Foraging behaviour of three primate species in a Costa Rican coastal lowland tropical wet forest

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ABSTRACT

Primates are predominantly distributed across tropical regions, many of which are threatened by deforestation. Removal of mature trees can harm primate populations by reducing available food resources. Understanding the dietary requirements of primates at local levels can help identify key habitats to conserve, and protect plant species on which primates rely. Little is known about local diets of *Alouatta palliata* (mantled howler monkey), *Ateles geoffroyi* (black-handed spider monkey), and *Cebus capucinus* (white-faced capuchin) in Costa Rica's lowland tropical wet forests. Because diet and activity levels are closely connected, studies examining one provide insight into the other. We used group scan sample methods to record activity and diet, identifying all plant species on which the primates fed. We identified nine families of plants eaten by *Ateles geoffroyi*, four families eaten by *Alouatta palliata*, and two families eaten by *Cebus capucinus*. Activity budgets demonstrated that *Alouatta palliata* was the least active species and *Cebus capucinus* the most active. We also found differences in the type of plant parts consumed by the three primate species; *Alouatta palliata* and *Ateles geoffroyi* fed mostly on fruit and new leaves, whereas *Cebus capucinus* fed on fruit and insects. The nine families of plants identified in this study are potentially important for all three primate species locally, and warrant conservation.

INTRODUCTION

New World primates have evolved to fill specific niches through variable body size, activity levels, and dietary preference (Rosenberger, 1992). However, these distinct niches may be contingent on intact forest. Timber extraction increases interspecies competition by narrowing the number of preferred plant species, in addition to reducing the total biomass of food resources. Studying basic primate natural history by recording aspects such as diet can assist conservation land management prescriptions at a local scale by identifying key habitats and plants that primates use, and protecting them as food resources.

In recent history, Costa Rica has suffered habitat loss of up to 4% forest cover per annum, mostly from expanding agriculture and human frontiers (Myers et al., 2000; Sanchez-Azofeifa et al., 2001; Achard et al., 2002). The country sought to redress this issue by the formation of national parks, and has recently expanded these to include wildlife corridors that connect reserve land to benefit primates, among a myriad of diverse wildlife (Canet-Desanti & Finegan, 2010). Costa Rica is biologically di-

verse, and has four species of primates that live in its tropical forests; *Saimiri oerstedii* (Reinhardt, 1872) (Central American squirrel monkey), *Cebus capucinus* (Linnaeus, 1758) (white-faced capuchin), *Alouatta palliata* (Gray, 1849) (mantled howler monkey), and *Ateles geoffroyi* (Kellogg et Goldman, 1944) (Geoffroy's or black-handed spider monkey). Despite their iconic status within Costa Rica's eco-tourism industry, surprisingly little is known about the diet of *A. palliata*, *Ateles geoffroyi*, and *C. capucinus* among these reserve lands, especially at local levels.

Group size and social structure can mitigate intra- and inter-species competition for food resources. Mantled howler monkeys form large, stable groups ranging from 2-39 individuals (Crockett & Eisenberg, 1987). They can live in large groups without intense food competition because their fitness is limited by access to mates rather than food; leaves are an abundant and easily accessible food source (Di Fiore & Campbell, 2007). Species with a higher proportion of fruit in their diet often use grouping strategies that allow access to this widely dispersed food source. Black-handed spider monkeys have a fission-fusion social structure (Di Fiore & Campbell, 2007), and live in groups of 15-25 individuals, forming sub-groups of 3 individuals (Robinson & Janson, 1987). Fission-fusion social structures may be a way of avoiding direct competition over food resources with conspecifics, by dispersing in small groups to scattered fruit sources (Di Fiore & Campbell, 2007). White-faced capuchins also feed predominantly on fruit, and form mixed-sex groups of 10-35 individuals (Robinson & Janson, 1987; Jack, 2007). Large group size might be a way to increase frequency of detecting fruit sources and defending these sources against other groups (Janson, 1988). Capuchins' smaller body size means that they have to intake fewer calories, mitigating competition within each group.

This study was performed at Caño Palma Biological Station, 8 km north of the coastal village of Tortuguero, in NE Costa Rica. Caño Palma is a small 5,000 m² reserve of mixed lowland tropical wet forest with dominant stands of *Manicaria* and *Raphia* palms (Lewis et al., 2010). The main objective of this study was to identify plant species and parts consumed by *A. palliata*, *Ateles geoffroyi*, and *C. capucinus*. In addition, each primate species was monitored for activity budget and food competition,

to create an ethogram to determine whether they fed on overlapping plant species and plant parts.

MATERIALS AND METHODS

The study period lasted 28 survey days from 8 April to 20 May 2011. Each day, the study site was surveyed commencing at 06:00. The first located species of primate was followed and monitored through the day until nightfall or until they became inaccessible. Observational frequency of all three primate species was adjusted in the field to ensure equal time budgets were allocated to each species. Namely, if one species had been followed more often than another, but was the first to be located during a survey, this species was immediately followed until an encounter with a less frequently observed species. For each data point, GPS coordinates were recorded to create distributional maps of each primate species across the site.

Activity budget data were collected using a group scan sample method (Martin & Bateson, 1993). At two-minute intervals the activity of each individual was recorded as one of four categories; inactive, travelling, feeding, and social interaction (Pavelka & Knopff, 2004). The age and sex of each individual was also recorded. Juveniles were not divided by sex, and adults of unknown sex were not included in analysis. Infants were excluded from activity budgets because of dependence on mothers for food (Pavelka & Knopff, 2004). When an individual was feeding, the species of plant and/or plant part was recorded. The five categories of plant parts were new leaf, mature leaf, unknown leaf, fruit, and stalk (Pavelka & Knopff, 2004). Plant parts that could not be identified were recorded as 'unknown'. Unknown plant species were included in the analysis of activity budget and plant parts, but discounted in analysis of plant species. For insectivores, such as *C. capucinus*, the number of insect feeding bouts was recorded, but the species of insect was not identified due to the complexity of deciphering specific species for each insect.

Data analyses of activity budgets and food budgets were conducted using R (version 2.11.1). Food budgets were sub-divided into separate analyses for plant species and plant parts. Individual identification of primates was not possible, and therefore, repeat sampling of some groups likely occurred. We

attempted to control for repeat sampling by using group scan sampling. The time budget spent for each activity was measured as a proportion of the time observed (Pavelka & Knopff, 2004). Therefore, time spent by a primate on an activity, the dependent variable, was measured as a percentage. Activity budget analyses used a 3 (species) x 2 (age) x 2 (sex) three-way ANOVA on mean frequency of each activity. Variation in plant parts consumed was analyzed by a 2 (sex) x 2 (age) x 3 (species) three-way ANOVA on mean frequency of type of plant part consumed.

RESULTS

The dataset comprised 28 survey days, of which monkeys were observed on 17 days, for a total of approximately 49 hours. Totals of 933 *A. palliata*, 368 *Ateles geoffroyi*, and 156 *C. capucinus* observations were recorded. Individual monkeys often provided multiple observations upon encounter.

Population and Distribution

A. palliata were found in groups of 3-4 individuals, *Ateles geoffroyi* in groups of 3-7 individuals, and *C. capucinus* in groups of 12-20 individuals. Distribution maps for each primate species indicated that most groups were located, and foraged, in edge and transitional (occasionally flooded) habitat (Fig. 1). Only *A. palliata* were found farthest north of the reserve among *Manicaria* swamp habitat (Fig. 1).

Activity Budgets

Overall activity budget for *A. palliata*, including all age and sex groups, indicated they spent 77% of time inactive, 14% moving, 7% feeding, and 2% engaging in social behaviour. *Ateles geoffroyi* spent 41% of time moving, 31% inactive, 20% feeding, and 8% engaging in social behaviour. *C. capucinus* spent 76% of time moving, 10% engaging in social behaviour, 8% feeding, and 6% inactive (Fig. 2). A 3 (species) x 2 (age) x 2 (sex) three-way ANOVA on mean frequency of each activity produced a statistical interaction between activity and primate species. The percentage of time spent on each activity differed significantly between primate species, $F_{(6, 192)} = 8.2069$, P = 0.001 (Fig. 2).

Diet

For time engaged in feeding, *A. palliata* spent 35% feeding on new leaves, 32% on fruit, 30% on unknown leaves, 2% on stalks, and 2% on unknown plant parts. *Ateles geoffroyi* spent 44% feeding on new leaves, 28% feeding on fruit, 17% on unknown leaves, 11% on plant stalks, and 1% on mature leaves. *C. capucinus* spent 77% of the time feeding on fruit, 15% on insects, and 8% on unknown parts (Fig. 3). A 2 (sex) x 2 (age) x 3 (species) three-way ANOVA on mean frequency of type of plant part consumed produced an interaction between plant part and primate species. Primate species ate different plant part, $F_{(10, 291)} = 2.347$, p = 0.0123, but not different plant families (Table 1).

Nine families of plants were identified as food for *A. geoffroyi*; Anacardiaceae, Araceae, Arecaceae, Clusiaceae, Melastomaceae, Moraceae, Myrtaceae, Rubiaceae and Tiliaceae. *A. palliata* fed on four plant families (Anacardiaceae, Araceae, Arecaceae, Clusiaceae), and *C. capucinus* fed on two plant families (Anacardiaceae and Melastomaceae) (Table 1).

DISCUSSION

Population and Distribution

All three species of primate were observed around Caño Palma's reserve land without disturbing normal activity. This suggested that all three species were habituated to human presence, likely due to the long-term presence of researchers at Caño Palma Biological Station and regular ecotourism to the area.

Caño Palma Biological Station's reserve land features lowland tropical wet forest edge, lowland tropical wet transitional (occasionally flooded) forest, and *Manicaria* swamp forest (Lewis et al., 2010). All three species of primates in this study were located, and observed foraging among edge and transitional vegetative zones within Caño Palma's reserve land. Only *A. palliata* was located in *Manicaria* swamp forest habitat. This is possibly due to the higher diversity of food providing trees and high vegetation within the transitional forest zone (Lewis et al., 2010). The observations of group numbers of *A. palliata*, *Ateles geoffroyi*, and *C. ca-*
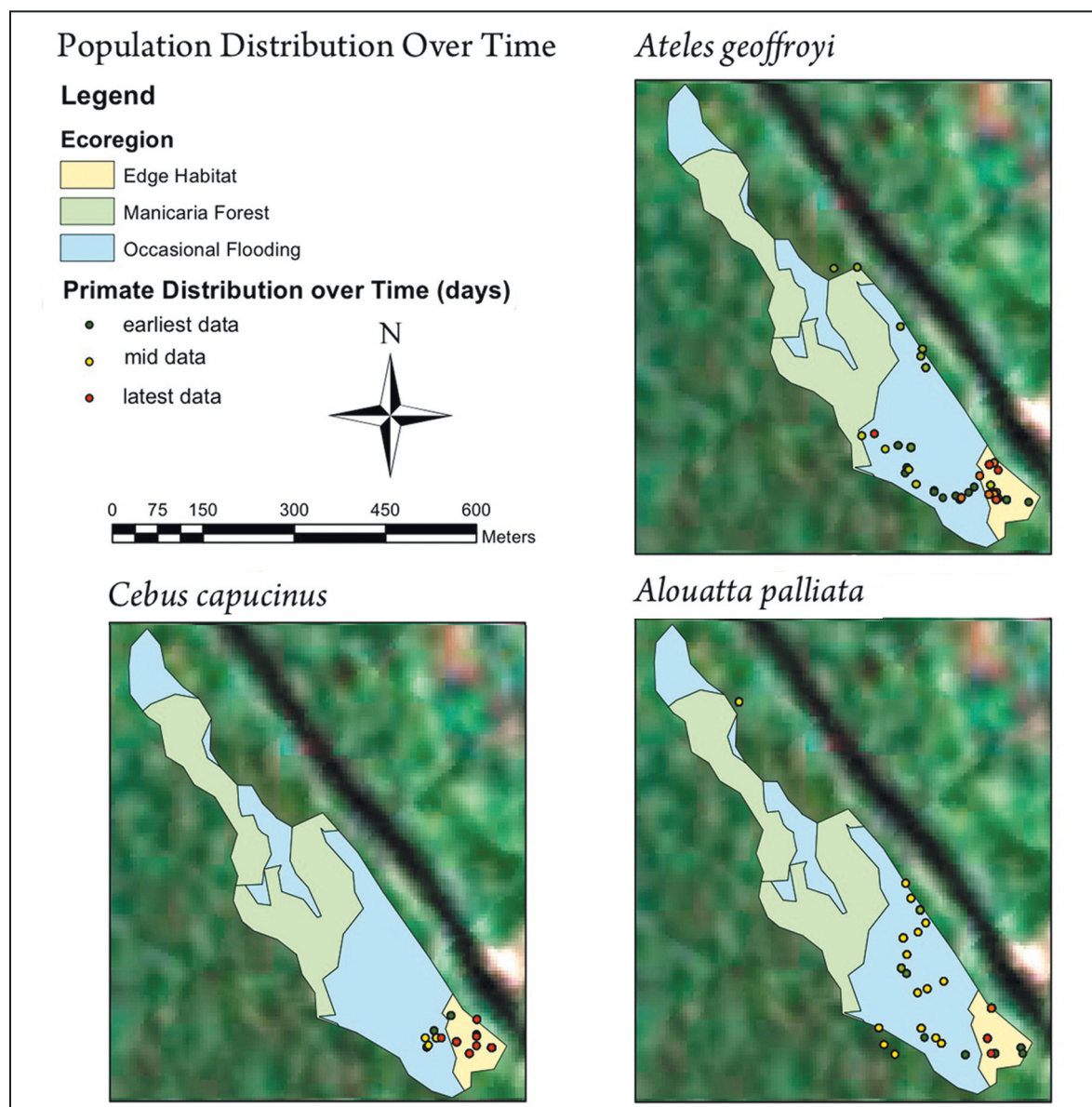
Figure 1. Distribution of each primate species across the study site as a function of time.

pucinus concurred with known group numbers for each species. *A. palliata* were found in groups of 3-4 individuals, within the reported range of 2-39 individuals (Crockett & Eisenberg, 1987). *Ateles geoffroyi* were found in small groups of 3-7 individuals that were possibly sub-groups, although they have been observed at Caño Palma Biological Station in larger groups (P. Grant & R. Ballard, pers. comm.). *Ateles geoffroyi* are usually found in fission-fusion structured social groups of 15-25 individuals, and form sub-groups of up to three individuals (Robinson & Janson, 1987; Di Fiore & Campbell, 2007). These fission-fusion social structures may be a way of avoiding direct competition over food resources with conspecifics (Di Fiore & Campbell, 2007). *C. capucinus* groups ranged from 12-20 and are known to form mixed-sex groups of 10-35 individuals (Jack, 2007; Robinson & Janson, 1987). *C. capucinus* were only observed on 3 non-consecutive days of 28 survey days, travelling through the study site. It is possible that Caño Palma's reserve is only a portion of this group's range.
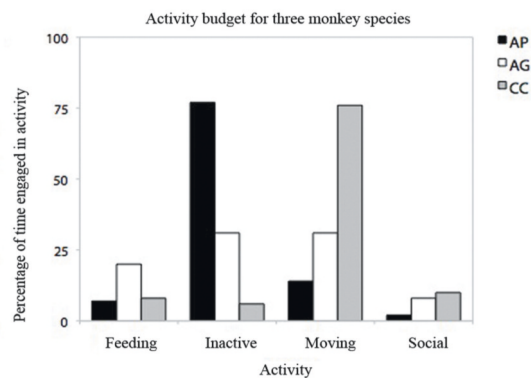
Figure 2. Activity budget by species (*Ateles geoffroyi* - black, *Alouatta palliata* - white, *Cebus capucinus* - grey); percentage of total time observed performing each activity. The percentage of time spent on each activity differed significantly between primate species, F (6, 192) = 8.2069, P = 0.001.
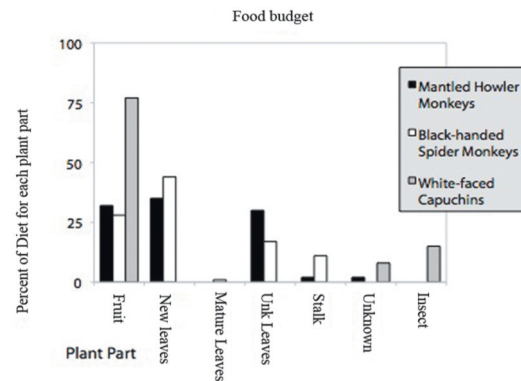

Figure 3. Food budget by species (*Ateles geoffroyi* - black, *Alouatta palliata* - white, *Cebus capucinus* - grey); percentage of total time observed feeding on each plant part.

Table 1. Food budget by species, age, and sex; percentage of total time observed feeding on each plant species.

Species	*Ateles geoffroyi*				*Alouatta palliata*				*Cebus capucinus*			
Age	All	A	J		All	A	J		All	A	J	
Sex	All	F	M	Unk	All	F	M	Unk	All	F	M	Unk
Anacardiaceae	23	15	28	50	44	41	47	50	8	14	0	0
Araceae	11	10	17	0	2	0	0	0	0	0	0	0
Arecaceae	23	29	22	0	5	5	7	10	0	0	0	0
Clusiaceae	1	2	0	0	18	20	20	10	0	0	0	0
Melastomataceae	4	6	0	0	0	0	0	0	46	43	0	100
Moraceae	7	6	6	10	0	0	0	0	0	0	0	0
Myrtaceae	1	2	0	0	0	0	0	0	0	0	0	0
Rubiaceae	5	6	0	10	0	0	0	0	0	0	0	0
Tiliaceae	16	15	17	20	0	0	0	0	0	0	0	0
Unknown	9	8	11	10	32	34	27	30	31	14	100	0
Insect	0	0	0	0	0	0	0	0	15	29	0	0

During this study, little interspecific competition was observed between primate species despite their overlapping distribution. This is possibly because each species foraging strategy led them to feed on different plant parts and plant species. It is possible that each primate species filled a specific niche, although a year-long study would clarify this concept and determine whether competition increases during periods of lower food availability.

Activity Budgets and Food Choice

A. palliata, *Ateles geoffroyi*, and *C. capucinus* exhibited different activity budgets, and fed on different plant parts to sustain activity. Differing activity budgets are known for all three species (Schoener, 1971; Crockett & Eisenberg, 1987; Di Fiore & Campbell, 2007). *A. palliata* was observed to consume mostly leaves and fruit, and did not

travel as much as *Ateles geoffroyi* or *C. capucinus*. These findings are consistent with the hypothesis that *A. palliata* exhibits a strategy of energy minimization. Namely, they receive less energy from the leaves they eat, and therefore exert less energy (Di Fiore & Campbell, 2007). *A. palliata* is primarily folivorous, with a diet similar to colobines and indriids, but without a specialized digestive tract to efficiently digest fibre (Milton, 1979). Although their capacious gut allows *A. palliata* to digest leaves, they do not extract the same amount of nutrients as their old world relatives (Milton, 1979). Across primate species, diets high in leaves correlate to low levels of activity (Dasilva, 1992). At Caño Palma, *A. palliata* exhibited a preference for young leaves, which may be because they contain higher protein content, and are generally lower in fibre, thus easier to digest (Milton, 1979). *A. palliata* can remain in stable social groups sharing the same area without intense competition because leaves are abundant and readily available in high density (Di Fiore & Campbell, 2007). At Caño Palma we did not observe intraspecific competition for food resources either within or between howler monkey groups.

Ateles geoffroyi are known to move to specific areas to exploit seasonally ripe fruit and can spend between 18.9% and 50.5% of their day feeding (Robinson & Janson, 1987). Spider monkeys in this study ate fruit and leaves from a wide variety of plant species, and were more active than *A. palliata*. Unlike *A. palliata*, *Ateles geoffroyi* live in fission-fusion societies, possibly as a response to their dietary preference for ripe fruit (Di Fiore & Campbell, 2007). Because fruit is a densely but sparsely distributed resource, spider monkeys often divide into sub-groups to avoid competition while foraging (Di Fiore & Campbell, 2007). This was evident within Caño Palma's spider monkey groups from the low group sizes encountered. *Ateles geoffroyi* maximize energy intake by moving quickly to sources of high-energy foods (Di Fiore & Campbell, 2007). To gain the energy required to travel and forage; they must eat fruit and, synchronously to eat fruit, they must travel to foraging areas. At Caño Palma, *Ateles geoffroyi* ranged constantly in the field as was observed in their distribution. *Ateles geoffroyi* do not have the capacious gut of *A. palliata* and therefore possibly cannot extract sufficient calories from leaves alone.

C. capucinus can spend 70-80% of their day foraging and move seasonally to find ripe fruit (Robinson & Janson, 1987). Our observations showed *C. capucinus* to be more active than *Ateles geoffroyi*, eating mainly fruit, as well as occasional insects. This diet of high energy fruit and insects could allow higher activity levels for capuchins. According to optimal foraging theory, individuals should select fruit based on caloric/nutritional profitability even when other familiar food sources are available (Schoener, 1971). Considering this, *C. capucinus* should consume the available fruit with the highest energy content. A study to investigate capuchin seasonal diet at Caño Palma would confirm this aspect. Diets between neighbouring groups of *C. capucinus* can vary and such differences in diet between groups at Caño Palma could be cultural, intraspecific, or due to food profitability (Chapman & Fedigan, 1990).

Diet Composition

In this study, the three primate species fed on a total of nine families of plants, some of which overlapped across two, or all three species. The difference in plant families consumed may be explained by the preferred plant parts of each primate species, and possibly by plant distribution. *A. palliata* has been known to consume mostly young leaves and fruit, and the morphology of their teeth suggests they have a predominantly folivorous diet (Crockett & Eisenberg, 1987; Di Fiore & Campbell, 2007). Past studies have shown that the proportion of fruit in the diet of *A. palliata* affects their activity levels, because fruit is a higher energy source than leaves (Pavelka & Knopff, 2004). At Caño Palma, *A. palliata* confirmed their known ecological behaviour trait as inactive frugivore-folivores by their selection of vegetative food (Table 1).

Our observations of *Ateles geoffroyi* diet confirm their ecological behaviour as active frugivore-folivores that prefer ripe fruit (Robinson & Janson, 1987; Di Fiore & Campbell, 2007). At Caño Palma, *Ateles geoffroyi* were seen consuming *Philodendron* sp. (Araceae). *Philodendron* is a genus known for its toxic properties due to the presence of calcium oxalate crystals (Genua & Hillson, 1985). Calcium oxalate crystals are a secondary compound that defends certain plant species against herbivores (Franceschi & Horner, 1980). Other mammal species, with ruminating or complex guts, have been known to eat high concentrations of oxalates (Freeland & Janzen, 1974). Humans also consume some oxalate

rich foods such as rhubarb, spinach, nuts, and tea, and over-consumption can lead to adverse health effects (Massey et al., 1993). *Ateles geoffroyi* may possess a tolerance to oxalate crystals that allow them to consume calcium oxalate rich plants, such as *Philodendron* spp., in conjunction with other plant foods when preferred sources are scarce (Franceschi & Horner, 1980). This food choice could also be an act of self-medication (Huffman, 1997). *Ateles geoffroyi* in certain parts of Costa Rica have lower parasite loads due to the ingestion of fig leaves (Glander, 1994), and it is possible that calcium oxalate acts as a similar vermicide.

C. capucinus confirmed their ecological behaviour as very active frugivore-insectivores (Robinson & Janson, 1987). Their diet is known to be variable, comprising mostly seasonal fruit or insects, and they are known to hunt small vertebrates (Jack, 2007). At Caño Palma, *C. capucinus* consumed species of plant not atypically described for the species at other sites across Costa Rica and the neotropics (Jack, 2007).

Habitat and Conservation for Primates at Caño Palma

Factors such as variable body size and feeding specializations may help New world primate species to mitigate interspecific competition. Additionally, each species' social structure can alleviate pressure from intraspecific competition and resource scarcity (Rosenberger, 1992). This self-regulating behaviour among and within species of primate highlights the importance of protecting areas that contain preferred food plants, especially in connected habitats like Caño Palma that buffer national reserves.

However, despite laws to regulate selective logging within the Barra del Colorado Refuge, unmonitored logging still occurs (Lewis et al., 2010; R. Ballard, pers. comm.). We recommend that any selective logging should avoid plant families and communities of local provenance to maintain the integrity of food resources for primates. Notwithstanding, regulation of selective logging on the vast Barra del Colorado Refuge is not always pragmatic. By studying and considering local foraging by primates, a strategy to conserve connected areas around Caño Palma could be realised, and is suggested. Further study of territory and distribution combined with disseminating information, and involvement of local communities, support this recommendation.

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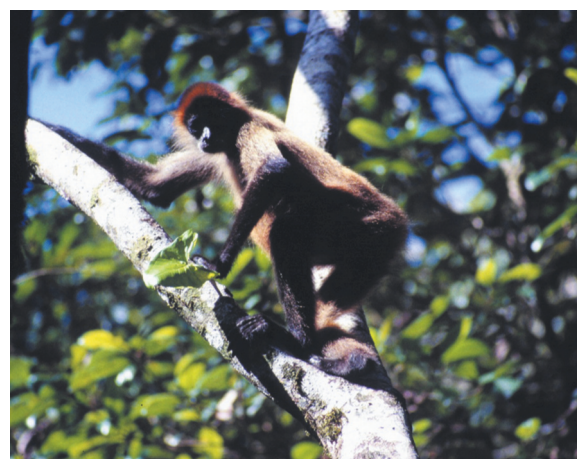
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Figure 4. White faced capuchin. Copyright Jamie Bowkett. Figure 5. Mantled Howler Monkey. Copyright Michelle Haines. Fig. 6 Black-handed Spider Monkey. Copyright Paul Grant.

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