Table 1. Physical characteristics around randomly selected *Inga* seedlings in primary (n=7) and secondary (n=7) forest sites at Corcovado N.P., Costa Rica. Differences in litter depth, O horizon depth, and soil moisture were significant (P<0.05, mean ± SE, see text).

Forest Type	Litter Depth (cm)	O horizon depth (cm)	Soil moisture (%)	Canopy Cover (%)	pH	Soil minus air temp °C
Primary	3.4 ± 0.7	2.7 ± 0.64	88.6 ± 0.9	79.6 ± 1.3	6.3 ± 0.07	1.4°C ± 0.1
Secondary	1.0 ± 0.4	0.7 ± 0.35	68.1 ± 3.7	77.6 ± 1.3	6.4 ± 0.08	1.3°C ± 0.2

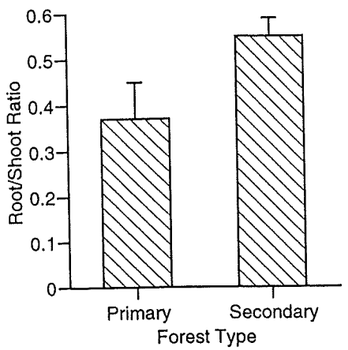

Fig. 1. Root/shoot ratio of *Inga sp.* seedlings in primary (n=7) and secondary (n=7) forest sites at Estacíon Sirena, Corcovado N.P., Costa Rica (mean ± 1 SE, P=0.07).

Discussion

The higher root/shoot ratio of *Inga* in the secondary compared to the primary forest was probably due to differences in the soil environment. Sunlight did not seem to be a factor differentially affecting seedling growth in the two forests, as the canopy cover over *Inga* did not differ significantly between secondary and primary forests. Therefore, *Inga* seedlings in the secondary forest were probably either nutrient or water limited, and required more roots per shoot mass than plants in the primary forest.

The difference in soil texture between forest types (sandy soil in secondary sites and loamy-clay in primary forest sites) probably is the main reason for the difference in root/shoot ratios. Sandy soils have a lower cation exchange capacity, and so hold fewer nutrients than clay. Therefore, the secondary soils may be more nutrient limited than the primary forest soils. In soils with low pH, base cations such as K^+, P^+, Ca^{2+}, and Mg^{2+}, which are important nutrients for plants, are replaced with protons and leached out of the soil. pH did not differ significantly between soils, so acidity did not seem a likely cause of differences in nutrient levels in these two tropical forests soils.

Greater soil moisture in the primary forest could be due to the greater litter layer and O horizon compared to the secondary forest, which would prevent water from evaporating. As well, clays dry out more slowly than sandy soils, thereby increasing soil moisture. Temperature did not differ significantly between sites, and thus could not affect soil moisture levels.

Differences in soil type may partially be the result of differences in past usage and geological history. Unlike the primary forest sites, the secondary forest sites I sampled were farmed until 1978, and therefore cleared of trees, which in tropical areas often results in nutrient leaching (D. Peart, *pers comm*). Also, the secondary forest sites I sampled were on flat land < 500 m from the ocean, which could explain the sandy soils there. The primary forest, however, was farther from the ocean and likely on volcanic or alluvial soils.

The deeper litter layer and O horizon in the primary compared to the secondary forest could be due to greater organic input rates. However, if the decomposition rates differ between forest types, then inputs might be equal. Slower decomposition, perhaps due to tougher leaves that resist decomposition, returns nutrients to the soil less quickly, implying that the primary forest could be less nutrient limited than the secondary forest.

In conclusion, significant differences in soil characteristics existed between sites, with the primary forest having a deeper litter layer and O horizon, greater soil moisture, and more clay-like soils than in the secondary forest. *Inga* seedlings in the secondary forest had a greater root/shoot ratio than in the primary forest. These findings suggest a lower nutrient availability in the secondary forests, which may be related to past use and geological history.

Factors influencing spider monkey (*Ateles geoffroyi*) group size and sex ratios

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Abstract: Spider monkeys, *Ateles geoffroyi*, live in groups of variable size and composition that may change multiple times during the day. We examined the relationships between group size, sex ratio and activity (foraging, resting or traveling) of spider monkeys in primary and secondary forest. We hypothesized that group size while foraging and traveling would be small to lessen intraspecific competition and increase travel efficiency. Group size, especially while resting, would be large when predation risks are high to increase predator detection. Similarly, sex ratios should be even in large groups, but skewed in smaller groups. We found no correlation between group size and sex ratio or group size and activity. Groups were significantly smaller in secondary forest, where food may be more limiting and travel costs may be higher than in primary forest.

Key Words: intraspecific competition, primate social organization, sex ratios, troop structure

Introduction

Spider monkeys, *Ateles geoffroyi*, live in groups that change in size and composition throughout the day (Klien 1972). They are among the most active monkeys in Costa Rica (Reid 1997), and must forage for leaves and fruit frequently during the day to meet their energy needs. Chapman (1990) found that spider monkey group size was related to food availability.

We hypothesized that group size would vary with activity and location (primary vs. secondary forest). Resources may be limited during the dry season or in secondary forest, so small group size may be preferable to reduce intraspecific competition (Janson 1986). However, if predation risks are high, large foraging groups may increase individual foraging efficiency because each individual may devote less time to searching for predators (Dums et al. 1997). Thus, we predicted that spider monkeys would aggregate into large groups when resting for defensive purposes. However, since large groups deplete resources rapidly, they must travel more often (Chapman 1990). We predicted that traveling groups would be small to enable fast travel between foraging sites, especially in secondary forest, which tends to have larger gaps than primary forest, increasing travel time (Dunn and Preuss 1993).

Furthermore, we hypothesized that sex ratio would vary with group size. We predicted that large groups would have more even sex ratios because sub-groups congregate to rest. Our rationale for this was that sub-groups that split off to feed and travel may be dominated by high ranking males with several females, while subdominant males form their own subgroups (Eisenberg 1983).

Methods

On 5-7 February 1999 we spent 60 person-hours searching for groups of spider monkeys on all trails within 3 km of Estación Sirena in Corcovado National Park, Costa Rica. When a group was encountered, we noted the time, type of forest (primary or secondary), group size, and sex ratio. Sex of monkeys was determined by looking at the genitalia: the testes of males and the lack of testes in females. Some females also possessed large pendulous external genitalia which could be confused with male structures (Reid, 1997). For each group we conducted two separate scan surveys 5 min apart, recording the behavior (foraging, resting or traveling) of each monkey at an instant in time to determine the modal behavior of the group. To correlate group size with activity, we categorized groups into "small," < 8 individuals, and "large," 8 individuals.

Results

We observed 22 groups of spider monkeys, ranging in size from 2 -16 individuals. Sex ratios were determined for 20 of the groups. Eight groups were observed foraging, six resting, and 10 traveling. Group size was not correlated with activity, since small and large groups participated evenly in all three activities (Table 1). The mean ratio of males to females did not differ by group size (Kruskal-Wallis: $X^2 = 0.49$, df = 1, P = 0.48), although small groups had a

much wider range of sex ratios than did large groups (small: 0.3-3, large: 0.6-2). Group sizes were significantly smaller in secondary forest than in primary forest (Fig. 1, t-test, t = 2.52, df = 20, P = 0.02).

Table 1. Number of individuals, sex, and activity type as a function of group size in Spider Monkeys (mean ± 1 SE).

		Number of individuals			% Time		
Group Size	n	Males	Females	Infants	Feeding	Resting	Traveling
Large (8 indiv.)	8	5.3 ± 0.61	5 ± 0.86	1.2 ± 0.40	40.3 ± 7.6	23.3 ± 10.3	32.9 ± 15.4
Small (< 8 indiv.)	14	2.2 ± 0.21	2 ± 0.28	0.7 ± 0.24	34.1 ± 9.2	32.0 ± 10.3	33.9 ± 11.1

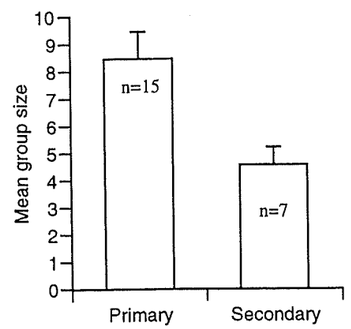

Fig. 1. Number of spider monkey individuals per group (mean ± 1 SE) in primary versus secondary forest near Estación Sirena, Corcovado National Park, Costa Rica (p=0.02).

Discussion

Contrary to our predictions, food limitation, foraging efficiency, and predation do not appear to influence group size during specific activities. Both small and large groups were found foraging, traveling, and resting in approximately equal proportions. All subgroups except one had more than two individuals, contrary to Freese's (1976) finding that spider monkeys are most frequently encountered in groups of two. Small groups had a wider range of male to female ratios, which may be due to dominance hierarchies within troops affecting sub-group sex ratios.

In primary forest, foraging took place in both small and large groups, suggesting that food resources may not be a limiting factor. Group size therefore, may not need to be reduced to decrease intraspecific competition in this habitat. Further, predation risk may not be the sole determinant of resting group size, since spider monkeys were seen in both small and large groups when resting. However, we did observe that the majority of subgroups in primary forest (13 of 14) contained five or more individuals, perhaps helping to increase predator surveillance during all activities.

In secondary forest, food may be more limiting, explaining why only small groups were found there. With small groups there is presumably less intraspecific competition and increased foraging efficiency (Janson 1986). Canopy cover is less dense in secondary forests, increasing the time and effort required for travel. Therefore, small group size may reduce energy costs of travel and travel time.

The relationships between group size and activity that we observed in primary and secondary forest are not completely explained by food limitation or predation risks; other environmental or social factors may be important in determining the size of spider monkey groups.

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