

High population density of black-handed spider monkeys (*Ateles geoffroyi*) in Costa Rican lowland wet forest

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Abstract The main objective of this study was to estimate the population density and demographic structure of spider monkeys living in wet forest in the vicinity of Sirena Biological Station, Corcovado National Park, Costa Rica. Results of a 14-month line-transect survey showed that spider monkeys of Sirena have one of the highest population densities ever recorded for this genus. Density estimates varied, however, depending on the method chosen to estimate transect width. Data from behavioral monitoring were available to compare density estimates derived from the survey, providing a check of the survey's accuracy. A combination of factors has most probably contributed to the high density of *Ateles*, including habitat protection within a national park and high diversity of trees of the fig family, Moraceae. Although natural densities of spider monkeys at Sirena are substantially higher than those recorded at most other sites and in previous studies at this site, mean subgroup size and age ratios were similar to those determined in previous studies. Sex ratios were similar to those of other sites with high productivity. Although high densities of preferred fruit trees in the wet, productive forests of Sirena may support

a dense population of spider monkeys, other demographic traits recorded at Sirena fall well within the range of values recorded elsewhere for the species.

Keywords *Ateles* · Neotropical primates · Line-transect survey · Corcovado National Park · Sirena Biological Station

Introduction

Knowledge of the distribution and population density of primate species is crucial for assessing their conservation status (NRC 1981; Rylands et al. 1997; Cowlshaw and Dunbar 2000). Among neotropical primates, larger-bodied frugivores, for example spider monkeys (*Ateles* spp.), face additional risk because of the combined pressures of hunting (Mittermeier 1987; Ráez-Luna 1995), habitat reduction (Estrada and Coates-Estrada 1996), and the pet trade (Cowlshaw and Dunbar 2000; Duarte-Quiroga and Estrada 2003). As ripe fruit specialists, spider monkeys require relatively larger areas of forest than do species that are folivorous–frugivorous (e.g. *Alouatta*), omnivorous (e.g. *Cebus*), or frugivorous–insectivorous (e.g. *Saimiri*) and are, therefore, not found in small forest fragments (Estrada and Coates-Estrada 1996; Cowlshaw and Dunbar 2000).

The largest (41,788 ha) remaining tract of Pacific lowland wet forest (as defined by Holdridge 1967) in Mesoamerica is protected as Parque Nacional Corcovado (Corcovado National Park), on the Osa Peninsula of Costa Rica. The park encompasses primary, secondary, and coastal forest (Herwitz 1981; Hartshorn 1983; Boza 1988). Because of its size,

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protected status, and potentially high productivity, Corcovado would be expected to harbor large populations of spider monkeys (*Ateles geoffroyi*) and of the other three primate species present—mantled howler monkeys (*Alouatta palliata*), white-faced capuchins (*Cebus capucinus*), and squirrel monkeys (*Saimiri oerstedii*).

Throughout Central and South America, high precipitation is coupled with high plant diversity and number of mammal-dispersed fruits (Gentry 1982, 1983). In a comparative study of dry, moist, and wet tropical forests, Gentry (1982) found that wet forest was the most diverse. Although plant density did not differ significantly among tropical forests, wet forest tended to have more large trees than either dry or moist forests.

Objectives

In this survey, most of which preceded a one-year study of behavioral ecology of *Ateles* at the study site, my objective was to compare the Sirena spider monkey population density and other demographic variables with those for spider monkeys at other sites. A pilot study showed Sirena to have a high abundance of spider monkeys (Weghorst 2001). I predicted that the female:male ratio at Sirena would be lower (i.e. relatively more males) than at other sites, because evidence from other studies of spider monkeys (Chapman et al. 1989; Nunes and Chapman 1997) has supported the post-weaning resource competition hypothesis (Clark 1978). This hypothesis essentially states that sex ratios will be skewed toward the sex that disperses (in *Ateles*, females; McFarland Symington 1987), because the dispersing sex will not compete in the future with natal group members for resources. Chapman et al. (1989) found a significant negative correlation between site productivity (mean annual rainfall) and sex ratio (i.e. relatively more males in more productive habitats).

Methods

Study site

The survey was conducted intensively from mid-July 2002 to October 2002 and then intermittently, usually for several days each month, from November 2002 to October 2003 at the Sirena Biological Station in Corcovado National Park, Costa Rica (8°26′–8°39′N, 83°25′–83°44′W) (Gilbert 1982; Boinski 1987). The study area is composed of lowland wet primary, secondary, and coastal forest (Hartshorn 1983). Sirena is

bordered on one side by the Pacific Ocean, approximately 1 km away from the station buildings. Mean annual rainfall from 2000–2003 was 5,657.3 mm (SD 952.9 mm) (unpublished station data). There is a dry season from approximately December to March, with average monthly rainfall 175.8 mm (SD 215.7 mm). During the rest of the year the area receives 619.3 mm (SD 313 mm) of rain, on average, per month.

Survey methods

A stratified, replicated line-transect survey was used to estimate local population density (Chapman et al. 1988; Buckland et al. 1993). Twelve existing trails, totaling 16.16 km (average 1.35 km, minimum 0.45 km, maximum 2.08 km) (Table 1), were selected as line transects. These trails traversed habitats representative of forest used by spider monkeys and approximated straight lines better than other possible transects. (The station's policy prohibited the cutting of new trails). The five main forest types represented by the twelve transects were coastal primary, lowland primary, lowland secondary, lowland swamp, and upland primary forests (described in Table 1). Each transect was replicated 35 times for a total transect distance of 565.6 km. Two observers walked transects between 0600 and 1730 hours, for approximately equal times, in the morning (0600–1200 h) and afternoon (1201–1730 h). Occasionally, because of illness or other circumstances, only one observer was able to walk transects, but the most this occurred within one transect was nine times out of thirty-five, which is not a large enough sample size to reliably signal a true difference between one or two observers (Mitani et al. 2003). Almost all replicate walking of the same transect was separated by a minimum of 1 day. On four occasions, however, replicates were separated by at least 6 h but were checked for independence through examination of subgroup size and composition. Transects had previously been marked at 25-m intervals (except for one trail at 50-m intervals) by researchers and were walked at approximate speeds of 1.0–1.5 km h⁻¹, with frequent stops to listen and scan the forest. Censuses were not conducted during heavy rain or wind.

When a spider monkey was sighted, observers remained with the subgroup for approximately 10 min, or until all individuals were counted, leaving the transect only if the sex and/or age of a monkey could not be determined from the transect (Chapman et al. 1988). If all or most of the subgroup was counted in less than 10 min but the subgroup was traveling ahead of and parallel to the transect, the observers began walking the

Table 1 Line-transect descriptions, density estimates, and abundance indices

Transect length (km)	Effective distance (m)	Density estimate ^a (inds km ⁻²)	Abundance		Main forest types
			# subgroups km ⁻¹	# inds km ⁻¹	
0.80	46.43	130.00	2.32	12.07	Coastal primary ^b and coastal secondary ^c
2.08	60.82	37.15	1.02	4.52	Lowland secondary ^d , primary ^e , and swamp ^f
0.45	50.00	57.78	1.65	5.78	Lowland secondary and swamp
0.92	54.17	34.11	0.81	3.70	Lowland secondary, coastal primary
0.81	60.26	61.76	1.73	7.44	Lowland secondary
1.81	61.41	48.19	1.37	5.92	Lowland secondary and primary
1.75	61.30	66.05	1.53	8.10	Upland primary ^g
1.97	46.59	66.00	1.42	6.15	Upland primary
1.90	52.34	90.64	2.05	9.49	Upland primary, lowland secondary
1.55	44.60	87.00	1.79	7.76	Lowland secondary, coastal secondary
1.20	53.19	81.24	1.24	8.64	Lowland secondary, coastal secondary
0.92	53.57	61.45	1.37	6.61	Lowland secondary
Mean ± SD					
1.35 ± 0.56	53.72 ± 6.13	68.45 ± 26.25	1.52 ± 0.42	7.18 ± 2.27	–

^a Density estimated using effective observer-to-animal sighting distance

^b Coastal primary forest characterized by flat terrain, sandy soils, open understory, and trees such as *Quararibea asterolepis*, *Faramea occidentalis*, *Nectandra umbrosa*, and *Chomelia microloba*

^c Coastal secondary forest characterized by flat terrain, sandy soils, open understory, and trees such as *Ficus insipida*, *Ochroma pyramidale*, *Cecropia* spp., and *Spondias mombin*

^d Lowland secondary forest characterized by flat terrain, dense understory, and trees such as *Ficus insipida*, *Ochroma pyramidale*, *Cecropia* spp., and *Spondias mombin*

^e Lowland primary forest characterized by flat terrain, open understory, and trees such as *Anacardium excelsum*, *Caryocar costariense*, and palm species

^f Swamp forest characterized by flat terrain, poorly-drained soils, and trees such as *Symphonia globulifera*, *Luehea seemannii*, and *Crateva tapia*

^g Upland primary forest characterized by uneven, sometimes steep, terrain, well-drained soils, open understory, and trees such as *Viola koschnyi*, *Brosimum* spp., and *Protium* spp.

transect again to minimize the probability of counting the same individuals more than once. Spider monkeys estimated to be approximately within 150 m of one another and engaged in generally coordinated activity were considered to belong to the same subgroup (Chapman et al. 1993). Numbers of adults, subadults, independently locomoting juveniles, dependent juveniles, and infants of both sexes were recorded. On the first sighting, other data were recorded:

- 1 observer-to-animal distance,
- 2 perpendicular transect-to-animal distance,
- 3 activity (rest, feed, travel, forage, other),
- 4 height and forest stratum, and
- 5 method of detection (auditory or visual).

Throughout the duration of the survey, observers practiced estimating distances and heights and checked them against measured distances and heights.

The mean density formula (Hayek and Buzas 1997) employed for *Ateles* was:

$$\bar{X} \equiv \sum_{i=1}^N \frac{X_i}{N}$$

where N is the number of transects sampled and X_i is a sampling unit (i.e. density calculated from one transect). Transect width was estimated by several methods—effective, mean, and maximum observer-to-animal and perpendicular transect-to-animal distances (NRC 1981; Chapman et al. 1988; Whitesides et al. 1988). To estimate the effective distance for each transect, histograms of sighting distances were examined to determine the fall-off sighting distance, which was the point at which sighting frequencies decreased by at least 50% from the previous sighting distance (Whitesides et al. 1988). Effective distance was estimated by multiplying the fall-off distance by the total number of independent sightings per transect divided by the number of independent sightings before the fall-off distance (Whitesides et al. 1988) (Table 1). The mean and maximum distances were simply the mean and maximum, respectively, of all sighting distances for a transect.

The area covered by a transect was estimated as its length multiplied by its estimated width. Ninety-five percent confidence intervals were calculated for each density estimation (Hayek and Buzas 1997). To assess

the accuracy of population densities estimated from survey data, the estimated group size and home range were available for one focal social group monitored during the one-year behavioral ecology study.

When perpendicular transect-to-animal distances were compared to observer-to-animal sighting distances, standard deviations were always closer to the mean of the perpendicular distances, and mean perpendicular distances were always lower than mean sighting distances, primarily because of the abundance of perpendicular distances of zero, when animals were directly over the transect. For these reasons, densities were not estimated with perpendicular distances to reduce the risk of underestimating the area sampled and thus overestimating population density.

A normal distribution was observed for scatterplots of the total number of spider monkeys observed, and of the number of independently locomoting individuals (ILI) observed, plotted against the sighting distances. No interaction was noted between transect length and density.

Focal study group

From the one-year behavioral ecology study, the size of the social group whose members included at least two radio-collared focal subjects was estimated to be approximately 85 individuals (Weghorst, unpublished data). Using the minimum convex polygon method of home range calculation, a preliminary, broad estimate of this same social group's home range was approximately 1 km² (Weghorst, unpublished data). Thus, the population density estimate based on behavioral following of focal subjects was approximately 85 individuals km⁻² (inds km⁻²).

Results

Ateles geoffroyi has extremely high density estimates at Sirena Biological Station. Population density estimates calculated by employing the effective, mean, and maximum sighting distances varied, and the twelve transects also varied in their density estimates (Table 1). There was, however, no pattern of density differences among habitat types.

The population density estimate calculated from the effective sighting distance for spider monkeys at Sirena was 68.45 ± 26.25 inds km⁻², with a 95% confidence interval (CI) of 53.60–83.30 inds km⁻² (ILI only: 62.59 ± 24.94 inds km⁻², 95% CI 48.48–76.70 inds km⁻²). Use of mean sighting distances resulted in a much higher density estimate of 142.87 ± 57.28 inds km⁻², 95% CI

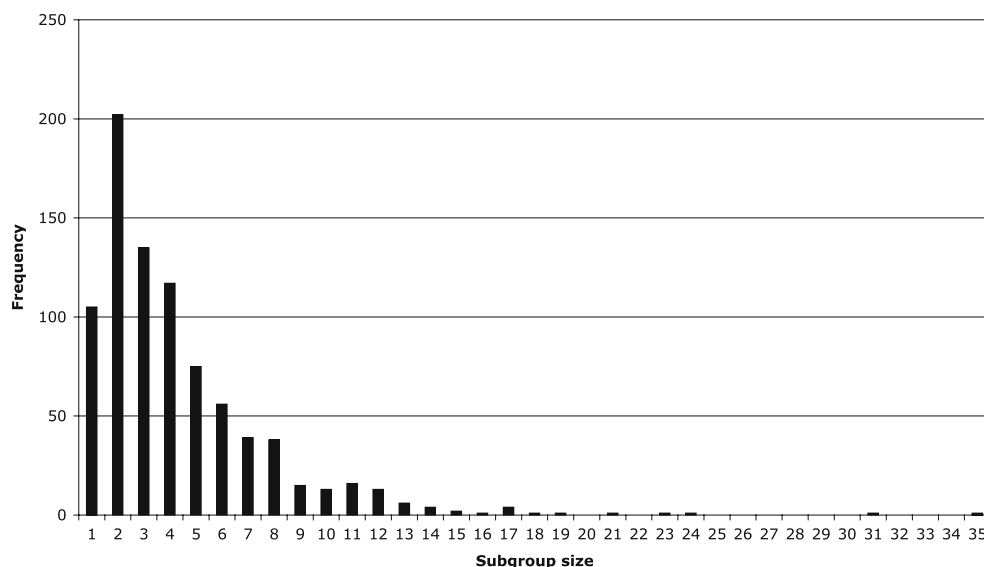
110.46–175.27 inds km⁻² (ILI: 130.92 ± 54.50 inds km⁻², 95% CI 100.08–161.75 inds km⁻²). Calculation of density by use of maximum distances resulted in the lowest estimate of 51.53 ± 15.35 inds km⁻², 95% CI 42.85–60.21 inds km⁻² (ILI 47.15 ± 14.68 inds km⁻², 95% CI 38.84–55.45 inds km⁻²).

Spider monkeys were sighted more often with the aid of auditory cues (67.85%) rather than visual (32.15%). These cues included vocalizations, rustling tree crowns, and dropping fruit. Active monkeys (81.31%) were spotted more frequently than resting ones (18.69%). Spider monkeys were found most often (65.39%) in the middle canopy layer, at average heights between 10 and 20 m. The high canopy (21–40 m) was the stratum used second-most frequently (27.33%), followed by the low canopy (1–9 m; 6.92%). Only one census sighting (0.12%) out of 836 was of spider monkeys on the ground.

There were 848 independent sightings of spider monkey subgroups during the survey, a total of 4,010 individuals across the 35 replicates (3,686 ILI). When subgroups were considered as ILI only, mean subgroup size was 4.35 ± 3.54 , with a median of 3.00 (Fig. 1). The most commonly seen subgroup contained two monkeys. The adult female-to-male ratio was 1.57:1 ($N_{\text{females}} = 1459$, $N_{\text{males}} = 927$) and the sub-adult female-to-male ratio was even at 1:1 ($N_{\text{sub-adult females}} = 261$, $N_{\text{sub-adult males}} = 261$). The juvenile female-to-male ratio was 1:0.66 ($N_{\text{juv. females}} = 158$, $N_{\text{juv. males}} = 238$), the reverse of the pattern for the adult sex ratio. Infants were more difficult to sex because their genitalia were more often concealed, with only 11 females and 7 males seen, giving a small-sample ratio of 1.57:1. The ratio of adults to immatures, which includes all individuals for which age but not necessarily sex was identified, was 4.28:1 ($N_{\text{adults}} = 2,827$, $N_{\text{immatures}} = 661$).

Of a total of 700 subgroup sightings that could be classed as single-sex or mixed-sex subgroups, most (52.86%) were composed of adult females only, with or without immatures (including sub-adult males). Approximately one-third (34.14%) of the subgroups contained both adult males and females. The least common category was all-male (including subadult males) subgroups, at 13%. Mixed-sex subgroups were larger than either all-male or all-female subgroups and averaged 7.43 ± 4.41 independently locomoting monkeys. The most common mixed-sex subgroup size was five (range 33). All-male subgroups and all-female subgroups had similar average sizes— 2.60 ± 1.82 for all-male and 2.86 ± 1.72 for all-female. The most common all-male subgroup size was one, however, whereas two was the most common all-female subgroup size. Females and males did not differ in their

Fig. 1 Subgroup size frequencies for independently locomoting spider monkeys at Sirena, Corcovado National Park, Costa Rica. Total number of independent sightings was 848. Mean subgroup size was 4.35 ± 3.54



frequencies of being alone ($z = -0.50$, $P > 0.05$, $N = 65$).

Discussion

The data from this survey enhance our knowledge and understanding of Mesoamerican demographic statistics of *Ateles*. Sirena Biological Station has one of the highest population densities of spider monkeys ever recorded (Table 2). Although it is impossible to extrapolate from density estimates at Sirena to the rest of the park, primarily because the flora of Sirena differs substantially from that of the other stations in the park (R. Aguilar, personal communication), it could safely be assumed that Corcovado National Park as a whole harbors an extremely large population of spider monkeys.

The complex variables that determine primate population densities include historical events, environmental quality, food availability, predation, disease, and interspecific competition (Struhsaker 1973; Dittus 1977; Cant 1980; Butynski 1990; Oates et al. 1990; Peres 1994; Tutin et al. 1997). It seems likely that several factors have worked synergistically to create the high density of spider monkeys in the forest surrounding Sirena station.

First, the spider monkeys of Sirena inhabit a protected national park. The closest road and village are 19 km away, providing even more protection by limiting access to the station. Thus, Sirena functions as a virtual island of protection from human encroachment. Groups of parkguards patrol the park regularly for poachers and illegal gold miners (Cuello et al. 1998).

Spider monkeys are not reported to be prey targeted by poachers (Altrichter and Almeida 2002), but they could be taken opportunistically.

Second, if spider monkeys were hunted before the park was established in 1975 (Christen 1995), they would have had over 25 years to recover. Spider monkeys are especially sensitive to hunting pressure, because of their relatively slow life history pattern, which includes a late age of sexual maturity and an interbirth interval of 2–4 years (Milton 1981).

Third, the fig family, Moraceae, was found to be the most diverse plant family at Sirena (A. Gentry, personal communication to L. Gilbert). Moraceae was the most-represented family in the Sirena spider monkeys' diets (Weghorst unpublished data) and has been found to be important in spider monkeys' diets at other studied sites (Chapman 1987; McFarland Symington 1987; Russo et al. 2005).

Fourth, some forest in its current stage of succession produces much fruit eaten by spider monkeys. When Corcovado was established as a national park some of the flat land surrounding Sirena was devoted to cattle pasture (Christen 1995; Cuello et al. 1998). This survey was conducted 27 years later, and the former cattle pastures are now regenerating secondary forest. This secondary forest has a high density of trees of *Ficus insipida* (Moraceae) and *Spondias mombin* (Anacardiaceae), which are both important food sources for spider monkeys (Weghorst, unpublished data). *Ficus insipida*, in particular, was one of the most frequently eaten food species (infructescences and leaf buds) and was available all year round. Its high density in regenerating secondary forest, asynchronous and frequent

Table 2 Comparison of high population densities of *Ateles* determined by use of line-transect surveys

Species	Location	Forest type	Location Size (km ²)	Density ^a (inds km ⁻²) ^k	Average subgroup size	Adult sex ratio (F:M)	Census duration (months)	Ref.
<i>A. Geoffroyi</i>	Otoch Ma'ax Yetel Koooh Sanctuary, México	Semi-deciduous	53.67	89.5 ^b (all inds)	–	–	12	Ramos-Fernández and Ayala-Orozco (2003)
<i>A. Geoffroyi</i>	Sirena, Corcovado National Park, Costa Rica	Wet	418	68.45 ^c (all inds); 62.6 (ILL)	4.73 (all inds); 4.35 (ILL)	1.57:1	14	This study
<i>A. Geoffroyi</i>	Tikal, Guatemala	Semi-deciduous	576	56.4 ^d (all inds)	4.7 (all inds)	1.61:1	0.27	Estrada et al. (2004)
<i>A. Geoffroyi</i>	Tikal, Guatemala	Semi-deciduous	576	45 ^e (all inds)	–	2.23:1	3	Coelho et al. (1976)
<i>A. Geoffroyi</i>	Tikal, Guatemala	Semi-deciduous	576	27.8 ^f (all inds)	4.3 (all inds)	1.76:1	11	Cant (1978)
<i>A. Geoffroyi</i>	Muchukux forest, Quintana Roo, México	Moist	–	27.11 ^g (all inds)	4.55 (all inds)	2.6:1	12	Gonzalez-Kirchner (1999)
<i>A. belzebuth</i>	Cerro Bran, northern Colombia	Moist	0.83	33.3 ^h (all inds)	3.34 (all inds)	–	9	Green (1978)
<i>A. paniscus</i>	Noel Kempff Mercado National Park, Department Santa Cruz, Bolivia	Moist	15,000	32.1 ⁱ (all inds); 23 (ILL)	6.2 (all); 4.5 (ILL)	–	15	Wallace et al. (1998)
<i>A. paniscus</i>	Cocha Cashu, Manu National Park, Peru	Moist	15,328	31 ^j (ILL)	3.15 (ILL)	2.53:1	2	White (1986)

^a Methods of transect width estimation by study

^b Perpendicular transect-to-animal distance (no method specified)

^c Effective observer-to-animal distance

^d Observer-to-animal distance (no method specified)

^e No method specified

^f Effective perpendicular transect-to-animal distance

^g Observer-to-animal distance (no method specified)

^h 100 m transect width

ⁱ Perpendicular transect-to-animal distance; width estimated by use of DISTANCE software with Fourier series transformations

^j Effective perpendicular transect-to-animal distance

^k Density estimates using all individuals (all inds) and independently locomoting individuals only (ILL) are specified

fruiting pattern (Milton 1991), large size (diameter at breast height averaging approx. 85 cm), and status as a preferred food, and a fallback food, of spider monkeys make it a leading candidate for the currently large numbers of *Ateles* at Sirena. *Ficus insipida*, and, more inclusively, Moraceae, is a very important resource for spider monkeys at Sirena. McFarland Symington (1988) compared population densities of *Ateles* across four forests and concluded that variation in their abundance was best explained by the presence of keystone resources. Tikal, Guatemala, a site that has had a relatively high population density of spider monkeys now (56.4 inds km⁻², Estrada et al. 2004) and over 30 years ago (45 inds km⁻², Coelho et al. 1976; 27.8 inds km⁻², Cant 1978), has a high density of trees of *Brosimum alicastrum* that were cultivated by the Maya, the fruits and young leaves of which are now eaten by spider monkeys (Coelho et al. 1976). McFarland Symington (1988) suggested that this tree species was a important resource for spider monkeys at Tikal and that it was partly responsible for their high abundance there. McFarland Symington (1988) proposed that the high population density of *Ateles* (28 inds km⁻²) at Cocha Cashu, Manu National Park, Peru could be related to the abundance of large strangler figs.

Although the results of this survey clearly showed a high population density for spider monkeys at Sirena, population density point estimates differed, depending upon whether the effective, mean, or maximum sighting distance was used to estimate transect width. Previous studies have revealed the effects that different survey methods and transect width estimation methods have on resulting estimates of population density (NRC 1981; Whitesides et al. 1988; Fashing and Cords 2000). Without other, non-survey information about a population, choosing among different estimates would be challenging. The data from the one-year behavioral ecology project provide a means for choosing among the three methods, however. Three transects—0.80, 0.81, and 0.92 km long—were located completely within one focal social group's home range. This social group's population density was approximately 85 inds km⁻². When transect width was estimated using the effective sighting distance, the mean density estimate using only these three transects—densities 130.00, 61.76, and 34.11 inds km⁻²—was 75.29 inds km⁻², consistent with results from behavioral data.

Comparison of population statistics of *Ateles* across studied sites and over time

Surveys of spider monkeys have been conducted in many forests throughout Central and South America

(Freese 1976; Pruetz and Leason 2002; Haugaasen and Peres 2005). High densities (at least 25 inds km⁻²) have been recorded for three different species of spider monkey in seven different forests ranging in area from 0.83 to 15,328 km² (Table 2). Forest types varied from semi-deciduous to wet. Survey duration ranged from 8 days (Estrada et al. 2004) to 15 months (Wallace et al. 1998). To facilitate cross-site comparisons of population density, Table 2 also provides the transect width estimation method used in each census. Several studies did not describe these methods, however, whereas others published only partial methods of transect-width estimation. Because the method of estimating transect width has a clear effect on the final density estimate, it is important to include full descriptive details of transect methods to facilitate cross-study comparisons.

Before this survey, the most recent survey of spider monkeys at Sirena was conducted for 1.5 months in 1991, when the estimated mean population density was 5.4 inds km⁻² (Piñeros 1994). There could be several explanations of the vast discrepancy between this study's mean population density estimate (68.45 inds km⁻²) and that of the survey conducted in 1991. One explanation could be methodological differences—the previous survey was conducted by different observers, on several different transects, over a shorter time period, and with fewer replicates (10), all of which could result in strikingly different estimates of the density (Mitani et al. 2003). I performed 199 resamples, however, with replacement of ten randomly-chosen replicates for each transect, keeping the respective effective distance constant for each transect. The mean was 68.06 ± 7.28 inds km⁻², and the 95% confidence interval was 56.11–83.90 inds km⁻². These resampled results suggest that ten replicates for each transect were sufficient. Another explanation of the discrepancy between the two surveys is that 11 years before this survey was conducted the population density of spider monkeys was actually much lower than it was during the span of this study. Forest succession—specifically, progression of cattle pastures into secondary forest—was probably an important factor in the growth of the spider monkey population around Sirena.

The results from this survey showed that the mean subgroup size of 4.35 for spider monkeys at Sirena was within the range of those in other sites studied in which densities of *Ateles* were relatively high (Table 2).

Adult sex ratios (females:males) for Sirena spider monkeys now and 11 years before this survey are virtually the same (1.64:1, Piñeros 1994; 1.57:1, this study). When compared with spider monkeys with high

densities at other sites, spider monkeys at Sirena have the lowest sex ratio (i.e. relatively more males; Table 2). Three of the five sex ratios published after these surveys are from the same site, however, Tikal. The low sex ratio at Sirena further supports the conclusion of Chapman et al. (1989) that there is a negative relationship between mean annual rainfall and the number of female to male spider monkeys.

Age ratios differed between the two Sirena surveys: 1:0.42 11 years ago (Piñeros 1994) and 1:0.23 now. That there are relatively fewer immatures now may reflect a real demographic change in the population over time. The large number of immatures recorded by Piñeros (1994) could have reflected an expanding population.

Increases in population densities for spider monkeys, howler monkeys, and white-faced capuchins have been observed in regenerating dry forest in Santa Rosa National Park (now called Área de Conservación Guanacaste), Costa Rica (Sorensen 1998). Similarly, an increase in population density of mangabeys (*Cercopithecus*) was found over a 20-year period at another site and was attributed mainly to regenerating forest (Olupot et al. 1994). This has important implications for conservation of spider monkeys and other primates. Spider monkeys may also aid forest succession in their ability to disperse seeds far away from the parent tree. Hladik and Hladik (1969) found that seeds of *Ficus* sp. that had passed through spider monkeys' guts germinated at a higher rate than seeds that had not.

The spider monkeys of Sirena are a model system for study of a dynamic, fission–fusion social system, all within a protected national park. As the secondary forest matures and no longer contains an abundance of trees of *Ficus insipida* or *Spondias mombin*, the high spider monkey population density will most probably decrease naturally as competition for fruit increases. Long-term monitoring of the Sirena groups could be very informative for answering questions about the relationship between demography and social system dynamics, or for designing conservation strategies.

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