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Positional adaptations and ecology of the Pitheciini

Walker, Suzanne Eve, Ph.D.

City University of New York, 1993

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POSITIONAL ADAPTATIONS AND ECOLOGY OF THE PITHECIINI

by

SUZANNE E. WALKER

A dissertation submitted to the Graduate Faculty in
Anthropology in partial fulfillment of the requirements for
the degree of Doctor of Philosophy, The City University of
New York.

1993

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This manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

POSITIONAL ADAPTATIONS AND ECOLOGY OF THE PITHECIINI

by

Suzanne E. Walker

Advisor: Professor Warren Kinzey

The aim of this study was to investigate positional behavior in a tribe of specialized seed-eating platyrrhines, the Pitheciini, in their natural habitats in Venezuela and Brazil. Data were collected on the positional behavior, habitat use and habitat characteristics of Pithecia pithecia, Chiropotes satanas and Cacajao calvus. These data were used to investigate the influence of a number of ecological and phylogenetic variables on positional behavior, and to draw inferences about the evolution and divergence of the pitheciins.

Pithecia frequently engages in leaping, and exhibits numerous behavioral and anatomical specializations for vertical clinging and leaping. It often uses the lower canopy, which is comprised primarily of vertical and angled supports. Vertical clinging used in feeding allows Pithecia to cling to the bole of one tree while reaching food from the terminal branches of a neighboring, smaller tree.

Chiropotes and Cacajao, the larger pitheciins, are similar to one another in their positional adaptations. They engage primarily in quadrupedalism and pronograde

clambering. Although leaping is important in their locomotor repertoires, they do not demonstrate anatomical adaptations to it. These species occupy the middle and upper canopies. Pedal suspension is often utilized by both species, particularly when feeding, and features for hindlimb eversion are apparent in their pedal anatomy.

Based upon shared behavioral characteristics of these primates, the primitive pitheciin pattern is presumed to have consisted primarily of quadrupedalism and pronograde clambering, with considerable leaping. This pattern accords well with that inferred for the extinct pitheciin Cebupithecia, for which postcranial remains are well preserved.

Each pitheciin species presents a mosaic of primitive and derived features: P. pithecia is more derived in terms of its positional adaptations, due primarily to its specialization for vertical clinging and leaping, while C. satanas and C. calvus are more derived dietarily. Two hypotheses are presented to explain these differences, both dealing with Pithecia's descent to the lower canopy to expand its resource base. One hypothesis envisions the impetus for this shift to have been due to competition with sympatric Chiropotes, and the other to seasonal fluctuations in food availability.

ACKNOWLEDGEMENTS

Numerous people have had much influence on my academic career, from its beginning to the present.

The members of my dissertation committee have inspired and helped me in different ways. As my advisor, Professor Warren Kinzey was positive and encouraging, and always gave generously of his time for discussion or answering my questions. I hope I can someday be as good an advisor to my students as he has been to me. I thank Warren for his guidance, and both he and his wife, Julie Kelly, for their special friendship.

To Professor John Oates I owe my first, wonderful field experience, when he took me to his site in Sierra Leone. I have a great deal of respect for him as an ecologist, and his critical mind has been an important influence for me. His friendship and sense of humor have helped me through tedious times.

Professor Fred Szalay has been a great influence on my thinking, and instilled in me an enthusiasm for morphology and systematics.

Professor John Fleagle has been involved in this project since its early stages. I thank him very much for his support, his time in critically reading drafts of my proposal and dissertation, and for inspiring me to think about important issues of primate positional adaptations.

A special thank-you goes to Professor Elizabeth

Strasser, whose generosity is much appreciated. She has provided an important influence since my early days as graduate student. I thank her for taking time to discuss projects, critically read drafts of the dissertation, arrange for me to use the faculty computer facilities at Cal State University Sacramento, and for sharing many meals with me.

Professor Eric Delson has been a tremendous help since I first started in this program. I am grateful to him for his support (financial and moral), and for introducing me to the wonderful world of the American Museum of Natural History, an incredible place to work and study.

I am grateful to Professor Todd Olson for a few reasons: for providing employment, for assisting with my second comprehensive exam, and especially for sending me in the right direction - to the NAC Building (he'll know what I mean)!

Professors Sara Stinson and Patricia Bridges have provided guidance and friendship over the years, and helped make teaching at Queens College a pleasure.

Several other people have been involved in one way or another, since the beginning of the project, and have been of tremendous help. Professor Mike Rose has been of assistance at every stage, from discussing field methods to reading drafts of the dissertation. I am very grateful for his help and encouragement, and for simply "being around."

Professor Paul Garber spent a great deal of time with me on the telephone, discussing statistical methods, and (probably unknowingly) offering a great deal of moral support and encouragement in the process. His enthusiasm for my project, and helpful discussions with him, are much appreciated. Dr. Marcio Ayres provided a great deal of assistance and encouragement as well. Other people provided advice or discussions of methods of data collection and/or analysis. They include: Professors Miguel Schon, John Cant, and Roy Fontaine, Charles Janson and Thomas Struhsaker.

Professor Marilyn Norconk was very helpful in the field at Guri. She provided encouragement and advice, as well as friendship. A number of other people came to the field site at Guri, Venezuela, with whom I formed strong friendships. They include: Julie Sherman, Christian Meyer zur Heyde, Pia Parolin, Sara Lee, and Jennifer Ashley. The dedicated field workers Ingo Homberg and Angela Peetz made data collection move more smoothly.

I am grateful to have had the opportunity to examine museum collections, and thank those responsible: Dr. Guy Musser, Mammalogy Department at the American Museum of Natural History; Dr. Paolo Emilio Vanzolini, Museo de Zoologia de Universidade de Sao Paulo; Sueli Marquez, Museo Emilio Geoldi, Belem; Dr. Camache, Museo Nacional de Rio de Janeiro. Wolfgang Fuchs provided assistance at the AMNH.

Frank Jr. and Sharon Dumond allowed me to conduct a

pilot study at Monkey Jungle, and to stay in the research house.

Funds for this project were provided by an Explorer's Club Exploration Club Grant, The Graduate Center of the City University of New York, a Wenner Gren Anthropological Institute Grant, a National Science Foundation Dissertation Improvement Grant (BNS 89-13349) and a National Science Foundation Grant to W. Kinzey (BNS 87-19800).

My fellow graduate students at CUNY and at NYU have helped me to survive both New York and graduate school. A special thank you goes to Sharon Sawitzke, who always has room for me to stay whenever I come through New York. Likewise, Dr. Dave Maynard, Wanda Knauss and Linda Brown made it possible for me to carry on outside of New York, while they took care of my affairs here. Thanks to Colleen McAnn and Bob Smith for their friendship. The early days of my graduate career were influenced by Bob Kluberdanz; I appreciate his intelligence, sense of humor, and extensive reprint collection.

Former CUNY Ph.D.'s, finishing before me or during my early days as a graduate student, served as role models, and provided much encouragement. They are: Dr. Marleni Ramirez, and Professors Alfred Rosenberger and Patricia Wright.

At California State University Sacramento, I am grateful to Professor Lorraine Heidecker for permission to

use the computer facilities, to Professor Emeritus Louanna Pettay, who influenced me as an impressionable undergraduate at CSU Sacramento and again as a doctoral candidate, and to Charles Coupar, who just helped out. I also appreciate encouragement of Professors Lois Lippold and Patricia Scollay at San Diego State University.

At the CUNY Graduate Center, I appreciate the help of Professor Jane Schneider, Miss Terri Vulcano and Mrs. Judith Attride, who made things go smoothly for me.

Numerous people that I encountered in my field work in Brazil and Venezuela deserve much gratitude. In Brazil, they are: Chico dos Santos Martins, João Alves and Alejandro Salles. In Venezuela, members of the ecology department of EDELCA were incredible in their logistical support. Special thanks go to Luis Balbás. It would be impossible to name everything he did for us, but working at Guri probably would not have been possible without him. I appreciate both he and his wife, Dora Peretti Balbás, for their friendship. Martín and Marini Lubin were my parents away from home. Other ecology department members were: Teotiste de Aponte, Cleofe Rodriguez, Antonio León, Asterio Farreras, Ali Acuña and Jesús (Quique) Pacheco. Quique's concern and caring followed me from Guri Lake to the United States. Angelica and Alfonso Vega provided assistance in many ways, and a friendship that will always be valued.

My various cousins here in New York, whom I'd met one or fewer times before arriving, took me in and treated me like family. Many thanks to Jimmy and Alice Walker, Bobbie and Gene Zinbarg, and Stellie and Stanley Brill.

My entire family has been encouraging and supportive throughout this entire process.

My husband, Quique, was willing to be plucked from a successful career in his native country in order to share the life of a struggling student. He has provided support and encouragement, knowing that his sacrifices were helping me to speed the process towards achieving my goal. My parents provided everything a kid could want, and supported me in every possible way. It is to my parents and to my husband that this dissertation is dedicated.

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Chapter 1. INTRODUCTION

A. Objectives and Scope

Among the important questions of general interest to evolutionary biologists are those which concern the nature of adaptation and the origin of taxonomic groups. Due to the influence of the fossil record in addressing these questions, the historical emphasis has been on dental features, partly because dental remains are more common than are those of the postcranial skeleton. Recent studies (e.g. Rose, 1983; Ford, 1986; Szalay and Dagosto, 1988) have demonstrated that examination of the postcranium can be equally useful. However, in order to interpret postcranial adaptations, knowledge of positional behavior of animals in their natural habitat is of critical importance.

Objectives

The aim of this study is to investigate the positional behavior of a monophyletic group of platyrrhine primates, the Pitheciini, in their natural environment. The data collected on positional behavior, habitat use, and diet, will be used to draw inferences as to the evolution of positional behaviors and their adaptive significance for obtaining certain dietary items, or for movement in certain forest types.

One representative of each genus, Pithecia, Chiropotes and Cacajao was studied. The pitheciins are medium-sized

platyrrhines, with some significant size differences among members of the tribe. They occur, sometimes sympatrically, in a variety of habitat types in northern South America. Chiropotes and Cacajao are more restricted than is Pithecia in terms of their geographical range and habitat type.

The unique positional adaptations of each genus of the Pitheciini can be differentiated from those which unite the tribe, and thereby provide clues to their divergence. Therefore, three general types of questions are investigated. The first two questions deal with the selective advantage of positional adaptations; the first one concerns proximate causation, and the second, ultimate causation. The third question deals with phylogeny. As an aid in addressing these three major questions, some specific predictions and questions will be examined. These were formulated based on previous studies of positional behavior of the study species, as well as other species, and some theoretical ideas adopted from the literature.

1) How are particular behavioral solutions advantageous to positional problems?

a. Problems of locomotion and posture are typically imposed by the habitat and by an animal's anatomy, which limit the way a habitat can be used (Cant and Temerin, 1984). Primates of large and small body size are each faced with different problems relating to balance, support use and to the crossing of gaps in the canopy (Cant, 1992). Since

balance atop fine supports appears to be a problem for larger primates (Grand, 1972; Cartmill and Milton, 1977), the size of the supports used should be positively correlated with their body size (Fleagle and Mittermeier, 1980). Therefore, we should expect that the large-bodied Chiropotes and Cacajao would use larger supports than would the small-bodied Pithecia. We could also predict that the larger species of pitheciins would engage more frequently in lying behavior, since sitting would be more difficult for them in terms of balance.

As predicted by Cartmill and Milton (1977), and demonstrated by Fleagle and Mittermeier (1980), larger primates would be expected to cross gaps in the canopy by climbing (or bridging), and smaller primates by leaping.

b. Assuming that particularly efficient ways exist to move about in different forest types or canopy levels, we may expect to see some parallels in the way different species utilize the same forest types or levels. For example, changes in canopy level should be accompanied by changes in positional behavior such that when Chiropotes and Cacajao enter lower canopy levels or use lower tree portions, they leap more frequently. This prediction is based on the assumption that leaping is associated with portions of the canopy which have a low degree of connectedness (Napier, 1967; Fleagle, 1977). Davies (1984) demonstrated that Presbytis rubicunda spent more time

leaping when in the discontinuous lower canopy than when in the higher levels. Convergent behavior in similar parts of the forest would indicate a solution to problems posed by habitat structure.

2) How did environmental forces select for adaptations, and under what conditions did they evolve?

This challenging question must be approached based upon information from both ecological and phylogenetic realms.

a. Positional adaptations can evolve as a result of any one of a number of factors, or a combination of them. These factors may include: competition, shift in food availability (perhaps related to a very harsh season), or the colonization of new areas. Some clues which may assist in addressing this question of ultimate causation lie in the previous proximate question. By demonstrating that some positional behaviors appear to be more efficient for use in certain habitats, on particular supports, or to exploit certain food resources, the selective advantage for these behaviors might be inferred. Of great importance to this end is the use of intraspecific comparisons; especially valuable may be the comparison of positional behavior and habitat use with seasonal variations in diet or food availability, as well as with characteristics of the habitat.

b. Possible conditions under which positional

adaptations evolved may be inferred based upon knowledge of the divergence of the pitheciin taxa from one another. Crucial to this end is information about the paleoenvironment of the Amazon basin, the association of certain river types and vegetation with geological formations (as discussed in Ayres, 1986), and the current distribution, habitats, and ecology of extant pitheciins. Studies comparing allopatric and sympatric populations of the same sets of species are of great importance, particularly in terms of inferring whether or not competition may have played a role in selecting for certain (positional or dietary) adaptations.

3) Which positional adaptations are ancestral for the tribe Pitheciini and which are taxon-specific for each genus?

a. Determining the patterns common to all group members can be helpful in discerning which behaviors are ancestral for the group. Previous studies of sympatric primates (e.g., Fleagle, 1978; Fleagle and Mittermeier, 1980), have demonstrated that feeding positions differ less than do traveling positions. In this study (although conducted with the species in allopatry), if feeding positions differ less than those used in other activities (i.e., travel and rest), we would expect that during feeding, more behaviors would be exhibited which are shared among the species. Presumably, these shared behaviors

represent the ancestral pattern.

b. Based on the underlying assumption that the behavioral patterns common to group members are the ancestral ones, we can use a second method to search for ancestral patterns. Subsequent to allopatric speciation, many congeners or other closely related forms often enter a situation of sympatry once again. In this case, divergence in forest use and/or diet is often exhibited in order to avoid direct competition. For example, sympatric Pithecia and Chiropotes demonstrate preferences for different canopy levels (Fleagle and Mittermeier, 1980), possibly as a result of having adapted to a great degree of overlap in general dietary adaptations.

If such species are then encountered in an allopatric situation after a period of sympatry, they may exhibit behaviors not observed when they occurred together. This situation in which each of the species occurs without the other may allow for "competitive release", enabling each to expand and exploit different parts of the habitat or different foods than is typical for the species when sympatric. If we assume that the ancestral patterns of positional behavior are retained by the group members, each species may independently revert to these ancestral patterns.

Scope of study

The members of the taxon Pitheciini were chosen to investigate the above questions of phylogeny and adaptation. The three genera were represented in this study by Pithecia pithecia, Chiropotes satanas satanas and Cacajao calvus calvus. Pithecia and Chiropotes were studied in Venezuela for fifteen and ten months, respectively, and comparative data for Cacajao were collected in Brazil for six weeks. Both Pithecia and Chiropotes were observed through various seasons and different habitat types within their range. The range of positional behaviors was delimited, then categorized in a detailed fashion. The data collected demonstrate the use of positional behaviors in various contexts, and can be related to habitat use by the three species and to the structure of the habitat in which they live. The relationship of positional behavior to diet is examined with regard to the location of the primates' food in the canopy. These data are then synthesized with ecological and morphological information for the Pitheciini in order to draw conclusions about the evolutionary history and adaptations of this tribe.

B. History of Primate Positional Behavior Studies

Reasons for studying positional behavior

Primate positional adaptations have been studied as a means to achieve various ends, including those dealing with

hominid origins, comparative and functional anatomy, and ecology. Early studies of primate positional behavior were primarily concerned with making inferences about the locomotor behavior of the earliest hominids, using the living great apes as analogies (e.g. Wood-Jones, 1929). Brachiating adaptations were often focused upon (e.g. Avis, 1962; Napier, 1959), since brachiation was sometimes considered to be transitional between a quadrupedal and a bipedal pattern (e.g. Morton, 1926; Erikson, 1963; Napier, 1967). Knuckle-walking was sometimes emphasized for the same reason (e.g., Washburn and Moore, 1974). Comparative anatomical studies examined the range of variation within and among primates (Campbell, 1937), and often attempted to categorize locomotor groups based on their results (e.g. Ashton and Oxnard, 1963). More recently, positional behavior has been studied for its own sake or with regard to its wider implications for ecology. Positional behavior has been related primarily to diet (e.g., Andrews and Groves, 1976), to primates' ability to reach food (e.g. Grand, 1972), or to the level occupied by the primates in the canopy (Napier, 1966).

Terminology

Positional behavior, a term coined by Prost (1965), refers to the establishment of certain spatial relationships between the body mass of an individual and its environment.

Prost described positional behavior as encompassing both locomotion (the process of organic activity occurring during organism displacement) and posture (the organic activity which occurs while the summary displacement of body mass is less than a threshold value). Studies conducted since Prost have utilized this distinction between locomotion and posture, and used Prost's terminology (e.g. Rose, 1974; Kinzey, 1977).

Locomotor behaviors have often been emphasized at the expense of postural behaviors, although the latter as well are important in the process of selecting for morphological features; known specializations for resting or sleeping include morphological features (ischial callosities; Washburn, 1957) and behavioral ones (the "foot-prop" posture; Rose, 1974).

The entire range of behaviors of which an animal is "capable" may be somewhat different than those actually "expressed" in its day-to-day life (Morbeck, 1976). First Prost (1965), then Ripley (1967) distinguished between those behaviors which may not occur often, but are crucial to survival, and those that are typically used in most situations. Prost (1965) referred to these seldom-used but important behaviors as "critical", and may be used, for example, in predator escape. Other behaviors in the animal's repertoire he referred to as "frequent". Ripley (1967) referred to the crucial, little-used behaviors as

"primary locomotion".

Primates are characterized by exhibiting a great deal of behavioral flexibility, and the pitheciins are no exception. A wide range of behaviors are possible, limited primarily by anatomical constraints and body size. A great degree of overlap exists among primate species, and very few behaviors appear to be completely exclusive for any one species. The important differences are exhibited in the frequency, the context in which they occur, and the qualitative nature of the behaviors.

Classifications of positional behavior

Prost (1965) stressed the importance of a standardized system to classify the locomotor behavior of primates - one that would allow more concise comparison among studies. The lack of concordance among studies, he suggested, was based primarily on the lack of a good definition of locomotion. He proceeded to provide a general definition (discussed in the previous section). Studies of primate positional behavior have since flourished, and have become increasingly sophisticated and detailed.

Studies of comparative primate anatomy began long before the commencement of field studies which focused on positional behavior. Therefore, classifications of primate positional behavior were initially devised by anatomists (e.g. Ashton and Oxnard, 1963; Napier, 1963). However,

these classifications were based upon observations of zoo animals, anecdotal observations of wild primates, or solely on anatomy. The problem with the categories that were devised was that they were very broad, and that many diverse forms were lumped together which actually exhibit very different positional behavior from one another (Ashton and Oxnard, 1963). Erikson (1963) based his comparison of Old and New World brachiators on the (primarily) anatomically-based classification of Krieg (1930).

The results of a 1965 symposium on primate locomotion demonstrated the importance of distinguishing between categories of locomotor behavior and those based on skeletal anatomy (Kinzey, 1967). Even some of these classifications based on behavior were inaccurate, partly because they were not derived from natural behavior, and were devised to fulfill certain expectations based on the phylogeny of the animals. For example, in the classification of Napier and Napier (1967), primate species were placed into categories of behaviors in which they seldom actually engage. For example, gorillas were placed into the "brachiator" category, although field observations (e.g., Schaller, 1963) demonstrated that they rarely brachiate. Other classifications have used unspecific categories for behaviors in which no primate actually engages (Ripley, 1976); the non-existent behavioral category "semi-brachiation" is an example.

Current studies have based classifications of locomotion and posture on behavior of natural primate populations rather than on anatomy or the behavior of captive animals. Therefore, these classifications are biologically relevant. They tend to be thorough, and more detailed in nature (e.g., Schön and Schön, 1987; Cant, 1988; Fontaine, 1990; Boinski, 1989; Doran, 1992; Hunt, 1992), reflecting such information as limb segment positioning (e.g., Schön and Schön, 1987), forces thought to be transmitted through limbs (ibid.), and number of cheiridia or body parts in contact with supports (e.g., Hunt, 1992).

However, even in current studies of positional behavior, the difference in the manner in which each positional mode is utilized by various species has not yet been investigated. Each species may have its own particular way of moving, and although a general category may adequately describe the positional mode for two different species, there may be qualitative differences between them due to differences in anatomy, limb proportions and support use. One important example, leaping, will be discussed in Chapter 6.

Ecological considerations

The focus of studies of positional behavior as it relates to ecology initially emphasized the relationship between locomotion and diet in the attempt to discover broad

correlates (Napier, 1962; Avis, 1962; Napier, 1967; Andrews and Groves, 1976). Studies attempting to identify such correlates among sympatric primates have found instead that species with broadly similar diets differ in their locomotor behavior (Charles-Dominique, 1971; Stern and Oxnard, 1973; Fleagle, 1978; Fleagle and Mittermeier, 1980; Fleagle, 1984). Two proposed associations between locomotion and diet (forelimb suspension with frugivory: Avis, 1962; Napier and Napier, 1967; Andrews and Groves, 1976; and vertical clinging and leaping with gummivory: Fleagle, 1984) are characterized by confounding variables and exceptions. For example, many frugivorous primates (e.g., pitheciins) do not habitually use forelimb suspension. Vertical clinging and leaping tends to occur not only with gummivory, but in forests with many vertical substrates (Stern and Oxnard, 1973). Some primates exploit gum but do not demonstrate any "gummivore" specializations (see Fleagle, 1984); others are vertical clingers and leapers but are not gummivorous. However, for some callitrichid primates, studies have demonstrated clear evidence for the selective advantage of positional strategies for a particular diet (Kinzey et al., 1975; Garber, 1980; Sussman and Kinzey, 1984). In these studies, vertical clinging was shown to be related to exudate feeding, particularly from large vertical supports, which demonstrates an important relationship between the substrate type and the positional strategy rather than the

food per se. Fleagle (1984) demonstrated how the traditional classification of food into such groups as leaves, fruit and insects does little to elucidate the relationship between diet and positional behavior. Therefore, the correlation of diet with positional strategies must not depend on the food type, but its location in the canopy and in individual trees.

While diet directly influences locomotor behavior by determining and/or limiting energy intake, it also provides an indirect influence by determining the path to be traversed in order to reach food. Behavioral adaptations for feeding (e.g., suspension or vertical clinging) are made possible by anatomical specializations (a mobile shoulder joint or claw-like nails and small body size; Erikson, 1963; Grand, 1972; Sussman and Kinzey, 1984). A number of environmental variables provide selective pressures for positional behaviors, and researchers (listed below) often emphasize the influence of one or more of these as well as document the context in which they occur (feeding, foraging, travel, etc.). Habitat structure is often shown to figure importantly in determining positional behavior. For example, canopy level and/or substrate characteristics influenced positional behavior in Callicebus torquatus (Kinzey, 1977), Alouatta palliata (Mendel, 1976), Presbytis cristatus and P. obscura (Fleagle, 1978), P. rubicunda (Davies, 1984), and Pongo (Cant, 1987). Ripley (1979), in

her study of Presbytis entellus, was one of the first researchers to demonstrate how tree form affects primate activities, including positional behavior. Garber (1984) and Crompton (1984) observed differential habitat utilization and locomotor patterns of Saguinus oedipus and two Galago species, respectively, to exploit foods located in different parts of the habitat and on different substrates. The latter study was the first to document locomotor changes in response to seasonal food availability. Rose (1979) analyzed positional activities of Colobus guereza and Cercopithecus aethiops, relating them to maintenance and social behaviors as well as to habitat structure. Fleagle and Mittermeier (1980) investigated the correlations between diet, forest strata and support size with locomotion in seven sympatric primates in Surinam.

Biomechanical and morphological considerations

Gravitational and frictional forces pose problems for primates; solutions to these problems may be behavioral or anatomical, or a combination of the two. Functional morphology uses the laws of physics to demonstrate a causal relationship between morphology and behavior. The correlation alone of certain morphological features with particular behaviors is not sufficient - a strong case must be made for a biomechanical advantage of a particular form. Numerous studies have done so; Fleagle's (1977a and b)

provide examples. In his research, the analysis of field behavior and anatomy were combined for two species of Presbytis, and differences were documented between them in both the skeleton and associated musculature. A biomechanical analysis demonstrates causally linked patterns of locomotor behavior with anatomy. For example, the longer hindlimbs of P. melalophos are related to the capacity to "increase the distance over which the accelerating force is exerted..." when leaping (Fleagle, 1977b, p. 442).

Various methods of functional morphology have been used to explain the diversity of morphological structures, especially: skeletal anatomy (joint architecture, cortical bone thickness, limb indices; e.g. Erikson, 1963; Sarmiento, 1983; Godfrey, 1988; Strasser, 1988); allometry (e.g. Jungers, 1985; Strasser, 1992); muscular anatomy (muscle attachments, muscle weights, electromyography; e.g. Basmajian, 1974; Tuttle and Basmajian, 1974; Ashton and Oxnard, 1963; Grand, 1968a and b; Stern, 1971; Stern and Wells, 1976; Rodman, 1979; Sarmiento, 1985); cineradiography (e.g. Fleagle and Jenkins, 1975) and range of motion studies on cadavers or anesthetized animals (e.g. Kinzey, 1967; Ziemer, 1978; Gebo, 1985).

Body size has been shown to be an important limiting factor for positional behavior and support use, and can secondarily influence the evolution of some specialized anatomical features. As pointed out by Rose (1974),

differences between New World and Old World monkeys in size as well as in postural behaviors may explain the lack of ischial callosity development in New World monkeys. The smaller body size of most New World primates is one factor which lessens problems of balance. In addition, New World monkeys tend to lie, rather than sit, to sleep and rest. An additional example of the effects of body size on anatomical and behavioral adaptations is demonstrated by the callitrichids. Along with claw-like nails, small body size allows these primates to cling to and move about upon large vertical supports (e.g., Garber, 1980; Sussman and Kinzey, 1984).

Fleagle and Mittermeier (1980) found substantive correlations between locomotor behavior and body size. Some of these correlations supported predictions by Napier (1967) and Cartmill and Milton (1977), which suggested that smaller primates would be more likely to leap, and larger ones to climb (or bridge) across gaps in the canopy. These authors, as well as HersHKovitz (1970), predicted that larger primates would be more likely to suspend below branches than smaller ones, as balance on top of branches becomes increasingly difficult as body size increases. Avis (1962) found that, in a captive setting, monkeys spent less time on the small branches than did the larger apes. The monkeys were observed to utilize relatively larger supports.

C. Theoretical Considerations

Introduction

Many aspects of an animal's behavioral repertoire contribute to its survival. Positional behaviors enable an animal to achieve certain goals: attain food, escape from predators and maintain balance (especially important for arboreal animals). Theoretically, each individual should attempt to achieve its goals in the most efficient manner possible; that is, the manner in which a minimum of energy is expended. Features which are "well-adapted" (sensu Bock, 1980) to the environment allow biological role(s) to be performed by an individual with a minimum of energy expenditure. Behavioral features do not act in isolation from the morphologies which permit and constrain certain functions. The study of positional behavior encourages an "holistic" approach by encompassing a range of interacting variables, drawn from behavior, morphology and phylogeny. While the mechanics (function) of a feature can be studied in a laboratory, the biological role can be determined only by observing the use of a feature in its natural environment (Bock and von Wahlert, 1965). The study of a species in its species-specific habitat (microhabitat) is essential in order to begin to assess the selective forces acting on a species (Bock, 1980).

Ecological considerations

The early studies which attempted to make broad correlations between positional behavior and aspects of ecology (discussed on p. 12) were useful in that they caused researchers to think about new and important issues in primate ecology. However, the picture doesn't seem to be as simple as was once thought. It seems crucial to gather more information on the behavior and ecology of primates in order to make these types of correlations. We need to look more specifically at the variables influencing positional behavior, such as the location of food in the canopy matrix and the form of feeding trees. Studies of habitat use should include not only canopy levels, but the relative height at which primates are found within trees, the tree portion, and characteristics of individual supports used. We should search for the consistent use of certain positional behaviors on similar supports across species. Such constancy may indicate the most efficient way of moving on certain supports, therefore elucidating the selective advantage provided by these positional behaviors.

Biomechanical and morphological considerations

Although this study deals primarily with the ecological aspects of positional behavior, another important aspect is that inferences can be drawn for morphological studies. In this study, categories of positional behavior have been

defined in such a way as to allow such inferences about the forces acting upon the musculoskeletal system when it is involved in various positional behaviors upon a variety of support types (as in Schön and Schön, 1987). The effects of forces on living organisms depend upon their form and their features (e.g. body size and limb length), and upon characteristics (e.g. size, inclination and deformability) of the supports they use.

Investigation of the manner in which laws of physics affect primate positional behavior must include consideration of the lever arms of gravity and the muscles resisting gravity, types of stresses, force application, force absorption and friction.

The musculoskeletal system works about axes of rotation (fulcrum) so that a series of levers produce movement as a consequence of the size and architecture of muscles and their distance of attachment from joints. Mechanical advantages for particular movements at each joint depend upon the lengths of power and load arms (due to muscle insertions, limb length and segment positions). For example, in Presbytis melalophos, the moment arm of the hamstrings about the hip is increased by the relatively long ischium, resulting in the powerful thigh retraction which permits efficient leaping (Fleagle, 1977b).

The influence of gravity poses an important problem for animals (particularly if arboreal), as balance must be

maintained. A tree branch generally provides a primate with a narrow base of support, over which the center of gravity must be balanced (Napier, 1967). There are four possible solutions to overcome this problem (Cartmill, 1985): shortening limbs morphologically or behaviorally, prehensility, underbranch suspension and smaller body size. These solutions are significant if a branch is horizontal. However, the center of gravity shifts with increasing inclination of a support; it becomes displaced either forward (if the body is angled up) or rearward (if the body is angled down).

When angled supports are used, the importance of friction in positional behavior comes into play, since there is a potential for slippage. A horizontal support poses no problem in terms of friction if the base of support is large, while increasing the inclination of a support increases the shear force exerted between the feet and the branch (Hildebrand, 1982). On angled supports, therefore, behavioral strategies (such as limb flexion) or morphological adaptations (such as claws or volar pads and prehensile capabilities - Cartmill, 1979) are called into play in order to maintain the center of gravity over the base of support. Primates are subjected to, as well as exert, forces, the latter in order to effect a change in velocity (to move). A change in velocity can be increased in two ways: a force of greater magnitude can be applied,

and/or the period of time over which force is applied can be lengthened. For example, crouching immediately prior to leap take-off is presumably a strategy to increase the time over which propulsion is applied against the take-off support by a leaping primate. In order to stop the momentum of an object in motion (again, for example, a leaping primate), velocity must be changed (decreased) to zero. The forces of impact upon landing can be reduced by increasing either the landing surface area or the time over which forces are distributed. Landing on all four limbs maximizes the surface area over which compressive forces are spread, and limb flexion or landing on a flexible substrate, acts to increase the time over which forces are distributed.

Reconstructing positional behavior of extinct primates

Causal links between features of anatomy and behavior can be established through functional morphological analyses, and comparative anatomy employed to establish the form of the physical features of fossil remains. Subsequently, the positional adaptations of extinct animals may be reconstructed by analogy to form-function complexes in living animals. The study of paleobiology should be undertaken within the framework of evolutionary morphology (sensu Szalay, 1988), recognizing the constraints imposed by morphology, ecology and phylogeny, and the interplay between the three. Examples of these kinds of studies include Jolly

(1972), Szalay and Decker (1974), Morbeck (1975), Szalay and Dagosto (1980 and 1988) and Fleagle and Simons (1982), Rose (1983,'88,'92), Sarmiento (1987) and Ford (1988).

For many taxonomic groups, no fossil record exists; nevertheless, ancestral behaviors can be inferred based on behavior patterns and their functional correlates in their living representatives, as discussed on p. 5.

D. Organization of Dissertation

Chapter 2 provides background information about the Tribe Pitheciini (sensu Rosenberger, 1992). It begins with interpretations of the phylogeny of the group. The chapter continues with a description of the distribution, habitats and home range sizes occupied by its members, as well as the endangered status of natural populations of Pitheciini. This is followed by a section on dietary adaptations and one on positional adaptations of the group members. The chapter ends with a brief presentation of a few interpretations of the locomotor behavior of now-extinct pitheciins.

Chapter 3 introduces the study sites in Venezuela and Brazil, and includes information about weather patterns in the regions and mammalian species which co-exist with the study species. The composition of the study groups observed at each site, as well as the active day length and the habituation process for each, are discussed.

The theory behind the methods of data collection used

in this study, the use of frequency data in studies of positional behavior and problems in applying statistical tests to these data are discussed in Chapter 4. The rationale for the statistical analysis performed in this study is also presented.

Chapter 5 provides a comparison of vegetation types before and after the inundation of the Caroni River Basin in Venezuela, in which forested islands have been formed, now providing the habitat for the pitheciin primates observed for this study. The chapter also presents the results of data collected on the habitat types at the Venezuelan site. A comparison of the form of the five major species of feeding tree of Pithecia and Chiropotes is presented here.

At the beginning of Chapter 6, the categories of positional behavior are defined, having been distinguished both in the field and from video analysis. The results of the analyses are presented in three sections. The first compares the two groups of Pithecia living on two different islands. The second presents the results of the positional behavior of each species (the data from two groups of Pithecia are pooled). The third section compares positional behavior among the three species (Pithecia pithecia, Chiropotes satanas and Cacajao calvus). The chapter concludes with a presentation of the qualitative and quantitative differences in leaping behavior of Pithecia and Chiropotes.

Chapter 7 is a discussion which synthesizes the various aspects of positional adaptations, correlating the positional behavior of each species with habitat and support use, habitat types, and anatomical features. The influence of habitat differences on the positional behavior and habitat use of the pitheciins is discussed, as is the relationship between positional behavior and diet.

In Chapter 8, the range of variability in a number of ecological and behavioral features is outlined. Partly from this information, inferences are drawn as to the possible ancestral locomotor pattern for pitheciins, and the possible conditions by which members of the taxon diverged.

A summary and conclusions are presented in Chapter 9.

Chapter 2. WHAT IS A PITHECIIN?

A. Taxonomy and Phylogeny

Classification

The monophyly of the three genera: Pithecia, Chiropotes and Cacajao, has been widely accepted for a long time (e.g. Hill, 1960; Rosenberger, 1981; Ford, 1986). Their placement in the tribe Pitheciini (as in Rosenberger, 1992) within the subfamily Pitheciinae is accepted here. Callicebus and Aotus are also accepted as their sister-group, the two together forming the subfamily Pitheciinae (ibid.). However, Ford (1986) and Kay (1990) place Callicebus and Aotus outside the pitheciine clade. In this dissertation, only members of the tribe Pitheciini (Pithecia, Chiropotes and Cacajao) will be considered.

These three genera share a number of derived cranio-dental (Rosenberger, 1979) and postcranial (Ford, 1986) traits. It is generally agreed that Cacajao and Chiropotes are more closely related to one another than either is to Pithecia (e.g. Hill, 1960), as the two share a number of derived features not shared with Pithecia, particularly in dental and mandibular morphology (Rosenberger, 1988; Kinzey, 1992).

The two species of Pithecia previously recognized (e.g. Hill, 1960) were P. monachus and P. pithecia, the former with four geographic variants and the latter with two (Tate, 1939). The variants of P. monachus have since been

separated into four allopatric species (Hershkovitz, 1987a) within the species-group P. monachus. This group includes P. monachus (formerly P. hirsuta), P. aequatorialis (formerly P. monachus), P. albicans and P. irrorata (ibid.). Members of this species-group, all of which occur south of the Rio Amazonas, can be distinguished from the P. pithecia species-group on a number of variables. These are noted by Hershkovitz (1987a): features of pelage and degree of pelage difference between the sexes, cranial characteristics and skeletal metrics; and by Peres (in press): body size, vertical use of the forest and locomotor behavior. While Hershkovitz' classification is provisionally accepted here, greater emphasis is placed on the differences between the two species-groups, Pithecia pithecia and Pithecia monachus.

Chiropotes comprises two species, Chiropotes satanas and Chiropotes albinasus (Mittermeier and Coimbra-Filho, 1981).

Two species of the genus Cacajao are recognized: C. calvus and C. melanocephalus (e.g. Hershkovitz, 1972; Mittermeier and Coimbra-Filho, 1981; Hershkovitz, 1987b). C. calvus includes a red form and a white form, often considered separate subspecies: C. c. calvus and C. c. rubicundus (e.g. Hershkovitz, 1972; Mittermeier and Coimbra-Filho, 1981).

Fossils

The tribe Pitheciini is thought to have diverged from its ancestral platyrrhine stock by the early Miocene, and the dental features typical of modern pitheciins to have evolved by the middle Miocene (Rosenberger, 1992). The affinities of some possible fossil representatives of the subfamily are questionable, and only a single fossil genus, Cebupithecia, is agreed upon as a pitheciine, and has been considered as such for a few decades (e.g. Hill, 1960). Both Kay (1990) and Rosenberger (1992) would place Cebupithecia sarmientoi, from the middle Miocene of La Venta, Colombia, in the pitheciine clade based on dental and postcranial evidence. Kay considers the taxon to represent a sister-group to living pitheciines, as it lacks some of the dental specializations of extant pitheciines. Ford (1990) postulates that while many aspects of the postcranium of Cebupithecia are comparable to those of Pithecia, the similar features evolved independently, precluding its status as an ancestor to Pithecia.

Rosenberger (1992) recognizes Soriacebus ameghinorum as another, earlier member of this clade, while Kay (1990) considers the dental features of this primate to represent convergent specializations to a similar diet rather than a synapomorphic pitheciine adaptation to sclerocarpic foraging (sensu Kinzey, 1992).

While commenting on the dearth of evidence, Kay

recognizes the possibility that Mohanomico herskovitzi (which he considers synonymous with Aotus dindensis) represents a primitive pitheciine, rather than a callitrichine relative (as in Rosenberger, 1992).

Body Size, Sexual Dimorphism and Sexual Dichromatism

Body size of pitheciines ranges from an average of 1.4 kg (female Pithecia pithecia) to 3.8 kg (male Cacajao calvus) (from Ford and Davis, 1990; see Table 2.1). The genus with the largest body size is Cacajao, and Chiropotes is slightly smaller. Pithecia has the smallest body size, although members of the P. monachus species-group are considerably larger than P. pithecia (Herskovitz 1987a; Ford and Davis, 1990; Peres, in press).

Overall, members of this tribe exhibits little to moderate sexual dimorphism (Hill, 1960; Robinson et al., 1981). Female body weight ranges from about 76% of that of males (members of P. monachus-group) to 86% (C. satanas) (from data in Ford and Davis, 1990). Within the genus Pithecia, the largest members (the P. monachus-group) are the most sexually dimorphic, and the smallest (P. pithecia) is the least sexually dimorphic (ibid.).

Pithecia is the only genus to exhibit differences in pelage between males and females. P. pithecia exhibits striking sexual dichromatism in body coat color as well as facial markings, and the males of this species are thought

to be the most highly derived of the genus (Hershkovitz, 1987a). Members of the P. monachus group exhibits some differences in facial pelage between males and females, although they are by far the most marked in P. aequatorialis (ibid.).

B. Distribution

Members of the tribe Pitheciini occur in northern South America (Figure 2.1). The northern-most point of their distribution is the southern portion of the Orinoco Delta in northeastern Venezuela and the most southerly along Rio Manu in Peru (Hershkovitz, 1979). The western-most distribution is reported to be Baeza in Ecuador (ibid.), and they occur as far east as the eastern side of Rio Tapajós in northern Brazil (ibid.). Pithecia is the most widely distributed genus, members of which make up the northern, southern and western limits of the range of the Pitheciini. Pithecia species are often found sympatrically with Chiropotes, and less frequently with Cacajao, while the latter two appear to occur only allopatrically with one another.

Members of the genus Pithecia inhabit much of northern South America, and the two species-groups are separated by the Rio Amazonas. P. pithecia is found throughout the Guayanas and in northern Brazil (Wolfheim, 1983). Its northern and western limits in Venezuela are formed by the

Rio Orinoco (Bodini and Pérez-Hernández, 1987) and the Rio Caroni, respectively. In Brazil, the boundaries for P. pithecia distribution are formed by the Rio Negro on the west and Rio Amazonas on the south. The members of the P. monachus group occur to the south of the Rio Amazonas and southwest of the Rio Negro. The range of P. monachus is from the west bank of the Rio Tapajóz in Brazil, west to the Andes of Peru, Colombia and Ecuador (Hershkovitz, 1979). P. aequatorialis is distributed from southern Colombia to northern Bolivia, and east to the Rio Juruá and Japurá/Caqueta (Hershkovitz, 1979). P. albicans occurs on the southern bank of the Rio Solimões, between the lower Rio Juruá and lower Rio Purús (Hershkovitz, 1979; Peres, in press). P. irrorata occurs in southwestern Brazil between the south bank of the Rio Juruá and the south bank tributary, the Rio Tarauacá (Hershkovitz, 1987a).

The two species of Chiropotes occur in the eastern part of the Amazon basin (Napier, 1976), in forests on the Brazilian and Guayana shields (Ayres, 1989). Two subspecies of C. satanas (C. s. satanas and C. s. utahicki) occur south of the Rio Amazonas in Brazil, to the east of the Xingú River (Hershkovitz, 1985). C. s. chiropotes occurs north of the Rio Amazonas, and the Rio Negro forms its western limit. This subspecies is distributed throughout the forests of French Guayana and Surinam, and through much of Guayana (Ayres, 1986). In Venezuela, C. s. chiropotes is found in

the southern Amazon region (Handley, 1976; Bodini and Pérez-Hernández, 1987), and to the north it occurs on the west bank of the Rio Caroni (Kinzey et. al., 1988), north of the confluence with the Rio Paragua. C. albinasus is found south of the Rio Amazonas in Brazil, between the rivers Madeira and Xingú (Ayres, 1989).

The two forms of Cacajao calvus are found in the western Amazon basin (Napier, 1976). They occur in northwestern Brazil, eastern Peru and southeastern Colombia (from Ayres, 1989). The red form (C. c. rubicundus) and the white form (C. c. calvus) are allopatric. C. c. rubicundus is found west of the Rio Japurá on the north bank of the Solimões, and C. c. calvus on the south bank of the Rio Solimões, with the Rio Japurá forming its eastern limit (Fontaine, 1981; Hershkovitz 1987b; Ayres, 1989). Cacajao melanocephalus also occurs in northwestern South America, from eastern Colombia and southern Venezuela into northern Brazil (Fontaine, 1981; Bodini and Pérez-Hernández, 1987). It is found to the north of the main rivers between the Rio Negro basin and the east bank of the Rio Japurá (Ayres, 1989).

These distribution patterns, and the incidence of sympatry among the pitheciins, are discussed further in Chapter 8.

C. Habitats

Members of the tribe Pitheciini occur in widely varying habitats, some representatives being more limited in their distribution and habitat preference than others. The two larger pitheciin genera, Chiropotes and Cacajao, are more limited in their habitat preference, while Pithecia can survive in a wide range of habitat types.

Of the members of its genus, P. pithecia has the widest range of habitat preferences. It occurs in inland high tropical rainforest, mountain savanna forest, liane forest, ridge forest, savanna forest, riverbank marsh lee forest, swampwood and secondary forest (Mittermeier, 1977). Durham and Durham (cited in Wolfheim, 1983) have reported it in gallery forest, open canopy Mora forest, palm forest and coastal scrub. In Venezuela, it most often inhabits moist evergreen forest and sometimes dry deciduous forest, and ranges from 150 to 350 meters elevation (Handley, pc to Wolfheim, 1983). It has also been observed in small patches of dry forest interspersed with scrub vegetation in eastern Venezuela (Kinzey et al., 1988; W. Kinzey, pers. comm.).

Information on the habitat preferences of each species of the P. monachus group is probably not accurate, due to the differences in the classification schemes followed by various authors. Thus, the following information on habitat preferences probably includes all members of the P. monachus species-group unless otherwise specified. P. monachus

inhabits humid lowland primary rainforest (Wolfheim, 1983) of Colombia. In Peru and Bolivia it can be found in evergreen, mesophytic, broadleaf forest on high ground in white-water drainage and on floodplains of black-water rivers (Freese, 1982). This species may occur up to an elevation of 762 m in Peru, and in Brazil it inhabits primary terra firme and primary várzea forests (Mittermeier and Coimbro-Filho, 1977). It has been observed in primary lowland rainforest of Peru (Happel, 1982).

P. albicans occurs in primary terra firme forest in Brazilian Amazonia, but also uses igapó (seasonally flooded forest along black-water rivers) along the Rio Urucu, as well as creekside forest and palm swamps (Peres, in press).

Chiropotes is generally found in primary forest on terra firme (nonflooded, high forest) (Ayres, 1989), but may also use riverine forests along clear-water rivers (Johns and Ayres, 1987). In Venezuela, C. satanas is found most often in evergreen forest near streams, as well as in deciduous forest between 135 and 161 meters elevation (Handley, pc to Wolfheim, 1983). In Surinam it has been reported mostly in high tropical rainforest, riverbank high forest and mountain savanna forest (Mittermeier, 1977). In Brazil, C. satanas occurs in igapó forest of black or clear water, in the high forest (ibid.; Dean et al, 1971, cited in Wolfheim), and is also reported to use the palm swamps of eastern Maranhão (Johns and Ayres, 1987). C. albinasus

inhabits the igapó forests of clear-water rivers (Mittermeier and Coimbra-Filho, 1977), terra firme and sometimes várzea (Ayres, 1986).

The two species of Cacajao have been reported almost exclusively in floodplain environments, although they have been reported as well in high terra firme forest (Aquino, 1988; Ayres, 1989). Cacajao calvus lives in the várzea forests (floodplains of white-water rivers) (Ayres, 1986). C. melanocephalus has been observed in igapó forests in Brazil (Mittermeier and Coimbra-Filho, 1977; Ayres, 1989). In Venezuela, this species is found in evergreen forests near streams between sea level and 500 meters elevation (Handley, pc to Wolfheim, 1983) and in seasonally flooded forests of black-water rivers (G. Aymard, pers. comm., 1991).

D. Home Range Size

Home range size is dependent upon type of diet, and can vary intraspecifically. However, it can be instructive to examine the overall picture of home range size, especially since each pitheciin species (or species-group) appears to conform to the same general pattern.

Home ranges sizes have been established, at least tentatively, for several species of pitheciins. P. pithecia appears to have by far the smallest home range, estimated by Buchanan (1978) to be between four and ten hectares. Setz

(1988) observed P. pithecia in a nine-hectare patch of forest. For the current study, the size of the island upon which the group of P. pithecia occurs was less than 20 hectares. P. albicans, on the other hand, has a home range of at least 172 hectares (Peres, in press).

The other two genera undoubtedly range over greater areas. Chiropotes albinasus was observed to have a home range of 250 to 350 hectares (Ayres, 1981), and that of C. satanas 200 to 250 hectares in Surinam (van Roosmalen et al., 1981). Of an estimated total home range size of 500 to 550 hectares for Cacajao calvus, Ayres (1989) estimated that they primarily used 250 to 300 hectares.

E. Status of Wild Populations

Population Density

The population density of at least one species of each genus has been estimated based on census studies. Freese (1975) estimated that P. monachus had a population density of between 2.5 and 9.0 individuals per km² in Peruvian Amazonia. P. albicans is estimated to have a density of 4.1 individuals per km² in terra firme forest (Peres, in press). Mittermeier and van Roosmalen (cited in Buchanan et. al., 1981) report P. pithecia's density as 3.6 individuals per km² in terra firme high forest of Surinam. Oliveira et. al. (1985) estimate a density of 40 per km² in Brazil, in an area completely protected from hunting and from primate

competitors. This area consisted of a few vegetation types: selectively logged high forest, lower forest on white-sand soils, old secondary forest and patches of palm forest.

C. albinasus (Ayres, 1981) and C. satanas (van Roosmalen et al., 1981) each have population densities of between 7 and 8 individuals per km² in terra firme forest. C. calvus has been estimated to have a population density of 10 to 11 individuals per km² (Ayres, 1986) in flooded forests of white-water rivers.

Endangered Status

Three pitheciin species are listed as Vulnerable in the 1990 IUCN Red List of Threatened Animals: Cacajao calvus (both subspecies), C. melanocephalus and Chiropotes albinasus. Both Cacajao species have vulnerable status in Brazil, Colombia and Peru; C. albinasus is considered vulnerable in Brazil. Chiropotes s. satanas, the southern bearded saki, is listed as Endangered in Brazil, and according to Johns and Ayres (1987) it is the most endangered Amazonian primate. Its situation has been brought on primarily by extensive habitat encroachment, most often in the form of timber logging and flooding for dam construction.

Pithecia is hunted for both its meat and its tail in Brazil (Mittermeier and Coimbro-Filho, 1977), Peru (Soini, 1972), Surinam (Husson, 1957; Mittermeier, 1977) and

Venezuela (Mondolfi, 1976). In Surinam, P. pithecia is kept as a pet (Husson, 1957; Mittermeier, 1977), as is P. monachus in Brazil (Mittermeier, Coimbro-Filho and Van Roosmalen) and Peru (Castro, 1976).

Chiropotes albinasus and C. satanas are hunted for food and bait in Brazil (Mittermeier and Coimbro-Filho, 1977; Ayres, 1978), and for food in Venezuela (Mondolfi, 1976) and Surinam (Husson, 1957; Mittermeier, 1977). Individuals are killed for their tails to be used as dusters in Brazil (Mittermeier and Coimbro-Filho, 1977) and ornaments in Venezuela (Mondolfi, 1976), and C. satanas may be taken as a pet in Surinam (Husson, 1957).

C. calvus is hunted for its meat only in Peru (Grimwood, 1969), while C. melanocephalus is hunted in Colombia (Hernandez-Camacho and Cooper, 1976) and Venezuela (G. Aymard, pers. com.). In Brazil, its meat may be used as cat bait (Mittermeier and Coimbro-Filho, 1977). C. calvus may be captured for pets in Peru (Castro, 1976; I.U.C.N., 1978).

F. Feeding Adaptations

Diet

Members of the tribe Pitheciini are primarily seed predators, each genus specialized to a varying degree for the ingestion of seeds. Dietary adaptations of Cacajao and Chiropotes are more similar to one another than to those of

Pithecia (Ayres, 1986; Kinzey, 1992).

Data on annual diets of Cacajao calvus and Chiropotes albinasus are documented in Ayres (1986), and on C. satanas from Van Roosmalen et al. (1988) and Kinzey and Norconk (1990, 1993). Comparative long-term data for Pithecia, previously lacking in the literature, are available in Kinzey and Norconk (1993) for P. pithecia and Peres (in press) for P. albicans.

Fruit: Fruit parts comprise the major portion of pitheciin diets. Averaged over a year, at least 90% of the dietary intake of Chiropotes and Cacajao (Ayres, 1986; Van Roosmalen et al., 1988), about 88% of that of P. pithecia (Kinzey and Norconk, 1993) and 80% for P. albicans (Peres, in press) consisted of fruits. Seeds account for 36% to 75% of total fruit intake in all three genera, and usually for at least 63% (Ayres, 1986; van Roosmalen et al., 1988; Kinzey and Norconk, 1993; Peres, in press). While Ayres (1986) and van Roosmalen et al. (1988) report Chiropotes and Cacajao to concentrate on immature seeds, Kinzey and Norconk (1993) document avoidance of seeds of some species of unripe fruits, especially by Pithecia, possibly due to a high level of condensed tannins. At the Venezuela site, Pithecia depends on seeds to a lesser degree than does Chiropotes (61% compared to 75% of total fruits ingested), and more on other fruit parts, leaves, flowers and insects (ibid.). Seeds comprise a total of 46% of the diet of P. albicans in

Brazil (Peres, in press). Previous short-term studies (Mittermeier and van Roosmalen, 1981 and Oliveira et al., 1985) document a high percentage of fruit (79% and 93%) in Pithecia diets, but a lower ingestion of seeds (22% and 36%) than for Pithecia in Venezuela. This difference may be due, in part, to habitat differences between the sites, as the Guri forest is drier, and may have a lower availability of fleshy fruits (Kinzey and Norconk, 1993).

Nonfruit: The importance of dietary items besides fruits varies within the Pitheciini and may account for between 1% and 28% of the total intake. The following table lists the percentages of non-fruit items in the diets of Cacajao calvus (cc), Chiropotes satanas (cs), C. albinasus (ca), P. pithecia (pp) and P. albicans (pa):

	<u>cc</u> (1)	<u>cs</u> (1)	<u>ca</u> (1)	<u>cs</u> (2)	<u>cs</u> (3)	<u>pp</u> (3)	<u>pa</u> (4)
Flower/nectar	6	11	3	3	0.4	2	8
Insect/arthropd	5	-	-	-	0.5	2	0.4
Leaves	-	-	-	-	0.2	7	10
Petioles, young twigs	-	-	-	0.4	-	-	-
Other	3*	16*	7*	-	-	-	1**

(1) Ayres, 1986 * leaves, petioles, bark, unidentified

(2) van Roosmalen et al., 1988

(3) Kinzey and Norconk, 1993

(4) Peres, in press ** exudates, bark

(Johns, 1986b, reports 30% leaves for pa; Happel, 1982, reports 16% for pm)

Although actual ingestion of insects by Chiropotes is rarely recorded, individuals often manipulate dead leaves, presumably to search for insects (pers. obs.).

Seasonal variation: P. pithecia utilizes a high percentage of flowers only in the dry season when fruit availability was low (Kinzey and Norconk, 1993). It depends to a large degree on two plant species (Licania discolor and Connarus venezolanus) for seed consumption, and when these fruits are scarce, feeding on flowers as well as a wider variety of other seed species increased (ibid.). Seasonal variation is also noted in relation to an apparent change in chemical properties, with Pithecia choosing fruits at times when tannin levels are moderate to low, and lipid and protein content is higher. During February and March of 1991, an especially dry season prevailed, and Pithecia was seen to ingest large quantities of leaves (pers. obs.), as well as an egg taken from a bird's nest (I. Homburg, pers. comm.). While Pithecia depends on a wider variety of foods such as flowers, leaves and others when fruits become scarce (Setz, 1988; Kinzey and Norconk, 1993; pers. obs.), Chiropotes eats seeds from fruits with hard pericarps (Kinzey and Norconk, 1990, 1993).

Seasonal diversity in diet is reported for Chiropotes albinasus and Cacajao calvus by Ayres (1986). Both species exhibit a marked increase in seed consumption in the dry season, with a concomitant decrease in mesocarp consumption. Conversely, the rainy season brings about a shift towards higher mesocarp, and lower seed intake (ibid.) For Cacajao, at least, dietary diversity increases with fruit

availability at Lake Teiú (ibid).

Species and characteristics of food eaten by pitheciins:

Although the várzea habitat of Cacajao and the terra firme forest of Chiropotes albinasus in Brazil differ considerably in terms of variety in fruit species (the latter with a much wider variety), fruits from the same families, and even the same genera, are consistently chosen by both pitheciin species. For Cacajao, one half of the annual diet is derived from the four families: Hippocrataceae, Lecythidaceae, Annonaceae and Moraceae. Chiropotes albinasus has a more varied diet, but depends to a high degree on Palmae, Sapotaceae and Leguminaceae, and to a lesser degree on Bignonaceae. Chiropotes satanas in Brazil (Ayres, 1986) and Surinam (van Roosmalen, 1981) use several species of both Sapotaceae and Lecythidaceae. Sapotaceae and Lecythidaceae are also heavily depended upon by P. albicans (Peres, in press), although Pithecia's diet diverges more from the other two both in terms of families of food species eaten and hardness of fruits consumed (see below) (Oliveira et al, 1985; Kinzey and Norconk, 1993; pers. obs.). Fruits eaten by Cacajao and Chiropotes also share some common morphological features (besides hardness), noted by Ayres (1986); for example, they often have yellow lipid- and protein-rich pulp, as opposed to white pulp low in protein and lipids but high in sugar.

Kinzey and Norconk (1993) tested for the hardness of

pericarps of fruits eaten by Pithecia pithecia and Chiropotes satanas in Venezuela, as well as the crushing resistance of the seeds. They found that the seeds inside hard-shelled fruits were relatively soft, and were masticated and digested. There was little overlap in the fruit species used by the two pitheciins, and Chiropotes used fruit whose maximum hardness was higher than that of Pithecia. Ayres (1986) noted that Cacajao calvus used more lianas for feeding, while Chiropotes albinasus used relatively fewer. C. satanas in Surinam used fruit from lianas almost 20% of the time for feeding (van Roosmalen, 1988). Liana species comprised 1% of the foods used by P. albicans (Peres, in press).

Although Buchanan et al. (1981) reported that drinking in wild Pithecia had not been documented, P. pithecia in Venezuela was observed to do so on numerous occasions, usually by dipping its hand into a fork or hole in a tree, then holding the hand up and licking it (pers. obs.).

Dentition

A unique dental apparatus enables the pitheciins to exploit these resources (Rosenberger, 1988; Kinzey, 1992). The three genera exhibit shared derived traits of both anterior and posterior dentition, which can be functionally correlated with the preparation of hard-shelled fruits and the mastication of relatively soft seeds. Chiropotes and

Cacajao share more such traits with one another than with Pithecia. These shared traits of Chiropotes and Cacajao are said to be derived for these specialized seed predators (Rosenberger, 1988; Kinzey, 1992).

Features of the anterior dentition include: styliiform lower incisors; upper and lower incisors anteriorly inclined; large, laterally splayed canines; and buccolingually tapered canines (Rosenberger, 1988; Kinzey, 1992). The incisor form allows efficient "nipping" or "cropping" (ibid.). The size and shape of the canines are functionally correlated with their use in opening hard fruit, and their orientation enables fruits to be punctured with a great deal of force, without interference of the incisors, due to the position of the diastema (ibid.).

In the posterior dentition, $Pm^{4/4}$ is enlarged and molariform, and $Pm^{3,4/3,4}$ are often crenulated on their occlusal surfaces. Occlusal relief on the molars is low, and they are crenulated. The biorole of the posterior dentition is said to be mastication of the relatively soft seeds, often found in fruits with hard pericarps (Kinzey, 1992). The crenulated premolars and molars may serve to better grip the smooth seeds for grinding (rather than crushing) motions (ibid.). The opening of hard pericarps with the anterior dentition to obtain relatively soft seed kernels which are masticated by the posterior dentition has been referred to by Kinzey and Norconk (1990)

as sclerocarpic foraging.

G. Positional Adaptations

Differences in both positional behavior and morphology among the genera of pitheciins are better documented than are the features shared by members of the tribe (except Ford, 1986). One such feature is the pitheciin hand, characterized by the fact that grips are taken between the second and third digits, rather than first and second, as in many primates (e.g. Erikson, 1957; Hill, 1960; Kay, 1990).

Positional Behavior

Representatives of all three genera use both quadrupedalism and leaping to a high degree (Buchanan et al., 1981; van Roosmalen et al., 1981; Fontaine, 1981), although there are significant differences in the form of these behaviors (see p.) and in the frequency of their use in various contexts. The two shared forms of locomotion among the genera are obviously not unique to this group, as they are also used by most platyrrhines. Previous long-term field studies of pitheciin positional behavior are lacking, although short-term research has been conducted. Mittermeier (1977) and Fleagle and Mittermeier (1980) studied sympatric primate species in Surinam, including Pithecia and Chiropotes.

Pithecia

Short-term observations were conducted for P. pithecia in Suriname (Mittermeier, 1977; Fleagle and Mittermeier, 1980), although its positional behavior remained little documented. Individuals were unhabituated and difficult to follow, which made significant quantitative data collection impossible. However, some features of microhabitat preference and positional behavior were observed. These primates demonstrated a preference for vine tangles in lower levels of liane and high forests (Fleagle and Mittermeier, 1980), and for relatively small supports. Seventy-five percent of its observed travel bouts involved leaping behavior; other locomotor modes observed were quadrupedal walking and climbing, the latter relatively frequently. For rapid locomotion, bipedal hopping was common, and used along with bounding, jumping and leaping when individuals were excited (Mittermeier, 1977). Leaps greater than 10 meters were observed. Slow movement was achieved by quadrupedal walking. Ascent was accomplished on thin twigs by climbing, and on thicker supports by shinnying, or sometimes hopping or jumping. Leaping was observed as a descent mode, and gaps were crossed by bounding, galloping or bipedal hopping. Short distances could be covered by bipedal walking, which was less common than hopping. Hindlimb suspension was recorded in feeding Pithecia.

Happel (1982) observed "P. hirsuta" (= P. monachus) for

a short time in Peru, and found that these primates were using different parts of the forest than had previously been reported for the genus. Feeding and resting were observed in the upper canopy and emergents (15 - 24 m), and travel in the more continuous understorey (10 - 19 m). Horizontal quadrupedal walking was the most common locomotor pattern observed (49%), followed by leaping (33%). Vertical quadrupedal walking was also used fairly frequently (10%), and other behaviors (horizontal quadrupedal run, vertical quadrupedal run, gallop and quadrupedal walk on ground) relatively infrequently. The locomotor behaviors were not defined in the paper, and again, the sample size was very limited (N=153 observations).

In his long-term study of the ecology of P. albicans, Peres collected data on vertical use of the habitat, and made some anecdotal observations on locomotor behavior. He described P. albicans as a "canopy species", rarely found in the understorey, but most frequently in the lower canopy (25 - 30 m). This species used tall trees in proportions higher than expected for their availability. The most common locomotor pattern was a quadrupedal gait, usually on large branches. Vertical clinging was rare. Leaps were also observed between terminal twigs or different tree crowns. Mostly inflexible branches were used.

Previous to the current study, Pithecia had not been reported on the ground.

Chiropotes

Chiropotes satanas was studied more extensively by Mittermeier (1977) and by Fleagle and Mittermeier (1980) than was Pithecia pithecia. Chiropotes demonstrated a preference for upper forest levels. Quadrupedal walking and running comprised 80% of all bouts in travel, and leaping 18%. Leap landings were often onto forelimbs first (for short leaps) or all four limbs (longer leaps). Climbing and bridging were relatively rare. Quadrupedal travel was accomplished on relatively large branches, and leaping on somewhat smaller supports. Quadrupedal climbing was used for both ascent and descent. Locomotion during feeding (movement within a feeding tree) was also primarily quadrupedal (walking and running). Hindlimb suspensory postures were used to increase the feeding sphere. Smaller supports were utilized for movements within a feeding tree than during travel. Chiropotes uses its tail for balance as well as communication. Tail-wagging has been reported for individuals in a state of general excitement (e.g. van Roosmalen et. al., 1981). This species was never observed on the ground.

Cacajao

The locomotor behavior of wild Cacajao has not been the focus of any study; however, some data were collected on substrate use and positional behavior by investigators

focusing on other aspects of ecology (i.e. Ayres, 1986). Ayres, in fact, collected preliminary data of locomotor behavior during travel for C. c. calvus in Brazil. He found that quadrupedalism was the most frequently used, at just under 50% of samples, followed by leaping, at about 40% of samples (pers. comm.). Climbing was noted about 12% of the time (ibid.). Ayres (1986) also described feeding techniques and substrates used. Cacajao often moves about in terminal branches to collect fruit, then carries it in the mouth; the individual may either to a more solid support if manipulation is required to open the fruit, or it can be eaten while traveling. Also mentioned is the use of hindlimb suspension for obtaining access to fruit, but points out that this behavior is used more often in play. Ayres also observed extensive use of the ground by Cacajao, particularly for the driest months at Teiú, when they were estimated to spend as much as 30 to 40% of their time foraging on the ground.

Fontaine (1981) thoroughly documented the positional behavior of captive Cacajao living in a large, natural-type enclosure at Monkey Jungle, Florida. The most important behavior was quadrupedalism, usually observed on solid boughs. Leaping was the second-most important behavior. Momentum could be gained before leap take-off by either rocking the branches or by using a running start for solid supports. Gallop and bounding were used for rapid

locomotion and crossed extension quadrupedal gaits for slow locomotion. For ascent of large boughs, Cacajao "often move by pushing in unison with the hindlimbs while using their forelimbs as pivot struts" (ibid.). This probably describes the category here referred to as shinnying. Gaps were crossed by leaping, armswinging or bridging. Some bipedal locomotion was observed in play or while food-carrying. Vertical clinging was observed sometimes, usually as a momentary pause between leaps. Both bipedal suspension and bipedal standing were used in feeding. Resting postures included the sprawl, a flexed resting posture, or sit.

Differences were noted between age-sex classes (ibid.). Generally, adult males were slower and more cautious, and engaged in less leaping and armswinging than did females or juveniles. Bridging was more common in adults than in juveniles.

While Cacajao's tail is too short to assist in balance during locomotion or posture, it is used in tail-wagging displays.

Morphology

Morphological comparisons of the postcranial skeleton between Pitheciini and other platyrrhines (including the other Pitheciinae, Aotus and Callicebus) demonstrate the existence of a number of features, particularly of the humerus (pers. obs.) and femur (Ford, 1980), which appear to

be shared among members of this tribe; see list below.

From Ford (1980 and 1986):

Femur

low transverse trochanteric breadth
 oval to round insertion area for the iliopsoas
 tendon on the lesser trochanter
 thick, posteriorly directed lesser trochanter
 medial and lateral patellar borders which are rounded
 and subequal in anterior extent
 distal epiphysis relatively symmetrical - the condyles
 are subequal in size, and in distal and posterior
 extent

Hand

digit ray formula: 4>3>5>2>1

Features of the knee attest to approximately equal use of both condyles in weight-bearing, and little abduction at the hip. Not all of the features listed about are unique to pitheciins; only low transverse trochanteric breadth and an oval to round insertion area for the iliopsoas tendon on the lesser trochanter are derived for the group (Ford, 1986). The relatively long fourth digit in pitheciins may be related to the ability to grasp large-diameter supports; this may be similar to the situation described for the foot of colobine monkeys (Strasser, in press).

A number of humeral, and a few femoral, features (pers. obs.) are listed below, compared with those of the atelines and the cebines (Saimiri and Cebus). The pitheciins appear to fall in between atelines and cebines in terms of most

features.

Humerus

	pitheciin	ateline	cebine
orientation of proximal humerus:	somewhat medial	more	less
orientation of humeral head:	1° posterior	medial	posterior
size discrepancy between greater and lesser tuberosity:	some	little	much
size of tuberosities:	medium	small	large
cranial extent of tuberosities in relation to humeral head:	medium	low	high
placement of greater and lesser tuberosities on proximal humerus:	sltly. anter.	anterior	lateral and medial
articular surface area of humeral head:	medium	most	least
bicipital groove:	medium	narrowest	widest

The medial orientation of the proximal humerus appears to be due to both curvature and torsion. The size and placement of the tuberosities in relation to the humeral head, and the articular surface of the head, indicate that the role of stability at the shoulder joint is less important for pitheciins than it is for cebines. A wider range of motion is permitted in pitheciins than at cebines at this joint, although less so than in atelines.

Femur

posterior proximal femoral ridge less pronounced,
more rounded (contra Ford, 1980 for Cacajao)
patellar groove wide and shallow (contra Ford,
1980, p. 233 for Chiropotes).

A wide, shallow patellar groove indicates a relatively high degree of mobility at the knee joint.

Postcranial features which distinguish among the pitheciin genera abound (particularly between Pithecia vs. Chiropotes and Cacajao). These appear to be functionally related to aspects of locomotion (Fleagle and Meldrum, 1988). Functional correlates of behavior and anatomy were based on the behavioral data collected by Fleagle and Mittermeier (1980). As previously mentioned, Chiropotes behavior is much better known than that of either Pithecia or Cacajao. Most anatomical features documented by Fleagle and Meldrum (1988) attest to a primarily quadrupedal pattern for Chiropotes, and one of leaping and clinging for Pithecia. Their results, correlated with the data collected for the present study, are discussed in Chapter 8.

Locomotor adaptations of fossil pitheciins

Reconstruction of the locomotor morphology of pitheciins is limited to the taxon Cebupithecia sarmientoi, for which a considerable part of the postcranial skeleton has been preserved (Meldrum and Fleagle, 1988; Ford, 1990;

Meldrum et al., 1990). Ford (1990) compares Cebupithecia to Pithecia and to habitual leapers as she discusses features of the humerus, femur, talus and calcaneum.

Femoral morphology suggests a moderate degree of lateral rotation and abduction at the hindlimb; that of the talus and calcaneum, a stable ankle joint; humeral features indicate a stable elbow. Hindlimb features may represent adaptations to leaping; those of the forelimb to a frequent clinging posture, particularly on angled or vertical supports. Ford (1990) proposed that Cebupithecia exhibited a mixed behavioral repertoire which included quadrupedal branch running, leaping, some climbing and suspensory positions. Meldrum et al (1990) report on a distal humerus from the same species, but focus on its similarities to Pithecia. They discuss several features which they attribute to likely adaptations to a habitual clinging posture.

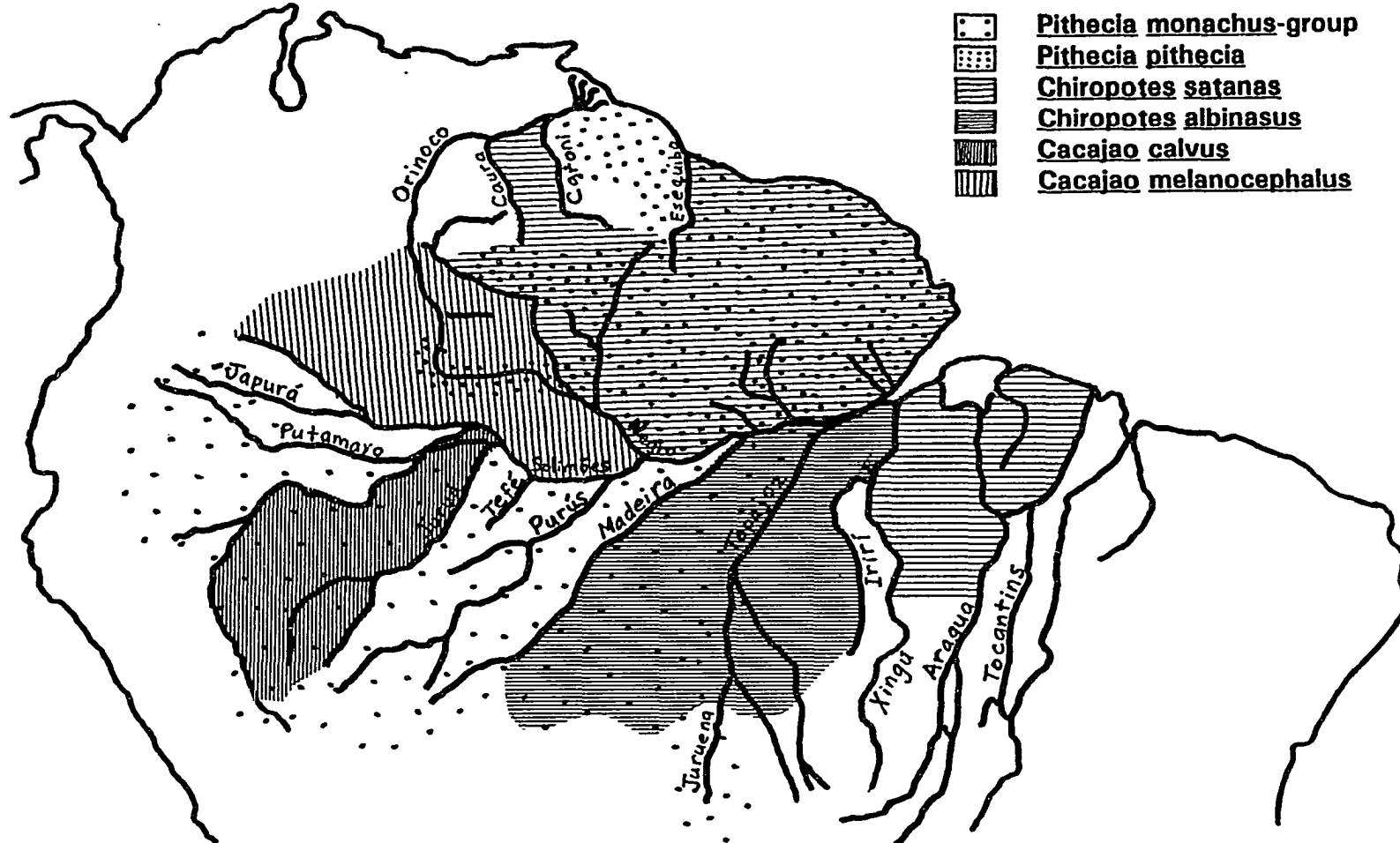


Figure 2.1. Distribution of pitheciins

Table 2.1. Body weights of pitheciin primates.

Species	Average Weight (kg)	
	Males (N)	Females (N)
<u>Pithecia monachus-group</u>	2.6 (17)	2.0 (20)
<u>P. pithecia</u>	1.8 (32)	1.4 (19)
<u>Chiropotes albinasus</u>	3.1 (20)	2.5 (18)
<u>C. satanas</u>	3.0 (73)	2.6 (72)
<u>Cacajao calvus</u>	3.8 (2)	3.2 (3)
<u>C. melanocephalus</u>	-	2.7 (2)

Compiled from Ford and Davis (1990)

Chapter 3. STUDY AREAS

A. Teiú Lake, Northwestern Brazil

A short-term study of Cacajao calvus was conducted for six weeks, from July to September, 1988, in the forest at Lake Teiú, in Brazilian Amazonia. This species is found in the seasonally flooded "várzea" (floodplains of white-water rivers) forests (Ayres, 1986).

Location

This study site is located on the shores of Lake Teiú, a small oxbow lake between the Japurá River and Lake Mamirauá of northwestern Amazonas (3.22°S, 64.42°W). It is 47.5 km west of the town of Tefé (Ayres, 1986). (See map, Figure 3.1). It can be arrived at by boat from Tefé in approximately five hours, via the Solimões River to the long, ribbon-like Lake Mamirauá. Near the end of the lake is the camp (a floating house), constructed by Ayres for his 1983/84 study; it is now a station for a biological reserve.

Climate

Temperatures were recorded over a period of twelve months in 1983/84 (Ayres, 1986). The mean temperature near the site (approximately 21 km away) in 1984 was 29.5° C, with the mean maximum and mean minimum at 31.3° and 21.7° C, respectively (ibid.). Daily temperatures vary much more than the monthly averages. The lowest temperature recorded

by Ayres (1986) was 18° C in June, 1984.

Rainfall

Annual rainfall (between December 1983 and November 1984) was 2850 mm, considerably higher than the average yearly rainfall for the Amazon basin (2300 mm) (Ayres, 1981). January through April had the highest amount of rainfall, and the driest month recorded in 1984 was September (Ayres, 1986). The fluctuation in rainfall results in a difference of approximately eleven meters in water level at the study site. Water levels were generally highest in late May/early June and lowest in September and October (ibid.). From the start of my study in late July to the end in early September, water level dropped approximately 3.5 meters.

Mammalian fauna

There is a low mammalian diversity at the site, compared with that from "terra firme" areas. Ayres (1986) observed 22 species, including the four primates: Cacajao calvus, Cebus apella, Alouatta seniculus and Saimiri vanzolinii. Hunting was virtually nonexistent due to the inaccessibility of the site, as well as to the absence of major game animals, such as tapir (Tapirus terrestris), peccary (Tayassu tajacu and T. pecari), deer (Mazama spp.), paca (Cuniculus paca) and agouti (Dasyprocta agouti).

Felids present at the site include jaguars (Panthera onca), ocelots (Felis pardalis) and margays (Felis weidii), which may be possible monkey predators (along with the rare harpy eagle, Harpia harpija) (Ayres, 1986). Other common mammals include the two genera of sloth (Bradypus and Choleopus), capybara (Hydrochoerus), red squirrel (Sciureus cf pyrronotus), and anteater (Tamandua) (Ayres, 1986 and personal observation).

Study site, general habitat characteristics

Ayres developed a trail system in the form of a grid, with trails each 100 meters, with more than 30 km of total trails (see map, Fig. 3.2), which he used in his study of Cacajao ecology in 1983 and 1984.

The general habitat type covering the entire study area is várzea. Included in this forest type are the higher and lower restingas (levees) and chavascal (backswamp) (Ayres, 1986). In general, plant biomass is considerably lower than in non-flooded habitats (Pires, 1973 cited in Ayres, 1986). The higher restinga, which covers considerably less area than does the lower, is distinct from the latter in both structure and species composition. Covered by dense vegetation, this higher ground is much more species-rich, and has a relatively higher number of trees, which may reach 35 or 40 meters in height, particularly along riverbanks (Ayres, 1986). Predominant tree families include:

Annonaceae, Euphorbaceae, Leguminaceae, Apocynaceae, Lecythidaceae and Lauraceae. Very little of the ground on the higher restinga is flooded -- one to two-and-a-half meters at the most, and only for a short time (ibid.).

The lower restinga, found between the higher restinga and the chavascal, is sometimes flooded up to five meters, and is characterized by many more lianas than found on higher ground. The most common tree families include: Euphorbaceae, Leguminaceae, Lecythidaceae, Annonaceae and Myrtaceae (ibid.).

Chavascal, or backswamp, is relatively more open, and is covered by flood waters up to a depth of six to seven meters, from six to eight months of the year. Common vegetation includes Bombacaceae (Bombax), Euphorbiaceae and Moraceae (especially Cecropia and Ficus) (ibid.).

Study group

Ayres' main study group of 1983/84 consisted of 48-50 individuals, including a number of adult males and females and their offspring. This approximate group count applies for my 1988 study as well. Since Ayres' study, this Cacajao group had not been observed by researchers, therefore had become unaccustomed to the presence of people. My stay was too short to re-habituate them. In fact, they had never been habituated enough to allow for close observation, but were tolerant only if the observer stayed at a distance of

at least thirty meters (Ayres, 1986). Fortunately, however, they remained sufficiently high in the canopy that noises from the forest floor could go undetected, so they could often be observed for periods of time without their apparent knowledge. When human presence was detected, however, the monkeys usually gave alarm calls, split up and moved quickly out of view. During my stay, as the dry season progressed and water level dropped, fruit became increasingly sparse. The Cacajao group responded to the lower fruit availability by splitting into small feeding subgroups, which were more difficult for me to locate and follow.

B. Guri, Eastern Venezuela

Behavioral observations of Pithecia pithecia in their natural habitat in Venezuela were conducted from October 1989 to May 1991, and of Chiropotes satanas from December 1989 to May 1991. The two species were studied on three separate islands in Guri Reservoir. The two northerly islands are located in an area known as Las Carolinas, and the island 40 km to the south in a zone called Danto Manchado. In this region of Venezuela, Pithecia is found in tropical dry forest and Chiropotes in "transitional" moist tropical forest (Kinzey and Norconk, 1993).

Location, general habitat characteristics

Guri Lake (mouth at 7.30°N, 63.00°W) is located in

Bolívar State, eastern Venezuela (Fig. 3.3), on the northern part of the Guayana shield (Schubert, et al., 1986). The 4300 km² lake was created by the construction of the Raul Leoni hydroelectric dam in 1963 on the Caroni River, and its subsequent inundation to 215 m above sea level beginning in 1968. The lake reached its current level of 270 m above sea level in 1986 (Alvarez et al., 1986). The dam, the lake, and the strip of land within one kilometer of the 270 m mark surrounding the lake are administered by EDELCA (Electrificación del Caroni), a subsidiary company of the government corporation CVG (Corporación Venezolana de Guayana). The inundations have isolated patches of savanna and forest habitat into islands, upon which occur a wide variety of reptilian, avian and mammalian fauna (see p.58).

The Caroni River is a black-water river whose contributing waters originate on the tops of several tepuis (sedimentary-stone plateaus) to the south in the Gran Sabana, in the southwest portion of the Caroni River Basin (Huber, 1986). This basin was formed by the rivers Paragua and Caroni, and covers approximately 95,000 square kilometers (Schubert et al., 1986).

A widely varied mosaic of forest and savanna types cover the entire area, and are described by Huber (1986). The greatest portion (over one half) of the area is forest-covered, followed by savanna, which occurs mostly in the north and southwest parts of the basin. Guri Lake is

located in the northern part of the Caroni River Basin. Of the land surrounding Guri Lake, much of the northern shore is covered by "bosques tropofilos macrotermicos" (ibid.). These forests are deciduous or semideciduous, with the highest trees ranging from 12 to 18 meters. The forest is of medium density, and the presence of lianas (especially Arrabidaea) is marked. Common tree species are: Tabebuia crisantha and T. millsii, Tapirira guianensis, Apeiba echinata, Bourreria cumanensis and Bursera simaruba (ibid.). Much of the eastern and western shores of the reservoir are savanna-covered, with some patches of forest similar to that mentioned above. The southern-most part of the lake's shores, and continuing to the south, are "bosques ombrofilos", higher, wetter forests (pluvial forests), which cover a large part of the lowlands (Huber, 1986). This terrain is undulating, with clayey soils and great variation in vegetation type. These forests are evergreen and taller, the emergents reaching to more than 40 meters in height. The understory is not well developed, presumably due to the dearth of light which reaches the forest floor. Common tree species for the upper canopy are: Aspidosperma, Erisma uncinatum, Drypetes variabilis, Sandwithiodoxa egregia, Hymenea courbaril, Anacardium giganteum, and Sclerolobium chrysophyllum. For the middle canopy, the most common species are: Bocageopsis multiflora, Licania discolor, Himantanthus articulata, Inga alba, Tetragastris

panamensis, Eschweilera subglandulosa and Jessenia sp.

Of the 4300 square kilometers now covered by Guri Lake, approximately 54% was originally savanna, and about 46% was covered by various types of forest (Pernia, 1985). Presumably, these forests lined the river's edge before the flooding.

Effects of this enormous lake on the environment include slightly higher humidity, and somewhat higher levels in the water table of nearby areas (Morales and Gonzales, 1986).

Climate

The mean annual temperature for the Caroni River Basin is 27.1° C (Morales and Gonzales, 1986). In Guri, meteorological data are recorded daily by EDELCA's División de Cuencas e Hidrología. Temperatures between 1986 and 1988 ranged from a minimum of 20.1° C to a maximum of 34.5° C, with a mean annual temperature of 26.6° C (EDELCA).

The coolest months of the year are January and February, which are the windiest as well, and the warmest mean temperatures occur first in April and May, and again in September and October.

Average monthly temperatures for the islands of the study site are presented in Figure 3.4. These represent data collected daily from thermometers placed just inside the entrance to each forest, between January 1988 and

December 1991 for Las Carolinas, and July 1989 to December 1991 for Danto Manchado (with the exception of September through December). The average minimum and maximum temperatures for Las Carolinas are 23.1° and 29.4° C, respectively. For Danto Manchado, they are 22.4° and 29.0° C.

Rainfall

The Caroni River Basin has a mean annual rainfall of 2561 mm, and the relative humidity is 76% (Morales and Gonzales, 1986). At the confluence of the rivers Paragua and Caroni (in the central part of the Caroni Basin), the two tributaries of Guri Lake, mean annual rainfall varies from 1800 to 2200 mm (Huber, 1986). Within the Caroni Basin, precipitation is lower towards the north. For example, the average yearly rainfall recorded from 1986 to 1990 by EDELCA at the town of Guri, at the northern part of the basin, was 1186 mm.

The dry season generally begins in late December or January and lasts through April or May, when the rainy season begins. The rains intensify in late May or early June, and are relatively heavy until September or October, when they slacken considerably.

Rainfall data were collected daily on each island from a rain gauge placed in a relatively open area. Average yearly rainfall differs somewhat between the two islands;

data are presented in Figure 3.5. The average for Las Carolinas was 1123 mm, and that of Danto Manchado was 1245 mm.

Mammalian fauna, hunting pressure

Four species of primates are found on islands in Guri Lake: Chiropotes satanas, Pithecia pithecia, Cebus olivaceus and Alouatta seniculus. Sightings of Aotus trivirgatus have been reported for this region (Alvarez, pers. comm.), but have not been confirmed by published reports. Members of three of the four genera are often found sympatrically, but the two pitheciins have not been found on the same island in the reservoir. Previous to the inundation of the valley which now forms Guri Lake, the islands upon which the two pitheciin species are found were separated by the Caroni River, with Pithecia occurring on the east side and Chiropotes on the west. In fact, these two species have not been reported to occur sympatrically at any location in Venezuela, although they are sympatric throughout most of their range in the Guayanas (discussed in Chapter 2, p. 30).

Mammalian fauna are far more plentiful and diverse on the Danto Manchado island than in Las Carolinas. Access to the reservoir is limited to employees of EDELCA, the Guardia Nacional, and other individuals, such as researchers, who are granted permission to enter. However,

entrance does occur from some of the surrounding mainland areas, which occasionally attract hunters. Although illegal anywhere in the lake or the surrounding area administered by EDELCA, hunting does occur, particularly on the southern islands, including Danto Manchado. Hunting concentrates mostly on the tortoise Geochelonia denticulata, which is served in a traditional Easter dish, and thus most heavily consumed around that time of the year ("semana santa"), and somewhat less so in other seasons. Also, tapir (Tapirus terrestris), deer (Odocoileus virginianus) and capybara (Hydrochaeris) are commonly hunted. The monkeys are not hunted here.

Possible predators on the island's primates could include large raptors such as the harpy eagle (Harpia harpija), seen in the mainland area near Danto Manchado, the ornate hawk-eagle (Spizaetus ornatus), and large cats such as jaguars (Panthera onca) and pumas (Felis concolor). Five howler monkeys (of all age-sex classes) of a group of six disappeared from Pithecia Island I between August and December of 1988. Fur and/or bony-fleshy remains were left in all cases but one (Peetz et al., 1991; pers. obs.).

Field sites, study groups

Three islands were chosen for this research, and support the ongoing research of Kinzey and Norconk (e.g. Kinzey et al., 1988; Kinzey and Norconk, 1993). Two islands

have groups of Pithecia, and one supports Chiropotes. The "Pithecia" islands (I and II) are found in Las Carolinas, approximately 13 km east of the town of Guri. "Chiropotes" island, in Danto Manchado, is located further from town, at 40 km to the south (see Fig. 3.3).

Island situations such as these present both advantages and disadvantages. First and foremost is the obvious consideration that this is no longer a completely natural situation; animals have been isolated from both conspecifics and members of other species, due to the most part, by chance. The study of intergroup interactions, migration, etc. is not possible. The long-term effects (such as reduced variability in the gene pool and local extinctions) are serious and irrevocable.

On the other hand, some advantages provided to researchers by this situation are:

- 1) It offers the opportunity of observing Pithecia, known for its wary and cryptic nature, in a small island habitat where individuals can be habituated relatively easily. This genus is known to be difficult to study in the wild (Buchanan et al, 1981). Additionally, here, the boundaries of the home range of Chiropotes (which is normally very large) are easily established, as it is limited to the island's shores. The island's size appears appropriate in terms of normal home range sizes for Chiropotes (van Roosmalen et al., 1981; Ayres, 1989), since

the group uses the entire 365 hectare island. This allows for increased feasibility of data collection. Neither of the two species are well-known in terms of their behavior or ecology.

2) The few previous studies which document habitat utilization in Chiropotes satanas and Pithecia pithecia have been conducted only where they are sympatric, and have revealed differential use of forest canopy levels between the species. The allopatric situation presented here will allow for valuable comparisons to be made with the results from these other studies.

Additionally, intergroup interactions, migration and the like are not a consideration of a study of positional behavior. Before the inundation, these animals occurred in much the same habitat types (Pernia, 1985; L. Balbás, pers. comm.), and therefore have survived for a very long period of time in this environment. The site is natural in that the relationship between the habitat and the positional behavior of the primates has been conserved.

Although the forests on these islands can be described in general terms as semi-deciduous and dry, the two island zones differ greatly in soil type, moisture content and vegetation (and of course diversity and density of fauna). Some of the differences are due to the size of the islands; the Danto Manchado ("Chiropotes") island is a great deal larger than either of the Las Carolinas islands.

As will be described in Chapter V, a detailed analysis of the habitat was conducted on each island, and the results of this analysis are discussed there. However, a few general features of these habitats and the groups of monkeys which occur on them are described here.

The two Las Carolinas islands ("Pithecia" islands I and II), located in the northern part of the lake, are best classified as having tropical dry forest (Ewal et al., 1976). The soil is very fine, dry and often reddish, and the ground extremely rocky. These islands are less diverse in both flora and fauna than the more southerly island, Danto Manchado. "Pithecia" Island I is about 70 ha, with six forest patches of various sizes interspersed with savanna. Separated from the nearest forest patch by a large expanse of savanna, one three hectare forest patch supports two (formerly three) fully habituated Pithecia (Group I). Another group of five to six unhabituated individuals travels among the five other forest patches, and was not the subject of this study. "Pithecia" Island II is a completely forested island of about 15 hectares which is located approximately one km to the west of "Pithecia" Island I, and supported a group of seven habituated animals (Group II).

Previous to October 1988, a group of six howlers inhabited "Pithecia" Island I; one remains (see p. 67). A small group of capuchin monkeys (between one and three) crosses the savanna from the other forest patches every few

months, and stays from one day to several weeks at a time.

The Danto Manchado site ("Chiropotes" Island), further south, is approximately 365 ha in size. It is almost completely forest-covered, with the exception of two hilltops, which are mostly grassy or bamboo-covered. Although much of the island is relatively flat, many portions have undulating hills. The habitat can generally be referred to as a transitional moist forest (as in Kinzey and Norconk, 1993). It is much more diverse in terms of numbers of plant species and of distinct habitat types than are the Las Carolinas islands. The forest is moister and taller, and the soil darker and richer (especially in the lower elevations). There are very few rocks. There has been more evidence of habitat disturbance on this island, such as remains of fires and an old road. Most of the fires are limited to the island's shores, where they are used by hunters to flush out the tortoises. Additionally, some of the vegetative growth is secondary vegetation. Parts of the island resemble Chiropotes' habitat in Surinam (W. Kinzey, pers. comm.).

The number of individuals in the Chiropotes group fluctuated between fifteen and nineteen over the course of the study. For most of the study, there was only one (formerly at least two) adult male. Several groups of Cebus olivaceus and Alouatta seniculus also occur on the island.

Habituation process, activity patterns

The habituation process of Pithecia Group I was already complete upon my arrival, and a trail system in this forest had been established. The trails on "Pithecia" Island II were cut between July and November, 1989. A trail system in the "Chiropotes" forest was completed over the period of June through December, 1989. The process of habituation for Chiropotes took place between June and October 1989, and of Pithecia Group II, from November 1990 through February 1991. The two species behave quite differently from one another in terms of their strategies for avoiding unwanted observers.

The adult male Pithecia (and sometimes an adult female) may threaten the observer while the rest of the group moves quickly and quietly away, then follows the others. Individuals may stop suddenly, and hide for long periods of time, making it difficult for the observer to know whether they have continued traveling or still remain in the same location. Another Pithecia strategy is to stop and hide, then sneak quietly away, using movements resembling those of a slow loris. It is virtually impossible to observe Pithecia without their knowing, due in part to their frequent use of the lower canopy and tree trunks.

Chiropotes, on the other hand, is similar to Cacajao in that it may sometimes be observed undetected, as it travels in larger, noisier groups, and is found higher in the canopy. When unhabituated Chiropotes is disturbed, one or

more individuals will deliver a threat "whistle" at the observer, the others will respond with vocalizations, and the group may move quickly away. When followed by several observers, unhabituated Chiropotes may divide into a few sub-groups, each of which move off in different directions.

The groups of both species were habituated relatively rapidly, although the habituation process was undoubtedly slowed by the constraint that the researchers studying the monkeys were few in number and could not be on both islands at once. Therefore, neither of the species was in constant contact with the observers during the habituation process. Problems of observation were never altogether eliminated, as dense foliage, thick undergrowth, and the often rapid travel of the primates contributed to losing them (or at least the focal animal) momentarily or for the rest of the day (see Chapter IV for discussion of biases in data collection). The more difficult problem in studying Chiropotes, as well as Pithecia Group II, was finding them initially rather than, once found, following and observing them. This was especially true for Chiropotes, which inhabits and uses virtually all of its 365 hectare, forest-covered island. However, it became clear that after the habituation process was complete, I was having a minimal effect on the normal behavior of these primates.

The activity patterns for Pithecia and Chiropotes differ greatly from one another. Pithecia tend to start the

day later, and departure from their sleeping tree varies from 6:30 to as late as 9:00 AM, with an average of slightly before 7:00. Their active day length is very short, as they return to their sleeping tree as early as noon, although the end of their normal active day ranges from 1:00 to 3:00 PM.

Pithecia Group II tended to have a longer active day than did Group I. The tendency for this species to have an exceptionally short day was also noted by Setz (1988). There is no evidence for movement later in the afternoon or at night.

Chiropotes begin moving and feeding while it is still dark under the forest canopy, at approximately 5:45 AM. They are active until at least 4:00 PM, when they may settle in a sleeping area, and appear to fall asleep between 4:30 and 5:00 PM.

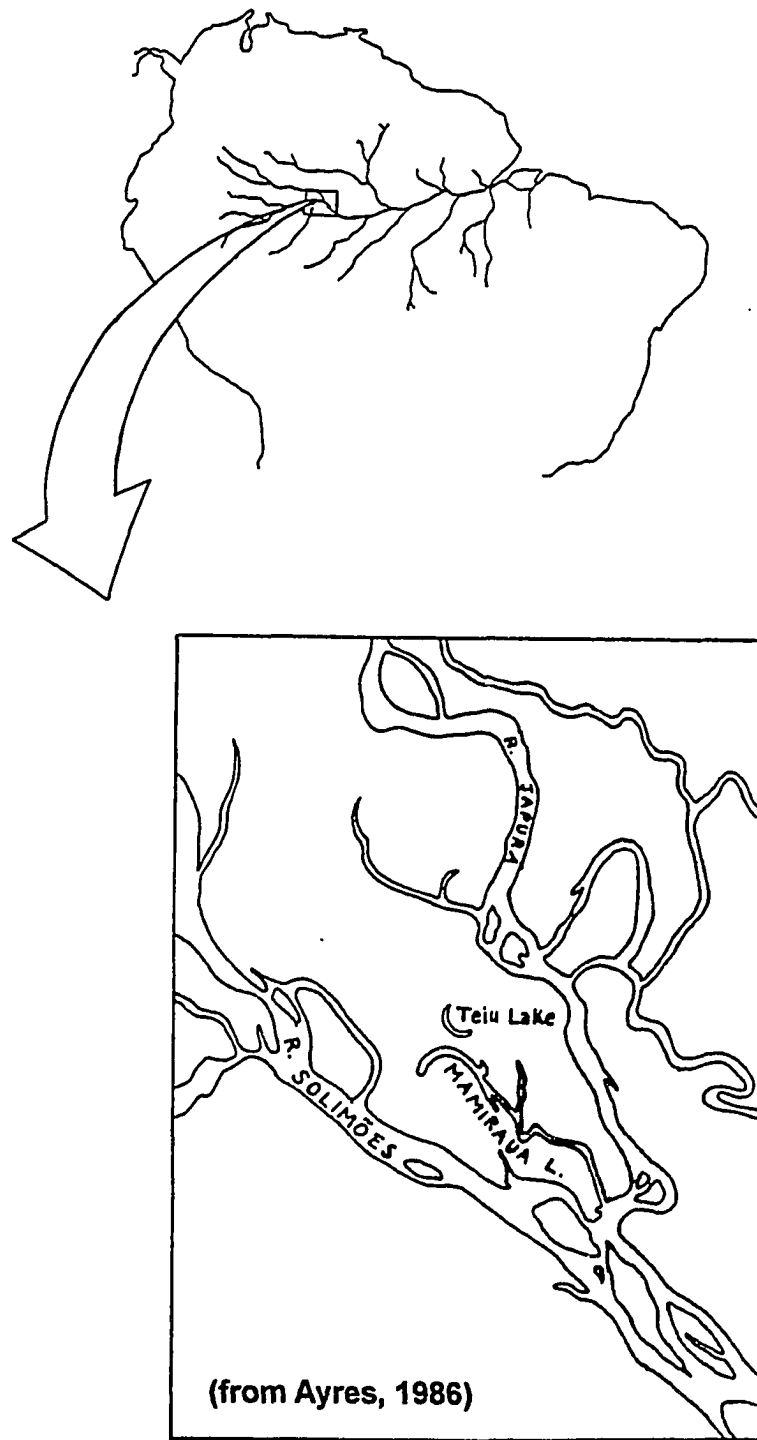


Figure 3.1. Map of northern South America with inset of Teiu Lake, Brazil

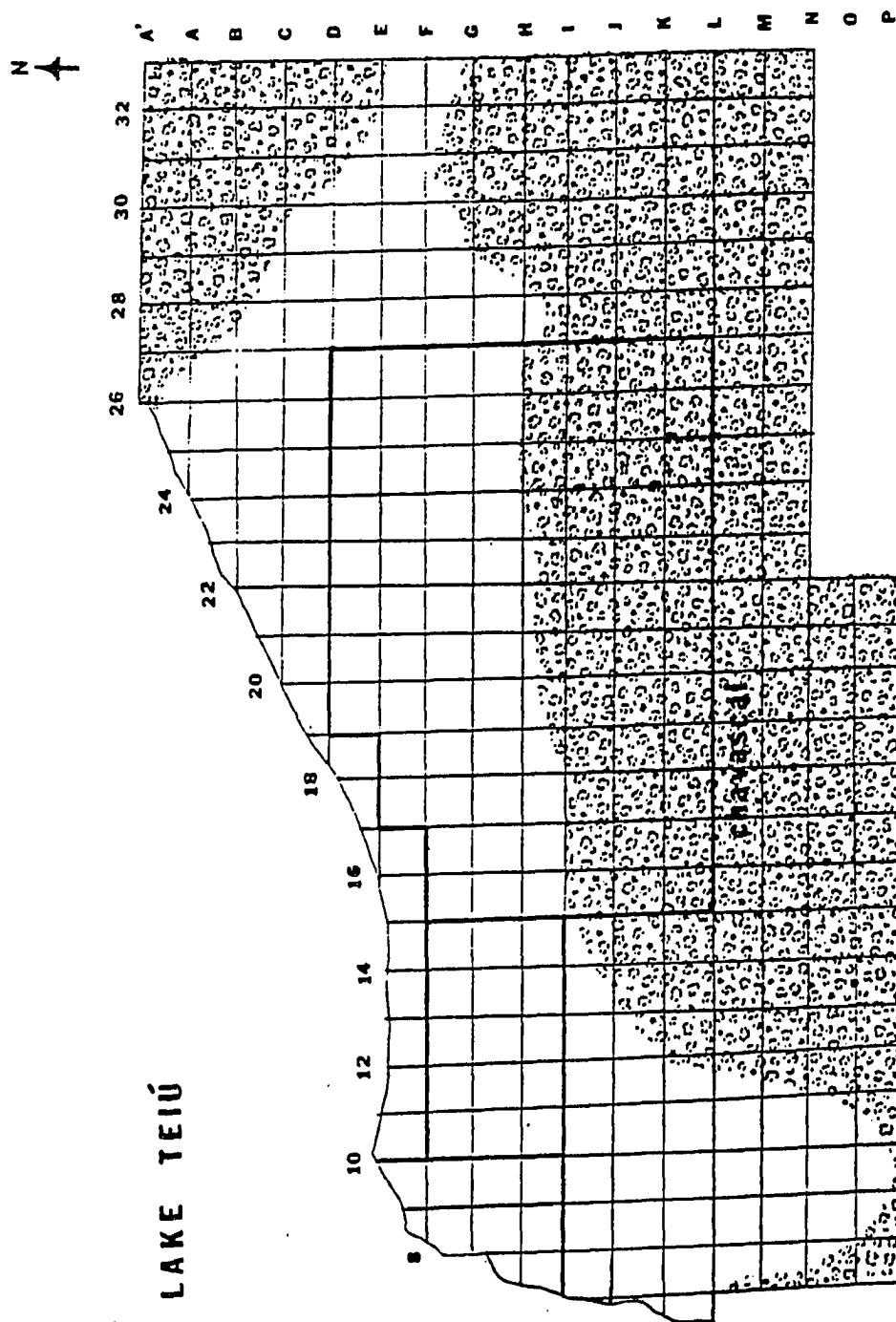


Figure 3.2. Trail system - Lake Teiú (from Ayres, 1986)

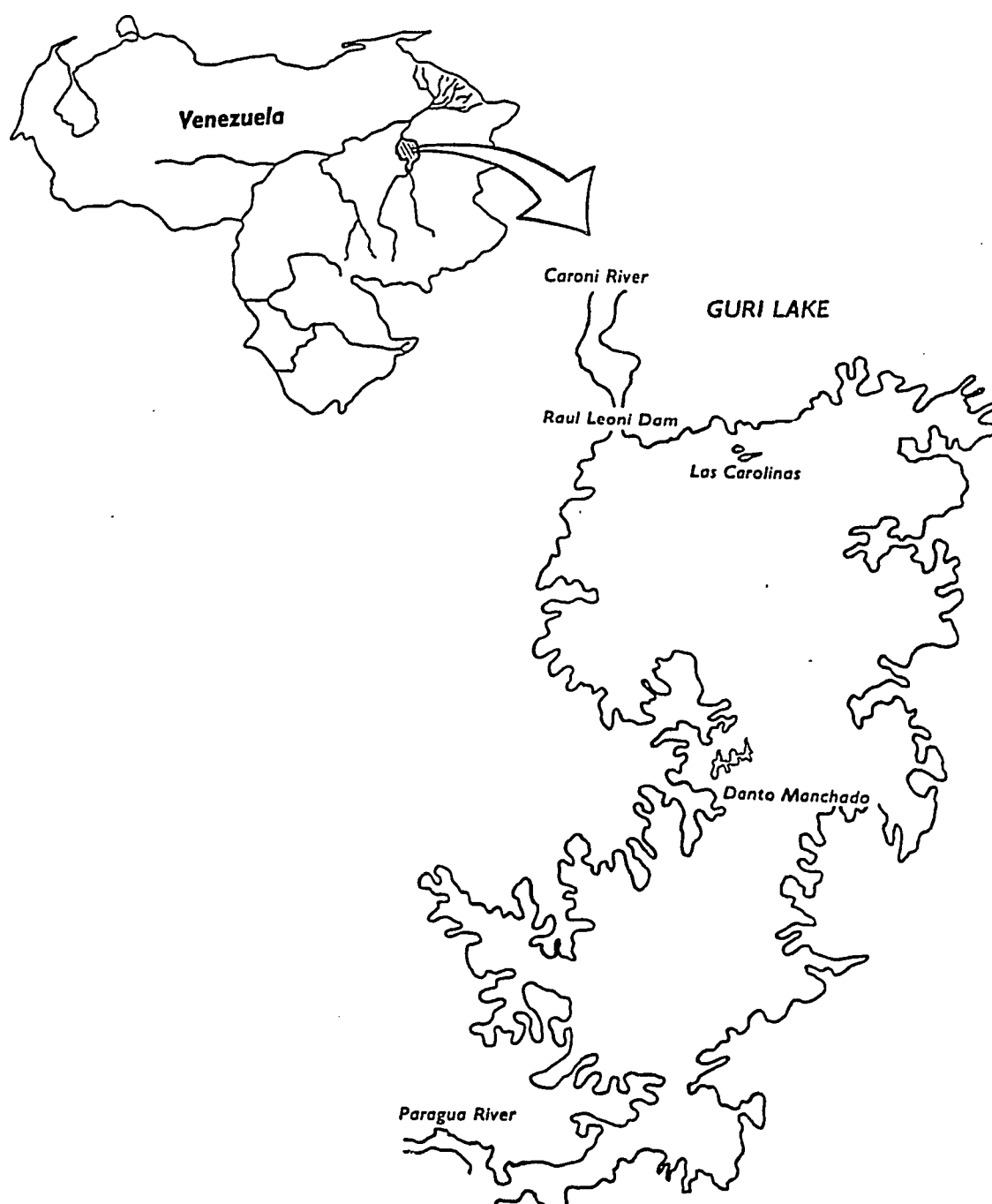


Figure 3.3. Map of Venezuela with inset of Guri Lake

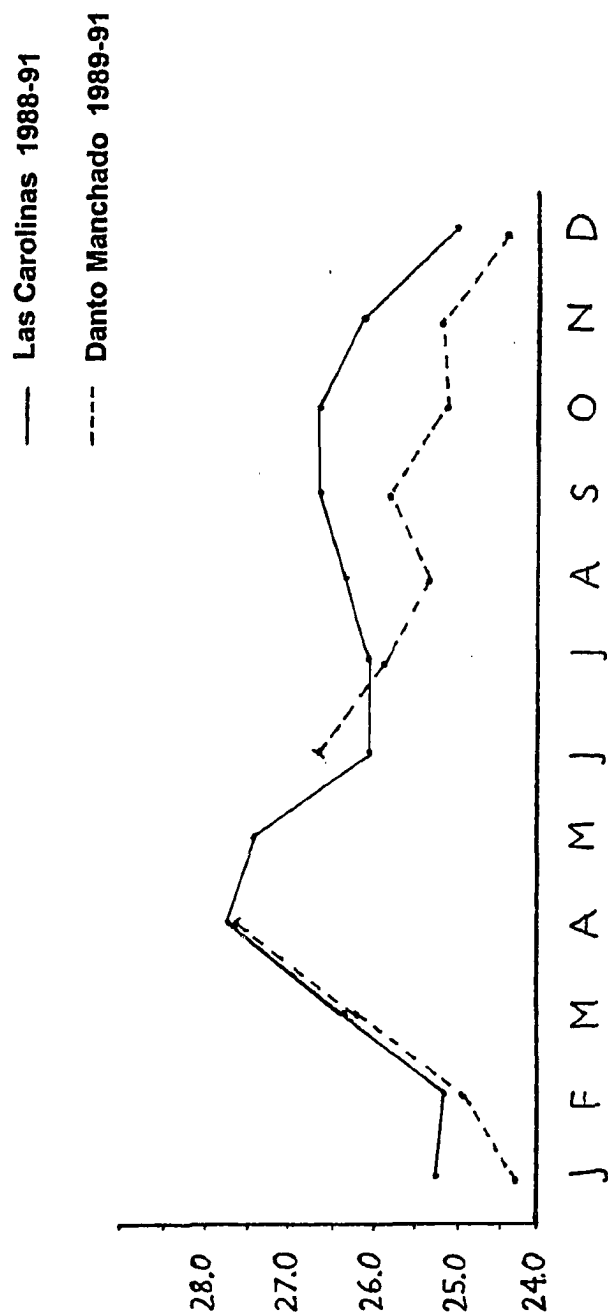


Figure 3.4. Mean monthly temperature on study islands

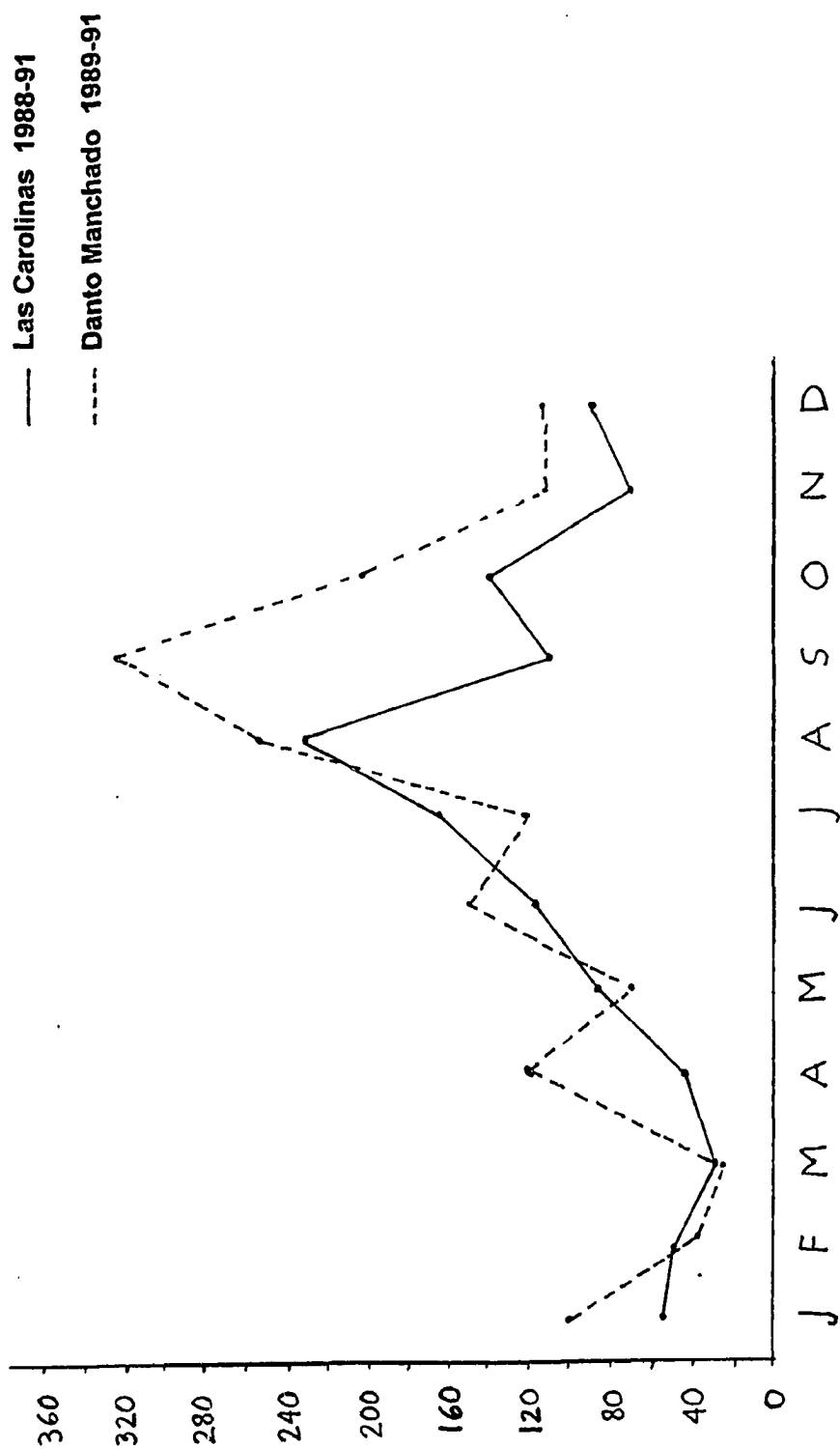


Figure 3.5. Mean monthly rainfall on study islands

Chapter 4. METHODS

A. General Introduction

Habituated groups of Pithecia pithecia and Chiropotes satanas were observed in Venezuela for fifteen and ten months, respectively, and an unhabituated group of Cacajao c. calvus was observed in Brazil for six weeks. Systematic behavioral sampling was carried out for a total of 84 days for Pithecia, 39 for Chiropotes and eight for Cacajao (see Table 4.1 for research schedule). Data collection day lengths reflected the active day lengths for Pithecia and Chiropotes (discussed in greater detail on p. 72). Thus, data collection usually averaged six and a half hours for Pithecia and eleven hours per day for Chiropotes. Due to the difficulty in finding and subsequently following Cacajao, an average of only three hours of data per day was collected for this species. Data on a number of environmental, behavioral and dietary variables were collected using a focal animal instantaneous sampling technique at two-minute intervals. In Venezuela, separate detailed information was collected on habitat plots and on strips along the trail system in each forest, in order to obtain a sample of the various habitat types and supports available for the animals to choose from. Statistical tests verify the observable differences among the frequencies of positional behavior and support use of the three species. These data provide a base from which to investigate

questions about the relationship between positional behavior, habitat use and diet in the pitheciin primates.

B. Methods of Data Collection

Introduction

The study of positional behavior in natural populations of animals is intrinsically difficult, in large part because positional behaviors do not have clear-cut distinguishing characteristics, but may grade into one another in time sequences. This can make their categorization difficult; videotaping and photography provided an invaluable asset in categorizing positional behavior.

Difficulties of field observations are discussed by Garber (1980), who, following Aldrich-Blake (1970), outlines the problems of visibility limitations and their contribution to observational bias. One important problem is that of the overestimation of highly conspicuous behaviors and individuals, the latter of which may be more highly represented among some particular age-sex classes. I found this to be a valid problem in the current study. For example, "travel" (activity bouts defined in Table 4.2) is the most conspicuous activity bout, and may be recorded at disproportionately high rates at the beginning of a sampling period, particularly after the animal had been lost from view. The degree of conspicuousness of "feeding" behavior depends upon the type of food eaten. A feeding primate can

attract attention to itself as it drops remains of large or heavy foods on the ground. "Resting" primates are the most difficult to find in a forest; however, once found, consecutive samples are easy to record while the animals are engaged in this activity bout.

A second problem is that many social interactions go unseen or are misinterpreted due to poor visibility of one or more individuals. These problems are exacerbated when studies are conducted in forests.

Sampling Techniques

A number of different techniques have been utilized to study positional behavior of primates in their natural habitat, most often involving the selection of a focal animal to observe during the sampling period. Focal animal sampling (Altmann, 1977) has been said to be a good choice for observing animals in the field, because it can yield a great deal of information while providing a relatively unbiased account of behavior. It is considered unbiased, in part, because it involves following an individual through all situations and behavior patterns where it may not ordinarily be observed (ibid).

Two of the most commonly used sampling methods for the study of positional behavior are bout sampling (e.g. Fleagle, 1976; Mittermeier, 1978; Crompton, 1983; Gebo, 1992; Cant, 1988; Doran, 1992) and instantaneous sampling

(e.g. Mendel, 1976; Garber, 1980; Cant, 1986; Boinski, 1989; Fontaine, 1990; Doran, 1992; Hunt, 1992). Both involve collection of positional data on a focal animal.

Bout sampling was initially used by Fleagle (modified after Prost, 1965) in his study of siamangs (Fleagle, 1976). It involves following an individual in order to record continuously the positional mode as well as the distance traveled and support size used while in that mode. Cant (1988) described the bout sampling method wherein the basic unit is a bout of distance moved, and the bout changes when any one of the behavioral or support variables changes. Cant used the same technique as Fleagle, although he added a few variables. These included information on substrate type (tree or liana), substrate angle and direction of focal animal's movement, whether or not a gap in the canopy was crossed during the bout, and if so, how that was achieved (walk-through, leap or drop).

Sampling instantaneously (Altmann, 1977) at predetermined time intervals allows for a sample of behavioral states to be recorded. It is especially suited to the collection of nonsocial data such as locomotion (Martin and Bateson, 1986) because it can be used to record behaviors that "can unequivocally be said to be occurring or not occurring at an instant in time" (ibid.). The percent of time is estimated from the samples in which a given activity was recorded, and so "readily provides data

appropriate to estimating the percent of time spent in various activities..." (Altmann, 1979).

Doran (1992), in her research on the locomotor behavior of chimpanzees, utilized both bout sampling and instantaneous sampling in order to compare the two methods in terms their accuracy for estimating frequencies for locomotion and substrate use. She found no significant differences in the results obtained by the two sampling methods, provided the bout sampling was weighted with distance traveled for each bout. She discussed the advantages of each method. The most significant advantage of instantaneous sampling is that it allows for the collection of a large number of variables at once, while the advantage of bout sampling is its greater reliability in recording rare and/or rapidly-occurring behaviors (such as leaping). Doran concluded that a combination of the two methods would provide the most accurate and complete record of positional behavior.

In the current study, for each species studied, I first utilized an *ad libitum* approach (Altmann, 1977) while initially characterizing behaviors and continuing the habituation process of the primate groups. Data were collected in this fashion for approximately 40 hours. Subsequently, both bout sampling and instantaneous sampling were utilized in order to investigate the relative feasibility of each for long-term data collection. The two

methods appeared to result in similar frequencies of positional behavior; however, instantaneous sampling was chosen as the primary data collection method for two main reasons. First, I wanted to collect data upon a wide range of behavioral and environmental variables (sometimes as many as sixteen variables at once). It is very difficult to collect more than a few variables at once using bout sampling; the highest number of variables recorded for this method has been six (Cant, 1988; Doran, 1992). Second, the time-consuming process of data transcription from tape recorder to field book discouraged me from continuing to use this technique, especially since the study was to be a long-term one, and the amount of data to transcribe on three species would have been voluminous. I attempted to compensate for the possible dearth of data on rare or rapidly-occurring behaviors by recording them if they occurred within five seconds of the instantaneous sample. Leaping fell into this category; a leap was recorded if observed in any of its stages, and all take-off and landing information was recorded as well (if possible). Although I collected data for approximately 50 hours using bout sampling, only results from instantaneous samples are presented as frequencies and used in the statistical analysis.

Collecting instantaneous data at predetermined intervals on a focal animal allowed me to collect

information on a large number of behavioral and environmental variables in approximately fifteen seconds. This information could then be utilized to determine the relative importance of the different variables (based on percentages of time the pitheciins devoted to particular positional modes) in shaping the positional repertoire of Pithecia, Chiropotes and Cacajao, and in establishing any correlations between particular positional strategies and environmental variables.

The same method of instantaneous focal animal sampling was used successfully by Garber (1980) in his study of positional behavior in the Panamanian tamarin, Saguinas geoffroyi, as well as by Hunt (1992) in his study of chimpanzee locomotion.

Sampling procedures utilized for the collection of
behavioral and dietary data on pitheciins

Data were collected using an instantaneous focal animal sampling technique (Altmann, 1977) from the time the animals exited their sleeping tree (or when first located in the morning) until the time they returned to the sleeping tree (or were lost from view). Sampling was conducted during all active hours of the day, with a few exceptions. On some occasions, for example, on the final day of a monthly Chiropotes sample, observations ended at midday or in the early afternoon. Likewise, on the first day of monthly

samples for either species, the animals may not have yet been found; therefore, a partial sampling day resulted.

An individual was selected at random (always with a five-second pause before data collection began) and observed until lost from view, at which time another (preferably from the same age-sex class and engaged in the same activity bout) was selected and used as the focal animal. An attempt was made to sample males and females equally. For Pithecia, only adults were observed; for Chiropotes, a small percentage (probably about 10%) of the samples were on juveniles, with the majority of sampling time reserved for adults. For Pithecia, the majority of the samples were conducted on four adult individuals; however, sampling for two others was also carried out on some occasions. Chiropotes individuals (particularly females) were somewhat more difficult to identify individually; however, females could often be identified by the size of their infants. At least five (and probably seven) adults were consistently observed, and, less frequently, two juveniles.

The following variables were recorded at two-minute intervals on a prepared data check-sheet (see Fig. 4.1), and are defined in Table 4.2: age-sex class (females with carried infants were placed in their own class), activity bout (Feed, Travel, Rest, Social, Other), positional behavior (see Chapter 6 for classification), number of supports, support inclination and diameter, flexibility of

support, height of animal and of supporting tree, food species (if feeding), and location of food and of animal in tree or on liana (Fig. 4.2), quadrat in the forest, and any additional comments. If a leap was exhibited for the sample period, further information was collected on the positional behavior and tree portion used, and the number, inclination and diameter of supports in both take-off and landing. For the midflight phase, leap distance was recorded.

If no individual was in sight at the interval, data were recorded five seconds after the next sighting to prevent biases in recording the most conspicuous behaviors.

At each sample, a note was made as to whether or not the positional behavior was the same as that of the previous one, or if the individual had moved at least one body length between samples. This permitted me to eliminate later those samples in which a behavior continued for more than one sample, in order to satisfy assumptions of independence for statistical tests (see below, p. 95).

By recording the height of the focal animal and of its supporting tree at each sample, a relative height index could later be obtained which provided the relative height at which the animals were found in the tree. By dividing the animal's height in the tree by the tree's total height, I arrived at a ratio that expressed an animal's height in the tree as the percentage of the tree's height.

Data collection was more thorough for Pithecia and

Chiropotes than for Cacajao. Cacajao was the first species to be studied, and data collection was more limited in terms of the number of variables recorded at each sample. Additional variables were added later in the study at the Venezuelan site. Of the three pitheciins, Cacajao was the most difficult to encounter, and to subsequently follow.

Pitheciin foods were classified according to species and to their location in the tree or liana in which they were found (see Fig. 4.2). Food species eaten by Pithecia and Chiropotes were identified by a visiting Venezuelan botanist, Gerardo Aymard, and trees were labelled by a City University of New York graduate student. Additional identifications were obtained by consulting Van Roosmalen (1985).

Sampling procedures utilized for the collection of environmental data

It was imperative to document differences both among the islands and among the various parts of each island, since a variety of habitat types was observed for each. Detailed comparative analyses of the forests on the three islands were undertaken for two main reasons:

- 1) An accurate idea of the supports which are actually available for the animals to use is necessary in order to gauge the primates' preference for certain supports.
- 2) By establishing and quantifying the differences among

the various habitat types found in each forest, comparisons could be made of different positional modes used in these different areas for both species. The comparisons of positional behavior, support use and forest structure between Pithecia groups on the two different islands were especially instructive.

Two procedures were utilized to describe and analyze quantitatively the vegetation: strip sampling and habitat plots.

Strip sampling

In this procedure, each island was traversed in order to collect a series of variables at predetermined intervals along the trails. These intervals differed among the different-sized islands, partly in order to utilize trail markers and trail intersections. (See Figures 4.3 to 4.5 for trail maps of each island.) Data were collected on "Pithecia" Island I at 20 m intervals, on "Pithecia" Island II at 25 m intervals, and at 50 m intervals on Danto Manchado ("Chiropotes") island. The following variables were recorded (and are defined in Table 4.3): first and second most common tree heights within 20 meters of the trail marker, number of trees within a 5 meter radius of the trail marker and the dbh (diameter at breast height) category of each, undergrowth density and predominant form of undergrowth, liana density, liana form and location, predominance of rocks, soil color and texture, and

additional comments such as the presence of specialized vegetation or steepness.

Habitat plots

Detailed information on the form of various parts of the forest, particularly those used by the primates, was obtained by the analysis of a number of 5 x 20 m plots on each island (see Figures 4.6 to 4.8 for the location of these plots). The following variables (defined in Table 4.4) were recorded for each tree and liana at least 2 cm dbh on the two "Pithecia" islands: species, dbh, tree height, bole height, inclination of first branch, crown diameter, climber load, percent crown overlap, crown shape, and branch orientation (as in Garber, 1980) in the top, middle and lowest 1/3 of the canopy. On "Chiropotes" Island, dbh only was recorded for those trees between 2 and 10 cm dbh, and the other variables recorded on those trees larger than 10 cm dbh. Trees with a diameter of less than 10 cm dbh were seldom used by Chiropotes, therefore information on the form of the small trees was not collected. On all three islands, each plot was mapped for its distribution of all trees and lianas with a dbh of at least 2 cm, in order to gauge, in as much detail as possible, the supports available for use and their distance from one another.

Data from the plot analyses together with that of the strip sampling provided an accurate assessment of the forest pathways in various habitat types. Results of the habitat

analysis are presented in Chapter V.

Photography, video recording

I used a Sony Handycam CCD-V99 high resolution 8 mm camcorder to videotape Pithecia and Chiropotes in their natural habitat. The zoom capability for the videocamera was 8X (approximately 300 mm). For still photos, I used a Nikon F2, with a 200 mm lens and a 2X converter.

Videotaping, along with still photography, proved to be highly useful for investigating in detail movement patterns and gaits, and categorizing and subcategorizing positional behaviors. Use of the still frame feature on the videocamera allowed detailed analysis of limb positions. This was essential for those behaviors which normally occur too rapidly to document limb positions, such as running, leaping and continuous bounding. Additionally, hand and foot positions are usually very difficult to see accurately in the normal course of data collection, but can be observed when captured on still or motion film. The videotape was especially important in aiding the analysis of the qualitative differences between Pithecia and Chiropotes for the same behavioral categories. Studies of individual frames of video footage can aid in determining differences between the species in terms of the amount of force applied to a support during leap take-off. This is accomplished by simply counting the number of frames in which the hindlimbs

were being used in propulsion to push off against the support (at 30 frames per second), and by taking into account the approximate known weight of the animals.

Anatomical data collection

Osseous anatomy was studied in representatives of all three pitheciin genera, at museums in both the United States and Brazil (see Table 4.5 for sample). The focus was on muscle insertion areas (which indicated their advantage for certain activities) and joint articular surfaces (which are reliable indicators of the degree of movement occurring at the joint). I also collected data on limb and body proportions. These data are presented in Chapter 2. In Chapter 7, positional behavior is correlated with descriptions of pitheciin postcrania discussed in the literature (Ford, 1986; Fleagle and Meldrum, 1988).

Data analysis

Introduction: frequency as an implication of the importance of behaviors

Establishing the locomotor and postural behaviors which are the most important to a primate's survival is difficult, since the frequency of occurrence of a particular behavior is not necessarily an accurate reflection of how vital that behavior is in the life of an individual. Behaviors which occur infrequently may play a more significant role in the

survival of an individual. These "critical" behaviors (Prost, 1965) may enhance escape from or avoidance of a potential predator.

The primary tool we have by which to gauge the importance of various positional behaviors is how often they are performed by the animals. Therefore, data are often collected and analyzed in terms of frequencies. An indication of the importance of frequency data is demonstrated by previous studies (e.g. Fleagle, 1977; Rodman, 1979; Ward and Sussman, 1979) which have established a functional correlation between certain often-used behaviors and particular anatomical features.

In this study, data are presented in terms of frequencies with the assumption that they indicate, to a large degree, the relative importance of certain behaviors to an individual primate's survival.

Statistics

Statistical tests provide a means of assessing whether differences between species observed in the data are in fact significant, and to ensure that apparent differences are not an artifact of small sample size.

A rigorous set of statistical tests have rarely been applied to results of studies of positional behavior, with the exception of Boinski (1989) and Fontaine (1990). Often, statistical tests are not used to evaluate positional data, but only frequencies are presented. It has been noted that

data on positional behavior are not particularly amenable to statistical testing, primarily because of problems of non-independence of the data (e.g. Cant, 1987; Hunt, 1992), since the independence of data is a requirement for performing most statistical tests.

The problem of the lack of independent data can involve sequential time (e.g. Cant, 1988) or repeated observations on an individual (e.g. Sussman et al., 1979). As stated by Cant (1988), "locomotor bouts (of distance) cannot be assumed to be independent because some of them are sequential... proportions of time spent in various postures cannot be tested directly because units of time (e.g. seconds or minutes) are not independent observations..." It was found in this study that the only positional behaviors for which there are potential problems involving lack of independence of data are postural behaviors, which are the only ones which may continue from one sample to the next.

In this project, the problem of independence was first dealt with in the field during data collection by noting the samples which involved a continuation of behavior from the previous sample (discussed on p. 88). I later had the option of simply eliminating those (presumably) non-independent samples before performing statistical tests. Comparisons of the "independent" and "non-independent" data sets demonstrated that the results of frequencies of raw data and those of Chi-square tests of the two were virtually

identical. Therefore, eliminating consecutive samples may not be necessary, and may, in fact, result in an unnecessary loss of data in terms of numbers of observations. This technique of elimination of repeated samples is similar to that of "pooling" instantaneous samples into artificial bouts when consecutive samples were the same (Hunt, 1992). In Hunt's study, however, behaviors which were the same in two (or more) consecutive samples were pooled into one bout without knowing whether or not a different behavior had interceded between them. Therefore, it is possible that many samples were eliminated which were, in fact, independent, since it was not recorded in the field whether or not the postural bout was a continuous one. In both the current study and that of Hunt, this additional step of eliminating continued samples ensures that assumptions of independence are not violated, and that appropriate statistical tests can confidently be applied.

Differences existed between the major activity bouts (Feed, Travel, Rest) in terms of the percentage of repeated samples (continuation of behaviors) from one two-minute sample to the next. As would be expected, no continuation of behaviors occurred in Travel, while 6% of the Feeding samples were repetitious. Rest was the activity for which the highest degree of samples were continued to the next (34%).

The data collected on positional behavior seldom

satisfy the assumptions of most parametric tests, since the majority of these data are on a nominal, or at most, ordinal scale. In some studies (e.g. Fleagle, 1976; Cant, 1988; Boinski, 1989; Doran, 1992; Hunt, 1992), nonparametric tests such as the Mann Whitney U, Fisher's Exact, G-test or Chi-square have been utilized in order to compare the locomotor behavior between different species, or to test for the association of behavioral with environmental variables in the same species. Nonparametric tests make fewer assumptions about normalcy in the data distribution or the independence of samples, but at the same time provide rigorous and robust techniques for hypothesis-testing and investigating the source of variation within and between populations.

The Chi-square test is a nonparametric test of association which can be performed on frequency data. The primary assumption to be satisfied in order to utilize this test is that of the independence of data. The Chi-square test can be used to determine whether or not two variables are statistically associated. For example, one can investigate if an association exists between a particular species and a particular set of positional behaviors. This test was an appropriate one to apply to my frequency data on behavioral and environmental variables of the three pitheciins, and was used to determine whether or not statistical associations exist between each pitheciin

species and an exclusive set of positional behaviors, tree portions, support characteristics or heights in trees.

Data were grouped for analysis according to activity bout (Feed, Travel, Rest). Since the goals of feeding, traveling and resting are very dissimilar, one would expect that the means to achieve them would also differ. In fact, previous studies (e.g. Fleagle and Mittermeier, 1980) have demonstrated that locomotor behavior differs greatly between Feeding and Travel. Therefore, the most instructive comparisons to make are of the positional behavior and habitat use of each species while engaged in the same major activity bout.

Chi-square tests were used to gauge the significance of overall differences in a number of comparisons, both within and between species, for each activity bout. Differences were deemed significant if the associated chi-square statistic had a probability of less than .01. Comparisons were made of positional behavior and support use between different groups of the same species on different islands (Pithecia), and later, interspecific comparisons were made among the three pitheciins.

Since the Chi-square test indicates only an overall association between variables, an additional application, the Z - test, was performed on specific positional behaviors in order to examine which contributed the most to the overall differences between the species.

Data were imported from a spreadsheet program (Quattro pro) into a SYSTAT program, which was subsequently utilized to perform the statistical tests. The sample size N represents the number of observations, which is equal to the number of instantaneous samples.

The analysis of the habitat data could be conducted with parametric statistics, since much of those data were continuously and normally distributed.

Table 4.1. Research schedule - data collection using instantaneous sampling.

<u>Group</u>	<u>Months sampled</u>	<u># of days</u>
<u>Cacajao</u> ¹		
	1988: July	4
	August	4
	Total hours: 24	
<u>Pithecia I</u> ²		
	1989: July	1
	August	3
	October	6
	November	10
	December	9
	1990: January	11
	March	4
	April	8
	May	8
	June	2
	August	4
	Total hours: 429	
<u>Pithecia II</u> ³		
	1991: February	2
	March	4
	April	6
	May	6
	Total hours: 135	
<u>Chiropotes</u> ⁴		
	1989: October	1
	December	7
	1990: January	1
	March	4
	April	2
	June	4
	July	2
	August	2
	1991: February	5
	April	6
	May	5
	Total hours: 429	

¹ average of three hours per day

² average of seven hours per day

³ average of six hours per day

⁴ average of eleven hours per day

Table 4.2. Variables for the collection of data using instantaneous focal animal samples.

Time: Data were recorded at 2-minute intervals.

ID: Age/sex class of the focal animal, or individual identification if known.

Bout (main activity in which the focal animal was engaged):

Travel: continuous movement, particularly between feeding trees or in long-distance travel - may include momentary pauses (<15 seconds) while traveling

Feed: preparation and ingestion of food

Travel/Feed: movement within a feeding tree, or carrying food

Rest: non-movement for at least fifteen seconds. Brief movements within an overall period of rest were scored as rest rather than travel if the individual moved for fewer than five seconds.

Social: includes grooming or play with other individuals

Other: activities other than those defined, including vigilance behavior

Note: for analysis, Travel/Feed was lumped with Feed, and Social (Grooming) with Rest. Travel and Social (Play) were each analyzed separately.

Positional Behavior: Specific postural or locomotor positions of the focal animal. If a leap occurred within five seconds of the sample, that was the behavior recorded. Estimated distance of leaps were also recorded. Behavioral categories and subcategories are defined in Chapter IV.

Same/Different: At each sample, it was noted whether or not the same positional behavior was continued in the subsequent sample. This distinguishes between two different bouts of postural behavior (for example "sit") which have been interrupted by movement more than one body length, from one continuous bout of "sit". This aids in establishing whether or not samples are independent from one another.

Support number: one, two or several (three or more) supports

Support inclination:

horizontal (0 - 20°)

angled (20 - 70°)

vertical (70 - 90°)

deformable (if support deformed under body weight)

mixed (combination of supports of various angles)

Table 4.2. (cont'd.)

Support diameter: < 2 cm
 2 - 5 cm
 6 - 10 cm
 11 - 15 cm
 > 15 cm
 mixed (combination of supports of various diameters)

2nd Support number: same as support number above; used if the behavior involved was a leap, drop, hop or bridging.

2nd Support inclination: same as support inclination above; used if the behavior involved was a leap, drop, hop or bridging.

2nd Support diameter: same as support diameter above; used if the behavior involved was a leap, drop, hop or bridging.

Tree quadrant - animal: portion of the tree in which the focal animal was observed (see Figure 4.2).

Tree quadrant - food: portion of the tree from which food was obtained (see Figure 4.2). Also recorded was 1) if the food had been carried from one part of the tree to another or from a different tree, and 2) if the substrate providing support to the focal animal was from the same tree, or a different one from which it was feeding.

Food: species (if known), plant part

Height - animal: height from ground (in meters)

Height - tree: total height (in meters) of supporting tree

Location: coordinates within trail system

Comments: social behaviors, weather, disturbances, etc.

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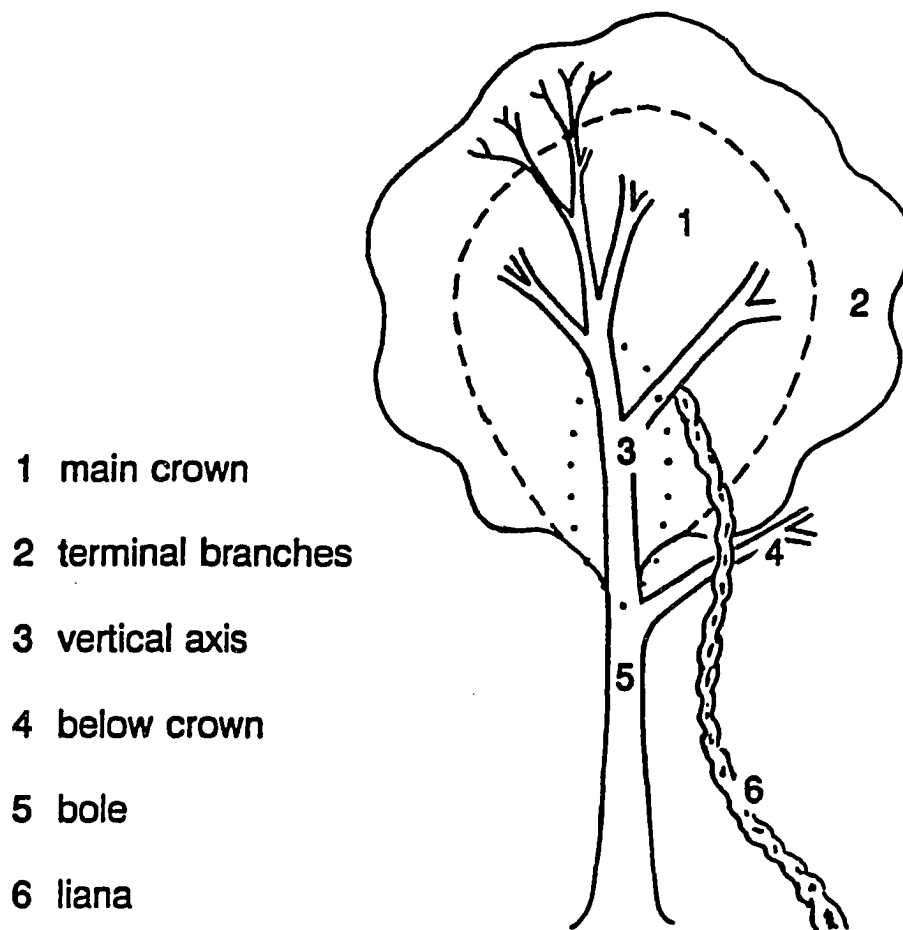


Figure 4.2. Tree portions

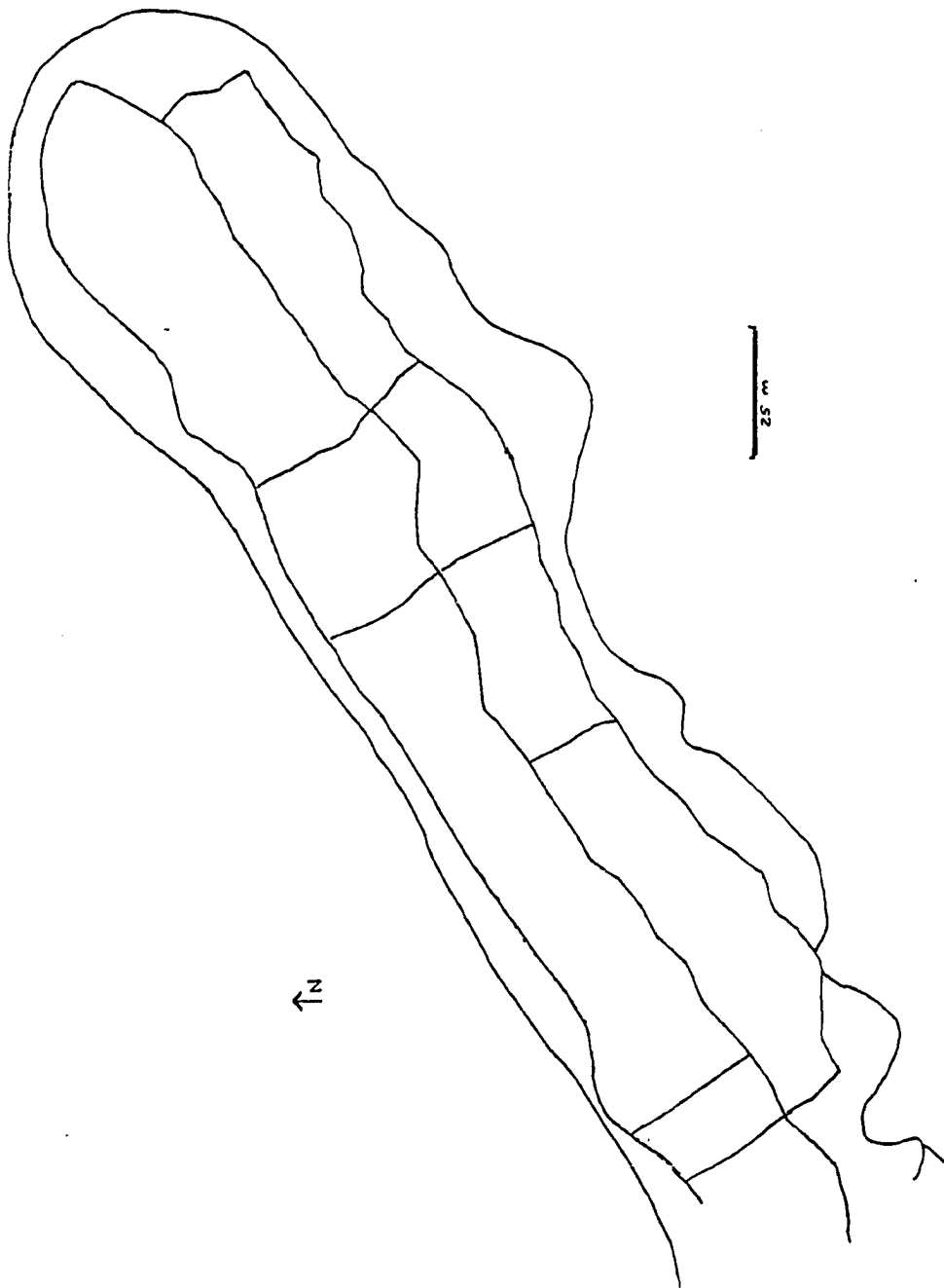


Figure 4.3. Trail map, "Pithecia" Island I

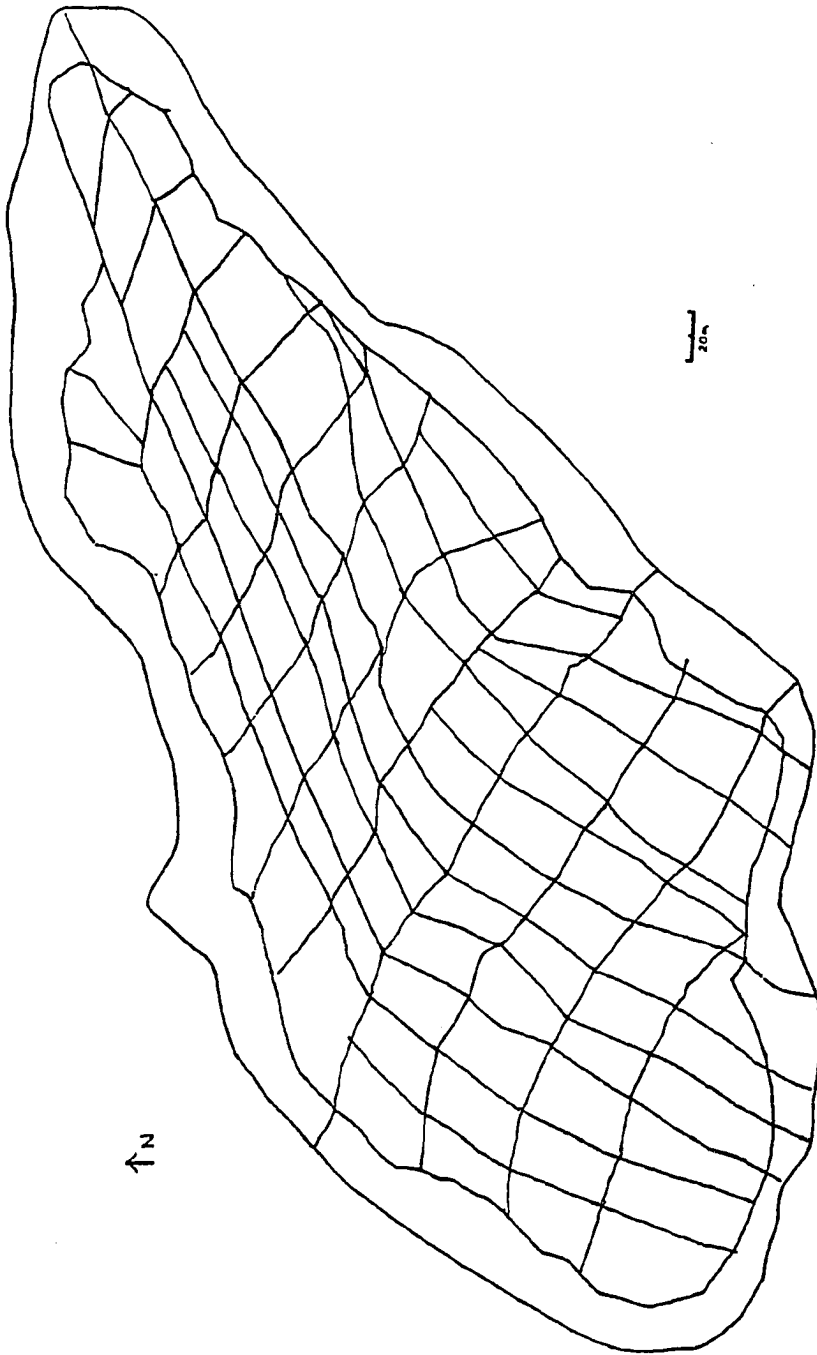


Figure 4.4. Trail map, "Plithecia" Island II

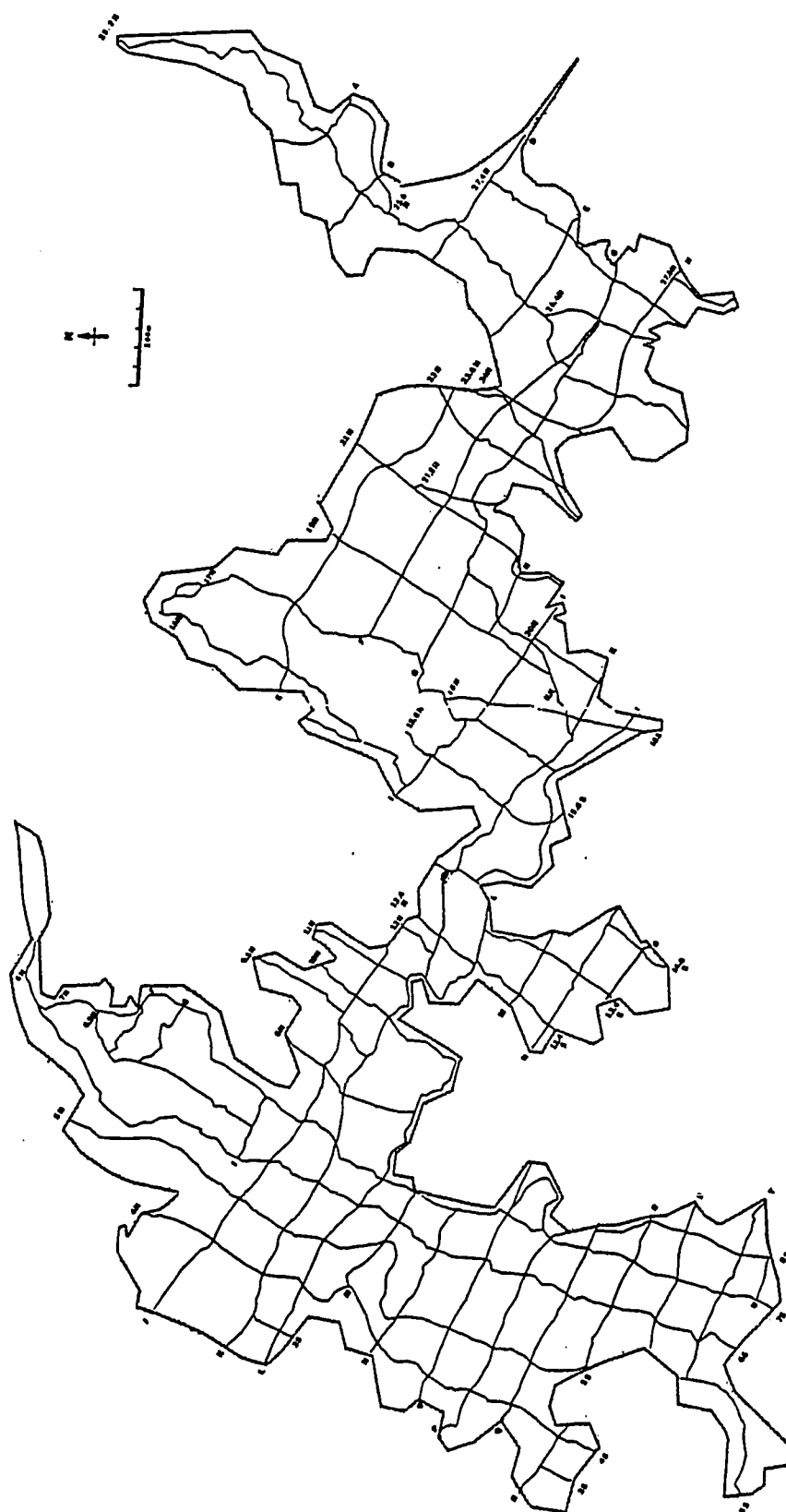


Figure 4.5. Trail map, Danto Manchado

Table 4.3. Variables for vegetation analysis - strip sampling.

Location: coordinates within trail system

Dominant Tree Height 1: most common height range of trees within 20 meters of trail marker

Dominant Tree Height 2: second-most common height range of trees within 20 meters of trail marker

DBH Category: number of trees in each DBH category within a 5 meter radius of trail marker:

Category	#1 (2 - 5 cm)
	#2 (6 - 10 cm)
	#3 (11 - 15 cm)
	#4 (16 - 20 cm)
	#5 (> 20 cm)

Undergrowth Density: amount of coverage of the forest floor with various undergrowth types; estimation based on a scale from 0 - 4

Predominant Form(s) of Undergrowth: most common undergrowth type; sapling (<2 cm dbh) shrub, grass, bamboo, etc.

Liana Density: estimated density of lianas based on a scale of 0 - 4

Liana Form: single liana or vine tangle; location - on ground or in tree crown

Soil Color: description of color, e.g. light red, red-brown, dark brown, etc.

Soil Texture: fine, pebbly, lumpy, sandy, etc.

Rock Density (for Las Carolinas islands only): area of forest floor covered with rocks of various sizes; estimations based on a scale of 0 - 4

Comments: presence of specialized vegetation, steepness of area, etc.

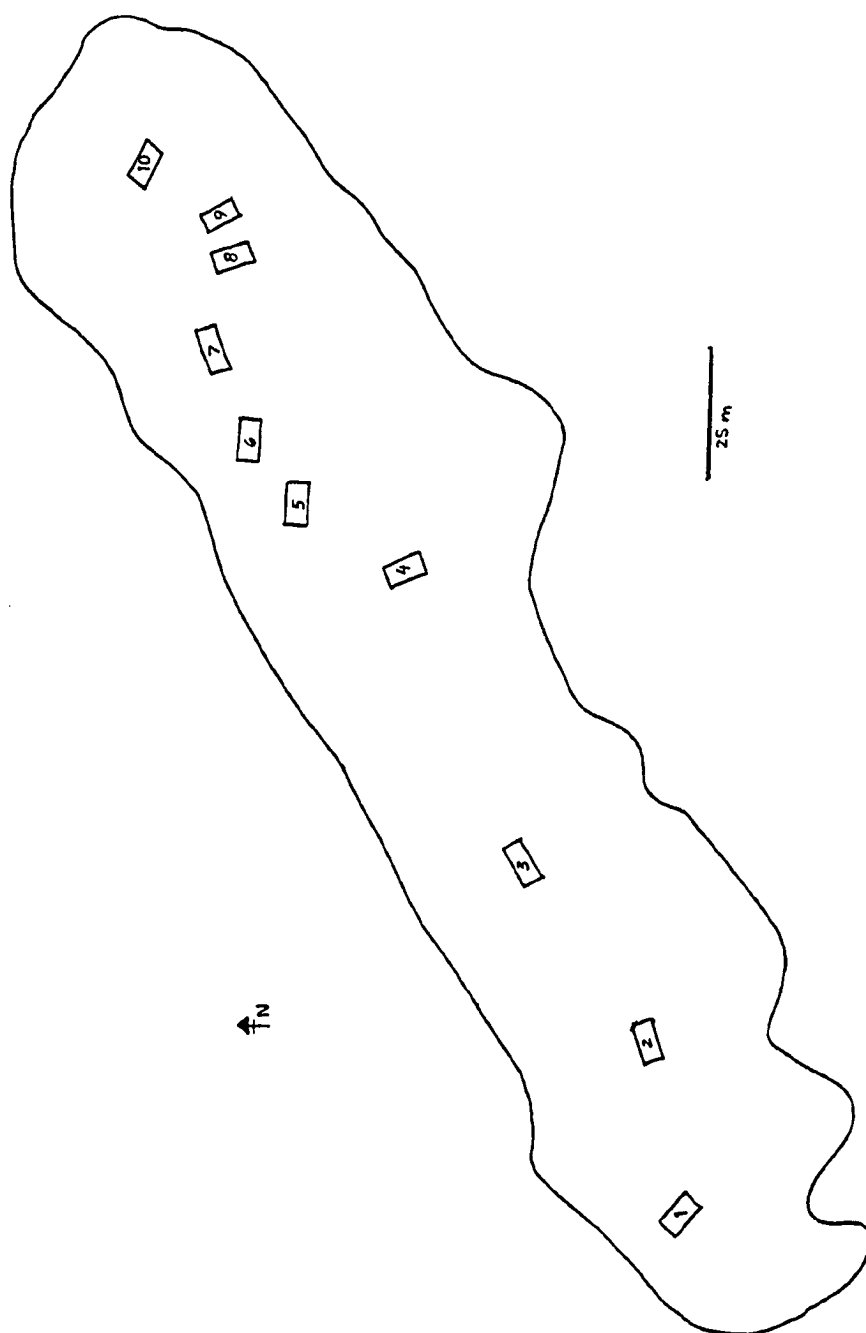


Figure 4.6. Locations of habitat plots, "Pithecia" Island I

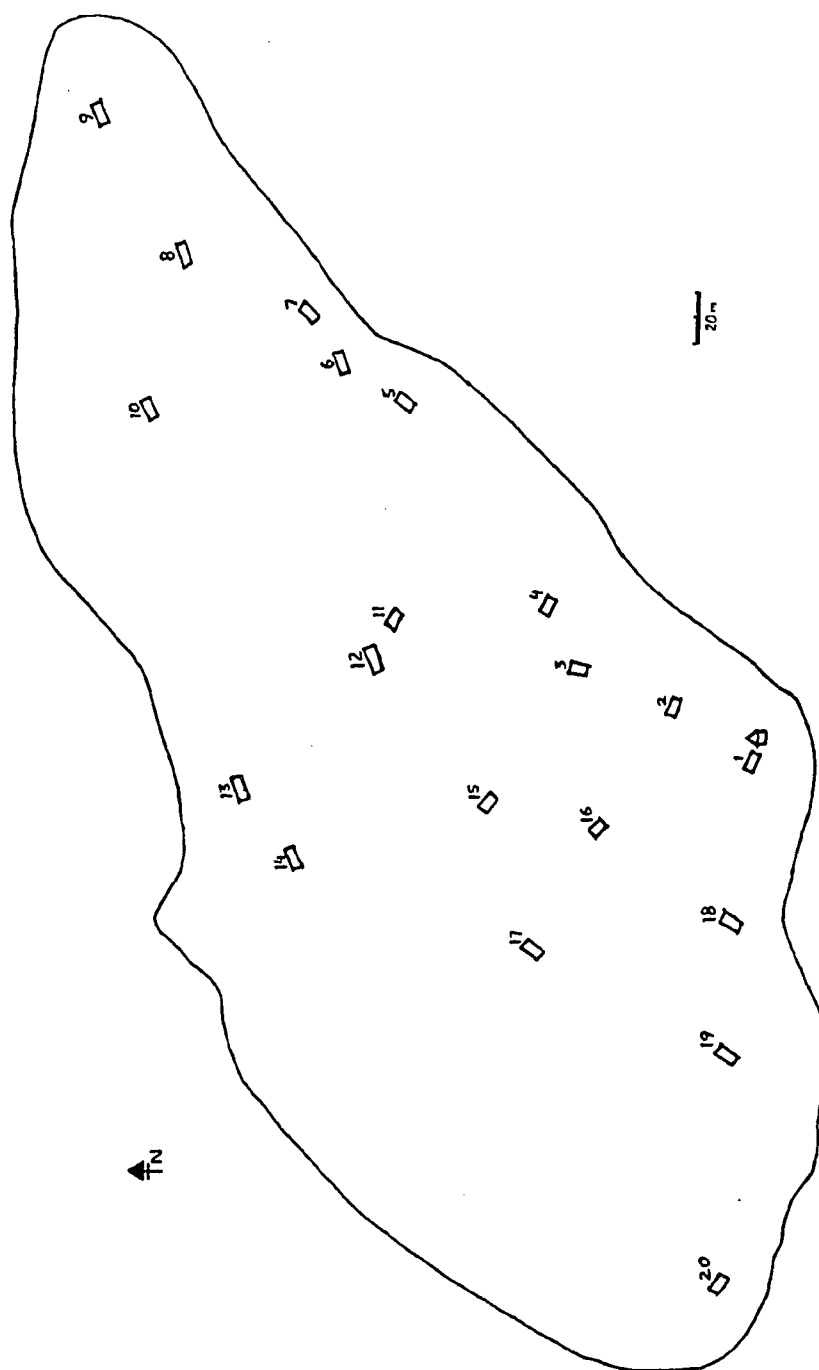


Figure 4.7. Locations of habitat plots, "Pithecia" Island II

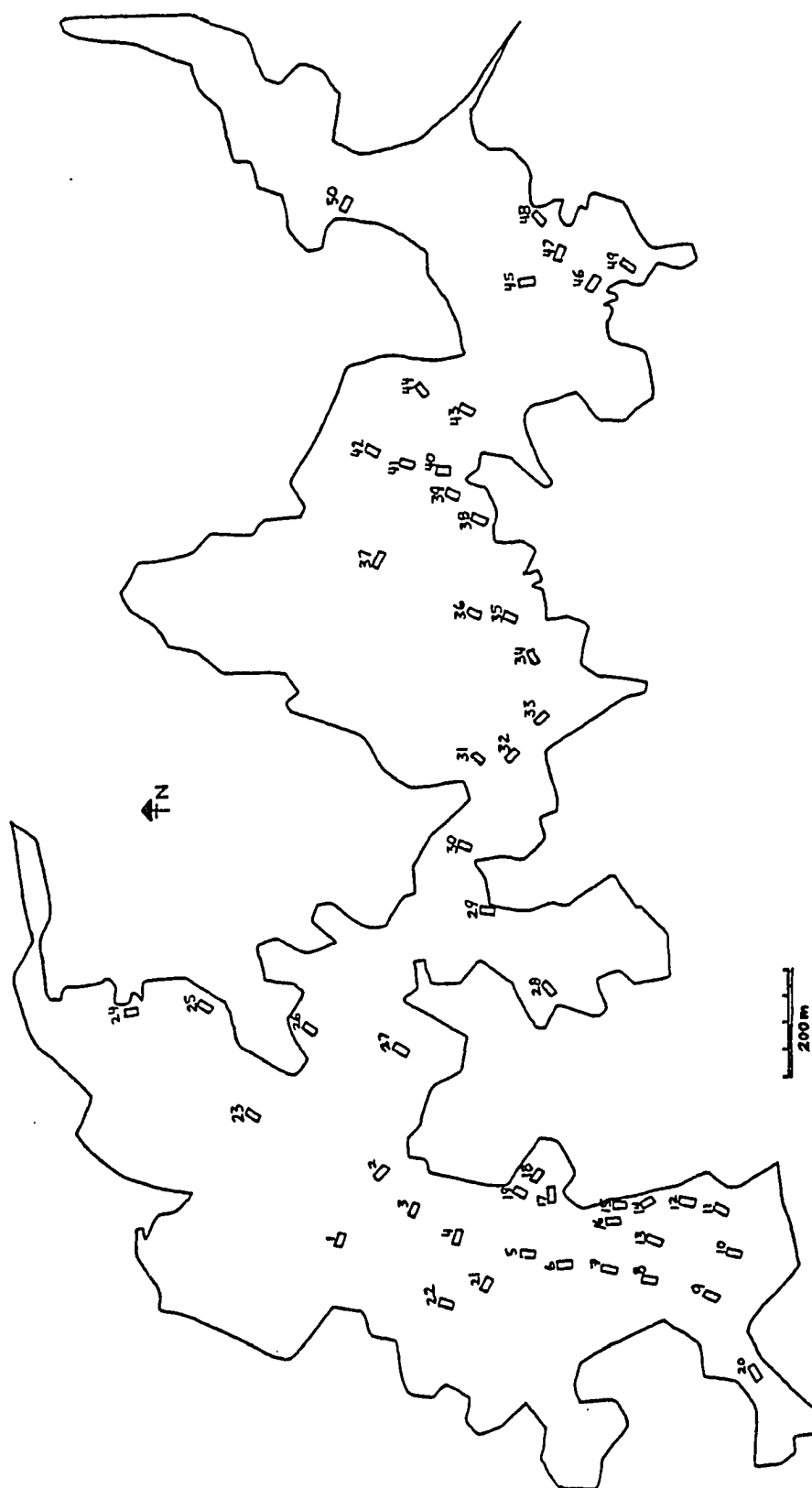


Figure 4.8. Locations of habitat plots, Danto Manchado

Table 4.4. Variables for vegetation analysis - habitat plots.

Tree Number: Many trees had been previously identified and labeled through the project of W.G. Kinzey and M.A. Norconk or their graduate assistant. Trees without a number were assigned one.

Species: For trees not previously identified, an attempt was made to identify it, based on identifications of known trees.

Diameter at Breast Height (dbh): Recorded for all trees larger than 2 cm on all three islands

Tree Height: Estimations of total tree height were practiced with the assistance of a clinometer until proficiency was achieved in estimating by eye.

Bole Height: height of tree trunk from ground to first main branch

Inclination of first main branch: vertical, near vertical, highly angled, angled, near horizontal, horizontal

Crown Diameter: diameter (in meters) of crown at widest point. If crown was very long in shape, an average was calculated with the narrowest dimension.

Percent Contact with Neighboring Crowns: estimate of percent of contact of tree (or near-contact, within 1 meter) with neighboring trees

Crown Shape: In data collection, crown shapes were recorded as regular or irregular; drawings and photographs were used in order to establish common shapes for each species

Branch Inclination: inclinations of most branches at:
Bottom 1/3 of Crown
Middle 1/3 of Crown
Top 1/3 of Crown

Table 4.5. Sample of postcranial skeletal specimens.

	<u>Pithecia</u>	<u>Chiropotes</u>	<u>Cacajao</u>
American Museum of Natural History New York	5	1	0
Museo Nacional de Rio de Janeiro Rio de Janeiro, Brazil	1	2	7
Museo de Zoología de Universidade de São Paulo Sao Paulo, Brazil	2	5	2
Museo Emilio Geoldi Belem, Brazil	0	1	1

Chapter 5. HABITAT - VENEZUELA

A. Introduction

While Chapter 3 briefly introduced the Caroni River Valley, the three study islands and the basic differences between them, this chapter details the results of habitat analyses on each island, and draws from the data of other habitat studies conducted in this area.

The first section provides a comparison of forest types in the Guri area before and after the third inundation (Pernía, 1985). The results of the quantitative habitat analyses carried out for this study are then presented within the framework of a general overview of forest structure and other characteristics of the islands. The third section consists of a presentation of several of the physical characteristics of five important species of feeding trees for Pithecia and Chiropotes.

B. Comparison of Forest Types Before and After the Third Inundation

The area in which the pitheciin habitat occurs in the Guri area in Venezuela was modified by the inundation of the Caroni River Basin. One would expect that if their new habitat were considerably different, with different potential resources than those upon which they had been depending, they would not have been able to make the shift successfully after the inundation. Therefore, it is

important to compare the habitat types available before (or at least in earlier stages of) the inundation to those afterward, and establish whether or not great changes in food availability and habitat type for the pitheciins would have occurred.

Before the final inundation, which would cover more than 125,000 hectares of land in the Caroni River Basin, Pernía (1985) conducted a series of surveys of vegetation at various levels, predicting which habitat types would be the most affected by the inundation. He distinguished six main types of forest, plus savanna and savanna-mixes. The forest types were: high (25 m +), medium (12 - 25 m), low (<15 m), hilltop, gallery and secondary. The various forest types were distributed over the area to be inundated as follows:

high	12.7%
medium	51.7%
low	22.4
hilltop	0.1
gallery	8.7
secondary	4.4

Pernía predicted that the islands to be formed would have the following forest distribution:

high	1.9%
medium	41.6%
low	49.7
hilltop	2.2
gallery	1.4
secondary	3.2

Therefore, the distribution of forest types would be expected to change after the flooding, such that low forest should be predominant, followed closely by medium forest.

The percentage of high forest and gallery forest would be altered the most dramatically. Danto Manchado was one of the areas with much high forest; some of this was preserved despite the flooding, providing a habitat for Chiropotes.

Although surveys were not conducted subsequent to inundation, Pernía's study was quite extensive, and thought to be very accurate. Therefore, it appears that although the proportions of the forest types have changed, those utilized by the monkeys still exist and are available for their use. Since Chiropotes tend to use primarily higher forest, they may have been affected more than was Pithecia, which can survive in a wider variety of habitats, including low, scrubby forest.

C. Island Habitats

"Pithecia" Island I is a primary forest, as its vegetation is probably undisturbed. It has the fewest small, young trees, although few mature trees reach more than 13 m in stature. The mean height of trees in habitat plots is 6.7 m, with a bole height of 3.2 m and average relative bole height of 48% (Table 5.1). The average crown diameter is 3.8 m.

The forest is quite heterogenous in terms of plant species for such a small forest patch, with more than 120 species identified (Kinzey and Norconk, tree list). The terrain of the forest is flat, and tree density relatively

low compared to the other two islands. The average density for the trees sampled within a 5 m radius of the sample points is 27.8 (Table 5.2). Mean dbh of trees in plots is 7.4 cm (Table 5.1). Sixty percent of the trees sampled for their density fall into the smallest dbh category (2-5 cm) (Table 5.2). Twenty percent are in the 6-10 cm range, 10.0% in that of 11-15 cm; 7.2% have a dbh of 16-20 cm and 2.4% a dbh greater than 20 cm. The average amount of overlap of tree crowns with their neighbors is 45%.

Lianas are fairly common (much more so than "Pithecia" II, but less so than Danto Manchado); on a scale of 0 to 4, the density of lianas averages 1.7 (Table 5.3). Locations of lianas in the forest are as follows: in 4.7% of the samples they were recorded on or near the ground (or on trunk), 14.0% in the crowns, and they occur both near the ground and in the crown in 81.4% of samples. They are most often single (61.4%) rather than in a vine tangle (20.5%). They occur as both single lianas and vine tangles 18.2% of the time.

Density of undergrowth is less than on other islands, with an average score of 2 (on a 0 to 4 scale) (Figure 5.1). The most predominant form of undergrowth is saplings (trees of less than 2 cm dbh) which constitute 61.2% of the undergrowth. Vines and lianas are next, being predominant 23.9% of the time. Shrubs (herbs or small plants less than 1 m in height) make up 11.9%; grasses and bushes are the

least common, each being the predominant form of undergrowth only 1.5% of the time.

Various forest types can be distinguished, some with high, some with low, and some with a mix of high and low vegetation. In higher forest, the density of the undergrowth is moderate, while the high/low forest mix usually occurs over a very dense undergrowth. The scrubbiest, lowest vegetation occurs over a rocky area; the mean density of rocks on "Pithecia" I is 2.2 (on a scale of 0 to 4), which means that slightly over one-half of the surface of the soil is covered by rocks of various sizes. Much of this rocky area is covered by densely packed small trees, but little undergrowth.

"Pithecia" Island II: This island is drier and rockier than the other islands, with vegetation typical of wind-swept areas. It was the site of a thorough vegetation analysis (Parolin, 1992 and 1993), and data from that study are drawn upon to describe some of the characteristics of the forest and its various habitat types. Parolin distinguished four types of forest on the island, each with its own characteristic plant species, soil features, etc. The types are: high forest, intermediate forest, low forest and savanna.

High forest (12-14 m) covers almost 70% of the island, and is the only one to occur on the southeastern part of the

island, which is the most exposed to wind and rain (ibid.). Trees are taller in this forest type; even those of the same species occurring in other forest types are shorter and more slender than those growing in high forest. Areas of high forest are more varied in terms of numbers of tree species, and a higher percentage of them are deciduous.

Invariably occurring between high forest and low forest is a belt of intermediate forest, which shares more species and characteristics with the high and low than either of the latter do with one another (ibid.).

Low forest consists of many xerophytic plant species, with adaptations to drought (ibid.). Stem density is greatest in low forest. Savannas cover very little of the island; they are characterized by grasses or sedges covering hard-packed, dry soil.

In general, this island has a high percentage of small-diameter trees, and the fewest large trees. The mean tree height is 7.6 m, and bole height is 4.0 m and average relative bole height 52% (Table 5.1). Average crown diameter is slightly larger than "Pithecia" I, at 4.1 m.

Tree density is higher than on "Pithecia" Island I; the average number of trees within a 5 m radius at each sampling point is 41.4 (Table 5.2). Mean dbh is 6.6 cm (Table 5.1), and the distribution of dbh sizes is as follows: frequency of trees in the smallest category averages 74% (Table 5.2). Trees of 6-10 cm dbh make up, on

the average, 13.7% of the trees, those of 11-15 cm 6.8%, and 16-20 cm trees 4.1%. Only 1.3% of the trees are larger than 20 cm dbh. The amount of overlap between neighboring tree crowns averages 43%.

Liana density is much lower than on either of the other islands, averaging only 0.6 on the 0-4 scale (Table 5.3). When they occur, they are most often single (89.1% of the time) as opposed to occurring in vine tangles (only 2.2%). In 8.7% of the samples in which lianas were observed, they occurred both singly and in vine tangles. Most often (53.3%), they are both in the crowns and on the ground. Thirty two and-a-half percent of the time they are only on or near the ground, and were seen only in the crowns in 14.1% of the samples. Although typical lianas are few, there are trees, particularly from the species Connarus venezuelanus, which are liana-like in form, or may occur as true lianas, and depend on other trees for support. All lianas, including the liana form of Connarus, occur most frequently in the intermediate forest type. Parolin suggests that this forest type allows favorable growing conditions (i.e., light) for lianas. I would speculate that the liana form of this species is adapted for fast growth - less energy should be required for growth as a liana than as a tree. The liana-like trees have no regular crown, but the bole or vertical axis extends far vertically or obliquely without branching (or with only two main branches), before

leafing out into a small crown.

Undergrowth density is higher than that of "Pithecia" Island I; the mean undergrowth density (based on the 0-4 scale) is 2.44, over one-half (54.5%) of which are saplings (Figure 5.1). The second most common undergrowth type is shrub (29.9%), followed by grass or sedge (8.5%). Mature bamboo and bushes occur equally often as the predominant undergrowth type at 2.7% each; bamboo is virtually nonexistent on "Pithecia" Island I. Lianas are relatively uncommon, and count in the dominant undergrowth only 1.7% of the time. "Pithecia" II is the only forest with "razor-grass" (Scleria bracteata), a sedge, which appears to occur with drier vegetation. There are other types of grasses and sedges as well, which are generally more predominant on this island than on either of the other two.

The average score for the predominance of rocks is 2; over some portions of the island, the ground is covered with rocks or boulders. The most extreme of these are here referred to as "rock forest", and are characterized by a high percentage of epiphytes and philodendrons. Parolin (ibid.) found these areas to be associated with a high undergrowth density (including Scleria), and were often on steep terrain.

In the tree crowns, vertical supports comprise 13.1% of the branches in the crown, angled supports 71.8%, and horizontal 15.1% (Table 5.4).

Danto Manchado, the "transitional moist forest" (Kinzey and Norconk, 1993), is wetter than either of the others, especially in the valleys. These areas, protected from the wind and with less run-off, retain more water. Vegetation here is moister and greener, less deciduous, with more palms. The island is covered with undulating hills, although no steep slopes. There is a greater range of tree heights than on the other islands, with more very large (30 m +) trees. Trees potentially used by Chiropotes (those at least 10 cm dbh) were sampled; the mean height was 11.8 m, average bole height 5.1 m and average relative bole height of boles is 41%. The average diameter of their crowns was 7.7 m (Table 5.1).

There is evidence of disturbance, with an old road and remains of fires. Secondary vegetation in some areas is evidenced by a high density of scrubby undergrowth, and many Cecropia trees, which are commonly found where vegetation disturbance exists. Tree density is much lower than on "Pithecia" II, approximating "Pithecia" I in its density rating (25.6 trees within a 5 m radius of each sampling point) (Table 5.2). Of the 1328 trees in the plots, the mean overall dbh is 8.4 cm (Table 5.1). Fewer than 300 of these are over 10 cm dbh. Of these larger trees, the smallest dbh category (2-5 cm) averages 75.4% of the samples (Table 5.2). Trees in the other categories average 12.4% (6-10 cm), 5.8% (11-15 cm), 3.8% (16-20 cm) and 2.7% (larger

than 20 cm). The average amount of crown overlap is 37% (Table 5.1).

Lianas density is high, at 2.9 on the average (on the 0-4 scale); in almost one-half of the samples, liana density scored a 4 (very high density) (Table 5.3). The form of the lianas are both single and in vine tangles about 50% of the time; however, when one or the other predominates, vine tangles alone occur 35% of the time as compared to 9.9% occurring singly. In most samples, they are equally predominant in the crowns and on or near the ground (83.6%), and split evenly between the ground and crown in the rest of the cases (8.4% and 8.0%, respectively). On this island, the vine tangles are usually made up of larger lianas, usually of the genus Bauhinia (Caesalpiniaceae) or the species Cydista diversifolia (Bignoniaceae).

Overall undergrowth density is the highest of the three islands, though only slightly higher than that of "Pithecia" II. It averages 2.6 on the 0-4 scale, with bamboo (particularly young bamboo) and saplings together making up one-half of the growth (24.8% and 23.9%, respectively) (Figure 5.1). Both young and mature bamboo are common in drier areas; mature bamboo is also common in the higher areas, often covering much of a hilltop or slope. Some hilltops are covered with grasses other than bamboo. Lianas and vine tangles are each the predominant undergrowth 34.4% of the time. Shrubs occur in 12.0% of the samples as one of

the dominant forms. Grasses (other than bamboo), bushes, and palms are rare, predominating at only 2.3%, 1.8% and 0.8% of samples, respectively.

Unlike the two "Pithecia" islands, Danto Manchado is not rocky.

Supports in the tree crowns are comprised of 14.4% vertical, 61.4% angled and 24.2% horizontal branches (Table 5.4).

D. Characteristics of Five Primary Feeding Trees

Data were collected for five species of Pithecia feeding trees on Island II, and for Chiropotes on Danto Manchado. These important food species were also among the most abundant and/or dominant tree species, particularly for "Pithecia" Island II. All are included in the top 11 (for abundance) or 15 (for dominance) species on this island (Parolin, 1992). Each species is quite homogenous in form; branching pattern, inclination of supports, etc., is species-specific.

"Pithecia" Island II (Table 5.5): The mean dbh of the feeding trees for Pithecia is 14.5 cm. Tree height averages 12.0 m, with a bole height of 4.8 m; relative bole height is 37%. The mean crown diameter is 8.2 m, and crown overlap averages 53%.

Crown shape is sometimes irregular; two of the five species consistently have irregular branching patterns

and/or crown shape. Branch orientation in the canopy was recorded as follows: 18.7% of the branches are vertical, 57.3% angled and 24.0% horizontal (Table 5.6).

Danto Manchado (Table 5.5): The mean dbh of Chiropotes feeding trees is 37.2 cm. Heights of these trees average 15.4 m, and bole height 6.0 m. The relative bole height is 34%. Crown diameter has a mean of 12.6 m, and an overlap of 31%.

Only one species of the five has an irregular crown shape. Orientation of branches in the crowns are: vertical branches comprised 15.2%, angled 52.2%, and horizontal 33.2% (Table 5.6).

E. Summary

Pernía's 1985 study of the affects of the third and last inundation of the Caroni River Basin indicated that high forest and gallery forests would be the most drastically altered. While medium forest predominated previous to the flooding, low forest (although followed closely by medium) would be the dominant forest type after.

The three islands are very distinct from one another in their distribution of forest type and habitat characteristics. Plant species differences, although not discussed here, are much more similar between the two "Pithecia" islands than to those on Danto Manchado.

"Pithecia" Island I is a primary forest, with the lowest percentage of the smallest-diameter trees. Overall, though, mean tree height and dbh is lower than that of the other two islands. Lianas are more common here than on Island II.

"Pithecia" Island II also appears to consist of undisturbed, or primary, vegetation. It has the highest tree and undergrowth densities, and there are very few true lianas. Much of the island is covered with rocks, and some parts are of very steep inclination. The vegetation over some portions of the island is adapted to high winds; others, to aridity. Danto Manchado is the wettest island, with the largest trees and the most lianas. With undulating terrain, valleys are green and vegetation indeciduous, and hilltops are covered with bamboo or other grasses.

In comparing feeding trees to those of the habitat plots, the following is revealed. Dbh is about twice as large for Pithecia feeding trees than for average plot trees on Island II; Chiropotes feeding trees have a dbh over four times as large as all sampled trees on Danto Manchado. The dbh measurement was recorded for all trees >2 cm; remaining variables were collected on Danto Manchado only for trees with a dbh larger than 10 cm (see Chapter 4). That notwithstanding, both height and crown diameter is much greater in feeding trees than other sampled trees on both islands. Relative bole height is less in feeding tree than for plot trees. Crown overlap is greater in feeding trees

of Pithecia than plot trees on Island II; for Chiropotes feeding trees, crown overlap is less than for the plot trees on Danto Manchado.

Branch orientation of feeding trees also differs from that of most island trees. For Pithecia, feeding trees have a somewhat higher frequency of vertical supports, considerably fewer angled and more horizontal supports. Chiropotes' feeding trees have approximately the same percentage of vertical supports as the others, fewer angled supports and a considerably higher frequency of horizontal supports. Comparing the branch inclinations between the habitats of Pithecia (on Island II) and that of Chiropotes, availability of vertical supports appears to be approximately equal. More angled supports are available on "Pithecia" Island II than on Danto Manchado, and more horizontal supports are available on Danto Manchado.

Implications of the differences in habitat structure on each island, taken together with information on habitat use by the primates, are discussed in Chapter 7.

Table 5.1. Characteristics of trees in habitat plots.

	<u>"Pithecia"</u> I	<u>"Pithecia"</u> II	Danto Manchado
$\bar{X}$:			
dbh (cm)	7.4 (517)	6.6 (915)	8.4 (1328)
height (m)	6.7 (508)	7.6 (868)	11.8 (270)*
bole height (m)	3.2 (498)	4.0 (801)	5.1 (264)*
relative bole height (%)	48 (498)	52 (801)	41 (264)*
crown diameter (m)	3.8 (444)	4.1 (729)	7.7 (252)*
crown overlap (%)	45 (464)	43 (769)	37 (265)*

* trees with dbh greater than 10 cm

(N) - different sample sizes are due to missing variables

Table 5.2. Density and dbh of trees - strip sampling.

	<u>"Pithecia" I</u> (N=1444)	<u>"Pithecia" II</u> (N=9947)	Danto Manchado (N=8589)
$\bar{X}$ number of trees within 5 m radius of each sample point	27.8	41.4	25.6
% of trees with diameter of:			
2 - 5 cm	60.4%	74.0%	75.4%
6 - 10 cm	20.0	13.7	12.4
11 - 15 cm	10.0	6.8	5.8
16 - 20 cm	7.2	4.1	3.8
> 20 cm	2.4	1.3	2.7

Table 5.3. Liana density and liana form.

Liana Density (0 - 4 scale)	$\bar{X}$
" <u>Pithecia</u> " Island I	1.7
" <u>Pithecia</u> " Island II	0.6
Danto Manchado	2.9

Liana Form	single	vine tangle	both
" <u>Pithecia</u> " Island I	61.4%	20.5%	18.2%
" <u>Pithecia</u> " Island II	89.1	2.2	8.7
Danto Manchado	9.9	35.0	55.1

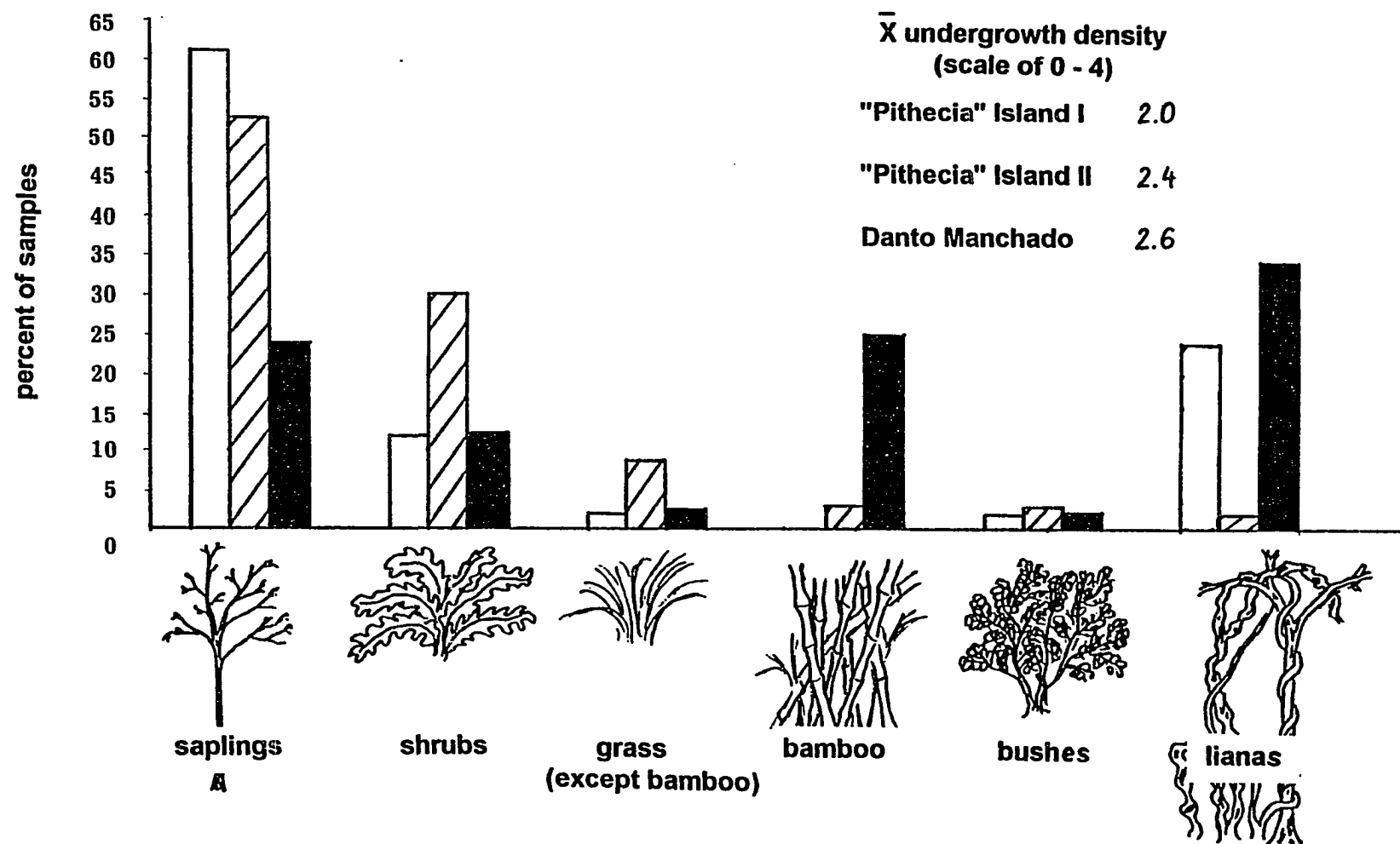


Figure 5.1. Density and predominant type of undergrowth

Table 5.4. Branch orientation of trees in habitat plots.

<u>Pithecia</u> Island II (N=1963)	Danto Manchado (N=884)
Horizontal: 15.1%	Horizontal: 24.4%
Angled: 71.8%	Angled: 61.4%
Vertical: 13.1%	Vertical: 14.4%

Table 5.5. Characteristics of primary feeding trees.

<u>"Pithecia"</u> Island II (N=44)	Danto Manchado (N=42)
<u>Peltogyne floribunda</u> (10)	<u>Pradosia caracasana</u> (8)
<u>Connarus venezuelanus</u> (10)	<u>Brosimum guianense</u> (7)
<u>Licania discolor</u> (10)	<u>Chrysophyllum lucentofolium</u> (7)
<u>Erythroxylum steyermarkii</u> (9)	<u>Melicoccus bijugatus</u> (8)
<u>Coccoloba latifolia</u> (5)	<u>Coccoloba fallax</u> (12)

	<u>"Pithecia"</u> Island II	Danto Manchado
dbh (cm)	14.5	37.2
height (m)	12.0	15.4
bole height (m)	4.8	6.0
relative bole height (%)	37	34
crown diameter (m)	8.2	12.6
crown overlap (%)	52.9	30.8

Table 5.6. Branch orientation of feeding trees of Pithecia and Chiropotes.

<u>Pithecia</u> Island II (N=171)	Danto Manchado (N=184)
Vertical: 18.7%	Vertical: 15.2%
Angled: 57.3	Angled: 52.2
Horizontal: 24.0	Horizontal: 33.2

Chapter 6. RESULTS: POSITIONAL BEHAVIOR AND HABITAT USE

A. Classification of Positional Behavior and Gaits of Pithecia and Chiropotes, and Cacajao

Categories for the positional behavior of the three pitheciins were initially established in order to collect data in the field. Since these positional behaviors grade into one another in a time sequence, and are difficult to observe and analyze in a natural situation, they were later defined in further detail with the use of slow motion video playbacks of the study populations (for Pithecia and Chiropotes). This allowed an analysis of gait patterns, limb positions, body orientation and tail position for each positional category. The detailed definitions presented below will permit inferences to be drawn as to the types of forces generated through the limbs for the various positional behaviors. To this end, the classification was devised in an anatomically meaningful way (as in Jolly, 1965), and will also aid in future analysis of anatomical features and their functional correlates.

Some positional categories (e.g., angled sit, vertical cling, pronograde clamber) are dependent upon, and defined at least partially by, characteristics of the supports in use (e.g. Ripley, 1967; Cant, 1988). The number of supports, their angle, diameter and the amount of deformation they undergo under an animal's body weight are of particular importance. The angle of a support can act to

increase or decrease the way certain types of forces are distributed. Subtle differences in the use of certain behaviors within a species (for example, various sitting modes) may also play a role in the distribution of forces, depending upon the orientation of the body to the support and the use of various body segments in weight-bearing. Here, these subtle differences are defined as subcategories in the classification of positional behavior, but are pooled into major categories for the quantitative analysis. Further investigation into the effects of these minor differences on anatomy and on habitat use can be conducted at a later time. Additionally, possible variations of each positional behavior were noted as qualifiers during data collection, and are presented under the categories listed below under Posture and Locomotion.

The same general categories may be used for the positional behavior of all three species, although they are used to a different extent by the various pitheciins, and exhibit some qualitative differences. The most apparent difference between the species is that of body orientation, and secondly, that of limb segment positioning (particularly the degree of flexion during positional activities). These qualitative differences must be taken into account, as anatomy, limb proportions and support use influence the form of the positional behavior exhibited by each species. For example, Pithecia tends to maintain a more vertical body

orientation throughout its positional repertoire, which correlates with its propensity for clinging to and leaping from vertical or highly angled supports. Additionally, the length of Pithecia's hindlimbs dictates a higher degree of hindlimb flexion in pronograde activities than in the other two genera. Some of the relatively minor qualitative differences among the species in their use of the positional modes are mentioned in the classification of positional behavior in the following section, while the most notable example of qualitative differences, leaping, is discussed in greater detail beginning on p. 205.

The categorization of positional behaviors for Cacajao was not undertaken as thoroughly as for the other two species (only still photographs were utilized; no video was taken), although the form of most categories is quite similar to that of Chiropotes, based on my personal observations of behavior in the wild, observations of the positional behavior of captive animals (Fontaine, 1981) and anatomical similarity (Fleagle and Meldrum, 1988).

Posture

Qualifiers noted in postural behaviors primarily included such variations as the degree of flexion of the back, the number of limbs used in support and weight bearing and the orientation of the body in relation to the support. Categories may be distinguished from one another based on

the supports used.

Sit (Figure 6.1): Occurs on horizontal or low-angled supports, with the body generally upright. A high degree of hindlimb flexion is exhibited at both the knee and the hip, while the forelimb is primarily extended at both the elbow and the shoulder. Positions of the hands and feet vary depending on the number, size and inclination of supports used, and on the orientation of the anteroposterior body axis to the support (whether parallel, perpendicular or oblique). The two subcategories of sit are perpendicular and parallel.

The qualifiers for sitting are: hunched, facing up or facing down (if using angled support), leg dangle, haunches on support, haunches off support.

Note: The pitheciins rarely assume the "foot-prop" postures typical of Old World Monkeys with ischial callosities (Rose, 1974), and the haunches are often not resting on the support.

Perpendicular sit (Figure 6.1A): The more common of the subcategories, in which the anteroposterior body axis is more or less perpendicular to the substrate. The weight is borne by the feet (which grasp the branch) with or without support from the haunches. The haunches, while often not resting on the substrate, may contribute to balance of the body by pressing against the supporting branch. Depending on support size, the hallux may be in line with other pedal

digits (if support is large) or opposed to the others (if support is small). Forelimb positions vary depending upon whether the hands are grasping the same branch upon which the body is resting, another branch, or none at all. The forelimbs are often not involved in weight-bearing. Perpendicular sit is most frequently used during feeding and while on smaller supports.

Parallel sit (Figure 6.1B): The anteroposterior body axis is aligned with the support. The feet grasp the branch in front of the haunches with the sole on one side and the digits on the other, one foot behind the other. The haunches rest on the support. The forelimbs more often play a weight-bearing or support role in parallel than perpendicular sit, and the hands may be used to grasp either the same branch that the body is on or a nearby branch. The posture may appear to be a "dog-like" sit. Parallel sit is more frequent during resting than feeding, and usually occurs on larger supports.

Bipedal Stand (Figure 6.2): The upper body is raised (by hindlimb extension) from a quadrupedal stand, sit or perch, then a branch is quickly grasped by at least one hand for additional balance. This is often used in order to reach for food, and is usually exhibited on medium-sized or small supports far out in the crown.

Angled sit (Figure 6.3): The anteroposterior body axis is oriented either perpendicular to or parallel with the support. This category was recorded separately from sit (above), since, due to friction, the distribution of forces on the body resting on a highly angled support differ from those of a body on a horizontal support.

Qualifiers are straddle-sit and hindlimb dangle.

Lean: This position is similar to sit, except that some of the animal's body weight is distributed through an additional support against which the individual is leaning.

Perch (Figure 6.4): This posture is similar to perpendicular sit, but the haunches are not involved in either weight-bearing or balance; the weight is transmitted and the body balanced over the feet alone, which grasp the support. The body is often hunched forward to aid in balance. The tail may be draped over a branch, and may provide additional support. Perching is typically exhibited on small supports, often during feeding.

Stand (Figure 6.5): The three subcategories of stand differ in the degree of flexion of the various limbs and the back. This posture occurs on horizontal or low-angled supports.

Parallel stand (Figure 6.5A): This is a relatively stable posture due to its large base of support. The long

axis of the body is approximately parallel to the support and the long axes of limbs approximately 90° to the body. The limbs are primarily extended and adducted. Since the hindlimbs are longer than the forelimbs, they are slightly flexed at the hip and the knee (more so in Pithecia than in Chiropotes or Cacajao). The support may be grasped by the hand between digits II and III rather than between the pollex and the other digits. This is particularly notable for Pithecia. The grasp taken depends on support size, and may affect the degree of pronation (increasing pronation as the central weight-bearing axis moves laterally in the hand).

Perpendicular stand (Figure 6.5B): This posture is less stable because of its smaller base of support. It is usually a momentary posture between locomotor bouts, and involves a degree of back flexion. Generally the feet grasp the support with the hallux opposed to the remaining digits, while the hands grasp with all digits in line. Typically, the hands are to the outside of the feet; however, they are sometimes on the inside.

Crouch: Involves flexion of all limbs in addition to the back. This posture is often used as a take-off position for a leap (Figures 6.13 and 6.14).

Vertical Cling (Figure 6.6): This orthograde position is typical for Pithecia, but uncommon for Chiropotes and

Cacajao. The long axis of the body is approximately parallel to the vertical or highly angled support. The hindlimbs are abducted at the thigh. The hindlimbs are strongly flexed at all their joints, and the sole of the foot is appressed to the support, with the digits encircling it, and hallux opposed to them. The forelimbs are also flexed, but not as strongly as the hindlimbs.

The primary qualifier to vertical cling is "vertical cling with feet", where the feet alone are used for support while the hands are involved in feeding from a neighboring tree or vine. Another qualifier was whether the support is vertical or near vertical as opposed to highly angled (approximately 70°). A third qualifier is "hindlimb dangle", in which one hindlimb releases the support and dangles for a short time, so that the other hindlimb and the forelimbs are used to support body weight.

Lie (Figure 6.7): Relaxed posture, whereby the length of the body rests along a single support or across multiple supports.

Ventral lie (Figure 6.7A): A ventral sprawl is common, in which the forelimbs are usually flexed, resting on the support just anterior to the head, or under the chin. This posture is exhibited more frequently by Chiropotes and Cacajao. Chiropotes sometimes arches its tail over its back while in this position. Alternatively, the body may be in a

hunched position, with the hindlimbs highly flexed and on the support rather than dangling.

Lie on side (Figure 6.7B): This posture often occurs on at least two supports, and appears somewhat less stable on a single support than does ventral lie. Lie on side is more common for Pithecia than for Chiropotes. The body may be in a curled position (back and limbs flexed). Often, dual supports at a fork are used.

Suspension (Figure 6.8): Suspensory behaviors take place underneath the support, with the hindlimbs, forelimbs or a combination of the two used in grasping. Supports used for this posture are of small to medium diameter and usually occur in or near the terminal branches during feeding or play. Flexible supports are often used in play, where their springiness is utilized to aid in play.

Qualifiers to suspension involve limb usage, which may include any combination of fore- and hindlimbs. Bipedal suspension is by far the most common, and was sampled only for Chiropotes and Cacajao. For Cacajao, this category includes a behavior which involves vigorous swinging while suspended by the hindlimbs; the flexed forelimbs are rapidly protracted and retracted to build momentum, which has the affect of swinging the entire body back and forth. This is apparently used for display, or while playing. Suspended locomotion is very rare, but was observed in a few isolated

incidents outside of the sampling period.

Cling (Figure 6.9): This posture, observed primarily for Chiropotes, is similar to suspension in that the limbs are under tension. The body is angled up or nearly vertical. The hindlimbs are flexed at both the hip and the knee; the forelimbs are abducted at the shoulder and the elbows are flexed. Supports are grasped with the feet and the hands, although one hand is often used for feeding. Cling is often used as a momentary pause between bouts of pronograde clamber, and occurs on terminal branches.

Locomotion

The qualifiers noted here (up, down) indicate whether progression deviates from horizontal to involve ascent or descent.

Quadrupedal walk (Figure 6.10 - Pithecia; Figure 6.11 - Chiropotes): Pronograde locomotion for pitheciins typically involves the symmetrical gait of diagonal sequence/diagonal couplets (Hildebrand, 1967). Diagonal sequence refers to the sequence of footfalls, in which the footfall of a hindlimb will be followed by that of an opposite forelimb (Hildebrand, 1967; Rose, 1973; Rollinson and Martin, 1981). For example, the footfall of the left hindlimb is followed by that of the right forelimb, then the right hindlimb, and

last the left forelimb, after which point the cycle is repeated. Diagonal couplets refer to the support sequence: the paired limbs which are supporting the body at any particular moment. The footfalls of two limbs that occur together (or almost together), thus providing the support, are said to be couplets. When the two limbs are from opposite sides of the body, they are diagonal (rather than lateral) couplets. As quadrupedal walk is characterized by footfalls which are evenly spaced in time, the gait is said to be symmetrical. While pitheciins fit the normal primate pattern of diagonal sequence/diagonal couplets gait, most non-primates exhibit a lateral sequence gait. It has been proposed that the more posterior center of gravity of primates compared to non-primate mammals calls for a diagonal gait pattern (Rollinson and Martin, 1981). Non-primates carrying weights which effect a posterior shift in their center of gravity have been seen to use diagonal gaits (Tomita, 1967, cited in Rollinson and Martin, 1981).

Quadrupedal walk is exhibited along a single support. The overall position in relation to the support is similar to that of stand, with the long axis of the body approximately parallel to the support and the long axes of the limbs approximately perpendicular to the body. The four limbs are used in propulsion and remain mostly extended. A slight degree of abduction occurs in the swing phase, when each limb protracts (and comes around) to be placed upon the

support. The feet are dorsiflexed and inverted. The forearms are primarily pronated, and the hands abducted at the wrist to grasp the supporting branch. As in stand, hand placement upon the branch is often such that digits I and II oppose the others, rather than the more common anthropoid condition where the pollex opposes the remaining digits in grasping. The tail is usually in an arched position posterior to Pithecia, and often over the back in Chiropotes.

Qualifiers of quadrupedal walk are the direction of progression (up or down), since the distribution of forces and the effects of friction are different on an angled support (e.g. Cartmill, 1979). The amount of flexion increases with the need for a more anterior (if up) or posterior (if down) center of gravity, and to lower the center of gravity for increased stability.

Quadrupedal run: The gait is similar to that of quadrupedal walk in that the diagonal sequence/diagonal couplets is used; however, the opposite limbs strike the support closer together in time, so that the gait approximates a trot, and the speed of progression is increased.

Scamper: Used by juvenile Chiropotes (and probably Cacajao) in play, this springy gait has more of an upward component than does quadrupedal run.

Pronograde clamber (Figure 6.12): Follows Cant (1988), where movement is across multiple substrates in a horizontal or diagonal direction. These multiple supports are often of various sizes, inclinations and orientations. The gait pattern is often irregular. More limb abduction is exhibited at the hip and shoulder than in a quadrupedal walk, as well as more flexion in the hip, knee and elbow. Therefore, the body (and thus the center of gravity) is lower. This type of locomotion is typically used to move around in the terminal branches.

Qualifiers are up or down, along or across. If two parallel supports were used to move along, the behavior is similar to quadrupedal walk. However, the supports were often of mixed orientations and inclinations, and the animal walks across them at a more irregular pace.

Pronograde clamber-run: Basically similar to pronograde clamber, but it occurs at a faster speed of progression.

Climb up: Following Rose (1979) and Cartmill (1985) climbing refers to locomotion on supports with vertical or steeply sloping surfaces. Here, climb up is recorded for movement upward along a single support. It is similar to quadrupedal walk up in terms of the gait used. Since the support used in this case is closer to vertical, different forces will act on the hindlimbs than on the forelimbs.

Hindlimbs play a greater propulsive role, while the forelimbs appear to act more as stabilizers, although they possibly exert some tension to help pull the body up. The more vertical the support, the more simultaneously the opposite limbs strike the substrate. This causes the spine to flex from side to side, and results in a swaggering appearance. Except while reaching for the next grasp, the limbs are flexed. A degree of abduction is exhibited at both the hip and the shoulder.

Climb down: Vertical or near-vertical movement downward along a single support. This is a relatively rare form of descent in either species, and was especially rare for Pithecia.

Qualifiers are head-first and tail-first.

Side-down (Figure 6.13): This locomotor behavior is used for descent. From a vertical cling position, the first part of the descent is achieved by moving the upper body down so that the hands grasp the support at a level equal to or lower than that of the feet. The lower body is then allowed to swing down so that the feet are again lower than the hands. This is repeated until the animal has lowered itself to the desired level on the support. This is used primarily for descent along a bole.

Pull-Up: This behavior involves the use of the arms in tension to pull the body up to a higher support.

Shinny up: Used for ascent on a single vertical support, generally of at least 8 cm in diameter. The sets of fore- and hindlimbs each move together, the forelimbs extending upward to grasp the support, then hindlimbs flexing upward, continuing until the desired level has been reached.

Shinny down: Basically similar to shinny up, except used to descend, and no propulsion is required.

Swing down: The forelimbs extend to grasp a neighboring support, then the body is allowed to swing down.

Bridge (Figure 6.14): This behavior is used to cross gaps in the canopy, and is accomplished by quadrupedally walking or pronograde clambering towards the end of a support (often a terminal branch) until the branch becomes too unstable (deformable). The forelimbs are then used to reach forward to grasp a support across the gap. The body is then pulled across while the new support is being pulled towards the body, until the hindlimbs are close enough to grasp this second support. Continuous progression, usually pronograde clambering, follows.

Leap (Figure 6.15 - Pithecia; Figure 6.16 - Chiropotes):
Used to cross gaps in the canopy; this behavior involves rapid progression between discontinuous supports through propulsion by the hindlimbs. Following Rose (1973), a leap can be divided into several stages: preparatory, take-off, flight (here referred to as midflight), landing and recovery (the last phase is not considered here). Since the goal of leaping is often to travel as far as possible, the amount of force applied to a take-off support must be maximized. This is accomplished in two ways, both of them having to do with increasing the time over which muscular force is applied against the support. Both Pithecia and Chiropotes exhibit behavior which is appropriate to achieving this goal.

1) In the preparatory phase (just prior to take-off), a crouching posture is often assumed from the original position (particularly if this position is stand, sit or quadrupedal walk). This crouch, which is characterized by rapid flexion of all four limbs and the back, is immediately followed by extension of these same body segments. This is similar to a "counter-moment jump" in humans (e.g. Bosco et al., 1981), and can serve to "potentiate" (e.g. Cavanagh, 1977) the muscles to be used in the leap. Muscle potentiation can enhance the power output of a muscle by utilizing previously stored energy in the muscle for immediate use (ibid). During eccentric muscle contractions (whereby a muscle is forcibly stretched while under

tension), mechanical energy is absorbed by the muscle; this energy can either be dissipated into heat or stored within the muscle. It can then be re-utilized in subsequent active (concentric) contraction of the muscle. Part of the energy is derived from the passive recoil of the muscle, and therefore acts to decrease the time for which it is necessary for chemical energy to be transferred into mechanical energy. For example, Alexander (1974) showed that the ankle extensors (gastrocnemius and plantaris) of a leaping dog acted essentially as passive elastic bodies. They seemed to absorb as much energy while they were being stretched (eccentric contractions) as they subsequently performed as work when they shortened (concentric contractions). Alexander postulated that most of the energy was stored in the tendons of these muscles.

A crouching primate in preparation for a leap may be potentiating the same muscles (i.e. gastrocnemius and plantaris) by lengthening them while under tension. These muscles would therefore absorb some degree of mechanical energy, and re-use a portion of it together with their elastic recoil when they contract to leap. The stored energy must be utilized immediately or it will be lost to heat; therefore, a faster crouch can initiate a more powerful leap.

2) The utilization of the sets of limbs and the back in a temporal sequence pattern also serves to generate more

force, in part by lengthening the time over which force is applied to the support (R. Robertson, pers. comm., for human locomotion). The process begins with a combination of back flexion and forelimb extension; the back flexes as arms extend and are thrown forward. This is followed by hindlimb extension from the proximal to the distal limb segments. The final propulsive thrust comes from the action of the calf muscles, providing plantar flexion against the support.

Together, muscle potentiation and use of the limbs in a temporal sequence pattern can maximize the propulsive force of a leap.

Leaping is influenced by supports, position and speed of progression at take-off, which affect leap distance and body orientation. Take-off positions include: quadrupedal walk, quadrupedal run, pronograde clamber, pronograde clamber-run, vertical cling and stand. The pitheciin species differ considerably in the frequency of the use of various positions and supports for take-off and landing, and in qualitative aspects of leaping, with Pithecia exhibiting notable differences from Chiropotes and Cacajao. Leaping differences between the species are discussed on p. 205.

Drop (Figure 6.17): Dropping is used to cross vertical gaps in the canopy. It provides rapid descent with little or no propulsive exertion by the limbs, and little horizontal displacement. The body tends to be primarily horizontally

oriented when dropping onto flexible supports, and is often angled downward when dropping onto solid supports. Landings onto flexible supports are most often accomplished with all four limbs striking the substrate at the same time; landing onto solid supports is often forelimbs first. Drops (particularly longer drops) are more frequently onto terminal branches, although Figure 6.17 demonstrates the sequence of a drop down to a solid support, with the body angled downward.

Hop: Both the take-off and landing phases are hindlimb-dominated, and the other leap phases (preparatory, mid-flight, recovery) are very short. The primary difference between hop and leap is that very little displacement occurs between take-off and landing. Hops are usually used within rather than between trees.

Continuous bound: This mode of locomotion is used by Pithecia for rapid and/or long-distance locomotion. The take-off position is often from a vertical cling, and several consecutive leaps are exhibited, with each take-off directly following a previous landing. Upon landing, hindlimb flexion is used to absorb the compressive forces of landing. As described in the previous section on leaping, some of the muscles used in landing are eccentrically contracted in the same way as are those in a crouch. Energy

is thus stored in these stretched muscles, a portion of which can be recovered if they are (immediately) concentrically contracted in leaping. This elastic recoil property can be used to reduce the total muscular effort of those muscles which have been potentiated. The principle is well documented in kangaroos, for which about 40% of the concentric contractions in the leg muscles was sustained by the elastic recoil of the gastrocnemius and plantaris tendons (Alexander and Vernon, 1977).

Bound: Chiropotes, while locomoting rapidly, use bounding interspersed with quadrupedal locomotion.

Use of the tail in positional activities

In general, the tail does not play an active role in locomotion, but appears to be used as a counterbalance for Pithecia and Chiropotes in some locomotor activities, and is often draped over a nearby branch for added support in postural activities, as seen in Callicebus (Kinzey, 1977). The tail of Cacajao is probably too short to be used in this manner. Use of the tail as an aid in locomotion is especially apparent in leaps of Pithecia, in which it may be used as a "rudder" (see p. 218) to direct turning of the body in the mid-air phase.

B. Results of Quantitative Analysis

Some overall patterns of activity levels and positional behavior emerge from the quantitative data; these may be kept in mind while reading this results section. First, comparisons of the time spent feeding, traveling and resting by each species demonstrate that: Pithecia spends the most time resting, Chiropotes spends the most time feeding, and Cacajao spends the most time traveling. Overall, Pithecia is the least active of the three, and Cacajao the most active.

Following from this, comparing the use of locomotor versus postural behaviors produces a similar result. Pithecia, the least active, spends one-third of its time in locomotion, and two-thirds in posture. On the other hand, Cacajao engages in locomotor and posture each almost one-half of the time, with postural behaviors slightly more frequent. Chiropotes falls almost exactly between Pithecia and Cacajao in the use of locomotion versus posture. These differences are, to a large degree, due to the fact that Cacajao spends considerably more time engaged in locomotor activities while feeding than does either of the other two species.

As will be seen clearly from the quantitative data, the frequency of the primary locomotor mode differs considerably between the species. For most behaviors, Pithecia and Cacajao are at opposite ends of the spectrum, and Chiropotes

falls between them, consistently nearer to Cacajao. Pithecia leaps much more than either of the other two species, but spends much less time in pronograde clamber/bridge or quadrupedal walk/run. It seldom drops from a higher substrate to a lower one. Quadrupedalism is the primary locomotor mode for both Chiropotes and Cacajao, followed by pronograde clamber/bridging. Dropping is exhibited much more frequently in these two species.

The presentation of the quantitative data is divided into three portions: 1) intraspecific differences between two Pithecia groups, 2) description of species-specific behavior for each of the three pitheciins, and 3) interspecific comparisons. The quantitative results are presented as frequencies of positional behavior and habitat use (tree portion; height in tree; number, inclination and diameter of supports) while engaged in the three major activity bouts of Feed, Travel or Rest. Results for each of these major activities are presented separately; locomotor behaviors are presented first, followed by postural behaviors. For Chiropotes only, data are also presented for Play. Tables 6.5 - 6.11 each include data from all three species, and may be referred to for interspecific comparisons and the results of statistical tests. Behaviors which did not represent at least 1.0% of the samples were listed separately, and their cumulative total is presented in each table under the category "other".

Two data sets were utilized; the original is presented as raw frequencies in the text and in the tables. A second data set was created in order to eliminate repeated samples of postural behaviors to be used for statistical tests (as discussed on p. 95). The main portion of this data set is presented in Appendices 1-5. As previously mentioned, data on more variables are presented for Pithecia and Chiropotes than for Cacajao.

Intraspecific Differences

(Comparisons between Pithecia groups on two islands)

The following comparison demonstrates some of the intraspecific differences between Pithecia groups on different islands. It should be noted that the qualitative aspects of positional behaviors were consistent within species, and can be contrasted with the qualitative differences observed among species.

Positional Behavior

Feeding (Table 6.1): While some of the behaviors exhibited by Pithecia during feeding differ little between the two groups, a number of them differ considerably ($\chi^2 = 57.10$, $df = 8$, $P < 0.001$). Group I exhibits more pronograde clambering (11.5% compared to 7.9%), more quadrupedal walking (2.0% compared to <1%), and more leaping (1.3% compared to <1%) than does Group II. Group I vertically

clings more than does Group II (12.1% compared to 8.6%). Group II sits with greater frequency than does Group I (58.9% compared to 51.2%), and stands bipedally more (2.6% compared to 1.3%).

Travel (Table 6.2): Differences in positional behavior between the two groups are significant ($\chi^2 = 92.4$, $df = 16$, $P < 0.001$), although most of the differences are noted for the behaviors which are used relatively infrequently by Pithecia. For example, Group I exhibits the locomotor behaviors climb up (2.3%), climb down (1.0%) and swing down (1.2%) more than does Group II, which uses these behaviors, respectively, in 1.6%, <1%, and <1% of samples. Group II uses continuous bound (3.8%), hop (3.9%), drop (2.7%) and sidle down (1.2%) more than does Group I, which uses these behaviors, respectively, in 2.7%, 1.0% <1% and <1% of samples. The most notable difference of the postural behaviors is the use of sit, used in 7.0% of Group I samples, and 4.7% of Group II samples.

Rest (Table 6.3): The most frequently used postural behavior during rest differs little between the groups, but other behaviors differ considerably ($\chi^2 = 101.12$, $df = 7$, $P < 0.001$). Vertical cling is used more frequently by Group I (13.4%) than by Group II (9.0%). Ventral lie is much more frequently used by Group II (12.2%) than by Group I (4.7%), while lie on side is used more often by Group I (5.0%) than by Group II (1.2%). Stand was sampled more for Group I than

for Group II (3.1% compared to 1.8%). Neither lean nor perch were sampled for Group I; in Group II they were recorded in 2.0% and 1.0% of samples, respectively.

Tree Portions Used (Table 6.4)

Feeding: Use of the tree portions differ greatly during feeding ($\chi^2 = 210.44$, $df = 7$, $P < 0.001$). The difference in terminal branch use is extremely notable; Group II uses terminal branches more than one-third as frequently as does Group I (61.0% compared to 36.6%). Group I uses the portions below crown (8.8%), bole (8.4%), liana (6.7%), vine tangle (3.5%) and ground (1.2%) more often in feeding than did Group II, for which the frequency of use of these portions are, respectively, 3.4%, 2.1%, 2.6%, 1.0% and <1%.

Travel: Differences between the Pithecia groups in tree portion use during travel are apparent as well ($\chi^2 = 158.97$, $df = 6$, $P < 0.001$). Group I uses both the main crown (37.3%) and the terminal branches (13.5%) less than does Group II, which uses these portions in 47.5% and 26.0%, respectively. Although the vertical axis is used less often by Group I than by Group II (6.0% compared to 8.1%), the other two lower tree portions, below crown and bole, are used more frequently by Group I (14.3% and 16.6%) than by Group II (8.8% and 6.5%). Both lianas and vine tangles are used more by Group I (9.6% and 2.7%,) than by Group II (2.3%

and <1%).

Rest: Resting tree portions differ considerably between the two groups ($\chi^2 = 162.39$, $df = 6$, $P < 0.001$). Use of the main crown and below crown is approximately equal, while all others differed. The terminal branches and vertical axis are used more by Group II (8.1% and 8.5%) than by Group I (1.2% and 5.6%), while the bole, lianas and vine tangles are used more frequently by Group I (9.8%, 9.3% and 2.3%) than by Group II (1.8%, 6.8% and <1%).

Relative Height in Tree

Feeding: Although statistically significant ($\chi^2 = 31.10$, $df = 6$, $P < 0.001$), relative heights of the two groups are not as divergent as are positional behaviors and tree portions. Group I tends to be found more often than Group II in lower portions (10.8% of Group I samples below 60% of tree's height vs. 6.0% of Group II samples), and Group II slightly more often than Group I in higher portions (94.0% as opposed to 89.2%).

Travel: The Pithecia groups differ from one another while traveling as much as they do while feeding, with Group I again using the lower portions more, and Group II using the higher portions more ($\chi^2 = 22.91$, $df = 6$, $P = 0.001$). Group I uses the lower portions (below 60% of tree's height) in 20.5% of samples, while Group II uses this portion in 12.6% of samples. Group II uses the higher portions (above

60% relative height) in 87.4% of samples; for Group I this figure is 79.5%.

Rest: Differences between the groups in relative height while resting are also significant ($\chi^2 = 44.77$, $df = 6$, $P < 0.001$). The total frequency for use of the lower portions (below 60% of tree height) by Group I is 20.2%, while for Group II it is 12.2%. Group I uses the higher portions in 79.8% of samples and Group II in 87.8%.

**Species-Specific Positional Behavior and Habitat Use by
Pithecia, Chiropotes and Cacajao**

Pithecia

(pooled data from the Pithecia groups on two islands)

Positional Behavior

Feeding (Table 6.5): While feeding, Pithecia uses locomotor behaviors in fewer than 15% of the samples, and postural ones in over 83%. Of the few sampled locomotor behaviors, pronograde clambering is used the most at 10.4%. Quadrupedal walk was observed in 1.5% of the samples and leap in 1.0%.

Sitting is by far the most common feeding posture (53.3%), followed by quadrupedal or tripodal stand (9.8%) and clinging to vertical or highly angled supports (10.5%). Perch is employed in 9.3% of samples, and bipedal standing while feeding is used in 1.7%.

Travel (Table 6.6): The single most frequent locomotor behavior is leaping (39.7%), followed by pronograde clamber (15.6%). Quadrupedal walk comprises 15.1% of the travel samples, quadrupedal run 4.6% and continuous bound 3.0%. Climb up is used in 2.1% of observations, hopping in 1.8%, drop in 1.1% and, pronograde clamber-run and swing-down each in 1%. The postural behavior most frequently observed in the momentary pauses during travel was sit (6.4%), followed by vertical/angled cling (3.6%). Standing was recorded in 2.1% of samples.

Rest (Table 6.7): Pithecia spend the vast majority of resting time in a sitting position (71.8%), while vertical/angled cling makes up 11.3% of the samples. Lying was observed in 11.1% of samples (7.5% on ventrum and 3.6% lying on side). Standing accounts for 2.5% of rest samples, and leaning for 1.1%.

Tree Portions Used (Table 6.8)

Feeding: The terminal branch portion of the tree is that most commonly used for feeding (44.0% of samples), followed by the crown (28.7%). The other portions are used as follows: below crown (7.2%), bole (6.5%), lianas (5.5%), vertical axis (4.6%) and vine tangles (2.7%). Pithecia was observed on the ground in 1.0% of their feeding samples.

Travel: The tree portion in which Pithecia was observed most often while traveling was the crown (39.9%).

Terminal branches are used in 16.8% of travel samples. The bole is observed in use 14.0% and below crown 13.0% of travel time. Lianas are used in 7.7% of the travel samples and the vertical axis in 6.5%. Vine tangles were observed 2.2% of the time.

Rest: The tree portion most frequently used by resting Pithecia is the crown (51.0% of samples), followed by below crown (21.9%). Other tree portions comprise significantly fewer of the resting samples. Lianas were observed in use in 8.3% of samples, the bole in 6.8% and the vertical axis in 6.7% of samples. The terminal branches are used in 3.8% of samples and vine tangles in 1.6%.

Tree Portions from which Food is Obtained (Table 6.9)

Pithecia obtains most of its food from the terminal branches (64.3%). The location that is second-most important in providing food is the liana (17.9%), followed by the crown (12.5%). Food is found on the ground in 2.5% of the samples, and the remaining tree portions (bole, vertical axis, below crown and vine tangle) each provide a food source in fewer than 1% of samples.

Absolute Height in Tree (Figure 6.18)

The mean height at which Pithecia is found in the trees was 6.8 meters, and the mean height of the trees which they use was 9.6 meters.

Relative Height in Tree (Figure 6.19)

Feeding: The relative tree heights at which Pithecia is found while feeding varies, with the portions which occurred between 80 and 90% of the tree's height most frequently utilized (34.5%). The relative height of 70-80% is used in 28.2% of the samples, and that of 90-100% in 13.8%. At the relative height of 60-70%, Pithecia was observed feeding in 14.2% of the samples. At 50-60% of the tree's height, feeding was observed in 5.4% of the samples, and under 40% of the tree's height, in 2.5%. 1.4% of the samples were recorded at the 40-50% portion.

Travel: While traveling, Pithecia was most often seen at a relative height of 70-80% of the tree's height (34.1%). The height portions immediately above and below that level (80-90% and 60-70%) are used approximately equally (19.7% and 24.2%, respectively). The level at 50-60% of the tree's height is used in 13.1% of travel samples, and the uppermost portion (90-100%) in 3.7%. Pithecia was observed at 40-50% of the tree's height in 3.3% of samples, and below 40% in 1.8%.

Rest: Pithecia is most often found at the relative height of 70-80% (in 28.3% of samples), followed closely by the portion 80-90% (28.0% of samples), and that of 60-70% (19.5% of samples). In 12.4% of resting samples, Pithecia is found between 50 and 60% of the tree's height, and in the uppermost portion (90-100% of tree height) for 8.8% of the

samples. Pithecia rests at the height 40-50% for 2.0%, and below 40% in 1.1% of the samples.

Support Use

Feeding (Table 6.10)

Number of Supports: While feeding, Pithecia uses a single support and several (three or more) supports with similar frequencies (46.4% and 38.2%, respectively); two supports are used for 15.4% of the samples.

Inclination of Supports: Branches which deform under the weight of Pithecia are the most frequently used for feeding (34.1%), followed first by angled supports (26.0%), then by horizontal supports (16.8%). In 14.5%, a mix of supports are used. Vertical supports were observed used by Pithecia in 8.6% of the feeding samples.

Diameter of Supports: The branch size most frequently used by Pithecia while feeding is between 2 and 5 cm in diameter (37.5% of the samples). The smallest supports (less than 2 cm) are used in 22.8% of the samples, and a combination of these two smallest support categories is often used (22.0%). Branches 6 to 10 cm in diameter are used in 12.0% of the feeding samples, and those 11 to 15 cm in only 3.0%. In 2.0% of samples, combinations of size classes other than <2 with 2-5 cm are utilized. Supports larger than 15 cm are observed 1.0% of the time.

Travel (Table 6.11)

Number of Supports: Pithecia was observed using a single support for travel in 71.8% of the samples. Several supports (three or more) are used in 21.1% of the samples, and two supports in 7.0%.

Inclination of Supports: Pithecia most often uses angled supports while traveling (35.2%). The two other inclinations (horizontal and vertical) are used almost equally (20.5% and 19.8%, respectively), and branches that deform under body weight are used in 16.1% of samples. A mix of support inclinations were observed in 8.4% of samples.

Diameter of Supports: While traveling, Pithecia most frequently uses supports with a diameter of between 2 and 5 cm (42.7%), followed by those between 6 and 10 cm (29.7%). Supports smaller than 2 cm are used in 9.5% of travel samples. Pithecia frequently (9.1%) uses a combination of supports in the two smallest size categories (<2 and 2-5 cm). Those between 11 and 15 cm are used in 6.1% of samples, and a combination of branches in categories other than the two smallest (<2 with 2-5 cm) in 1.6%. The largest support category (>15 cm) is used for 1.3% of samples.

Rest (Table 6.12)

Number of Supports: Pithecia uses a single support in 60.3% of rest bouts, and dual supports in 31.9%. Three or more supports are used in 7.8% of samples.

Inclination of Supports: Pithecia used angled supports more than the other inclinations (40.7%) for resting. Horizontal supports were used in 34.1% of observed rest bouts, and vertical ones in 7.6%. A mix of supports are used in 16.2% (two-thirds of which were angled with horizontal), and deformable branches 1.4% of samples.

Diameter of Supports: For Pithecia, the most commonly used rest supports are 2-5 cm in diameter (44.8%), followed by those in the size range 6-10 cm (30.9%). Supports 11-15 cm in diameter are used in 5.8% of samples, and were the largest size class observed for resting Pithecia. Combinations of two size classes are used as well: 2-5 with 6-10 cm (9.8%), <2 with 2-5 cm (5.3%) and other combinations (2.5%).

Supports Used in Each Tree Portion (Table 6.13)

Supports used by Pithecia on the bole are virtually always single, usually vertical, and sometimes angled. Diameter of these supports are primarily 5-10 cm, followed by 2-5 cm, then 11-15 cm. The vertical axis is used primarily as a single support as well, but dual supports are sometimes taken. Angled supports, followed by vertical, are those most commonly used by Pithecia. Their most common diameter is 2-5 cm, followed by 5-10 cm. Below crown is virtually identical to vertical axis in terms of the number of supports used; support inclination is by far most

frequently angled, and much less frequently horizontal. Diameter of the supports used in this portion are primarily from the size classes 2-5 cm and 5-10 cm. In the crown, a single support is most frequently used, with dual supports used one-half as often. Inclination of the primary supports used in this portion are divided evenly between horizontal and angled, and they are most frequently 2-5 cm, and much less often, 5-10 cm. In the terminal branch portion, supports used are by far most often multiple, deformable and of the smallest (<2 cm) size class, that of the 2-5 cm class, or a mix of the two. Lianas are typically taken as a single support, most often angled, but also relatively frequently horizontal. By far the most often-used diameter for lianas used by Pithecia is that of 2-5 cm; that of 5-10 cm is used about one-third as frequently. Supports used in vine tangles are most often taken several at a time, are deformable or of mixed inclination, and are from the smallest size class (<2 cm), or the smallest mixed with that of 2-5 cm.

Use of Positional Behaviors in Various Tree Portions

(Table 6.14)

Crown: Leap was the primary locomotor behavior observed in the crown (12.7%), followed by quadrupedal walk (7.7%). Pronograde clamber was observed 5.7% of the time, quadrupedal run in 2.1% and continuous bound in 1.0%.

Sitting comprises 51.8% of the samples in the crown, and is much more common than the second most frequent behavior, stand, which comprises only 3.9%. Angled/vertical cling was observed 3.5% of the time, and ventral lie 3.2%. Lie on side is used in 2.7% of samples and perch in 2.0%.

Terminal Branches: The locomotor behavior most often used in the terminal branches is pronograde clamber (25.2% of samples). Leaps comprise 5.8% of the samples and quadrupedal walk 2.3%. Sitting in the terminal branches was observed 40.8% of the time, perch 11.0% and stand 9.6%. Bipedal stand is used for 1.2% of the samples.

Below crown: Leaping is used in 12.4% of samples in the tree portion below the crown. Quadrupedal walk comprises 5.6% of samples, quadrupedal run 2.6% and continuous bound 1.1%. Sit is the most common postural behavior (52.7% of samples), followed by angled/vertical cling (11.0%). Ventral lie was observed in 5.3% of samples, stand in 3.3%, lean in 1.4% and perch in 1.0%.

Vertical Axis: While using the vertical axis, the most common locomotor behavior is leap (20.2%). The other behaviors are much less frequently used: quadrupedal walk (3.3%), climb up (2.0%), climb down (1.4%), quadrupedal run (1.0%) and swing down (1.0%). The most often observed postural behaviors are sit (39.9%) and angled/vertical cling (23.2%). Stand was observed 2.9% of the time, perch 1.2%, and lean 1.0%.

Bole: Leaping is the most frequent positional activity (36.8%) when the bole is being utilized. Other locomotor behaviors are used relatively rarely: climb up (2.1%), quadrupedal walk (1.9%), climb down (1.2%), quadrupedal run (1.1%), sidle down (1.0%) and continuous bound (1.0%). Angled/vertical cling is the postural behavior most often exhibited (38.5%). Sit is observed in 11.9%, and stand in 1.1% of samples.

Liana: The locomotor behavior most frequently used while on lianas is quadrupedal walk (9.4%), followed by leap (8.9%). Pronograde clamber is used in 4.2% of samples, quadrupedal run in 2.9% and climb up in 2.2%. Sitting was observed 41.0% of the time, angled/vertical cling 16.2% and stand only 4.4%. Pithecia was observed perching in 2.7% of samples and standing bipedally in 1.0%.

Vine tangle: The primary locomotor mode used in vine tangles is pronograde clamber (37.1%). The others are used very infrequently: leaping (3.9%) and hopping (1.7%). Sitting postures were assumed in 37.1% of the samples, stand in 10.7%, perch in 4.5% and vertical/angled cling in 1.1%.

Ground: Pithecia was observed on the ground only 26 times during sampling bouts, making the percentages of each positional behavior suspect to sampling error, and therefore may not be representative of their positional repertoire while on the ground. Of these, 26.9% of the samples were quadrupedal walk, 11.5% hop, and 3.9% quadrupedal run.

Stand was observed in 26.9% of these samples, sit in 23.1% and bipedal stand in 7.7%.

Use of Positional Behaviors on Various Supports (Table 6.15)

Positions vary significantly with substrate use.

Behaviors assumed depend on the number of supports, their inclinations and their diameters.

Number of Supports: The most common locomotor behavior observed on a single support is leaping (18.7%). Quadrupedal walk is used in 9.6% of the samples recorded on one support, and quadrupedal run in 2.7%. The other locomotor behaviors used are climb up (1.1%) and continuous bound (1.0%). For postures assumed on a single support, the most common is sit (41.4%), followed by angled/vertical cling (14.2%). Stand is used in 2.7%, perch in 2.4% and ventral lie in 1.9%.

The two locomotor activities observed on dual supports were pronograde clamber (4.9%) and leap (3.5%). The most frequent postural mode is sitting (64.1%). Stand is used in 6.8% of the samples on dual supports, ventral lie in 5.2%, perch in 4.6% and lie on side in 3.5%. Vertical cling was observed 3.4%, bipedal stand 1.1% and lean 1.0% of the time.

The range of locomotor behaviors observed while using several supports at once is relatively small. The locomotor mode most frequently observed is pronograde clamber (35.5%). Leaps were observed in 5.8% of samples, pronograde clamber-

run in 1.2% and hop in 1.0%. Sitting postures are associated with the use of multiple supports 35.0% of the time, standing 9.8% and perch 6.7% of the time. Ventral lie was observed with dual supports 1.4% of the time and lie on side 1.0%.

Inclination of Supports: Five types of locomotor behavior were observed in use on horizontal supports, the most frequent of which were quadrupedal walk (9.7%) and leap (9.3%). Quadrupedal run is used in 3.1% of samples and pronograde clamber in 2.5%. Of the postural behaviors, the most frequently used is sit (57.0%). The other postures are used far less frequently: ventral lie (5.5%), stand (4.6%), lie on side (3.8%) and perch (2.1%).

On angled supports, leap is the most frequently used locomotor behavior (11.9% of samples), followed by quadrupedal walk (9.3%). Quadrupedal run is used in 2.5% of observations, pronograde clamber in 1.6% and climb up in 1.1%. Again, sit is by far the most commonly used postural behavior (51.8%); angled/vertical cling comprised 8.5% of samples. Stand is used in 3.1% of samples, perch in 2.6%, ventral lie in 2.5% and lean in 1.0%.

On vertical supports, Pithecia uses a much wider variety of locomotor than postural modes. Leap comprises almost one-half of samples (41.3%). Climb up was observed 2.4% of the time, climb down 1.8%, continuous bound 1.2%; swing down and shinny down were each used in 1.0% of the

samples. The sole postural behavior observed was vertical cling (47.9%).

Pronograde clamber is the locomotor behavior most often used on deformable supports (30.9%). Leaping was observed in 7.6% of samples, quadrupedal walk in 1.5% and hop and bridge each in 1.0%. Sit (31.6%) is the most common postural behavior, followed by stand (11.0%) and perch (10.4% of samples). Bipedal stand (1.4%) and angled/vertical cling (1.3%) are used relatively rarely.

On supports of mixed inclinations, pronograde clamber is the primary locomotor activity (18.6%). Others are: drop (4.0%), pronograde clamber-run (1.0%) and climb up (1.0%). Sitting was observed in 57.7% of mixed-support positions, stand 7.6% and perch 3.9%. Lie on ventrum and vertical cling were each observed in 1.5% of the samples.

Diameter of Supports: While using the smallest support category (<2 cm in diameter), pronograde clamber is the primary locomotor mode (33.8%). Leap was observed in 4.7% of samples, and quadrupedal walk and bridge each in 1.0%. Postural behaviors are mostly comprised of sit (30.2%), perch (12.8%) and stand (11.0%). Vertical cling was observed 1.9% of the time and bipedal stand 1.1%.

The positional repertoire is more varied on supports 2-5 cm in diameter. Leap was the most frequently observed locomotor mode (13.2%), followed by quadrupedal walk (8.2%). Pronograde clamber was observed in 3.7% of the samples,

quadrupedal run in 1.5% and climb up in 1.2%. Sit is the primary postural behavior (46.5%), followed by angled/vertical cling (10.6%). Stand was observed 4.3% of the time, perch 3.5% and ventral lie 2.1%. Lie on side and bipedal stand are each used in 1.0% of the samples.

While engaged in locomotor activities, the branch size category 6-10 cm is most often used for leaping (20.6%). Quadrupedal walk was observed in 8.0% of samples, and quadrupedal run in 3.4%. Climb up was observed 1.0% of the time. Sit is used in 41.5% of the samples and angled/vertical cling in 12.7%. The three other postural behaviors are: ventral lie (4.0%), stand (2.2%) and lie on side (1.7%).

The support category 11-15 cm is used primarily with leaping behavior (24.8%) as well. Quadrupedal walk is used in 4.9% of samples, quadrupedal run in 2.2% and continuous bound in 1.2% of samples. Sit was observed 42.5% of the time, vertical cling 18.5% and stand 1.2%.

The most common locomotor behavior associated with the largest support category (>15 cm) is also leaping (24.4%). Quadrupedal run was observed in 7.3% of the samples on these supports, quadrupedal walk in 3.7% and drop and sidle down each in 2.4%. The following locomotor modes are each used in 1.2% of the samples: hop, swing down and shinny down. The most common postural behavior is vertical cling (28.1%), followed by sit (18.3%). Stand was used 6.1% of the

observed time and ventral lie 3.7%.

Support size categories are often mixed when multiple supports are used. By far the most common combination of support categories is the use of the two smallest (<2 with 2-5 cm). However, all mixed support combinations are pooled for this comparison. The primary locomotor behavior used on mixed supports is pronograde clamber (21.0%). Other locomotor behaviors were infrequent: leap (3.7%), quadrupedal run (1.1%) and hop (1.0%). Sit was used in 53.0% of samples on mixed supports. Stand is used in 8.1% and perch in 4.4% of samples. The other postural behaviors were: ventral lie (2.6%), lie on side (1.6%) and vertical cling (1.2%).

Chiropotes

Positional Behavior

Feeding (Table 6.5): Chiropotes uses postural behaviors in 77% of the feeding samples, and locomotor behaviors in 19%. Sitting accounts for 51.0% of the time observed in feeding, and standing quadrupedally or tripedally for 12.8%. Perching behavior was observed in 8.3% of the samples, bipedal stand in 3.5% and hindlimb suspension in 1.2%.

The three locomotor behaviors used (pronograde clamber, quadrupedal walk, quadrupedal run and leap) were observed in 11.5%, 5.3%, 1.5% and 1.2% of the samples, respectively.

Travel (Table 6.6): The two most frequently used behaviors in travel are leap (24.5%) and quadrupedal walk (22.9%). Pronograde clamber was observed in 16.7% of travel samples, quadrupedal run in 12.3% and drop from higher to lower support in 7.6%. Pronograde clamber-run is used in 2.6%, climb up in 2.1% and bridge in 2.0% of samples. Hop (1.1%) is one of the most infrequently recorded locomotor behaviors for Chiropotes. The postural behaviors utilized while engaged in travel bouts are stand and sit (3.3 and 2.9%, respectively).

Rest (Table 6.7): Chiropotes uses sitting postures in 56.8% of rest bouts, followed by lie (35.8%). Ventral lie comprises 29.8% of samples and lying on side comprised 6.1%. Standing was observed in 5.0% of samples. During rest bouts, Chiropotes exhibit some brief movement using quadrupedal walk (1.0%).

Play (Table 6.16): Of the locomotor behaviors used in play, the most frequently used is pronograde clamber-run (17.7%). Quadrupedal run (including scamper) is used in 9.3% of play samples, and leaping in 14.3%. Pronograde clamber is used in 4.6%, and hop and drop each in 2.9% of samples. Of the postural behaviors, suspension is the most common (17.1%). Bipedal suspension is that most commonly used, with bimanual or a combination of pedal and manual suspension observed much less frequently. Sitting postures are adopted in 16.6% of play samples, quadrupedal or

tripedal stand in 6.3%, and bipedal stand in 2.3%. The remaining four postural behaviors used in play - dorsal lie, vertical cling and perch- are each used in 1.1% of samples. Ventral lie and lie on side are each used in fewer than 1% of samples.

Tree Portions Used (Table 6.8)

Feeding: As for Pithecia, the terminal branches are most often used for feeding (49.9%), followed by the crown (41.1%). Other portions are used relatively infrequently: lianas (3.1%), below crown (2.6%) and vine tangles (2.5%). The vertical axis is used in 1.0% of feeding samples.

Travel: Chiropotes spends one-half of their travel time in the crown (49.5%), followed by that spent in the terminal branches (34.3%). Other tree portions are used relatively infrequently for travel: below crown (7.9%), lianas (5.6%), vine tangle (1.4%) and vertical axis (1.0%).

Rest: The overwhelming majority of Chiropotes' resting time is spent in the crown (79.5%). The portion below the crown is used in 8.9% of samples, and terminal branches in 8.0%. The vertical axis and lianas were each observed 1.5% of the time.

Play: The crown is the most frequently used tree portion for play (63.8%), followed by the terminal branches (24.7%). Lianas are used in 6.3% of play samples, below crown in 2.3% and vine tangles in 1.7%. The vertical axis

was observed used during play for fewer than 1% of samples.

Tree Portions from which Food is Obtained (Table 6.9)

Chiropotes also finds the majority of its food in the tree crown (68.1%). The crown is used to obtain food in 18.3% of samples, and lianas in 12.0%. Food is obtained in vine tangles in 1.0% of samples, and the portions of vertical axis and below crown each provide less than 1% of Chiropotes' food.

Absolute Height in Tree (Figure 6.18)

The mean height at which Chiropotes is found in the trees was 13.5 meters, and the mean height of the trees in which they were found was 18.0 meters.

Relative Height in Tree (Figure 6.19)

Feeding: The most frequently used height category for Chiropotes while feeding was that which occurs at 80-90% of the tree's height (40.7% of the samples). The tree portion at 70-80% of tree height is used in 30.8% of samples, and that of 60-70% in 12.7% of samples. The uppermost tree portion (90-100% of the tree's height) is used in 10.1% of samples, and that of 50-60% in only 5.0%. Portions below 50% of the tree's height are used in fewer than 1% of feeding samples.

Travel: Chiropotes was most often observed at 70-80%

of the tree's height (32.9%), followed by the 80-90% height portion (30.6%). The relative height portion of 60-70% is used in 20.0% of travel cases, and that of 50-60% in 8.5% of cases. Chiropotes was observed traveling in the uppermost portion (90-100%) in 5.9% of the samples, and the 40-50% portion in 1.7%. Fewer than 1% of samples were recorded for travel below 40% of tree height.

Rest: Chiropotes most often rests at 70-80% of the tree's height (35.9%), followed by the 80-90% portion (32.2%). The portion at 60-70% relative height is used in 20.1% of the resting samples, and that of 50-60% in 6.2%. The uppermost portion (90-100%) is used in 4.8% of samples. (Fewer than 1% of samples were below 50% relative height.)

Play: The two relative height categories which make up the two portions between 80-90% and 70-80% of the tree's height are used the most frequently by playing Chiropotes (44.9% and 35.9%, respectively). The relative height 60-70% is used in 9.0% of samples. The uppermost portion (90-100%) is used 7.1% of the observed time, and that of 50-60% for 1.3% of samples. The portion between 40 and 50% of tree height was observed 1.3% of the time.

Support Use

Feeding (Table 6.10)

Number of Supports: While feeding, Chiropotes most often uses one support (47.0%). Several supports are used

in 32.8% of samples, and two supports in 20.2% of samples.

Inclination of Supports: As for Pithecia, branches that deform under Chiropotes' body weight are from the category most frequently used in feeding (38.1%) Horizontal supports are used in 24.8% of the feeding samples, followed by angled supports (23.8%). A mix of various support inclinations is used in 12.9% of samples, and vertical supports in fewer than 1% of samples.

Diameter of Supports: The most often-used size category used by feeding Chiropotes is 2-5 cm (37.6%). A mix of supports of the two smallest categories (<2 with 2-5 cm) are also often used (20.9%). Branches between 6 and 10 cm are used in 17.1% of samples and those from the smallest category (<2 cm) in 16.3%. Branches 11-15 cm diameter are used in 3.9% of samples, and a combination of branches from size categories other than <2 with 2-5 cm are used in 2.7%. Those larger than 15 cm were observed in use 1.6% of the time.

Travel (Table 6.11)

Number of Supports: Chiropotes also uses single supports most frequently while traveling (60.8%). Several supports were observed in 31.0% of the travel samples, and two supports in 8.1%.

Inclination of Supports: The support inclination most often used by traveling Chiropotes is angled (33.8%), followed closely by deformable branches (31.3%). Horizontal

supports are used in 24.9% of the samples, and a mix of support inclinations is utilized in 8.4%. Vertical supports are used in only 1.7%.

Diameter of Supports: The most frequently used support diameter for traveling Chiropotes is 2-5 cm (28.7%), followed closely by those 6-10 cm (27.8%). Branches less than 2 cm in diameter are used in 15.8% of travel samples; a combination of this smallest size class with that between 2 and 5 cm is used in 12.4%. In 9.9% of samples, Chiropotes was observed using branches with a diameter between 11 and 15 cm, and in 3.4% of samples, those larger than 15 cm. A combination of size classes other than <2 with 2-5 cm is used in 2.0% of samples.

Rest (Table 6.12)

Number of Supports: Chiropotes spends 63.7% of rest time on a single support, and 29.8% on two supports. Several supports are used for rest in only 6.5% of the samples.

Inclination of Supports: Chiropotes most often uses horizontal supports for resting (56.0%), followed by angled (32.9%). Mixed supports are used in 8.5% of samples (two-thirds of these were horizontal with angled). Deformable branches are used in 2.4% of samples.

Diameter of Supports: Chiropotes most frequently uses branches between 6 and 10 cm in diameter while resting (33.0%). The smaller size class of 2-5 cm is used in 20.7%

of samples, and that of 11-15 cm in 18.8%. Supports larger than 15 cm are used in 12.2% of samples. The most common combinations of various support sizes used are: 2-5 with 6-10 cm (7.5%) and <2 with 2-5 cm (3.1%). Other combinations were used in 4.7% of samples.

Play (Table 6.17)

Number of Supports: In play, Chiropotes most often uses a single support (59.8%). Several branches are used at once in 31.4% of samples, and two branches in 8.9%.

Inclination of Supports: Deformable branches are used in 39.0% of play bouts, horizontal supports in 27.9% and angled ones in 24.4%. A mix of branches are used in 7.6% of bouts, and vertical supports in 1.2%.

Diameter of Supports: The branch size most frequently employed by Chiropotes during play is of 2-5 cm in diameter (30.5%). Combinations of the two smallest size classes (<2 with 2-5 cm) are used in 21.0% of samples. The size category 6-10 cm also comprises 22.8% of samples, and that of 11-15 cm, 9.6%. The smallest category (<2 cm) is used in 8.4% of samples. Supports larger than 15 cm in diameter are used 4.8% of the time observed in play. The support combination 2-5 cm with 6-10 cm is used in 3.0% of samples.

Supports Used in Each Tree Portion (Table 6.13)

The supports used by Chiropotes in the vertical axis are overwhelmingly single, but a significant percentage are

used as dual supports. The primary inclination used in this tree portion is angled, with other inclinations used much less frequently. Diameters of the main supports used by Chiropotes in this portion are divided almost evenly between the >15 cm, 6-10 cm and 11-15 cm size classes. Virtually all supports used in the below crown tree portion are single, primarily angled and secondarily horizontal. Support diameters are most frequently 11-15 cm, followed by >15 cm and 6-10 cm. In the main crown, most supports are taken singly, but in a significant number of samples, dual supports are used. Horizontal supports are those most frequently used by Chiropotes in this portion, followed by angled. The 6-10 cm size category, followed by that of 2-5 cm, are those primarily used in the crown. Multiple supports are the most frequently used in the terminal branches, with a single support used less than one-half as often, and dual supports just slightly less than that. Most supports used by Chiropotes in this tree portion are deformable. The size of the supports used in this portion are primarily in the 2-5 cm category, followed closely by both those mixed <2 with 2-5 cm, and the smallest (<2) category alone. Lianas are most frequently taken as single supports, but sometimes as dual supports as well. Inclination of lianas used are primarily angled, deformable or horizontal. Most of them are 2-5 cm; about one-half as frequently they are 6-10 cm. Vine tangles are most often

used as multiple supports of mixed inclination, followed by deformable supports; they usually consisted of a mix of the two smallest size classes, followed by those from the smallest class alone.

Use of Positional Behaviors in Various Tree Portions

(Table 6.19)

Crown: The locomotor behavior most often observed was quadrupedal walk (11.3%), followed by leap (6.9%) and quadrupedal run (6.0%). Pronograde clamber is used in 5.1% of samples, pronograde clamber-run in 1.3% and drop in 1.1%. Sitting is by far the most common posture assumed (42.3%). Ventral lie (11.4%) and stand (6.5%) are the next most frequent; the other behaviors are lie on side (2.0%), bipedal stand (1.8%), perch (1.7%), and suspension (1.0%).

Terminal Branches: In the terminal branches, the primary locomotor mode used is pronograde clamber (18.4%), followed by leap (10.0%). Drop is observed 5.0% of the time, quadrupedal walk in 3.5% and bridging in 1.9%. Pronograde clamber-run is used in 1.7% of the samples and quadrupedal run in 1.0%. The primary postural mode is sit (33.1%), followed by stand (10.9%), then perch (8.0%). Bipedal stand is used in 1.9%, suspension in 1.8% and ventral lie in 1.3% of the samples.

Below Crown: The two locomotor behaviors most frequently used below the crown are quadrupedal walk and

quadrupedal run, which comprise 18.7% and 12.4% of samples, respectively. Leaping is used in 7.8% of samples, drop in 1.2% and pronograde clamber 1.0%. Sitting is observed 31.4% of the time, ventral lie 12.7% and stand 5.2%. Lie on side is used in 6.1% of the samples, and angled/vertical cling was observed 1.0% of the time.

Vertical Axis: The vertical axis is used relatively infrequently as well (65 observations). While using this tree portion, the locomotor behaviors most commonly used are climb up and quadrupedal walk (each used in 7.7% of samples) and leap (6.2%). Both quadrupedal run and drop were observed in 3.1% of samples. Bridging is used in 1.5% of samples. The postural behavior most frequently used in the vertical axis is sit (40.0%), followed by stand (18.5%). Ventral lie and lean were each observed 4.6% of the time, and angled/vertical cling in 1.5% of samples.

Bole: Chiropotes uses the bole to such an infrequent degree (six observations), that those cases are not included in this analysis.

Liana: On lianas, the most frequent locomotor category used is quadrupedal walk (18.4%). Pronograde clamber is the second most frequent (7.8%), followed by climb up (6.9%). Quadrupedal run was observed 5.5% of the time; leap and climb down each 4.6%. Sitting is used in 28.6% of the samples, stand in 6.9% and angled/vertical cling in 3.7%. Suspension was observed 2.8% of the time, perch 2.3% and

bipedal stand 1.8%.

Vine Tangle: Vine tangles are used relatively infrequently by Chiropotes; the most common locomotor activity while in this portion is pronograde clamber (36.5%). Pronograde clamber-run was observed 2.8% of the time, and quadrupedal walk and leap each 1.9% of the time. Climb down and hop were each sampled 1.0% of the time in vine tangles. Sit was observed 32.7% of the time spent in vine tangles, followed by stand (11.2%). Perch is used in 5.6% of samples, suspension in 2.8%, and bipedal stand in 1.9% and ventral lie in 1.0%.

Ground: Chiropotes was observed on the ground in only one isolated incident, under a set of unusual circumstances. An infant gave several shrill vocalizations, immediately followed by a state of general excitement for much of the group. Several group members also vocalized, and appeared to chase an individual (a small adult female or subadult female or male). As this individual fled, it descended lower and lower in the canopy, moving toward me without seeing me. It leapt down to a bole, landing in a vertical cling position, then leapt two times in quick succession (landing between the leaps on another bole in a vertical cling position), with its final landing substrate being the ground. It quadrupedally ran for a few strides, then leapt up to a bole, where it leapt a second time from a vertical cling position, and continued moving rapidly, using bounding

interspersed with quadrupedally running.

Use of Positional Behaviors on Various Supports (Table 6.20)

Number of Supports: Chiropotes traveling on a single support were most often observed to quadrupedally walk (16.6%). Leaping was observed in 8.6% of samples, and quadrupedal run in 8.1%. Drops were observed in 1.5% of samples and climb up in 1.0%. Sitting was by far the most frequent postural behavior observed (40.9%). Ventral lie was observed in 7.7% of samples, standing in 5.8%, and perch in 3.4%. Bipedal stand is used in 2.1% of samples, suspension in 1.3% and lie on side 1.1%.

While using dual supports, pronograde clamber is the primary locomotor category (7.0%). Other locomotor categories are: leaping (2.3%), climb up (1.2%), pronograde clamber-run (1.1%) and drop (1.0%). The most-used postural category is sit (48.5%), followed by ventral lie (13.4%). Stand is used in 11.2% of samples, lie on side in 4.5%, perch in 4.2% and bipedal stand in 1.9%. Suspension was observed 1.5% of the time on dual supports.

Pronograde clamber is also the most frequently used locomotor behavior used on several supports (33.4%), followed by leaping (9.6%). Drop was used 5.5% of observed time and pronograde clamber-run 4.5%. Bridging was observed in 1.9% of samples. Sit was used in 23.7% of observations on several supports, with stand used 10.8% of the time. In

4.6% of the samples, perch was recorded. Ventral lie was recorded in 2.7% of samples and suspension in 1.0%.

Inclination of Supports: Chiropotes, while on horizontal supports, uses quadrupedal walk as the primary locomotor activity (10.9%). Leap is sampled 5.9% of the time, quadrupedal run 4.5%, pronograde clamber 2.1% and drop 1.0%. Sit was the most often-observed postural behavior on a horizontal support (45.0%). Ventral lie is sampled 15.0% of the time, stand 6.4% and perch 2.4%. Lie on side is used in 2.4% of samples, bipedal stand in 2.0% and suspension in 1.0%.

On angled supports, the primary locomotor mode is quadrupedal walk (16.8%), followed first by quadrupedal run (9.7%), then by leaping (7.9%). Pronograde clamber is used in 1.5% of samples, drop in 1.2% and hop in 1.0%. Sit was observed in 41.8% of samples on angled supports, stand in 6.4% and ventral lie in 6.0%. Lie on side was recorded in 2.3% of samples, perch in 2.0% and bipedal stand in 1.1%.

Vertical supports were only observed used by Chiropotes 50 times. Of these, the locomotor behaviors recorded are as follows: climb up (36.0%), climb down (12.0%), leap (10.0%), quadrupedal run, pronograde clamber and shinny up (each 4.0%). Angled/vertical cling is the most common postural behavior (10.0%), followed by sit (8.0%), stand and bipedal stand (each 2.0%).

While using supports which deform under Chiropotes'

body weight, pronograde clamber is the locomotor behavior most frequently used (22.1%). Leaping is used in 11.3% of the samples, dropping in 6.3% and pronograde clamber-run in 2.9%. Quadrupedal walk was recorded 2.8% of the time and bridge 2.3%. Of the postural modes, sit is assumed in 26.4% of samples, stand in 10.3% and perch in 8.2%. Suspension comprises 2.9% and bipedal stand 1.8% of samples.

While using a combination of supports of various angles, pronograde clamber (41.9%) is the primary locomotor behavior, followed by pronograde clamber-run (9.1%), then leap (5.4%). Sit was recorded for 23.7% of the samples on supports of mixed inclinations, stand for 14.0%, perch for 2.2% and ventral lie 1.1%.

Diameter of Supports: While using the smallest support category (<2 cm), Chiropotes were most often observed in pronograde clamber as the primary locomotor mode (25.9%), followed by leaping (12.4%). Drops comprise 7.9% of the samples, bridge 3.6%, pronograde clamber-run 1.5% and quadrupedal walk 1.0%. For the postural behaviors, sit was observed 21.5% of the time, stand 9.4% and perch 9.4%. Suspension was recorded in 3.1% of samples and bipedal stand in 1.7%.

While using the support size category 2-5 cm, the most frequently observed locomotor behavior was quadrupedal walk (9.5%), followed by leap (9.0%) and pronograde clamber (7.0%). Quadrupedal run was observed in 3.1% of samples,

drop in 1.7%, pronograde clamber-run in 1.4% and climb up in 1.2%. While engaged in postural behaviors, the most frequent is sitting (40.3% of samples). The second-most frequently used postural behavior is stand (8.4%), followed by perch (5.7%). Ventral lie, bipedal stand and suspension are used in 5.2%, 2.8% and 1.6% of samples, respectively.

The most frequently used locomotor behavior for the 6-10 cm category is quadrupedal walk (16.6%), followed by quadrupedal run (9.8%). Leaping is used in 7.8% of samples and drop in 1.0%. Once again, the primary postural category is sit (41.7%). Ventral lie comprises 10.4% of samples, stand 5.8%, bipedal stand and lie on side each 1.3% and perch 1.1%.

The locomotor category associated the most frequently with the support size class of 11-15 cm is quadrupedal walk (15.9% of samples). Quadrupedal run is used in 9.3% of samples, leap in 5.7% and drop in 1.0%. Sit (42.0%) is the most frequently used posture on these large supports, followed by ventral lie (14.4%). Stand was observed in 4.7% of samples and lie on side in 3.8%.

The largest size category (>15 cm), used more by Chiropotes than Pithecia, is most frequently associated with the locomotor behavior of quadrupedal walk (12.2%). Quadrupedal run was observed in 5.7% of these samples and leap in 2.7%. Sit (47.3%) is the most common posture, followed by ventral lie (17.1%) and stand (7.4%). Lie on

side was observed in 2.4% of samples.

The most frequent locomotor behavior used on mixed supports was pronograde clamber (24.3%). Other behaviors were infrequent: leap (4.6%), pronograde clamber-run (3.9%), drop (2.8%), climb up and climb down (each 1.0%). Sit was the most common postural behavior (35.1%), followed by stand (11.9%). Other behaviors were: ventral lie (5.9%), perch (3.8%), lie on side (2.1%), bipedal stand (1.5%) and suspension (1.0%).

Cacajao

Positional Behavior

Feeding (Table 6.5): The primary posture used by feeding Cacajao is sit (40.6% of samples), followed by stand (9.7%). Perch was observed 4.2%, bipedal suspension 3.1% and bipedal stand 1.4% of the time. A vertical cling is used in 1.0% of the samples, and the remaining postural behaviors (lean and suspension from a combination of hands and feet) are each used in fewer than 1% of samples. While travel-feeding, Cacajao most frequently uses pronograde clambering (19.1% of samples), followed by quadrupedal walk (11.8%). Leap was observed in 3.1%, drop in 2.1% and quadrupedal run in 1.0% of feeding samples. The remaining behaviors are: quadrupedal run, climb up, climb down and hop. These were each observed less than 1% of the time.

Travel (Table 6.6): The three most frequently used

behaviors in travel are quadrupedal walk (22.2%), leap (21.3%) and pronograde clamber 20.5%. Quadrupedal run was observed in 11.7% of travel samples and drop from higher to lower support in 9.6%. Pronograde clamber-run and climb up are each used in 2.5%, and bridge in 1.0% of samples. Hop (at less than 1%) is one of the most infrequently recorded locomotor behaviors for Cacajao. The postural behaviors utilized while engaged in travel bouts are sit (4.2%), stand (2.5%) and bipedal suspension (1.3%).

Rest (Table 6.7): Cacajao uses sitting postures in 58.9% of rest bouts, followed by ventral lie (28.1%). Stand comprises 3.4% of samples. Several behaviors each represent 1.4% of samples: dorsal lie, lie on side, vertical cling and bipedal suspension. During rest bouts, Cacajao exhibits some brief movement using quadrupedal walk (2.1%). Other movements that were observed, but recorded in fewer than 1% of samples, were: pronograde clamber, drop and bridge.

Absolute Height in Tree (Figure 6.18)

The mean height at which Cacajao is found in the trees was 16.2 meters. The height of the trees used is unknown; however, Cacajao tends to use the taller trees in the Teiú forest, which are between 25 and 35 meters (Ayres, 1986).

Support Use

Feeding (Table 6.10)

Number of Supports: While feeding, Cacajao most often uses several supports (47.0%). A single support is used in 41.8% of samples, and two supports in 11.2% of samples.

Inclination of Supports: Branches that deform under Cacajao' body weight are the most frequently used in feeding (41.5%) Horizontal supports are used in 35.4% of the feeding samples, followed by angled supports (15.0%). A mix of various support inclinations are used in 6.1% of samples, and vertical supports in 2.0% of samples.

Travel (Table 6.11)

Number of Supports: Cacajao uses single supports most frequently while traveling (58.5%). Several supports were observed in 35.8% of the travel samples, and two supports in 5.7%.

Inclination of Supports: Traveling Cacajao most often uses deformable supports (35.5%). The most common definable inclination is horizontal (31.8%), followed by angled branches (24.8%). A mix of support inclinations is utilized in 5.1% of samples, and vertical supports are used in 2.8%.

Rest (Table 6.12)

Number of Supports: Cacajao spends 61.6% of rest time on a single support, and 24.7% on two supports. Several supports are used for rest in 13.7% of the samples.

Inclination of Supports: Cacajao most often uses

horizontal supports for resting (60.4%), followed by angled (28.5%). Deformable branches are used in 8.3% of samples. Vertical supports as well as a combination of support inclinations are each used in 1.4%.

Use of Positional Behaviors on Various Supports (Table 6.21)

Number of Supports: Cacajao traveling on a single support were most often observed to quadrupedally walk (25.1%). Leaping was observed in 9.5% of samples, and quadrupedal run in 9.0%. Climb up was observed in 2.3% of samples and drops in 2.0%. Sitting was by far the most frequent postural behavior observed (33.5%). Ventral lie was observed in 5.2% of samples and standing in 3.8%. Suspension is used in 1.7% of samples, vertical cling in 1.2% and bipedal stand in 1.0%.

While using dual supports, pronograde clamber is the primary locomotor category (7.4%). Other locomotor categories are: leaping (3.7%), pronograde clamber-run (2.5%) and drop (1.2%). The most-used postural category was sit (50.6%), followed by ventral lie (14.8%). Stand is used in 7.4% of samples and suspension in 4.7%. Lie on side and perch are each observed in each in 3.7%, and lean in 1.2% of the time on dual supports.

Pronograde clamber is also the most frequently used locomotor behavior used on several supports (34.7%), followed by leaping (10.5%). Drop was used 9.3% of observed

time and pronograde clamber-run 4.0%. Bridging was observed in 1.2% of samples. Sit was used in 21.8% of observations on several supports, with stand used 7.7% of the time. Ventral lie was recorded in 4.4% of samples. Perching was recorded in 2.8% of the samples, suspension in 2.0% and bipedal stand in 1.0%.

Inclination of Supports: Cacajao, while on horizontal supports, uses quadrupedal walk as the primary locomotor activity (19.6%). Quadrupedal run was sampled 6.3% of the time, and leap and pronograde clamber each 5.8%. Drop was observed in 1.7% of samples and pronograde clamber-run in 1.3%. Sit was the most often-observed postural behavior on a horizontal support (40.0%). Ventral lie is sampled 10.0% of the time, stand 3.3%, suspension 2.1% and bipedal stand 1.3%. Lie on side is used in 1.0% of samples.

On angled supports, the primary locomotor mode is quadrupedal walk (24.1%), followed first by quadrupedal run (10.5%), then by leaping (9.0%). Pronograde clamber is used in 2.3% of samples and drop in 1.5%. Sit was observed in 33.1% of samples on angled supports, ventral lie in 9.0% and stand in 6.8%. Lie on side was recorded in 1.5% of samples.

Vertical supports were observed only thirteen times in use by Cacajao, and are therefore not included in this analysis.

While using supports which deformed under Cacajao's body weight, pronograde clamber is the locomotor behavior

most frequently used (30.7%). Leaping is used in 9.8% of the samples, dropping in 8.3% and pronograde clamber-run in 4.4%. Quadrupedal walk was recorded 2.4% of the time and bridge 1.5%. Of the postural modes, sit is assumed in 22.9% of samples, stand in 8.3%, perch in 3.9%, and suspension in 3.4%. Ventral lie comprises 2.4% of samples and bipedal stand 1.0%.

While using a combination of supports of various angles, pronograde clamber (31.0%) is the primary locomotor behavior, followed by both pronograde clamber-run and leap (each 6.9%). Sit was recorded for 37.9% of the samples on supports of mixed inclinations, stand for 13.8% and suspension for 3.5%.

C. Interspecific Comparisons of Positional Behavior and Habitat Use

Positional Behavior

Feeding (Table 6.5): Positional behaviors used during feeding differ greatly between all combinations of species pairs (Pithecia/Chiropotes: $\chi^2 = 388.67$, $df = 11$, $P < 0.001$; Pithecia/Cacajao: $\chi^2 = 300.89$, $df = 12$, $P < 0.001$; Chiropotes/Cacajao: $\chi^2 = 118.82$, $df = 11$, $P < 0.001$). One of the most apparent differences is Cacajao's more frequent use of locomotor behaviors than the other two species while feeding. Pronograde clamber is used almost twice as frequently by Cacajao as by Pithecia or by Chiropotes,

although for Pithecia, pronograde clamber is virtually the only locomotor behavior used. Quadrupedal walk was also sampled much more for Cacajao than for either Pithecia or for Chiropotes. The most notable difference in terms of postural behaviors is Pithecia's frequent use of vertical cling while feeding, which was not sampled at all for Chiropotes, and seldom for Cacajao. Perch is more frequent for both Pithecia and Chiropotes than for Cacajao. Bipedal stand was sampled more for Chiropotes than for either Pithecia or Cacajao. Pedal suspension, not sampled for Pithecia, was observed occasionally in Chiropotes' feeding samples, and more often in Cacajao's.

Travel (Table 6.6): Differences in locomotor behavior during travel are most apparent between Pithecia and the other two species (Pithecia/Chiropotes: $\chi^2 = 553.01$, $df = 18$, $P < 0.001$; Pithecia/Cacajao: $\chi^2 = 216.00$, $df = 14$, $P < 0.001$). Differences between Chiropotes and Cacajao during travel are not significant. Leaping contributes considerably to the overall difference in locomotor behavior; Pithecia leaps in over one-third of samples, while Chiropotes and Cacajao do so less frequently. Quadrupedal walk was observed less often for Pithecia than for Chiropotes and Cacajao. Quadrupedal run is exhibited much less by Pithecia than by Chiropotes and Cacajao. Continuous bound was sometimes observed in Pithecia's travel samples, but was not recorded for either Chiropotes or Cacajao. The

use of dropping is rare in Pithecia, while it played an important role in the locomotor repertoire of Chiropotes and Cacajao. Pronograde clamber-run was less frequently observed for Pithecia than for Chiropotes or Cacajao. Bridge, not sampled for Pithecia, was sometimes recorded for Chiropotes and for Cacajao.

Pithecia sat more than did Chiropotes or Cacajao, and engaged in vertical clinging while in momentary pauses of travel bouts, which was not recorded for Chiropotes nor Cacajao. Pedal suspension while in travel bouts was observed for Cacajao alone.

Rest (Table 6.7): Great differences between the three species in positional behavior during resting bouts are apparent (Pithecia/Chiropotes: $\chi^2 = 359.40$, $df = 7$, $P < 0.001$; Pithecia/Cacajao: $\chi^2 = 170.51$, $df = 9$, $P < 0.001$; Chiropotes/Cacajao: $\chi^2 = 44.1$, $df = 8$, $P < 0.001$). Pithecia does not exhibit locomotor behaviors during resting bouts, while Chiropotes and Cacajao do. Pithecia engages in sitting behavior more and lying behavior less than do the other two species. Vertical cling is used virtually only by Pithecia; it was not sampled for Chiropotes, and very rarely for Cacajao. Again, pedal suspension was observed only in Cacajao. Lean was observed only for Pithecia.

Tree Portions Used (Table 6.8)

Feeding: Data on use of tree portions were not

collected for Cacajao; Pithecia and Chiropotes exhibit significant differences in tree portion use while feeding ($\chi^2 = 415.30$, $df = 7$, $P < 0.001$). Chiropotes feeds more frequently in the main crown than does Pithecia, while terminal branch use is almost equal. Pithecia was sampled in the three lower tree portions more often than Chiropotes. Pithecia was sampled more on lianas than was Chiropotes, and sometimes uses the ground to feed from, which was not observed for Chiropotes.

Travel: Pithecia and Chiropotes exhibit significant differences in use of tree portions while traveling ($\chi^2 = 553.01$, $df = 6$, $P < 0.001$). Chiropotes uses both the main crown and terminal branches more than does Pithecia. The lower tree portions were recorded more often for Pithecia than for Chiropotes. Pithecia uses both lianas and vine tangles somewhat more than does Chiropotes.

Rest: Resting tree portions also differ between the two species ($\chi^2 = 350.39$, $df = 6$, $P < 0.001$). Chiropotes uses the main crown and terminal branches more than does Pithecia. Pithecia uses the vertical axis, below crown and bole more than does Chiropotes. Lianas are used for resting by Pithecia much more than by Chiropotes. Pithecia sometimes rests in vine tangles; this was not recorded for Chiropotes.

Absolute Height (Figure 6.18): Over all activities, Pithecia is consistently observed at a much lower from the ground than either Chiropotes or Cacajao. The mean height at which Pithecia was observed is 6.8 m, while for Chiropotes it is 13.5 m and for Cacajao 16.2 m.

Relative Height (Figure 6.19)

Feed: Overall differences between the species in relative height while feeding are significant ($\chi^2 = 90.71$, $df = 6$, $P < 0.001$). Pithecia uses the uppermost relative tree height (90-100% of tree height) slightly more frequently than does Chiropotes. The two following tree relative tree heights are used slightly more by Chiropotes than by Pithecia. Pithecia was observed in the remaining relative heights, from 70% of tree height to less than 40%, somewhat more than was Chiropotes.

Travel: Relative heights in the trees differ between species during travel as well ($\chi^2 = 84.95$, $df = 6$, $P < 0.001$). Chiropotes is consistently found in one of the three highest tree portions, those comprising the uppermost 70% of the tree, more frequently than is Pithecia. The lower four portions (below 70%) are used more by Pithecia.

Rest: The two Pithecia groups also differ in relative tree heights while resting ($\chi^2 = 72.29$, $df = 6$, $P < 0.001$). The uppermost portion at 90-100% of tree height is used in more Pithecia samples than those of Chiropotes. The

portions 80-90% and 70-80% are both used somewhat more frequently by Chiropotes. Portions below 60% of tree height are used over twice as much by Pithecia.

Support Use

Feeding (Table 6.10): Differences in the number of supports used by the three species are significant between Pithecia and Chiropotes ($\chi^2 = 37.60$, $df = 2$, $P < 0.001$) and between Chiropotes and Cacajao ($\chi^2 = 26.42$, $df = 2$, $P < 0.001$). Pithecia and Chiropotes use a single support for feeding in almost one-half of samples, while Cacajao uses one support slightly less often. Chiropotes uses dual supports more frequently than do either Pithecia or Cacajao. Several supports are used most by Cacajao, followed by Pithecia, and least by Chiropotes.

Differences in the inclination of supports used while feeding is significant for all pairs of species (Pithecia/Chiropotes: $\chi^2 = 253.31$, $df = 4$, $P < 0.001$; Pithecia/Cacajao: $\chi^2 = 85.14$, $df = 4$, $P < 0.001$; Chiropotes/Cacajao: $\chi^2 = 33.37$, $df = 4$, $P < 0.001$). Pithecia uses horizontal supports less than does Chiropotes or Cacajao. Both angled and vertical supports are used more by Pithecia than by either Chiropotes or Cacajao. Deformable branches are used least by Pithecia and most by Cacajao. Supports of mixed inclinations are used most by Pithecia, followed closely by Chiropotes, and least by Cacajao.

Support diameter was recorded for Pithecia and Chiropotes only, and significant differences are exhibited ($\chi^2 = 82.86$, $df = 6$, $P < 0.001$). Pithecia were observed on the smallest supports (<2 cm) in about one-fifth of samples; for Chiropotes, this figure was somewhat less. Supports in the class 2 - 5 cm are used equally by the two species, and those of 6 - 10 cm diameter are used more frequently by Chiropotes than by Pithecia. Supports of 11 - 15 cm and those larger than 15 cm are used more by Chiropotes than by Pithecia, and supports of mixed diameters are used virtually equally by the two species.

Travel (Table 6.11): Differences in the number of supports used while traveling are significant between Pithecia and each of the other species; those between Chiropotes and Cacajao are not significant (Pithecia/Chiropotes: $\chi^2 = 63.58$, $df = 2$, $P < 0.001$; Pithecia/Cacajao: $\chi^2 = 26.23$, $df = 2$, $P < 0.001$). Pithecia uses a single support more frequently than does either Chiropotes or Cacajao. Dual supports are used approximately equally by Pithecia and Chiropotes, and somewhat less frequently by Cacajao. Pithecia uses several supports for travel less often than does Chiropotes or Cacajao.

The inclination of supports used in travel differ among all of the species (Pithecia/Chiropotes: $\chi^2 = 399.51$, $df = 4$, $P < 0.001$; Pithecia/Cacajao: $\chi^2 = 94.14$, $df = 4$, $P < 0.001$; Chiropotes/Cacajao: $\chi^2 = 13.29$, $df = 4$, $P = 0.01$). Pithecia

uses horizontal supports less frequently than does Chiropotes or Cacajao. Angled supports are used to approximately the same degree by Pithecia and Chiropotes, and less often by Cacajao. Pithecia were sampled on vertical supports one-fifth of the time in travel, while Chiropotes and Cacajao were rarely sampled on this support type. Deformable supports are used much less frequently by Pithecia than by either Chiropotes or Cacajao. Supports of mixed inclinations are used equally by Pithecia and Chiropotes, and less by Cacajao.

The diameter of supports used by Pithecia and Chiropotes differs significantly ($\chi^2 = 147.50$, $df = 6$, $P < 0.001$). Chiropotes uses supports with a diameter of less than 2 cm in more samples than does Pithecia. Supports between 2 and 5 cm in diameter are used more frequently by Pithecia than by Chiropotes. Those of 6 - 10 cm are used almost equally, and those of a diameter between 11 and 15 cm are used more by Chiropotes than by Pithecia. The largest size class (>15 cm) is used more by Chiropotes than by Pithecia, and supports of mixed diameters are used somewhat less frequently by Pithecia than by Chiropotes.

Rest (Table 6.12): Differences in the number of supports used while resting are significant between Pithecia and Cacajao and between Chiropotes and Cacajao, but not between Pithecia and Chiropotes (Pithecia/Cacajao: $\chi^2 = 9.88$, $df = 2$, $p < 0.005$; Chiropotes/Cacajao: $\chi^2 = 22.08$, $df =$

2, $P < 0.001$). The use of a single support differs little among the species; use of dual supports while resting is most frequent for Pithecia, followed closely by Chiropotes, and is least frequent for Cacajao. The use of several supports is less frequent for Pithecia and Chiropotes than for Cacajao.

The use of variously inclined supports is significant between all pairs of species (Pithecia/Chiropotes: $\chi^2 = 203.06$, $df = 5$, $P < 0.001$; Pithecia/Cacajao: $\chi^2 = 85.05$, $df = 5$, $P < 0.001$; Chiropotes/Cacajao: $\chi^2 = 22.52$). Pithecia uses horizontal supports less often than does Chiropotes or Cacajao. Angled supports are used more by Pithecia than by either Chiropotes or Cacajao. Vertical supports are used almost solely by Pithecia; not at all by Chiropotes, and in few Cacajao samples. Deformable supports are used least by Pithecia while resting, slightly more by Chiropotes, and considerably more by Cacajao. Supports of mixed inclinations are used much more frequently by Pithecia than by Chiropotes or by Cacajao.

Differences between use of supports of various diameters is significant between Pithecia and Chiropotes ($\chi^2 = 410.94$, $df = 7$, $P < 0.001$). The smallest size (<2 cm) is used infrequently by Pithecia and not at all by Chiropotes. The size class 2 - 5 cm is used over twice as much by Pithecia as by Chiropotes. Supports of 6 - 10 cm are used almost equally, and those between 11 and 15 cm are used more

by Chiropotes than by Pithecia. The largest size class (>15 cm) was sampled only for Chiropotes. Total use of mixed supports is somewhat greater for Pithecia than for Chiropotes.

D. Qualitative and Quantitative Differences in Leaping Behavior Among Pitheciin Species

Leaping behavior deserves close analysis for three main reasons: 1) It may play an important role in the avoidance of predators, as evidenced by its more frequent use in unhabituated individuals (pers. obs.). Thus, leaping may be a selective "critical" behavior (Prost, 1965), most likely to be used when necessary for survival.

2) Of all locomotor behaviors, it is the one which qualitatively differs the most among the pitheciin species.

3) Anatomical features would be expected to be functionally correlated with behavioral differences, since body orientation and support use influence the distribution of forces exerted on and by the body.

As previously mentioned, important qualitative differences are noted between Pithecia and the other two pitheciin genera in the form of their leaping behavior. Since considerably more quantitative data were collected on Pithecia and Chiropotes than on Cacajao, only features of Pithecia and Chiropotes leaping will be considered here. However, Cacajao is assumed to be much more similar to

Chiropotes (Fleagle and Meldrum, 1988; pers. obs.).

While several authors (e.g. Fleagle and Mittermeier, 1980) have defined Pithecia as a leaper, and Chiropotes primarily as a quadruped, leaping plays a significant role in the locomotor repertoire of both species. As demonstrated in the previous section and in Table 6.2, leaping was the locomotor behavior recorded in 40% of Pithecia's travel samples; for Chiropotes, this figure was 25%. However, the form that the behavior takes, as well as the supports and tree portions used for take-off and landing, differ greatly between the two species.

The various kinds of leaps are determined primarily by the take-off position used (which is partially determined by the take-off support) and the speed of progression at take-off. Quantitative data are presented for each species in terms of positional behavior, tree portions and supports used in both the take-off and landing phases of leaps. Qualitative differences are presented for the species in terms of body orientation, leap distance and the amount of vertical displacement exhibited during the midflight phase.

The above-mentioned quantitative and qualitative data are presented only for the leaps between trees, which were much more frequent than those within trees. Leaps for which take-off and landing occurred in the same tree were exhibited more by Chiropotes (31.7%) than by Pithecia (14.3%). For both species, within-tree leaps overwhelmingly

(approximately 82% of the time) commenced and terminated in the tree crown. These leaps tended to be shorter than those between trees.

Quantitative and Qualitative Results

Positional Behavior

Take-off position (Table 6.22): Leap take-offs occur from a variety of locomotor and postural positions, which differ greatly between the species ($\chi^2 = 340.04$, $df = 6$, $P < 0.001$). While Pithecia more frequently takes off from a stationary posture (63.2%), Chiropotes usually takes off while moving (76.2%). Pronograde clambering is used less than one-half as frequently by Pithecia as by Chiropotes (12.9% compared to 33.1%). Pithecia also uses quadrupedal walk (14.1%) and quadrupedal run (8.3%) less often as take-off positions than does Chiropotes (23.1% and 18.3%, respectively). Pronograde clamber-run was observed in fewer than 1% of Pithecia take-offs, and in 1.7% of those of Chiropotes. Climb was observed in 1.0% of Pithecia take-offs, but not sampled for Chiropotes. Pithecia takes off from a vertical cling posture in 51.3% of the samples; this behavior was recorded in fewer than 1% of Chiropotes' samples. Pithecia uses stand as a take-off position in 11.9% of samples; for Chiropotes this figure is 22.9%.

Landing positions: Landing positions are much less variable than take-off positions, and depend on the

orientation of the body during the leap, which for Pithecia is often vertical, and for Chiropotes is usually horizontal. Landing also depends on the leap distance. Pithecia typically lands with the feet striking the support first, and the hands shortly thereafter. This is particularly apparent in longer leaps, in which the longer hindlimbs flex upon contact, absorbing the compressive forces of landing. For shorter leaps, all four limbs may strike at the same time or the forelimbs may contact slightly before the hindlimbs. For Chiropotes, all four limbs typically encounter the substrate at the same time, unless the leap was very short, in which case the forelimbs may strike first. The degree of limb abduction (especially hindlimb) at landing depends upon support type (e.g. greater abduction for landing upon many flexible branches).

Tree Portions (Table 6.23; tree portions see Figure 4.2)

Take-off: Tree portions used for take-off also differ greatly between the two species ($\chi^2 = 338.82$, $df = 5$, $P < 0.001$), primarily in terms of use of the terminal branches and of the lower tree portions (bole, vertical axis, below crown). Terminal branches are used in only 10.0% of the samples for Pithecia, while they are an important take-off portion for Chiropotes (44.6%). The crown is used in 33.2% of Pithecia leap samples, and 46.1% of those of Chiropotes. The below crown portion is used as a take-off point for

Pithecia in 10.7% of samples, and 5.6% for Chiropotes.

Pithecia uses the vertical axis in 10.1% of samples and the bole in 30.6%; Chiropotes uses each of these in fewer than 1% of samples. Pithecia uses lianas somewhat more frequently for take-off than does Chiropotes (5.4% compared to 2.5%).

Landing: Landing tree portions are also significantly different between the two species ($\chi^2 = 333.40$, $df = 5$, $P < 0.001$). Pithecia lands in the terminal branches 20.6% of the observed time, while Chiropotes uses this portion by far the most of any (88.1%). Pithecia uses the crown for landings in 16.1% of the samples; Chiropotes uses it in only 5.7% of samples. The below crown portion is used for 11.3% of Pithecia's leaps and 3.1% of those of Chiropotes. Pithecia uses the vertical axis for landing in 11.6% of samples, and Chiropotes not at all. The landing tree portion used most frequently by Pithecia is the bole (35.1%), while Chiropotes lands in this portion fewer than 1% of recorded leaps. Lianas are used in only 5.4% of Pithecia and 2.6% of Chiropotes landings.

Number of Supports (Table 6.24)

Take-off: Significant differences are observed in the number of take-off supports used ($\chi^2 = 108.55$, $df = 2$, $P < 0.001$). Pithecia takes off from a single support in the great majority of leaps (85.0%), as does Chiropotes (60.7%).

Dual supports are used in only 4.1% of Pithecia's take-offs, and 4.7% of Chiropotes'. Several supports were used 10.8% of the observed time for Pithecia leap take-offs, and 34.6% of those of Chiropotes.

Landing: The number of supports used in landing differs substantially between the species as well ($\chi^2 = 235.27$, $df = 2$, $P < 0.001$). Pithecia landings are also performed primarily on a single support (84.3%), while fewer than one-half (41.3%) of Chiropotes' leaps end on a single support. Dual supports are seldom used in landing for either species (1.7% for Pithecia and 2.5% for Chiropotes). Several supports are used in only 14.0% of Pithecia landings, but in 56.3% of Chiropotes landings.

Inclination of Supports (Table 6.25)

Take-off: Differences were observed between Pithecia and Chiropotes in the frequencies of use of supports of various inclinations in leap take-off ($\chi^2 = 329.03$, $df = 4$, $P < 0.001$). Horizontal supports are used less often by Pithecia (13.1%) at take-off than by Chiropotes (24.5%). Angled supports are used almost equally by the two species in take-off; Pithecia uses them in 26.2% of the samples, Chiropotes in 29.2%. One of the most notable difference in support inclination for leap take-off is in Pithecia's frequent use of vertical or near vertical supports (45.9% of the samples); Chiropotes uses them in only 1% of samples.

Deformable supports are used for take-off to a much lesser degree by Pithecia (10.7%) than by Chiropotes (41.2%). Supports of mixed inclinations are used to the same degree in leap take-offs by the two species (4.2%).

Landing: Inclination of landing supports differs between the species as well ($\chi^2 = 287.49$, $df = 4$, $P < 0.001$). Horizontal supports are used less by Pithecia in landing than by Chiropotes (8.2% as compared to 14.2%). Angled supports are used more frequently by Pithecia (28.7%) than by Chiropotes (19.9%). Pithecia most often lands on vertical supports (41.4% of samples), while Chiropotes does so very infrequently (2.5%). Deformable supports are used for landing in only 19.9% of the Pithecia samples, but for 62.4% of the Chiropotes samples. Supports of mixed inclinations are infrequently used for landings by either species (1.7% for Pithecia and 1.1% for Chiropotes).

Diameter of Supports (Table 6.26)

Take-off: Differences between the species in the diameter of supports used in take-off are notable ($\chi^2 = 126.24$, $df = 6$, $P < 0.001$). Pithecia uses the smallest branch size as a take-off support in relatively few samples (4.1%), while Chiropotes uses this support category for 20.2% of leap take-offs. Both species use the second support size (2-5 cm) approximately equally in leap take-off: 41.2% for Pithecia and 33.9% for Chiropotes. Support sizes from 6 to

10 cm in diameter are used more frequently by Pithecia (38.0%) in take-off than by Chiropotes (25.1%), and supports of the size class 11-15 cm are used somewhat more often by Pithecia (10.3%) than by Chiropotes (6.9%). The largest size class (larger than 15 cm) is used infrequently both species (1.9% for Pithecia and 1.5% for Chiropotes). A mix of the two smallest size classes are used less frequently by Pithecia (3.7%) than by Chiropotes (11.1%). Mixed supports of other diameters are relatively infrequent (1.0% for Pithecia and 1.5% for Chiropotes).

Landing: The two species also use various support sizes to different degrees while landing after leaps ($\chi^2 = 222.97$, $df = 5$, $P < 0.001$). The smallest support class is used much less frequently for Pithecia landings (10.7%) than for those of Chiropotes (42.4%). Supports between 2 and 5 cm are those most frequently used by Pithecia when landing (41.3%), while Chiropotes uses this size about half as frequently (17.5%). Pithecia landings occur on supports between 6 and 10 cm in 32.3% of samples; Chiropotes lands on this support size class in 16.7% of samples. Supports between 11 and 15 cm are used in 9.3% of Pithecia landings, and 7.1% of Chiropotes landings. Neither species often use the largest support size class to land (1.5% for Pithecia and 1.1% for Chiropotes). Mixed supports of the two smallest size classes are used relatively infrequently by Pithecia (5.0%), but three times as often by Chiropotes

(15.3%).

Leaping and Relative Height in Trees (Table 6.27)

Relative tree heights used for leaping are presented with those tree heights used in all travel bouts in Table 6.24. Relative heights used for various activity bouts will be further discussed in Chapter 7.

The relative height at which leaping most often occurs differs between the species. For Pithecia, that portion of the tree 70-80% of its total height is the most frequently used (32.1%), followed by the next lower portion, 60-70% relative height (24.6% of samples). The two relative heights 50-60% and 80-90% are used equally (16.7 and 16.3% of samples, respectively). The portions of tree heights 40-50% and those less than 40% are used in 4.8 and 3.2% of samples. The portion least often used for leaping by Pithecia is the top (90-100%) of the trees, used in only 2.3% of samples.

Chiropotes uses the two portions at 70-80 and 80-90% virtually equally for leaping (33.3 and 32.9%, respectively). The relative height 60-70% is used about one-half as often (15.4%), followed by the portion 50-60% of tree height (8.2% of samples). The top 90-100% of the tree's height is used in 7.7% of leap samples. The portion by far the least used by Chiropotes are those 40-50% and less than 40% of relative tree height (1.6 and 1.0% of

samples.

Qualitative Aspects - Leap Phases (Figures 6.15 and 6.16)

The qualitative aspects of leaping differences between the species can be observed in the leap phases of each. Following is a detailed description of the stages of a leap from the same crouched take-off position for an individual of each species, in order to highlight contrasts in the different aspects of the "same behavior" in the two species.

Preparatory: The preparatory phase of leaping is similar for both species. The body is quickly lowered into a crouch by flexion of all four limbs and the back (Figure 6.15 and 6.16 - Preparatory), followed by immediate extension of the hindlimbs and back to initiate take-off. Extreme crouching serves to: 1) increase the amount of time over which force is applied to the support during extension, and 2) "potentiate" the muscles and tendons used in leaping (see p. 150). Subsequent leap phases differ between the species.

Pithecia

Take-Off: At take-off, near simultaneous movement is exhibited at the hindlimb, back and forelimb. Pithecia extends its hindlimbs, first at the hip, then at the knee. The back begins to extend at the same time as the hindlimbs extends at the hip, and the torso becomes angled almost vertically. The forelimbs release the support and begin to

protract and abduct slightly. Pithecia continues to extend its hindlimbs (at both the hip and the knee) and back, raising its body and propelling it forward. The forelimbs continue to protract. When hindlimb extension is almost complete, the feet provide the final propulsive thrust against the support for take-off (Figure 6.15, Take-Off).

Midflight: The fullest hindlimb extension occurs immediately after take-off. Once the substrate has been released, the fully extended hindlimbs begin to flex both at the hip and at the knee. This flexion continues until the body is tucked into a ball, with back flexed and head down (Figure 6.15, Midflight 1). This can serve to minimize the mass moments of inertia about the animal's transverse axis, as reported by Peters and Preuschoft (1984) for leaping Tarsius. An orthograde body orientation is maintained throughout the leap, most apparent at the midpoint of the leap, when the body is tucked, and the hindlimbs are flexed approximately 90° at both the hip and the knee. The forelimbs are flexed and somewhat abducted. From this position, Pithecia subsequently begins to extend the hindlimbs (at the knee first, then at both the hip and the knee), which will contact the landing substrate first. Extension of the back immediately follows (perhaps at least partly as a result of hindlimb extension), and the tail is raised, possibly due to the contraction of the back extensor musculature (Figure 6.15, Midflight 2). The body is angled

slightly posteriorly. The hindlimbs continue to extend at the hip and the knee as the body approaches for landing.

Landing: Landing occurs with the hindlimbs near full extension; they contact the support first, flexing at both the hip and the knee. The back flexes, and the forelimb contacts the landing substrate immediately after the hindlimb, flexing as well. Flexion continues for the longest time in the hindlimbs, until the body is again at rest on the landing substrate.

Chiropotes

Take-Off: From its crouching position, Chiropotes quickly extends its back, lifting the upper torso and moving it forward. At the same time, the forelimbs extend, pushing against the support. Upon release of the support by the hands, the forelimbs begin to protract and abduct, and the hindlimbs begin to extend at the hip and knee. The body is oriented upward, although it is less orthograde than that of Pithecia (Figure 6.16, Take-Off). Extension of the back continues, accompanied by further protraction and abduction of forelimbs until elbows are approximately lateral to the head, and arms are nearly fully extended. Hindlimb extension continues as well, ending with plantar flexion of the foot for a final propulsive thrust. The hindlimbs are usually almost fully extended and adducted at take-off.

Mid-flight: The hindlimbs become completely extended

after take-off, and the forelimbs are fully protracted as well (Figure 6.16, Midflight 1). The orthograde body orientation observed at this stage is maintained throughout the leap. Immediately after full extension is reached, the hindlimbs begin to flex on the hip, and abduct. Passive flexion of the knee occurs as a by-product of the flexion at the hip, which continues until the hindlimbs are flexed at about a 45° angle with the body. At this point, all limbs are abducted as well (Figure 6.16, Midflight 2). The hindlimbs extend slightly at the hip when the body nears the landing support. The forelimbs, having been maintained in a very protracted position throughout most of midflight portion, begin to retract until they are positioned at approximately a 90° angle to the body. The elbows remain somewhat flexed. After having extended at take-off, the back remains extended during much of the flight phase, then begins to flex slowly as the body draws closer to the landing substrate.

Landing: Since a pronograde body orientation is usually maintained throughout the leap, all four limbs are at approximately the same level at landing. The hindlimbs are still highly flexed at the hip and the knee, and the back is flexed. At landing, limbs undergo more flexion as compressive landing forces are transmitted through the body.

For short downward leaps, Chiropotes exhibits little extension of the back, but simply falls forward, then the

hindlimbs are used to provide propulsion away and down from the support.

Use of the Tail in Leaping of Pithecia

The tail of Pithecia may play a role in aiding the control of leaps, as has been demonstrated for Tarsius (Peters and Preuschoft, 1984) and Lemur catta (Dunbar, 1988). This may be accomplished in two ways:

1) In the midflight phase, as the body prepares for landing, the body "untucks" through hindlimb and back extension. As the back extends, the tail rises. Peters and Preuschoft (1984) cite this phenomenon in Tarsius as "...upswing of the tail and a resulting rotation of the body head rearward..." in order to move the upper body out of the way of the landing substrate, upon which the hindlimbs will strike first.

2) In leaping from one vertical support to another, the body must complete a 180° rotation in order to prepare for landing. Rotation about the longitudinal axis is initiated at take-off, and the swing of the tail stops this rotation (Peters and Preuschoft, 1984).

Although the extent to which tail movements affect body rotations in Pithecia is unknown, both types of tail movement (the upswing of the tail as the body untucks, and the lateral swing of the tail as the body turns in mid-air to face the landing support) are exhibited by Pithecia in

the midflight phase of leaping.

Leap Distance, Amount of Vertical Displacement

As Ripley (1969) demonstrates, leap distance and the amount of vertical displacement undergone in a leap are closely intertwined, since upward or downward components of a leap can drastically affect the total horizontal distance covered.

Pithecia can easily leap at least six meters in a straight horizontal plane, while Chiropotes was observed to leap only about two and a half meters if no downward component was involved. Pithecia usually maintains the same vertical level while traveling, and often leaps straight across gaps without either ascending or descending in level. Chiropotes, on the other hand, more often leaps from a higher to a lower support. Thus, involvement of a downward component greatly increases the potential distance, and leaps to a lower support can exceed ten meters in horizontal distance.

Some General Properties (Correlates) of Leaping Behavior

Some interrelated features can be noted between leap distance and landing patterns, and are related to use of the tree portions and supports within them. Strategies for landing after various leap distances differ between the species.

The amount of propulsion generated (therefore distance of leap) is greater from more solid supports, which Pithecia tends to use for take-off in the majority of leaps. Landing patterns for short leaps differ somewhat between the species; those for long leaps differ considerably.

When landing after a short leap, the common pattern for both species is for the forelimbs to strike the substrate first, or, for Pithecia, all four limbs may strike simultaneously.

When landing after a long leap, limb use and landing support type differ between the species. Pithecia lands with the hindlimbs first, usually onto solid, often vertical branches.

Chiropotes lands on all four limbs, virtually always onto flexible terminal branches.

E. Summary

Positional Behavior

As evident from these results, the pitheciins exhibit a very wide range of behaviors. Some of them occurred only rarely, and were observed only outside of sampling periods. A tremendous amount of overlap among the three species is apparent, and very few behaviors appear to be exclusive for any one species. Differences among the species are exhibited in the frequency, the context and in the qualitative nature of the behaviors.

While feeding, Pithecia engages in relatively fewer locomotor behaviors than postural, compared to Chiropotes and especially to Cacajao; the latter spends almost one-third of its feeding time engaged in locomotor behaviors. The main difference in postural behavior between the species is Pithecia's frequent use of vertical supports, which was not sampled for Chiropotes and rarely for Cacajao. Chiropotes engages in more bipedal standing while feeding than do the other two species, and only Chiropotes and Cacajao were sampled in bipedal suspension, which was most frequent for Cacajao.

During travel, Pithecia leap more frequently than do either Chiropotes or Cacajao; Pithecia is the only species sampled using continuous bound. Chiropotes and Cacajao exhibit more quadrupedal walking and running, and more often drop from a higher to a lower support than does Pithecia. Pronograde clamber-run and bridge were observed more frequently for Chiropotes and Cacajao than for Pithecia. In the momentary pauses during travel, Pithecia sits more frequently than the other two species. Vertical cling was recorded only for Pithecia, and pedal suspension during travel bouts only for Cacajao.

During resting bouts, Pithecia sits considerably more than does either Chiropotes or Cacajao, while both of the latter use lying postures much more frequently than does Pithecia. Again, vertical cling was observed for Pithecia

alone. While engaging in resting bouts, pedal suspension is used only by Cacajao.

Only Chiropotes was sampled during play, for which pronograde clamber-run, leap and quadrupedal run were the most frequent locomotor behaviors. Pedal suspension and sit were the postural behaviors most often observed; other behaviors occur relatively infrequently.

Tree Portions

Use of tree portions was recorded only for Pithecia and Chiropotes.

Through all activities (i.e. feed, travel, rest), Chiropotes uses the main crown much more frequently than does Pithecia. Terminal branches are used more by Chiropotes than by Pithecia in both travel and rest. The lower and central tree portions (bole, vertical axis and below crown) are used more frequently by Pithecia than by Chiropotes in feed, travel and rest. Pithecia uses lianas and vine tangles more than does Chiropotes in all activities.

Of these two species, only Pithecia was observed on the ground; this occurred during feeding bouts. Ayres (1986) observed Cacajao on the ground feeding on seedling clumps with great frequency (up to 30 or 40% of the time) in the dry season at Lake Teiú.

Play bouts of Chiropotes took place primarily in the

crown, and almost one-half as frequently in the terminal branches. Lianas were also used in a number of samples.

Tree Portions from which Food is Obtained

The location of foods in the canopy differs little between Pithecia and Chiropotes; the primary location is the terminal branch portion. Either lianas (for Pithecia) or the crown (for Chiropotes) is the secondary portion. Other parts of the canopy provide very little food.

Absolute and Relative Heights in Trees

Pithecia was observed at a mean height much lower than that for either Chiropotes or Cacajao. Through all activities, Pithecia consistently uses the relative height of 60-70% and lower more than does Chiropotes. Chiropotes generally uses the relatively higher tree portions more than does Pithecia, with the exception of the portion at 90-100% of tree height. During feeding and resting, Pithecia was more often observed at this relative height than was Chiropotes.

Support Use

During feeding, Chiropotes uses dual supports the most frequently, and Cacajao the least. Several supports are used most often by Cacajao and least often by Chiropotes. The primary difference in the inclination of supports used is the use of fewer horizontal supports and more vertical supports by Pithecia.

Supports which deform under an individual's body weight are used most often by Cacajao, and least often by Pithecia. The diameter of supports used was recorded only for Pithecia and Chiropotes. The smallest supports (<2 cm) are used slightly more frequently by Pithecia than by Chiropotes, while supports in the range of 6 to 10 cm are used somewhat more often by Chiropotes than by Pithecia.

While traveling, Pithecia uses single supports in more samples than do either Chiropotes or Cacajao, while the latter two species use several supports considerably more than does Pithecia. Horizontal supports are used least by Pithecia and most by Cacajao. Cacajao uses angled supports considerably less often than the other two species. Vertical supports were sampled frequently for Pithecia, and very infrequently for either Pithecia or Chiropotes, while deformable supports were used about twice as often by Chiropotes and Cacajao as by Pithecia. Chiropotes uses the smallest support size class (<2 cm) more than does Pithecia, while the next smallest category (2 - 5 cm) is used more by Pithecia. Supports in the two largest size classes are used more by Chiropotes than by Pithecia.

During resting, few difference are exhibited in support use, the primary one being in Cacajao's use of several supports for resting, which was about twice as frequent as for Pithecia or Chiropotes. Chiropotes and Cacajao use horizontal supports in the majority of their resting bouts, while Pithecia uses primarily angled supports. Vertical supports were used almost

solely by Pithecia, although Cacajao used vertical supports in a small percentage of rest bouts. Deformable supports were used to a significant degree only by Cacajao. Pithecia used the smallest two support size classes more than did Chiropotes, while Chiropotes used the largest two classes much more than did Pithecia.

Supports Used in Each Tree Portion

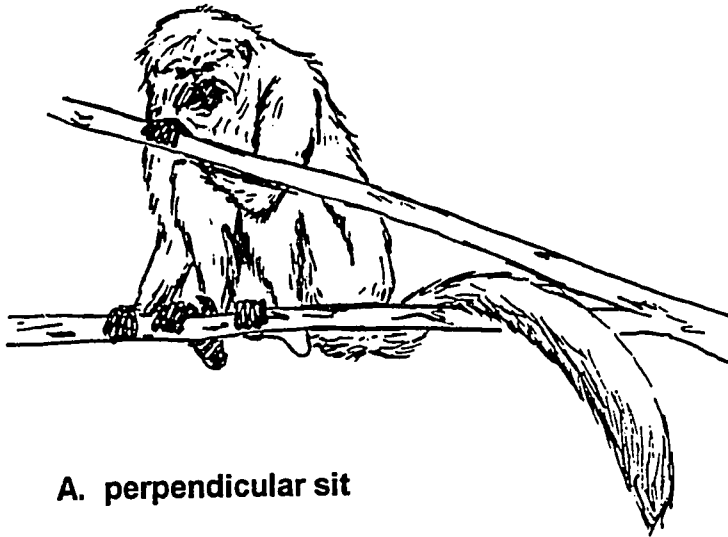
The supports used in each tree portion is very similar between the species. In the lower tree portions, particular the bole and the vertical axis, supports used were typically vertical or angled. Below the crown, supports were usually angled, and sometimes vertical; in the main crown, supports used are either angled or horizontal. In all of these portions, single supports are the most commonly used. The terminal branch portion is the only one in which several supports are used most often; these branches are often small and deformable. Lianas are usually taken as single supports, usually angled. Supports within vine tangles are similar to those in terminal branches.

Leaping

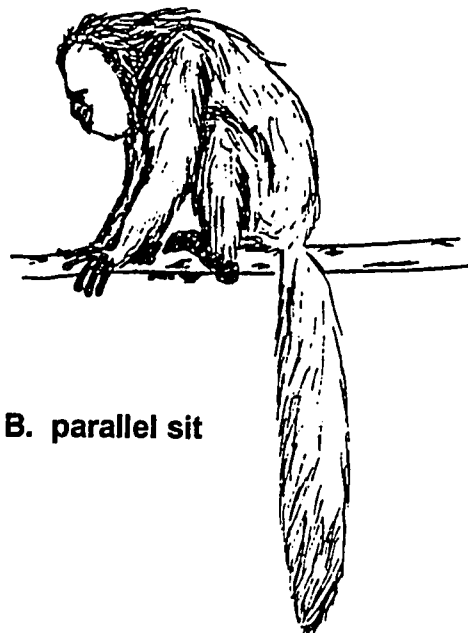
Pithecia uses vertical clinging as a take-off position one-half of the time; this behavior was never sampled for Chiropotes. Chiropotes uses pronograde clamber, quadrupedal walk, run and stand as take-off positions approximately twice as frequently as does Pithecia.

Tree portions used in take-off differed primarily in that Pithecia often uses the bole, which wasn't sampled for Chiropotes, while Chiropotes uses the terminal branches for take-off much more frequently than does Pithecia. Landing tree portions also differ mainly in the frequent use of the vertical axis and bole by Pithecia, and the almost exclusive use of the terminal branches by Chiropotes.

In both take-off and landing, Pithecia prefers to use a single support, which tends to be vertical, and of the size class 2-5 cm or 6-10 cm. Chiropotes prefers to use a single support for take-off and several deformable ones for landing. Chiropotes uses larger supports for take-off than for landing, which is typically onto supports of less than 2 cm in diameter.



A. perpendicular sit



B. parallel sit

Figure 6.1. Sit

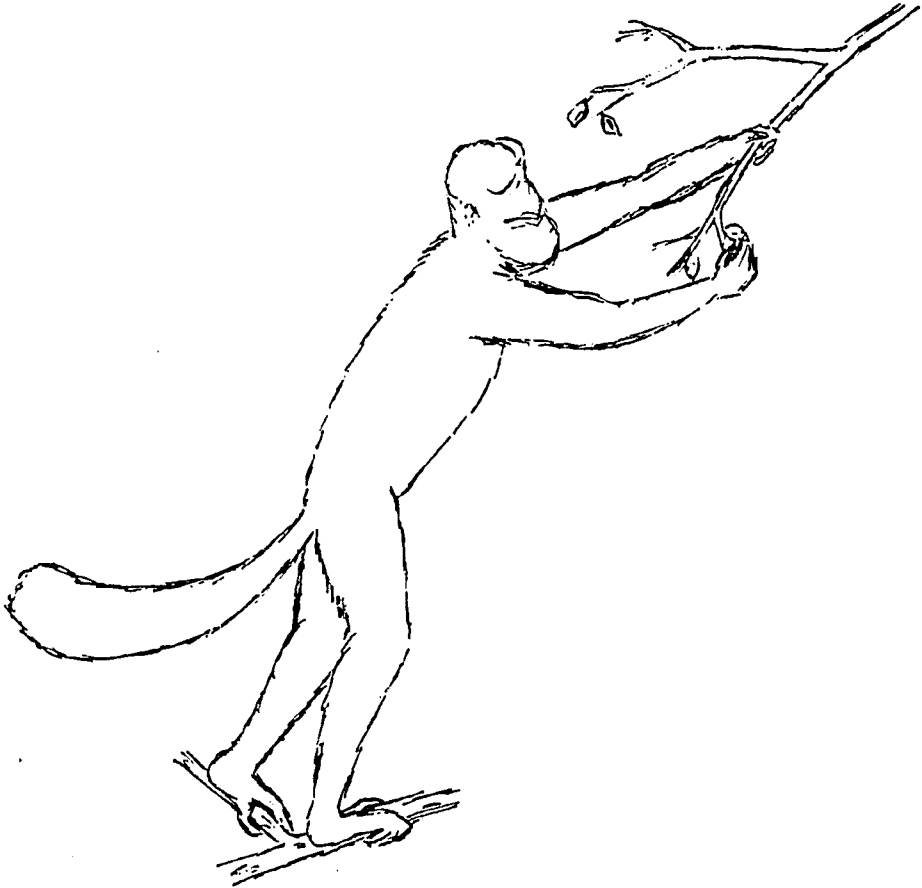


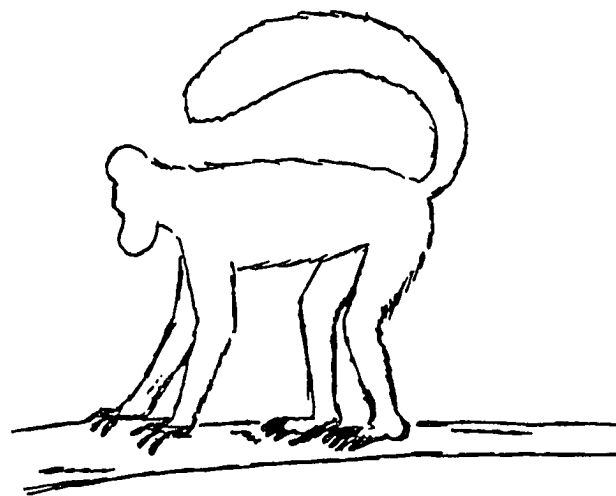
Figure 6.2. Bipedal stand



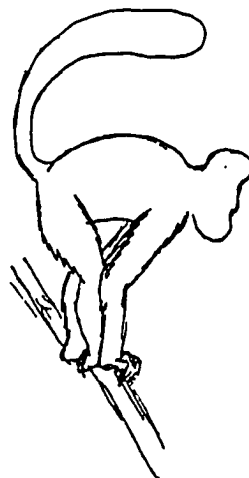
Figure 6.3. Angled sit



Figure 6.4. Perch



A. parallel



B. perpendicular

Figure 6.5. Stand

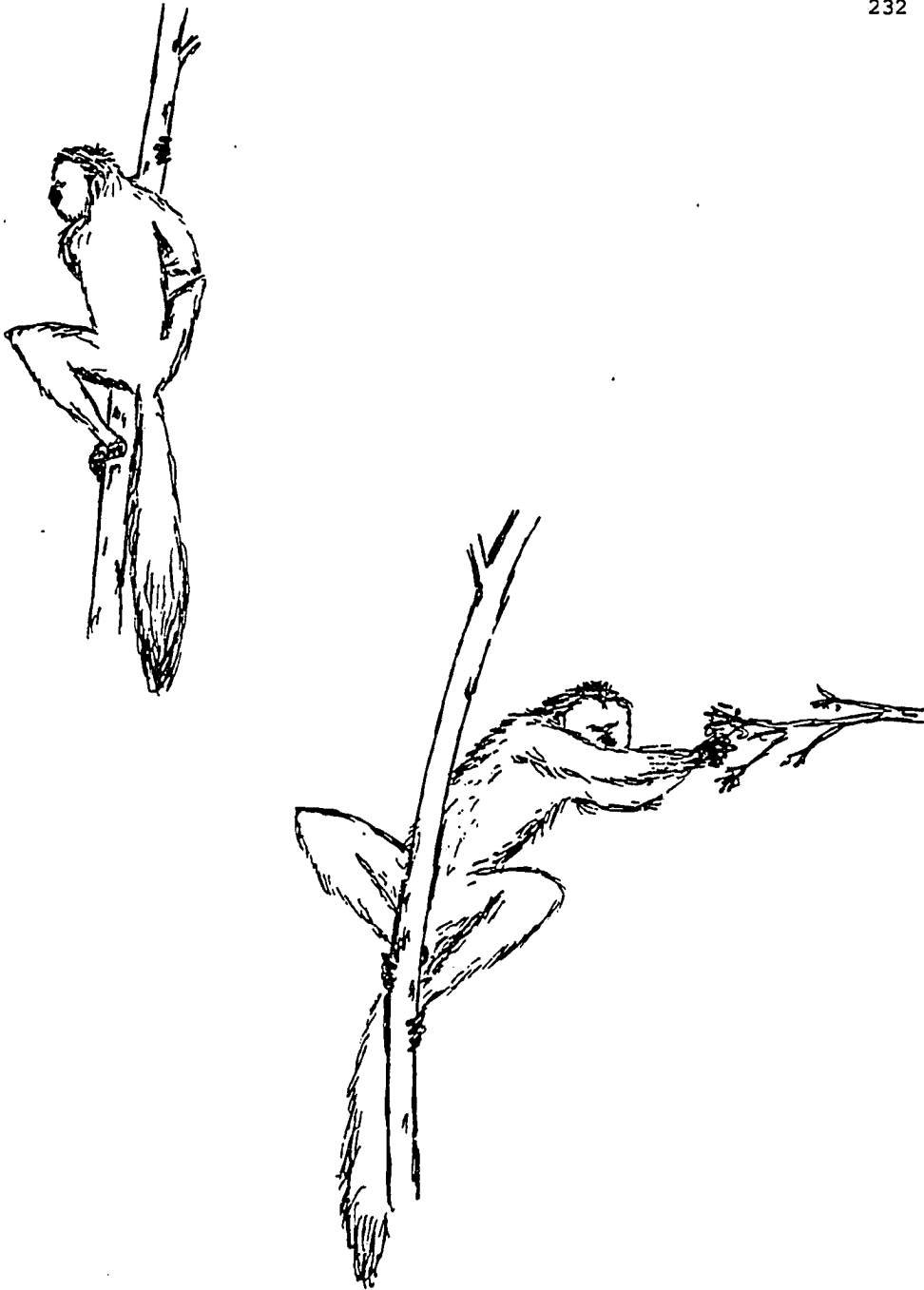


Figure 6.6. Vertical cling

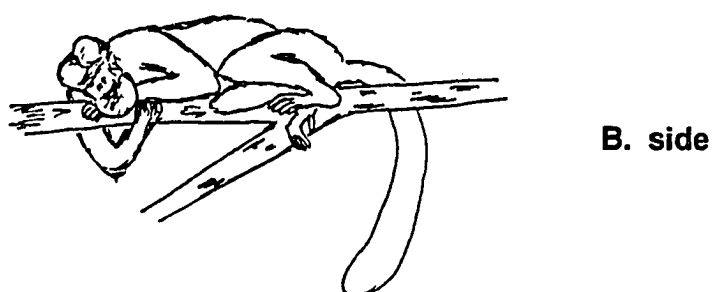
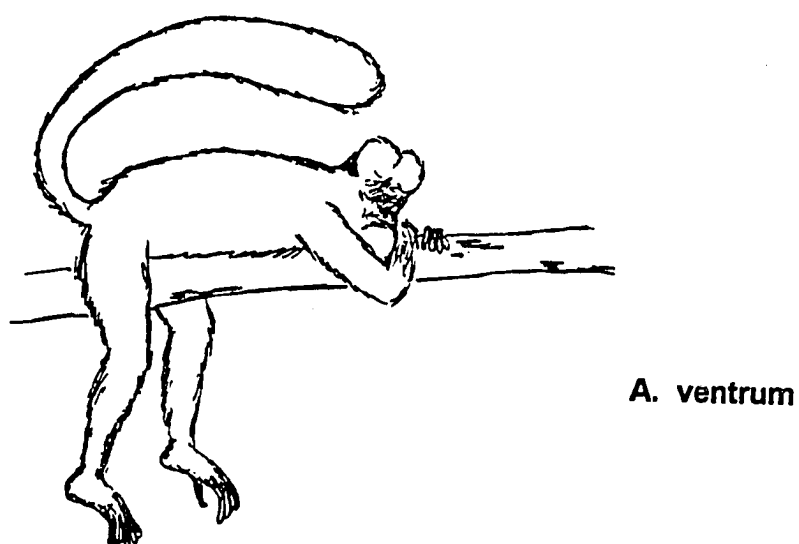


Figure 6.7. Lie

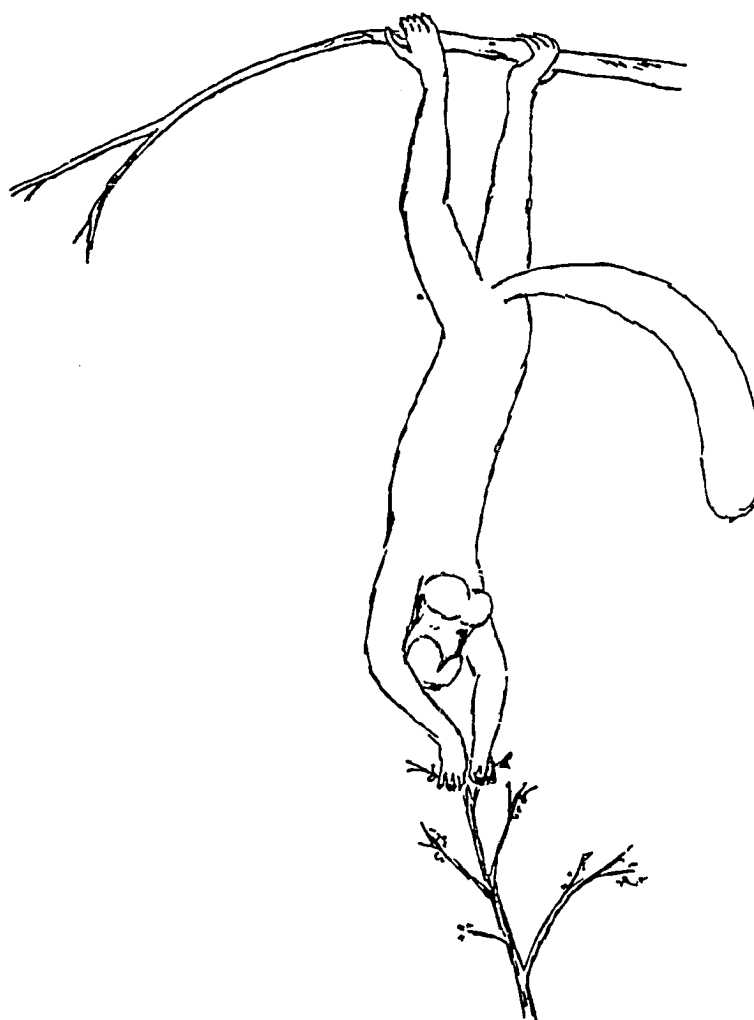


Figure 6.8. Bipedal suspension



Figure 6.9. Cling



Figure 6.10. Quadrupedal walk - Pithecia

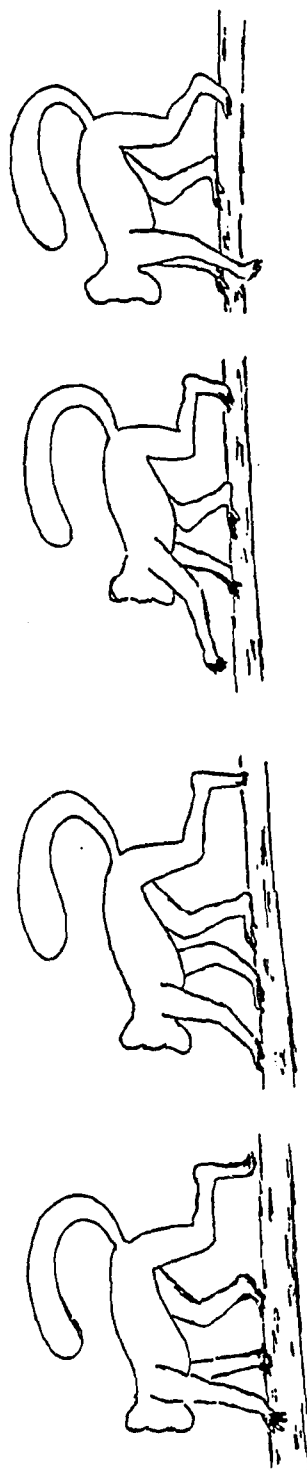


Figure 6.11. Quadrupedal walk - Chiropotes

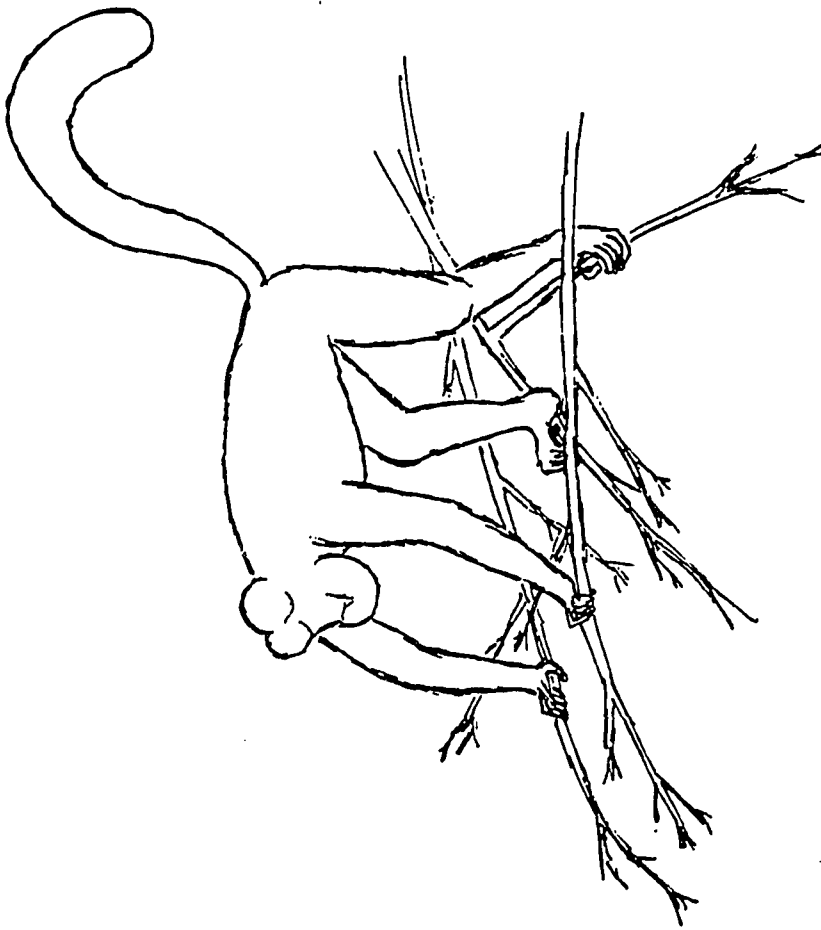


Figure 6.12. Pronograde clamber

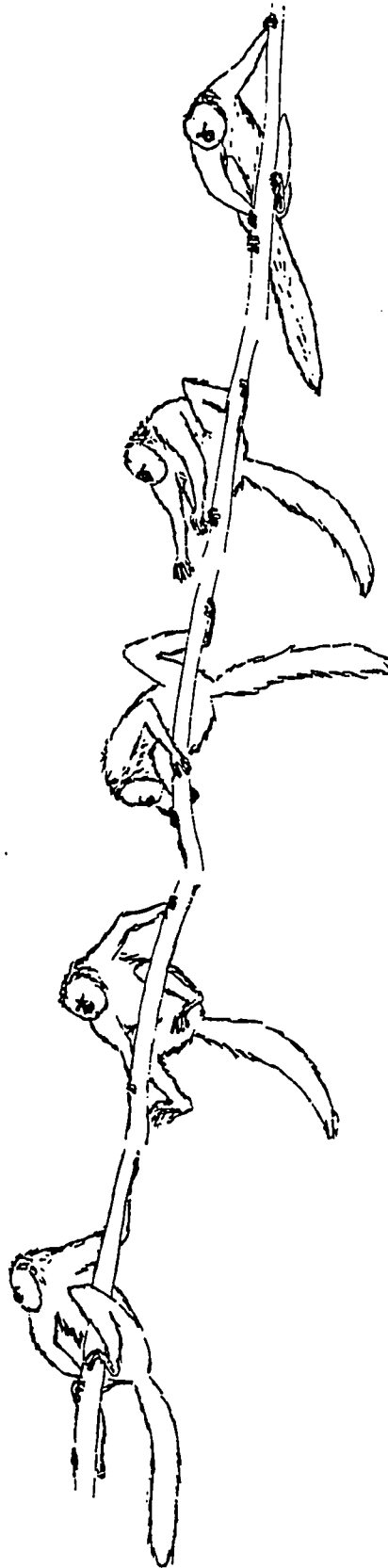


Figure 6.13. Side down

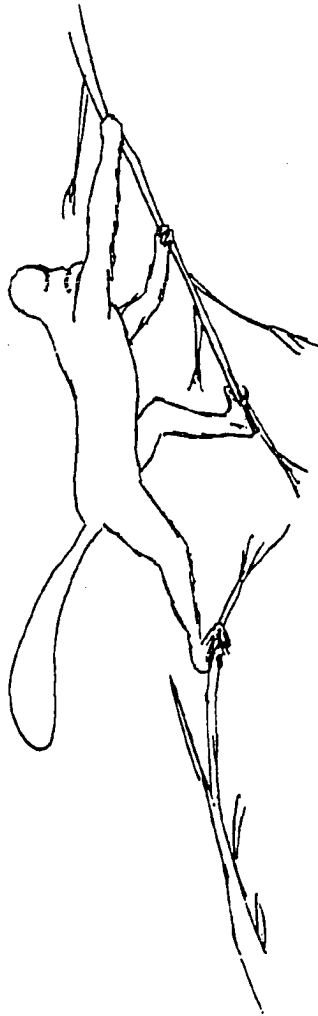


Figure 6.14. Bridge

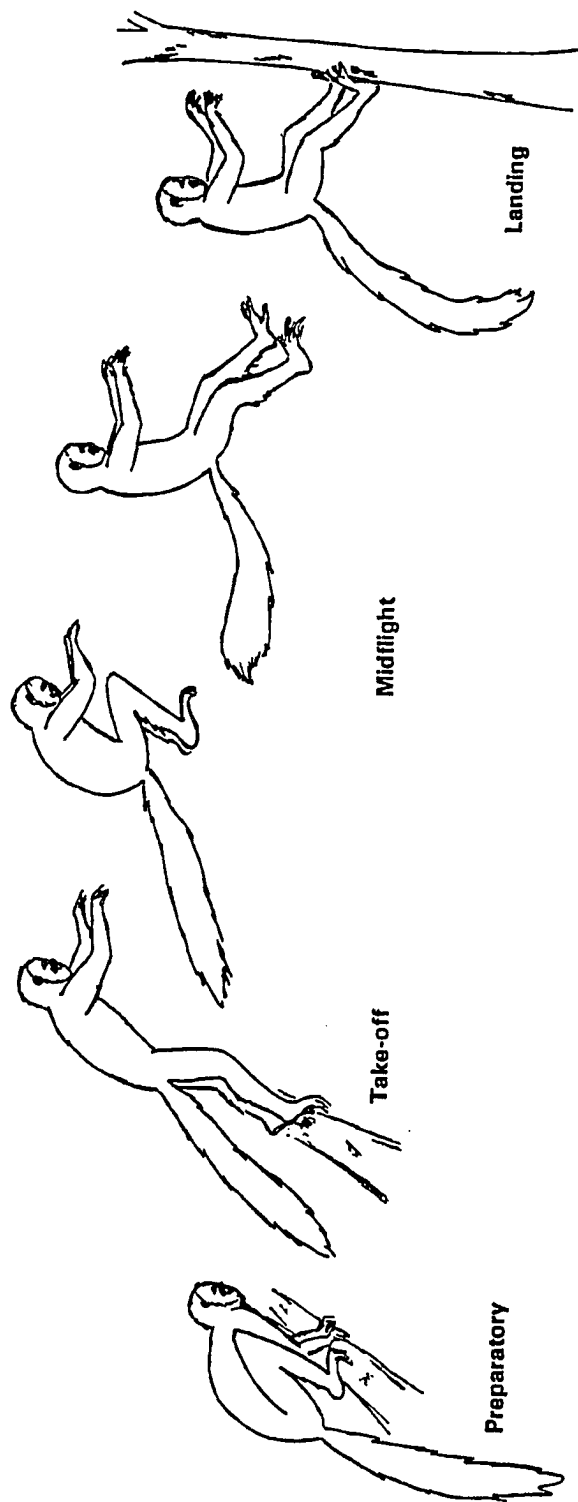


Figure 6.15. Leap sequence - Pithecia

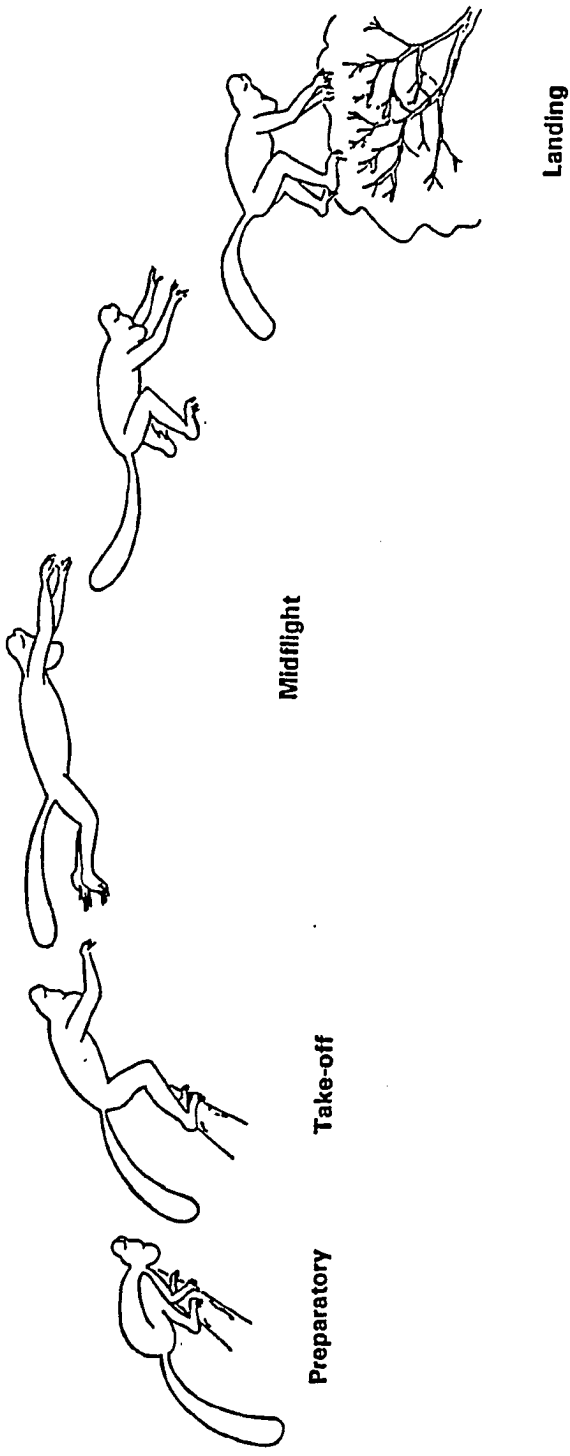


Figure 6.16. Leap sequence - Chiropotes

Figure 6.17. Drop (from flexible to solid support)

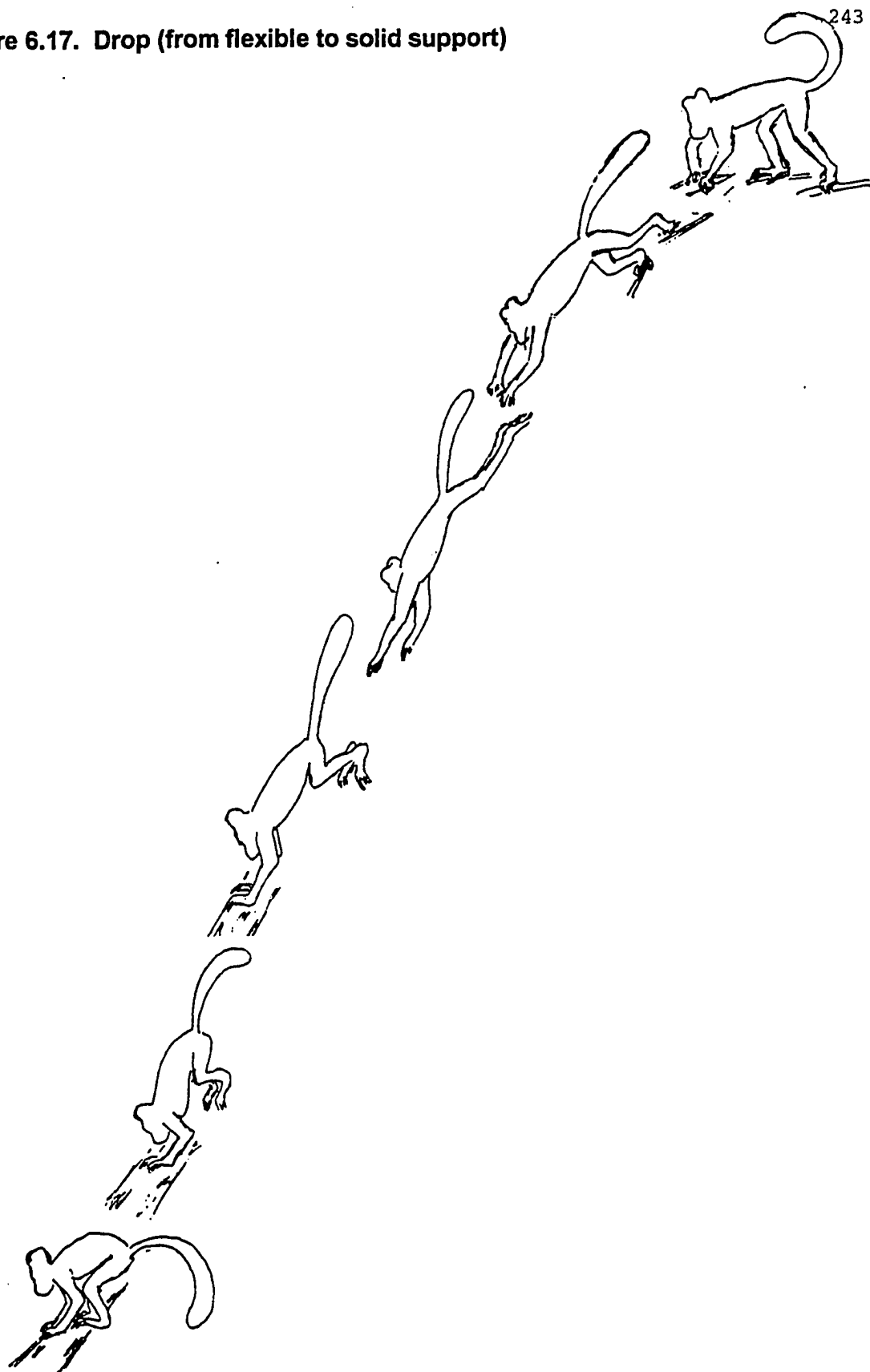


Table 6.1. Positional behavior during feeding.

	<u>Pithecia</u> Group I (N=2236)	<u>Pithecia</u> Group II (N=976)
Positional Behavior		
Locomotor		
pronograde clamber	11.5%	7.9%
quadrupedal walk	2.0	-
quadrupedal run	-	-
leap	1.3	-
drop	-	-
Total	14.8	7.9
Postural		
sit	51.2%	58.9%
stand	9.5	10.7
vertical cling	12.1	8.6
perch	9.0	9.9
bipedal stand	1.3	2.6
pedal suspension	-	-
Total	83.1	90.7
Other (cumulative total of those behaviors each of which comprised <1% of samples)	2.1%	0.7%

Chi-square value = 57.10
df = 8
p<0.001

Table 6.2. Positional behavior during travel.

	<u>Pithecia</u> Group I (N=2170)	<u>Pithecia</u> Group II (N=766)
Positional Behavior		
Locomotor		
leap	40.2%	38.8%
pronograde clamber	15.5	16.1
quadrupedal walk	15.1	15.1
quadrupedal run	5.0	3.3
continuous bound	2.7	3.8
climb up	2.3	1.6
climb down	1.0	-
hop	1.0	3.9
drop	-	2.7
pronogr. clamber-run	1.0	1.3
swing down	1.2	-
sidle down	-	1.2
Total	85.0	87.8
Postural		
sit	7.0%	4.7%
vertical cling	3.8	3.0
stand	2.4	1.6
perch	-	1.0
Total	13.2	10.3
Other (cumulative total of those behaviors each of which comprised <1% of samples)		
	1.1	1.2
Chi-square value = 92.43		
df = 16		
p<0.001		

Table 6.3. Positional behavior during rest.

	<u>Pithecia</u> Group I (N=1614)	<u>Pithecia</u> Group II (N=983)
Positional Behavior		
Postural		
sit	71.8%	72.3%
vertical cling	13.4	9.0
lie - ventrum	4.7	12.2
lie - side	5.0	1.2
stand	3.1	1.8
lean	-	2.0
perch	-	1.0
Total	98.0	99.5
Other (cumulative total of those behaviors each of which comprised <1% of samples)		
	2.0%	0.6%

Chi-square value = 101.12
df = 7
p<0.001

Table 6.4. Tree portions used during major activities.

	<u>Pithecia Group I</u>			<u>Pithecia Group II</u>		
	Feed N=	Travel	Rest	Feed	Travel	Rest
	2196	2024	1608	954	692	963
Tree Portion						
main crown	30.1%	37.3%	49.7%	25.5%	47.5%	53.1%
terminal branches	36.6	13.5	1.2	61.0	26.0	8.1
vertical axis	4.6	6.0	5.6	4.4	8.1	8.5
below crown	8.8	14.3	22.2	3.4	8.8	21.5
bole	8.4	16.6	9.8	2.1	6.5	1.8
liana	6.7	9.6	9.3	2.6	2.3	6.8
vine tangle	3.5	2.7	2.3	1.0	-	-
ground	1.2	-	-	-	-	-
Total	99.9	100	100.1	100	99.2	99.8

	Chi-square value	df	Probability
Feed:	210.44	7	<0.001
Travel:	158.97	6	<0.001
Rest:	162.39	6	<0.001

Table 6.5. Positional behavior during feeding.

	<u>Pithecia</u> (N=3212)	<u>Chiropotes</u> (N=2788)	<u>Cacajao</u> (N=288)
Positional Behavior			
Locomotor			
pronograde clamber	10.4%	11.5%	19.1%
quadrupedal walk	1.5	5.3	11.8
quadrupedal run	-	1.5	1.0
leap	1.0	1.2	3.1
drop	-	-	2.1
Total	12.9	19.5	37.1
Postural			
sit	53.3%	51.0%	40.6%
stand	9.8	12.8	9.7
vertical cling	10.5	-	1.0
perch	9.3	8.3	4.2
bipedal stand	1.7	3.5	1.4
pedal suspension	-	1.2	3.5
Total	84.6	76.8	60.4
Other (cumulative total of those behaviors each of which comprised <1% of samples)			
	2.5%	3.8%	2.3%

Species	Chi-square value	df	Probability
<u>Pithecia/Chiropotes</u>	388.67	11	<0.001
<u>Pithecia/Cacajao</u>	300.89	12	<0.001
<u>Chiropotes/Cacajao</u>	118.82	11	<0.001*

* significance test suspect (few cases in Cacajao cells)

Table 6.6. Positional behavior during travel.

	<u>Pithecia</u> (N=2944)	<u>Chiropotes</u> (N=1818)	<u>Cacajao</u> (N=239)
Positional Behavior			
Locomotor			
leap	39.7%	24.5%	21.3%
pronograde clamber	15.6	16.7	20.5
quadrupedal walk	15.1	22.9	22.2
quadrupedal run	4.6	12.3	11.7
continuous bound	3.0	-	-
climb up	2.1	2.1	2.5
hop	1.8	1.1	-
drop	1.1	7.6	9.6
pronogr. clamber-run	1.0	2.6	2.5
bridge	-	2.0	1.0
swing down	1.0	-	-
Total	85.0	91.8	91.3
Postural			
sit	6.4%	2.9%	4.2%
vertical cling	3.6	-	-
stand	2.1	3.3	2.5
pedal suspension	-	-	1.7
Total	12.1	6.2	8.4
Other (cumulative total of those behaviors each of which comprised <1% of samples)			
	2.9%	1.9%	0.42%
Species	Chi-square value	df	Probability
<u>Pithecia/Cacajao</u>	553.01	18	<0.001
<u>Pithecia/Cacajao</u>	216.00	14	<0.001
<u>Chiropotes/Cacajao</u>	23.63	12	<0.05 (ns)

Table 6.7. Positional behavior during rest.

	<u>Pithecia</u> (N=2603)	<u>Chiropotes</u> (N=1512)	<u>Cacajao</u> (N=146)
Positional Behavior			
Locomotor			
quadrapedal walk	-	1.0%	2.1%
Postural			
sit	71.8%	56.8%	58.9%
vertical cling	11.3	-	1.4
lie - ventrum	7.5	29.8	28.1
lie - side	3.6	6.1	1.4
lie - dorsum	-	-	1.4
stand	2.5	5.0	3.4
pedal suspension	-	-	1.4
lean	1.1	-	-
Total	97.8	97.7	96.0
Other (cumulative total of those behaviors each of which comprised <1% of samples)			
	2.7%	2.0%	2.0%

Species	Chi-square value	df	Probability
<u>Pithecia/Chiropotes</u>	359.40	7	<0.001
<u>Pithecia/Cacajao</u>	170.51	9	<0.001*
<u>Chiropotes/Cacajao</u>	44.1	8	<0.001*

* significance test suspect (few cases in Cacajao cells)

Table 6.8. Tree portions used during major activities.

Tree Portion	N=	<u>Pithecia</u>			<u>Chiropotes</u>			
		Feed 3212	Travel 2722	Rest 2603	Feed 2788	Travel 1757	Rest 1512	Play 174
main crown		28.7%	39.9%	51.0%	41.1%	49.5%	79.5%	63.8%
terminal branches		44.0	16.8	3.8	49.9	34.3	8.0	24.7
below crown		7.2	13.0	21.9	2.6	7.9	8.9	2.3
vertical axis		4.6	6.5	6.7	1.0	1.0	1.5	-
bole		6.5	14.0	6.8	-	-	-	-
liana		5.5	7.7	8.3	3.1	5.6	1.5	6.3
vine tangle		2.7	2.2	1.6	2.5	1.4	-	1.7
ground		1.0	-	-	-	-	-	-
Total		100.2	100.1	100.1	100.2	99.7	99.4	98.8

<u>Pithecia/Chiropotes</u>	Chi-square value	df	Probability
Feed:	415.30	7	<0.001
Travel:	553.01	6	<0.001
Rest:	350.39	6	<0.001

Table 6.9. Tree portion in which food was obtained in feeding bouts of Pithecia and Chiropotes.

	<u>Pithecia</u> (N=2290)	<u>Chiropotes</u> (N=2031)
Crown	12.5%	18.3%
Terminal Branches	64.3	68.1
Below Crown	0.9	0.4
Vertical Axis	0.4	0.3
Bole	0.7	-
Liana	17.9	12.0
Vine Tangle	0.8	1.0
Ground	2.5	-
	<u>100.0</u>	<u>100.1</u>

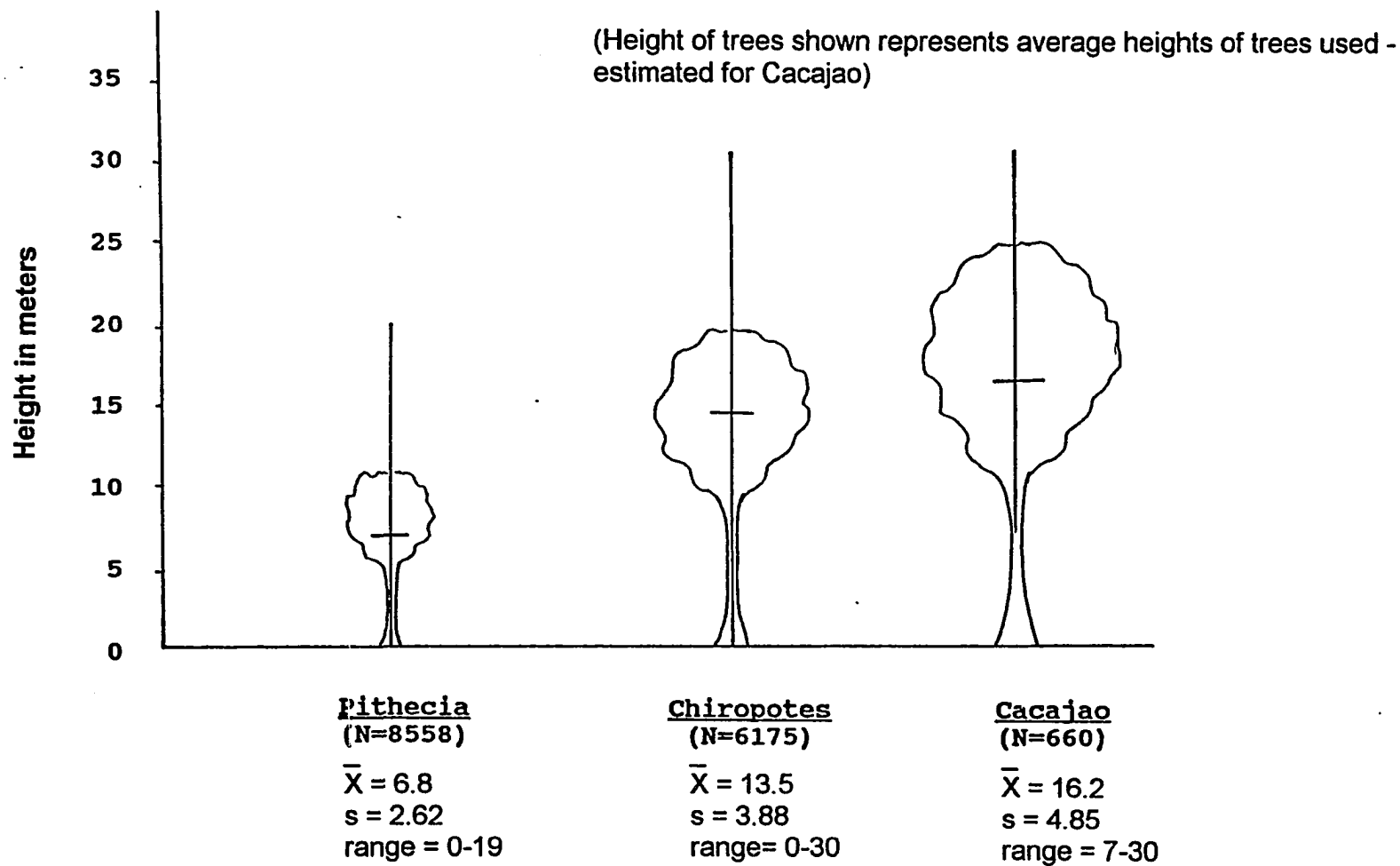


Figure 6.18. Mean height in tree (with range shown)

Figure 6.19. Relative height in trees during major activity bouts

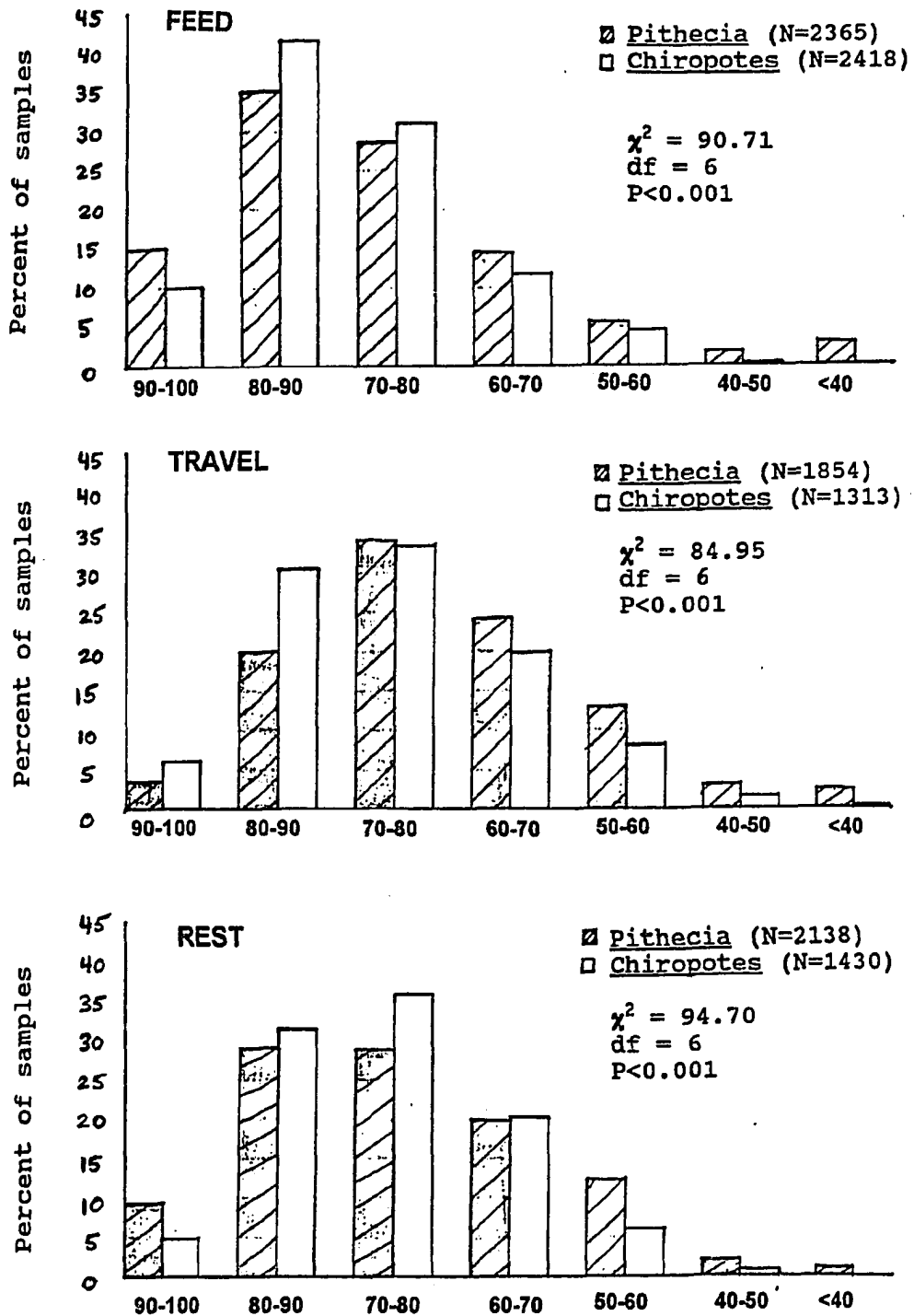


Table 6.10. Support use during feeding.

	<u>Pithecia</u>	<u>Chiropotes</u>	<u>Cacajao</u>
Number	(N=3167)	(N=2778)	(N=285)
one	46.4%	47.0%	41.8%
two	15.4	20.2	11.2
several	38.2	32.8	47.0
Total	100	100	100
Inclination	(N=3164)	(N=2775)	(N=246)
horizontal	16.8%	24.8%	35.4%
angled	26.0	23.8	15.0
vertical	8.6	-	2.0
deformable	34.1	38.1	41.5
mixed	14.5	12.9	6.1
Total	100	99.6	100
Diameter	(N=3158)	(N=2777)	
<2 cm	22.8%	16.3%	
2 - 5 cm	37.5	37.6	
6 - 10 cm	12.0	17.1	
11 - 15 cm	3.0	3.9	
>15 cm	1.0	1.6	
mixed, <2 & 2-5 cm	22.0	20.9	
other mix	2.0	2.7	
Total	100.3	100.1	

Table 6.10. (cont'd.)

Probability	Species	Chi-square value	df	
Number	<u>Pithecia/Chiropotes</u>	37.60	2	<0.001
	<u>Pithecia/Cacajao</u>	6.72	2	0.035 (ns)
	<u>Chiropotes/Cacajao</u>	26.42	2	<0.001
Incl.	<u>Pithecia/Chiropotes</u>	253.31	4	<0.001
	<u>Pithecia/Cacajao</u>	85.14	4	<0.001
	<u>Chiropotes/Cacajao</u>	33.37	4	<0.001
Diam.	<u>Pithecia/Chiropotes</u>	82.86	6	<0.001

Table 6.11. Support use during travel.

	<u>Pithecia</u>	<u>Chiropotes</u>	<u>Cacajao</u>
Number	(N=2779)	(N=1762)	(N=229)
one	71.8%	60.8%	58.5%
two	7.1	8.1	5.7
several	21.2	31.1	35.8
Total	100.1	100	100
Inclination	(N=2773)	(N=1757)	(N=214)
horizontal	20.5%	24.9%	31.8%
angled	35.2	33.8	24.8
vertical	19.8	1.7	2.8
deformable	16.1	31.3	35.5
mixed	8.4	8.4	5.1
Total	100	100.1	100
Diameter	(N=2764)	(N=1752)	
<2 cm	9.5%	15.8%	
2 - 5 cm	42.7	28.7	
6 - 10 cm	29.7	27.8	
11 - 15 cm	6.1	9.9	
>15 cm	1.3	3.4	
mixed, <2 & 2-5 cm	9.1	12.4	
other mix	1.6	2.0	
Total	100	100	

Table 6.11. (cont'd.)

Probability	Species	Chi-square value	df	
Number	<u>Pithecia/Chiropotes</u>	63.58	2	<0.001
	<u>Pithecia/Cacajao</u>	26.23	2	<0.001
	<u>Chiropotes/Cacajao</u>	3.13	2	0.21(ns)
Incl.	<u>Pithecia/Chiropotes</u>	399.51	4	<0.001
	<u>Pithecia/Cacajao</u>	94.14	4	<0.001
	<u>Chiropotes/Cacajao</u>	13.29	4	0.01
Diam.	<u>Pithecia/Chiropotes</u>	147.50	6	<0.001

Table 6.12. Support use during rest.

	<u>Pithecia</u>	<u>Chiropotes</u>	<u>Cacajao</u>
Number	(N=2606)	(N=1513)	(N=146)
one	60.3%	63.7%	61.6%
two	31.9	29.8	24.7
several	7.8	6.5	13.7
Total	100	100	100
Inclination	(N=2601)	(N=1506)	(N=144)
horizontal	34.1%	56.0%	60.4%
angled	40.7	32.9	28.5
vertical	7.6	-	1.4
deformable	1.4	2.4	8.3
mix	16.2	8.5	1.4
Total	100	99.8	100
Diameter	(N=2602)	(N=1506)	
<2 cm	1.0%	-	
2 - 5 cm	44.8	20.7	
6 - 10 cm	30.9	33.0	
11 - 15 cm	5.8	18.8	
>15 cm	-	12.2	
mix of <2, 2-5 cm	5.3	3.1	
mix of 2-5, 6-10 cm	9.8	7.5	
other mix	2.5	4.7	
Total	100.1	100.0	

Table 6.12. (cont'd.)

Probability	Species	Chi-square value	df	
Number	<u>Pithecia/Chiropotes</u>	8.55	2	0.014
	<u>Pithecia/Cacajao</u>	9.88	2	0.007
	<u>Chiropotes/Cacajao</u>	22.08	2	<0.001
Incl.	<u>Pithecia/Chiropotes</u>	203.06	5	<0.001
	<u>Pithecia/Cacajao</u>	85.05	5	<0.001
	<u>Chiropotes/Cacajao</u>	22.52	4	<0.001
Diam.	<u>Pithecia/Chiropotes</u>	410.94	7	<0.001

Table 6.13. Supports used by Pithecia within each tree portion.

Number of Supports:	1	2	3	(N)
Crown	61.6%	25.1%	13.4%	(3228)
Terminal Branches	18.1	14.7	67.2	(1906)
Bole	98.7	1.2	0.1	(754)
Vertical Axis	81.2	16.9	1.8	(490)
Below Crown	81.7	17.0	1.2	(1138)
Liana	88.0	3.4	8.6	(594)
Vine Tangle	9.0	3.4	87.6	(177)

Support Inclination:	H	A	V	D	M	(N)
Crown	38.8	39.3	2.6	7.3	12.1	(3222)
Terminal Branches	8.7	9.6	0.4	69.7	11.6	(1905)
Bole	1.5	23.9	73.3	0.9	0.4	(754)
Vertical Axis	10.9	45.2	32.2	4.5	7.2	(487)
Below Crown	23.2	59.6	8.9	1.3	7.0	(1138)
Liana	27.6	38.9	14.3	9.4	9.8	(594)
Vine Tangle	8.5	6.2	0.6	46.3	38.4	(177)

H: horizontal A: angled V: vertical D: deformable
M: mixed

Table 6.13. (cont'd.)

Support diameter (cm)	<2	2-5	6-10	11-15	>15	<2,2-5	7.0%	7.0%	mix of 2-5 & 6-10	other mix
Crown	2.4%	52.0%	28.4%	1.9%	0.2%	7.0%	7.0%	1.2%		
Terminal Branches	40.4	22.1	1.2	0.1	-	36.1	0.1	0.1		
Bole	0.8	29.8	42.3	21.0	5.3	-	-	-		
Vertical Axis	1.2	42.7	31.8	12.2	2.3	3.3	5.6	1.0		
Below Crown	0.3	42.7	37.6	10.0	2.0	2.0	4.0	1.5		
Liana	5.6	58.4	20.2	2.0	-	7.7	5.4	0.7		
Vine Tangle	51.4	18.2	0.6	-	-	28.3	1.7	-		

Table 6.14. Use of positional behavior in various tree portions. (*Pithecia*, N=8375)

	crn	tb	va	bc	bo	lia	vt	gr
Positional Behavior								
Locomotor								
leap	12.7%	5.8%	20.2%	12.4%	36.8%	8.9%	3.9%	-
quadrupedal walk	7.7	2.3	3.3	5.6	1.9	9.4	-	26.9
pronograde clamber	5.7	25.2	-	-	-	4.2	37.1	-
quadrupedal run	2.1	-	1.0	2.6	1.1	2.9	-	3.9
contin. bound	1.0	-	-	1.1	1.0	-	-	-
climb up	-	-	2.0	-	2.1	2.2	-	-
climb down	-	-	1.4	-	1.2	-	-	-
hop	-	-	-	-	-	-	1.7	11.5
sidle down	-	-	-	-	1.0	-	-	-
swing down	-	-	1.0	-	-	-	-	-
Total:	29.2	33.3	28.9	21.7	45.1	27.6	42.7	42.3

Table 6.14. (cont'd.)

	crn	tb	va	bc	bo	lia	vt	gr
Postural								
sit	51.8%	40.8%	39.9%	52.7%	11.9%	41.0%	37.1%	23.1%
stand	3.9	9.6	2.9	3.3	1.1	4.4	10.7	26.9
vertical cling	3.5	-	23.2	11.0	38.5	16.2	1.1	-
perch	2.0	11.0	1.2	1.0	-	2.7	4.5	-
lie-side	2.7	-	-	-	-	-	-	-
lie-ventrum	-	-	-	5.3	-	-	-	-
bipedal stand	-	1.2	-	-	-	1.0	-	7.7
lean	-	-	1.0	1.4	-	-	-	-
Total:	63.9	62.6	68.2	74.7		65.3	53.4	57.7

Totals may together equal less than 100, since each positional behavior which was exhibited in fewer than 1% of samples is not presented here.

Table 6.15. Use of positional behavior on various supports. (*Pithecia*, N=8512)

	1	Number 2	sev	H	Inclination A V		D	mixed
Positional Behavior								
Locomotor								
leap	18.7%	3.5%	5.8%	9.3%	11.9%	41.3%	7.6%	-
quadr. walk	9.6	-	-	9.7	9.3	-	1.5	-
pron. clamber	-	4.9	35.5	2.5	1.6	-	30.9	18.6
quadr. run	2.7	-	-	3.1	2.5	-	-	-
pron. clamber-run	-	-	1.2	-	-	-	-	1.0
contin. bound	1.0	-	-	-	-	1.2	-	-
climb up	1.1	-	-	-	1.1	2.4	-	1.0
climb down	-	-	-	-	-	1.8	-	-
hop	-	-	1.0	-	-	-	1.0	-
sidle down	-	-	-	-	-	-	-	-
swing down	-	-	-	-	-	1.0	-	-
shinny down	-	-	-	-	-	1.0	-	-
bridge	-	-	-	-	-	-	1.0	-
drop	-	-	-	-	-	-	-	4.0
Postural								
sit	41.4%	64.1%	35.0%	57.0%	51.8%	-	31.6%	57.7%
stand	2.7	6.8	9.8	4.6	3.1	-	11.0	7.6
vertical cling	14.2	3.4	-	-	8.5	47.9	1.3	1.5
perch	2.4	4.6	6.7	2.1	2.6	-	10.4	3.9
lie-side	-	3.5	1.0	3.8	-	-	-	-
lie-ventrum	1.9	5.2	1.4	5.5	2.5	-	-	1.5
bipedal stand	-	1.1	-	-	-	-	1.4	-
lean	-	1.0	-	-	1.0	-	-	-

Table 6.15. (cont'd.) Use of positional behavior on various supports.

	Diameter					
	<2	2-5	6-10	11-15	>15	mixed
Positional Behavior						
Locomotor						
leap	4.7%	13.2%	20.6%	24.8%	24.4%	3.7%
quadr. walk	1.0	8.2	8.0	4.9	3.7	-
pron. clamber	33.8	3.7	-	-	-	21.0
quadr. run	-	1.5	3.4	2.2	7.3	-
pron clamber-run	-	-	-	-	-	1.1
contin. bound	-	-	-	1.2	-	-
climb up	-	1.2	1.0	-	-	-
climb down	-	-	-	-	-	-
hop	-	-	-	-	1.2	1.0
sidle down	-	-	-	-	2.4	-
swing down	-	-	-	-	1.2	-
shinny down	-	-	-	-	1.2	-
bridge	-	-	-	-	-	-
drop	1.0	-	-	-	2.4	-
Postural						
sit	30.2%	46.5%	41.5%	42.5%	18.3%	53.0%
stand	11.0	4.3	2.2	1.2	6.1	8.1
vertical cling	1.9	10.6	12.7	18.5	28.1	1.2
perch	12.8	3.5	-	-	-	4.4
lie-side	-	1.0	1.7	-	-	1.6
lie-ventrum	-	2.1	4.0	-	3.7	2.6
bipedal stand	1.1	1.0	-	-	-	-
lean	-	-	-	-	-	-

Table 6.16. Positional behavior of Chiropotes during play.
(N=175)

Positional Behavior	
Locomotor	
quadrapedal run	8.6%
pronograde clamber	4.6
pronogr. clamber-run	17.7
leap	14.3
drop	2.9
hop	2.9
scamper	1.7
Total	52.7
Postural	
sit	16.7%
stand	6.3
perch	1.1
vertical cling	1.1
bipedal stand	2.3
pedal suspension	17.1
lie - dorsum	1.1
Total	45.7
Other (cumulative total of those behaviors each of which comprised <1% of samples)	1.7%

Table 6.17. Support use of Chiropotes during play.

Number	(N=169)
one	59.8%
two	8.9
several	31.4
Total	100.1

Inclination	(N=172)
horizontal	27.9%
angled	24.4
vertical	1.2
deformable	39.0
mixed	7.6
Total	100.1

Diameter	(N=167)
<2 cm	8.4%
2 - 5 cm	30.5
6 - 10 cm	22.8
11 - 15 cm	9.6
>15 cm	4.8
mix, <2 & 2-5cm	21.0
mix, 2-5 & 6-10cm	3.0
Total	100.1

Table 6.18. Supports used by Chiropotes within each tree portion.

Number of Supports:	1	2	3	(N)
Crown	71.2%	20.3%	8.5%	(3286)
Terminal Branches	24.5	19.0	56.4	(2130)
Bole	100.0	-	-	(6)
Vertical Axis	69.2	27.7	3.1	(65)
Below Crown	92.8	6.9	0.3	(346)
Liana	67.6	21.8	10.7	(216)
Vine Tangle	7.4	7.4	85.2	(108)

Support Inclination:	H	A	V	D	M	(N)
Crown	47.5%	38.2%	0.3%	7.8%	6.3%	(3276)
Terminal Branches	10.8	10.1	0.1	71.5	7.5	(2130)
Bole	33.3	16.7	50.0	-	-	(6)
Vertical Axis	15.6	48.4	12.5	6.3	17.2	(64)
Below Crown	37.7	57.7	1.2	1.5	2.0	(345)
Liana	24.1	30.6	10.2	27.8	7.4	(216)
Vine Tangle	13.9	1.9	-	30.6	53.7	(108)

H: horizontal A: angled V: vertical D: deformable
M: mixed

Table 6.18. (cont'd.)

Support diameter (cm)	<2	2-5	6-10	11-15	>15	<2,2-5	mix of 2-5 & 6-10	other mix
Crown	1.7%	30.0%	39.1%	12.7%	5.4%	4.1%	5.4%	1.7%
Terminal Branches	29.6	35.2	2.0	0.1	-	31.6	0.7	0.9
Bole	-	-	50.0	33.3	16.7	-	-	-
Vertical Axis	-	15.4	21.5	20.0	24.6	3.1	6.2	9.2
Below Crown	-	4.1	25.7	39.0	29.5	-	0.6	1.2
Liana	12.0	50.5	25.5	0.5	-	10.2	0.9	-
Vine Tangle	34.6	18.7	-	-	-	45.8	0.9	-

Table 6.19. Use of positional behavior in various tree portions (Chiropotes, N=6193).

	crn	tb	va	bc	lia	vt
Positional Behavior						
Locomotor						
quadrupedal walk	11.3%	3.5%	7.7%	18.7%	18.4%	1.9%
leap	6.9	10.0	6.2	7.8	4.6	1.9
quadrupedal run	6.0	1.0	3.1	12.4	5.5	-
pronograde clamber	5.1	18.4	-	1.0	7.8	36.5
pron. clamber-run	1.3	1.7	-	-	-	2.8
drop	1.1	5.0	3.1	1.2	-	-
bridge	-	1.9	1.5	-	-	-
climb up	-	-	7.7	-	6.9	-
climb down	-	-	-	-	4.6	1.0
hop	-	-	-	-	-	1.0
Total	31.7	41.5	29.3	41.1	47.8	45.1
Postural						
sit	42.3%	33.1%	40.0%	31.4%	28.6%	32.7%
stand	6.5	10.9	18.5	5.2	6.9	11.2
lie-ventrum	11.4	1.3	4.6	12.7	-	1.0
lie-side	2.0	-	-	6.1	-	-
bipedal stand	1.8	1.9	-	-	1.8	1.9
perch	1.7	8.0	-	-	2.3	5.6
suspension	1.0	1.8	-	-	2.8	2.8
lean	-	-	4.6	-	-	-
vertical cling	-	-	1.5	1.0	3.7	-
Total	66.7	57.0	69.2	56.4	46.1	55.2

Table 6.20. Use of positional behavior on various supports (*Chiropotes*, N=6204).

Positional Behavior	Number			sev.	H	Inclination			
	1	2	A			V	D	M	
Locomotor									
quadr. walk	16.6%	-	-	10.9%	16.8%	-	2.8%	-	
leap	8.6	2.3	9.6	5.9	7.9	10.0	11.3	5.4	
quadr. run	8.1	-	-	4.5	9.7	4.0	-	-	
pron. clamber	-	7.0	33.4	2.1	1.5	4.0	22.1	41.9	
pron clmbr-run	-	1.1	4.5	-	-	-	2.9	9.1	
drop	1.5	1.0	5.5	1.0	1.2	-	6.3	-	
bridge	-	-	1.9	-	-	-	2.3	-	
climb up	1.0	1.2	-	-	-	36.0	-	-	
climb down	-	-	-	-	-	12.0	-	-	
hop	-	-	-	-	1.0	-	-	-	
shinny up	-	-	-	-	-	4.0	-	-	
Total	35.8	12.6	54.9	24.4	38.1	70.0	47.7	56.4	
Postural									
sit	40.9%	48.5%	23.7%	45.0%	41.8%	8.0%	26.4%	23.7%	
stand	5.8	11.2	10.8	6.4	6.4	2.0	10.3	14.0	
lie-ventrum	7.7	13.4	2.7	15.0	6.0	-	-	1.1	
lie-side	1.1	4.5	-	2.4	2.3	-	-	-	
bipedal stand	2.1	1.9	-	2.0	1.1	2.0	1.8	-	
perch	3.4	4.2	4.6	2.4	2.0	-	8.2	2.2	
suspension	1.3	1.5	1.0	1.0	-	-	2.9	-	
lean	-	-	-	-	-	-	-	-	
vertical cling	-	-	-	-	-	10.0	-	-	
Total	62.3	85.2	42.8	74.2	59.6	22.0	49.6	41.0	

Table 6.20. (cont'd.) Use of positional behavior on various supports.

Diameter:	<2	2-5	6-10	11-15	>15	mixed
Positional Behavior						
Locomotor						
quadr. walk	1.0%	9.5%	16.6%	15.9%	12.2%	-
leap	12.4	9.0	7.8	5.7	2.7	4.6
quadr. run	-	3.1	9.8	9.3	5.7	-
pron. clamber	25.9	7.0	-	-	-	24.3
pron clmbr-run	1.5	1.4	-	-	-	3.9
drop	7.9	1.7	1.0	1.0	-	2.8
bridge	3.6	-	-	-	-	1.0
climb up	-	1.2	-	-	-	1.0
climb down	-	-	-	-	-	-
hop	-	-	-	-	-	-
shinny up	-	-	-	-	-	-
Total	52.3	32.9	35.2	31.9	20.6	37.6
Postural						
sit	21.5%	40.3%	41.7%	42.0%	47.3%	35.1%
stand	9.4	8.4	5.8	4.7	7.4	11.9
lie-ventrum	-	5.2	10.4	14.4	17.1	5.9
lie-side	-	-	1.3	3.8	2.4	2.1
bipedal stand	1.7	2.8	1.3	-	-	1.5
perch	9.4	5.7	1.1	-	-	3.8
suspension	3.1	1.6	-	-	-	1.0
lean	-	-	-	-	-	-
vertical cling	-	-	-	-	-	-
Total	45.1	64.0	61.6	64.9	74.2	61.3

Table 6.21. Use of positional behavior on various supports (*Cacajao*, N=675).

	Number			Inclination				
	1	2	sev.	H	A	V	D	M
Positional Behavior								
Locomotor								
leap	9.5%	3.7%	10.5%	5.8%	9.0%	23.1%	9.8%	6.9%
quadr. walk	25.1	-	-	19.6	24.1	7.7	2.4	-
pron. clamber	-	7.4	37.9	5.8	2.3	-	30.7	31.0
quadr. run	9.0	-	-	6.3	10.5	7.7	-	-
contin. bnd	-	-	-	-	-	-	-	-
climb up	2.3	-	-	-	1.0	23.1	-	-
climb down	-	-	-	-	-	-	-	-
hop	1.0	-	-	1.0	-	-	-	-
sidle down	-	-	-	-	-	-	-	-
swing down	-	-	-	-	-	-	-	-
shinny down	-	-	-	-	-	-	-	-
bridge	-	-	1.2	-	-	-	1.5	-
drop	2.0	1.2	9.3	1.7	1.5	-	8.3	-
pron. clmbr.-run	-	2.5	4.0	1.3	-	-	4.4	6.9
Postural								
sit	33.5%	50.6%	21.7%	40.0%	33.1%	15.4%	22.9%	37.9%
stand	3.8	7.4	7.7	3.3	6.8	-	8.3	13.8
vertical cling	1.2	-	-	-	-	15.4	-	-
perch	-	3.7	2.8	-	-	-	3.9	-
lie-side	-	3.7	-	1.0	1.5	-	-	-
lie-ventrum	5.2	14.8	4.4	10.0	9.0	-	2.4	-
bipedal stand	1.0	-	1.0	1.3	-	-	1.0	-
lean	-	1.2	-	-	-	-	-	-
bipedal suspension	1.7	2.5	1.6	9.8	-	-	2.4	-
bimanual suspension	-	1.2	-	-	-	-	1.0	3.5

Table 6.22. Take-off positions for leaping.

	<u>Pithecia</u> (N=939)	<u>Chiropotes</u> (N=420)
Locomotion		
pronograde clamber	12.9%	33.1%
quadrupedal walk	14.1	23.1
quadrupedal run	8.3	18.3
pronograde clamber-run	-	1.7
climb	1.0	-
Total	36.3	76.2
Posture		
vertical cling	51.3	-
stand	11.9	22.9
Total	63.2	22.9
Other	0.5	1.0

Chi-square = 340.04

df = 6

p<0.001

Table 6.23. Tree portions used in take-off and landing.

TAKE-OFF		
Tree Portion	<u>Pithecia</u> (N=879)	<u>Chiropotes</u> (N=408)
Main Crown	33.2%	46.1%
Terminal Branches	10.0	44.6
Vertical Axis	10.1	-
Below Crown	10.7	5.6
Bole	30.6	-
Liana	5.4	2.5
Total	100	98.8

Chi-square value = 338.82

df = 5

p<0.001

LANDING		
Tree Portion	<u>Pithecia</u> (N=647)	<u>Chiropotes</u> (N=227)
Main Crown	16.1%	5.7%
Terminal Branches	20.6	88.1
Vertical Axis	11.6	-
Below Crown	11.3	3.1
Bole	35.1	-
Liana	5.4	2.6
Total	100.1	99.5

Chi-square value = 333.40

df = 5

p<0.001

Table 6.24. Number of supports used in take-off and landing.

TAKE-OFF		
	<u>Pithecia</u> (N=896)	<u>Chiropotes</u> (N=407)
Number of Supports		
one	85.0%	60.7%
two	4.1	4.7
several	10.8	34.6
Total	99.9	100
Chi-square value = 108.55		
df = 2		
p<0.001		

LANDING		
	<u>Pithecia</u> (N=824)	<u>Chiropotes</u> (N=366)
Number of Supports		
one	84.3%	41.3%
two	1.7	2.5
several	14.0	56.3
Total	100	100.1
Chi-square value = 235.27		
df = 2		
p<0.001		

Table 6.25. Inclination of supports used for leap take-off and landing.

TAKE-OFF		
Inclination	<u>Pithecia</u> (N=892)	<u>Chiropotes</u> (N=408)
horizontal (0-20°)	13.1%	24.5%
angled (20-70°)	26.2	29.2
vertical (70-90°)	45.9	1.0
deformable	10.7	41.2
mixed	4.2	4.2
Total	100.1	100.1
Chi-square value =	329.03	df = 4 p<0.001

LANDING		
	<u>Pithecia</u> (N=828)	<u>Chiropotes</u> (N=367)
horizontal (0-20°)	8.2%	14.2%
angled (20-70°)	28.7	19.9
vertical (70-90°)	41.4	2.5
deformable	19.9	62.4
mixed	1.7	1.1
Total	99.9	100.1
Chi-square value =	287.49	df = 4 p<0.001

Table 6.26. Diameter of supports used for leap take-off and landing.

TAKE-OFF		
Diameter	<u>Pithecia</u> (N=887)	<u>Chiropotes</u> (N=407)
<2 cm	4.1%	20.2%
2-5 cm	41.2	33.9
6-10 cm	38.0	25.1
11-15 cm	10.3	6.9
>15 cm	1.9	1.5
mix, <2 & 2-5 cm	3.7	11.1
other mixed	1.0	1.5
Total	100.2	100.2
Ch-square value = 126.24 df = 6 p<0.001		
LANDING		
Diameter	<u>Pithecia</u> (N=821)	<u>Chiropotes</u> (N=366)
<2 cm	10.7%	42.4%
2-5 cm	41.3	17.5
6-10 cm	32.3	16.7
11-15 cm	9.3	7.1
>15 cm	1.5	1.1
mix, <2 & 2-5 cm	5.0	15.3
Total	100.1	100.1
Chi-square value = 222.97 df = 5 p<0.001		

Table 6.27. Leaping and relative height in trees.

Pithecia

Relative Ht. in tree	All Travel (N=1847)	Leaping (N=816)
90 - 100%	3.4	2.3
80 - 90	19.8	16.3
70 - 80	34.3	32.1
60 - 70	24.3	24.6
50 - 60	13.2	16.7
40 - 50	3.3	4.8
< 40	1.8	3.2

Chiropotes

Relative Ht. in tree	All Travel (N=1311)	Leaping (N=441)
90 - 100%	5.9	7.7
80 - 90	30.6	32.9
70 - 80	32.9	33.3
60 - 70	20.1	15.4
50 - 60	8.5	8.2
40 - 50	1.7	1.6
< 40	-	1.0

Chapter 7. PATTERNS OF PITHECIIN POSITIONAL ADAPTATIONS

A. Introduction

As stated in Chapter 1, the aim of this study is to investigate the positional adaptations of the Pitheciini in order to address some general questions concerning these adaptations and their evolution (from Chapter 1):

- 1) How are particular behavioral solutions to problems of locomotion and posture advantageous?
- 2) How did environmental forces select for adaptations, and under what conditions did they evolve?
- 3) Which positional adaptations are ancestral for the taxon Pitheciini and which are taxon-specific for each genus?

These questions can be addressed using either ecological or morphological lines of investigation, each with underlying phylogenetic constraints. In this study, variables from the ecological realm are investigated more thoroughly, although those dealing with morphological aspects are also considered. Many of the differences recorded between the species in positional behavior and habitat use can be correlated with variables from both of these aspects. Each ecological or anatomical variable imposes its own limits on positional behavior. For example, the location of food, particularly when located in the terminal branches, poses problems for the primates who try

to reach it. Forest structure and tree form (both of which differ between the forests inhabited by the various pitheciins) influence the positional behaviors that can be used within them. Body size constrains activities by limiting larger primates to certain portions of the tree, or by forcing them to evolve specializations enabling them to move within the entire tree. Smaller primates encounter problems in crossing gaps in the forest, and must compensate through behavioral or anatomical adaptations. Anatomical features thus serve to enable some kinds of behaviors to be performed more efficiently, as well as to constrain the range of positional behaviors. Positional behaviors are dependent upon the supports upon which a primate must move or balance itself. Thus, consistent associations are found between the positional behaviors exhibited by each species and the use of particular tree portions and supports.

Therefore, the behavioral repertoire of each species represents a mix of interacting variables, including body size, anatomical features, phylogenetic constraints on behavior and diet, forest structure and the location of food. These present a complex picture of intertwined causes and effects, making it difficult to tease apart the influence of each on the observed positional behavior. In order to begin to piece together (or rather pull apart) the puzzle is to investigate each variable separately, examine the associations between the variables, and test predictions

relating to each.

In the course of the following discussion, the specific predictions presented in Chapter 1 will be addressed in order to determine whether or not the data collected conform to the expected behavioral patterns. These predictions include: the relationship of body size with support use, gap crossing and balance; differences in positional behavior among the species while feeding, traveling and resting; comparisons of the species in the allopatric situation studied here with some of the same species when sympatric; and the effect of changes in canopy level on positional behavior.

These specific questions and predictions form part of the general questions concerning the phylogeny and adaptations of the Pitheciini, which will be addressed in the concluding chapter, having been synthesized with information dealing with ecology and morphology.

B. Considerations of Ecology

Positional behavior ultimately depends on habitat structure, with the intermediary of habitat use (height in tree, tree portions and characteristics of supports used). For each species, the use of particular tree portions and supports is associated with certain positional behaviors. All of the above, however, are dependent upon the location of food resources.

The first section below presents an overview of the patterns of positional behavior and habitat use exhibited by each species, and demonstrates how they are correlated with one another. The second section outlines features of the habitats of Pithecia and Chiropotes, and the implications of the observed differences for positional behavior and habitat use. In each section, intraspecific differences for Pithecia (if any) are discussed first, followed by interspecific comparisons; locomotor behaviors are discussed before postural behaviors. In the third section, an attempt is made to elucidate the nature of the relationship between positional behavior and diet in pitheciin primates, drawing from information on the location of food, characteristics of the feeding trees, and seasonal differences in positional behavior.

Correlations between positional behavior and habitat use

Intraspecific differences

Use of locomotor behaviors are quite similar between the two Pithecia groups; those used during feeding are the main exception. Group I uses more types of locomotor behavior (particularly pronograde clamber) while feeding, and with higher frequency, than does Group II (Table 6.1). This appears to be a partial result of more food-carrying by members of Group I. On Pithecia Island I, a juvenile howler monkey often followed the two Pithecia, and displaced them

from feeding trees. On many of these occasions, the Pithecia individuals frequently carried their food to another tree in order to feed.

Postural behaviors differ more than do locomotor behaviors between the groups. The most apparent difference is in the use of vertical clinging, which is more frequent in Group I than for Group II (Tables 6.1 and 6.3). This is related to the fact that the former tends to use the lower tree portions more frequently, particularly while feeding and traveling, and is consistently found at a lower height in the trees than is Group II. Group II used both the crown and the terminal branches more often, particularly for traveling (Table 6.4), while Group I seems to have substituted the use of lower tree portions.

Lying behavior differs in that Group II lies somewhat more frequently overall, and more often on the ventrum (Table 6.3). Interestingly, the males of Group II were seen lying exclusively on their ventrum, while the females were seldom observed in ventral lie (discussed again briefly on p. 327). The females of Group I divided their lying time between their ventrum and their side.

Although many of the differences between the groups in positional behavior and habitat use are statistically significant, each Pithecia group differs in the same way from Chiropotes and Cacajao, and are much more similar to one another than either is to Chiropotes or Cacajao.

Accordingly, pooled data for the two Pithecia groups are compared to that for Chiropotes and for Cacajao.

Interspecific differences

Differences among the species in positional behavior are far more apparent than are those within species. In general, while feeding (and, to a lesser degree, while resting) Pithecia engages in relatively fewer locomotor behaviors than postural, compared to Chiropotes and Cacajao (Table 6.5). During travel bouts, Pithecia was more often observed in momentary pauses, engaging in postural behavior (Table 6.6). In general, this species was less active than was either Chiropotes or Cacajao. Perhaps their lower activity level was contributed to by a lower quality diet, in that Pithecia consumes more leaves than the other two, and may need more time to digest them (e.g. Struhsaker and Oates, 1974). Another possibility is that its inactivity relates to its crypticity.

Throughout all activities, quadrupedalism is more frequent for Chiropotes and Cacajao than for Pithecia (Tables 6.5 to 6.7). In feeding, the use of quadrupedal walking can be related to both the location of food in the trees and to the structure of the trees used. After reaching fruit, most often located in the terminal branches, Chiropotes and Cacajao often carry it to a more solid support on which to feed. They also feed in trees which

have larger crowns, therefore requiring more traveling within each tree. In travel as well, quadrupedalism was observed more often for Chiropotes and Cacajao, probably because Pithecia often leaps where the former two would walk or run quadrupedally. Pithecia was not observed to engage in locomotor activities during resting bouts; Chiropotes and Cacajao each (although infrequently) walk quadrupedally (briefly) while engaging in resting bouts (see Table 4.2).

For Pithecia, pronograde clamber accounts for virtually all of the locomotor behavior during feeding (Table 6.5). However, for Chiropotes, and especially for Cacajao, other behaviors are used as well, and together equal almost the total percentage of pronograde clamber. This can be partially explained by the greater use of quadrupedal walk by Chiropotes and Cacajao, discussed in the previous paragraph.

Bridging was not observed during sampling for Pithecia, and was infrequently recorded for the other two species (Table 6.6). However, taken together with pronograde clambering and pronograde clamber-running, these activities do occupy a more substantial amount of time for the two larger genera; all of these behaviors typically take place in the terminal branch portion of the trees (Tables 6.12 and 6.16). While terminal branch use during feeding is similar for Pithecia and Chiropotes, this portion is used much more by Chiropotes than by Pithecia in travel and rest (Table

6.8).

Sitting behaviors, particularly during momentary pauses in travel, and while resting, are more frequent for Pithecia than for Chiropotes or Cacajao (Tables 6.6 and 6.7). Often, an angled sit is used, in the lower and central tree portions (bole, vertical axis, below crown), which are characterized by many highly angled supports. Sitting behavior, together with the frequent use of non-horizontal supports, may reflect the general tendency of Pithecia to maintain a more orthograde posture. Sitting, or other upright postures may be more conducive to vigilant behavior, which is possibly more important in a species with both a smaller group size and a smaller body size. Fleeing can be commenced more easily from a sitting than a lying posture; leaping especially can be initiated from the former.

Both standing and lying were more frequently observed for Chiropotes (and to some degree, Cacajao), and usually occurred on horizontal or near-horizontal supports, found primarily in the main crown (Tables 6.5 to 6.7). Chiropotes and Cacajao spend more time in this portion and on horizontal supports than does Pithecia (Tables 6.8, 6.10 to 6.12). Both of these species tend towards a more pronograde body orientation throughout their positional repertoire. While one-half of the lying samples for Pithecia are on their side, both Chiropotes and Cacajao spend the overwhelming majority of the time lying on their ventrum

(Table 6.7). Differences in the supports used by the species can be correlated with the behavioral differences. Pithecia, when lying, sometimes uses multiple (often two parallel) supports, and lies on its side, often with its back and legs flexed. Chiropotes and Cacajao more often lie on a single, large, horizontal support, and sprawl on their ventrum. For all species, a sprawl, the most efficient position for heat dissipation, appears to be more common for resting bouts during the day, while hunched sitting or lying postures are more commonly assumed for sleeping at night. In general, during the day, all species tend to rest lower in the trees, often on large supports, in a relatively open area of the crown or below crown. At night, all species move up higher in the trees. Pithecia tends to hide somewhat, and discourages being followed to its sleeping tree. Pithecia Group I sleeps in the same tree or set of trees, which are full-crowned with evergreen foliage; the animals can remain quite well hidden here. Chiropotes and Cacajao individuals are distributed throughout several adjoining large trees, often on the relatively solid forked branches nearest the fine supports in the terminal branch portion. This is probably, as Ayres (1986) discussed for Cacajao, an anti-predator strategy, allowing good visibility as well as the probability of feeling any vibration in the tree which would indicate the presence of predators. In the resting bouts during the day, some group members sleep

(probably lightly) while others groom or play. Therefore, some individuals are always alert enough to remain vigilant during these rest periods. When Chiropotes sleeps at night, the tail is often curled around the front of the body.

A very important difference among the species in postural behavior is in the use of vertical clinging by Pithecia, a behavior which is rarely used by either Chiropotes or Cacajao (Tables 6.5 to 6.7). This behavior is correlated with the frequent use of the lower tree portions, which are more likely to be vertical. During feeding, Pithecia sometimes clings to the bole of one tree while feeding from the terminal branches of a neighboring, smaller tree. In travel, vertical clinging is associated with momentary pauses between leaps. Differences in leaping, dropping and bounding among the pitheciins will be discussed in a separate section below. Vertical clinging was sampled in more than one-third of Pithecia's resting time on the vertical or near-vertical supports of the lower and central tree portions.

Pedal suspension was not recorded for Pithecia, and was observed in only one isolated incident (not during sampling), for descent between terminal branches. It plays a more important role in Chiropotes', and especially Cacajao's, positional repertoire (Tables 6.5 to 6.7). It was recorded most often in the context of terminal branch feeding; pedal suspension is also frequently used in play.

Cacajao uses this behavior more than does Chiropotes, engaging in it briefly even in momentary pauses during travel, and during resting bouts. Both Chiropotes and Cacajao were sampled more than Pithecia on branches which deform under their body weight, particularly during traveling and resting (Tables 6.10 to 6.12). Suspensory behaviors are most closely associated with terminal branch activities. It has been demonstrated (Grand, 1972), and may be the case here, that when food cannot be obtained by balancing on top of branches, underbranch postures are adopted, particularly by larger primates (discussed in more detail on p. 186).

Both Pithecia and Cacajao have been observed foraging on the ground (Ayres, 1986 for Cacajao; Kinzey and Norconk, 1993 and pers. obs. for Pithecia). Pithecia was also observed to descend to the ground twice to retrieve a fallen infant. Chiropotes does not forage on the ground, but was seen on the ground in only the one incident, described on p. 186. Ayres (1986) suggested that Cacajao may descend to the ground due to the lack of competition by terrestrial mammals in várzea forest, while Chiropotes does not because more potential competitors are found in terra firme forest. I would suggest that Cacajao may also be prompted to descend to the ground due to the lower fruit availability in the dry season, particularly since there is a lower overall species diversity in várzea than in terra firme forest (Ayres,

1986). Members of only one of the two Pithecia groups (Group I) come to the ground to forage, particularly in order to exploit the seeds of Capparis and Chrysophyllum, which have a higher protein content (Kinzey and Norconk, 1993). It must be kept in mind that Group II may also descend to the ground to feed, but it has not yet been observed. Since this has been observed a number of times for Group I and not at all for Group II, it is thought that this represents a real difference between the groups. The phenomenon of ground foraging by Group I and not by Group II could be due to one of several factors, including: lower food availability in this much smaller forest, which may be much more pronounced in the dry season, and the absence of potential terrestrial competitors, such as agouti, deer and curassow, which regularly inhabit Island II but not Island I.

Features of the habitats and implications for positional
behavior and habitat use

Crucial to the understanding of the characteristics that comprise species-specific positional behavior is establishing that the observed differences among species are due to the intrinsic nature of the animals, and not to the influence of the structure of the habitats in which they live. In order to establish this, and to tease apart the effects of habitat from inherited positional adaptations

(habitus vs. heritage: Gregory, 1914), features of the habitat must be quantitatively documented.

In this study, habitat analyses were conducted which provide an indication of the connectedness of the canopy, and aspects of support availability, tree form and tree size. A thorough quantification of these variables is extremely difficult, due to the complex nature of forests. Partly for the same reason, it is not possible to compare directly the availability with the use of various trees and supports. However, we can observe whether or not differences in support use and characteristics of trees used by the different species depart from one another in the same way as do the differences in availability of trees of various sizes and supports of various types in each habitat. Thus, each species may demonstrate its preference for trees and supports of particular aspect, and allow us to infer that the observed differences in positional behavior and habitat use are independent of the differences between habitats.

In this section, features of each habitat and the differences between them will be discussed in terms of their implications for positional behavior, and the observed positional behavior and habitat use are correlated with habitat structure. Characteristics of feeding trees, and location of pitheciin food in the trees will be discussed in the following section.

By examining different groups of a single species, we can hold constant the effects of anatomy and phylogeny, and assume that the variation observed between members of a single species is due to differences in habitat, food location and/or food availability. These intraspecific comparisons can indicate the kinds of differences that may be expected to occur with certain habitat features.

Connectedness of canopy

The connectedness of the canopy can be indicated to some degree by the percentage of overlap between neighboring tree crowns and by the density of trees. The presence of lianas, especially when single in form, can provide pathways between trees and eliminate the necessity for leaping or bridging between terminal branches.

Intraspecific differences

Crown overlap is approximately equal on the two "Pithecia" islands (average of 45% and 43%). This feature is a good indicator of potential pathways for primates which travel between crowns by using the terminal branches for access. However, since Pithecia often travels relatively low in the canopy using lower tree portions, tree density is a more relevant measure of canopy connectedness for this species. Average tree density differs greatly between the two "Pithecia" islands, with "Pithecia" Island II much more densely packed with trees than "Pithecia" Island I (41

compared to 28 trees within a 5 m radius of each sample point) (Table 5.1). In a forest with trees close together, with fewer discontinuities, it would be expected that leaping behavior may decrease. However, members of both groups leap to virtually the same degree (Table 6.2). Leaping behavior remains constant in spite of the fact that use of tree portions differs greatly (Table 6.4).

Lianas are approximately one and-a-half times more common on "Pithecia" Island I (Table 5.2) than on Island II (density is 1.7 and 0.6, respectively, on a 0 - 4 scale); corresponding to this difference in availability, Pithecia Group I used lianas and vine tangles more frequently than did Group II (Table 6.4). Group I frequently used a vine tangle "hideout" for resting and sometimes for feeding.

Interspecific differences

Overlap between crowns of neighboring trees potentially used by the pitheciins is somewhat greater on the "Pithecia" islands than on Danto Manchado, averaging 43 and 45% on the former, and 37% on the latter. As mentioned on the previous page, the relevance of canopy connectedness to the primates depends upon the level at which the animals cross gaps between trees.

Although crown overlap is greater on "Pithecia" islands, Pithecia does not take advantage of this overlap to cross gaps. Instead, Pithecia often descends to lower

levels or the lower part of the crown, often leaping between tree portions not in contact with one another.

Chiropotes tends to travel (including gap crossing) at a greater relative height in the trees than does Pithecia (Figure 6.19). Trees potentially used by Chiropotes are large (larger than 10 cm dbh) and often emergent, partly explaining the somewhat lower degree of overlap between their crowns than those used by Pithecia. These factors influence gap crossing behavior, which is typically leaping, dropping or bridging, primarily between terminal branches of neighboring trees (discussed further in section on leaping and habitat use, p.227). Therefore, Chiropotes travels more in the terminal branch portion than does Pithecia (Table 6.8), and uses more pronograde clambering and dropping, which, along with leaping, are the most important locomotor modes used in this portion (Table 6.19).

Tree density (for all trees greater than 2 cm dbh) is approximately equal on "Pithecia" I (28) and on Danto Manchado (26), while "Pithecia" II has much higher tree density (41) (Table 5.2). Pithecia uses trees of all sizes, while Chiropotes uses only the larger ones. Therefore, Pithecia has more trees close together available to it. The trees that Chiropotes uses are farther apart from one another for two reasons: 1) this species uses only about 20% of trees (those larger than 10 cm dbh), and 2) because the trees are quite large. It would not be possible for

Chiropotes to cross gaps at lower levels in their trees, since it can't cover the distance between them in a leap. Chiropotes uses higher tree portions (and relative heights) to cross gaps than does Pithecia.

In spite of the fact that lianas are the most common on Danto Manchado (density of 2.9 on a 0 - 4 scale) (Table 5.3), Pithecia uses lianas and vine tangles more than does Chiropotes in all activities (Table 6.8); this is particularly apparent for Group I. This may be partially explained by the fact that while Danto Manchado has the highest overall density of lianas, the form in which they occur is the least preferred for Chiropotes supports. Chiropotes much more frequently uses single lianas than those occurring in a liana or vine tangle. In only 10% of the strip sampling data points did lianas occur singly on Danto Manchado; most of the time they occurred together with liana/vine tangles (55%), or liana/vine tangles (35%) occurred alone (Table 5.3). This figure for singly-occurring lianas is much lower than for the other islands, for which it was 61% ("Pithecia" I) and 89% ("Pithecia" II).

Lianas can be used as a pathway to cross between trees, a support on which to sit while feeding, or from which to obtain food. They are used in very different ways by the pitheciin species. Of all samples in which lianas were used by Pithecia, fewer than 30% were for locomotor positions, while 65% of the samples were postural (Table 6.14).

Chiropotes, on the other hand, uses lianas virtually equally for locomotor and for postural positions (Table 6.19). It is possible that lianas are acting to increase canopy connectedness for Chiropotes, and this species uses them to cross between trees on Danto Manchado.

Support availability

Support use reflects the goal of a given activity, and therefore differs greatly between feeding, travel and rest. In feeding, the goal is to gain access to food, which is usually located in the terminal branches, or on fine supports within the main crown. It would be expected that travel modes are chosen which would allow an animal to move from one place to another in the most direct manner possible, expending the least amount of energy. Stability and balance are the important goals of resting behavior, allowing a primate to relax and/or sleep. Therefore, greater differences are observed among activities (feed, travel, rest) than among the species for any one activity.

Branch orientation and use of supports of various inclination

On "Pithecia" Island II and Danto Manchado, branch orientation was documented at three levels in each sampled tree, to be used as an indicator of the availability of supports of various inclinations. The frequency of vertical supports was virtually the same on both islands (13 and 14%)

(Table 5.4). However, Pithecia chose these supports more frequently in feed (9%), travel (20%) and rest (8%) than did Chiropotes for any activity (only 1.7% in travel). Angled supports were more common on "Pithecia" Island II (72%) than on Danto Manchado (61%) (Table 5.4). However, in both feeding and travel, use of angled supports was approximately equal between the two species (Tables 6.10 and 6.11). Only in rest did Pithecia choose somewhat more angled supports than did Chiropotes (41% compared to 33%) (Table 6.12). A higher frequency of horizontal supports were sampled for trees on Danto Manchado than on "Pithecia" II (24% compared to 15%) (Table 5.4). Chiropotes does, in fact, use considerably more horizontal supports than does Pithecia in all activities (Tables 6.10 - 6.12), but this is most evident during resting bouts (Table 6.12).

Supports used by Pithecia and Chiropotes in each tree portion

An additional way of gauging support availability is by their use by the primates, which has implications for the availability of supports in different parts of the tree. Primates consistently choose certain types of supports within each tree portion, and comparisons between pitheciin species demonstrate that support use in each tree portion is quite similar among species (for example, between Pithecia and Chiropotes, for whom these data were collected). Ideally, these data should be compared to information about

the actual form of the trees, in order to examine what is preferred by the primates relative to what is actually available. Data were collected to this end in this study for the inclination of branches in the tree crowns. A means to accurately assess support preference has yet to be discovered (Rose, 1979), and must involve some way of quantitatively detailing the form of trees in a forest. However, for now, we can compare the data on support preference to information which we intuitively know about most trees. Although the diameter of supports depends on overall tree size, we know that each tree portion characteristically has certain numbers and inclinations of supports available to any primate which may be passing through or resting in it. For example, the vertical axis and bole of most trees is usually vertical or highly angled, and usually offers only one support at a time for a primate to use. On the other hand, a typical terminal branch portion has many relatively small, often deformable, supports. A crown is more variable, but is usually composed of horizontal and angled supports. The results outlined below on support preference in each tree portion can be compared to these very general statements above, and it is evident that the two are very comparable. I believe that the types of supports the primates are choosing in each tree portion provide a relatively accurate representation of what is available, based partly on the fact that the two species

compared are so similar in this regard as well as the consistency of support types in each tree portion (as discussed above). The differences in habitat use between the primates is related primarily to the choice of different tree portions by each species, and the relative heights at which they occur. Data were presented in Tables 5.8 and 5.9 (to be moved to Chapter 6), and are summarized below. Only the primary two or three variates for each variable are mentioned in this summary.

Only Pithecia uses the bole; supports taken on the bole are virtually always single, usually vertical, and sometimes angled. Diameter of these supports are primarily 5-10 cm, followed by 2-5 cm, then 11-15 cm. The vertical axis is used primarily as a single support by both species, but dual supports are sometimes taken, more often by Chiropotes than by Pithecia. Angled supports are the primary ones used by both species; Pithecia uses vertical supports as well. Pithecia uses smaller supports in the vertical axis than does Chiropotes. Below crown is virtually identical to vertical axis in terms of the number of supports used; support inclination is by far most frequently angled, and secondarily horizontal (more for Chiropotes than Pithecia). Again, the diameter of the supports used in this portion differ, with Chiropotes using larger branches. In the main crown, a single support is most frequently used, but dual supports are used quite often as well. While the

inclination of the primary supports used in this portion are divided evenly between horizontal and angled for Pithecia, Chiropotes uses somewhat more horizontal than angled supports. Larger supports are used by the latter species. In the terminal branch portion, supports used are by far most often multiple, deformable and of the two smallest (<2 and 2-5 cm) size classes, or a mix of these two classes. Lianas are typically taken as a single support by both species. Supports used are most often angled, but also relatively frequently horizontal, and in the case of Chiropotes, sometimes deformable. By far the most often-used diameter for lianas used by Pithecia is that of 2-5 cm; that of 6-10 cm is used much less frequently. Supports used in vine tangles are most often taken several at a time, are deformable or of mixed inclination, and are from the smallest two size classes.

Size and form of trees

The presence of trees of various sizes and forms can be documented by the collection of data on several variables: dbh, tree height, bole height and crown diameter. Again, feeding trees will be discussed separately.

Intraspecific differences

Trees are, on the average, about three-quarters of a meter shorter on "Pithecia" Island I than on Island II (6.7 m compared to 7.6 m) (Table 5.1). Group I tends to

remain, overall, lower in the canopy by an average of almost one meter (p. 160), and even came down to the ground a number of times to forage (p. 159).

Differences between the other tree characteristics (relative bole height and crown diameter) on the two "Pithecia" islands are few (Table 5.1).

Interspecific differences

The differences listed below are all related to the presence of larger trees on Danto Manchado than on the "Pithecia" islands. Of these trees, Chiropotes chooses to use the largest.

On "Pithecia" island I and II, average dbh for trees larger than 2 cm dbh was 7.4 cm and 6.6 cm, respectively (Table 5.1). On Danto Manchado, the average dbh for all trees larger than 2 cm dbh was 8.4 cm. Of these, only 20% were greater than 10 cm, large enough to be used by Chiropotes. The remaining variables discussed for trees on Danto Manchado refer only to these larger trees.

On "Pithecia" islands, trees potentially used by Pithecia (at least 2 cm dbh) average 7.2 m in height, while the average height of trees used by Pithecia is 9.6 m. Trees on Danto Manchado potentially used by Chiropotes (at least 10 cm dbh) average 12 m; the average height of trees actually chosen by Chiropotes is 18 m. More relevant than the absolute height of trees and of the height at which

pitheciins occurred, is the relative heights at which the monkeys are found, which is independent of the differences in tree heights between the islands. Pithecia is found at lower relative heights than is Chiropotes.

Relative bole height is greater on the "Pithecia" islands (average of 50% of tree height) than on Danto Manchado (41%) (Table 5.1), signifying that larger (taller) average crowns occur on the latter island. Many trees used by Pithecia (particularly on Pithecia Island II) have very short (vertically) crowns, with a very long bole or vertical axis. In these trees, branching occurs only near the vertical extent of the tree.

Crown diameter is much larger for Danto Manchado trees than those on "Pithecia" islands (7.7 m compared to 3.9 m) (from Table 5.1). Trees used by Chiropotes are often wide-crowned, and characterized by many large, horizontal or near-horizontal supports in the main crown. The use of the main crown is especially apparent for resting Chiropotes (Table 6.8), for which large, horizontal supports are those primarily used (in about 60% of resting bouts) (Table 6.12). Likewise, Cacajao uses mainly single, large, horizontal supports for resting. Tree structure, therefore, may partially explain the more frequent use of the main crown by Chiropotes than by Pithecia. Pithecia more often uses trees with small, often irregular crowns.

Summary: significance of habitat differences

Intraspecific differences

As mentioned previously, intraspecific comparisons can provide important clues to the intrinsic nature of a species, with the differences between conspecifics attributed to habitat, food availability, etc. The differences in positional behavior between the two groups of Pithecia are different enough to exhibit statistical significance. However, the high X^2 statistic may be due, in part, to the large number of observations involved, and it must be kept in mind that comparisons that are statistically significant may not necessarily be biologically significant. Overall, differences in positional behavior are not great between the two Pithecia groups, and are much more similar to one another than either is to Chiropotes or Cacajao.

The primary differences between the two groups is in use of tree portions (Table 6.4), where Group II uses the terminal branches and main crown more extensively than does Group I. The latter remains lower in the canopy, using the lower tree portions. These differences are difficult to explain in terms of habitat characteristics. Further investigation into the distribution of food in the two forests should be conducted in order to elucidate whether this is a factor contributing to the observed differences.

Differences between the habitats of the two islands are exhibited primarily in tree density, liana density and tree

size. It is not known what effect, if any, the difference in tree density has on the positional behavior and habitat use of the two Pithecia groups. It would be expected that lower tree density should lead to more leaping between the trees, but leaping behavior remains constant between the two groups. Second, with the knowledge that leaping is virtually the same, it might be expected that in a forest such as that on "Pithecia" I, with lower tree density (and therefore more discontinuous canopy), "Pithecia" Group I might move to higher levels, move to branch ends using pronograde clamber, or quadrupedal walk/run, and cross gaps by leaping (often downward), dropping or bridging (as does Chiropotes, and presumably Cacajao). However, on "Pithecia" Island I, even lower canopy levels are used.

Difference in liana density on the two islands is in fact correlated with liana use; both the availability of lianas and their use is much higher on "Pithecia" I than on "Pithecia" II.

Tree heights are different as well, and the group which tends to be lower in the canopy by an average of approximately one meter occurs in a forest ("Pithecia" I) in which trees are, on average, about one meter shorter than on "Pithecia" Island II.

Overall, positional behavior is quite similar among groups of the species P. pithecia. This is comparable to the results of Garber and Preutz (1993), who found that

despite habitat differences, positional behavior was highly similar between two groups of Saguinus mystax, although support use differed somewhat.

In order to separate the effects of various factors on positional behavior and habitat use, intraspecific comparisons are more relevant and useful than are those made between species.

Interspecific differences

Again, the differences in habitat structure are difficult to compare directly with habitat use and positional behavior, but we can observe whether the differences of each fall in the same direction. An additional confounding factor is that some features of the habitat may influence the habitat use and/or positional behavior of one species, but not another. For example, the degree of crown overlap is probably more relevant for Chiropotes than for Pithecia. This is primarily due to the use of different forest levels by the two species, with Pithecia using lower levels than Chiropotes.

The features relating to canopy connectedness: crown overlap, tree density and lianas, are dependent upon the canopy level used; it is therefore difficult to separate the effects of habitat on positional behavior and habitat use from species-specific behavior.

Comparing support availability with support use appears

to be quite useful. Predicting support use of Pithecia and Chiropotes from the availability of sampled supports, it would be expected that vertical supports would be used equally by the two species, angled supports slightly more by Pithecia than by Chiropotes, and horizontal supports somewhat more by Chiropotes. However, vertical supports are chosen much more frequently by Pithecia than by Chiropotes in any activity. Use of angled supports is similar by both species. Throughout all activities, Chiropotes chooses horizontal supports more than does Pithecia. This is to be expected; however, the degree of difference in the use of horizontal supports appears to be greater than would be predicted by their availability.

Given a particular tree form, both species use supports with similar characteristics in each tree portion (Tables 6.13 and 6.18); indeed, the overall availability of certain types of supports in each tree portion appears to be similar among the trees on all islands (discussed on p. 299). The exception is that diameters of supports in some portions are larger, due to the presence of much larger trees on Danto Manchado than on the other islands. The more apparent, and more important, differences lie in the tree portions used, which determine the supports available.

Both Pithecia and Chiropotes choose to use trees which are taller than average, with even larger trees chosen for feeding (discussed in the next section). When comparing the

relative bole height of the primates in the trees, differences in tree structure between the two islands should be kept in mind. Trees on Danto Manchado tend to have taller crowns. Therefore, at the same relative height, Pithecia may be in a lower tree portion than Chiropotes. For example, at 60% of tree height on the "Pithecia" islands, Pithecia is likely to be in the vertical axis or below crown portion, while on Danto Manchado, Chiropotes may be well into the main crown.

Relationship between diet and positional behavior

One of the goals of this study was to attempt to elucidate the nature of the relationship of diet to positional behavior. It has been demonstrated in previous studies (i.e., Fleagle, 1984) that no direct relationship exists between positional behavior and diet per se.

Rarely has a biorole relating to diet been discerned for a particular pattern of positional behavior. An exception, Cebuella (Kinzey et al., 1975) or Callithrix (e.g., Garber, 1980) is due to the fact that the observed positional behaviors were related to the location of food (gum on vertical trunks), not the type of food eaten. Animals go where their food is, and the modes used to arrive depend on the supports available enroute and the location of the food.

Location of food

The location of pitheciin foods in the canopy can be inferred to a large degree by where the primates actually obtain it. The tree portion from which food was obtained was recorded for Pithecia and Chiropotes (Table 6.9). The part of the tree most often used to reach food is the terminal branch portion, from which food is obtained in about two-thirds of the samples for both species. The main crown of the tree and lianas also provide significant amounts of food, together comprising almost the other one-third of the samples. However, Pithecia and Chiropotes each uses these portions to differing degrees; Pithecia uses lianas somewhat more frequently, while Chiropotes uses the main crown. Very little food is obtained in other portions, except for a small percentage from the ground (Pithecia only), and from vine tangles.

Although highly variable, certain classes of foods typically occur in particular tree portions, and each tree species exhibits a characteristic distribution of foods within its crown. In general, fruit most often occurs in the outer portions of a tree, on the terminal branches. It can occur within the main crown as well, on small branches. Flowers, of course, occur in the same locations of the fruits which will replace them. Young leaves (typically the only ones eaten by Pithecia) usually occur near the ends of terminal branches. Insects can be found anywhere; the ones

eaten most often by Pithecia, ants, are usually taken from large supports on the vertical axis, below the crown or in the main crown. Chiropotes often forages for insects in dead leaves. This species often uses a branch in the main crown or below crown for support, sometimes standing bipedally to reach a bunch of dead leaves on small branches within the crown.

When examining the location of food in the tree, the form and size of the tree must be taken into account, as the feasibility of reaching for food can differ depending on the distance from the vertical axis to the terminal branches. The location of foods in the particular species of feeding trees used by Pithecia and Chiropotes will be discussed below, together with qualitative and quantitative characteristics of their feeding trees, and how they are utilized by the primates.

Location of food compared to where eaten

A comparison of the tree portions used by feeding Pithecia and Chiropotes (Table 6.4) to the tree portions from which the food was obtained (Table 6.9), demonstrates that these primates often do not eat in the same place where food is found. The pattern is similar for both species. The crown is used approximately twice as frequently for a support alone as for when food is obtained there as well. The terminal branches provide most (over two-thirds) of the

food, but only one-half (or fewer) of their supports. Likewise, lianas are used three to four times as frequently for obtaining food as for supports (they provide more frequent supports for Pithecia than for Chiropotes). On the other hand, vine tangles seldom provide food, but are sometimes used as supports while feeding. For Pithecia, the central and lower tree portions make up one-fifth of their feeding supports, but less than two percent of their food is found there.

These results clearly indicate that individuals are reaching for their food from a different tree portion (or different tree), or that food is often carried to a different location from where it was harvested. The former is exhibited by Pithecia much more frequently than by Chiropotes or Cacajao, while the two larger species often carried their food before settling down to eat. The latter may be related to body size; Chiropotes and Cacajao may have more problems balancing in the terminal branches, so move to larger supports on which to feed. While in the lower tree portions, most of the feeding time spent by Pithecia is in a vertical cling, harvesting food from the terminal branches of a neighboring, smaller tree. All pitheciin species stand bipedally in the crown to reach for food in the terminal branches, and Chiropotes (and Cacajao) accomplishes the same goal by bipedal suspension. When Pithecia obtains food from the ground, it most often descends only to pick up some

fruit, or perhaps to search for more, then returns to the safety of a tree.

Characteristics of feeding trees and some strategies for harvesting foods

In comparing feeding trees of Pithecia and Chiropotes (Table 5.5) with those of the sampled trees in plots on "Pithecia" Island II and Danto Manchado (Table 5.1), some consistent patterns emerge. Preliminary observations of the feeding trees of Cacajao demonstrated that they were quite similar to those of Chiropotes in size and form. Analysis of trees in Cacajao's habitat was not conducted. Both Pithecia and Chiropotes, but particularly Chiropotes, feed from trees which are much larger than most trees in the forest, as evidenced by comparison of measurements of dbh, tree height and crown diameter. The crowns of feeding trees tend to be larger (taller) - that is, relative bole height is shorter for these trees than for other island trees. The overlap with neighboring trees is higher for Pithecia feeding trees than it is for other sampled trees on Island II, perhaps because many of these trees are in the intermediate or higher forest, and because there are few emergents. On Danto Manchado, however, the crowns of Chiropotes' feeding trees tend to overlap less with their neighbors than do most trees on the island (even taking into account that the sample comprises the larger trees, with dbh

greater than 10 cm). Chiropotes tends to feed from larger trees, whose crowns are often higher than much of the surrounding vegetation; a number of individuals can feed in the same such tree at once.

Outlined below is the location of food in five species of feeding trees of Chiropotes and Pithecia (from Table 5.5), as well as a description of the general form of the trees. Typically, location of food and tree form are very consistent within a species.

Of the five primary feeding tree species used by Pithecia, two consistently have irregular branching patterns. The form of Connarus venezuelanus and Coccoloba latifolia influence the supports used by Pithecia to obtain food. Fruits of Connarus (of which Pithecia eats the seeds) are located primarily in the terminal branches. The crown of this tree is often small, and while Pithecia may harvest the food while sitting in the terminal branch portion, it may also sit (or stand) on a support within the main crown and reach up into the terminal branches. The small drupes of Coccoloba are located in the terminal branches as well as the main crown, the latter of which is small and irregular. Terminal branches can often be reached easily from the few supports in the main crown or from the vertical axis. Erythroxylum steyermarkii's small fruits are found in the terminal branches. This tree species is often quite small, and the terminal branches too fine to support even Pithecia.

Pithecia often uses the bole or vertical axis of a neighboring tree in order to harvest the fruits from the terminal branches of Erythroxylum. The two remaining tree species listed in Table 5.5, Peltogyne floribunda and Licania discolor, are large, and their crowns have a regular shape. Fruits of both (from which seeds are utilized) are located in the terminal branches as well as on small branches in the main crown.

The tree species used by Chiropotes on Danto Manchado are generally large, with regular branching patterns and large-diameter crowns, with the exception of one. Coccaloba fallax is similar in form to the species of Coccaloba utilized by Pithecia, mentioned in the previous paragraph. Chiropotes obtains fruits from these trees as well from the vertical axis or main crown. Chrysophyllum lucentofolium typically has a rounded, regular crown, and fruits are distributed evenly throughout. Most fruit appears to be obtainable to Chiropotes from a sitting or standing (sometimes bipedally) position, and it is most often eaten where it is harvested. Pradosia caracasana, Brosimum guianense and Melicoccus bijugatus are all large trees, and are usually emergent over the surrounding vegetation (particularly the latter two). For Pradosia, fruits are located in the terminal branches as well as in the main crown; those of the other two species are more often distributed in the terminal branches, and less in the crown.

Of these five feeding tree species, it is most often in the latter three that pedal suspension is exhibited; Chiropotes suspends from a branch relatively far out in the crown, or in the terminal branches, to reach fruit in this portion. Much locomotion during feeding occurs in these three tree species (or others with the same form); after grasping fruit, Chiropotes often carries it in its mouth or hand to a branch in the main crown, where it sits to feed. Pradosia, which has the hardest husk (of these three species), is most often carried to a solid support for feeding, since preparation time is greater for this fruit.

Seasonal variation in positional behavior

It would be expected that if differences in positional behavior and habitat use between wet and dry months were in fact related to a discernable variation in food availability, differences would be more apparent in feeding bouts than in travel or especially in rest. Comparisons between positional behavior and habitat in these different seasons did not provide any clear picture of divergence corresponding to differences in food availability. Month-to-month variation, at least for some pairs of months, appear to be as great as that between seasons.

Differences in positional behavior and habitat use would only be expected if the dietary shifts influence the tree portions to be used. However, for example, in dry

seasons, when Pithecia eats more flowers and more leaves (Kinzey and Norconk, 1993), flowers are found in the same tree portions as the fruits, and the latter further out at the ends of branches. No differences could be distinguished relating to either an increase in terminal branch feeding, or feeding from a bole while harvesting leaves on neighboring small trees.

The diet of Chiropotes does not shift greatly in times of low fruit availability. Generally, a few key species (e.g., Pradosia) are depended upon; these do not differ from those used during more abundant months. Although a particularly dry month was evidenced during the course of the study (February 1991), no differences in either species could be discerned which related to associated dietary shifts. It is possible that only in a very lean season, where a dietary shift is drastic, that differences in positional behavior or habitat use could be distinguished.

Feeding strategies and their relation to food location and tree form

Positional strategies used for feeding differ among the species, based partly on the form of their feeding trees, and on body size. Location of food is similar in trees used by both Pithecia and Chiropotes, and is primarily in the terminal branches. Pithecia probably has the fewest problems in reaching food in this portion, and in balancing

there. Chiropotes and Cacajao, while in the terminal branches, exhibit more locomotion than does Pithecia, perhaps because it is easier for these larger-bodied platyrrhines to move across small supports than to balance on top of them (see Tables 6.14 and 6.19, for positional behavior in tree portions). Additionally, pedal suspension may be a specialization for obtaining food otherwise unreachable by Chiropotes and Cacajao (see also p. 327 for discussion of body size). Pithecia has the ability to access food in locations probably inaccessible for Chiropotes (or Cacajao), on the terminal branches of very small trees, which it reaches by vertically clinging to the bole of a neighboring tree.

Summary and conclusions: relationship of diet to positional behavior?

As discussed by Fleagle (1984), and corroborated in this study, the relationship between positional behavior and diet is probably not a direct one, and its nature still eludes us. I don't believe it is fruitful to search for a direct correlation between a food type and a set of positional behaviors. Of greater importance is the location of foods, and the form of the trees (and lianas) in which they are found. These factors influence how (and if) the food can be reached. Even so, examining only the relationship between feeding and positional adaptations may

not be enough. It is probable that no one selective force (such as diet or location of food sources) influences the evolution of positional adaptations, but they are due to a number of interrelated factors, both ecological and phylogenetic. Since the pitheciin species obtain the bulk of their food from a similar location (the terminal branches), it may be expected that their positional behavior and habitat use should be similar as well. The fact that it is not, and that they exploit their food in different ways, indicates that other variables are involved. Obviously, positional adaptations which evolve for certain feeding modes will influence locomotor behavior in travel as well, since the same body carries out both activities. The opposite is true as well. For example, Pithecia is specialized in its locomotor adaptations as a vertical clinger and leaper, which appears to be associated with the use of lower forest levels, lower/central tree portions, and more specifically, vertical and angled supports. I presume that this specialization evolved as a locomotor adaptation, for traveling. Pithecia differs from Chiropotes and Cacajao in its feeding behavior, to a large degree, because of its use of vertical supports in a vertical cling posture (in 11% of its feeding samples). This capability allows Pithecia access to foods in the terminal branches of small trees, which is probably inaccessible to Chiropotes or to Cacajao. Thus, an adaptation which originally evolved for efficient

traveling is used for feeding as well. Unlike some of the other vertical clingers (e.g., Cebuella), whose adaptation is related to the exploitation of gum on large vertical supports, Pithecia's specialization may not relate to feeding at all. In fact, a range of evidence suggests that positional behaviors associated with traveling may be more conservative than are those associated with feeding.

The similarities in positional behavior and canopy level between the two groups of Pithecia are most apparent in travel (Table 6.2 and Figure 6.19), while the groups differ in feeding and rest (Table 6.1, 6.3 and Figure 6.19). Pithecia in Guri ascends into the canopy to feed, and descends somewhat to travel and to rest. Compared to observations in Surinam (although sparse), Pithecia was observed feeding only at lower levels (W. Kinzey, pers. comm.). This may indicate some degree of competitive release at the Guri site, whereby Pithecia can exploit some areas of the forest which it only uses in the absence of Chiropotes. Additionally, a similar degree of leaping occurs in both Pithecia groups at Guri, even though canopy connectedness differs. While highly speculative, these factors indicate that behaviors used in travel are more conservative than are those used in feeding. This is the opposite of that which would be expected, since feeding behaviors have been shown to differ less among (sympatric) species than do traveling behaviors (see p. 5).

It is possible that feeding behaviors are more labile in order for individuals to cope with changes in their environment (e.g., seasonal differences in food availability), or possibly the presence of competitors. If locomotor behaviors used in travel are in fact more conservative than the (primarily) postural behaviors used in feeding, this may reflect the importance of "critical behaviors" (presumably most locomotor) in shaping the behavioral repertoire. These behaviors have presumably been selected for their maximum efficiency in predator escape. More data are needed, however, particularly regarding the canopy levels used by P. pithecia where sympatric with Chiropotes.

The location of food differs from where it is eaten, due, for Chiropotes and Cacajao, to their larger body size. These two species carry food from the terminal branches to more solid supports on which to feed. For Pithecia, it is due to its vertical clinging capabilities, which allows it to harvest food from the terminal branches of small trees while clinging to a nearby bole.

Trees used for feeding are larger than average trees on each island; for Chiropotes especially, they are very large, with wide, deep crowns, and are usually regular in form. Trees used by Pithecia are more likely than those of Chiropotes to be irregular in their branching pattern, and have small crowns; food in their terminal branches can often

be reached from one of the branches in the main crown, or the vertical axis. Tree size and tree form may influence the observed behavior, such that more movement would be expected to occur within large tree crowns, with spreading branches and food out on the terminal branches. The influence of body size, which makes postural behavior on terminal branches more difficult (probably more so for the short-tailed Cacajao), would also tend to encourage that more solid supports would be sought for food preparation. On the other hand, the small crowns of Pithecia trees would discourage much locomotion during feeding. Food can be obtained with less movement around the feeding tree; it is often possible to sit on a solid support in the main crown and harvest food from the terminal branches. However, while tree form and features of the habitat appear to influence the immediate behavior of the primates, they may not have been an important factor in their evolution.

The comparison of data from different seasons did not distinguish any differences associated with seasonal dietary shifts, as the use of tree portions remains similar from month to month. Most of the differences exhibited between the wet and dry months were also exhibited between different months of the same season. However, the occurrence of a lean season and a more drastic dietary shift, for example making it necessary to depend on a single type of food which is somewhat different than usual, may cause greater

differences. It is possible that lean seasons initially had a great deal of influence in the shaping of dietary and positional adaptations (if, in fact, positional adaptations are formed partly as a result of diet).

Therefore, looking at diet alone in the search for the evolutionary forces selecting for positional adaptations appears too narrow an endeavor. A range of variables need to be examined, including the distribution of food in the forest, group size, ranging patterns, lean seasons, possible effects of competition for both space and food, and predation.

C. Considerations of Morphology

Because of the differential forces on bodies and features of various forms and sizes, differences in both features of skeletal anatomy and in body size affect positional behavior. It should be kept in mind that in the classification of positional behavior each category must be examined in terms of the qualitative differences that exist between species. The diverse forms of the "same" behavior may result in different anatomical adaptations, each evolving in response to a different set of forces acting on the body. The form, or manner, by which a behavior is conducted may be at least as important as its frequency in selecting for anatomical features.

Differences in morphology and body size are examined

below, in relation to the associated behaviors of the three pitheciin species. Concluding this section is a brief analysis of the form and use of the tail in pitheciins.

Positional behavior and skeletal anatomy

Shared features of the three pitheciins were outlined on p. 51. These features, compared with those of atelines and cebines, demonstrated that pitheciins have more mobility at the shoulder than do cebines, but less than atelines. A relatively mobile knee joint is also exhibited by pitheciins. Capabilities for a wide range of motion at the shoulder, and a mobile knee, may be important for the pitheciins. While the cebines (particularly Saimiri) and the other smaller platyrrhines (callitrichids, and the Aotini) may have little problem with balance because of a large branch/body size ratio, the larger pitheciins are faced with more such problems, as the base of support becomes smaller as the branch/body size ratio decreases. Abduction of the limbs can lower the center of gravity, reducing these problems; relatively mobile joints make these abducted positions possible.

Within the Pitheciini, the primary behavioral differences between Pithecia and Chiropotes/Cacajao are the use of vertical clinging and leaping by the former species, as well as differences in the manner in which they leap, and the more frequent use of quadrupedal activities (including

pronograde clambering and bridging) by the latter two. Only Chiropotes and Cacajao utilize pedal suspension. Leaping and its associated anatomical features are discussed separately in the following section.

The following anatomical features, recorded by Fleagle and Meldrum (1988) can be correlated with the observed behavioral differences in Pithecia and Chiropotes. These features can be grouped into several functional classes. These classes: allow either a wide range of motion, or greater stability, at the shoulder; relate to a retracted humerus and flexed elbow; reflect the relative importance of the hindlimb or the forelimb in locomotion; and indicate the range of motion of the foot, and specifically, foot eversion. Fleagle and Meldrum's preliminary analysis on a small sample of Cacajao showed that it resembled Chiropotes in most features.

1) The greater range of motion at the shoulder joint in Pithecia than Chiropotes is attested to by the shape of the glenoid fossa, which is rounded in Pithecia and more elongate in Chiropotes, as well as the form of the humeral head, which has a more expanded articular surface in Pithecia. More stability in the forelimb of Chiropotes is apparent, demonstrating a more important role in weight-bearing than for Pithecia. The humerus is more robust, and the greater and lesser tuberosities are larger than for Pithecia. The elbow joint of Chiropotes is more stable than

that of Pithecia. Greater stability at the forelimb joints would be expected from a more quadruped primate - these features are evident in Chiropotes.

2) Capability for powerful humeral retraction in Pithecia is indicated by a large flange on the scapula (for the origin of the teres major muscle), which can lengthen the muscle's moment arm. Pithecia exhibits an almost cylindrical (rather than lipped) humeral trochlear shape, reflecting the use of the elbow in a habitually flexed position. These features may correlate with frequent clinging behaviors.

3) Limb proportions, particularly the relatively longer hindlimbs of Pithecia (mean intermembral index is 76), indicate the importance of the hindlimbs in Pithecia locomotion, particularly in providing propulsion for leaps. The intermembral index is higher in Chiropotes (mean is 83), indicative of approximately equal use of both fore- and hindlimbs in weight-bearing; therefore, more quadrupedal behaviors would be expected.

4) Range of motion at the foot of Chiropotes is demonstrated by: bulbous talar head with a dorso-lateral extension of the articular surface, laterally expanded calcaneocuboid articular surface, enlarged peroneal tubercle and short cuboid. As demonstrated by Jenkins and McClearn (1984) for some arboreal mammals, these features are associated with hindfoot reversal. They are thus thought to

be functionally related to the hindlimb suspension characteristic of Chiropotes (and especially Cacajao).

Positional Behavior and Body Size

As previously mentioned, body size may influence behavior in numerous ways. The prediction that the larger species of pitheciins would engage more frequently in lying behavior is supported here; the larger-bodied Chiropotes and Cacajao spend much more time in lying postures than does the smaller-bodied Pithecia, which sits more (Table 6.7). Male Pithecia, which are somewhat (22%) larger than the females, lie the most, particularly on the ventrum. The two larger pitheciin species use larger supports than does Pithecia while resting, although not while feeding or traveling (Tables 6.10 to 6.12).

Primates of different body sizes solve problems of balance and gap-crossing in different ways. Grand (1972) predicted that, in order to expand their feeding sphere, larger primates should utilize more underbranch suspension while feeding in the terminal branches. Chiropotes and Cacajao engage in suspensory activity (particularly pedal suspension) far more frequently than does Pithecia. While all three species utilized the terminal branches to approximately the same degree while feeding (Table 6.8 for Pithecia and Chiropotes), only Chiropotes and Cacajao were recorded using pedal suspension to reach for food in this

tree portion. The smaller-bodied Pithecia may have less of a problem clambering out to and perching upon these finer supports. For larger primates, moving across unstable supports seems easier than balancing on top of them.

Chiropotes and Cacajao (particularly the latter), the larger pitheciins, spend more time in locomotor behavior in the terminal branches than does the smallest pitheciin, Pithecia.

The problem of gap-crossing was solved differently by each species, with their solutions influenced by both body size and use of tree portions. The larger-bodied Chiropotes often bridged gaps, and the smaller-bodied Pithecia more often leapt across them. Additionally, although leaping is an important gap-crossing behavior for Chiropotes and Cacajao, the form of the behavior is different than in Pithecia. Cartmill and Milton (1977) have predicted, and Fleagle and Mittermeier (1980) subsequently demonstrated with sympatric primates, that smaller species tend to leap more, and larger ones more often to engage in climbing or bridging. These associations were supported by the data presented here of two allopatric species.

As previously mentioned, Chiropotes travels more frequently than does Pithecia in the terminal branches. Likewise, both Chiropotes and Cacajao use the smallest, deformable supports found in this tree portion more than does Pithecia while traveling (Tables 6.14 and 6.19); the

two larger species use smaller supports for quadrupedal activities than does Pithecia (Tables 6.15 and 6.20). This contradicts predictions and previous associations in which larger animals will tend to use larger supports (e.g., Fleagle and Mittermeier, 1980). Pithecia, while resting, uses the smallest support sizes more than does Chiropotes or Cacajao. Feeding pitheciins use the two smallest support size categories to a similar degree (Table 6.10). The frequent use of the terminal branches by traveling Chiropotes (Table 6.10) can be correlated with the positional activities in which this species is most often involve: leaping, dropping or bridging between the terminal branches of two trees, and pronograde clambering toward branch ends. These activities, frequent for Cacajao as well, are all carried out on several supports.

Pitheciin tail form and function

Within the Pitheciini, a great deal of variation exists in tail length and appearance. The number of caudal vertebrae ranges from an average of 26 in Pithecia (Flower cited in Hill, 1960) to 17-18 in Cacajao. The number of caudal vertebrae of Chiropotes was unavailable; however, tail length is quite similar to that of Pithecia.

The general appearance of the tails differs in terms of shape and hair distribution. That of Pithecia has long, fine hairs, which meet in the middle on the underside. The

tail ends in a point. In Chiropotes, the hair is shorter and coarser, and the tail's tip has a rounded aspect. Cacajao's short tail has hair which is longer and finer than that of Chiropotes, also ending in a blunt tip.

Tails are used in a variety of ways, including balance, communication, social bonding, and possibly guiding direction or assisting body rotation in leaps. A tail that hangs straight down below a primate sitting on a branch can act to lower somewhat the animal's center of gravity toward the branch (Rose, 1974). The draping of a tail over a branch to assist in balance was observed by Kinzey (1977) for Callicebus, and noted for both Pithecia and Chiropotes in this study. The role of the tail in maintaining stability has also been discussed by Rose (1974).

Tail use differs between the species primarily in the degree to which it is used in communication. The tail of Pithecia generally hangs straight down, while Chiropotes and Cacajao use their tails more actively, often for tail-wagging (mentioned in Chapter 2). Tail-wagging often occurs with vocalizations, near the end of a rest period before troop movement begins. In addition, in the midst of a bout of tail-wagging of two Chiropotes individuals when sitting or standing side-by-side, tail twining may occur, similar to that observed for Callicebus (Kinzey, 1977). Chiropotes usually carries its tail arched over its back, or held high behind its body.

The question of the variation in tail morphology in pitheciins is an interesting one, particularly where it concerns Cacajao. Its stump of a tail is certainly too short to play a role in balance or shifting of the body during leaps, but is certainly used vigorously for display. Since Cacajao's tail-wagging occurs with such frequency, it may play (or have played) an important role in communication, or expression of a general state of arousal. Selection pressure to have shortened the tail must have been quite strong to overcome the advantages of its use in social behavior. However, since a portion does remain, this indicates that those factors leading to tail reduction were not strong enough to have completely overcome the selection pressure for maintaining it for display. Among primates, numerous groups lack tails (e.g. all hominoids, lorisids); however, the only monkeys to lack tails are some terrestrially adapted species of the Old World. While Cacajao may spend up to 30 or 40% of its time foraging on the ground in the dry season (Ayres, 1986), tail loss wouldn't seem to be due to terrestriality alone, especially in light of the fact that members of the genus Cebus are often more terrestrial than Cacajao. However, the element of sometime-terrestriality, together with features of the habitat, may have had an influence on the evolution of Cacajao's tail. Although quite speculative, perhaps lack of a tail provides an advantage in moving about in a viney,

flooded area (chaparral), in which caiman abound at certain times of the year. Interestingly, the only arboreal mammal in the neotropics which lacks a tail is the sloth, which frequently comes to the ground, to cross gaps and to defecate.

Cacajao's lack of a substantial tail presumably has some implications for its positional behavior, which are worth investigating. Predictions about these effects could be formulated based upon tail use in the other pitheciins and in other primates. Since the primary use of the tail in pitheciin positional behavior appears to be balance, particularly while engaged in postural behavior in terminal branches, Cacajao may solve its problems of balance by substituting other behaviors. The positional behavior of this species when in terminal branches differs from that of the other two in that it uses more hindlimb suspension, and more locomotor behavior (see especially subtotal of locomotor behavior in Table 6.5). Greater use of underbranch suspension may be expected if it is presumed that suspension is somewhat "easier" than balance on top of small branches. Cacajao also may be moving more in order to move to more solid supports (to feed, for example).

In sum, perhaps the combination of a short tail and large body size has lead to more frequent locomotor behaviors in the terminal branches, and more suspensory behavior, relative to the other pitheciins.

D. Leaping Adaptations in Pitheciins

The qualitative and quantitative differences in leaping behavior between Pithecia and Chiropotes, presented in Chapter 6, enable us to draw some generalizations concerning the degree to which each is specialized for leaping.

Specializations for leaping in Pithecia

While leaping is an important component of the behavioral repertoire in both species, it is more so for Pithecia; because of the obvious importance of leaping for this species (discussed in Chapter 6) it warrants closer consideration. Certain behavioral and anatomical features are characteristic of specialized leapers, as discussed by Hildebrand (1982) and demonstrated by Peters and Preuschoft (1984) for Tarsius. Several of these can be distinguished in Pithecia, and set this species apart from the more generalized leaping of Chiropotes.

- 1) Pithecia tends to be stationary at take-off, and more frequently takes off from a postural than a locomotor position, while Chiropotes is much more likely to take off from a locomotor position than a postural one (see Table 6.22).
- 2) Body orientation tends toward the vertical; one-half of Pithecia take-offs were from a vertical cling posture (Table 6.22), reflecting their general tendency to a more orthograde body orientation, which is maintained throughout

the leap. Chiropotes, whose body orientation is more often horizontal through the leap phases, uses pronograde positions for take-off. As in Tarsius, the midflight portion of Pithecia's leap is characterized by extreme flexion of hindlimbs and back, and tucking of head until the body assumes a ball shape. It is questionable whether the tail is used to help rotate the body of Pithecia, as claimed for Tarsius (see below).

3) Anatomical features are present which reflect adaptations to saltation (as in Tarsius, Peters and Preuschoft, 1984). As discussed by Fleagle and Meldrum (1988), Pithecia exhibits numerous features of the hindlimb which can be functionally correlated with leaping.

Anatomical adaptations for leaping

Indications of habitual leaping behavior include anatomical features which demonstrate a biomechanical advantage for the characteristic movements and ranges of motion involved in leaping. As discussed in Fleagle and Meldrum (1988), these types of movements are listed below, followed by the primary anatomical features which are associated with them.

1) Adducted hindlimb excursion and limited rotation/lateral movements:

At the proximal femur, the articular surface of the femoral head extends more postero-superiorly, the fovea

capitis is more distally located, and the femoral neck is set approximately perpendicular to the shaft. At the distal femur, the femoral condyles are more symmetrical from the posterior aspect, and there is a pronounced adductor tubercle. The proximal tibial shaft is medio-laterally compressed, and the distal 10-20% of the tibia and the fibula are often joined by connective tissue, and sometimes fused. The fibula, like the tibia, is more slender than that of Chiropotes, and is medio-laterally compressed.

2) Increasing the length of the hindlimb, which increases the distance (and time) for muscular force to be applied:

The hindlimbs are relatively long, as are the digit rays of the foot. The cuboid is elongated.

3) Increased trunk extension for leap take-off:

Pithecia has more lumbar vertebrae relative to thoracic than does Chiropotes.

4) Resistance of bending forces while leaping:

Femoral neck is short.

5) Evidence of muscular advantage:

The importance of m. vastus lateralis is demonstrated by the form of its origin, the greater trochanter, which is broad, proximally flattened and overhangs the femoral shaft anteriorly. This muscle is distinctive in Pithecia for its extensive development and proximal origin.

6) Prevention of patellar displacement:

The lateral side of the patellar groove is somewhat

expanded.

7) "Tibial stop" for dorsiflexed foot while clinging:

The anterior surface of talar trochlea extends onto the dorsal surface of the talar neck.

Leaping behavior and habitat use

The differences between the species can be accounted for by the anatomical adaptations of each, tree portions and supports used for take-off and landing, forest levels used and differences in the forest structure inhabited by the two species. The use of certain components of leaping behavior, such as take-off position and body orientation, can be correlated with the use of particular tree portions and supports. These in turn accord well with the anatomical features of each species in terms of expectations of the distribution of forces exerted by and upon the body during take-off and landing.

Pithecia tends to take off from the single, solid supports of the lower and central tree portions (bole and vertical axis) (Table 6.23), from which more propulsion can be derived. Its long hindlimbs allow force to be applied to the take-off support for a longer time, enabling it to leap farther than Chiropotes, and flexion of these longer hindlimbs allow the compressive forces of landing to be absorbed for a longer time, as landing is usually on a single, solid support (again, often a bole or vertical

axis).

Chiropotes is equally likely to take off from a single, solid support in the crown as from several terminal branches, but landing is almost exclusively on the multiple flexible supports of the terminal branch portion (Table 6.23), which decreases the amount of compressive forces exerted on the limbs. Its leaps were short, partly because its take-off supports were usually flexible terminal branches.

Differences in the structure of the forests and use of forest levels are also reflected in leaping behavior. Pithecia maintains a consistent level in the canopy while traveling, due to several factors: its ability to cover a large distance in a leap, few emergent trees in the forest make it unnecessary to ascend or descend to a large degree while traveling, and relatively frequent use of the lower canopy levels. Kinzey (1977), Fleagle (1978) and Davies (1984) found that leaping behavior is correlated with lower levels of the forest, an observation noted only for Pithecia in this study. In Table 6.27, the relative tree heights used for leaping may be compared to those used in all travel bouts. A different strategy is demonstrated by Pithecia than by Chiropotes. For Pithecia, the three highest tree portions (above 70% of relative tree height) are used slightly less when leaping than for overall travel bouts (all behaviors taken together). Below the 70% level,

leaping behavior **increases** somewhat compared to overall travel modes. Chiropotes follows the opposite pattern. At the highest three height levels, leaping is used slightly more than are all travel modes in general. Below 70% of tree height, leaping is used slightly less as a travel mode than are all behaviors taken together (all travel).

While these differences are slight, we can see that leaping is not associated with lower forest levels for Chiropotes. In fact, Chiropotes tend not to avoid crossing gaps at these lower levels, but to move up higher into the trees to do so. This correlates well with what has been presented for gap-crossing behavior and use of tree portions for traveling Chiropotes. Gaps are crossed primarily by leaping, and also by bridging, between the terminal branches of adjacent crowns. Therefore, Chiropotes tends to cross gaps higher in the canopy, and Pithecia tends to do so at the middle, and sometimes lower levels.

Chiropotes often leaps down, involving more vertical than horizontal displacement. In fact, Chiropotes frequently drops from a higher to a lower support while traveling, a behavior seldom recorded for Pithecia. This behavior can be correlated with the structure of Chiropotes' habitat, in which the various vegetation types diverged greatly in height. Chiropotes often uses trees which were emergent over the surrounding vegetation, making it necessary to descend or ascend while moving from one tree to

another. Trees in Chiropotes' habitat overlap less with neighbors than do those in the Pithecia habitat.

Dropping from the terminal branches of one tree to those of another result in a great deal of noise. Pithecia's use of more solid supports in leaping allows it to move quickly as well as quietly.

Leaping behavior and body size

Fleagle and Mittermeier (1980) found that leaping correlated negatively with body size, such that in eight sympatric species, the smallest ones tended to leap more. More recently, Gebo and Chapman (submitted; pers. comm.) found quite the opposite to be the case in sympatric species of cercopithecids. In Sierra Leone as well, anecdotal observations of three colobine species showed that the smallest (Procolobus verus), leapt the least (pers. obs.).

Certainly, within the Pitheciini, the smallest genus, Pithecia, leaps the most. Adding strength to this association, the larger members of the genus Pithecia (e.g., P. monachus and P. albicans) appear to leap much less than does the smaller (P. pithecia) (Happel, 1982; Peres, in press).

Role of the tail in leaping behavior

It has been proposed (Peters and Preuschoft, 1984; Dunbar, 1988; discussed in Chapter 6) that the tail is

important in aiding the control of leaps. The two ways that have been discussed are assisting in rearward rotation of the body by an upswing of the tail, and reducing the rotation of a leap in which the body has turned 180° in mid-air.

I believe that while the second of these may be plausible, the first is less likely to be. First, lifting of the tail should result in a forward, not rearward, rotation of the body, and it is doubtful that the weight of the tail of any of these species (Pithecia, Tarsius, Lemur) is sufficient to rotate the entire body from top to bottom. Secondly, since the tail rises as the back extends, this movement of the tail is most probably a by-product of the extensor musculature of the back, extending the tail as the back extends (Sarmiento, pers. comm.).

Leaping (and related behaviors) as predator avoidance strategies

As previously mentioned, leaping is likely one of the most important behaviors used for predator avoidance, as evidenced by its more frequent use by unhabituated individuals, particularly of Pithecia. Possibly, there is an increased risk of predation for Pithecia due to its use of lower forest levels, and to its smaller body size. A suite of "critical" behaviors (sensu Prost, 1965) seem to be exhibited by Pithecia: rapid vertical clinging and leaping,

freezing, and a slow creeping walk. Unhabituated individuals often make a series of long-distance vertical cling-leaps in the attempt to lose followers. As previously mentioned, these leaps tend to be relatively quiet, as little movement of the vegetation is produced. Silence is aided by the small group size. If several individuals are fleeing together, one of the adults may act as a decoy, vertically clinging and leaping out in the open. Once distracted, a potential predator may not notice the other group members, allowing them to move quietly away. On one occasion, a fully habituated female Pithecia was attempting to retire (unnoticed) to the sleeping tree. She was lost momentarily from my view, having "frozen" in a postural behavior after rapid locomotion. When I spotted her again, she was beginning to move very slowly, with movements resembling a slow loris, creeping forward in slow motion. When she glanced my way, and saw me observing her, she immediately began to walk quadrupedally (and normally) away.

Conclusions - pitheciin leaping adaptations

Pithecia exhibits a number of the behavioral and anatomical features of a specialized leaper, while Chiropotes exhibits those of a more generalized leaper. The latter species lacks anatomical specializations for leaping, and in fact demonstrates components of leaping behavior which indicate its generalist position, as discussed by

Hildebrand (1982). Chiropotes often initiates leaps while moving, utilizing some of the momentum from the forward movement to increase the distance of the leap. A frequent downward component in Chiropotes' leaps can also serve to increase horizontal distance.

Chiropotes deals with problems (such as landing forces) through behavioral adaptations (e.g., landing on flexible substrates), while Pithecia has done so through anatomical adaptations (e.g., longer hindlimbs). This demonstrates that Pithecia has taken its leaping adaptations one step further than has Chiropotes. Presumably, due to the highly labile nature of primate positional behavior and to the flexibility allowed by the anatomy, a behavior can begin to be utilized by an individual in its lifetime; only after selective pressures act to produce genetic adaptations can the anatomy change, making the behavior more efficient. The "Red Queen Effect" (Van Valen, 1973), refers to this fact that genetic (morphological) change always follows any adaptations of an individual to its environment during its lifetime.

Leaping behavior is important due to the exhibition of dramatic difference between species in its use, as well as to its apparent role as a predator avoidance strategy.

E. Conclusion

This chapter has outlined the major differences among

the pitheciins in terms of positional behavior, habitat use and anatomy, with a particular emphasis on leaping adaptations, especially for Pithecia pithecia. Obviously, the sections of this chapter are closely intertwined. We can correlate positional behavior with use of the habitat, as well as with anatomical features. We can also observe that the differences in the habitats have some implications for the positional behavior and habitat use in each pitheciin. However, the fundamental question has not been answered: Why are they different? A few possible hypotheses are discussed in Chapter 8.

Chapter 8. ADAPTATION AND EVOLUTION OF PITHECIINS

A. Introduction

One of the ultimate goals of a study of evolutionary ecology/biology is to draw inferences about the evolution of a taxon. Aspects about which inferences can be made include: presumed patterns exhibited by the common ancestor, distinguishing the more primitive members of the group from those which are more derived, and possible reasons leading to the divergence of taxa from their common ancestor. The first two aspects can be investigated by a series of steps, the first of which involves the compilation of information for a range of variables in order to demonstrate the overall pattern of ecological and behavioral variability of each genus.

The distribution of these patterns can be examined in several ways. Features which are shared among all or most of the taxa are presumed to be primitive, and likely present in the common ancestor. As stated by Simpson (1961), "within a taxon, the characters of the common ancestry are primitive and others are more or less specialized in proportion to their departure from the ancestral condition." The relative plasticity, or flexibility, of a taxon can provide clues as to its relative position of primitive vs. derived. Although generalized should not be used synonymously with primitive, especially in the absence of additional evidence (Simpson, 1961), this concept can be of

assistance in that "primitive animals are often relatively generalized...less narrowly or specifically adapted to a particular niche..." (ibid.). Comparisons with sister taxa, outgroup comparison (Hennig, 1966), is also useful in sorting out the relative positions of taxon members along a continuum of primitive to derived.

In the following sections, a number of ecological as well as behavioral features are outlined for the members of the tribe Pitheciini, having been discussed more thoroughly in chapters 2 and 6. These features include: geographical distribution, sympatry with other members of the taxon, habitat types, habitat use, feeding adaptations and positional adaptations. Shared features among group members, patterns of variability and a comparison with a member of their sister taxon, Aotini (following Rosenberger, 1988), can assist in revealing clues to the adaptations and evolution of the pitheciin primates.

B. Ecological and Behavioral Variability

Distribution

The genus Pithecia has the widest geographical distribution of the pitheciins, encompassing much of the range of the entire tribe. In its distribution, it overlaps that of both Chiropotes and Cacajao; in fact, a comparison of general maps of pitheciin distribution suggests that various species of Pithecia are sympatric with both

Chiropotes and Cacajao in many areas. However, the only consistently observed situation of sympatry within the pitheciins occurs with Chiropotes satanas and Pithecia, which are sympatric throughout most of the Guayanas. The fact that Pithecia and Chiropotes are not sympatric in Venezuela, while they are in other parts of the Guayanas is due to the fact that each species migrated into Venezuela taking a different route. While Pithecia crossed the Esequibo River to the north (along with Alouatta, Cebus and Saimiri), Chiropotes has not yet crossed the Esequibo; this species migrated further west before moving north into Venezuela. Its eastern expansion to the west bank of the Caroni River may be relatively recent, and the Caroni may not be a permanent boundary for either Pithecia or Chiropotes (W. Kinzey, pers. comm.).

Although Pithecia monachus overlaps in general geographical distribution with Cacajao calvus, a basic difference in habitat preference (discussed in next section) probably keeps them from being syntopic. Other possibilities for sympatry among the pitheciins include an area of apparent overlap between Pithecia irrorata and Chiropotes albinasus, to the east of the Rio Madeira, and west of the Tapajóz and Jureuná (Peres, in press). However, they may exclude one another (or, more likely, Chiropotes may exclude Pithecia) from co-existing in the same micro-habitat, due to a high degree of dietary overlap. Also

pointed out by Peres (although not apparent from HersHKovitz' 1987 distribution maps) is an area of sympatry between Cacajao calvus and Pithecia (monachus or irrorata) in the várzea along the Juruá river. Mittermeier and Coimbra-Filho (1977) as well report that Pithecia occurs syntopically with Cacajao at the western end of the Paraná do Panaua. Members of the Pithecia monachus-group have been studied (P. monachus in Peru: Happel, 1982; P. albicans in Brazil: Johns, 1986b; Peres, in press) only where they occur allopatrically from other pitheciins. Chiropotes and Cacajao are clearly not sympatric throughout most of their respective ranges; however, distribution maps of Eisenberg (1989) suggest their overlap near the confluence of the Orinoco and Casiquiare rivers in Venezuela.

The two species-groups of Pithecia are separated by the Amazon River, with the pithecia-group to the north, and the monachus-group to the south. Differences between these two species-groups will be discussed later in this chapter.

Habitats

The three genera differ both in terms of the range of habitats in which they can survive, and the characteristics of those habitats.

Pithecia occurs in a variety of terra firme habitats (e.g., Mittermeier, 1977; Durham and Durham, cited in Wolfheim, 1983; Kinzey et. al., 1988). Although this genus

survives in secondary growth or edge habitats, it appears to occur in higher densities in primary terra firme forests (Ayres, 1986). Its distribution in terra firme as opposed to flooded forests explains its more frequent sympatry with Chiropotes than with Cacajao. Ayres suggested that Pithecia can survive in poor habitats due to its smaller body size and smaller group size. The fact that Pithecia is dietarily more variable (Kinzey and Norconk, 1991) than other pitheciins is probably a contributing factor to its ability to survive in a range of habitats.

The two species of Chiropotes are mostly limited to high terra firme forests, often igapo of black- or clear-water rivers, and rarely in várzea (Johns and Ayres, 1987; Ayres, 1989).

Cacajao calvus occurs in várzea forests of white-water rivers, while Cacajao melanocephalus is found in igapo forest of black-water rivers (Johns and Ayres, 1987).

Ayres points out that although there are many similarities between Chiropotes and Cacajao, Cacajao is not found in terra firme even in areas where Chiropotes is absent. He explains the possible answer in terms of body size and avoidance of competition. Cacajao, the heavier of the two, requires large quantities of fruits, which can be provided by várzea forests, but not terra firme forests. Cacajao is not found in the terra firme forests within its geographical range in order to avoid competition with

potential primate competitors, which have a higher diversity in terra firme than várzea forests, particularly in the western Amazon. He cites the lack of Chiropotes in these western terra firme forests which overlap Cacajao's distribution as being due to the same reason: avoidance of competition.

However, the difference in body size between Chiropotes and Cacajao (2.8 kg and 3.4 kg, respectively) is probably not great enough to warrant different dietary requirements. In addition, pitheciins probably overlap relatively little dietarily with other primates; even for those food species which are shared, pitheciins (particularly Chiropotes and Cacajao) could exploit them at an earlier stage than other primates, when husks are too hard for most. Cebus, which can break open hard fruits as well, should probably not be serious competition for a sclerocarpivorous specialist, which possesses dental adaptations enabling them access to tough-husked fruits.

A more likely explanation of the non-occurrence of each in the habitat of the other may be that each genus is simply specialized for its own particular environment, with limited ability to colonize new ones. In addition, the dietary specializations possessed by Chiropotes and Cacajao, and (especially in the case of Cacajao), the unique environment in which they live, would inhibit the colonization of unfamiliar areas.

Lagothrix, a frugivorous primate which also possesses robust canines may in fact be a potential competitor for Chiropotes. The two are allopatric throughout their respective ranges; Lagothrix may prevent Chiropotes from expanding into its habitat, and/or vice versa (W. Kinzey, pers. comm.).

As previously mentioned, Pithecia and Cacajao may overlap geographically, but since Pithecia occurs in terra firme, and Cacajao in flooded areas, sharing of a habitat between the two is unlikely. For example, in Brazil, Pithecia albicans occurs at Lake Tefe, in a terra firme, selectively logged forest (Johns, 1986a; pers. obs.). Approximately 40 km away, Cacajao calvus is found in the flooded forests of white-water rivers, Japurá and Solimões, and their tributaries, including Lake Mamirauá.

Home range size

Of the pitheciins, Chiropotes and Cacajao have by far the largest home ranges (200-350 and 500 hectares, respectively (Ayres, 1981; van Roosmalen et.al., 1981; Ayres, 1989). P. albicans may have a home range as large as 172 hectares (Peres, in press), while that of P. pithecia is much smaller. Home range size is variable within species, and depend upon a number of factors, including phylogeny, general dietary adaptations, resource distribution and resource availability. Home range size

correlates to some degree with group size (e.g. Eisenberg et.al., 1979), which is small for Pithecia. In addition, a higher degree of leaf-eating in Pithecia, should allow it to utilize more resources in a smaller area.

Therefore, small group size together with a relatively eclectic diet (compared to Chiropotes and Cacajao) can allow P. pithecia to survive in small forest patches. Additionally, Pithecia can utilize parts of the habitat not used by Chiropotes (see next section). The more specialized frugivores, Chiropotes and Cacajao, which have much larger group sizes, must depend on larger food patches, which may not be so evenly or abundantly distributed. Their home ranges must be larger in order to obtain sufficient food for the entire group. Additionally, feeding trees used by both Chiropotes and Cacajao are usually very large, and spaced farther apart.

Habitat use

In terms of use of the various canopy levels and the various tree portions, Pithecia is the most flexible, while Chiropotes appears to be the least so.

The species of the genus Pithecia vary in terms of canopy use. P. pithecia uses all forest levels, including the ground, and all portions of the trees. This species uses the lower forest levels and lower tree portions more than does any other pitheciin. Members of the monachus

species-group appear to prefer the middle and upper canopy (Happel, 1982; Johns, 1986b; Peres, in press).

Chiropotes demonstrates a definite preference for the upper part of the canopy, very rarely descending to the understorey or shrub layer, and virtually never to the ground. This species is most often found in the main crown or the terminal branches, and seldom in other portions.

Cacajao is usually observed in higher canopy levels, but is more variable than Chiropotes in its use of the forest, inclusive of the fact that it has been observed foraging on the ground (Ayres, 1986). In general, both of the larger pitheciins are limited primarily to the middle and upper canopies.

Feeding adaptations

All members of the Pitheciini specialize in seed predation, but differ greatly in foraging strategies (Ayres, 1986).

Chiropotes and Cacajao are more highly specialized for seed-eating (and sclerocarpivory, sensu Kinzey, 1992) than is Pithecia, based on dental and mandibular morphology, and on diet. Pithecia eats a wider range of food items, and includes more (young) leaves in its diet than do either Chiropotes or Cacajao (Happel, 1982; Johns, 1986; Kinzey and Norconk, 1993; pers. obs.). Cacajao and Chiropotes appear to be quite similar in terms of dietary variability and

number of species used, with each taking food from between 80 and 85 plant species (Ayres, 1986; van Roosmalen et. al., 1988).

Pithecia eats fewer large-seeded fruits than do the other pitheciins. According to Ayres (1986), the lower degree of seed-eating is related to its smaller body size. However, I am inclined to think that it is related more to the lack of such a specialized apparatus for processing tough husks as is possessed by the two larger species. On the other hand, since it is known that Pithecia is capable of coping with moderately high levels of condensed tannins in seeds (Kinzey and Norconk, 1993), this may be part of the genus' own specialization. However, data have not yet been analyzed for Chiropotes to investigate whether or not they do the same. This capability may also be important for Pithecia's leaf-eating tendencies, as leaves often have high tannin levels (Oates et. al., 1980). Food passage rates, typically long for leaf-eaters, appear to be longer for Pithecia than for Chiropotes and Cacajao (Milton, 1984). Possibly correlated with this is the gut morphology of Pithecia, in which the small intestine is somewhat reduced, and the colon increased in size (Fooden, 1964).

Interestingly, one of the dietary differences between P. pithecia and P. albicans involves the use of plant families which have fruits with hard husks, and are used by the larger pitheciins. Lecythidaceae and Sapotaceae are

among the most important families for P. albicans, and are also a major component of the diets of Chiropotes and Cacajao. These families (particularly the Lecythidaceae) are much less frequently used by P. pithecia. Therefore, the monachus-group (at least P. albicans) may have retained a more primitive dietary adaptation, as did Chiropotes and Cacajao, or was permitted to expand due to competitive release from sympatric pitheciins (Peres, in press).

Positional adaptations

Pithecia is the most diverse in terms of positional behavior, using most behaviors exhibited by Chiropotes and Cacajao. Within the genus, P. pithecia exhibits the most leaping, particularly using vertical cling as a take-off position. Anatomical features are associated with this behavior. Members of the monachus-group (e.g., P. albicans: Peres, in press; P. monachus: Happel, 1982) appear to be more quadrupedal, and leap much less frequently. Preliminary observation of postcranial anatomy appears to confirm these differences between the species-groups (Meldrum and Lemelin, 1991; J. Meldrum, pers. comm.).

Both Chiropotes and Chiropotes are primarily quadrupedal. Chiropotes is less variable than is Cacajao in its positional repertoire. Although leaping plays an important role for both species as evident by its relatively high frequency, anatomical adaptations for this behavioral

mode are not exhibited. Features are present in the foot which are related to pedal suspension, in which they frequently engage, Cacajao much more frequently than Chiropotes.

C. Evolution of the Pitheciini

As demonstrated above, ecological and behavioral features differ widely among the pitheciins. The distribution of the features and the pattern of their differences can be examined in order to make inferences about the common pitheciin ancestor, distinguish conservative features from those which are more recent, and possible reasons leading to the divergence of pitheciin taxa.

Shared ecological and behavioral patterns, and their implications

Most pitheciins, as well as the aotins (particularly Callicebus - Kinzey, 1977), share a primary adaptation to quadrupedalism and pronograde clambering, with a considerable amount of leaping. Although no systematic sampling has been conducted on the locomotor behavior of Pithecia monachus, it appears to fit a similar pattern to that of Chiropotes and Cacajao (from Happel, 1978; Peres, in press). Only Pithecia pithecia diverges in its basic positional adaptations and habitat use, engaging in more

leaping and using more vertical supports than do the other pitheciins.

In terms of canopy use, P. pithecia is once again unique, in its frequent use of the lower canopy, while the other pitheciins remain mainly in the middle and upper canopies. Supports available at these levels differ from one another; lower tree portions are comprised of vertical and angled supports, and the main crowns of trees which occur in the higher canopy levels have numerous horizontal supports as well.

The patterns shared by most pitheciins: quadrupedalism, pronograde clambering and considerable leaping, along with use of the middle and upper canopies, are presumed to be the features primitive for the Pitheciini, and present in their common ancestor. This pattern is similar to the inferred behavioral repertoire of Cebupithecia, reported by Ford (1990), based on postcranial remains.

As with most taxa, each pitheciin genus exhibits a mixture, or mosaic (Simpson, 1961) of primitive and derived forms of features. Pithecia, as a genus, appears to be the most generalized, more diverse and adaptable in its distribution, habitat, diet and positional behavior than are the other two pitheciin genera. In terms of dietary adaptations, Pithecia is the most primitive, compared to the highly derived dental and mandibular morphology of

Chiropotes and Cacajao, the latter two which are accordingly more specialized for sclerocarpivory. However, Pithecia may be specialized in its gut morphology and passage rates, and in possibly in its ability to process higher tannin levels, although more data are needed.

Chiropotes and Cacajao share more features with one another than either does with Pithecia in terms of habitat use, positional behavior and dietary adaptations. Presumably, pedal suspension (together with its anatomical correlates) is a derived feature for Chiropotes and Cacajao, evolving after their divergence from the Pithecia line. Of the two larger genera, Cacajao, although exhibiting a wider range of behaviors, seems the most derived, based on a few factors. In terms of ecology, Cacajao is more limited in its unique habitat and smaller geographic distribution, while Chiropotes is more widely distributed. Cacajao is also more highly specialized for pedal suspension. Although both species exhibit this behavior as well as anatomical correlates for foot eversion (Fleagle and Meldrum, 1988), in Cacajao its use is more frequent, and occurs in a wider variety of contexts (feeding, play, social/display). This indicates a more specialized form of this features. Additionally, the loss of most of Cacajao's tail is derived within the Pitheciini.

Within the genus Pithecia, many differences are observable between the pithecia- and the monachus-group. P.

pithecia has a reduced body size (1.6 kg vs. 2.3 kg in P. monachus-group, based on data from Ford and Davis, 1992 - male and female weights averaged), exhibits a specialized form of locomotion (vertical clinging and leaping) together with anatomical correlates, a distinct karyotype (DeBoer, 1975), and pelage differences (HersHKovitz, 1979), with the pelage of male P. pithecia more differentiated from that of the female than is that of members of the P. monachus species-group. HersHKovitz presumes the center of Pithecia (and in fact, pitheciine) evolution to be in the range of P. monachus; P. pithecia is therefore the species to migrate the furthest from its site of origin. These features indicate that P. pithecia is derived within its genus. Vertical clinging and leaping in Pithecia may, in fact, be related to body size, as smaller primates have been shown to leap more than do their larger counterparts (e.g. Fleagle and Mittermeier, 1980; but see Gebo and Chapman, submitted).

Members of the P. monachus-group are more similar to Chiropotes and Cacajao in terms of positional behavior and forest use than they are to P. pithecia. Although they are little-studied thus far, no unique specializations of positional behavior or anatomy has been noted for P. monachus.

In terms of positional adaptations, therefore, P. pithecia appears to be the most derived, while in terms of dietary adaptations, Cacajao and Chiropotes are more

derived. The basic ancestral positional repertoire for pitheciins appears to be retained primarily by the Pithecia monachus-group, and to a large degree, by Chiropotes and Cacajao.

Possible reasons for divergence

In Chapter 7, differences between Pithecia, Chiropotes and Cacajao were discussed, but the question of why those differences exist was not addressed; the answer probably lies in the events leading to the divergence of these taxa. Although speculative, these events may be inferred based on what we know of the paleoenvironment, current distribution and other ecological and behavioral factors of the pitheciins. Two alternative hypotheses are presented.

As discussed by Ayres (1986), Chiropotes and Cacajao may have diverged during the Tertiary, when the Andes arose and a large inland sea was formed. This brought about the "early várzea", later evolving into what is currently terra firme. The ancestral stock split into populations which were separated, those later giving rise to Chiropotes to the eastern portion of Amazonia, and those giving rise to Cacajao in the western portion.

Pithecia is thought to have diverged from the Chiropotes/Cacajao stock previous to the divergence of the latter two (e.g., Kay, 1990). At this time, this early Pithecia was probably somewhat specialized in its

adaptations for seed-eating (perhaps similar to Cebupithecia in that regard), and similar in body size to P. monachus, possibly with similar ecological and behavioral features. Based on what we know about Pithecia's capability for surviving in diverse environments, it probably colonized new, diverse habitat types.

Although populations of Pithecia migrated to the north at some point, it is not known when this occurred; it is hypothesized here that P. pithecia evolved its specializations after becoming sympatric with Chiropotes in north-eastern Brazil north of the Amazon, and in the Guayanas. This sympatric situation may have had numerous affects. A similar diet of seeds, and use of the middle and upper canopies may have made co-existence difficult or impossible. As a more specialized seed predator, Chiropotes would have had the advantage in that it could exploit harder foods, therefore allowing it a wider fruiting season for each plant species than permitted for Pithecia. Pithecia may have been forced to broaden its resource base in order to survive in sympatry with Chiropotes. A change in diet in order to exploit a wider range of foods, including leaves, and a shift in canopy level to a lower one than that used by Chiropotes, would allow Pithecia to avoid direct competition with this ecologically similar primate. Dietary shift is discussed by Milton (1984), who points out that the differing digestive strategy of Pithecia may reduce its

dietary overlap with other pitheciines. Pithecia tends to turn to leaves and flowers in times of food shortages (dry season), and Chiropotes to hard-covered fruits. A number of related effects on Pithecia may have resulted from this dietary and locational (canopy level) shift. Smaller body size may have been selected for in order to allow lower amounts (and quality) of food. The use of lower forest levels and the vertical supports found at these discontinuous levels would have selected for the most efficient gap-crossing locomotor adaptation, which for Pithecia was vertical clinging and leaping.

Use of lower canopy levels, together with smaller body size, may have increased the risk of predation, also selecting for efficient leaping ability, and perhaps for crypticity. (Leaping as a predator avoidance strategy is also discussed in Chapter 7.) Although use of higher canopy levels can increase risk of exposure to raptors, particularly for a smaller primate, based on the behavior of other species, risk appears to be an important factor for primates when they descend to low forest level or the ground. For example, Cacajao's behavior while utilizing the ground for foraging supports the idea that predation risk is higher when near or on the ground. Only part of the group will descend at a time; others remain high in the canopy, apparently being vigilant (Ayres, 1986). Human observers were detected by the individuals up in the canopy, which

alerted those on the ground (ibid.). In the Old World, Procolobus verus, like Pithecia, has a small body size and small group size, and uses lower canopy levels and cryptic behaviors (Oates and Whitesides, 1990). Their primary anti-predator strategy is polyspecific association, usually with a Cercopithecus spp. (ibid.).

Members of the genus Pithecia which were not sympatric with Chiropotes (i.e. the monachus-group) retained the original positional adaptations (primarily quadrupedal), use of higher canopy levels, food species with somewhat harder husked fruits and larger body size.

Therefore P. pithecia due to the impetus from avoidance of competition with sympatric Chiropotes) has differentiated more from the common ancestor that it shared with P. monachus, while members of the latter species-group are considered to be the most primitive (as in Hershkovitz, 1979).

Alternatively, P. pithecia's specializations may have evolved for other reasons. For example, a season of particularly low food abundance could have forced Pithecia to broaden its resource base, possibly driving it to search for food in all levels of the canopy. This search may have caused it to descend to lower levels. The capabilities for exploiting food in these areas of the forest could then be advantageous in allowing it to cope with other primates in subsequent (or existing) situations of sympatry.

D. Fossil Pitheciins - Interpretations

Researchers who have examined the postcranial skeletal material of Cebupithecia sarmiento present similar interpretations of its morphological and presumed behavioral patterns. However, their results of comparisons with extant taxa differ.

Davis (1987 and 1988) studied the hindlimb of Cebupithecia, comparing it to a wide range of extant platyrrhines. She reports that Cebupithecia exhibited morphological similarities primarily to callitrichines, and to a lesser degree, to small-bodied cebids such as Saimiri and Callicebus (*sensu* Ford, 1986). The features in which Cebupithecia resembles these primates are those which appear related to leaping, and reflect: adduction and lateral rotation of the thigh, stability at the patellofemoral and knee joints, and stability at the ankle during dorsiflexion. Davis interpreted the postcranium of Pithecia as exhibiting a different form of the features which relate to leaping.

Meldrum and Fleagle (1988) and Meldrum et. al. (1990) also demonstrate the features of Cebupithecia as relating primarily to clinging and leaping, with a morphological pattern comparable to those of vertical clingers and leapers such as Pithecia, the indrids and the callitrichines. They also see these features as representing an affinity with Pithecia.

Ford (1990) compared Cebupithecia to a hypothesized

ancestral platyrrhine as well as to a range of extant taxa. She presumed that it frequently used non-horizontal supports for leaping, climbing or suspensory positions. While several features were functionally correlated with leaping, Ford pointed out that some of them (long posterior articular surface on calcaneum, deep cuboid pivot and serial transverse tarsal joint) could also represent adaptations for climbing. She concluded that Cebupithecia exhibited a mixture of locomotor behaviors, retaining the ancestral platyrrhine pattern of arboreal quadrupedalism, and differing in the use of leaping and suspension, and probably the use of many non-horizontal supports. Differences from Pithecia were also mentioned, and while the behavioral repertoire may have been similar to that of Pithecia, she believes that these behaviors and their structural adaptations were acquired independently in the two taxa. It is interesting that she discussed the probable importance of suspension and climbing in Cebupithecia; a relatively mobile forelimb in extant pitheciins (discussed on p. 53) may thus be shared by all known pitheciin taxa, extinct and extant.

Meldrum and Lemelin (1991) examined vertebral remains of Cebupithecia, and found some unique features, particularly a vinculum laminum, as well as overall vertebral proportions, shared with P. monachus. This is particularly interesting when compared with the ecological,

distribution, genetic and locomotor (although sparse) data, which indicate that P. monachus is the least differentiated from the common ancestor.

Although I haven't had the opportunity to examine the fossils, a perusal of the literature and comparisons of the various interpretations have led me to conclude the following. While there is general agreement that leaping played an important role in the locomotor repertoire of Cebupithecia, differences in interpretation lie mostly in the comparisons with extant taxa, and particularly with Pithecia. It became apparent while examining the literature that systematic comparisons of Cebupithecia with both species-group of Pithecia are of great importance, considering the possible anatomical differences between them, and are only recently starting to be conducted out (e.g. Meldrum and Lemelin, 1991).

E. Predictions, Direction for Future Study

Further research on the pitheciins is needed in order to examine more closely the adaptations of this group, as well as to test some principles of competition and niche overlap in sympatric, closely related primates.

The most instructive studies should focus on members of the P. monachus-group when (and if) in true sympatry with Chiropotes albinasus or Cacajao calvus. These data need to be compared to the species in allopatry, in order to examine

any evidence for shifts which may have occurred in diet, habitat use or positional behavior, prompted by dietary or spatial overlap.

Within the P. monachus-group, the range of variation should be established in order to see whether or not they fit a pattern similar to that of P. albicans. This pattern includes a primarily quadrupedal adaptation with relatively little leaping, use of the middle and upper canopy levels, diet consisting of fruits from the families Lecythidaceae and Sapotaceae. These, taken together with a body size larger than that of P. pithecia, cause the monachus-group species to appear more "Chiropotes-like."

Dietary adaptations should be investigated for each species, including a quantitative analysis of the hardness of fruits eaten (as in Kinzey and Norconk, 1990). Members of the monachus-group probably fall dietarily between the range of P. pithecia and that of Chiropotes in this regard. It would be instructive to examine the dentition, from which we may be able to infer dietary differences.

Studies of positional behavior might reveal that P. pithecia is the only species to exhibit vertical clinging and leaping, particularly to the extent, and with the anatomical adaptations, evident in this species. I would also expect that P. monachus-group members would differ less from Chiropotes/Cacajao (and the presumed common ancestor) than does P. pithecia, in their positional repertoire. This

appears to be the case based upon vertebral morphology (Meldrum and Lemelin, 1991). Functional anatomical analyses should be conducted for all members of the genus Pithecia; behavioral and anatomical differences may be found between the two species-groups, similar to those demonstrated for Presbytis obscura and Presbytis melalophus (Fleagle, 1977a and b). I would suspect that members of the monachus-group would retain a more conservative postcranial skeleton, with some features (those related to a primarily quadrupedal adaptation) more similar to Chiropotes and Cacajao.

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Chapter 9. SUMMARY AND CONCLUSIONS

A. Introduction

The aim of this study was to investigate the adaptive significance of certain positional behaviors, using data collected on their positional adaptations and their ecology. In examining this body of information, a picture emerges which represents an overall pattern of positional adaptations of each pitheciin representative, and allows us to draw inferences about presumed features of the common ancestor of the pitheciins as well as to suggest the events leading to the divergence of the taxa.

The questions proposed at the outset of the study are addressed below, followed by general summary of important positional adaptations of each pitheciin.

B. Questions of Adaptation and Evolution in the Pitheciini

1) How are particular behavioral solutions advantageous to positional problems?

Problems are imposed on a primate by anatomical constraints and characteristics of its habitat. Some important problems which must be dealt with include body size and balance on small supports, and crossing gaps in the canopy. Use of supports use differs among Pithecia, Chiropotes and Cacajao, due, at least in part, to differences in body size. Support use differs among bouts

of feeding, travel and rest as well.

Support use in feeding

In feeding, a primary concern is to obtain access to the terminal branches, from where most (about two-thirds) of the food is found for the pitheciins. This tree portion poses special problems for animals of larger body size. One predicted solution is that of underbranch suspension to reach for fruit which would be otherwise unobtainable, therefore expanding the feeding sphere. Chiropotes and Cacajao, the larger pitheciins, do indeed utilize suspension, primarily by their hindlimbs. This is not exhibited by Pithecia. Anatomical correlates have been functionally associated with this ability to suspend by the feet. Pithecia is expected to be presented with fewer problems of locomotion or posture in the terminal branches because of its smaller body size. To reach the fruit in terminal branches of very small trees, Pithecia vertically clings to boles of neighboring trees. Chiropotes and Cacajao tend to move more in the terminal branches, rather than remain stationary. It is probably easier to move across than to balance unmoving on small supports, and often, food is carried by these larger species to more solid supports on which to feed.

Support use in travel

In travel, predictions concerning support use and body size are not supported. Chiropotes and Cacajao often use

smaller supports for the activities in which they most frequently engage: pronograde clambering and bridging, and leaping and dropping between the terminal branches of neighboring trees. Pithecia more often uses larger supports on which to travel.

Support use in rest

In rest, data do conform to the expected pattern, whereby larger animals tend to use larger supports, and vice versa.

In general, for postural activities in pitheciins, sizes of supports used are positively correlated with body size. For locomotor activities, support sizes used are negatively correlated with body size.

Crossing Gaps

Pithecia virtually always crosses gaps by leaping, typically from and to solid supports. Chiropotes and Cacajao use leaping often as well, but tend to use deformable supports, especially for landing. The latter are also likely to use bridging or dropping to cross gaps, as would be predicted by their larger body size. Pithecia's frequent leaping may relate to some degree to its smaller body size (gaps in the canopy seem relatively larger), but as well, the gaps may be absolutely larger, especially when using the lower tree portions rather than the canopy with its frequently overlapping branches.

2) How did environmental forces select for adaptations and under what conditions did they evolve?

Numerous selective forces could be at work to shape positional adaptations. They may be related to diet, competition, predation or the habitat. Two possible hypotheses are presented to explain the major differences in positional adaptations of Pithecia, Chiropotes and Cacajao. They relate primarily to the evolution of a specialized form of leaping in Pithecia.

The first is that the pattern presented by Pithecia pithecia is due to the adoption of non-overlapping dietary strategies and spatial avoidance of Chiropotes when in sympatry. Due to the presence of the sclerocarpivorous specialist Chiropotes, an early Pithecia (with less specialized dental and mandibular features for opening hard fruits) may have been displaced to lower forest levels to search for food, and to avoid direct competition with Chiropotes. Lower food availability while adapting to this new forest level may have selected for smaller body size. Small size, together with the frequent use of low forest levels (including the forest floor) probably placed this animal under increased risk from predation; hence, the evolution of the specialized form of leaping and other associated "critical" behaviors.

An alternate hypothesis is that of a forced dietary shift, caused either by a drastic lowering of food abundance

in a particularly harsh season, or by the colonization of an unknown area. Pithecia, faced with one of these, or a similar situation, may have attempted to expand its resource base and use lower areas of the forest in its search for food.

3) Which positional behaviors are ancestral for the taxon Pitheciini and which are taxon-specific for each genus and species?

This question can potentially be answered (as proposed in Chapter 1) in one of two ways. In the first, the shared patterns in extant primates could be determined. Overall patterns of positional behavior which were shared among the taxa (and with the sister-group, Aotini) consist of quadrupedal walking/running and pronograde clambering, with a high degree of leaping (although the leaping is qualitatively different among species). Based on preliminary observations of members of the Pithecia monachus species-group, (Happel, 1982; Peres, in press), the described positional pattern may quite similar to members of this group.

As mentioned in Chapter 1, shared patterns may be found during feeding bouts, as sympatric primates often differ less in positional behavior while feeding than while traveling. In this study, feeding positions do differ less among the species than did traveling positions. However, an

intraspecific comparison of two Pithecia groups on different islands brought interesting results to light: feeding is the activity for which the groups differ the most. It is unknown what variable caused this difference - whether it was the habitat, location of food, or form of the feeding trees. Positional behavior during travel differed little between the groups.

A second method by which to infer ancestral behaviors is by utilizing the phenomenon of "competitive release", with the assumption that allopatric species which were previously sympatric may revert to behaviors which have been retained. This also requires the underlying assumption that competition is playing a role in determining the behavioral patterns; if not, it would not make a difference as to whether or not the species were sympatric. Therefore, Pithecia was observed with the assumption that if competition with Chiropotes had influenced the adoption of new behaviors, the absence of the latter species would allow it to expand once again. Possible evidence for this may be in Pithecia's use of the middle and upper canopy levels while feeding, more so than in travel. However, a dearth of comparative data on the use of the canopy by Pithecia where sympatric with Chiropotes prevents us from confirming it. Additional data on the P. monachus spp., both in sympatry with and allopatry from Chiropotes or Cacajao may provide further insight into niche separation and competitive

release, since it appears that there is considerable overlap between Pithecia monachus spp. and Chiropotes in terms of positional behavior, habitat use and diet.

The fact that positional behaviors associated with feeding in Pithecia differ between habitats, where travel behaviors do not, and that Pithecia ascends to feed, but stays lower in the canopy to travel and to rest, may indicate that behaviors used in travel are more conservative, possibly because of the influence of "critical behaviors" in shaping the behavioral repertoire. Those used in feeding may be more labile in order to cope with seasonal changes or a potentially difficult period.

Positional behaviors specific to each pitheciin species, as well as their relative position in terms of primitive or derived, are outlined in the next section.

C. Patterns of Positional Behavior and Habitat Use

Pithecia

Pithecia pithecia, the smallest member of the tribe, spends more time in resting and postural behavior than do the other two genera. It tends to maintain an orthograde position, as evident in its vertical clinging behavior, upright posture through all leap phases, and frequent use of the vertical and angled supports of the central and lower tree portions. Its most frequently used behavior is leaping, and it possesses anatomical correlates for this

specialization.

Its leaping capabilities provide the most efficient means of moving among the vertical trunks of the lower tree portions, as well as within and between tree crowns. It may serve as a "critical" behavior, allowing for efficient predator avoidance. The particular specialization of Pithecia pithecia, allowing take-off from vertical positions, and the capability for very long leaps, allows rapid escape, and leaping between solid supports makes very little noise. This species possesses other features which assist in the avoidance of predators, such as a small group size and relatively low activity level, which attract little attention. Once discovered by a potential predator, other abilities may be utilized: acting as a decoy to distract the predator from other group members, and the use of slow creeping behavior to move away unnoticed. While resting, Pithecia uses sitting postures much more frequently, and lying postures less often, than the other genera. This may be a function of its tendency to use a more upright posture; on the other hand, sitting can be used as a leap take-off position much more easily than can reclining postures.

Overall, Pithecia pithecia is derived for pitheciins in terms of its positional adaptations, due to its anatomical specializations for clinging and leaping. However, it lacks the specializations for hindlimb suspension, as in Chiropotes and Cacajao, which may relate to the larger body

size of the latter two genera. Members of the P. monachus-group appear to retain a more primitive positional repertoire.

Chiropotes and Cacajao

Quite similar in many ways to one another, Chiropotes satanas and Cacajao calvus are more generalized in their positional adaptations than is Pithecia pithecia. They are both more active than is Pithecia; Chiropotes spends more time feeding than the other two genera, while Cacajao spends the most time traveling. Cacajao engages in more locomotor activities in general, compared to the other species. The primary behavioral mode for both Chiropotes and Cacajao is quadrupedalism, followed by pronograde clambering. Both maintain a pronograde body orientation, using primarily horizontal or low-angled supports in the main crown, and deformable ones in the terminal branches. A pronograde body position is maintained throughout all leap phases (after take-off). Although leaping plays an important role in the locomotor repertoire of these species, the anatomical correlates of leaping present in Pithecia are not exhibited in either Chiropotes or Cacajao. Leaping appears to be important in predator avoidance for these species also, as it allows the rapid crossing of gaps; leaping is a frequently used mode for startled or unhabituated individuals. Fontaine (1981) reported that Cacajao uses

more leaping and armswinging when under stress, and often crosses gaps using either behavior. Most leaps and drops of Chiropotes and Cacajao occur between the terminal branches of neighboring trees, and they are quite noisy. Vigilance, made effective by the large group sizes of these species, plays a more important role than any attempted crypticity in these species. For example, when Cacajao group members are foraging on the ground, other individuals remain in the trees to keep watch (Ayres, 1986).

In terms of positional adaptations, these species are primitive relative to Pithecia. However, both of these species are more derived than is Pithecia in their dietary adaptations, as evidenced by the mandibular and dental morphology, specialized to a higher degree for sclerocarpivory.

Cacajao is more derived than is Chiropotes, due to its more specialized use of hindlimb suspension, shortened tail, and adaptations to the unique habitat in which it lives.

D. Direction for future studies

There remains much to investigate in this field. Studies should be designed to pull apart and examine the many possible variables contributing to positional adaptations. I suspect, however, that we should look to behaviors associated with travel as a possible primary adaptation, as some evidence suggests that, at least for

Pithecia, locomotor behaviors used during travel have played an important part in shaping its positional repertoire, and are only secondarily used in feeding. Additionally, in examining the relationship between diet and positional behavior, it may be a good idea to look beyond the food itself to its distribution in the forest, and at potential "key" resources which may be utilized in difficult times.

The most valuable contributions to be made, I believe, will be in thorough comparisons of members of the same species, as well as those of sets of different species, in both a sympatric and and allopatric situation.

APPENDIX 1. Positional behavior during feeding
(frequencies for which repeated samples have been
eliminated).

	<u>Pithecia</u> (N=2919)	<u>Chiropotes</u> (N=2708)	<u>Cacajao</u> (N=288)
Positional Behavior			
Locomotor			
quadrupedal walk	1.7%	5.4%	11.8%
quadrupedal run	-	1.5	1.0
pronograde clamber	11.5	11.9	19.1
pronogr. clamber-run	-	-	-
leap	1.1	1.2	3.1
drop	-	-	2.1
Total	14.3	20.0	37.1
Postural			
sit	50.8%	49.9%	40.6%
stand	10.6	13.1	9.7
perch	9.4	8.4	4.2
vertical cling	10.5	-	1.0
bipedal stand	1.9	3.6	1.4
pedal suspension	-	1.3	3.5
Total	83.2	76.3	60.4
Other (cumulative total of those behaviors each of which comprised <1% of samples)	2.6%	3.7%	2.3%
Total	100.1	100.0	99.8

APPENDIX 2. Positional behavior during rest (frequencies for which repeated samples have been eliminated).

	<u>Pithecia</u> (N=1653)	<u>Chiropotes</u> (N=1068)	<u>Cacajao</u> (N=146)
Positional Behavior			
Locomotor			
quadrupedal walk	-	1.2%	2.1%
Postural			
sit	69.8%	61.2%	58.9%
stand	3.8	7.0	3.4
lie - ventrum	6.2	24.8	28.1
lie - dorsum	-	-	1.4
lie - side	2.6	3.3	1.4
vertical cling	13.9	-	1.4
pedal suspension	-	-	1.4
lean	1.0	-	-
Total	97.3	96.8	95.7
Other (cumulative total of those behaviors each of which comprised <1% of samples)			
	2.7%	2.0%	2.0%
Total	100.0	100.0	99.8

APPENDIX 3. Tree portions used during major activities
(Frequencies for which repeated samples have been eliminated.)

	<u>Pithecia</u>			<u>Chiropotes</u>			
	Feed	Travel	Rest	Feed	Travel	Rest	Play
N=	2865	2722	1626	2703	1757	1063	174
Tree Portion							
main crown	27.9%	39.9%	47.6%	40.8%	49.5%	78.9%	64.0%
terminal branches	45.3	16.8	4.6	50.5	34.3	7.2	24.9
vertical axis	4.5	6.5	7.3	1.0	1.0	1.8	-
below crown	6.6	13.0	22.5	2.5	7.9	9.5	2.5
bole	6.5	14.0	7.9	-	-	-	-
liana	5.4	7.7	8.4	2.8	5.6	1.8	6.5
vine tangle	2.9	2.2	1.8	2.4	1.4	1.0	1.9
ground	1.0	-	-	-	-	-	-
	100.1	100.1	100.1	100.0	99.7	100.2	99.8

APPENDIX 4. Support use during feeding (frequencies for which repeated samples have been eliminated).

	<u>Pithecia</u>	<u>Chiropotes</u>	<u>Cacajao</u>
Number	(N=2876)	(N=2698)	(N=285)
one	45.0%	46.5%	41.8%
two	15.2	20.3	11.2
several	39.8	33.2	47.0
Inclination	(N=2872)	(N=2695)	(N=246)
horizontal	15.8%	24.6%	35.4%
angled	25.1	23.3	15.0
vertical	8.7	-	2.0
deformable	35.8	38.6	41.5
mixed	14.6	13.0	6.1
Diameter	(N=2866)	(N=2697)	
<2 cm	23.6%	16.6%	
2 - 5 cm	37.0	37.4	
6 - 10 cm	11.0	16.8	
11 - 15 cm	2.8	3.8	
>15 cm	1.0	1.6	
mixed, <2 & 2-5 cm	22.8	21.1	
other mix	1.9	2.7	

APPENDIX 5. Support use during rest (frequencies for which repeated samples have been eliminated).

	<u>Pithecia</u>	<u>Chiropotes</u>	<u>Cacajao</u>
Number	(N=1651)	(N=1069)	(N=146)
one	64.7%	68.6%	61.6%
two	28.6	27.1	24.7
several	6.7	4.3	13.7
Inclination	(N=1647)	(N=1066)	(N=144)
horizontal	33.1%	55.2%	60.4%
angled	41.8	34.2	28.5
vertical	9.3	-	1.4
deformable	1.8	2.8	8.3
mix of angled & horiz.	8.9	5.2	-
other mix	5.2	2.3	1.4
Diameter	(N=1648)	(N=1066)	
<2 cm	1.2%	1.0%	
2 - 5 cm	45.0	20.1	
6 - 10 cm	32.2	34.9	
11 - 15 cm	6.3	19.0	
>15 cm	-	13.4	
mix of <2 & 2-5 cm	5.0	2.8	
mix of 2-5 & 6-10 cm	8.1	5.8	
other mix	1.6	3.1	

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