The Effects of Forest Fragment Age, Isolation, Size, Habitat Type, and Water Availability on Monkey Density in a Tropical Dry Forest

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INTRODUCTION

The future of many primate species is uncertain. Countries with primate populations are losing 125,140 km^2 of forest annually and this destruction is considered to be a major threat to their survival (Chapman and Peres, 2001; Cowlishaw and Dunbar, 2000). Human disturbance of tropical forest is not

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only leading to habitat destruction but also to massive habitat fragmentation. In many areas of the world, fragmented habitats are becoming the dominant geographic feature (Laurance, 1999). The present study focuses on how the age of forest fragments since disturbance as well as the isolation and size of fragments affect the population density of white-faced capuchins (*Cebus capucinus*), black-handed spider monkeys (*Ateles geoffroyi*), and mantled howlers (*Alouatta palliata*) in tropical dry forest, in Costa Rica. Additionally, the present study examines how the habitat types and dry-season water availability within forest fragments affect the population density of these three primates. Using the line transect method, we censused the three monkey species within the megapark "Area de Conservación Guanacaste" (ACG). We conducted censuses in three parts of ACG where all three primates were present: Sector Santa Rosa (Santa Rosa National Park, SRNP), Sector Cerro el Hacha, and Sector Murciélago. We use these data to draw comparisons with previous primate census studies.

The conservation of primates living in tropical dry forest has received little attention, and there are only a few studies that provide the necessary information to produce conservation management plans for monkey species found in dry forests (Chapman *et al.*, 1989). Such data are needed because tropical dry forest is the most severely threatened of all major tropical habitat types, with less than 0.02% remaining in the world (The Government of Costa Rica, 1998). The near extinction of this forest type and the lack of information on primates living in dry forest fragments indicate that studies on this topic are urgently required. Our study contributes to this body of knowledge.

Background

One major variable we examine is the effect on monkey population densities (hereafter referred to as densities/density) of age since disturbance of the forest fragment. In SRNP, Sorensen and Fedigan (2000) found that capuchins returned to abandoned pastures after 14–25 years, howlers returned after 30–60 years, and spider monkeys returned after 60–80 years. These authors report that densities of all three primates were higher in older patches of forest (Sorensen and Fedigan, 2000). The current study examines whether these findings apply not just to SRNP but to other sectors of ACG, as well.

A second variable we examine is the effect of forest fragment isolation, measured as the distance between forest fragments, on primate density within the

fragment. Comparisons are made with the Estrada and Coates-Estrada (1996) study of mantled howlers where the density of primates was influenced by fragment isolation. Estrada and Coates-Estrada found that there were fewer individuals of *A. palliata* in more isolated habitat fragments. We also compare our results to the Onderdonk and Chapman (2000) study where the presence or absence of a primate species was affected by fragment isolation. Onderdonk and Chapman found that fragment isolation affected the presence of Pennant's red colobus monkeys (*Procolobus pennantii*); specifically that these monkeys were more likely to be present in forest fragments that were closer to Kibale National Park, Uganda. We believe that a discussion of the presence/absence of a species is relevant to density values because the absence (or extinction) of a primate population in an area may be the result of small population size, which is expressed as density values (Cowlishaw and Dunbar, 2000).

The third variable we examine is the effect of forest fragment size on primate density. As with isolation, comparisons are made with studies where the density, and presence or absence of primates was found to be related to fragment size. Estrada and Coates-Estrada (1996) found that larger habitat fragments supported larger populations of *A. palliata* in Mexico. Additionally, Kumar *et al.* (1995) determined that the presence of lion-tailed macaques (*Macaca silenus*) and Nilgiri langurs (*Presbytis johni*) in habitat patches was positively related to patch size. Lastly, red colobus monkeys (*Procolobus badius*), crested mangabeys (*Cercocebus galeritus*), and Syke's monkeys (*Cercopithecus mitis*) were usually more likely to be found in larger habitat patches, compared to smaller ones, along the Tana River in Kenya (Cowlishaw and Dunbar, 2000).

The fourth variable we examine is the effect of habitat type on primate density. Prior studies in ACG and SRNP (e.g. Freese, 1976; Fedigan *et al.*, 1998; Sorensen and Fedigan, 2000) have produced conflicting results about what can be considered optimal habitat for mantled howlers, whether it is deciduous or evergreen forest. As for spider monkeys, Freese (1976) found that, in SRNP, they occur in evergreen forests and in small, isolated islands of evergreen trees in semi-deciduous forests. However, Chapman *et al.* (1989) found spider monkeys in all major forest types except for some riverine strips in other sectors of ACG. Several studies of white-faced capuchins in SRNP found that they occur in all forest types (e.g. Freese, 1976; Chapman *et al.*, 1989; Sorensen and Fedigan, 2000). The present study re-examines the issue of which habitat types in ACG contain the highest densities of all three primates.

The fifth and last variable we examine is the effect of dry-season water availability on primate density. White-faced capuchins become central-place foragers near standing sources of water during the dry season in SRNP (Rose and Fedigan, 1995), which may affect their density around such areas. This chapter describes how each of these five variables (forest fragment age, isolation, size, habitat type, and dry-season water availability) affects primate density and compares our results to the two previous primate transect census studies in ACG (Chapman *et al.,* 1989; Sorensen and Fedigan, 2000).

Forest Fragmentation

The vegetation in ACG has been fragmented from the once continuous dry forest into much smaller pieces (Janzen, 1986). The patches of forest under investigation range in size from 0.07 to 95.71 km^2, and we suggest that these patches can be regarded as forest fragments for at least two reasons. First, two other studies have considered patches of forest that are within the size range of those under investigation in the present study, except the largest fragment of 95.71 km^2, as forest fragments (e.g., Goncalves *et al.* (2003) and Ferrari *et al.* (2003)). Additionally, Chiarello (2003) classified habitat patches much larger than 95.71 km^2 as forest fragments. Second, there is often a different microclimate near the periphery of a fragmented habitat, and this "edge effect" may render areas near edges inhospitable, thus leading to an effective reduction in fragment size for some species (Turner, 1996). Therefore, all of the area in the study fragments are not likely to be available to the primates, and the effective size of the study areas may be smaller than reported here.

METHODS

Study Site

In total, ACG is approximately 153,000 ha in size (110,000 ha is terrestrial habitat and 43,000 ha is marine) (Blanco, pers. comm.), and constitutes 2% of Costa Rica's landmass (The Government of Costa Rica, 1998), ranging from sea level to 1916 m (Chapman *et al.*, 1989). Dry successional deciduous forest is the predominant habitat type in the park, varying from 20 to 400 years of regeneration (Janzen, 1986). Regeneration is occurring quickly as vegetation and fauna spread into abandoned pastures and reconstitute themselves (The Government of Costa Rica, 1998).

We collected data in three sectors of ACG, northwestern Costa Rica. The forests in ACG have received nearly four centuries of highly heterogeneous damage due to a number of factors (The Government of Costa Rica, 1998); therefore, each sector has a different history of disturbance. There are little detailed data on the levels of disturbance in each sector, but what is known is reported here. In general, the logging, burning, hunting, ranching, and agriculture that occurred across ACG were not sufficient to completely eliminate any habitat type or any species, except for the green and scarlet macaw (The Government of Costa Rica, 1998).

The first study area is Sector Santa Rosa, or SRNP, which was established in 1971 and is approximately 10,800 ha in size (Fedigan *et al.*, 1985). SRNP is located approximately 35 km northwest of the town of Liberia in Guanacaste province, and is situated between the Pan-American Highway and the Pacific Ocean (Fedigan and Jack, 2001). Map coordinates of the Area Administrative in Sector Santa Rosa are 10 51′ N Lat and 85 37′ W Long (The Government of Costa Rica, 1998). Much of Guanacaste Province was originally covered in tropical dry forest (The Government of Costa Rica, 1998). The landscape is a series of stepped plateaus from the foothills of volcanic mountains down to the Pacific coastal plain (Fedigan *et al.*, 1998) and ranges in elevation from 300 m down to the ocean (Chapman, 1988).

There are two seasons at Santa Rosa, and the vast majority of the rain (approximately 900–2500 mm annually) falls in the wet season, usually between mid-May and mid-December. The non-riparian trees lose their leaves during the dry season, and most waterholes and streams gradually dry up. The strips of riparian and evergreen forests are more likely than other forest types to retain their leaves throughout this time (Fedigan and Jack, 2001).

The second oldest ranch in Costa Rica is located in Sector Santa Rosa (The Government of Costa Rica, 1998). This area was originally covered with dry deciduous forest dominated by clumps of oak forest (*Quercus oleoides*) (Chapman, 1988); but over the past 300 years, half of the upper plateau area was cleared for cattle pasture and planted with the East African jaragua grass (*Hyparrhenia rufa*). The forests in this area were selectively logged primarily for mahogany (*Swietenia macrophylla*) (Fedigan *et al.*, 1998) and fires entered Santa Rosa from runaway grass fires set outside the park by ranchers to keep woody vegetation out of their pastures. Additionally, attempts were made to grow dryland rice and cotton in this area. Specific types of disturbance in the Santa Rosa transects in this study include fire and wind damage to trees, and logging for fencepost

material. Since the establishment of Santa Rosa National Park in 1971, this area has been protected from fire, poaching, ranching, farming, and logging (The Government of Costa Rica, 1998).

In Santa Rosa, as in the other sectors of ACG, restoration is occurring rapidly as tree seedlings establish themselves spread onto abandoned fields and pasture-land. The establishment of woody vegetation is enhanced by fire prevention, which allows the introduced East African jaragua grass to continue to grow until it chokes itself out, leaving the small tree seedlings (The Government of Costa Rica, 1998). Due to the history of differential disturbance and protection of areas in Santa Rosa, the landscape is a mosaic of regenerating forest. There are fragments of evergreen, riparian, oak, mangrove, and early secondary forest in former pastures (Fedigan and Jack, 2001). No data are available on the proportional representation of each habitat type within this sector.

The second study area is Sector Murciélago, which is 12,200 ha in size (Janzen, 1986), and is located on the western coast bordering the Pacific Ocean. Map coordinates for the guard station in this sector are 1054.074′ N Lat and −85 43.754′ W Long (Medina, pers. comm.). This sector is composed of evergreen forest, semi-deciduous forest, deciduous forest, mangrove forest, and shrub vegetation surrounded by grassland (Medina, pers. comm.). The proportional representation of these forest types is presently unknown. Murciélago was incorporated into ACG in 1980 as an addition to SRNP. The forests in this area were differentially disturbed by centuries of European use (The Government of Costa Rica, 1998), and logging was detected in some of the transects. The forests began to recover in the mid-1980s after the cessation of ranching (The Government of Costa Rica, 1998).

The third study site is Sector Cerro el Hacha, which is 5000 ha in size, and is located on the northern boundary of the park near Nicaragua. Map coordinates for the guard station are 11 01.931′ N Lat and −85 31.691′ W Long (Medina, pers. comm.). This sector is composed of evergreen forest (which has ever-flowing creeks even in the dry season), native grasses, and secondary forest in varying stages of regeneration surrounded by grassland (Janzen, 1986). The proportional representation of these habitat types is unknown. Cerro el Hacha was incorporated into ACG between 1988 and 1989 (Blanco, pers. comm.). Some of the lower slopes in this sector still have virgin forest, while the upper slopes were largely deforested and were covered with native grasses. Some areas were used for growing corn and beans (Janzen, 1986). In this sector, logging and fire damage were detected in the transects. All

three sectors can be characterized as a series of forest fragments surrounded by grassland.

Data Collection

We collected data using the line transect method (Brockelman and Ali, 1987). We collected line transect data between January and June 2003 (mostly dry season, and a few weeks of the wet season) on 28 transects (8 in Santa Rosa, 8 in Cerro el Hacha, and 12 in Murciélago). Transects were approximately 600 m in length (mean: 612 ± 56). We walked transects between 18 and 43 times (mean: 31 ± 8) each. Difficulties with transportation and accessing some sites during the rainy season made it impossible to acquire equal sample sizes from all areas.

Line transects were located in a total of six forest fragments for Sectors Murciélago and Santa Rosa (labeled A–F) (Figure 1). Santa Rosa contained Fragments A, B, and E, while Murciélago contained the remaining Fragments

Scale: 1: 200,000

Figure 1. Forest fragments A–F containing line transects in Sectors Murciélago and Santa Rosa, in the megapark Area de Conservación Guanacaste. Fragments A, B, and E are located in Santa Rosa, while Fragments C, D, and F are located in Murciélago.

Table 1. Line transect locations within six forest fragments

	Santa Rosa	Murciélago	Total no. of transects
Fragment A	4 Transects	Not in this sector	4
Fragment B	1 Transect	Not in this sector	1
Fragment C	Not in this sector	6 Transects	6
Fragment D	Not in this sector	1 Transect	1
Fragment E	1 Transect	Not in this sector	1
Fragment F	Not in this sector	1 Transects	1
Not in a fragment	2 Transects	4 Transects	6
Total no. of transects	8	12	20

C, D, and F. Out of the 20 transects in Santa Rosa and Murciélago, four were in Fragment A, one was in Fragment B, six were in Fragment C, one was in Fragment D, one was in Fragment E, one was in Fragment F, and six transects were not located in a fragment (Table 1). We were able to plot the geographical waypoint locations of each transect in Sector Cerro el Hacha (waypoint locations were recorded for each transect in all three sectors), but there were no satellite images available for this sector, so it was not possible to determine the size and isolation of forest fragments in which these transects were found.

We recorded the perpendicular distance, sighting distance, and sighting angle (Brockelman and Ali, 1987) from the geometric center of the *C. capucinus* and *A. palliata* groups (Brockelman and Ali, 1987; Anderson *et al.*, 1979). However, for *A. geoffroyi*, we recorded all measurements for each individual separately (Brockelman and Ali, 1987). We measured distances with a range finder, or we estimated them, when using the rangefinder was not possible because of environmental conditions. We conducted inter-observer reliability testing between the two observers, ensuring 90% accuracy, before data collection began and once or twice each month in the following period.

We recorded the availability of water along a transect during the dry season as a "yes/no" variable. Water was available either from streams or artificial waterholes, such as horse troughs, but not from tree hollows, which evaporate during the dry season. There were nine transects in total that contained water; two transects with water were located in Murciélago, four in Cerro el Hacha, and three in Santa Rosa. Additionally, we hired a local botanist to classify the habitat type of each transect. We grouped habitat types into three categories: Habitat Type 1 consisted of deciduous and/or semi-deciduous forest; Habitat Type 2 was mainly semi-deciduous forest, but at least 100 m of the transect

consisted of forest in which up to 50% of the species were evergreen; Habitat Type 3 included transects where there were both semi-deciduous and evergreen forest, or simply evergreen forest. Habitat types were determined based on the majority of species present. For example, if 50% or more of the species present in a transect were evergreen then that forest was classified as evergreen. There were 6 transects classified as Habitat Type 1 (2 in Murciélago, 2 in Cerro el Hacha, 2 in Santa Rosa), 12 classified as Habitat Type 2 (8 in Murciélago, 1 in Cerro el Hacha, 3 in Santa Rosa), and 10 classified as Habitat Type 3 (2 in Murciélago, 5 in Cerro el Hacha, 3 in Santa Rosa). Lastly, the botanist also determined the approximate age since disturbance of each transect based on species composition, canopy height, and history of the area. The forest ages ranged from 14 to 118 years (mean: 33 ± 27).

Forest fragment size and isolation were determined with the Geographical Information System software ArcGIS (v.8.1). Geographical waypoint locations were marked with a Global Positioning System at the beginning and the end of each transect. These points were then plotted onto a satellite image of ACG that had been classified into general categories of forested and non-forested habitat based on 80% canopy closure (Sanchez-Azofeifa and Calvo, 2004). The transects that were classified as being "not in a fragment" were located in areas of vegetation that did not meet this 80% criteria.

We calculated the size of forest fragments surrounding our study transects in Sectors Murciélago and Santa Rosa using a buffer zone of 30 m. Any patch of forest that was located within 30 m of the fragment containing a line transect was included in the size calculation for that study fragment. Forest fragments outside this 30 m buffer zone were used to calculate the isolation distance of each census fragment. The closest distance to the next nearest patch of forest from the edge of any forest fragment within the 30 m buffer zone from a census fragment was considered to be the isolating distance. If there were no forest fragments within 30 m of a census fragment, then the distance from the edge of the census fragment to the next nearest patch of forest was considered to be the isolating distance. A buffer zone of 30 m was chosen because it is a short enough distance that it would not act as a barrier to any of the three species moving terrestrially between forest patches. The size of the census fragments ranged between 0.07 and 95.71 km^2 (mean: 35 ± 44 km^2) (Table 2). Forest fragments in SRNP containing line transects exceeded the boundaries of the park and, therefore, the size for all these fragments combined is larger than the size of the park itself. Additionally, the isolating distances for all census

Table 2. Table showing the size of census fragments (those containing a line transect), the size of forest fragments beyond 30 m from a census fragment (those that were used to determine isolation), and the isolating distances between them

Census fragments in Murciélago and Santa Rosa		Fragments beyond 30 m from a census fragment		
Fragment name	Size (km²)	Label	Size (km²)	Distance from census fragment (m)
		1	0.06	40.67
		2	0.12	40.67
A	95.71	3	0.21	40.67
		4	0.39	40.67
		5	0.07	40.67
		6	0.06	40.67
B	47.30	7	0.06	40.67
		8	0.25	40.67
C	19.26	9	3.16	655.84
D	5.28	10	0.06	333.21
E	0.08	11	0.06	626.46
F	0.07	12	0.60	3814.19

fragments ranged from 40.67 to 3814.19 m (mean: 140 ± 239 m) (Table 2). It is important to note that eight fragments were isolated from census fragments (those containing a line transect) by a distance of 40.67 m. This is due to the resolution of the image; distance measurements are only discernable in increments that reflect the size of the pixel, which in this case was 40.67 m.

Density Analysis

We calculated densities as per the National Research Council (1981). Absolute density (individuals/km²) was calculated as:

$$\text{Density:} \quad \frac{\text{Estimated animal population}}{\text{Census area}} = \frac{\text{Number of animals seen in sample area}}{\text{Sample area}}$$

The sample area was calculated as: Area: $l \times w$; where l is the length of the transect line (multiplied by the number of times the transect was walked) and w is the strip width, or the width on one side of the transect line multiplied by two (since data were taken on both the sides).

We used the maximum distance method (National Research Council, 1981) to designate strip width using sighting distances (the maximum distance of all

sightings were used to demarcate the area sampled). We recorded both the perpendicular and sighting distances during data collection but, by comparing density estimates based on both methods in areas of known primate density in SRNP, found that sighting distances yielded more accurate density estimates. We truncated the data by removing 5% of the most distant measurements as the farthest sighting events provide little information about density (Buckland *et al.*, 1996). We excluded solitary capuchins and howlers from analysis to avoid over counting individuals (Fedigan *et al.*, 1998). Few solitaries of these species were seen throughout the course of the study, and, therefore, this was not problematic.

Statistical Analyses

We conducted all statistical analyses using the statistical program SPSS (v.11.5). We performed standard multiple regressions for each species separately to examine the combined influence of forest fragment age since disturbance, isolation, and dry-season water availability on monkey absolute density (individuals/km^2). We eliminated forest fragment size from the multivariate model due to multicollinearity; size was correlated with forest fragment age since disturbance ($r = 0.759$) beyond an acceptable limit (Tabachnick and Fidell, 1996). Therefore, Pearson's product–moment correlations were used to test for the relationship between forest fragment size and the absolute density of monkeys. Lastly, we ran Kruskal–Wallis two-tailed tests to examine the effects of forest fragment habitat type on monkey absolute density. Habitat type was not included in the multiple regression analyses because it is not a continuous or dichotomous independent variable, which is required by the model. Habitat type was grouped into three categories based on the dominant species present, as mentioned above.

RESULTS

Absolute densities for all monkey species for each transect are reported in Table 3. Additionally, transect sample size and forest fragment age, size, isolation, habitat type, and dry-season water availability are reported in this table. These results indicate that the highest densities for capuchins and howlers were in Sector Santa Rosa (capuchins: 34.47 individuals/km^2, howlers: 28.64

Table 3. Primate densities, transect sample size, and forest fragment age, isolation, size, habitat type, and dry-season water availability for all transects

Transect	No. of times walked	Age (years)	Habitat Type	Size (km^2)	Isolation (m)	Water	Capuchin density (per km^2)	Spider density (per km^2)	Spider density (per km^2)
ME1[a]	30	16	2[b]	19.26	655.84	No	0.00	0.00	1.98
ME2	30	23	2	19.26	655.84	No	0.00	0.00	.00
ME3	30	18	2	19.26	655.84	No	0.00	0.00	17.81
ME4	30	16	1[c]	19.26	655.84	No	3.17	0.00	10.42
ME5	30	25	2	19.26	655.84	No	3.47	0.00	1.63
ME6	21	23	3[d]	0.07	3814.19	No	14.43	0.00	5.67
ME7	30	15	2	0.00[e]	0.00[f]	No	0.00	0.00	0.00
ME8	19	18	2	0.00	0.00	No	2.51	0.00	8.12
ME9	30	30	3	19.26	655.84	Yes	9.26	1.68	9.92
ME10	28	14	1	0.00	0.00	No	0.00	0.00	3.92
ME11	32	16	2	5.28	333.21	No	0.00	0.00	4.46
ME12	30	15	2	0.00	0.00	Yes	0.00	0.00	0.00
CH1[g]	30	20	3	Not available	Not available	No	3.05	0.00	2.22
CH2	30	23	3	Not available	Not available	Yes	18.52	5.70	26.50
CH3	30	25	3	Not available	Not available	Yes	11.06	0.00	4.87
CH4	30	16	1	Not available	Not available	No	0.00	0.00	0.00

CH5	19	30	3	Not available	Not available	Yes	31.52	0.00	12.53
CH6	18	18	1	Not available	Not available	No	0.00	0.00	0.00
CH7	22	19	2	Not available	Not available	Yes	0.00	0.00	0.00
CH8	19	20	3	Not available	Not available	No	0.00	0.00	0.00
SR1[b]	43	33	2	0.00	0.00	No	3.75	8.24	0.00
SR2	42	28	2	0.00	0.00	No	8.63	5.75	7.35
SR3	41	48	1	0.08	626.46	Yes	29.51	19.27	1.81
SR4	42	58	2	95.71	40.67	Yes	34.47	0.00	0.00
SR5	40	68	1	95.71	40.67	Yes	4.80	0.00	0.00
SR6	40	103	3	47.30	40.61	No	20.23	0.00	0.00
SR7	40	80	3	95.71	40.67	No	4.81	8.01	13.89
SR8	41	118	3	95.71	40.67	No	19.83	28.64	6.54

[a] Murciélago transects.

[b] Semi-deciduous forest, but at least 100 m of the transect consisted of forest in which up to 50% of the species were evergreen.

[c] Semi-deciduous and/or deciduous forest.

[d] Both semi-deciduous and evergreen forest, or simply evergreen forest.

[e] Zeros indicate that line transects were not located in a fragment, and therefore there were no values for this variable.

[f] Zeros indicate that line transects were not located in a fragment, and therefore there were no values for this variable.

[g] Cerro el Hacha transects.

[h] Santa Rosa transects.

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individuals/km^2), whereas the highest densities for spider monkey came from Cerro el Hacha (26.50 individuals/km^2). Throughout ACG, capuchin densities ranged from 0.00 to 34.47 individuals/km^2, howler densities ranged from 0.00 to 28.64 individuals/km^2, and spider monkey densities ranged from 0.00 to 26.50 individuals/km^2. Capuchins were found in all Santa Rosa transects but they were absent in 11 transects in Cerro el Hacha and Murciélago. Howlers were rare throughout ACG as indicated by their absence from 21 transects from all three sectors. Lastly, spider monkeys were absent from 11 transects in all three sectors.

In the multiple regression model, the age of the forest fragment ($T = 3.247$, $F(3,16) = 6.838$, $p = 0.005$) and dry-season water availability ($T = 3.050$, $F(3,16) = 6.838$, $p = 0.008$) both made significant contributions to explaining capuchin absolute density, whereas degree of isolation did not. Age made the strongest unique contribution. The model accounts for 56.2% of the variance in capuchin absolute density (Table 4).

Age of the forest fragment ($T = 2.990$, $F(3,16) = 3.147$, $p = 0.009$) made the only strong, unique, significant contribution to explaining howler monkey absolute density in the multiple regression model. This model explains 37.1% of the variance in this species' density (Table 4). No variable in the model made a strong, unique, significant contribution to explaining spider monkey absolute density. The model accounts for only 3.7% of variance in this dependent variable (Table 4).

We used Pearson's product–moment correlations to test for the relationship between forest fragment size, and the absolute density of monkeys. We found no significant results. There was a positive relationship between size and capuchin absolute density ($r = 0.411$, $df = 18$, $p = 0.071$), but it did not reach statistical significance (Table 4).

We ran Kruskal–Wallis tests to examine the effects of forest fragment habitat type on monkey absolute density. We obtained significant results only for capuchin absolute density ($\chi^2 = 7.274$, $df = 2$, $p = 0.026$). Capuchin density was highest (had the highest rank) in transects where there were both semideciduous and evergreen forest, or simply evergreen forest (Habitat Type 3). Although not reaching a level of statistical significance, howler monkey absolute density ($\chi^2 = 1.446$, $df = 2$, $p = 0.485$) and spider monkey absolute density ($\chi^2 = 4.133$, $df = 2$, $p = 0.127$) are all highest in Habitat Type 3, as well (Table 4).

Table 4. Table showing results from statistical tests

Variable	Statistical test	Capuchin density[a]	Howler density[b]	Spider density[c]
Age	Multiple regression			
	P	0.005**[d]	0.009**	0.965
	T	3.247	2.990	0.045
Isolation	P	0.112	0.999	0.567
	T	1.683	0.001	0.584
Dry-season water availability	P	0.008**	0.981	0.564
	T	3.050	−0.025	0.590
	R^2	0.562	0.371	0.037
	$F\,(3,16)$	6.838	3.147	0.208
Size	Pearson's product–moment correlation			
	P	0.071	0.210	0.814
	R	0.411	0.293	0.056
	df	18	18	18
Habitat Type	Kruskal–Wallis			
	K	3	3	3
	P	0.026*[e]	0.485	0.127
	HT 1[f] Rank	12.50	13.67	11.83
	HT 2[g] Rank	11.00	13.33	12.42
	HT 3[h] Rank	19.90	16.40	18.60
	df	2	2	2

[a] $\Upsilon = 0.213 + 3.589\ \text{E} - 03 + 11.290 + -4.383$.
[b] $\Upsilon = 0.147 + 1.952\ \text{E} - 06 + -0.068 + -2.134$.
[c] $\Upsilon = 2.702\text{E} - 03 + 1.140\text{E} - 03 + 1.998 + 3.747$.
[d] Significant at the 0.01 level.
[e] Significant at the 0.05 level.
[f] Semi-deciduous and/or deciduous forest.
[g] Semi-deciduous forest, but at least 100 m of the transect consisted of forest in which up to 50% of the species were evergreen.
[h] Both semi-deciduous and evergreen forest, or simply evergreen forest.

DISCUSSION

Forest Fragment Age

Age of a forest fragment since disturbance is an important variable in explaining capuchin and howler monkey absolute density in ACG. Higher densities of capuchins and howlers were found in transects where there was older forest. These findings are in accordance with a previous study by Sorensen and Fedigan (2000) in SRNP in which they found that capuchin and howler densities were positively related to forest age since disturbance. Sorensen and Fedigan (2000)

also found that capuchin food biomass (measured as the combined biomass of fruit and leaves from trees that constituted at least 2% of the species' diet based on published accounts) increased linearly with forest age in SRNP. Therefore, older forests may exhibit higher densities of capuchin monkeys because these areas contain higher food biomass for this species.

Furthermore, forest fragment age is the only significant independent variable in the multiple regression model for explaining howler monkey density. There may be at least two reasons why older forests have higher densities of howlers. First, in SRNP, howlers prefer to forage in larger trees (Larose, 1996), and these trees are found in older areas of forest. Second, food biomass for the howlers (measured as the combined biomass of fruit and leaves from trees that constituted at least 2% of the species' diet based on published accounts) was found to increase linearly with forest age in SRNP, just as it did for the capuchins (Sorensen and Fedigan, 2000). The proportion of evergreen trees in this sector also increased linearly with forest age (Sorensen, 1998). Therefore, more leaf food sources are available in older areas, assuming that evergreen trees produce uniformly palatable leaves that howlers consume (Sorensen and Fedigan, 2000). Then, it is to be expected that howlers would have higher densities in older forests that contain the trees that they prefer as well as high food biomass.

Sorensen and Fedigan (2000) found that in SRNP spider monkeys returned to abandoned pastures after 60–80 years of regeneration and that forest fragment age was significant in explaining their density. The present findings are different from the prior study in that we did not find forest fragment age to affect spider monkey density and we also found spider monkeys in much younger forest than previously reported. We found spider monkeys in Santa Rosa in 28-year-old forest (7.35 individuals/km^2), in Murciélago in 14-year-old forest (3.92 individuals/km^2), and in Cerro el Hacha in 20-year-old forest (2.22 individuals/km^2).

We suggest that since the time of the earlier study, spider monkeys may have simply expanded their ranges to include younger as well as older areas of forest in SRNP. This might explain why our findings are different from those of Sorensen and Fedigan (2000). If spider monkeys have expanded their ranges, then this would indicate that they can forage and travel in much younger areas than previously thought.

In summary, forest fragment age since disturbance was found to make a significant, positive contribution to explaining capuchin and howler monkey density in this study, whereas it made no contribution to explaining the density

of spider monkeys. Capuchins and howlers may have been found in older forests in higher densities because these areas contain higher food biomass for these species. Additionally, the large trees howlers prefer are located in older forest, which may also account for their higher densities in such areas. Spider monkey densities were not explained by fragment age, possibly because these primates have simply expanded their ranges to include older and younger areas of forest since earlier studies.

Forest Fragment Isolation

Isolation was not found to make a significant contribution to explaining the density for any of the three primates in this study. It is generally expected that as isolation increases, the probability of colonization, or immigration to a habitat fragment will decrease (Rodriguez-Toledo *et al.*, 2003). This immigration to a fragment could influence population density. We suggest that forest fragment isolation is not an important variable in explaining primate density in our study because of the size of fragments surveyed. Our study fragments ranged in size up to 95.71 km^2. It is possible that immigration occurs between the study fragments and surrounding ones, but that this exchange has little effect on density in most of the fragments surveyed. Most of the study fragments are large and may contain populations sufficient in size that demographic processes rather than rates of immigration regulate them.

Previous studies that have found forest fragment isolation to affect primate density, and presence/absence (e.g., Estrada and Coates-Estrada, 1996; Onderdonk and Chapman, 2000) came from research in forest fragments ranging in size between 0.8 and 1000 ha. Primate populations in such small forest fragments will likely be smaller in size than half the populations and the fragments surveyed in our study (three of the six forest fragments in our study were smaller than 1000 ha, while the remaining three were significantly larger). We suggest that immigration may have a more significant effect on the small populations studied by Estrada and Coates-Estrada (1996) and Onderdonk and Chapman (2000). It has been argued that the addition of individuals through immigration has a more significant effect on smaller populations because they are more vulnerable to extinction (Cowlishaw and Dunbar, 2000). The isolation distances in the two aforementioned studies ranged from 50 to 8000 m, and in our study they ranged from 41 to 3814 m. Since the isolation distances in the present study are within the range of those in the other two

studies, this suggests that some other variable is overriding the effects of isolation.

In summary, forest fragment isolation was not found to make a contribution to explaining the density of the three primates in this study. We contend that this is due to the large size of the fragments surveyed. Other demographic processes may be more important than immigration in regulating the study populations.

Forest Fragment Size

Forest fragment size was found to make little contribution to explaining primate density in ACG. Previous primate studies have found higher densities of primates in larger fragments of forest (e.g., Estrada and Coates-Estrada, 1996), or that primates were more likely to occur in larger patches of forest compared to smaller ones (e.g., Kumar *et al.,* 1995; Cowlishaw and Dunbar, 2000). Other studies have not come to this conclusion. For example, Rodriguez-Toledo *et al.* (2003) found the opposite: higher densities of *A. palliata mexicana* were found in smaller forest fragments. Additionally, Kowalewski and Zunino (1999) found that when forest patches in Argentina were reduced in size, a population of *Alouatta caraya* remained the same size. In the present study, no significant relationships were found between primate density and forest fragment size.

Therefore, we conclude that forest fragment size offers limited insight into primate density at our study sites. As with isolation, it may be that the large sizes of most of the forest fragments we surveyed explain why this variable made no explanatory contribution. The large patches that are under analysis here (up to 95.71 km^2) may not constrain primate population sizes the way a 10 ha fragment would. As with isolation, the primate populations living in the large ACG forest fragments may be big enough that fragment size has little or no effect on their population densities.

Gilbert (2003) argues that capuchins and spider monkeys cannot live in fragments under 1 km^2. Additionally, Ferrari *et al.* (2003) found that white-fronted spider monkeys (*Ateles marginatus*) were absent from fragments less than 1 km^2 in size. The results of the present study contradict those of the previous studies; the capuchins and spider monkeys were found in fragments as small as 0.07 km^2. This suggests that, in ACG, a lower size limit is required for capuchins and spider monkeys to exist in forest fragments. Studies of howler monkeys in fragments have found that this species can exist in those as small as 0.01 km^2 [red howlers

(*Alouatta seniculus*) in the Biological Dynamics of Forest Fragments Project in Brazil (Gilbert, 2003)], and 0.70 km^2 [red-handed howlers (*Alouatta belzebul*) along the Santarem–Cuiaba Highway in Brazil (Ferrari *et al.*, 2003)]. In the present study, howlers were found in fragments as small as 0.08 km^2.

In summary, forest fragment size was not important in explaining primate density at our study sights. We attribute this to the large size of the fragments surveyed. The study populations may be big enough that forest fragment size has little influence on their densities. Additionally, capuchins and spider monkeys were found in smaller fragments compared to previous studies, whereas the howlers were found in fragments that were in the size range of those they have been found in previously.

Habitat Type and Dry-Season Water Availability

The presence of evergreen forest is an important explanatory variable for primate species density in ACG. The absolute density of capuchins was significantly higher in transects where there was both semi-deciduous and evergreen forest, or simply evergreen forest (Habitat Type 3) (13.27 individuals/km^2). Additionally, although not reaching the level of statistical significance, howler monkey absolute density and spider monkey absolute density are all highest in Habitat Type 3 (4.40 individuals/km^2 and 8.21 individuals/km^2, respectively), compared to semi-deciduous or deciduous forest (Habitat Type 1) (howlers: 3.21 individuals/km^2, spider monkeys: 2.69 individuals/km^2), or semi-deciduous forest where at least 100 m of the transect consisted of forest in which up to 50% of the species were evergreen (Habitat Type 2) (howlers: 1.17 individuals/km^2, spider monkeys: 3.45 individuals/km^2).

The above finding is in accordance with previous studies from ACG on howler monkeys. Chapman and Balcomb (1998) found that howler monkey densities in ACG were highest in areas of semi-evergreen forest. Freese (1976) found that howler monkeys in ACG were almost completely confined to mature evergreen forest. Additionally, Chapman (1988) found that the core area used by howlers in Sector Santa Rosa (that is the area used in more than 10% of the observations) was wet semi-evergreen forest. Areas outside of this core tended to be dry semi-deciduous forest (Chapman, 1988). A study by Sorensen and Fedigan (2000) contradicts these findings, however. These authors found that, in 1996, howler densities in SRNP were not higher in old evergreen forests than in deciduous ones.

Spider monkeys, like the other two primates in ACG, were found to have higher densities in transects that contained semi-deciduous and evergreen forest, or simply evergreen forest (Habitat Type 3), although this relationship was not significant. However, this species was found in all habitat types we surveyed. These findings are in accordance with previous studies by Freese (1976) and Chapman *et al.* (1989).

Capuchin monkey density was significantly higher in transects where there was semi-deciduous and evergreen forest, or simply evergreen forest (Habitat Type 3). This finding is in accordance with previous studies by Chapman (1988), Chapman *et al.* (1989), and Freese (1976). Freese explained the extensive distribution of capuchins as a result of their diet and locomotor pattern; he argued that capuchins eat primarily fruit and insects, both of which are assumed to be available on a year-round basis in varying abundance in deciduous forests, and insects can also be found year-round in young secondary, deciduous growth. Additionally, these small primates move quadrupedally, which allows for easy movement through weakly structured, dense, short vegetation (Freese, 1976).

Capuchins in ACG may nonetheless reside preferentially in evergreen forests because these areas contain more water resources. During the dry season, capuchins in ACG usually visit areas with standing water daily (Chapman *et al.*, 1989). They try to maintain access to these limited resources (Fedigan and Jack, 2001), presumably because they cannot obtain the water they need from their foods alone (Freese, 1978). The importance of water to this species is evidenced by the fact that dry-season water availability made large contributions to explaining capuchin density in the multiple regression model. During the dry season in ACG, large evergreen trees provide more tree holes with drinking water (Sorensen and Fedigan, 2000), and evergreen vegetation lines the banks of the few springs and ever-flowing watercourses that are left at this time (Janzen, 1986). Thus, we conclude that capuchins can utilize all forest types within ACG, but preferentially inhabit evergreen areas because of water accessibility. This contention is supported by two previous studies. Fedigan *et al.* (1996) argued that, although SRNP capuchins use new secondary forest areas, they are not able to reside in them exclusively because of the difficulty of accessing fruit trees and water resources in these areas. Additionally, Rose and Fedigan (1995) and Chapman (1988), noted that Santa Rosa capuchins become central-place foragers around water resources in the dry season. If water is more abundant in evergreen forests during the dry season, then it is likely that capuchins would restrict much of their activities to these areas.

Dry-season water availability was not found to contribute to explaining howler and spider monkey density. This is consistent with a previous study by Freese (1978). This author found that spider monkeys and howlers in Santa Rosa did not drink from waterholes; he argues that these species probably obtain all the water they need from food. However, a study by Chapman (1988) found that in SRNP spider monkeys and howlers sometimes drank from waterholes. Another study by Gilbert and Stouffer (1989) found that both *A. palliata* and *A. geoffroyi* drank from a standing water source in the dry season in the tropical dry forest of Palo Verde National Park, Costa Rica. Despite these contradictions, it is clear that dry-season water availability is more important to capuchins than to the other two primates in Santa Rosa.

In summary, the presence of evergreen forest is an important explanatory variable for the density of all three primates in this study. Capuchins, howlers, and spider monkeys were all found in higher densities in Habitat Type 3 (semi-deciduous and evergreen forest, or simply evergreen forest), although the relationship was only significant for the capuchins. Capuchins may restrict some of their activities to evergreen forests because these areas contain more dry-season standing water, compared to deciduous forests. The availability of water was not found to contribute to explaining howler and spider monkey density.

SUMMARY

In summary, forest fragment age is an important explanatory variable for capuchin and howler density (higher densities were found in older areas of forest), whereas it makes no contribution to explaining the density of spider monkeys. The presence of evergreen forests in ACG is also important for explaining the absolute density of all three species, as there were higher densities in fragments containing evergreen forest. Transects where water was available in the dry season had higher capuchin densities; water availability appears to be more important for this species than for the spider monkeys and howlers. Forest fragment isolation and size made little contribution to explaining the density of any primate in ACG, probably due to the large size of forest fragments surveyed. Based on these findings, we conclude that older fragments of forest with dry-season standing water, and a substantial amount of evergreen forest should be preferentially protected to enhance the conservation of white-faced capuchins, black-handed spider monkeys, and mantled howlers in Costa Rica.

ACKNOWLEDGMENTS

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