ONTOGENETIC RESOURCE PARTITIONING IN WHITE FACED SAKIS (*PITHECIA PITHECIA)*

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CHAPTER I

INTRODUCTION

Primates exhibit a wide diversity of feeding strategies that are inherently linked to phenotypic differences that allow species to exploit some resources (i.e. fruits, leaves, insects) more efficiently (Anapol and Lee 1994). Phenotypic variation may also lead to differential feeding strategies among conspecifics (Agostini and Visalberghi 2005). Differences in body size associated with sex or age-class as well as differences in foraging experience associated with ontogeny are commonly cited as factors that may lead to within-species dietary variation (Clutton-Brock 1977, Janson and van Schaik 1993, Tarnaud 2004, Agostini and Visalberghi 2005). Variation in feeding ecology among primates may be important for establishing group size and home range size as well as the number of individuals that can stably coexist in an ecosystem (Svanback and Bolnick 2007).

The acquisition of juvenile foraging skills recently has received significant attention as juvenile's often experience high mortality rates associated with starvation (e.g. Janson and van Schaik 1993, Fragaszy and Boinski 1995, Gunst et al. 2008). Thus, any adaptations that improve a juvenile's ability to acquire food may be particularly important from an evolutionary perspective. Phenotypic variation between juveniles and adults may lead juveniles to adopt unique feeding strategies both to emphasize those resources best exploited by the juvenile phenotype and as a means to reduce competition for resources with adults. Many studies have focused on the acquisition of foraging skills among juveniles and thus, emphasized the behavioral aspect of within-species dietary variation (e.g. Harrison 1983, Fragaszy and Boinski 1995, 1997, Taurnaud 2004). Comparatively fewer studies have investigated how morphological limitations affect juveniles foraging ability (but see Gunst et al. 2008). In particular, the physical and mechanical properties of foods may limit the resources juveniles can potentially consume. This may be a particularly important factor in species that routinely target mechanically challenging foods, such as the pitheciins. In this study I investigate differences in feeding strategies between adult and juvenile white-faced sakis (*Pithecia pithecia*), and also address the role of physical and mechanical properties of foods in contributing to dietary variation.

Resource Partitioning

Schoener (1971) suggested that in order to coexist, species must vary in their use of resources in at least one niche dimension. This division of resources among species in a community is commonly referred to as resource partitioning. Schoener (1974) proposed three major dimensions by which species partition resources in decreasing order of importance: habitat, food type, and time, where partitioning can occur along one or more of these dimensions. Resource partitioning by habitat refers to differences in resource utilization by space including differences in either macrohabitat (e.g., vegetation zone) or microhabitat (e.g., forest strata). Partitioning by food type can be the differential use of food species, food chemistry, the physical and mechanical properties of food items, or differences in dietary diversity. Temporal resource partitioning is usually studied in terms of how animals differ in their use of habitat and food type on a daily or annual basis (Schoener 1974; 1986). In many cases, seasonal shifts in food availability or distribution lead to differences in resource usage, where species overlap significantly in food type or food species when food is abundant, but utilize different resources when food is scarce to avoid the effects of overexploitation (Schoener 1986, Overdorff 1993, Vasey 2000, 2002).

Resource partitioning is usually studied between sympatric species that share some similarity in feeding strategy (Schoener 1986), with the intent of understanding the limitations that competition places on the number of species that can stably coexist in an ecosystem (Schoener 1971). Resource partitioning is sometimes considered an evolutionary response to competition where species develop phenotypic and behavioral differences that allow them to exploit different resources (Walter 1991). In other instances, the term is simply applied to the differential use of resources among species, regardless of the origin of those differences or whether the differences are indicative of competitive interactions (Walter 1991).

Many studies of resource partitioning have treated members of the same species as ecologically equivalent, generally ignoring the variation that exists among individuals within a species. This is only appropriate if variation among conspecifics is limited or has little effect on their ability to exploit resources (Bolnick et al. 2003). Many times, individuals or groups of similar individuals within a species (i.e. sex classes, age classes, morphotypes) exhibit more phenotypic or behavioral variation than equivalent members (i.e. same sex, same developmental stage) of closely related species. Thus, the same principles that favor interspecific resource partitioning may also apply at the *intra*specific level (Polis 1984). Polis (1984) refers to subgroups of phenotypically similar individuals as “ecological species” because they partition resources similarly to separate species. Although intraspecific resource partitioning may be a product of phenotypic variation within a species, it is thought that sometimes natural selection maintains intraspecific variation to reduce competition among conspecifics (Svanback and Bolnick 2007).

Among primates, resource partitioning has been demonstrated along each of the major niche dimensions including microhabitat usage (e.g. Overdorff 1993, 1996, Vasey 2000; Grassi 2002), food type (e.g. Gautier-Hion 1980, Vasey 2000; dietary diversity, Fragaszy and Boinski 1995, Grassi 2002; chemical properties, Ganzhorn 1988,1989, Yamashita 2008; morphological characters, Gautier-Hion et al 1985; mechanical properties, Kinzey and Norconk 1990, Yamashita 1996, 1998), and temporal separation (e.g. Vasey 2000, 2002, Chapman 1987, Gautier-Hion 1980, Overdorff 1993). Comparatively fewer studies have investigated resource partitioning within primate species, although this factor may be considerably important (but see Gautier-Hion 1980, Vasey 2002, Grassi 2002). In a noteworthy study of African forest monkeys, Gautier-Hion (1980) found that intraspecific sex differences in diet sometimes exceeded interspecific differences. In this case, sex classes within a species fit Polis’s (1984) definition of ecological species.

Source of dietary variation

The relationship between an animal’s feeding efficiency and reproductive fitness is well established (Schoener 1971; 1974; 1986; Gaulin 1979). Failure to feed efficiently can delay sexual maturity, reduce fertility, reduce litter size, lower ovulation rates, shorten breeding seasons, cause lactational failure in females, and reduce sperm count, sperm motility, and success in competitive interactions in males (Gaulin, 1979, Janson and van Schaik 1989). Individuals that feed most efficiently grow the quickest; are least affected by predation, parasites, or starvation; and produce the most offspring. Thus, animals that feed most efficiently have the highest fitness and natural selection shapes feeding strategies to optimize feeding efficiency.

Models of foraging theory predict that animals should target food items that yield the most energy per unit foraging time (Schoener 1971; Gaulin 1979). A food item's energetic value can be roughly approximated with the following equation developed by Schoener (1971):

$$\frac{e_i}{t_i} = \frac{\text{potential energy- pusuit cost- handling and eating costs}}{\text{pursuit time+ handling and eating time}}$$

where e_i/t_i is an index of net energy yield per unit time for items of type i (Gaulin 1979). Different food items offer different net energy yields such that they can be effectively ranked by energy value. An individual can optimize its feeding efficiency by consuming foods with the highest net energy yield and avoiding those with the lowest. However, if an animal cannot acquire sufficient energy from the highest ranked food items, it should increase its consumption of lower ranked food items until it meets its metabolic requirements (Gaulin 1979).

An individual's feeding strategy reflects a complex interaction between intrinsic (e.g., phenotype: morphology, physiology, behavior) and extrinsic factors (e.g., environmental factors: resource characteristics, competition, social relationships, and predation) that affect the relative value of food items (Oates 1987, Bolnick et al 2003, Lambert 2007). Food items may vary in relative value among individuals with respect to the unique set of interactions between phenotype and environment. Thus, for every individual there exists a unique feeding strategy that maximizes feeding efficiency (Bolnick et al. 2003) and natural selection shapes phenotypes to cope with the environmental factors to improve feeding efficiency on a particular set of resources. Svanback and Bolnick (2005: 996) suggest that specialization on a particular set of resources "…occurs when individuals have different optimal diets due to variation in search, handling, or digestive abilities." The same phenotype-environmental correlation that leads to interspecific differences in diet strategy may also lead to differential feeding strategies among conspecifics. Differences in body size among conspecifics (Calder 1983, Werner and Gilliam 1984, Ford and Davis 1992, Marroig and Cheverud 2005) and *intra*specific competition (Clutton-Brock 1977, Janson and van Schaik 1989, Field et al 2005, Svanback and Bolnick 2005) are commonly cited as fundamental factors that lead to different feeding strategies within a species.

Body Size

Body size is a fundamental factor shaping an animal's feeding strategy as it has a predominant influence on an the animal's energetic requirements, potential to exploit resources, and susceptibility to enemies (Calder 1983, Werner and Gilliam 1984, Ford and Davis 1992). The scaling relationship between body size and metabolism is fundamental in determining energetic requirements and by extension, shaping an animal's feeding strategy (i.e. the Jarman/Bell principle, Gaulin 1979, Ford and Davis

1992). The Jarman/Bell principle is best understood by considering basic geometric relationships between surface and volume. The surface area of an object increases to the 2/3 power of volume such that smaller objects have relatively more surface area per unit volume than do larger objects (Gould 1966). In animals, surface-to-volume ratios are an important factor affecting heat loss, where smaller animals have a higher surface area per unit body mass so that they expel heat more rapidly than large animals. Consequently, smaller animals usually have higher metabolic rates than do larger animals, and must adapt feeding strategies accordingly. Age or sex classes within a species often exhibit similar or more variation in body size than equivalent members (i.e. same sex or developmental stage) of different species (Polis 1984, Werner and Gilliam 1984). As a result, groups of individuals within a species may adopt unique dietary strategies to cope with the unique physiological opportunities and constraints that result.

Larger conspecifics may be able to access some resources unavailable to small individuals simply because they are stronger. For example, adult male primates may be able to consume tougher fruits than immature primates because they have greater jaw strength that allows them to overcome the mechanical challenges of those food items (Janson and van Schaik 1993). Conversely, smaller individuals may experience some foraging advantages in that their body size allows them to utilize resources insufficient for larger animals, or simply unavailable to larger animals. For example, among brown capuchins, juveniles and subadults can hang by their feet beneath palm fronds to search for insects, while adult body size increases the chance of breaking the fronds and falling (Janson and van Schaik 1993).

Competition

Competitors are often considered one of the most important extrinsic factors shaping an animal's feeding strategy. Competitors can be any individuals that share common resources including members of other species as well as conspecifics (Schluter 2000). As the number of individuals sharing a common resource increases, the rate of resource depletion also increases. Thus, there is less available to each individual such that they are forced to include less valuable items in their diets (Schoener 1971; Gaulin 1979). If individuals must consume less valuable resources, they may have less energy available to allocate to reproduction and are more likely to succumb to starvation. Thus, any adaptations that reduce competition should have a selective advantage (Field et al. 2005).

Janson and van Schaik (1989) suggest that intraspecific competition may be more intense than interspecific competition. In this case, it would be highly advantageous for conspecifics to adopt different feeding strategies to avoid competition and avoid the potential to overexploit resources. Conspecifics may at times capitalize on phenotypic variation (e.g. body size) that allows them to exploit different resources than others. This may be particularly important for smaller individuals that are most likely to be competitively excluded. In primates, there is an inverse relationship between the amount of aggressive competition a juvenile receives and its likelihood of surviving to adulthood (Janson and van Schaik 1993). Thus, any alterations to a juvenile feeding strategy that reduce competition with adults should have a selective advantage.

Resource Partitioning by mechanical properties

Many studies suggest that the physical and mechanical properties of food items may provide a mechanism for resource partitioning (e.g. Gautier-Hion 1985, Kinzey, and Norconk 1990, 1993, Kinzey 1992, Rosenberger 1992, Yamashita1996, 1998, Lucas et al. 2000, Norconk et al. in press A). Generally, the physical properties of foods refer to the external factors including size, shape, roughness etc. The mechanical properties of foods are the internal properties that resist breakdown such as strength, toughness, and deformability (Yamashita 1998). The various components of fruits (or leaves, Teaford et al. 2006) pose different biomechanical challenges to herbivores, and provide a basis for morphological variation (Rosenberger 1992). Due to differences in masticatory morphology, some animals may be better than others at overcoming the mechanical challenges of foods (Hylander 1979).

To ingest most food items, a primate must first break off smaller pieces, often with its teeth, which involves overcoming the mechanical properties of the food (Lucas et al. 2000, Lucas 2004, Wright 2005). The application of teeth to a food item causes deformation of the item, and if sufficient deformation occurs, a crack begins to form. To successfully initiate a crack, an animal must generate a certain level of stress on the object, where stress is the force per unit cross sectional area over which it is applied. The two major mechanical defenses plants employ to deter herbivores are hardness and toughness (Lucas et al. 2000). Hardness has been described as “the resistance to deformation under indentation” and is measured as force per unit surface area of the crack generated (Lucas 2004). Hardness is considered a stress-limited defense (Lucas et al. 2000) in that consumers are limited by their ability to produce bite force or in the surface area of their teeth. Toughness is a displacement-limited defense. It is described as the resistance to crack propagation in a material and is measured as the work done in making a new area of crack. Foods that are considered “tough,” deter herbivores because their tissues deform without cracking, beyond the displacement a predator can generate by closing its jaws (Lucas 2004).

The relationship between the masticatory apparatus and body size is sometimes used to explain interspecific patterns of dietary variation (e.g. Norconk et al. in press B). The forces produced by the jaw muscles (i.e. temporalis, masseter) increase with body size (Dechow and Carlson 1990) with respect to differences in the physiological cross sectional area (PSA) of the muscle (Anton 1999). Consequently, smaller animals generate less bite force. Mandibular robusticity also varies with body size for the same reason. Norconk et al. (in press B) suggest that in resisting loads during mastication, a bigger mandible is better. Thus, smaller animals cannot dissipate forces as effectively during mastication.

Smaller individuals have smaller mouths and consequently, must have smaller teeth (Cochard 1985). In addition, deciduous dental patterns differ from adult patterns where adults have more teeth than immature individuals. The result is a reduced surface area over which foods can be processed, and a reduction of the rate at which foods can be consumed. Furthermore, larger teeth are generally considered an adaptation for processing hard-object foods (Norconk et al., in press A), such that small individuals may be at a disadvantage in processing mechanically challenging foods (Norconk et al. in press A). If a species is adapted to processing challenging food items, as in the case of sakis and uakaris, immature individuals may be at a significant disadvantage in harvesting resources.

Juvenile primates

The juvenile period is particularly important in primates as it is the first period of time when an individual is responsible for acquiring its own resources. Juveniles are considered to be at a disadvantage when foraging both because they are smaller than adults and thus cannot necessarily exploit all of the same resource that adults do, and are also less experienced foragers. Furthermore, small body size and lack of experience may lead juveniles to be competitively excluded by adults.

Foraging skills often require a learning period before an individual can maximize feeding efficiency. Thus, immature primates forage less efficiently than adults before they master the appropriate skills (Janson and van Schaik 1993; Fragaszy and Boinski 1995, Tarnaud 2004). During this time, immature individuals may favor more easily accessible resources to cope with reduced rates of food consumption. Furthermore, dietary breadth of immature individuals may be narrower. As primates age, they get progressively more efficient at exploiting resources. Janson and van Schaik (1993) cite three kinds of experience that allow immature primates to improve feeding efficiency: direct observation (of adults), trial and error, and practice.

Juveniles often experience higher mortality rates than adults due to starvation (Field et al 2005; Janson and van Schaik 1993). Thus, natural selection should favor any strategies that improve survivorship. Juveniles may adopt different foraging strategies than adults to make up for reduced feeding efficiency relative to adults and to cope with different physiological demands related to differences in body size. Additionally, juveniles may devote more time to foraging than adults. In a survey of 16 studies Janson and van Schaik (1993) estimate that juveniles spend an average of 5% more time foraging than adult females and 27% percent more time foraging than adult males (Janson and van Schaik 1993). To make up for narrower diet breadth, juveniles may consume a higher proportion of more easily obtained resources (Fragaszy and Boinski 1995). Juveniles also benefit from food sharing with adults. For the most part, food sharing occurs between mother and offspring when a resource is difficult for the offspring to obtain such as those resources that require considerable strength to access or complex skills to manipulate (Fragaszy et al. 1997).

Few examples exist in the literature relating the physical and mechanical properties of food to ontogenetic dietary differences. However, Terborgh (1983) found that in *Cebus apella*, the mechanical properties of palm nuts may inhibit smaller individuals from accessing them. Adult males can bite open the nuts with a 60% success rate. Females use one nut as an anvil on which to hit another achieving a 43% success rate. Juveniles bang the nuts against a palm frond, achieving a 33% success rate (Janson and van Schaik, 1993). As differences in strength and morphology affect an individual’s ability to cope with the mechanical properties of foods, differences in body size should be an important factor influencing the foods an individual can consume, particularly among age groups. In species that commonly target challenging food items, the mechanical properties of foods may be a major factor shaping differences in diet among age groups.

Platyrrhines and Pitheciins

The platyrrhines have been a common group in which to study resource partitioning (i.e. Hershkovitz 1977; Rosenberger 1992; Anapol and Lee 1994; Marroig and Cheverud 2001, 2005; Norconk et al. in press A). The adaptive radiation of the platyrrhines is associated with migration into new feeding niches accompanied by changes in body size (i.e. phenotypic variation), such that body size and diet are strongly correlated (Hershkovitz 1977, Ford and Davis 1992, Rosenberger 1992, Marroig and Cheverud 2005). Variation in body size among the plattyrhines and its consequences on resource exploitation provides an excellent mechanism for species to partition resource, and may have important implications for intraspecific resource partitioning.

Among the platyrrhines, the pitheciins (genera *Pithecia*, *Chiropotes,* and *Cacajao*), are characterized as seed predators because they consume the seeds of both ripe and unripe fruit (Kinzey and Norconk 1993, Norconk et al.1998, Norconk and Conklin-Brittian 2004, Norconk 2007). Seed consumption is advantageous because seeds are often rich in fat and protein such that they are high in calories per unit volume and provide valuable nutrients (Norconk and Conklin-Brittian 2004, Norconk et al. in press B). However, seeds are often protected by hard or tough outer layers to deter potential predators. Thus, animals that consume seeds routinely encounter mechanical challenges that they must overcome if they are to feed (Kinzey and Norconk 1990, 1993, Lucas et al. 2001). To access seeds, the pitheciins adopt a feeding strategy known as sclerocarpic foraging (Kinzey and Norconk 1990, Kinzey 1992, Norconk et al. in press B). This strategy is a multistage process for harvesting fruit that includes extracting a seed from the fruit or seed coating with the anterior dentition followed by mastication with the molars (Norconk in press B). Sclerocarpic foraging allows pitheciin monkeys to acquire nutritious seeds with reduced tannins that are softer than those ingested by other frugivores (Kinzey 1992, Norconk and Kinzey 1990, 1993, Norconk in press B).

Sclerocarpic foragers address mechanical challenges with the anterior dentition such that they exhibit a number of adaptations for resisting loads at the anterior of the mouth. Masticatory muscle leverage is more balanced between the masseter and temporalis than in other ceboids (define), which Anapol and Lee (1994) suggest is correlated with opening hard foods. The pitheciins exhibit an increased moment arm of the temporalis muscle relative to other primates, which increases muscle leverage along the length of the mandible (Anapol and Lee 1994). Pitheciins also have robust mandibles for resisting the forces produced during the processing of hard objects. Although the pitheciins commonly consume the seeds of hard food items, the seeds are usually soft (Kinzey and Norconk 1990, 1993; Kinzey 1992). Hence, mandibular robusticity is likely an adaptation to handle the forces generated while opening a fruit rather than chewing (Anapol and Lee 1994). The robusticity of the jaw extends through the symphysis, which increases its ability to resist bending and dorso-ventral shear (Hylander 1984; Anapol and Lee 1994).

All of the pitheciins have well-adapted anterior dentition including large, laterally splayed canines, for breaking open hard fruit and incisors that are "…inclined anteriorly from root to tip of crown, forming an efficient nipping or cropping device" (Kinzey 1992). While the anterior dentition of the pitheciines is adapted for overcoming mechanical challenges, the low occlusal relief and crenulated surface of the molars suggests an adaptation for masticating relatively soft dietary items (Kinzey 1992). Kinzey (1992) suggests that grinding, rather than crushing may be the major function of the pitheciine molars.

White-faced sakis (Pithecia pithecia)

Members of the genus *Pithecia* exhibit slightly smaller and less robust canines and incisors than do other members of Pitheciinae, as well as reduced mandible robusticity. This suggests that *Pithecia* may consume seeds from fruit that is slightly less challenging than fruit eaten by *Chiropotes* or *Cacajao*. Kinzey and Norconk (1993) found that *Pithecia pithecia* consumed seeds from fruit of a maximum puncture resistance of 6.8 kg/mm^2, which is much lower than the maximum resistance of seeds eaten by *Chiropotes* (37.8kg/mm^2), but still higher than those consumed by *Ateles paniscus*, a non-seed predators (1.4 Kg/ mm^2).

That *P. pithecia* routinely encounter mechanically-challenging foods has interesting implications for ontogenetic dietary variation. Immature individuals may be limited in their ability to exploit some of the more challenging items that adults may routinely consume. The difference in ability to exploit mechanically-challenging foods should affect a juvenile's foraging strategy. If juveniles cannot consume the most challenging food items, they may increase their consumption of less challenging food items, thus decreasing diet breadth. This may have additional effects on other aspects of resource partitioning as well. If age groups consume different proportions of certain foods, they may utilize different areas of the forest as well, in response to where preferred foods are most abundant. Juvenile white-faced sakis should alter their dietary strategies to compensate for reduced rates of feeding compared with adults. Thus, this group of platyrrhines should be ideal for investigating the effects of the mechanical properties of foods on ontogenetic resource partitioning.

CHAPTER II

HYPOTHESES

I investigated ontogenetic resource partitioning in white-faced sakis (*Pithecia pithecia*) following Schoener's (1974) three major niche dimensions. When investigating ontogenetic differences in food type, I also investigated differences in the mechanical properties of foods utilized. The following hypotheses were tested: (1a) age groups use different microhabitats during feeding bouts. This was tested by sampling differences in use of forest strata while feeding and measuring the size of feeding trees utilized. (1b) Microhabitat usage varies on a seasonal basis. If food availability shifts seasonally, individuals of different ages should shift their use of microhabitat to correspond to areas of highest food abundance. (2) Juveniles differ from adults in the food types they ingest (food types include fruit species, leaves, and flowers). I predicted that: (2a) the juvenile diet is less diverse than the adult diet, (2b) dietary diversity shifts on a seasonal basis but those differences vary between age groups, and (2c) age groups differ in resource consumption based on the physical and mechanical properties of foods.

1a. Small body size and predation cause juvenile white-faced sakis to differ from adults in their use of microhabitats. Juveniles should feed lower in the forest than adults for three reasons: first, juveniles may be more susceptible to predators than adults, so they avoid the upper canopy to avoid the increased chance of avian predation. Second, juveniles are smaller than adults, and thus may be able to use smaller trees than adults without the potential of breaking a support structure and falling. Third, if juveniles ingest different food types than adults, they may occupy different forest strata where those foods are more abundant.

Differences in juvenile and adult feeding strategies may be reflected in feeding tree size (diamteter at breast height (DBH)). DBH is often used as a predictor of tree crown volume and thus, feeding patch size (Chapman et al. 1992, Vasey 2000). If adults monopolize larger feeding patches, juveniles may be forced to acquire more resources from smaller food patches, where the difference should be reflected in the DBH of feeding trees.

1b. Seasonal shifts in food availability create differences in the extent of overlap of microhabitat usage between adults and juveniles. Primates have been known to vary in their use of habitat on a seasonal basis, where they differ in their use of forest strata according to fluctuations in resource availability (Overdorff 1993, Vasey 2002; Grassi 2002). When resources are abundant, juveniles and adults should overlap more in their use of microhabitat (i.e. less difference in feeding height and DBH of feeding trees), while when resources are limited, juveniles and adults should exhibit more difference in the height at which they feed and the size of the feeding patches they utilize (i.e. DBH of feeding trees).

2a. Due to small body size and inexperience, juvenile white-faced saki diets are less diverse than adult diets. Juveniles may be limited in the potential foods available to them due to constraints of body size as well as lack of experience. Body size and the accompanying differences in strength may prevent juveniles from accessing the more mechanically challenging resources that adults consume. Since juveniles are less experienced than adults, they may not have the knowledge of all food items that are available to eat and consequently eat a less varied diet. Thus, juveniles are predicted consume fewer food types than adults (e.g. lower dietary diversity), but should consume higher proportions of fewer foods. Juveniles are known to occasionally explore foods not eaten by adults, but most of these foods are rarely eaten again, and contribute little to juvenile food intake (Janson and van Schaik 1993).

2b. The extent of differences in dietary diversity between adults and juveniles shifts seasonally with changes in food abundance. Juveniles may respond differently to seasonality than adults. It has often been suggested that seasonal fluctuations in food availability affect primate's diets (Overdorff 1993, 1996, Norconk 1996, Vasey 2000, 2002, Cunningham and Janson 2006). In white-faced sakis, seasonal food scarcity has been found to cause both a decrease in dietary diversity (e.g. Cunningham and Janson 2006), and no difference in dietary diversity (e.g. Norconk 1996). In accordance with past studies, I predict that adult white-faced sakis will either maintain or decrease dietary diversity when food is scarce. Due to small body size and lack of experience, any decrease in dietary diversity should be more pronounced in juveniles.

2c Juvenile white-faced sakis are limited by the physical and mechanical properties of foods. Juveniles have absolutely smaller jaw muscles, smaller jaw gape, and smaller teeth than adults. Consequently they may be excluded from consuming the most physically and mechanically challenging food items in the adult dietary repertoire.

Here, I predict that adults will consume more challenging foods (i.e. harder, tougher, larger) than juveniles.

CHAPTER III

METHODS

Study Site

The study was conducted at Brownsberg Nature Park, Suriname (located between 04º 45’ 46” - 05º 59’ 44” North and 055º 07’ 58” -055º 15’ 23” West). Brownsberg Nature Park is approximately 27,500 ha of equatorial rainforest and is roughly 13.5 kilometers wide and 34 km long. The dominant feature of Brownsberg is a 1,400 ha lateritic plateau that rises roughly 500m above sea level. The plateau has a milder, cooler climate than the surrounding area, but maintains four distinct seasons: 1) the long rainy season between late April or May and mid-August; 2) the long dry season from mid-August through November or December; 3) the short wet season in December and January; and 4) the short dry season between February and April. Despite seasonal variation in rainfall, no month experiences fewer than 60mm of rain (De Dijn 2006). The data reported here were collected in late June through July, 2006 during the end of Suriname’s long wet season (Study period 1) and from mid-December through mid-January 2006-2007, during the short wet season (Study period 2).

The forests of Brownsberg Nature Park are typical of the Guayana Shield: the biodiversity hotspot that includes Guyana, Suriname, and French Guiana. Fitzgerald et al. (2002) classified 10 habitat types within the park including seven different forest habitats. The bottom of the plateau contains forest types typical of lowland rainforest while the plateau contains sub-montane rainforest and experiences occasional cloud forest-like conditions. Although the forests of Brownsberg are similar in structure to the rest of the Guayana Shield, the plateau is unique in both tree composition and taxa (De Dijn 2006).

Brownsberg contains all eight Guianan Shield primate species including golden handed tamarins (*Saguinus midas*), white-faced sakis (*Pithecia pithecia*), common squirrel monkeys (*Saimiri sciurius*), brown capuchins (*Cebus apella*), wedge-capped capuchins (*Cebus olivaceus*), bearded sakis (*Chiropotes satanas*), red howling monkeys (*Allouatta seniculus*), and black spider monkeys (*Ateles paniscus*) (Norconk et al. 2003). The study species, white-faced sakis (WFS), are the third most common primate species at Brownsberg (Norconk et al. 2003).

At Brownsberg, white-faced saki diets shift seasonally with changes in rainfall and fruit tree productivity. The majority of trees at Brownsberg flower during the long dry season when conditions favor pollination and fruit during the short wet and short dry seasons (De Dijn 2006, Vreedzam figure 3.1). Since WFS commonly feed on the seeds of unripe fruits, they experience food shortage during the long dry season when fruits are rare and experience food abundance during the short wet and short dry seasons when fruit is abundant. Norconk (2007) suggests that saki reproductive activity is seasonal such that birth and weaning occur during the time of peak fruit availability.

Study Subjects

Data were collected on a single group of white-faced saki monkeys (*Pithecia pithecia*). The home range of the group was restricted to the Northeast end of the Brownsberg plateau. Fitzgerald *et al.* (2002) classified the habitat types in this area as savanna forest, high forest, moss aspect, and secondary aspect. Previous reports of white-faced sakis at Brownsberg suggest that home range size is approximately 10.3 ha (Norconk et al. 2003).

The group contained six individuals during both study periods. During study period 1 (SP1), the group consisted of two adult males, one subadult male, one adult female, and two juvenile males. During study period 2 (SP2), the group was the same with the addition of a male infant and the loss of the younger adult male. The infant in the group during SP2 was carried low on its mother's thigh. This suggests that it was born only a few weeks prior to the onset of the second study period as the thigh position is only occupied for the first five weeks of life (Norconk 2007). The infant male did not forage independently so it was not included in the study. Assuming births are relatively consistent from year to year and the infant was born in November or December, the two juvenile males were approximately seven or eight months old during SP1, and about one year old during SP2. During both study periods, the juveniles foraged independently and did not engage in nursing bouts, but lacked the characteristic pelage of mature males. Both young males also frequently benefited from food sharing from each of the adults. Thus, they both fit the definition of a juvenile during both study periods.

Data Collection

I divide data collection into field and laboratory components. Data collected in the field include those related to microhabitat usage (height while feeding and DBH of feeding trees; i.e. hypothesis 1a) and dietary diversity (hypothesis 2a). Data collected in the lab include the physical and mechanical properties of food items (hypothesis 2b).

The field component is further divided into two study periods, as methodology differed slightly due to behavioral changes associated with the presence of the infant and seasonality. Hypotheses 1b and 2c (i.e. temporal resource partitioning) are tested with the data collected for the first two hypotheses, but include analyses between study periods.

Field component

Study Period 1 (June-July, 2006) I collected data on the study group between 0630 and 1630 hours while following the monkeys from sleep site to sleep site. A focal animal was identified at the beginning of each day and I conducted all occurrence sampling of feeding bouts (feeding bout= time entering feeding tree to time leaving tree). The focal animal was followed for as long as possible, but if it was lost from sight and not relocated within five minutes, a new focal animal was selected and sampling continued with the new animal. Juveniles and adults were alternated as focal animals in order to gather a similar amount of data on each age group.

The following data were collected during feeding bouts: plant species consumed, plant part consumed, diameter at breast height (DBH) of feeding tree (collected with a DBH tape measure), and the height in the tree while feeding (estimated to the nearest meter). If another individual was feeding in the same tree as the focal animal, a feeding bout was recorded for that individual as well. *Ad libitum* data were collected on variation in methods of food acquisition as well as unique food properties that may have influenced an individual's ability to ingest it (e.g. *Clusia* is dehiscent and requires no dental manipulation to access the edible parts (pulp), thus mechanical analyses of the pericarp are irrelevant).

During feeding bouts, food samples were collected from beneath the feeding tree for physical property analysis (see “lab analysis” below). If fewer than seven samples or no samples could be collected during a feeding bout, the tree was revisited at a later time to gather additional samples by climbing the tree or knocking fruits from the tree with a pole. Many of the lab tests required whole fruits for analysis (weight, maximum length, diameter), so mostly whole fruits were collected from beneath the feeding trees. Despite the numerous methods employed to collect fruit, only a limited number of whole-fruit samples could be collected on many occasions, which limited some of the subsequent measurements. Since hardness, toughness, and puncture resistance measurements did not require whole fruits, some partially eaten fruits were collected for these analyses.

Study Period 2 (December 2006- January 2007). Field data collection followed the same procedure as study period I with one exception: all observed feeding bouts were recorded without emphasizing a focal animal. The study group was more difficult to locate and to follow during this study period as they favored higher forest strata during feeding bouts (see results) and during travel such that a focal animal could not be followed for more than a few minutes. During SP2, I collected the same data during feeding bouts as during SP1.

Laboratory component

I tested fruits the same day they were collected or the following morning to minimize alterations to mechanical properties from rotting or drying. The following data were collected in the lab: fruit weight, diameter, puncture resistance, hardness, and toughness. For mechanical properties measurements, I tested only the pericarp of fruits. The pericarp is generally considered the most challenging part of the fruit that the sakis encounter, since the seeds they encounter once they overcome the pericarp are usually soft (Kinzey and Norconk 1990, Kinzey 1992, Norconk et al. in press B). Fruit weight was calculated with a 300 g maximum scale accurate to 0.1g. Maximum length and diameter were determined with calipers accurate to 0.1 centimeters. Puncture resistance data was collected with a Rimac® soil compression tester and a $2mm^2$ adapter (Kinzey and Norconk 1990) to generate a pressure measurement (Kg/mm^2). For the puncture test, the $2\ mm^2$ adapter was pressed into the fruit samples until it broke through the pericarp.

Hardness and toughness were measured with a portable mechanical properties tester (Darvell et al. 1996; Lucas et al. 2001; Lucas 2004). The tester consists of a mechanical testing frame, an electronics box, and a computer program. The mechanical testing frame includes a stage for placing fruit samples, testing jigs (specific for each properties test), a shaft encoder that controls displacement, and a mechanical crank for manually generating force and displacement. A load cell (10N or 100N) is attached to the mechanical frame to measure the forces created while testing a food item. The load cell and shaft encoder are linked to the electronics box which generates an analog output of force and displacement. The electronics box is linked to a computer that generates a digital output of force versus displacement on a graph. The data from the graph can be used to determine a particular mechanical property.

Hardness

The hardness test employs a Vicker's adapter (inverted pyramid) to the mechanical properties tester that is slowly pressed into the sample. Samples must be as flat as possible for a hardness test to control for the area of the indentation. Samples are shaped with a razorblade to as flat as possible prior to applying the hardness test. The Vicker's adapter is connected to the load cell and shaft encoder so that force and displacement values generated as the adapter presses into the sample are transferred to the shaft encoder and the computer. Hardness is measured as the maximum force on the force-displacement curve.

Toughness

The toughness test on the mechanical properties tester employs a set of high quality scissors which are slowly passed through a sample in order to determine the sample's resistance to the force created by the scissors. Before testing the sample, the scissors are compressed in an empty pass to remove the friction of the scissor blades from subsequent measurement generated while cutting foods. Since toughness is related to the area of a crack, the cross-sectional area of each sample is measured by cutting fruit samples into thin strips with a razorblade and measuring the width and depth of the strips with calipers. The scissor blades are pushed together slowly by turning the crank of the mechanical testing frame which lowers a wheel jig onto the upper scissor handle. The electronics box generates an analog output of the force and displacement created by closing the scissor blades across the sample. Toughness is measured as the area under the force-displacement curve.

Testing limitations

The data gathered with the mechanical properties instrument were somewhat limited due to the availability of the instrument and the nature of the fruit, which sometimes limited the tests which could be applied. For example, many of the fruits the sakis consumed were very small which limited the potential to shape a flat piece of pericarp for hardness tests without rendering the piece too thin. Furthermore, overly thin pieces risk damaging the load cell if the adapter contacts the stage after it pierces the sample.

Data Analysis

Field Component

Data for height while feeding were divided into five categories (0-5 meters, 5.01-10 meters, 10.01-15 meters, 15.01-20 meters, and >20 meters) to minimize potential error from estimations. I employed a three-dimensional chi square to analyze the differences between juveniles' and adult's use of forest strata both within and between seasons. To test for the difference in DBH of the trees used by each age group and between seasons, I used a univariate, general linear model, which tested for the difference between age groups, seasons, and for the interaction between age group and season. For both feeding height and DBH analyses, each feeding bout was included as a data point, regardless of whether or not the feeding tree had been used previously.

For analysis of dietary diversity, feeding bouts were categorized along three dimensions. First, they were divided according to age group (e.g. juvenile or adult). Second, these feeding bouts were grouped according to season such that each age group had two sets of feeding bouts; one for SP1 and one for SP2. Finally, the feeding bouts were grouped according to food type. To test for the difference in dietary diversity between juveniles and adults, the Shannon-Weiner index* of dietary diversity was calculated for juveniles and adults for each season and a Student's T test was used to compare difference in dietary diversity (Hutcheson 1970) between age groups and between seasons. I also calculated Morisita's index** of dietary overlap between age groups for each study period. Morista's index ranges from zero to one where a value of one indicates complete dietary overlap, while zero indicates no dietary overlap.

Laboratory Component

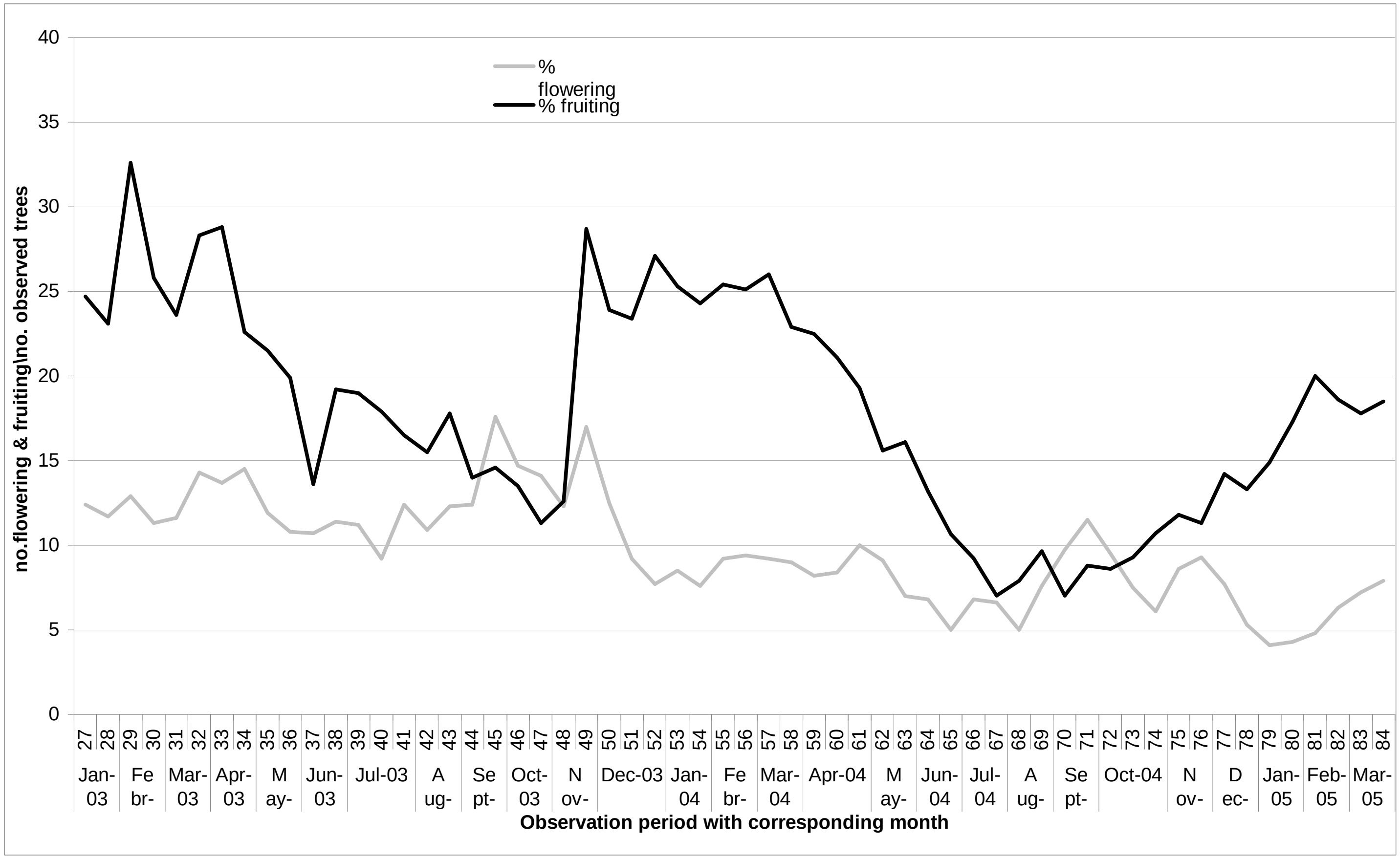
For each fruit species, I calculated the mean value of each physical and mechanical property. For each property, fruits were ranked in increasing order of the mean value of that property. If a monkey was observed feeding on a particular species, it was assumed that it could overcome the mean values of all the mechanical properties of that fruit. As all mechanical properties were not determined for each fruit species, only those for which the property was determined were included in each analysis.

* Shannon-Weiner index: $H= -\Sigma p_i \log p_i$, where p_i is the proportion of each food type to the rest of the diet.

** Morisita's index: $M_{jk}= [2\Sigma\ (x_{ij})\ (x_{kj})]/\ [\Sigma x_{ij}^2+ \Sigma x_{kj}^2]$, where x_{ij} is the occurrence of food *j* in the *i*th sample of a consumer and x_{jk} is the occurrence of the same food item in the *k*th consumer.

Juvenile feeding bout frequencies (for each fruit) were scaled in relation to the number of adult feeding bouts (i.e. juvenile feeding bouts – adult feeding bouts/ juvenile feeding bouts + adult feeding bouts). The scaled values were then regressed on the means of each food property. The mean values of each property were log-transformed to minimize the effects of heteroscedasticity. For fruit weight, diameter, and puncture resistance, fruits on which fewer than three feeding bouts were observed were not included in analysis. Since data for hardness and toughness were limited, all fruits were included in analysis, regardless of the number of feeding bouts observed on that particular fruit.

Figure 3.1. Phenology data for Brownsberg Nature Park From January 2003-March 2005. Figure and data provided by Ari Vreedzam.



CHAPTER IV

RESULTS

Hypothesis 1a and 1b (*Feeding Height and DBH*)

The three dimensional chi square yielded a significant relationship among age group, season, and usage of forest strata (χ^2=57.65, p<.000). Subsequent tests for partial independence found no relationship between age group and feeding height (χ^2=4.52, p>.05), but a significant relationship between season and feeding height (χ^2=51.04, p<.000). Thus, age groups did not differ significantly in their use of forest strata during either season, but the group as a whole, used significantly higher forest strata during SP2 (Figure 4.1). Nearly 90% of feeding bouts during SP1 occurred between 0-15m, while the same proportion of feeding bouts during SP2 occurred between 5-20m. As the early dry season at Brownsberg (i.e. SP1) is correlated with resource scarcity (De Dijn 2006) and the short wet season (i.e. SP2) is correlated with resource abundance, the white faced sakis appeared to shift their use of forest strata according to shifts in food availability (Figure 4.2).

The general linear model yielded a significant difference by age group (F=6.607, p<.011), by season (F=13.522, p<.000), and a significant interaction between age group and season (F=3.894, p<.049) according to the DBH of feeding trees utilized. Post-hoc, independent samples t-tests were performed to further delineate where the variation occurred. Juveniles used significantly smaller food patches (by DBH) than adults during

SP1 when juveniles fed in trees of an average DBH of 10.77 cm (±8.79cm) and adults fed in trees of average DBH 17.05 cm (±9.62cm) (t=5.821, p<.000). Age groups did not differ in the DBH of feeding trees used during SP2 (t=.275, p<.784). Juveniles used significantly larger trees during SP2 than during SP1 (t=6.135, p< .000), as did adults (t= 2.978, p<.01). Thus, both age groups used trees of larger DBH during SP2 than during SP1, but this difference was more pronounced in juveniles (Figure 4.3). As with differences in feeding height, juveniles and adults appeared to shift their use of trees according to differences in food availability.

Hypothesis 2a and 2b (*Dietary Diversity*)

Feeding bouts were distributed among 27 food types including 25 fruit species, one flower species, and leaves (leaves were grouped together as I was unable to collect any samples, so species could not be distinguished). Fruit and seeds made up the majority of feeding bouts for both age groups (87.2% Juveniles, 75.76% adults). Both age groups fed on a wider variety of foods during SP2 than during SP1 (Table 4.1).

Juveniles and adults differed significantly in dietary diversity during SP1 (*t*=6.72, p<.01), but not during SP2 (*t*= .307, p>.05). Juvenile dietary diversity differed significantly between study periods (*t*= 14.337, p<.001) as did adults (*t*= 3.4292, p<.01; Table 4.2). Juveniles also fed on considerably fewer food types than adults during SP1 (8/13) (Figure 4.4). During SP2, juveniles did not differ from adults in dietary diversity. Each age group was observed feeding on 15 different food types (Figure 4.5).

Calculations of Morisita’s index of dietary overlap yielded similar results to the Shannon-Weiner index. Dietary overlap between juveniles and adults was much less during SP1 (.598) than during SP2 (.936). Thus, dietary overlap was higher between juveniles and adults when foods were abundant than when foods were scarce.

Pausandra martinii made up 65.8% of juvenile feeding bouts (123/181) during SP1 but only 21.7% of adult feeding bouts during SP1 (32/147). The availability of *P. martinii* overlapped both study periods, but ingestion of *P. martinii* was significantly less during SP2 (Juveniles $\chi^2 = 65.37$, $p < .0001$; Adults $\chi^2 = 19.44$, $p < .0001$). Nevertheless, juveniles utilized *P. martinii* significantly more than adults during SP2 ($\chi^2 = 5.29$, $p = .0215$) (Figure 4.6).

Both age groups fed most often on *Micranda brownsbergens* during SP2 (juveniles: 21/71 feeding bouts, 29.6%; adults 24/84 feeding bouts, 28.8%). Both age group fed on significantly fewer leaves during SP2 than during SP1 (juveniles $\chi^2 = 5.44$, $p = .0197$; adults $\chi^2 = 8.00$, $p = .0047$), but juveniles devoted significantly fewer feeding bouts to leaves than adults during both study session (SP1 $\chi^2 = 13.7$, $p < .0001$; SP2 $\chi^2 = 4.037$, $p = .045$) (Figure 4.7).

Hypothesis 2c

(*Fruit Weight and Diameter*)

The largest fruits eaten by adults were greater than 286g (the mean *Clusia grandiflora* was actually higher because many fruits exceeded the maximum value of the scale, so they were recorded as 300g even though they were heavier) and an average of 9.21cm in diameter. The maximum size of fruit eaten by juveniles independently was 50.59 g (*Gustavia augusta*) and 5.00 cm in diameter (*Passiflora sp.*). Regression analysis of fruit size versus feeding bouts yielded a significant relationship, with juveniles consuming relatively fewer fruits than adults as fruit size increased (r^2= .479, t= 3.18, p< .01, df=12) (Figure 4.8). There was also a significant relationship between fruit diameter and relative feeding bouts (r^2= .382, t= 2.94, p<.05, df=15) (Figure 4.9).

(*Puncture Resistance*)

Abrus sp. was the most challenging fruit in terms of puncture resistance (9.67 Kg/mm² mean) and was not observed to be eaten by juveniles; however, only one adult feeding bout was recorded for this species. The next fruit species most resistant to puncture was *Inga* sp. with a mean resistance to puncture of 5.50 kg/mm². *Inga* sp. was eaten by both adults (n=11) and juveniles (n=9). Puncture resistance did not significantly influence difference in diet between adults and juveniles (r^2= .168) (figure 4.10).

(*Hardness*)

The hardest fruits eaten by the sakis were *Gustavia augusta* and "unknown #1," both of which had an average hardness of 2.38 MPa. Both age groups were observed feeding on each of these fruit species (*G. augusta* juvenile feeding bouts (JFB)=1, adult feeding bouts (AFB)=1; Unknown 1 JFB= 4, AFB= 9). Age groups did not differ significantly by proportion of foods eaten as ranked by hardness (r^2= .109, n= 9) (Figure 4.11).

(*Toughness*)

The toughest fruit eaten by the sakis was the *Inga* sp.(3589.06 J/m²), which was eaten by both juveniles and adults (AFB= 11; JFB= 9). Age groups did not vary significantly when feeding bouts were ranked by increasing toughness (r^2= .127, n=7) (Figure 4.12).

Figure 4.1. Comparison of feeding height between study periods. Age groups are combined.

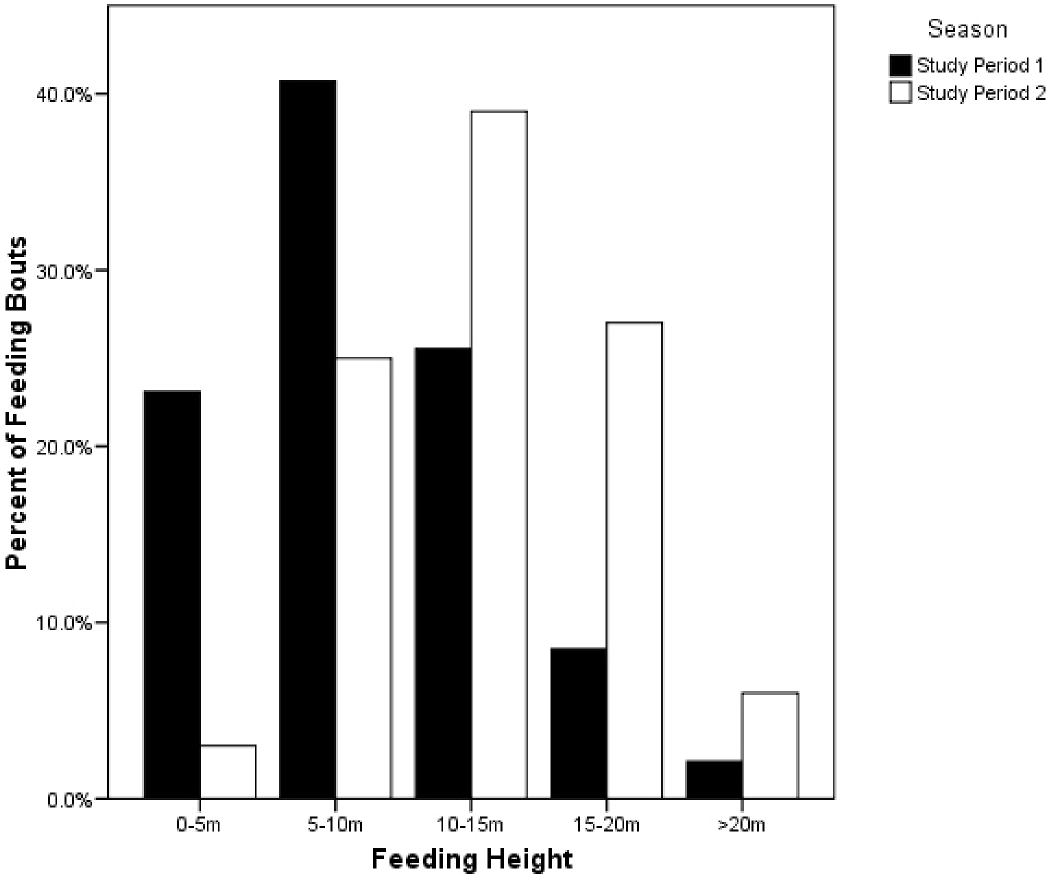


Figure 4.2. Comparison of forest strata used between age groups and study periods by percentage of feeding bouts taking place in each height category.

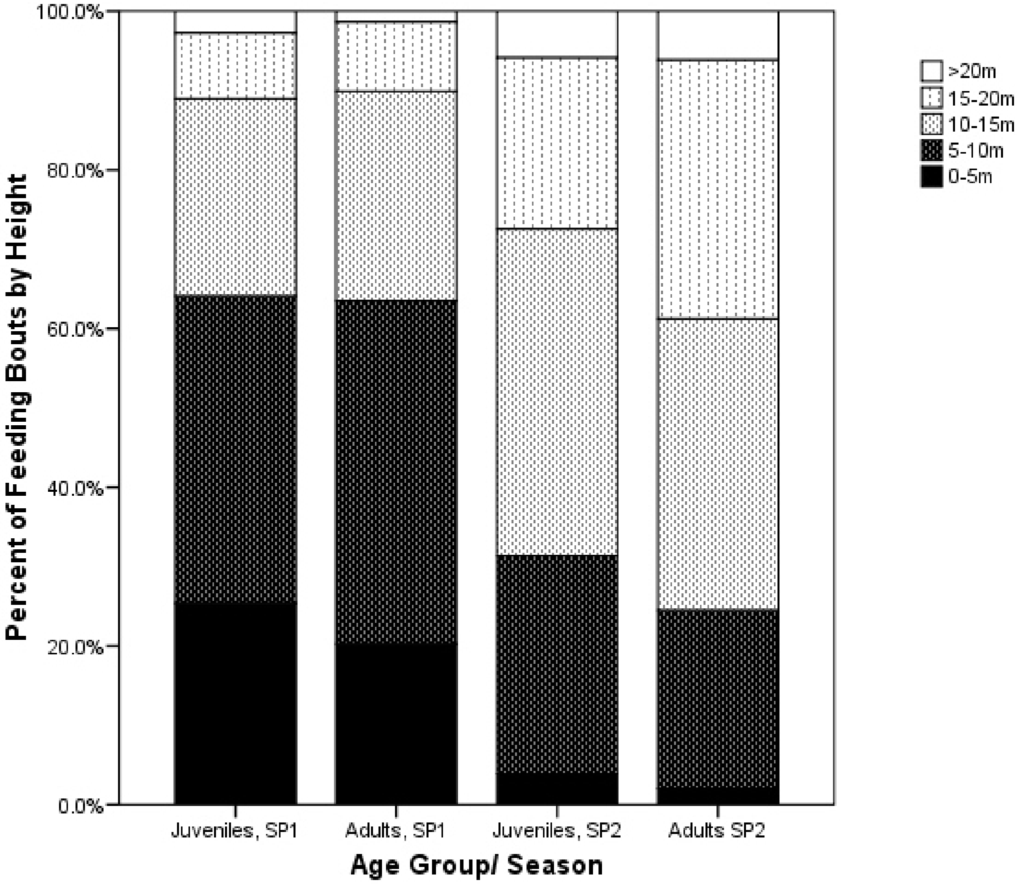


Figure 4.3. Comparison of average DBH of feeding trees by age and season. Error bars represent ± 1 SE.

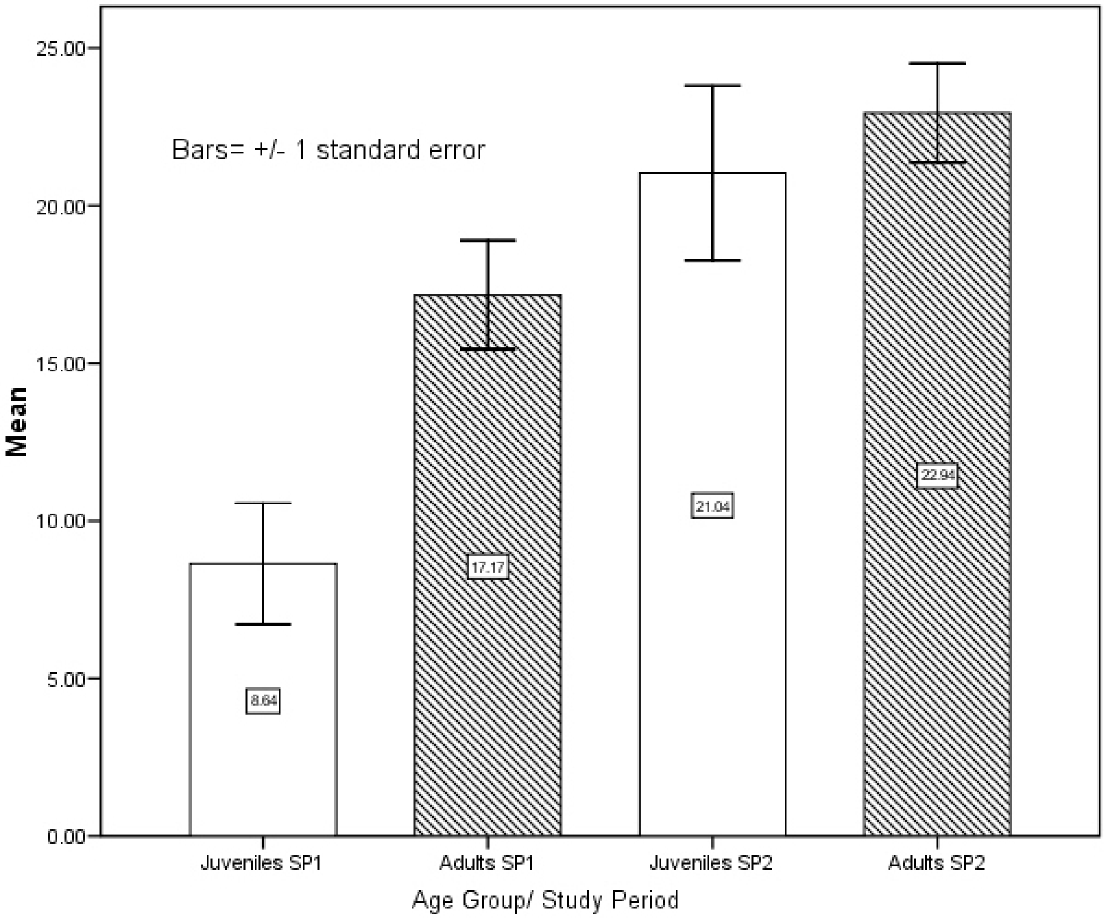


Figure 4.4. Comparison of juvenile and adult feeding bouts during SP 1 by food type. Some foods were eaten only by adults.

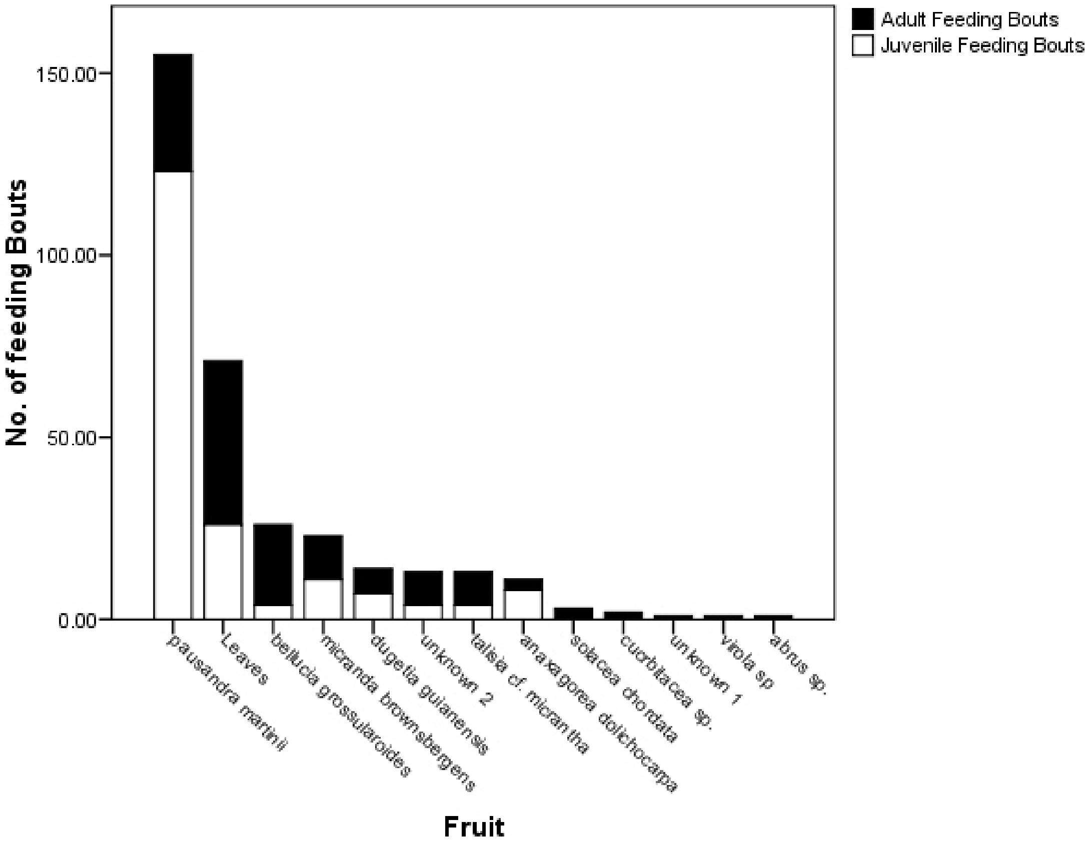


Figure 4.5. Comparison of juvenile and adult feeding bouts during SP 2 by food type. Some foods were only eaten by one age group.

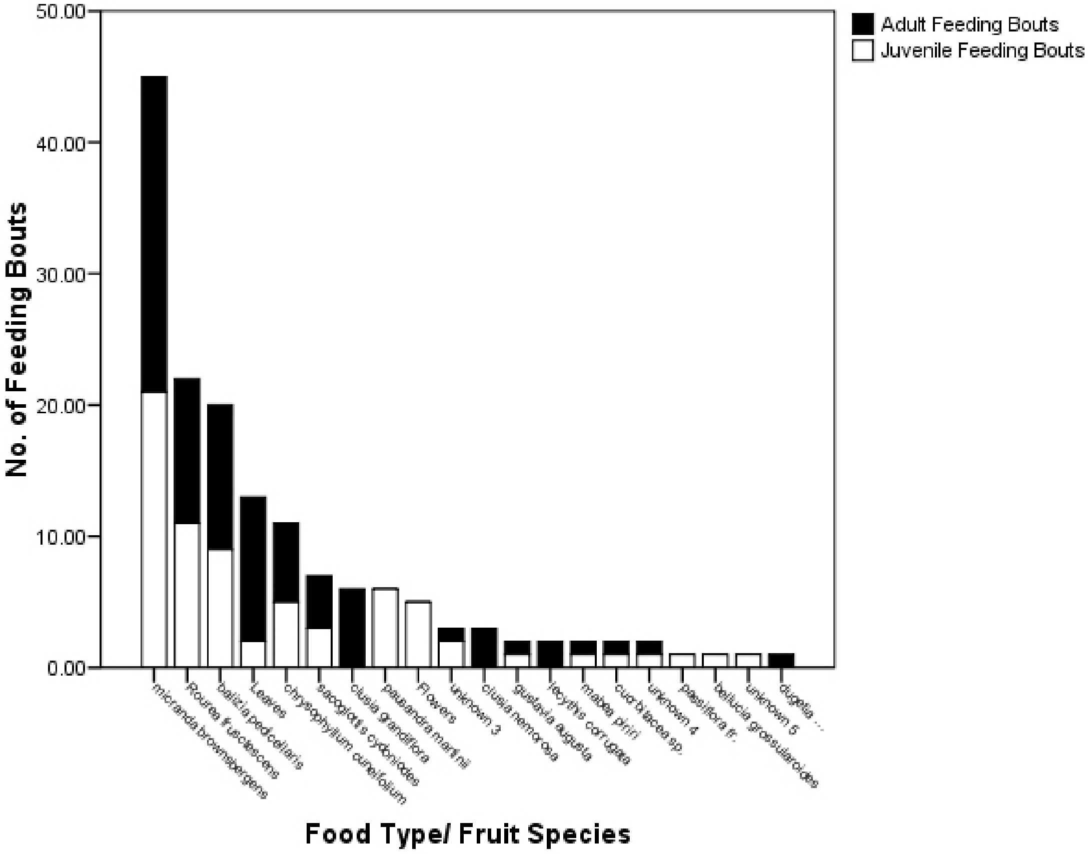


Figure 4.6. Comparison of *Pausandra martinii* feeding bouts by age group and season. Bars represent percentage of feeding bouts.

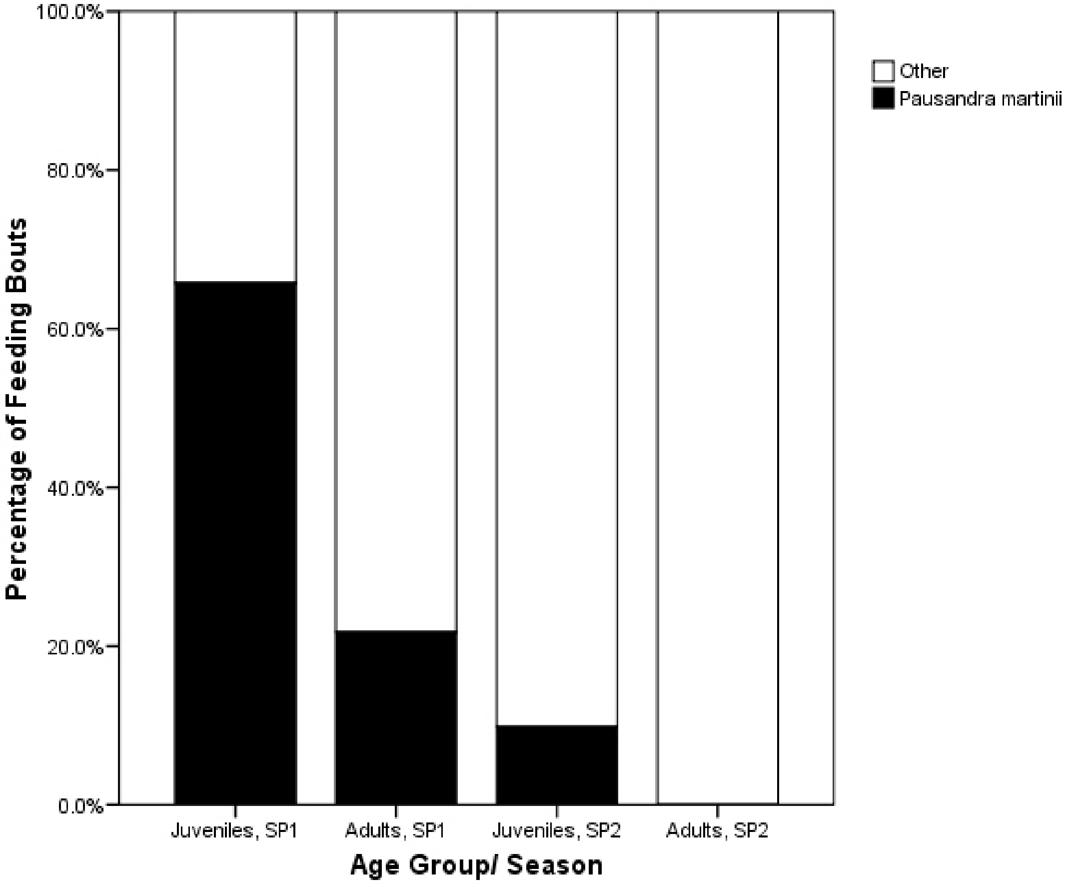


Figure 4.7. Comparison of leaf feeding bouts by age group and season. Bars represent percentage of feeding bouts.

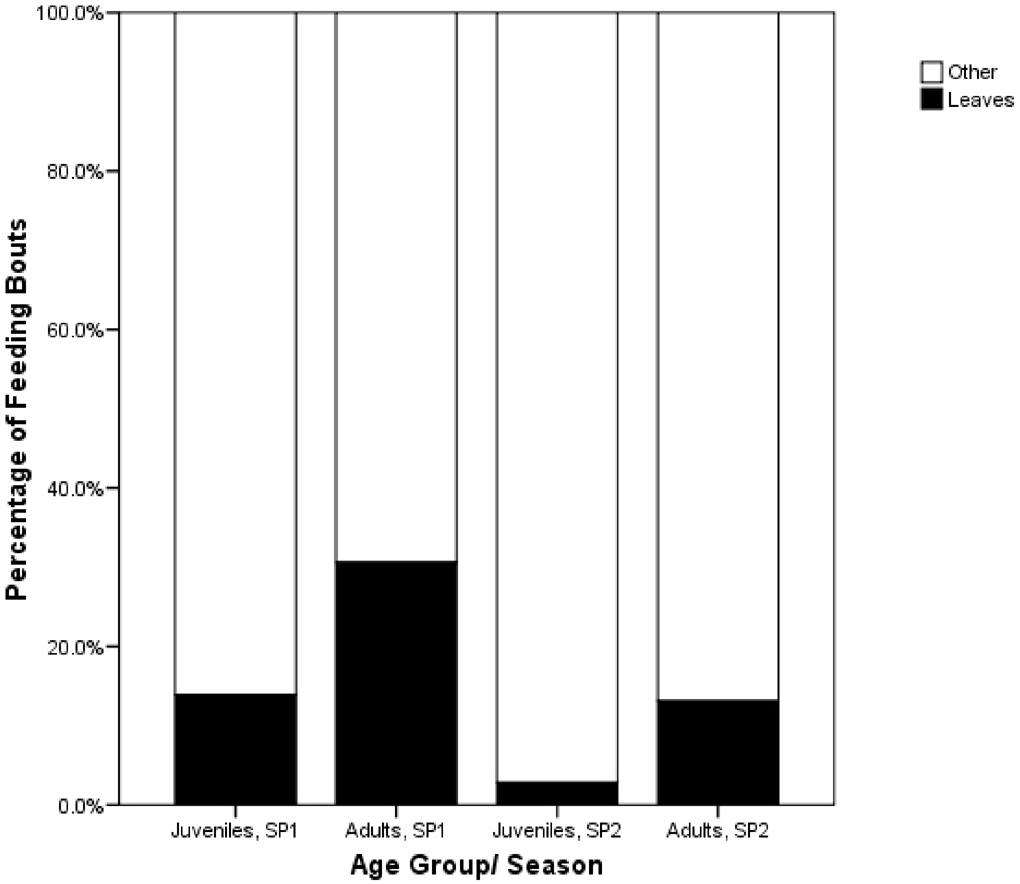


Figure 4.8. Regression analysis of scaled values of feeding bouts according to fruit weight. Data points closer to 1.0 are foods predominantly eaten by juveniles and data points closer to -1.0 represent foods predominantly eaten by adults. Curved lines represent 95% confidence interval.

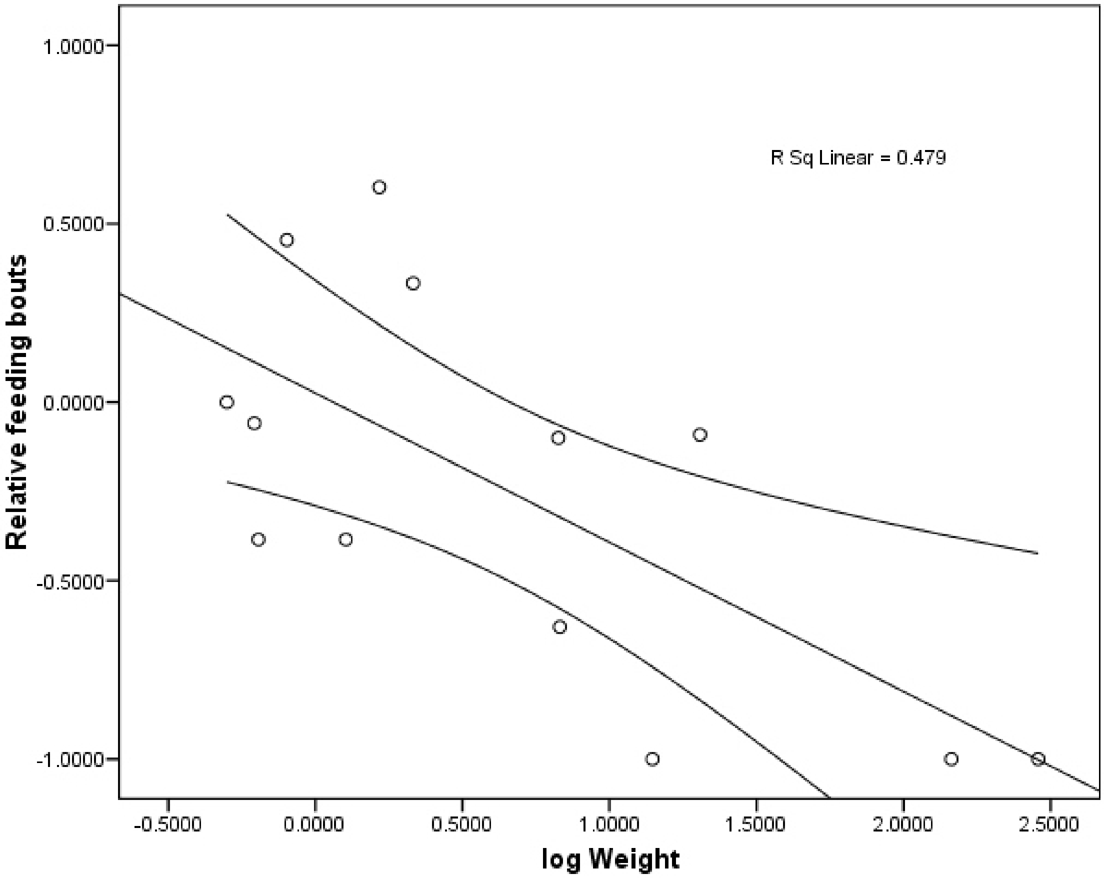


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Figure 4.9. Regression analysis of scaled values of feeding bouts according to fruit diameter. Data points closer to 1.0 are foods predominantly eaten by juveniles and data points closer to -1.0 represent foods predominantly eaten by adults. Curved lines represent 95% confidence interval.

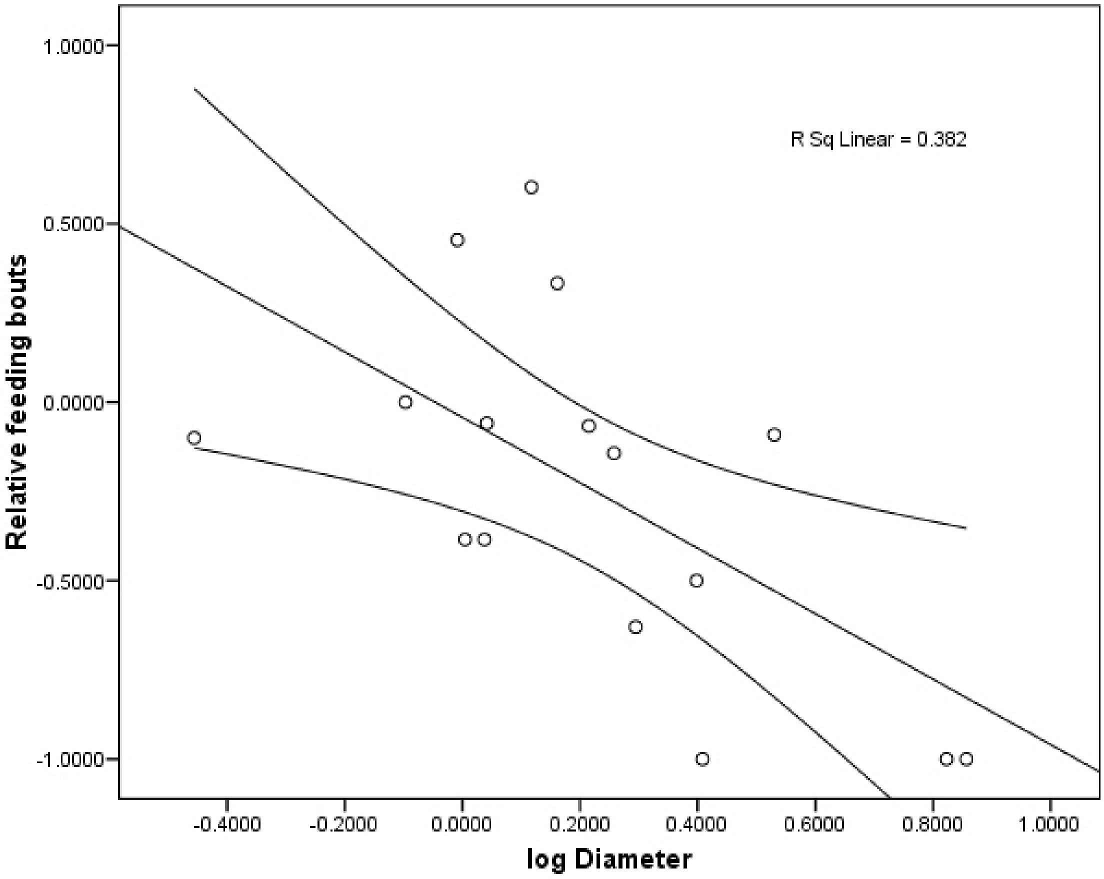

Figure 4.10. Regression analysis of scaled values of feeding bouts according to puncture resistance. Data points closer to 1.0 are foods predominantly eaten by juveniles and data points closer to -1.0 represent foods predominantly eaten by adults. Curved lines represent 95% confidence interval

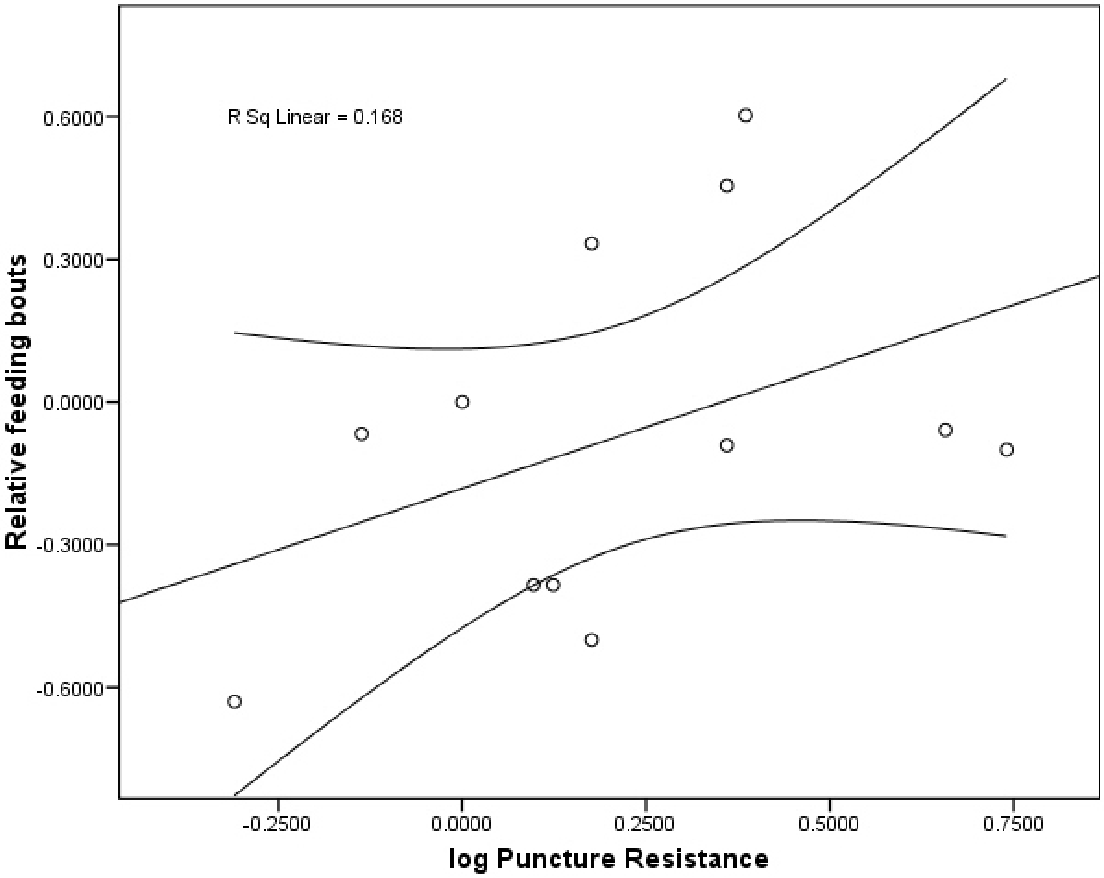

Figure 4.11. Regression analysis of scaled values of feeding bouts according to fruit hardness. Data points closer to 1.0 are foods predominantly eaten by juveniles and data points closer to -1.0 represent foods predominantly eaten by adults. Curved lines represent 95% confidence interval.

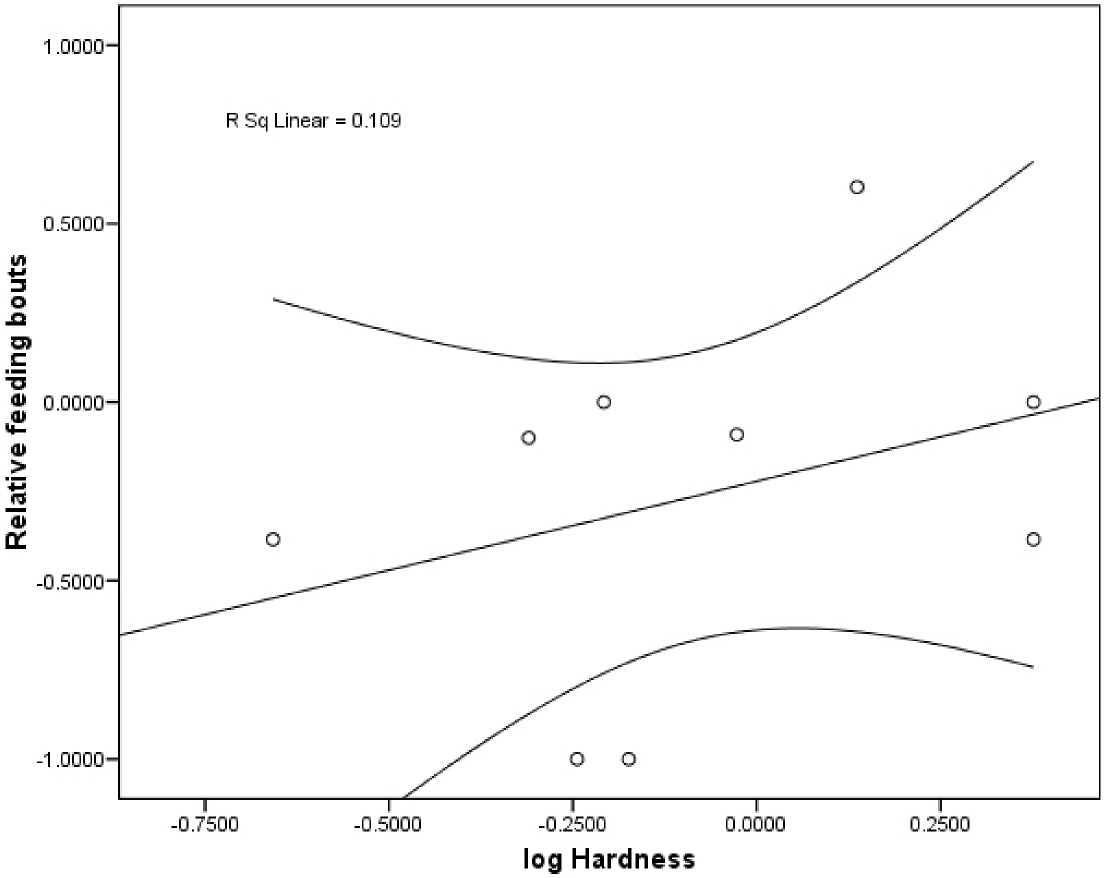

Figure 4.12. Regression analysis of scaled values of feeding bouts according to fruit toughness. Data points closer to 1.0 are foods predominantly eaten by juveniles and data points closer to -1.0 represent foods predominantly eaten by adults. Curved lines represent 95% confidence interval.

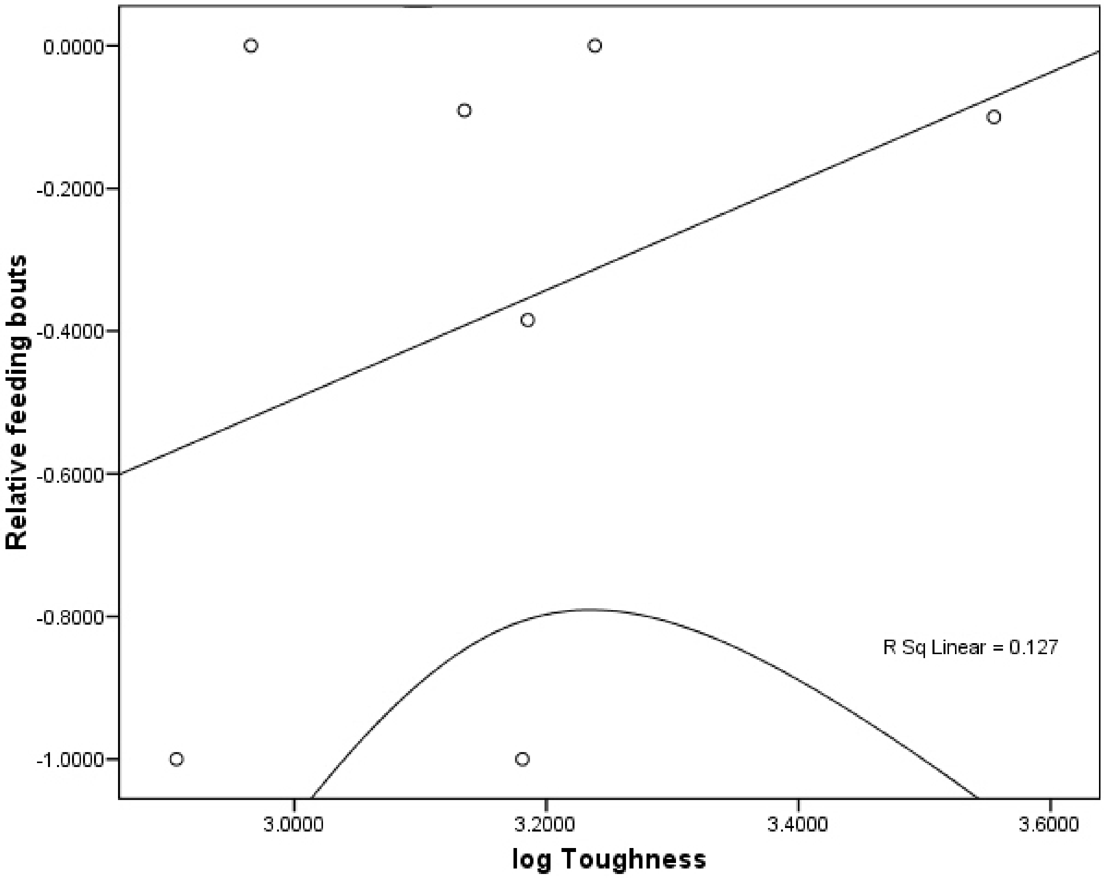

Table 4.1. Feeding bouts by study period, age group, and food type.

Study Period 1			Study Period 2		
Fruit Species	Juveniles	Adults	Fruit Species	Juveniles	Adults
Abrus sp.	0	1	*Bellucia grosslarioides*	1	0
Anaxagorea dolichocarpa	8	3	*Chrysophyllum cuneifolium*	5	6
Bellucia grosslarioides	4	22	*Clusia grandiflora*	0	6
Duguetia guianensis	7	7	*Clusia scrobiculata*	0	3
Gurania subumbellata	0	2	*Duguetia guianensis*	0	1
Micranda brownsbergensis	11	12	*Gurania subumbellata*	1	1
Pausandra martinii	123	32	*Gustavia augusta*	1	1
Salacia cordata	0	3	*Inga sp.*	9	11
Talisia cf. micrantha	4	9	*Lecythis corrugata*	0	2
Virola sp.	0	1	*Mabea piriri*	1	1
Unknown 1	0	1	*Micranda brownsbergeniss*	21	24
Unknown 2	4	9	*Passiflora* sp.	1	0
Leaves	26	45	*Pausandra martinii*	6	0
			Rourea fructescens	11	11
			Sacoglottis cydoniodes	3	4
			Unknown 3	2	1
			Unknown 4	1	1
			Unknown 5	1	0
			Leaves	2	11
			Flowers	5	0
Total	187	147	Total	71	84

Table 4.2. Dietary Diversity indices for each age group during each study period. Values in bold are statistically significant.

	Study Period 1	Study Period 2	*t**
Juveniles	.5305	.9766	**14.34**
Adults	.8639	.9568	**3.43**
*t**	**6.72**	.307	

**t* values are calculated using Hutchison's (1970) methods

Table 4.3. Physical and mechanical properties data for saki dietary items.

	Fruit Species/ Food type	Weight[1]	Diameter[2]	Puncture[3]	Hardness[4]	Toughness[5]	Juvenile FB	Adult FB
1	*Abrus* sp.	3.65	1.21	9.67	-	-	0	1
2	*Anaxagorea dolichocarpa*	0.80	0.98	2.29	-	-	8	3
3	*Bellucia grosslarioides*	6.78	2.44	0.49	-	-	5	22
4	*Chrysophyllum cuneifolium*	20.30	3.39	2.29	0.94	1364.30	5	6
5	*Clusia grandiflora*	286.60[§]	9.21	-	-	-	0	6
6	*Clusia scrobiculata*	14.00	2.56	-	-	-	0	3
7	*Duguetia guianensis*	-	1.76	0.73	-	-	7	8
8	*Gurania subumbellata*	-	2.50	1.50	-	-	1	3
9	*Gustavia augusta*	50.59	4.65	1.93	2.38	1731.47	1	1
10	*Inga sp.*	6.70	0.35	5.50	0.49	3589.06	9	11
11	*Lecythis corrugata*	10.08	2.77	1.69	.57	806.35	0	2
12	*Mabea piriri*	3.66	1.88	1.14	-	-	1	1
13	*Micranda brownsbergensis*	0.62	1.11	4.54	-	-	32	36
14	*Passiflora* sp.	19.45	4.14	0.40	-	-	1	0
15	*Pausandra martinii*	1.65	1.45	2.43	1.37	-	129	32
16	*Rourea fructescens*	0.50	0.80	1.00	-	-	11	11
17	*Salacea cordata*	145.40	6.70	-	0.67	1516.95	0	3
18	*Sacoglottis cydoniodes*	-	2.01	-	-	-	3	4
19	*Talisia cf. micrantha*	1.27	1.09	1.25	0.22	1531.80	4	9
20	*Virola sp.*	1.58	1.48	-	-	-	0	1
21	Unknown 1	3.28	1.66	2.31	-	-	0	1
22	Unknown 2	0.64	1.01	1.33	2.38	-	4	9
23	Unknown 3	2.15	1.45	1.50	-	-	2	1
24	Unknown 4	6.04	2.25	2.44	0.62	923.67	1	1
25	Unknown 5	2.35	1.37	2.50	-	-	1	0
26	Leaves	-	-	-	-	-	28	56
27	Flowers	-	-	-	-	-	5	0
Total							258	231

[1](grams); [2](centimeters); [3](Kg/mm^2); [4](MPa); [5](J/m)
[§]*Clusia grandiflora* maxed out 300gram scale, so mean weight is actually higher

CHAPTER V

DISCUSSION

Dietary differences between juvenile and adult white-faced sakis were most evident in dietary diversity, and were most pronounced when food items are least abundant (i.e. late wet season and early dry season). When foods were more abundant (i.e. short wet season), juvenile and adult diets did not differ significantly. These results are also consistent with the ecological literature on interspecific resource partitioning which predicts that individuals often overlap significantly in resource usage during times of food abundance, but segregate niches during times of food scarcity. These data must be interpreted cautiously however, as the difference in age of juveniles between study periods also may have contributed to dietary shifts. Microhabitat usage seemed somewhat less important for resource partitioning among age groups in white-faced sakis. Although juveniles used different sized food patches (as estimated by DBH) during SP1, they did not differ significantly in the forest strata they utilized. Aside from overall food size, the mechanical and physical properties of foods were not major factors influencing differential resource exploitation.

Hypothesis 1a and 1 b (Microhabitat usage)

The great vertical dimension in a rainforest can provide the means for species to avoid overlap in resource use and provide a mechanism for niche segregation (Grassi 2002; Vasey 2000, Overdorff 1993, 1996). The same principle can be applied at the intraspecific level. The differences in the use of forest strata among conspecifics can be explained by differences in body size, the need to decrease feeding competition, and difference in social roles (Grassi 2002). Furthermore, the distribution of food sources is important for interpreting differences in height use within the forest (Grassi 2002). White-faced saki age groups did not differ significantly in their use of forest strata during either study period ($\chi^2=4.52, p>.05$). Thus, hypothesis 1a was not well supported. Vasey (2000) suggests that shifts in use of forest height are often species specific tactics for behavioral thermoregulation and predator avoidance. Here, juveniles may occupy similar forest strata as adults both to reduce the chances of predation and to facilitate observation based learning from adults at the expense of increased competition for food. Juveniles often cannot reduce the risk of predation and starvation simultaneously and often favor reduced rates of food intake over increased potential for predation (Janson and van Schaik 1993). This may be because predation leads to immediate death, while reduced feeding efficiency can be overcome by food sharing with adults or the tendency for adults to allow juveniles to feed nearby. In this case, juveniles minimize risk by maintaining close contact with adults. This lends support to Janson and van Schaik’s (1993) “juvenile risk-aversion” hypothesis that suggests that juveniles adopt strategies to minimize the risk of death before reproductive maturity. Tarnaud (2004) suggests that foraging success for juveniles increases when a juvenile is in close contact with an experienced forager. Thus, juveniles may forage near adults to improve their foraging efficiency and reduce the need for trial-and-error learning, which is potentially risky due to the possibility of ingesting toxic food items.

The group as a whole fed significantly higher in the forest (χ^2=51.04, p<.000) and used larger food patches during SP2 than during SP1 (F=13.522, p<.000). These data are consistent to what Vasey (2002) reports for both *E. f. albifrons* and *V. v. rubra* in Madagascar, where each species uses significantly smaller feeding trees during seasonal food shortages. This strategy may be related to the relative availability of food in that when fruits are abundant, sakis favor larger patches. Larger food patches should yield a higher energy output per unit foraging time such that sakis take advantage of these when available. Conversely, when foods are less abundant, the sakis move lower in the forest to include fruit from smaller patches as well. The sakis may compensate for the reduced feeding patch size (During SP1) by increasing the amount of time they spend foraging during the day and thus, increasing the number of patches they visit during the day. Some anecdotal evidence supports this hypothesis. During SP1, nearly the entire day was spent foraging, while during SP2, the sakis often remained in the same place for several hours without feeding. Due to the difference in sampling methods between study periods, seasonal differences in patch usage per unit time cannot be quantitatively compared.

Both age groups avoided the upper forest strata (>25m) during both study periods. This may be partly to the increased chance of avian predation at this level. The major predators of white faced sakis are the Harpy eagle (*Harpia harpyja*, Rettig 1978) and the crested eagle (*Morphnus guianensis*, Gilbert 2000) (as cited in Miller and Treves 2007) which might limit the saki's use of the upper canopy. Grassi (2002) found that gray bamboo lemurs (*Hapalemur griseus*) respond to avian predators by reducing their height in the forest and becoming quiet, suggesting that the use of lower canopy strata is an effective means of reducing predation. Since adult white faced sakis only achieve adult body sizes of 1.5-2.5 Kg (Norconk 2007), it may be that the adult body size does not confer a significant advantage in avian predator avoidance. Thus, both age groups may avoid the upper canopy for similar reasons. Furthermore, the upper canopy may not provide the necessary food types that white faced sakis routinely consume. Thus, the tree species that form the upper canopy is essentially outside the realm of the saki dietary niche.

Although juveniles did not differ significantly from adults in their use of forest strata during SP1 (χ^2=4.52, p>.05), they used significantly smaller food patches than adults (t=5.821, p<.000). This difference may have been related to the difference in dietary diversity between adults and juveniles during SP1. Juveniles utilized *Pausandra martinii* trees extensively, which were small in DBH (6.48cm ± .32) and used frequently such that they made up a large proportion of observed feeding bouts and were responsible for reducing the average DBH of trees utilized by juveniles during SSI. During SP2, juvenile diets did not differ significantly from adults (see hypothesis 2) and consequently, they fed in many of the same trees. Thus, during SP2 juveniles did not differ significantly from adults in relation to the DBH of feeding trees.

Hypothesis 2a and 2b (Dietary Diversity)

Many studies have demonstrated shifts in dietary overlap between species and sex classes according to changes in fruit abundance (e.g. Vasey 2000, 2002, Gautier-Hion 1980, 1988, Overdorff 1993). Here, both age groups differed significantly in dietary diversity between seasons, but this difference was more pronounced in juveniles (juveniles: *t*= 14.337, p<.001; adults: *t*= 3.4292, p<.01; Table 2). Furthermore, juvenile dietary diversity was significantly lower than adults during SP1 (*t*=6.72, p<.01). These data support the predictions of hypothesis 2a. The seasonal shifts in dietary diversity correspond to seasonal shifts in food availability, where white-faced sakis at Brownsberg consume fewer food types during times of food scarcity and more food types during times of food abundance. Both age groups seem to compensate for the reduction in the diversity of food types they consume by consuming higher proportions of fewer food types. Adults compensated by increasing their relative leaf consumption, while juveniles compensated by consuming more *Pausandra martinii* fruits. These data are similar to what Overdorff (1993) found for *Eulemur rubriventer* and *Eulemur fulvus rufus*, which both decreased dietary diversity when food was scarce.

At Guri Lake, Venezuela, Norconk (1996) found a non-significant (r=-.477) inverse correlation between rainfall and plant species diversity and concluded that white-faced sakis did not vary in dietary diversity seasonally. She attributed this to the saki's ability to feed on fruit at different stages of ripeness. Conversely, Cunningham and Janson (2006), found that during a particular period of food scarcity, saki dietary diversity decreased significantly, where the majority of food came from one tree species: *Licania discolor*. The results presented here are somewhat intermediate between Norconk's (1996) and Cunningham and Janson's (2006) findings. The sakis at Brownsberg did not maintain dietary diversity as predicted by Norconk (1996), but did not reduce dietary diversity to the extent that Cunningham and Janson's (2006) study found. The adults decreased dietary diversity by only about 10% during this time period (.957 SP1 to .864 SP2, Shannon-Weiner index), while juveniles reduced dietary diversity by about 45% (.977 SP1 to .531 SP2, Shannon-Weiner index). These results suggest that white-faced saki feeding strategies can be quite variable, where groups alter diet strategies according to differences in fruit production. It may be their specialized feeding apparatus that allows this to be possible. Since white-faced sakis can use mechanically challenging foods, they may be capable of consuming a wider range of food types than other primate species.

Juvenile and adult white faced sakis appear to adopt different strategies to compensate for seasonal shifts in food availability. Juvenile increased their consumption of *Pausandra martinii* while adults increased their consumption of leaves. This difference may be a reflection of the different constraints of body size. The smaller body size of juveniles is accompanied by a shorter digestive tract, which reduced their absolute ability to extract nutrients from food items. Juveniles may require a relatively higher proportion of fast digesting carbohydrates and protein than adults to support increased metabolic rates and provide additional nutrients for growth. Adult white faced saki diets include anywhere from 4-18.4% leaves (Setz 1993 (as cited in Norconk 2007), Kinzey and Norconk 1993, Norconk 1996, 2007). Mature leaves tend to be difficult to digest and low in nutritional content (i.e. calories; Fleagle 1985, Marroig and Cheverud 2005) although they are widely available. It would make sense for juveniles to consume relatively fewer mature leaves than adults as these do not provide high quality, easily digestible nutrients. Conversely, small size allows juveniles the ability to subsist on less abundant, relatively higher quality resources (i.e. *P. martinii*). The large body size of adults may prevent them from relying on less abundant resources, but may allow them to consume lower quality resources due to a longer gut, which allows more time for nutrient extraction.

Juvenile's *Pausandra martinii* usage during SP1 greatly exceeded adult's use of leaves. There are two possible reasons for this. First, I was unable to estimate the volume of food that was consumed during feeding bouts. Thus, adult leaf-feeding bouts may have yielded a larger total volume of food than juvenile's *P. martinii* feeding bouts. Secondly, adult dietary diversity was significantly greater than juvenile dietary diversity during SP1, whereby adults may not have required as high a volume of each food item, particularly leaves. These results must be interpreted cautiously, as I do not have nutritional data for food items.

It is difficult to pinpoint the most important cause of dietary difference between juvenile and adult white-faced sakis. While difference in body size may have played a minor role in limiting juveniles from the largest food items or in causing juveniles to heavily exploit *P. martinii*, it was not likely a major factor limiting juveniles from other food sources that were not particularly challenging. Inexperience may have rendered juveniles less efficient at exploiting resources or simply naïve as to what foods were suitable to eat. Additionally, the presence of adults may have reduced the amount and variety of resources available.

Juveniles may have increased their consumption of foods with which they were familiar as a result of limited knowledge. It is also possible that juveniles purposefully favored fewer food items as specializing on a single food item can improve an animal's efficiency at exploiting that resource because it allows the individual to form a more effective search image (Bolnick et al. 2003). In this case, juveniles may have emphasized particular food items (e.g. *P. martinii*) because they could find and consume it relatively efficiently. The increase in dietary diversity during SP2 may have reflected juveniles increased knowledge and ability to find and consume foods.

Juveniles may be less efficient at acquiring resources during group feeding events such that they ingest fewer calories per unit time and fewer total calories. Janson and van Schaik (1993) suggest that juvenile foraging success is less than that of adults and that while consuming fruits, juveniles consume fruits at 81% the rate of adults. This may also explain juveniles' increased use of *P. martinii* relative to adults. If the juveniles consumed fewer calories during group feeding events in large patches, they may have made up for this by consuming more *P. martinii* while traveling between larger food patches.

If competition were indeed a factor contributing to dietary difference, the competition was exploitative rather than aggressive. Adults were never observed directing aggression towards juveniles and allowed juveniles to feed nearby during group feeding bouts. Furthermore, adults almost always yielded to juvenile solicited food sharing. This interpretation may be partly biased due to the genetic relatedness of the juveniles to the adults, where the adults effectively increased their own fitness by aiding the juveniles. In a situation with unrelated group members, competition may have been more obvious and involved aggressive interactions. Since I do not have specific data on rate of food intake during feeding bouts, it is not possible to quantitatively substantiate the effects of exploitative competition on age-related dietary variation.

It is important to comment on some of the limitations of the preceding interpretations. First, food items that juveniles acquired by sharing with adults were not included in the diversity estimate. Indeed, these foods are important in contributing to juvenile caloric intake; however they do not necessarily reflect a juvenile's ability to contribute to its own fitness. In this case, food sharing may be better interpreted as a means by which adults enhance fitness by aiding juvenile survival rates. Secondly, the difference in methodology and sample size between seasons may have affected interpretations. Since the group ranged higher in the forest strata during SP2 and were more difficult to observe, some of the feeding events were likely missed. Furthermore, fewer feeding bouts were recorded during SP2. However, any improvements in observation would have served to further exaggerate seasonal differences in dietary diversity as despite the limited visual ability, dietary diversity estimates during this period were already higher.

The difference in dietary variation between juveniles and adults between study periods may be confounded by the fact that the juveniles were older and more experienced during SP2. Thus, rather than purely seasonal differences in fruit abundance, the similarity in dietary diversity and dietary overlap between juveniles and adults during SP2 may have been due to the juveniles improved knowledge of what foods to eat and how those foods are most efficiently consumed. Indeed, Janson and van Schaik (1993) suggest that juvenile primates often achieve adult feeding efficiency before they reach adulthood. Conversely, if juveniles were feeding as efficiently as adults, adults may not have been willing to share food. Food sharing events were observed during SP2, suggesting that juveniles were still somewhat less efficient than adults at exploiting food. Thus, seasonal variation in food abundance was probably as least partly responsible for differences in dietary overlap.

Hypothesis 2c (Physical and mechanical properties)

Janson and van Schaik (1993) noted that juvenile primates often avoid certain large or tough fruits commonly eaten by conspecific adults. Yamashita (1998) found that variation in body size among lemurs contributes to variation in tooth morphology, and tooth morphology significantly influences an animal's ability to exploit particular resources (Anapol & Lee 1994; Lucas 2004; Wright 2005). Here, juveniles were limited only by food size (by weight ($r^2 = .479$, $t = 3.18$, $p < .01$, $df=12$) and by diameter ($r^2 = .382$, $t = 2.94$, $p<.05$, $df=15$)). Further support for this dietary limitation was provided by the observation of juvenile temper tantrums and food sharing events that were commonly associated with larger food items. Since juveniles were apparently unable to manipulate or extract food from the largest food items, they often solicited food sharing from adults while the adults were consuming these items. The mechanical properties of foods in the white-faced saki diet did not to influence dietary differences between juvenile and adult white-faced sakis based on the relative proportion of each food consumed.

It is likely overall body strength limited juveniles rather than jaw strength. The largest food item that adults consumed and juveniles did not, was *Clusia grandiflora*. This fruit was dehiscent such that it required no dental manipulation to access the interior pulp. Furthermore, the pulp was very soft, and would present no masticatory challenges, so the only limitation was juvenile's ability to hold and manually manipulate the fruit to extract the pulp. This inability to consume the largest fruits makes sense if we consider the body size of white faced sakis where adults range between 1.347 and 1.875 Kg. If juveniles are half to three-fourths this size, they should weigh approximately three-fourths to one Kg. Thus, the larger fruits in the saki's diet are about one quarter to one half the weight of juveniles, and may have been outside the range at which juveniles could comfortably hold the fruit and remove the pulp without dropping the fruit or falling from the tree themselves. In the case of *Salacea chordata* (the next largest fruit), it could have been the weight of the fruit or the combination of diameter and mechanical properties that prevented juveniles from consuming this fruit independently. Juveniles were observed eating this fruit during food sharing events with adults suggesting that the mechanical properties were not outside the range that juveniles could overcome. However, the diameter of the fruit may have required juveniles to open their jaws to maximum gape, where the potential bite force is significantly reduced.

The mechanical properties of the foods white-faced sakis consumed did not influence dietary differences between adults and juveniles. It may be the efficiency at which foods are ingested that contributes to differences between juvenile and adult food consumption. Juveniles may have the ability to consume the most challenging foods, but do not have the ability to do so as quickly as adults. This should be reflected in the relative proportions of foods eaten, where juveniles should consume a lower proportion of more challenging foods. Of the foods tested, juveniles did not consume a significantly lower proportion of any of the more challenging food items, according to the number of feeding bouts. It is possible that juveniles consumed fewer food items per feeding bout or consumed each food item at a slower rate, but I do not have data to comment on this difference at the current time. It is also possible that the major difference may be reflected in leaf consumption. Juveniles may consume a relatively lower proportion of leaves in relation to adults than fruit because the rate limiting step in leaf consumption is mastication, while the rate limiting step of fruit consumption is picking (Janson and van Schaik 1993). These data support this theory in that juvenile white faced sakis consumed significantly fewer leaves than did adults. However, this may also be related to digestive differences where juveniles are unable to acquire as much nutrition from leaves as are adults.

As mentioned previously, the data sets for hardness and toughness were limited due to the availability of the testing device. As I was unable to collect data on all of the foods the sakis consumed, I may have missed some of the more challenging food items which were not eaten by juveniles or at least eaten less often by juveniles. This discrepancy would most likely affect interpretations related to hardness and toughness as measurements of puncture resistance were obtained for nearly all relevant fruit species. Selection is often apparent during times of highest stress, or those times when food is in shortest supply (Schoener 1986, Overdorff 1993). Numerous studies have demonstrated that species can overlap significantly in niche dimensions outside the periods of highest stress, but then segregate in niche usage during stressful periods (Schoener 1986). It is possible in this case, that I was not present during the most stressful period when the sakis consumed the most challenging foods that would have segregated juveniles from adults. This is indeed possible since the study occurred during the early dry season and the short wet season. De Dijn et al. (2006) suggest that the dry season is the time of lowest fruit abundance at Brownsberg. Thus, it is possible that dietary differences based on the physical and mechanical properties of fruit are more evident later in the dry season.

Pausandra martinii and leaf consumption

The extreme proportion of the juvenile diet devoted to the consumption of *Pausandra martinii* during SP1 warrants further discussion. *P. martinii* may be an important fallback food for white faced sakis juveniles (at least at Brownsberg). Marshall and Wrangham (2007) define fallback foods as " …items assumed to be of relatively poor nutritional quality and high abundance, eaten particularly during periods when preferred foods are scarce." *P. martinii* was the most ubiquitous feeding tree and it produced fruits during both study sessions, but was consumed at a much higher frequency during the early dry season (reduced resource availability), particularly by juveniles. As juveniles increased the number of other foods they ate, *P. martinii* became less frequently utilized, as a fallback food predictably should. Adult white faced sakis may use *P. martinii* as a fallback food to at least some extent. Adults fed on *P. martinii* during SP1 (although significantly less than juveniles) but during SP2, adults were never observed feeding on *P. martinii*, although it was still widely available. Both age groups consumed a wider variety of food types during SP2 than during SP1, suggesting that when more alternative foods are present, white-faced sakis reduce their intake of *P. martinii*.

Milton (1993) proposed that frugivorous primate diets are characterized as relatively low in protein, but high in accessible calories. White-faced sakis appear to fit this trend as they tend to target foods that are rich in lipids (Norconk and Conklin-Brittain 2004). When considered in addition to the Jarman/Bell principle, this might explain, to at least some extent, the variation in the usage of *P. martinii* between juvenile and adult white faced sakis. Juveniles may select foods that are relatively higher in calories relative to those eaten by adults, to support increased metabolic rates and growth. Juveniles may favor *P. martinii* over leaves as seeds offer relatively more calories. Conversely, decreased metabolic rates combined with larger body size may allow adult white-faced sakis to consume a higher volume of leaves relative to adults. Additionally, variation in the use of *P. martinii* may be related to the patch size of *P. martinii*, which may reduce its potential benefits for large bodied adults. Ecological theory suggests that larger bodied animals cannot afford to consume resources that are in low abundance, even if the nutritional value of these resources is high. Instead, they must consume resources that are more abundant. Conversely, smaller individuals (i.e. juveniles) can consume less abundant food sources if they are higher in quality, because the high quality is necessary to support increased metabolic rates and they require fewer total calories to support their smaller body size.

Marshall and Wrangham (2007) suggest that leaves may be used as a fall back foods, and cite a number of studies in support (proboscis monkey, Yeager 1989; Indri, Powzyk and Mowry 2003; howling monkeys, Chapman 1987). White-faced sakis may also utilize leaves as fallback foods, but adults more so than juveniles. Both age groups consumed significantly fewer leaves during SP2 than during SP1, but adults consumed significantly more leaves than juveniles during both study sessions.

Janson and van Schaik (1993) suggest that the rate-limiting step in leaf consumption is mastication, where juveniles can only consume leaves at 44% the rate of adults. Thus, it would make sense for juveniles to target other resources that yield more total calories per unit time. The fact that both groups fed on a lower proportion of leaves during SP2 than during SP1 suggests that leaf consumption may be related to the availability of other foods such that when other foods are more abundant, sakis do not need to rely on leaves. This lends support to Milton's (1993) hypothesis that primate frugivore diets are highest in accessible calories. When available, sakis seem to select for higher calorie foods (e.g. seeds) but when these foods are less abundant, sakis acquire additional calories from leaves. These results are consistent with Cunningham and Janson (2006) who found that in Guri lake, Venezuela, when fruit feeding decreased, the sakis added more leaves and insects to their diets.

Implications of within-species dietary variation

Acknowledging individual variation within a species is necessary both because it generates a more complete description of biological systems and because it allows ecologists to generate models that more accurately predict the behavior of the system (Bolnick et al 2003). Studies that treat members of the same species as ecologically equivalent may overlook important variation within a species that puts individuals under different selective pressures. To recognize this variation is important because it results in differential fitness among individuals and has important evolutionary implications.

Indeed, it is that individual variation that provides the mechanism for diversification. In primates, individual variation may be more pronounced than in other clades due to the learning component of behavior. Learning allows primates to be extremely versatile in their feeding strategies, well beyond that which is controlled by genetics. This ability to alter behavior and feeding strategy is a major component of primate life histories.

Recognizing individual variation has important implications for conservation. If species management plans aim to protect a species resources by targeting the average resources used by the community, the plan may inadvertently harm those individuals that vary from the population mean (Bolnick et al 2003). Furthermore, this procedure may inadvertently reduce genetic diversity by favoring only a certain set of individuals that are most like the average. This may have further detrimental effects in that it reduces a population's or species' ability to cope with environmental change. Bolnick et al. (2003) suggest that variation within a population may buffer against loss of a particular habitat or resource and provide the genetic variation necessary to adapt to environmental change. In primates, the individual variation that occurs with respect to ontogeny is particularly important. Primates produce very few offspring during a lifetime such that survival through ontogeny is a decisive factor determining population viability. In a study of elephant seals, McMahon et al. (2003) found that juvenile survival was the most important factor affecting the population rate of change. Thus, when developing conservation plans for primates, it is especially important to consider the ecological requirements of immature individuals.

CHAPTER VI

CONCLUSIONS

1. Juvenile white-faced sakis exhibited decreased dietary diversity relative to adults when food was less abundant (i.e. SP1). This difference was likely related to differences in body size and experience that limited the foods the juveniles could potentially consume. Seasonal variation in dietary differences may have been related to niche partitioning during food scarcity, but may also have been a product of age differences between study periods.
2. Juvenile white-faced sakis utilized significantly smaller food patches than adults when foods were less abundant. This may have been a mechanism to reduce niche overlap with adults. It may also have been related to juvenile's small body size which renders smaller food patches more valuable. Like the difference in dietary diversity, the seasonal differences in size of food patches may have been related to the increase in age between study periods.
3. Among the food types the white-faced sakis consumed, age groups differed the most in the consumption of *Pausandra martinii* and leaves, where juveniles consumed a significantly higher proportion of *P. martinii* than adults and adults consumed significantly more leaves than juveniles. That both of these foods were consumed significantly less during SP2, when other foods were more abundant suggests that these resources may serve as important fallback foods for each age group.

4. Despite differences in dietary diversity and feeding patch size, adult and juvenile white-faced sakis maintain a similar height in the forest while feeding. Juveniles may adopt a strategy of feeding close to adults to facilitate observation based learning as well as to gain protection from predators.
5. Juveniles were unable to consume the largest fruits that adults consumed. This was likely related to overall body strength as the largest fruits presented no mechanical challenges.
6. The mechanical properties of fruits (hardness, toughness, puncture resistance) did not significantly contribute to differences in feeding strategy between adults and juveniles. The mechanical properties of foods may affect feeding efficiency, which was not addressed in this study.
7. That juvenile and adult white-faced sakis differ in feeding strategies for at least part of development suggests that it is important to recognize within–species variation in feeding strategies. Recognizing individual variation provides a more accurate description of ecological systems and is important for devising effective conservation strategies that protect a species’ resources.

REFERENCES

Agostini, Ilaria, and Elisabetta Visalberghi. 2005. Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (*Cebus nigritus*). *American Journal of Primatology*, 65: 335-351.

Anapol, Fred and Sarah Lee 1994. Morphological Adaptation to Diet in Platyrrhine Primates. *American Journal of Physical Anthropology,* 94: 239-261.

Anton, S.C. 1999. Macaque masseter muscle: internal architecture, fiber length and cross-sectional area. *International Journal of Primatology*, 20: 441-462.

Bolnick, Daniel I., Richard Svanback, James A. Fordyce, Louie H. Yang, Jeremy M. Davis, C. Darrin Hulsey, and Metthew L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist*, 161: 1-28.

Cachel, Susan. 1984. Growth and allometry in primate masticatory muscles. *Archives of Oral Biology*, 29: 287-293.

Calder, William A. 1983. Ecological scaling: mammals and birds. *Annual Review of Ecology and Systematics*, 14: 213-230.

Chapman, Colin. 1987. Flexibility in the diet of three Costa Rican primates. *Folia Primatologica*, 49: 90-105.

Chapman, Colin, L. J. Chapman, R. W. Wrangham, K. Hunt, D. Gebo, and L. Gardner. 1992. Estimators of fruit abundance of tropical trees. Biotropica. 24: 527-531.

Clutton-Brock, T.H. 1977. Some aspects of intraspecific variation in feeding and ranging behavior in primates. In Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys, and Apes. T.H. Clutton-Brock *eds*. Academic Press, London, pp 539-556.

Cochard, Larry R. 1985. *Ontogenetic allometry of the skull and dentition of the rhesus monkey* (*Macaca mulatta*). In Size and Scaling in Primate Biology. William L. Jungers *eds.* Plenum Press, New York pp 231-256.

Cunningham, Elena P. and Charles H. Janson 2006. *Pithecia pithecia*'s response to decreasing fruit abundance. *American Journal of Primatology*, 68: 491-497.

Darvell, B. W., P.K.D. Lee, T.D.B. Yuen, and P.W. Lucas, 1996. A portable fracture toughness tester for biological materials. *Meas. Sci. Technol*., 7: 954-962.

Dechow, Paul C. and David S. Carlson. 1990. Occlusal Force and Craniofacial biomechanics during growth in rhesus monkeys. *American Journal of Physical Anthropology*, 83: 219-237.

De Dijn, Bart, Iwan E. Molgo, Marilyn A. Norconk, L. Tremaine Gregory, Brian O'Shea, Christian Marty, Martina Luger, Max Ringler, Samuel Crothers, Brice Noonan, Kelly Fitsgerald, Sutrisno Mitro, Arioene Vreedzaam, and Dnarma Satyawam. 2006. The Biodiversity of Brownsberg.

Field, Iain C., Corey J. A. Bradshaw, Harry R. Burton, Michael D. Sumner, and Mark Hindell. 2005. Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (*Mirounga leonina*). *Oecologia*, 142: 127-135.

Fitzgerald, Kelly A., Bart P.E. De Dijn, and Sutrisno Mitro. 2002. *Brownsberg Nature Park Ecological Research and Monitoring Program 2001-2006*. STINASU Research Department.

Fleagle, John G. 1985. Size and adaptation in primates. In *Size and Scaling in Primate Biology*. William L. Jungers *ed*. Plenum Press, New York.

Ford, Susan M. and Lesa C. Davis. 1992. Systematics and body size: implications for feeding adaptations in new world monkeys. *American Journal of Physical Anthropology*, 88: 415-468.

Fragaszy, Dorothy M. and Sue Boinski 1995. Patterns of individual diet choice and efficiency of foraging in wedge-capped capuchin monkeys (*Cebus olivaceus*). *Journal of Comparative Psychology*, 109: 339-348.

Fragaszy, Dorothy M., J.M. Feuerstein, and D. Mitra. 1997. Transfer of food from adults to infants in tufted capuchins. *Journal of Comparative Psychology*, 111: 194-200.

Ganzhorn, Jorg U. 1988. Food partitioning in Malagasy primates. *Oecologia*, 75: 436-450.

Ganzhorn, Jorg U. 1989. Niche separation of seven lemur species in the eatern rainforest of Meadagascar. *Oecologia*, 79: 279-286.

Gaulin, Steven J.C. 1979. A Jarman/Bell model of primate feeding niches. *Human Ecology*, 7: 1-20.

Gautier-Hion, Annie. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *Journal of Animal Ecology*, 49: 237-269.

Gautier-Hion, Annie, J. M. Duplantier, R. Queris, F. Feer, C. Sourd, J.P. Decoux, G. Dubost, L. Emmons, C. Erard, P. Hecketsweiler, A. Moungazi, C. Roussilhon, and J.M. Thiollay. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia*, 65: 324-337.

Gilbert, K. A. 2000. Attempted predation on a white-faced saki in the Central Amazon. *Neotropical Primates*. 8: 103-104.

Gould, Steven Jay. 1966. Allometry and size in ontogeny and phylogeny. *Biology Review*, 41: 587-640.

Grassi, Christina. 2002. Sex differences in feeding, height, and space use in *Hapelemur griseus*. *International Journal of Primatology*, 23: 677-693.

Gunst, Noelle, Sue Boinski, and Dorothy M. Fragaszy. 2008. Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour*, 145: 195-229.

Harrison, Michael J.S. 1983. Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. *Animal Behaviour*, 31: 969-977.

Hershkovitz, P. 1977. Living mew world monkeys (Platyrrhini). University of Chicago Press, Chicago.

Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. *Journal of Theoretical Biology*, 29: 151-154.

Hylander, William L. 1979. The functional significance of primate mandibular form. *Journal of Morphology*, 160: 223-240.

Hylander, William L. 1984. Stress and strain in the mandibular symphysis of primates: a test of competing hypotheses. *American Journal of Physical Anthropology*, 61: 1-46.

Janson, Charles H. 1989. Intra-specific food competition and primate social structure: a synthesis. *Behaviour*, 1-15.

Janson, Charles H. and Carel P. van Schaik 1989. Recognizing the many faces of primate food competition: methods. *Behaviour*, 165-

Janson, Charles H. and Carel P. van Schaik. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In *Juvenile Primates: Life History, Development, and Behavior*, Michael E. Pereira and Lynn A. Fairbanks *eds*., Oxford University Press, New York, pp 57-74.

Kinzey, Warren G. 1992. Dietary and dental adaptations in the pitheciinae. *Americal Journal of Physical Anthropology*, 88: 499-514.

Kinzey, Warren G. and Marilyn A. Norconk. 1990. Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology*, 81: 5-15.

Kinzey, Warren G. and Marilyn A. Norconk 1993. Physical and chemical properties of fruit and seeds eathen by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *International Journal of Primatology*, 14: 207-227.

Lambert, Joanna E. 2007. Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In *Primates in Perspective*. Christina Campbell, Agustin Fuentes, Katherine C. MacKinnon, Melissa Panger, Simon K. Bearder *eds*. Oxford University Press, New York, pp. 123-138.

Lucas, Peter W. 2004. *Dental Functional Morphology: How Teeth Work*. Cambridge University Press, Cambridge.

Lucas, Peter W., Ian M. Turner, Nathaniel J. Dominy, and Nayuta Yamashita. 2000. Mechanical Defenses to Herbivory. *Annals of Botany*, 86: 913-920.

Lucas, P.W., T. Beta, B.W. Darvell, N.J. Dominy, H.C. Essackjee, P.K.D. Lee, D. Osorio, L. Ramsden, N. Yamashita, T.D.B. Yuen. 2001. Field kit to characterize physical, chemical, and spatial aspects of potential primate foods. *Folia Primatologica*, 72: 11-25.

Marroig, Gabriel and James M. Cheverud. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology and ontogeny during cranial evolution of new world monkeys. Evolution, 55: 2576-2600.

Marroig, Gabriel and James M. Cheverud. 2005. Size as a line of least evolutionary resistance: diet and adaptive morphological radiation in new world monkeys. *Evolution*, 59: 1128-1142.

Marshall, Andrew J. and Richard W. Wrangham 2007. Evolutionary consequences of fallback foods. *International Journal of Primatology*, 28: 1219-1235.

McMahon, C.R., H. R. Burton, M. N. Bester. 2003. A demographic comparison of two southern elephant seal populations. *Journal of Animal Ecology*. 72: 61-74.

Miller, Lynne E. and Adrian Treves. 2007. Predation on primates: past studies, current challenges, and directions for the future. In Primates in Perspective. Christina Campbell, Agustin Fuentes, Katherine C. MacKinnon, Melissa Panger, and Simon K. Bearder *eds*. Oxford University Press, New York, pp 525-542.

Milton, Katherine. 1993. Diet and primate evolution. *Scientific American*. 269: 86-93.

Norconk, Marilyn A. 1996. Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. In *Adaptive Radiations of Neotropical Primates*. Marilyn A. Norconk, Alfred L.Rosenberger, Paul A. Garber *eds*. New York, Plenum, pp. 403-423.

Norconk, M. A. 2007. Sakis, uakaris, and titi monkeys. In *Primates in Perspective*. Christina Campbell, Agustin Fuentes, Katherine C. MacKinnon, Melissa Panger, Simon K. Bearder *eds*. Oxford University Press, New York, pp. 123-138.

Norconk, Marilyn A. and Nancy Lou Conklin-Brittain. 2004. Variation on frugivory: the diet of Venezuelan white faced sakis. *International Journal of Primatology*, 25:1-25.

Norconk, Marilyn A., Brian W. Grafton, and Nancy L. Conklin-Brittain. 1998. Seed dispersal by neotropical seed predators. *American Journal of Primatology*, 45: 103-126.

Norconk, Marilyn A., Maryanne Raghanti, S. K. Martin, Brian W. Grafton, L. Tremaine Gregory, and Bart P.E. DeDijn. 2003. Primates of Brownsberg Natuurpark, Suriname, with particular attention to the pitheciins. *Neotropical Primates*. 11: 94-100.

Norconk, Marilyn A., Barth Wright, Nancy L. Conklin-Brittain, and Christopher J. Vinyard. In Press A. Mechanical and nutritional properties of food as factors in Platyrrhine dietary adaptations. In *South American Primates: Comparative*

Perspectives in the Study of Behavior, Ecology, and Conservation. Paul Garber, Alejandro Estrada, Julio Bicca-Marques, Eckhard Heymann, and Karen Strier *eds*.

Norconk, Marilyn A., Brian W. Grafton, and W. Scott McGraw. Morphological, physiological, and ecological adaptations to seed predation- a primate-wide perspective. In Press B. In *Evolutionary Biology and Conservation of Titis, Sakis, and Uacaris*. Adrian Barnett, Liza Veiga, Stephen Ferrari, and Marilyn Norconk *eds.*

Oates J. F. 1987. Food distribution and foraging behavior. In *Primate Societies*. Barbara B. Smuts, Dorothy L. Cheney, Robert M. Seyfarth, Richard W. Wrangham, and Thomas T. Struhsaker *eds*. Pp 197-209.

Overdorff, Deborah J. 1993. Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *International Journal of Primatology*, 14: 721-753.

Overdorff, Deborah J. 1996. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *American Journal of Primatology*, 40: 327-342.

Polis, G. A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *American Naturalist* 123:541-564.

Powzyk, J.A. and C.B. Mowry. 2003. Dietary and feeding differences between sympatric *Propithecus diadema diadema* and *Indri indri*. *International Journal of Primatology*, 24: 1143-1162.

Rettig, N.L. 1978. Breeding behavior of the Harpy Eagle (*Harpia harpyja*). AUK, 95: 629-643.

Rosenberger, Alfred L. 1992. Evolution of feeding niches in new world monkeys. *American Journal of Physical Anthropology*, 88: 525-562.

Schluter, Dolph. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.

Schoener, Thomas W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2: 369-404.

Schoener, Thomas W. 1974. Resource partitioning in ecological communities. Science, 185: 27-39.

Schoener, Thomas W. 1986. Resource partitioning. In *Community Ecology: Pattern and Process*. J. Kikkawa and D.J. Anderson *eds*. Blackwell Scientific Publications, London, pp 91-126.

Setz, E. Z. F. 1993. Ecologia alimentar de um grupo de paraucus (*Pithecia pithecia chrysocephala*) em um fragmento florestal na Amazonia central. Ciencias Biologicas (Ecologia) [PhD diss.]. Instituto Biologica, UNICAMP, Campinas, Brazil.

Svanback, Richard and Daniel I. Bolnick. 2005. Intraspecific sompetition affects the strength of individual specialization: an optimal diet theory method. *Evolutionary Ecology Research, 7*: 993-1012.

Svanback, Richard and Daniel I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. *Proceeding of the Royal Society of London B,* 274: 839-844.

Taurnaud, Laurent. 2004. Ontogeny of feeding behavior of *Eulemur fulvus* in the dry forest of Mayotte. *International Journal of Primatology*, 25: 803-824.

Teaford, M.F., P.W. Lucas, P.S. Ungar, and K.E. Glander. 2006. Mechanical defenses in leaves eaten by Costa Rican howling monkeys (*Allouatta palliata*). *American Journal of Physical Anthropology*, 129: 99-104.

Terborgh, J. 1983. *Five New World Primates: A Study in Comparative Ecology*. Princeton University Press, Princeton.

Vasey, Natalie. 2000. Niche separation in *Varecia variegate rubra* and *Eulemur fulvus albifrons*: I. interspecific patterns. *American Journal of Physical Anthropology*, 112: 411-431.

Vasey, Natalie. 2002. Niche separation in *Varecia variegate rubra* and *Eulemur fulvus albifrons*: II. intraspecific patterns. *American Journal of Physical Anthropology*, 118: 169-183.

Walter, G. H. 1991. What is resource partitioning? *Journal of Theoretical Biology*, 150: 137-143.

Werner, E.E. and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics*, 15: 393-425.

Wright, Barth W. 2005. Craniodental biomechanics and dietary toughness in the genus *Cebus*. *Journal of Human Evolution*, 48: 473-492.

Yamashita, Nayuta. 1996. Seasonality and site specificity of mechanical dietary patterns in two Malagasy lemur families (Lemuridae and Indriidae). *International Journal of Primatology*, 17: 355-387.

Yamashita, Nayuta. 1998. Functional dental correlates of food properties in five Malagasy lemur species. *American Journal of Physical Anthropology*, 106: 169-188.

Yamashita, Nayuta. 1998. Molar morphology and variation in two Malagasy lemur families (Lemuridae and Indriidae). *Journal of Human Evolution*, 35: 137-162.

Yamashita, Nayuta. 2008. Chemical properties of the diets of two lemur species in southwestern Madagascar. *International Journal of Primatology*, 29: 339-364.

Yeager 1989. Feeding ecology of the proboscis monkey (*Nasalis larvatus*). *International Journal of Primatology*, 10: 497-530.