and bulbs/tubers from *Watsonia* species (DeVore and Hall, 1965). Other important herbaceous materials in the diet of *P. ursinus* include: *Aristea*, *Salvia africana* (Wild sage), *Myrsine africana* (Cape myrtle), *Taaibos*,

and the fruits of: *Cassine peragua* (Bastard/Cape saffronwood), *Cassine maurocenia* (Hottentot's cherry), and *Olea europea* Africana (Wild olive) (Pauw and Johnson, 2001).

Baboons were observed to excavate holes to uncover roots and tubers, with considerable concentration on subsurface rhizomes. DeVore and Hall (1965) included insectivory as an important dietary preference of the Cape baboons, and had observed individuals turning over rocks looking for insects and reptiles, such as scorpions, centipedes and lizards. Hamilton, et al, (1978) noted that during a massive grasshopper infestation in the Cape region, baboons were more apt to ignore other food resources. Inhabiting coastal regions, *P. ursinus'* has demonstrated a proclivity for marine animals, particularly black mussels, limpets, sandhoppers and crabs (DeVore and Hall, 1965; Pauw and Johnson, 2001; Yeld and Barker, 2004), which further reveals the plasticity of *P. ursinus'* foraging strategies.

2.2: Evolutionary Perspectives on Foraging Adaptations:

The 21 genera and 96 species (Nowak, 1999) of Old World monkeys are taxonomically classified into the family Cercopithecidae, which is then divided into two subfamilies, Cercopithecinae and Colobinae, based on divergence from common ancestors during the middle to late Miocene (Delson, 1994). Cercopithecinae is phylogenetically divided into two taxonomic tribes: the *Cercopithecini* and *Papionini* (Distotell, 2000). There are six cercopithecine genera included in the extant group of *Papioni*, including: *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* (Singleton, 2002).

Most cercopithecines, particularly the papionins *Macaca* and *Papio*, have retained generalized morphological characteristics, in contrast to other more niche-specialized

primates, such as *Daubentonia madagascariensis* (Aye-aye). All cercopithecines, especially papionins, share a number of common morphological characteristics including: flaring molars, broad nasal apertures, relatively long faces, and a diploid chromosomal number of 42 (Singleton, 2002). Other shared features amongst this group include: a dental formula of 2-1-2-3, specialized cheek pouches that aid in the storage and digestion of plant material (Hayes et al., 1992; Napier and Napier, 1997), shorter forelimbs than hind limbs that are adapted for terrestrial locomotion, upper canine elongation, smaller premolars than molars, hands and feet that are capable of a wide range of grasping movements, and a lengthening of metacarpal V (Napier and Napier, 1997; Nowak, 1999).

The generalist skeletal characteristics of *Macaca* and *Papio*, particularly dentition that is suited toward omnivory, allow these species to also be generalist in their foraging strategies, which in turn increases their ability to exploit many different ecological niches (Napier and Napier, 1997). The evolutionary trajectory of *Macaca* and *Papio* establishes that the retention of these generalist morphological characteristics was selectively advantageous as it facilitated successful foraging abilities in a wide range of ecological habitats. Generalists were able to successfully forage on unfamiliar herbaceous materials, effectively compete with other primate species that were restricted to more specialized diets and also had the ability to survive the environmental challenges of resource seasonality and scarcity. This was accomplished by adapting their behavioral and foraging strategies by incorporating diverse food categories to meet nutritional needs (Reed and Bidner, 2004) All of these factors have allowed generalist species to become evolutionarily successful, with a higher degree of reproductive fitness and lower extinction rates than specialists (Hernandez-Fernandez and Vrba, 2005). Additionally,

omnivorous diets may have been a factor in the selection for an increase in relative brain size, as extractive food items, such as seeds and fruits, require a higher degree of cognition to successfully exploit (McKinney and McNamara, 1990).

Melnick and Pearl (1987) state that "if abundance, breadth of distribution, and diversity of habitat are measures of evolutionary success, then the cercopithecines are indeed successful." This statement particularly holds true for the genus *Macaca*, one of the most widely dispersed and environmentally adaptive genera within the primate order (Morales, et al, 1999); macaques are found in more habitats and climates than any other non-human primate (Nowak, 1999; Groves, 2001). There are 20 different species of macaques (Groves, 2001), living in variable habitats and environments ranging in location from North Africa (*M. sylvanus*) to *M. fuscata* populations in Japan (Nowak, 1999). While not as widely dispersed as *Macaca,* baboons are distributed throughout Sub-Saharan Africa, ranging from areas in Guinea (*P. papio*) and northern Egypt (*P. hamadryas*) to *P. ursinus* populations in South Africa (Nowak, 1999).

2.3: Habitat Ecology of *M. mulatta* and *P. ursinus*

M. mulatta populations and subspecies vary considerably in their habitat. *M. mulatta* can be found in semi-desert, dry deciduous, mixed deciduous and bamboo, and temperate cedar-oak forests (Fooden, 1971; Melnick and Pearl, 1987) in eastern Afghanistan, southeastern Pakistan, India and Nepal, northeastern China, Indochina and Hainan (Nowak, 1999).

Like macaques, baboons also dwell in a wide range of different vegetative types, such as: semi-desert, savanna, woodland, rainforest, high-altitude, and coastal areas (Wolfheim, 1983). In contrast to *M. mulatta*, *P. ursinus* has a more restricted geographic

range and habitat, being found in Angola, Mozambique, Namibia and South Africa. Common natural habitats of this species consist of: woodland, grassland, acacia scrub, semi-desert, mountain regions and seaside cliffs (Rowe, 1996). An important component of *P. ursinus'* habitat is the availability of safe sleeping locations, such as rocky cliffs with caves, to prevent predation from African felids (Napier and Napier, 1997).

Geographic variability and location directly influence the types of food resources that are available to *Papio* species. There is little overlap of plant resources in the geographic ranges of the five *Papio* species, particularly with reference to the habitats of *P. anubis* and *P. ursinus*, so it must be assumed that while these *Papio* species are utilizing different plant materials, overall dietary categories will be relatively consistent with expected degrees of dietary variability from ecologically-dependent food availability. For example, Ransom (1981) found that *P. anubis* populations in Gombe National Park consumed a larger quantity of fruits and relied less on terrestrial food resources, such as rhizomes and tubers. Alternatively, *P. hamadryas'* diet is composed of 90% grasses, a resource that is lacking in the Cape region (DeVore and Hall, 1965; Pochron, 2000).

P. ursinus is the largest of the *Papio* species (Wolfheim, 1983). Because of this, they must spend more time feeding to sustain their basal metabolic rates than smaller-bodied primates (Temerin et al, 1984), including other *Papio* species. *P. ursinus* must also spend increased amounts of time foraging because they inhabit an environment that contains only low-quality food resources (Paterson-Jones, 1997; Pauw and Johnson, 2001). Even when fruits are available in the summer months, these resources are limited and widely dispersed, so the baboons must exploit larger quantities of low-quality foods to balance and meet their energetic demands. In order to acquire adequate nutrition in this

environment, *P. ursinus* must spend a greater amount of its time foraging than its savannah counterparts (Pauw and Johnson, 2001). The winter season also has consequence on the number of daylight hours available for foraging activities and brings decreased temperatures, which places an even greater demand on energy requirements needed for effective thermoregulation (Hill (c), 2003). During the winter seasons, foraging activities must be compacted and heightened at the cost of other social behaviors because the days are shorter and colder. Although research was only conducted during the winter months of June and July, other researchers (Hill (c), 2003) have established that as daylight hours increase, time available for foraging also increases, resulting in more flexible foraging strategies that incorporate more opportunity for social behaviors.

2.4: Physiological Characteristics

Macaques are slighter in size and build than baboons, with a lessened degree of sexual dimorphism. In *M. mulatta*, males typically weigh 5.6-10.9 kg, while females range from 4.4-10.9 kg (Rowe, 1996; Napier and Napier, 1997; Groves, 2001). *M. mulatta* has a seasonal birthing period that is largely determined by environmental factors, such as abundance of food resources, rainfall levels and temperature. (Melnick and Pearl, 1987)

P. ursinus located in the Cape region of South Africa are the largest of the baboon species (Wolfheim, 1983), which may reflect the need for a larger body size due to the region's temperate climate. Males and females are differentiated from one another by the large degree of sexual dimorphism, which is seen at its most pronounced forms amongst cercopithecines in the *P*apio genera, as evidenced in canine and body size. Males' mean

weight is 20.4 kilograms – although older and dominant males can weigh up to 40 kilograms (Smithers, 1983) – and females average 16.8 kilograms (Rowe, 1996).

2.5: Social Organization of *M. mulatta* and *P. ursinus*

The social structure of *M. mulatta* follows the multi-male/multi-female pattern with a two-tiered class system that is established by a strict female-bonded matrilineal hierarchy (Rowe, 1996). The two-tiered descriptor of the class system represents separate dominance hierarchies for males and females and the tendency to mate according to hierarchical rank (Nowak, 1999). A hierarchical structure of dominance affects all aspects of the social interactions within *M. mulatta*, especially when determining priority access to desirable food commodities and reproductive partners (Bercovitch and Huffman, 1999). Females are philopatric and form strict matrilines, while males are often peripheral to the group and emigrate from their natal group to several different troops within their lifetimes (Parker, 1990). Social rank of offspring is dependent upon the status of its mother (Kawamura, 1959); daughters inherit their mother's social status and dominance rank. Dominance and hierarchical rank is strictly enforced in *M. mulatta*, more so than most other cercopithecoid monkeys (Bercovitch and Huffman, 1999). Daughters of high-ranking mothers receive less aggression from conspecifics than low-ranking individuals and have priority of access to food resources and grooming partners (Lindburg, 1971).

The social organizational pattern of *P. ursinus* is also multi-male/multi-female, with female philopatry and male emigration. However, *P. ursinus* has a less rigid dominance hierarchy than *M. mulatta*, particularly amongst females (Barrett et al, 2002). Another interesting aspect of *P. ursinus'* social organization is illustrated in their lessened degree

of alliance formations and coalitions, which are common in *M. mulatta*, particularly during intragroop and intergroup agonistic encounters (Henzi et al., 1997). This may be an effect of group size dynamics, as *P. ursinus* groups are often reduced in population when compared to *M. mulatta* and also employ fission-fusion to avoid feeding competition over ideal food patch distributions, thus reducing the selective pressure for coalitionary behaviors amongst kin. When *Papio* kinship coalition formation is present, female reciprocation and interference during disputes occurred at lower levels than was seen in *M. mulatta* populations (Matheson, et al, 2000; Silk et al., 2004).

When *P. ursinus* territories overlap over key resources, contact agonism is often avoided because smaller and weaker troops will usually retreat (Bowlig, 1957). Barrett et al. (2002) noted that female dominance and aggression in chacma baboons might be diffused by grooming bouts increased in both frequency and length. Female dominance rank remains stable and younger daughters assume a status position in the troop that is comparable to that of their mothers (Kawamura, 1959). Younger daughter ascendancy is seen in both *Macaca* and *Papio*, where younger sisters hold a higher rank than their older sisters (Cheney, et al., 2004).

2.6: Theoretical Approaches

The theoretical models applied in the research design of this study were activity budgeting of foraging behaviors (Ferrari and Rylands, 1994; Strier, 1997; Matsumoto-Oda, 2001; Vasey, 2002) and the Optimal Foraging Strategy (Post, 1984). These widely used theoretical models were chosen for application in this research design because they both are intended to provide a framework to specifically approach the analysis of primate foraging strategies.

Activity budgets and feeding-time equations are used as means to examine the affect that diet has on primate social behavior (Ferrari & Rylands, 1994; Strier, 1997; Dunbar, 2001; Matsumoto-Oda, 2001; Vasey, 2002). Primates tailor their activity budgets and time spent foraging according to the availability and type of food resources present. The variability of body size to diet ratio is another factor that influences the allocation of time and energy spent on foraging behaviors, as large-bodied folivores need to spend more time foraging than medium-bodied frugivores and small-bodied insectivores (Milton, 1984). Smaller insectivorous primates employ a time-minimizing strategy in order to meet daily nutritional requirements in the shortest time period possible (Ferrari, 1998), which may be influenced by metabolic rates and high levels of predation. In contrast, larger primates, particularly folivores, instead must maximize the amount of time spent feeding because the quality of food is lower and more substantial amounts of herbaceous material are required to satisfy nutritional demands (Strier, 1992). *P. ursinus'* budgeted foraging activities are directly influenced by both its large body size and the fact that it resides in such a nutritionally-poor environment, and because of these factors, *P. ursinus* must spend more time foraging than other smaller-bodied cercopithecines, such as *M. mulatta*.

The Optimal Foraging Strategy is used as a predictive device to determine how primates should forage when faced with multiple foraging opportunities. According to this model, primates should choose the strategy that "maximizes the expected fitness return," (Post, 1984) while taking into account all of the variables that may be affecting the individual during that time period. In order to promote optimal foraging, a primate must meet its basic needs through sufficient dietary intake of the proteins, minerals,

water, vitamin, and calories (Cant and Temerin, 1984) that are needed for sustaining its biological functioning. Other factors include the context of the environment, such as: climatic variables, the physical structure of the habitat, presence of predators or co-consumers, patch size and its spatiotemporal distribution (Cant and Temerin, 1984). It requires raw energy to process foods and there is a level of energy expenditure that is required to move from one feeding patch to another, and these costs need to be weighed against the body size, age, and sex of the foraging primate. Certain individuals will be affected more strongly by their foraging patterns and must optimize their foraging strategies to include foods that are higher in essential nutritional components, while reducing the amount of energy that is spent processing or locating resources.

The Optimal Foraging Strategy thus provides the framework by which the dietary optimization of the study group can be measured. If the subjects are most effectively optimizing their foraging strategies, they will prefer those resources that most directly meet their specific nutritional demands, while at the same time, balancing the energetic exertion that these resources require to procure. The differences in foraging behaviors in the subgroups will reveal how individuals are addressing separate energetic and nutritional demands, and will demonstrate with foraging activity budgets how much time each distinct subgroup is allocating for particular food resources.

2.7: Nutritional Pressures

All primates need to obtain carbohydrates, amino acids/protein, minerals, water and fatty acids in their diet (Glander, 1981, Serio-Silva, 1996). Foraging primates must seek to incorporate all of these nutritional elements at satisfactory and energy optimizing levels on a daily basis – a process that can be difficult even when there is an abundance

of food resources. Abundant resources may provide some nutritional components, but may be lacking in other critical constituents, such as carbohydrates or protein. Therefore, primates must determine when to continue exploiting abundant food resources and when to seek out scarcer resources that meet these nutritional needs.

Adult females are especially vulnerable to nutritional imbalance during periods of lactation and gestation, as these periods have high energy costs and involve specific nutritional requirements, such as increased requirements for proteins and fat (Lee, 1996; Nogueria, 1996; Power, 1999; Serio-Silva, et al., 1999). Lee (1996) states that most mammalian females must increase their non-reproductive energy intake – 1.5 times normal levels in *Papio* species – during periods of gestation and lactation to sustain energetic balance The success of gestational and lacational processes have also been found to be dependent upon the female's quality of diet even before reproductive events (Silk, 1986; Lee, 1996; Dunbar, et al., 2002), as quality of diet has dramatic consequences on neonatal health. If females are energy-limited prior to conception, they will provide milk at lower levels than normal, causing decreased growth rates in their infant (Altmann and Alberts, 1986; Lee, 1996), even if they have adequate access to nutritional resources during periods of gestation and lactation. Early growth retardation from inadequate maternally supplied nutrition severely affects infant/juvenile females, resulting in higher incidences of disease or parasitic infections and reduced adult size, effectively limiting female reproductive success (Lee, 1996) and continuing a vicious cycle. In highly dimorphic species, such as baboons, male infants/juveniles grow more rapidly and have higher metabolic requirements than female infants/juveniles (Altmann, et al., 1993; Lee, 1996). Males that are born to nutritionally stressed mothers will be

smaller in final body size, more prone to infections and have also lessened reproductive success – consequences that have lasting effects in a species where robusticity and strength are determinants in dominance and hierarchical relationships. Additionally, even juveniles that are born to healthy mothers face nutritional pressures during the process of growth and development. There is a critical time period during the formative years of a juvenile's life when growth rates are at their highest, and if adequate nutrition is not met during this period, final adult size and health will be limited. Juveniles must also spend increased time foraging to make up for lower foraging competency than adults (Janson and van Schaik, 1993). While adult males may be less affected by nutritional stresses on a physiological basis, social factors may exacerbate nutritional demands. In cercopithecine societies, adult males must be able to fulfill their roles during vigilance and maintain dominance and hierarchical rank within the group. If an adult male is not getting enough energy from the food resources that are being consumed, strength reserves will be lessened and he will not be able to defend himself or his group against peripheral males that may challenge his dominance status.

CHAPTER 3: METHODS

3.1: Study Site and Subjects: Morgan Island

Behavioral observation of rhesus macaques (*M. mulatta*) was conducted on Morgan Island, SC during one week in August of 2004, with a total of 12 hours of formal ethological observation. Morgan Island is a 4,500 acre barrier island complex located in the St. Helena Sound near Beaufort, South Carolina (32.465°N, 80.520°W). Approximately 400 acres (161.87 hectares) of this island complex is considered high ground and is current habitat for the *M. mulatta* colony (Gioielli and Crider, 2002). The island was leased in the 1970's for the purpose of utilizing it as a home to a domestic breeding colony of rhesus macaques (Gioielli and Crider, 2002). Like Cayo Santiago, Morgan Island offers field researchers a unique opportunity to study the behavior and ecology of *M. mulatta* in a semi-free ranging and non-indigenous environment.

Morgan Island is an unpopulated island, with no known predators or other large or medium sized mammals, except for the approximately 2, 400 rhesus macaques (at the time of data collection) inhabiting the island (Howell, 2004). The only other known animals to inhabit the area are raccoons, and various avian, amphibian and reptile species. The habitat of Morgan Island could be described as shrub/scrub, bare sand, grassland, and salt marshes (NC Colonial Waterbird Database, 2005), and the environment is dominated by old-growth oak and pine trees, which form a dense forest of deciduous and evergreen species at the center of the island.

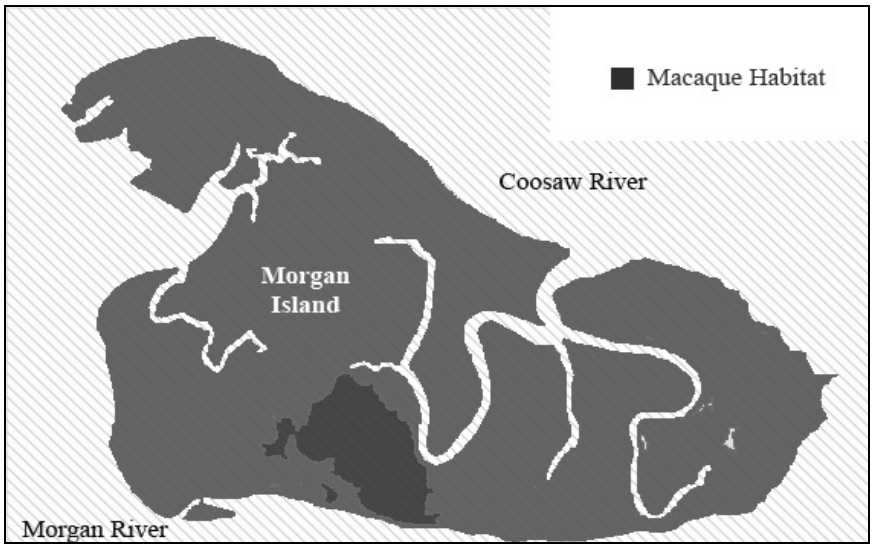

Figure 1. Morgan Island
Adapted from (Beaufort County GIS, 2002)

At the time of the study, there were 31 separate groups of macaques on Morgan Island, and observations were conducted on three of the groups (YA6, YP1, and R1). The groups were allowed to form and maintain naturally and without intervention, but group size on the island was much larger than would be seen in wild groups (Roonwal and Mohnot, 1977) due to artificial breeding environments and provisioned food resources. All of the island's *M. mulatta* groups were provisioned daily at approximately 9:00 AM at the 17 established provisioning stations, which also had water sources that could be manipulated by the macaques to provide fresh water. Documentation (Howell, 2004) was provided that estimated the size the home/day ranges of the macaque groups in relation to landmarks (such as the feeding stations). Given considerable overlap in the groups' home/day ranges, provisioning stations were the only "guarded" areas of the groups' territories and were fiercely defended following the day's provisioning. Only after all high-ranking group members had fed at the provisioning centers would the group move away from the immediate vicinity and allow smaller groups or those without their

own designated territories to feed at the station. Interestingly, territory size did not correlate with group size or number of males. The "C" (n=83, 15 males, 68 females) and "Is" (n=57, 19 males, 38 females) groups had the largest home/day ranges; however, they were smaller in group size and had fewer males than the "R1" group, which was composed of 157 individuals (56 males, 101 females).

Table 1. *M. mulatta* Group Composition

Group Label	Individuals	Males	Females
Y6A	42	16	26
YP1	36	8	28
R1	157	56	101

3.2: Study Site and Subjects: Table Mountain National Park

Behavioral observation of a group of *P. ursinus* was conducted in Table Mountain National Park, South Africa during the winter months of June and July 2006, providing a total of 65 hours of formal ethologically documented observations. The research area was located along the western coast of the Cape Peninsula, between the northern landmark of Menskop Point (34.252°S, 18.378°E), Duitserstent in the south (34.266°S, 18.387°E), and ranging as far east as Die Kloot (34.257°S, 18.387°E). The Cape Peninsula is bordered by the Atlantic Ocean on the west, the Indian Ocean at its southern points, and Bluff's Bay on its eastern coast. *P. ursinus* are indigenous primates to the Cape region of South Africa, an area that is well-noted for its unusual floral characteristics and relatively few contemporaneously surviving large and medium sized mammalian and avian species – as are seen in the rest of Sub-Saharan Africa. *P. ursinus* populations were once spread throughout Sub-Saharan Africa, and may have inhabited the Cape Peninsula for over 1 million years (Yeld and Barker, 2004), but the advent of European settlers brought the massive expansion of urban centers/dwellings (such as

Cape Town and the Cape Flats) which effectively separated the lower ranging Cape baboons from the Western Cape baboons and dramatically decreased their natural habitat (Yeld and Barker, 2004).

The study site was situated along the coastal regions of the Cape Floral Kingdom and Fynbos Biome. The Cape Floral Kingdom spans from the town of Vanrhynsdorp in the Northern Cape, to the Cape Peninsula and Cape Plains in the southern regions, and concludes at Grahamstown region in the Eastern Cape (Jones-Paterson, 2003; Department of Environmental Affairs and Tourism, South Africa, 2005). The entire area covers less than 90,000 square kilometers, yet supports over 8,578 different species of plants, including 955 plant genera and 6 plant families (Yeld and Barker, 2004). The Cape Floral Kingdom, composed of fynbos, is the smallest and richest floral kingdom with the highest concentration of plant species (1,300/10,000 square kilometers) in the world (Maneveldt, 1996). Fynbos literally translates to "fine bush," and was used as a blanket term for the distinctive vegetation types that are dominant in the southwestern and southern Cape regions of South Africa (Cowling and Richardson, 1995). Fynbos species are divided into subfamilies, including *Ericacea*, *Proteaceae*, and *Restinacea,* and various geophytes that consist of over 7,700 different species (Paterson-Jones, 2003). Seventy percent of these species are endemic to the area and are distinct in their leaf-shape composition (Maneveldt, 1996) and ability to grow in nutritionally poor soils (Cowling and Richardson, 1995). Grass is largely absent in this environment, but restiose plants – tall reed-like plants that grow in marshy areas – have filled the niche.

The region's fauna are dominated by herbivorous low-lying grazers/browsers from the Bovidae family, such as *Sylvicapra grimmia (*common duiker), *Raphicerus melanotis*

(grysbok), *Oreotragus oreotragus* (klipspringer), and *Damaliscus pygargus* (bontebok). Other medium-sized fauna found in the study area include: *Hystrix africaeaustralis* (Cape porcupine), *Mellivora capensis* (honey badger), *Orycteropus afer* (antbear), and several *Galerella* (mongoose) species.

There are a total of ten baboon groups, ranging in size from 13 to 100 individuals, native to the Cape Peninsula area (Kansky, 2002). Behavioral observations were focused on the Groot Olifantsbos group, which is one of the smaller groups in the region with only 27 individuals. The Olifantsbos troop was chosen for this particular study because it was one of the more easily accessible and semi-habituated groups in the Cape Peninsula. A group that had not been habituated to any degree would have required a very lengthy research period; as primates, particularly females with young infants/juveniles, are extremely wary of human observers, and males may be aggressive to outside interference.

Table 2. Groot Olifantbos Group Composition

Males	Females	Juveniles	Infants	Total
7	9	9	2	27

The territory of the Groot Olifantsbos group was mapped daily by marking latitudinal and longitudinal coordinates on a map of the Cape Peninsula (Slingsby, 2003). The study group's observed day range was approximately 300 hectares (3 square kilometers) in area and borders both the Olifantsbos and Scarborough regions of the Cape. This compares to the home ranges of other *P. ursinus* groups (Wolfheim, 1983) studied in this region on the smaller end of the scale (210-3367 hectares). An artificial pressure that likely limited the home range size of the study group was the "herding" of the group into designated areas by baboon monitors employed by the park. This "herding" was considered an important function as the baboon group had been known to pose problems in the past by

raiding residential and visitor areas for food (Yeld and Barker, 2004). The baboons retired to high cliffs at night, which were difficult to access on foot, and it is likely that the baboons exploited some of the herbaceous food resources in this area before descending in the mornings. The baboons were most frequently found on one of Table Mountain National Park's small visitor roadways directly in front of the gate of Olifantsbos cottage, and in several foliage patches bordering the beach coasts.

3.3: Data Collection

Classic ethological observation techniques were employed to document the dietary behaviors of the research groups of *Macaca* and *Papio*. Prior to data collection, a standard set of categorized ethological behaviors was compiled from a review of the literature (Hall and DeVore, 1965). All behavioral categories were defined using molecular behavioral units (Martin and Bateson, 1986) and were classified into various subcategories, including: affiliative, aggressive, dominant, foraging/food-related, infant/juvenile related, neutral, sexual or submissive behavioral classes. Antecedently defined behavior lists allowed for definitive and consistent recognition of behaviors and also facilitated the timesaving use of abbreviated codes during the process of data entry and analysis. Upon arrival in each study site and after site familiarization, approximately 2-3 hours were spent performing mock ethological trials to test the validity of the categorized behavior lists in representing the behaviors of the research subjects, and adjustments to the behavior lists were made at this point prior to the commencement of data recording. The ethological techniques employed for observation and data collection were *ad libitum*, scan sampling/zero-one recording, and focal animal sampling/continuous recording (Altmann, 1974; Martin and Bateson, 1986).

Ad libitum recording was used in each research site during the familiarization process in order to provide contextual information about group dynamics and behavioral trends. *Ad libitum* recording is lacking in methodological structure and the data collected by this method are not suitable for quantitative analysis; however, this lack of structure grants the observer liberty from rigid methodology in the hopes of noting any behaviors of interest that could be missed during quantitative ethological trials. During the *ad libitum* observation phase of the studies, description and categorization of the various plants species utilized by *P. ursinus* and *M. mulatta* was also undertaken for later identification of the specimens.

Scan sampling/zero-one recording was the predominant method of data collection with the Morgan Island macaques, and was chosen because it allowed for a better overview of plants being consumed by all group members during such a short observation period. Scan sampling involves the observation of all or multiple group members while zero-one recording defines the recording of behaviors if they are exhibited by the individuals within a defined interval (Martin and Bateson, 1986). Because this method involves recording the presence of simultaneously occurring behaviors amongst multiple group members during intervals of a trial, it provides a more relevant measure of the behavior of the group as opposed to a representative. The scan sampling/zero-one method is most appropriately used when comparing independent groups as it provides data that represent the behaviors of all group members across time and ecological conditions (Martin and Bateson, 1986).

The focal animal/continuous recording (Altmann, 1974) ethological technique was the primary method of data collection employed in the study of *P. ursinus*. In accordance

with this method, representative focal animals for observational trials were randomly selected from stratified groups (adult male, adult female, juvenile). Stratification of the subject animals permits quantitative analysis that provides better representation by segmenting the data amongst groups that are likely to exhibit differing behavioral patterns (e.g., adult vs. juvenile, male vs. female). The focal animal/continuous recording (Altmann, 1974) method facilities a more accurate and detailed representation of the individual's range and frequency of behaviors as the researcher is recording each and every behavior exhibited by the focal animal for the duration of the trial (Altmann, 1974; Martin and Bateson, 1986). This method also protects against much of the bias towards recording of conspicuous behaviors and individuals typical to the scan sampling method (Harcourt and Stewart, 1984; Bernstein, 1991). Focal animal observations collected at Morgan Island were collected via a specifically designed computerized ethological application entitled EthoTracker (Appendix). The usage of an electronic device during behavioral research minimized data processing time and facilitated more consistent data recording. In order to standardize data collection methods across all participating observers, traditional paper checklists were used for data recording during observational periods at the Cape region.

Recording of food-associated behaviors in ethological trials included the behavioral parameters: actor, behavior, plant consumed, part of plant, and level of manipulation. Focal animal sampling/continuous recording trials were also performed in a method that enabled the analysis of time-budget data; a timestamp was recorded for each behavior and change of behavioral state exhibited so that the duration of each behavior could be calculated and analyzed.

Three different observers participated at different points during the study of *P. ursinus*. Inter-observer reliability testing was facilitated by all researchers observing the same individuals concurrently for two focal animal trials. The frequencies of foraging behaviors targeted to specific food categories observed in these trials were tallied for analyses. The results of a Spearman rank correlation were found to be $r_s = +1.00$ between each observer and food category pair, indicating a high degree of reliability between observers in documenting dietary behaviors.

P. ursinus individuals and groups were also recorded with a Panasonic PV-GS32 handheld video recorder during the study period to facilitate additional and more detailed observation of foraging behaviors. Recorded video of foraging behaviors was transferred to a personal computer for review and analysis. Video recordings of foraging bouts for leaves and roots/tubers by 15 individuals (5 adult females, 5 adult males, 5 juveniles) were observed in single two-minute trials for each of the two food categories analyzed. Each two-minute trial involved continuous feeding activity without other behavioral interruption.

In order to properly identify and describe the food resources consumed, habitat and phenological data were collected at each study site to assess the following environmental properties: overall structure, dominant leaf shapes, and floralistic properties (Ganzhorn, 2003). A plant identification sheet with categories for vegetative type, general descriptive qualities, stalk, flower, and leaf shape was created prior to arrival at the study site to be filled out in the field after each instance of consumption by the subject animals was observed during the exploratory observation phase. Plant samples were collected, photographed, pressed for preservation, cataloged according to plant identification sheets,

and assigned numerical codes for later identification. Numerical coding also provided a more structured method for inputting data during focal animal sampling than textual descriptions. A pictorial illustration of dominant plants consumed during preliminary trials was created as a reference tool for plant identification in the field. Plants consumed by the Morgan Island macaques were identified with the help of the staff of Hunting Island State Park, located on another coastal barrier island that has a comparable climate and floral characteristics as Morgan Island.

3.4: Selection of Statistical Tests

In the analyses of the observational data collected, statistical tests were chosen on the basis of their ability to address the research questions posed as well as the ability of the data to meet the assumptions of the tests. The nature of the research questions, number of groups being compared, and the shape of the data distributions were factors used to determine the appropriateness of available tests when applied. All tests were executed in the software package SPSS 12.0 for Windows (SPSS Inc, 2003).

The research questions posed in this study address the differences in foraging strategies between discrete categories of focal animals. Therefore, tests that measure the significance of differences between unpaired groups were chosen. Such tests include: the independent samples *t*-test, one-way Analysis of Variance, the Mann-Whitney *U*-test, and the Kruskal-Wallis test (Dytham, 2003). As a single individual is not a reliable representative of the stratified group to which the individual is assigned, multiple observational trials for each stratified group were analyzed, and thus, these tests that compare unpaired groups can be described as comparisons of the means for the stratified groups. Of the tests identified as appropriate for these comparisons, the *t*-test and Mann-

Whitney *U*-test perform comparisons between only two groups while the other tests support comparisons between multiple groups concurrently. While multiple groups were being compared (such as: adult females, adult males, juvenile females, juvenile males) for each point of analysis, the research questions concern the differences between each of the groups individually (e.g. adult females versus adult males) and not the differences existing between all groups concurrently. The independent samples *t*-test and Mann-Whitney *U*-test were thus determined to be the two most appropriate tests for these group pair comparisons. However, the *t*-test, which is parametric, assumes that the data being analyzed fit a Gaussian distribution (Dytham, 2003), but the Mann-Whitney *U*-test is non-parametric and does not make this assumption. In general, non-parametric tests are more conservative and potentially less accurate than parametric tests (introducing risk of Type II errors), but if the requisite assumptions of the parametric tests are not met, parametric tests are prone to manifest the more dangerous Type I error (Martin and Bateson, 1986; Dytham, 2003).

To determine if the distributions of the data being tested could be accurately described as Gaussian, the Kolmogorov-Smirnov test was employed. This widely used test analyzes two sets of data to determine if they derive from the same distribution (Dytham, 2003). By analyzing the distribution of the data being tested against the Gaussian distribution, the Kolmogorov-Smirnov test reveals whether the distribution of the observational data can be described as Gaussian. For each element of analysis, if the Kolmogorov-Smirnov test revealed a significant ($p < .05$) difference from the Gaussian distribution, the more conservative Mann-Whitney *U*-test was chosen over the *t*-test.

3.5: Supplementary Foraging Analysis (*M. mulatta)*

The primary goal of the pilot study on *M. mulatta* of Morgan Island was to assess which natural food resources from the habitat the provisioned subjects might be exploiting to supplement the provisioned diet. To provide a prioritized list of the supplementary food resources most frequently exploited during observational trials, the frequencies of intervals in which a group member was foraging on a food item from a defined category were summed. These per-trial sums were then compared with Mann-Whitney *U* tests to analyze the significance of variance between the frequencies for each category.

3.6: Foraging Time Budgeted Analysis *(P. ursinus)*

In order to reveal any potential discrepancies between the foraging strategies of subgroups resultant from the time that the focal animals allocated for foraging behaviors, the total time spent in foraging activities per observational trial was summed and divided by the trial duration to calculate a proportion of time budgeted for foraging on a per trial basis. Differences between the proportions for the focal animal categories were analyzed with Mann-Whitney *U* tests.

3.7: Foraging Bout Durations Analysis *(P. ursinus)*

To further describe the foraging strategy exhibited by the research subjects and enhance understanding of foraging optimization, the durations of foraging bouts were analyzed. Foraging bouts were considered to be discrete, and included the procurement, manipulation, processing and consumption of a singular food resource, with a break in activity exceeding no more than 20 seconds. If the focal animal began feeding on another type of food resource, another part of the same food resource, locomoted to another

instance of the same type of food resource, or interrupted feeding activity for greater than 20 seconds, the feeding behaviors were analyzed as distinct foraging bouts. Mann-Whitney *U* tests were used to test the significance of the differences between bout durations for the defined categories of food resources.

3.8: Consumption Rates Analysis (*P. ursinus*)

While the time budgeted for food resources is considered the best metric for quantification of nutritional intake for free-ranging subject animals (Martin and Bateson, 1986), the units of food resource processed in the time budgeted for the resource may vary. Therefore, the rates of consumption for the two most exploited food resources were quantified, to elucidate any further potential differences between the subgroups. This rate was calculated for each consumption rate trial by dividing the number of units consumed by the seconds observed. Video-recorded food resource consumption rates were tested for significance of difference from the normal distribution with Kolmogorov-Smirnov tests. Independent sample *t*-tests were then used to determine the significance of differences between the focal animal categories in rate of consumption.

3.9: Food Resource Preference Analysis (*P. ursinus*)

To identify potential differences in food resource exploitation between subgroups and ultimately assess if the food resource exploitation was a response to the pressure of nutritional demands, the foraging time budgeted for each category of food per observational trial was summed and then divided by the total time spent in foraging activity to identify the proportion of foraging time spent on each food category. Mann-Whitney *U* tests were used to analyze the significance of variance of the proportion of foraging time spent for each food category between the focal animal categories.

CHAPTER 4: RESULTS

4.1: Supplementary Foraging (*M. mulatta*)

The frequency of foraging behaviors for bark or other wood objects observed during scan sampling observations (Figure 2) was significantly greater than that for roots/tubers (U=6.00, *p*=.001), insects (U=2.00, *p*=.000), seeds/nuts (U=5.50, *p*=.001) and lichen/moss (U=.00, *p*=.000). Likewise, the frequency of foraging behaviors focused on leaves (Figure 2) was significantly greater than that for roots/tubers (U=4.00, *p*=.000), insects (U =4.00, *p*=.000), seeds/nuts (U=7.00, *p*=.002) and lichen/moss (U=00, *p*=.000). The frequency of foraging behaviors between all other paired comparisons of food categories were not found to differ significantly.

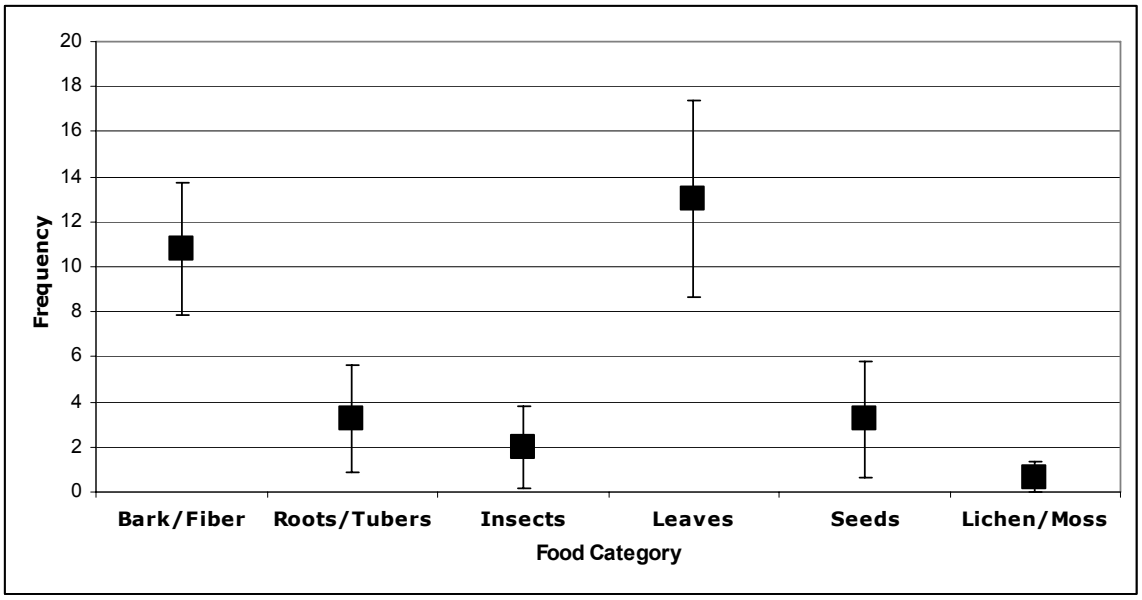

Figure 2. Supplementary Foraging Frequencies

4.2: Foraging Time Budgeted (*P. ursinus*)

The mean percentage of observation time budgeted by the focal animals for foraging activities was 59.74 (SD=26.96). No significant differences were found between the age and sex combinations in time budgeted for foraging (Table 3).

Table 3. Time Budgeted for Foraging (%)

Focal Animal	Time Budgeted for Foraging (%)
Adult Males (N=8)	x=50.02 (SD=35.25)
Adult Females (N=10)	x=64.51 (SD=24.81)
Juvenile Males (N=11)	x=62.74 (SD=25.04)
Juvenile Females (N=8)	x=59.37 (SD=25.58)

4.3: Foraging Bout Durations (*P. ursinus*)

A total of 303 foraging bouts were recorded with a mean bout duration of 133.85 seconds (SD=174.172). Mean bout durations ranged 65.59 seconds (SD=28.99) for flowers to 173.44 seconds (SD=257.85) for roots/tubers (Table 4). Foraging bout durations were not found to differ significantly between food categories.

Table 4. Foraging Bout Durations

Resource	Duration (Seconds)
Flowers (N=17)	x=65.59 (SD=28.99)
Leaves (N=180)	x=137.11 (SD=162.06)
Roots/Tubers (N=59)	x=173.44 (SD=257.85)
Seeds (N=14)	x=96.50 (SD=68.13)
Succulents (N=33)	x=96.30 (SD=95.29)

4.4: Consumption Rates (*P. ursinus*)

The distribution of observed consumption rates (from video-recorded trials) was determined to not significantly differ from the Gaussian distribution ($Z_{(30)}$=.936, p=.345). Adult males consumed units of leaves (Figure 3) at a significantly lower rate than adult females (t(8)=-2.63, p=.030) and juveniles (t(8), p=0.42). While adult males consumed units of foods in the roots/tubers category at a lower rate than adult females and juveniles, these differences are not significant.

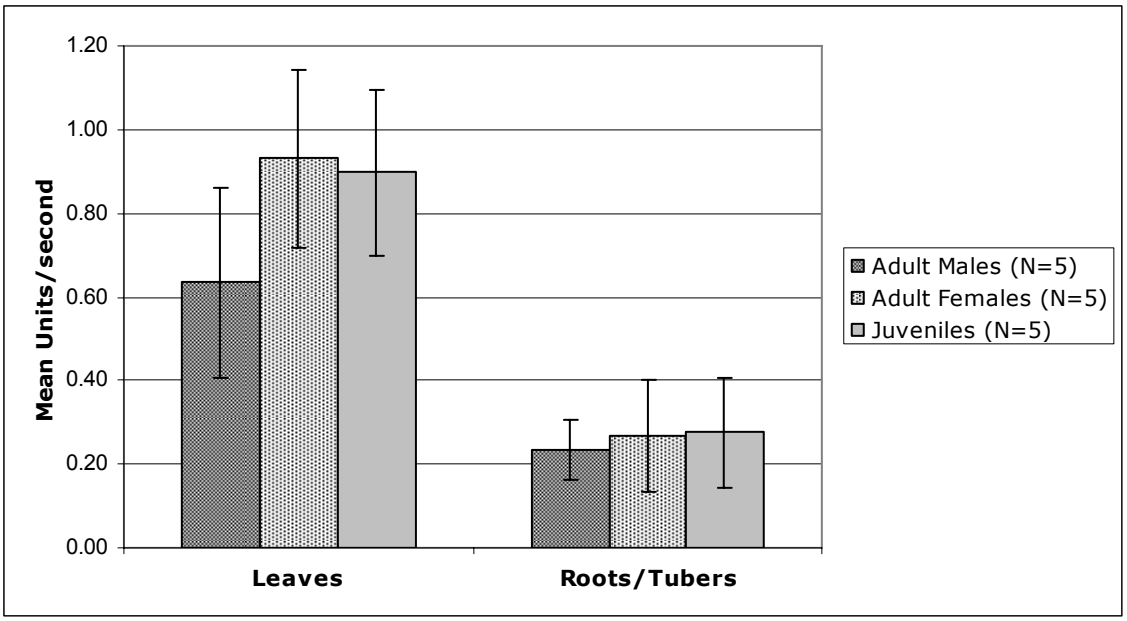

Figure 3. Mean Rate of Consumption

4.5: Food Resource Preference (*P. ursinus*)

The mean percentage of foraging time budgeted for leaves by adult males (Figure 4) was significantly lower than that of adult females (U=17.50, *p*=.045), juvenile males (U=11.50, *p*=.006), and juvenile females (SD=31.80; U=13.00, *p*=.045). Adult males preferred leaves and roots/tubers primarily, followed by succulents, seeds, and flowers. Adult females and juvenile females preferred leaves primarily, followed by roots/tubers, succulents, flowers, and then seeds (juvenile females were not observed in any foraging behaviors toward seeds). Juvenile males preferred leaves primarily, followed by succulents, roots/tubers, flowers, and seeds.

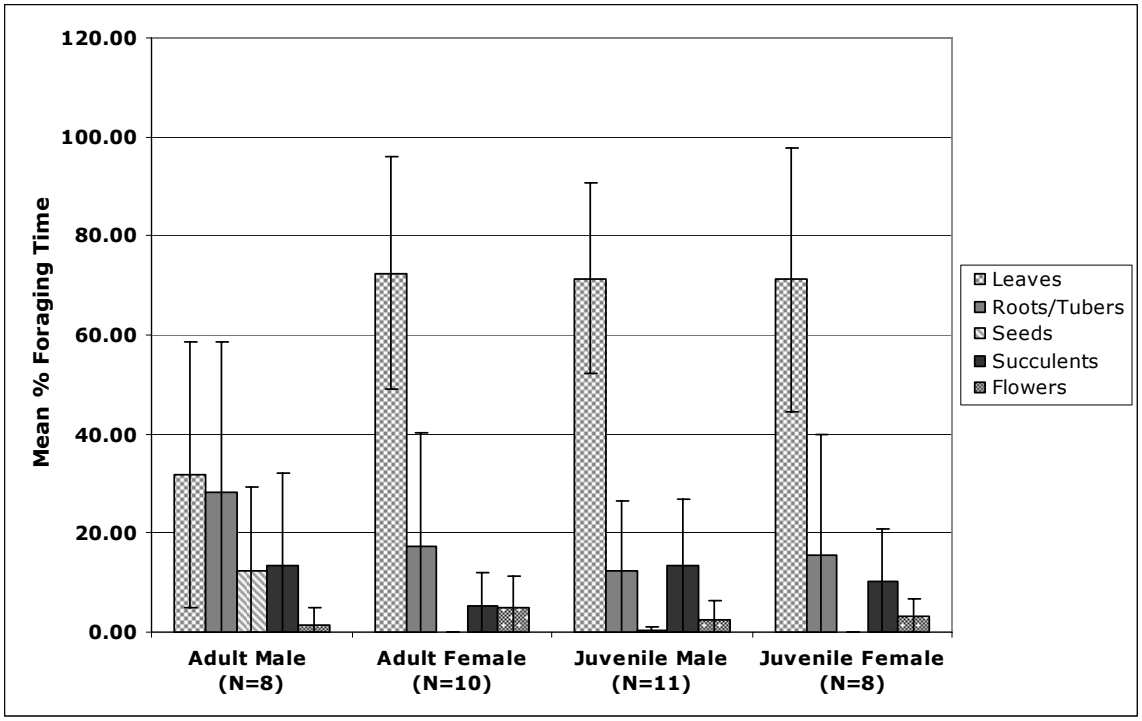

Figure 4. Food Resource Preference

CHAPTER 5: DISCUSSION

5.1: *Macaca mulatta*

Morgan Island offers an opportunity to observe the plasticity and adaptability of *M. mulatta*'s foraging preferences and dietary intake. The vegetative qualities of the island dramatically differ from what would be seen in *M. mulatta*'s natural habitat, yet still yield sufficient nutritional content when used as supplementary foods to a provisioned diet. The macaques supplemented their daily provisioned food of "monkey chow" with several different subcategories of herbaceous materials, including: bark, roots/tubers, leaves, seeds, and lichen, and they were also observed catching and processing various insects. Macaques were observed to eat the fresh and dried pine needles of *Pinus taeda* (Loblolly pine) and *Pinus elliotti* (Slash pine) and the leaves of *Quercus virginiana* (Virgina/Southern live oak), *Quercus laurifolia* (Laurel oak), *Serenoa repens/Sabal serrulata* (Saw palmetto), and *Sabel palmetto* (Cabbage palmetto). Pinecones, and subsequent seeds, from the two *Pinus* species were important food resources utilized by the macaques. Pinecones were pried open using the anterior teeth to access the pine nuts inside. Well-developed lichen specimens were prevalent in the interior old-growth forest sections of the island, growing on the lower portions of trees and fallen branches, which the macaques would scrape from fallen sticks with either their hands or teeth to ingest. Fallen trees were also common in the interior sections of the mixed *Pinus* and *Quercus* forest. Bark, in various states of decomposition and termite infestation, was either pulled directly from living trees or eaten off of the ground.

"Monkey chow" is a high carbohydrate food, but it does not provide much fiber, trace minerals or nutrients (Suhana, et al., 1999). As a food lacking in moisture, it can also cause dehydration during the consumption process, making it necessary for the macaques to consume large quantities of water after provisioning episodes. The frequency of observations of the consumption of leaves (Figure 2) reveals that they were an important supplementary resource. Adult females and juveniles would climb to the highest canopies of *Quercus* trees to gather young buds, a behavior that males did not engage in. It could be possible that adult females and juveniles preferred young leaves/buds and were using this resource as an additional source of protein. From the relatively high frequency of foraging events for bark and wood, one may infer that the subjects were supplementing their diet with this resource to specifically address the deficiency of fiber in their provisioned diet. Roots/tubers and seeds were the next utilized supplementary resource, providing the macaques with additional levels of protein, fatty acids, and carbohydrates.

The short pilot study undertaken at Morgan Island yielded valuable results for later application to the design of the study of *P. ursinus* in South Africa. The macaques exhibited supplementary foraging behaviors that appeared to be directed towards indigenous food resources that would have specific nutritional value. This is certainly noteworthy in a population of cercopithecines who are provisioned daily with "monkey chow" biscuits that are intended to meet all nutritional needs. While one may not expect to see *M. mulatta* consuming the raw fibrous material of bark and twigs, the prevalence of this behavior in the Morgan Island population strongly suggests that the subjects were seeking to address a very specific nutritional deficiency in their primary diet. This provided the framework for the hypothesis – that cercopithecines will seek out those food

resources that best meet their nutritional requirements – employed in the design of the dietary study of the Cape baboons.

The Morgan Island study also proved valuable in the refinement of ethological technique. While the scan sampling observational technique is ideal when applied to intergroup comparisons or when used in an exploratory role to quantify general group behaviors in a short period of time, the increased detail and intrinsic defense against observer bias of the focal animal sampling technique revealed it to be a better method of recording dietary preferences and patterns. Although the requirement to use standardized data collection methods across multiple participating observers in the Cape baboon study prevented the use of the computerized data recording application EthoTracker (Appendix), its use in the Morgan Island observations demonstrated that the employment of such an application expedites data-input greatly and facilitates more rigid standardization of behavioral definition, and thus it will certainly be used again in future studies

5.2: *Papio ursinus*

Baboons are known to be generalists in their foraging strategies and food preferences (Hall and DeVore, 1965), and this is evident from the ethological data collected on *P. ursinus* in the Cape region. Cape baboons were observed to exploit herbaceous materials from a few different subcategories of food resources, such as leaves, roots/tubers, flowers and seeds. Fruit eating was not observed during this time period as the resource was seasonally unavailable, but other researchers (Hall and DeVore, 1965; Cowling and Richardson, 1995; Pauw and Johnson, 2001) have noted its importance during the summer months. The Groot Olifantsbos troop was observed to eat roots and rhizomes

from *Ericacea* and *Restinacea* plants; flowers from *Nylandtia spinosa* (Tortoiseberry) and *Leucospermum conocarpodendron* (Tree pincushion); tubers from various bulb-bearing Ericaceae species, such as the iris, gladioli, orchid and watson plants; as well as the seeds from *Anthochortus capensis* and rooikran species. Leaves were predominantly Protea species and *Oxalis* (clover), and various unidentified succulents were also consumed.

During observational trials, individuals were not documented to eat any vertebrate or insect-prey, but were observed on a few occasions to collect *Docoglossa* (limpets) from the intertidal coastal areas. Individuals would scour the coastal rocks for large-sized limpets and pry them off using their incisors, sitting down among the rocks to scoop the contents out with either their mouths or front hands. This is a delicate and difficult task, as limpets will adhere to the rocks when they sense the slightest bit of movement, so a certain level of dexterity and quickness is required to effectively pry them off before they have time to enact their defense mechanisms. All subgroups (adult males, adult females, and juveniles) of the Groot Olifantsbos troop were observed exploiting this food resource, with females being observed exploiting the resource most frequently. However, it should be noted that this behavior was only witnessed around dusk and was thus outside of the hours of formal ethological observation.

Each food category holds distinct requisite manipulation levels that presupposed successful foraging. For instance, the baboons had to dig deep holes in the sandy soil to excavate roots/tubers and seeds. Grit and sand particles were then extracted from the food items by repeated movements between the hands, a behavior termed “hand washing” by the researcher. Low-lying succulents were also “hand washed” prior to consumption.

Leaves and flowers were merely picked from their respective plants and eaten in their entirety.

The rate at which a focal animal consumes a food resource could be influenced by such factors as the hunger level of the focal animal, the quality of the particular instance of the food resource, the focal animal's affinity for the food resource, or general distractions due to social interactions or vigilance. In regards to the roots/tubers food category, no significant differences were observed between adult females, adult males, and juveniles (Figure 3). In general, the three groups of focal animals for this analysis seemed to process and consume roots/tubers at the same rate. In contrast, adult males did exhibit a significantly slower rate of consumption for leaves than adult females or juveniles. The slower consumption rate for leaves (and to a lesser extent roots/tubers) evidenced by adult males could be the result of mitigated nutritional requirements for this resource, pressures to maintain observant vigilance during all activities, or likely, a combination of both factors. For this food category, juveniles and adult females exhibited virtually indistinguishable patterns of dietary behavior.

While still budgeting the highest percentage of their foraging time for leaves, adult males budgeted a comparable percentage of their total foraging time for roots/tubers (Figure 4) and the lowest percentage of their total foraging time for flowers. Alternatively, adult females budgeted over 70% of their total foraging time for leaves and the lowest percentage of their foraging time for seeds. The mean percentages of foraging time budgeted for leaves were significantly different between adult males and females, revealing a noteworthy discrepancy in foraging strategies. Juvenile males and females evidenced remarkable similarity to adult females in their observed food resource

preferences, allocating over 70% of their foraging time for leaves and the least percentage of their foraging time for seeds.

While these observational data demonstrate that the adult females and juveniles strongly preferred leaves over other food resources, it was noted that they also appeared to be more selective about the leaves that they procured than adult males and were often observed climbing to the tops of Protea shrubs to seek out the youngest and most tender leaves. Leaves, particularly young leaves, contain high levels of protein (Milton, 1979; 1981), and protein is the primary nutritional requirement of both the ontogenetic and female reproductive life stages (Lee, 1996). Adult males were often observed selecting more mature leaves from the base of the shrubs, and did not show a proclivity for younger leaves. In contrast to young leaves, mature leaves are lower in protein and higher in carbohydrates (Milton, 1984).

Adult males also evidenced an overall diet less dependent on leaves with an augmented dependency on roots/tubers (Figure 4), which are additional sources of starchy carbohydrates (Reusch, 1999). Adult males may be able to balance their energetic demands better than adult females and juveniles because the pressures to acquire easily accessible sources of protein are not as high in adult males as they would be in adult females and juveniles, and the nutritional consequences would not be as severe in adult males if needs for protein were not immediately met. Plant materials that are high in carbohydrates provide immediate energy, allowing males to sustain their higher metabolic rates and participate in the highly energetic-demanding activities, such as competition and agnostic encounters, that are involved in maintaining dominance hierarchies (Hall and DeVore, 1965; Packer, 1979; Anderson, 1981). Roots/tubers must

be dug out of the sandy soil at some depth; a process that expends substantial amounts of energy before even acquiring the needed resource. Adult males have the strength to access this food resource more efficiently than adult females and juveniles, making its potential nutritional gains more attractive. Cant and Temerin (1984) have established that the quantity of food items that each food patch yields is determined by the maximum number of items a consumer can harvest. Roots/tubers are found within an abundant food patch, located along the beach in coastal areas, yielding the resource to be yet more attractive to the adult males exploiting it.

With a mean foraging time allocated of over 12%, seeds represented an important food resource to adult males (Figure 4). Juvenile males, juvenile females, and adult females did not exhibit as substantial of a preference for this resource. Seeds are extremely high in protein and fatty acids (Heller, et al., 2002), and thus, seeds likely represent adult males' means of obtaining adequate levels of these nutritional components. Again, the manipulation and processing levels for seeds are higher than the procurement of young leaves, which may explain why males are exploiting this resource differentially.

Succulents store excess water in their roots, leaves and shoots (Sajeva and Costanzo, 1997), providing the baboons an excellent source of water and additional nutrients during foraging activities. Adult males, juvenile males and, to some extent, juvenile females were observed to engage in more vigorous activity than adult females, making it more necessary to replenish hydration through vegetation during foraging bouts and thus likely that they would more frequently exploit this resource.

To determine how effectively the baboons are optimizing their dietary choices, the Optimal Foraging Strategy (Post, 1984) can be applied to reveal further insight. It is evident that the baboons are seeking those resources that meet their specific nutritional needs, but the costs associated with resource procurement and processing also play an important part in the effectiveness of foraging strategies. Notably, adult males were more prone to expend the energy to procure and process roots/tubers and to some extent seeds. For this behavior to be optimal, the energetic return of the resources consumed must be greater than the amount of energy expended to obtain the resources. Since roots/tubers are likewise a rich source of starchy carbohydrates and seeds and are a rich source of protein and fatty acids, it can be inferred that the nutritional composition of these food resources did offset any net energy loss that was required to process them. Adult females and juveniles are meeting their energetic demands by eating higher quantities of leaves, particularly from Protea plants and substantial amounts of clover. It can be expected that these food resources contain sufficient quantities of proteins and carbohydrates to make them preferred over seeds and tubers.

5.3: Conclusions and Future Research

Even for a highly adaptive generalist feeder such as *P. ursinus*, maintaining proper nutritional intake in the nutritionally poor (Pauw and Johnson, 2001) Cape region is not without its challenges. Though the studied group of *P. ursinus* traveled and operated as a group with concurrent access to the same food resources, a discrepancy in foraging strategies between certain age/sex classifications was demonstrated. Adult males consumed leaves at a significantly slower rate, and exhibited a significantly lower preference for leaves – incorporating more roots/tubers – than did adult females, juvenile

males or juvenile females. Overall, adult females, juvenile males, and juvenile females exhibited very similar foraging strategies.

Through a review of the literature, it was surmised that a diet optimally addressing the most pressing nutritional demands would be: high in carbohydrates for the active adult males, high in protein for the ontogenetically-stressed juvenile males and females (Lee, 1996), and high in protein for gestating, lactating, or sexually receptive adult females (Lee, 1996). As adult males revealed an increased reliance on roots/tubers that are high in starchy carbohydrates and a tendency to consume higher carbohydrate mature leaves and adult females and juveniles exhibited a preference for high protein leaves (particularly the young leaves that they sought out), the subject animals optimized their foraging strategies to address those demands that were expected to be the most nutritionally prioritized. While the individual aptitude of the subgroups to procure certain food resources – such as adult males' ability to exert the strength and endurance required to dig for roots/tubers and juveniles' ability to climb higher in foliage due to lower body weight to procure younger leaves – likely provided extended motivation in the selection of dietary factors, nutritional pressure weighted most heavily in the selection of dietary resources.

The application of the Optimal Foraging Strategy (Post, 1984) to wild populations of primates is valuable in revealing which food resources are necessary for overall nutritional and energetic maintenance. This study lends credence to theories that primates are competent foragers, even in the harshest of conditions, and are able to make concise decisions during foraging bouts based on specific nutritional pressures. Additionally, this research has made apparent the discrepancies between subclasses of individuals and their

preference for food resources that are the result of separate physiological energetic constraints during social, ontogenetic and reproductive periods.

Evolutionarily, generalists have been extremely successful, which is confirmed by the abundance of primate generalists, especially *Macaca* and *Papio*, and the fact that the species of these genera are able to survive in a wide range of environmental conditions. Adult males, adult females and juveniles differ in their nutritional requirements and dietary intake of carbohydrates and protein. Therefore, it can be assumed that selective pressures have shaped generalist foraging behaviors within these subgroups as a means to incorporate a diversity of food items in order to meet the differential nutritional requirements. Dietary optimization directly influences reproductive fitness, and thus it can be inferred that these differences in dietary choice between subgroups has given cercopithecine species a fitness advantage throughout their evolutionary trajectories.

The results put forth in this study provide a foundation for substantial and fascinating future research. Notably, the execution of a multi-seasonal study of *P. ursinus* in the Cape region would reveal how dietary behaviors and preferences change with seasonal availability of food resources (such as fruits). Longitudinal studies of juvenile male baboons as they age into adulthood could demonstrate at what point their dietary behaviors break from the similarity to adult females and become like that of the adult males and provide further evidence to the changing nutritional requirements that correspond with the physiological changes of maturation. Likewise, more focused study on breeding adult females as they go through pregnancy and nursing might demonstrate how the heavy nutritional demands of gestation and lactation manifest in behavioral dietary change amongst *P. ursinus*. Comparative studies between *Papio* and the other

cercopithecine generalists, *Macaca,* in their natural habitats have the potential to reveal a more specific model for the selection of food resources due to nutritional demands, ecological availability, and energy costs of procurement, and such a model could possibly be applied to other generalist non-human primates.

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APPENDIX: ETHOTRACKER

Traditionally, ethological data recording has involved the use of paper checklists that are later input manually into computer spreadsheets for statistical analyses. Manual input of observational data is a time-consuming process and can be prone to error. To address these concerns for this and future research projects, a novel handheld-computer application, referred to as EthoTracker, was designed by the researcher to provide more efficient observational data entry and extraction.

The design involved an analysis of ethological checklist formats, behavior lists, and focal animal lists in order to define a desired user interface and data handling mechanisms for the application. EthoTracker was developed in Microsoft's Visual Basic.NET programming language for the Microsoft Windows PocketPC operating system. This platform was chosen for its ease of interoperability with the widespread Microsoft Windows personal computer operating system.

The EthoTracker application consists of two components: one for the handheld computer (Figure 5) and one for the desktop computer. The handheld computer application is used for observational data entry and the desktop component is used for data extraction and preparation for analysis. Behavior lists and focal animal lists can be modified from either component. The use of a computer application with predefined behavior lists allows the researcher to quickly input behaviors as they occur with automatic recording of the focal animal, timestamp, and duration of the behavior. As data are initially input into a database and do not require further manual input, the duplication of data entry is eliminated.

The development process for the EthoTracker application initially involved the presentation of a list of design goals and requirements to the software developer. A series of prototypes were analyzed and revised before a working product was put forth. This working product was then subjected to pilot testing by performing multiple observational trials on captive gorillas and lemurs at Zoo Atlanta. Data from these trials were extracted and analyzed with exploratory statistics and further revisions to the data recording and user interface aspects of the application were submitted to the developer. Further pilot testing, debugging, and revision were carried out prior to the application being utilized in data collection during the first stage of this research project.

Figure 5. EthoTracker User Interface