Distribution of three monkey species along a gradient of regenerating tropical dry forest

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Abstract

Only 2% of tropical dry forest in Central America remains undisturbed; consequently habitat regeneration is the best option to provide adequate areas of habitat for wildlife. This study examined the influence of a forest regeneration gradient (0–180 years since pasture abandonment) on the densities of white-faced capuchins (Cebus capucinus), howling monkeys (Alouatta palliata), and spider monkeys (Ateles geoffroyi) in the tropical dry forest of Santa Rosa National Park, Costa Rica. Monkey densities and tree characteristics were sampled using 600 m transects within each of 14 sites from February to June 1996. Densities of all three monkey species were higher in older forests and in forests with greater food biomass estimates. The results indicate that monkey habitat, and consequently viable monkey populations, can be regained through protection and natural regeneration of tropical dry forest.

1. Introduction

Tropical dry forest once covered much of Central America but now less than 2% of its original area is in an undisturbed state and only 0.09% is protected (Janzen, 1986a), rendering tropical dry forest the most threatened of all lowland tropical forest types (Janzen, 1988). Therefore, land restoration and subsequent habitat regeneration is the only management option left for tropical dry forest. What remains to be answered is how this regeneration affects the wildlife within the forest, and whether regenerating forests provide adequate habitat to attract and sustain wildlife. This study examines the influence of a regeneration gradient on the densities of white-faced capuchins (Cebus capucinus), mantled howlers (Alouatta palliata), and red spider monkeys (Ateles geoffroyi), in Santa Rosa National Park, Costa Rica.

Recent long-term studies have demonstrated that over a large spatial scale the numbers of capuchin and howling monkeys are increasing in Santa Rosa as the park regenerates from abandoned pastures (Fedigan et al., 1996, 1998). It is unlikely, however, that monkey densities are changing uniformly on a smaller spatial scale within the park. Monkey densities probably experience very little year-to-year change in undisturbed forests; whereas higher rates of change likely occur in rapidly regenerating forests. Conservationists and managers need to know the stage of regeneration at which monkeys return to a disturbed forest from local refugia, as well as when changes in densities are occurring most rapidly, and when the population has returned to a pre-disturbance state. Without this information it is very difficult to estimate available habitat or predict monkey population size. The current study examines monkey densities along a chronosequence of forest ages, and on a smaller spatial scale than previously studied, to estimate the time required for monkey populations to recover from habitat disturbance.

Many studies suggest that body size, proportion of fruit and flowers in diet, and home range size are negatively related to the ability of a primate species to survive in disturbed forests (Freese, 1976; Freese et al., 1982; Johns, 1985, 1992; Skorupa, 1986; Johns and Skorupa, 1987; Bearder, 1991). Furthermore, insectivorous species may benefit from high insect biomass in secondary forests.
(Freese, 1976; Lovejoy et al., 1986; Schwarzkopf and Rylands, 1989). Of our three study species, capuchin monkeys are the smallest in size and have the most diverse diet including insects; therefore we predict that capuchins will return first to regenerating forest. We predict that spider monkeys will return last to regenerating forest due to their large body size, large home ranges, and specialized diet. Although howlers are foli- vores, which suggests they might return early to regenerating forest, they are also large in body size and prefer to forage in large trees, which requires older forest. Therefore we predict that howler monkeys will return after capuchins but before spider monkeys.

Although the time required for wildlife populations to recover from habitat disturbance is the primary question to be answered, managers are also interested in understanding what factors attract the primates and improve the quality of the habitat. Food abundance is often assumed to influence primate density; however, attempts to correlate these two variables have had mixed results (Coelho et al., 1976; Skorupa, 1986). Skorupa (1986) found that the abundance of primates could be predicted by the abundance of food trees or by measures of forest structure. This study examines the influence of food abundance, and forest age, structure and species-composition on the densities of three monkey species.

2. Methods

2.1. Study site

Santa Rosa National Park (SRNP, est. 1971) is located (10° 50’ N, 85° 39’ W) 35 km northwest of Liberia, Guanacaste, Costa Rica, within the much larger (1100 km²) protected zone called “Area de Conservacion Guanacaste”. SRNP consists of 108 km² of tropical dry forest (Tropical Dry Forest and Premontane Moist Forest; Holdridge et al., 1971) covering an upper and lower plateau (300–0 m elevation). The park receives 800–2600 mm of rainfall annually (mean = 1473 mm) with mean high temperatures ranging from 21.6 (Sept.) to 34.4°C (April; Janzen, cited in Gerhardt, 1994). The area experiences a severe dry season from mid December to late May in which virtually no rain falls and deciduous trees lose their leaves (Janzen, 1986b). The original forest mainly consisted of semi-evergreen trees (Janzen, 1986a,b). Forest disturbances since the late 1500s have included clearing for pasture, agriculture, selective harvesting (e.g. Swietenia macrophylla), grazing, and ground fires. These disturbances have resulted in a mosaic landscape of various stages of regeneration.

When studying stages of succession simultaneously, one has to assume that all study sites were originally similar, and that the same successional processes proceeded at similar rates for all sites. In January of 1996, 13 patches of forest representing the entire range of natural regeneration (from 10 years old to relatively undisturbed) were chosen as study sites (Table 1, Fig. 1). Patch boundaries were obtained from a detailed forest cover map of the park (Pacheco and Morera, 1994). In addition to the forest sites, a current pasture was chosen as a time-zero data point (Table 1, Fig. 1). The topography of the upper plateau of Santa Rosa is undulating and all sites appeared to have similar representation of aspects and slopes. Sites were generally homogenous in age (Table 1). Although patch sizes varied (mean 35 ha, range 22–56 ha, Table 1), none of the patches were isolated from other forest and monkeys could freely travel into and out of patches (Fig. 1).

Furthermore, patch sizes were not correlated with forest ages ($R^2 = 0.034$, $p = 0.523$). Capuchins, howlers (Mittermeier, 1973; Larson, 1996; Stoner, 1996), and spider monkeys (Chapman, 1988b; Fedigan et al., 1988) are known to have home ranges smaller than these patches. The maximum distance between two sites was approximately 8 km (min. 0.6 km, Fig 1).

Forest ages (years since abandonment) were known for sites that were abandoned within the past 40 years, and estimated for older sites. Forest ages could not be calculated from annual growth rings since most species of tropical trees do not form these rings (Lieberman and Lieberman, 1985). On the other hand, allometric growth curves can be used to predict tree ages from their dimensions [e.g. diameter at breast height (dbh)]. Species-specific allometric growth curves were determined from 20-year incremental growth data on trees ranging from saplings to large trees (B. Enquist, unpublished). The largest individuals (minimum of five) of at least eight species from each site were aged using minimum and maximum growth curves. These analyses provided averaged and 95% confidence intervals for each forest’s age. Age estimates for areas that were selectively logged may be over- or under-estimated depending on the severity of the logging. Estimates from park botanists, park historians, and local people confirmed the values from the allometric growth curves.

2.2. Study subjects

Three monkey species inhabit the park, where they have been studied since the 1970s. Thus, much background biology is now available, including their overall numbers, diet, home ranges, group compositions, social behavior, and associations with generalized habitats.

White-faced capuchins (C. capucinus) are distributed from Honduras to Columbia (Rodriguez-Luna et al., 1996). Their diet consists of fruits (81%), insects (17%), and occasionally small vertebrates (Chapman, 1987; Chapman and Fedigan, 1990). There are approximately 528 capuchins in 30 groups in SRNP. Groups are multi-male and
Table 1
Location and disturbance histories of the 14 study sites at SRNP, Costa Rica

<table>
<thead>
<tr>
<th>Site</th>
<th>Age (years)</th>
<th>Average Area (ha)</th>
<th>95% C.I.</th>
<th>Known history</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0</td>
<td>Current pasture</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>10</td>
<td>26</td>
<td></td>
<td>Burned in 1986, rice field in early 1960s</td>
</tr>
<tr>
<td>C</td>
<td>14</td>
<td>31</td>
<td></td>
<td>Pasture before burn in 1982.</td>
</tr>
<tr>
<td>F</td>
<td>60</td>
<td>40–80</td>
<td>22</td>
<td>Transect outside stone wall enclosure. Pasture prior to late 1950s. Contains some large trees that were not cleared for pasture.</td>
</tr>
<tr>
<td>G</td>
<td>60</td>
<td>40–80</td>
<td>56</td>
<td>Abandoned pasture south of man-made laguna.</td>
</tr>
<tr>
<td>H</td>
<td>80</td>
<td>60–100</td>
<td>50</td>
<td>Heavily logged in 1940s. Transect crosses small ravine of older age (70–100).</td>
</tr>
<tr>
<td>I</td>
<td>90</td>
<td>60–120</td>
<td>31</td>
<td>Selectively logged in 1940s.</td>
</tr>
<tr>
<td>J</td>
<td>100</td>
<td>60–140</td>
<td>40</td>
<td>Heavily logged in 1940s for fence posts.</td>
</tr>
<tr>
<td>K</td>
<td>100</td>
<td>60–140</td>
<td>38</td>
<td>Selectively logged in 1940s for fence posts. Appears less disturbed than site I.</td>
</tr>
<tr>
<td>L</td>
<td>140</td>
<td>80–200</td>
<td>32</td>
<td>Lightly selectively logged in 1940s.</td>
</tr>
<tr>
<td>M</td>
<td>150</td>
<td>80–220</td>
<td>27</td>
<td>Relatively intact. Six trees were logged in the late 40s. Hilltops may have been damaged by wind.</td>
</tr>
<tr>
<td>N</td>
<td>180</td>
<td>100–260</td>
<td>28</td>
<td>Relatively intact. Part of transect is in the former Finca Jenny.</td>
</tr>
</tbody>
</table>

* Exact ages of forest patches younger than 40 years old were known. Forest ages for the two older sites are probably maximum tree ages rather than forest ages. Site letters refer to locations on Fig. 1.

Fig. 1. Map of Santa Rosa National Park, Costa Rica, and the 14 study sites. All sites were connected with other forests so that monkeys could easily travel into and out of all sites. Transects and study sites are labeled A to N, as in Table 1.
rarely subdivide into foraging parties like the other two monkey species (Chapman, 1990a); however, groups can be dispersed over a radius of 250 m (Chapman, 1990b). Estimated home range sizes for capuchins are usually less than 100 ha (range 32–179 ha; Baldwin and Baldwin, 1976; Freee, 1976; Chapman, 1987, Chapman et al., 1988).

Mantled howling monkeys (A. palliata) are distributed from southern Mexico to the west coast of Columbia and Ecuador (Crockett and Eisenberg, 1987). Howlers eat primarily leaves (49%) but opportunistically eat fruit (29%) and flowers (23%, Chapman, 1987, 1988a,b; Larose, 1996). There are approximately 620 howlers in 37 groups in the park. Howlers are usually associated with very large trees (mean diameter at breast height (dbh) = 62.6 cm; Chapman, 1988a). Howler groups are multi-male, consisting mostly of non-related adults and their offspring (Jones, 1980; Clarke and Glander, 1984). Home range sizes of groups vary from 5 to 108 ha (Baldwin and Baldwin, 1976; Larose, 1996) and neighboring home ranges exist with no overlap or up to 100% overlap (Baldwin and Baldwin, 1976).

Spider monkeys (A. geoffroyi) are distributed from Mexico to Panama (Rodriguez-Luna et al., 1996). Their diet is mostly fruit (78%) supplemented with leaves (12%) and flowers (9%, Chapman, 1987, 1988a,b). On average, spider monkeys use fairly large trees (mean dbh = 43.1 cm, range 7–185; Chapman, 1990a). Spider monkeys associate in dynamic, sex-segregated foraging parties (“fission–fusion communities”; Fedigan and Baxter, 1984; Chapman, 1990a). The home ranges of single spider monkeys vary between 25 and 98 ha with males having larger home ranges ($\bar{x} = 81.4$ ha) than females ($\bar{x} = 54.9$ ha, Fedigan et al., 1988; Chapman, 1990a).

2.3. Data collection

Line transects were used because they are a systematic, objective, and rapid method to compare population parameters between habitats (Cant, 1978; Buckland et al., 1996). A 600 m transect was surveyed within each site at a random compass heading (Fig. 1) with the restriction that the transect must remain within the forest patch. It became apparent from Global Positioning System (GPS) data that most transects were not exactly 600 m long ($\bar{x} = 558$ m, SE = 7). Transects were surveyed ca. 1 km apart (minimum 600 m) so that a single monkey group was unlikely to overlap multiple transects.

To sample the forest in each site, all stems within 10 m of the transect and $\geq 5$ cm dbh were measured, estimated for height, and identified to species. A total of 14.5 ha of forest was sampled. Nomenclature for tree species are from Janzen and Liesner (1980).

From February to July 1996, monkey densities were sampled by walking each transect every other day to maximize the similarity of tree phenomenologies between transects. It was assumed that any monkey group could randomly distribute itself within its home range on a daily basis; therefore transects walked on every other day were considered independent. Transects were walked slowly (45 min per transect), in random order, and during all daylight hours (06:00–17:00). Sampling effort was rebalanced after 1 month favoring sites where monkeys were observed. From early February to the middle of July, transects with monkeys present were walked on average 95.5 times (range 87–113) and transects without monkeys were walked on average 57 times (51–60). Half of the sampling effort for each site was in the dry season and half in the wet season; therefore monkey densities and food abundances are averaged across seasons.

When a monkey was observed on the transect, its horizontal distance ($r$) was measured using a range finder ($\pm 10$ cm at a distance of 15 m) and the angle of the monkey off the transect was recorded ($\theta$). Each monkey’s perpendicular distance from the transect was calculated as the product of $r$ and sine $\theta$ (Buckland et al., 1996).

2.4. Density analysis

Monkey densities were calculated using the program DISTANCE (Laake et al., 1996). DISTANCE calculates the density of monkeys from the equation

$$D = n/A$$

where $D$ is the density of monkeys, $n$ is the total number of monkeys observed for all walks of the transect, and $A$ is the area sampled. The area sampled was calculated from

$$A = 2L\mu$$

where $L$ is the total distance walked (length of the transect multiplied by the number times the transect was walked), and $\mu$ is the distance that one can effectively observe monkeys perpendicular to the transect (effective strip width). $\mu$ is calculated from the area under a plotted curve of the probability of detection, $g(y)$, vs. the perpendicular distance from the transect ($y$). The Fourier series detection function (uniform key function with a cosine series expansion) was used to estimate $\mu$ due to its accuracy and robustness with other primate species (Koster and Butynski, 1985). Detection functions are more accurately modeled when there is a large sample of distance measurements and density estimates therefore have less variance. Density estimates from sites with fewer observations of monkeys had proportionally higher variance.

Three DISTANCE estimates of $\mu$ appeared unrealistically low (9 m for capuchins in site F, 5 m for howlers...
in site G, and 10 m for spider monkeys in site L) and were substituted with \( \mu \) estimates from the most abundant species within each site (15.4 m from howlers in site F, 28 m from capuchins in site G, and 21.8 m from howlers in site L). This assumes that detection functions of distance are similar for all species of monkeys (visibility; Buckland et al., 1996).

The farthest observations provide relatively little information about density (Buckland et al., 1996); therefore, 5% of the most distant monkey sightings were not used to estimate \( \mu \) (truncated), as recommended by Buckland et al. (1996).

There are two ways to estimate density with the DISTANCE program: as individuals per area, or groups per area. Densities were analyzed as individuals in a area rather than groups per area due to difficulties in determining the distance to the middle of highly dispersed monkey groups (see also Green, 1978; Cant, 1982; Freese et al., 1982; Chapman et al., 1988; Johns, 1991; Weisenseel et al., 1993; Peres, 1999). Both of these methods result in similar density estimates, however the variance in individuals per area does not incorporate the variance in group size (Buckland et al., 1996).

### 2.5. Habitat characteristics

Several response variables were used in regressions against the estimated ages of the sites. Response variables included tree species diversity (Shannon-Wiener index; Krebs, 1989), tree density (stems/ha of all trees), and basal area/ha of canopy trees. Canopy tree species were defined as species that had a maximum height greater than 20 m or were described as canopy species in the literature (Croat, 1978; Janzen and Liesner, 1980; Opler et al., 1980; Janzen and Waterman, 1984).

### 2.6. Food abundance

Fruit (Peters et al., 1988; Niklas, 1993, 1994) and leaf biomass (Kittredge, 1944; Kira and Shidei, 1967; Attiwill and Ovington, 1968; Whittaker and Woodwell, 1968; Negi et al., 1983; Clough and Scott, 1989; Singh and Yadava, 1991) are known to be power functions of \( \text{dbh} \). Furthermore, studies of tropical trees have shown that single regressions can accurately explain fruit and leaf biomass for several tree species combined (Kira and Shidei, 1967; Ogawa and Kira, 1977; Peters et al., 1988). Food biomass estimates were therefore calculated using the following published allometric relationships,

\[
Fr = 47 \text{dbh}^{1.9}
\]

\[
(R^2 = 0.78, \text{ wild trees and shrubs, Peters et al., 1988; similar to Niklas, 1993})
\]

\[
L = 38.4 \text{dbh}^{1.65}
\]

(derived from equations in Whittaker and Woodwell, 1968).

Where \( Fr \) is the mass of fruit, \( L \) is the mass of leaves, and \( \text{dbh} \) (cm) is the diameter of food tree species. Food biomass for each tree was the sum of fruit and leaf biomass depending on the diet of each monkey species. The estimate of food biomass was then summed within each site for each monkey species. Food lists for each monkey species were obtained from diet studies in Guanacaste where the percent of total diet was presented (Glander, 1975, 1978; Freese, 1977; Chapman, 1987; Chapman and Fedigan, 1990; Larose, 1996; Sorensen, 1998). Food items were included if they constituted at least 2% of the published diet and were confirmed to be available during the study period.

Only adult trees (> 10 cm \( \text{dbh} \)) were included in fruit biomass estimates. Assuming a balanced sex ratio (see Bawa and Opler, 1975; Glander, 1975), half of the calculated fruit biomass was included from dioecious species (Barsera simaruba, Cecropia peltata; Chlorophora tinctoria, Sciadodendron excelsum, Simaruba glauca, Spondias mombin; Bawa and Opler, 1975; Croat, 1978; Glander, 1975, 1978). Peters et al. (1988) based their formula on two fig species so fruit biomass was not corrected for monoecious species. Brosimum alicastrum is a sequential hermaphrodite; therefore fruit biomass was only included for trees less than 70 cm \( \text{dbh} \) (see Peters, 1991). In addition, only trees greater than 20 cm \( \text{dbh} \) were included in the howlers’ diet because howlers rarely forage in smaller trees (< 0.02% of forage time; Leighton and Leighton, 1982; Chapman, 1990b; Larose, 1996), unlike capuchins and spider monkeys (34.6 and 25%, respectively, Chapman, 1990b).

The allometric relationship for flower biomass is not well documented for trees [shrubs studied by Midgley and Bond (1989) and Le Maitre and Midgley (1991)]; therefore flower biomass was not included in the food biomass estimate. Insect biomass constitutes an important proportion of capuchin diet (17% of foraging time; Chapman, 1987) but was not estimated in this study and therefore capuchin food biomass is underestimated in each study site.

### 3. Results

3.1. Forest regeneration

A total of 13,653 stems greater than or equal to 5 cm \( \text{dbh} \) were measured, consisting of 113 known species (28–65 species per site), 96 genera, and 47 families. Species diversity was higher in older forests (Table 2). Similarly, basal area/ha and average height of canopy trees were higher in older forests (Table 2). Tree density was highest in forests 10–60 years old (Table 2).
3.2. Monkey density and food abundance

Most of the variation in monkey density estimates (58–100% of variance) was due to variable encounter rates rather than the estimation of effective strip width (μ, 0–42% of variance). In other words, the average number of monkeys that were seen each time the transect was walked introduced the most variation to the density estimate.

Multiple regressions of monkey densities versus forest age, food biomass, tree density, and tree species diversity were used to examine the combined influence of environmental variables. Basal area/ha was removed from the model due to intercorrelation with other variables. Capuchin densities were positively associated with forest age (Fig. 2a), and food biomass (Fig. 2b; multiple regression, $R^2 = 0.805$, $p = 0.0001$). Residual fruiting trees in site F may have caused higher capuchin densities than the other 60-year-old forest, site G (Fig. 2a). The densities of capuchins did not appear to level off within the chronosequence of sites although the two undisturbed sites had the highest densities (59–61/km²; Fig. 2a).

Howler densities had a positive relationship with forest age but were highly variable after 60 years of regeneration ($p = 0.011$; Fig. 3a). The only habitat variable that was significant in the multiple regression model was food biomass ($p = 0.0004$; Fig. 3b). Simple regressions indicated that howler densities were more strongly related to leaf biomass ($R^2 = 0.689$, $p = 0.0002$) than to fruit biomass ($R^2 = 0.592$, $p = 0.001$) as one would predict from their relative proportions in howler diet. Residual fruiting trees in site F may have resulted in higher howler densities than naturally regenerated sites (Site G; Fig. 3a,b). The maximum density of howlers reached 85/km² in 80-year-old site H. Most (90%) of the howler sightings in site H were within two older portions of the transect (> 100 years old).

The multiple regression indicated that only forest age was significant in explaining variation in spider monkey densities ($p = 0.004$, Fig. 4a). Spider monkey densities were high in the two relatively intact forests (46 and 67/km²) but very low in all other sites (Fig. 4a). An exponential model fits the data ($y = e^{0.051x}$; $R^2 = 0.607$, $p = 0.001$) however the model is biologically inappropriate for spider monkey populations. The density of spider monkeys in site E was mostly due to travel through the patch rather than foraging. Although the multiple regression determined that forest age explained more variation, spider monkey densities were weakly related to food biomass estimates ($p = 0.030$; Fig. 4b). Spider monkey densities were better explained by fruit biomass ($R^2 = 0.328$, $p = 0.032$) than leaf biomass ($R^2 = 0.101$, $p = 0.268$) as predicted by relative proportions in their diet.

To examine when food biomass reaches maximum levels during regeneration, food biomass was regressed against forest age. Food biomass for capuchins ($p = 0.005$; Fig. 5a), howlers ($p = 0.001$; Fig. 5b), and spider monkeys ($p = 0.00002$; Fig. 5c) increased linearly with the age of the forest. Clearly, the food biomass estimate for site F is higher than the other 60-year-old forest, site G (Fig. 5a–c).

4. Discussion

4.1. Capuchins

Capuchin densities were linearly correlated with both forest age and food biomass. The densities did not appear to level off within the chronosequence but the
two undisturbed sites had similar high densities (59–61/km²). Although capuchin density in undisturbed forest was high, it was within the range of reported densities for the species (maximum 68–94/km², Baldwin and Baldwin, 1976). The range of regenerating habitat used by capuchins is consistent with suggestions that capuchins are habitat generalists (Freese, 1976; Chapman et al., 1989).

The third highest density of capuchins was in site F (44/km²) which suggests that densities can be artificially raised in younger forest by leaving residual fruiting trees in abandoned pastures. It also appears that capuchins are able to exist at variable densities depending on food abundance in the habitat.

4.2. Howling monkeys

Several studies suggest that howlers prefer older, more evergreen forest rather than younger, more deciduous forest (Freese, 1976; Heltne et al., 1976; Chapman et al., 1989; Chapman and Balcomb, 1998). The proportion of evergreen trees increased linearly with the age of the forest (Sorensen, 1998), but the highest howler densities were not in the oldest, most evergreen forest (site N) nor was there a trend in densities after 60 years of regeneration. Likewise, site F was very deciduous but had the third highest howler density (75/km²). The above results suggest that deciduous/evergreen distinctions and forest age may be inadequate to define optimal habitat for howlers.
Early studies suggested that howler densities were not limited by food resources and that home ranges included more food than groups could ever eat (Chivers, 1969; see Baldwin and Baldwin, 1976; Coelho et al., 1976). However, Glander (1975, 1978) and Jones (1980) later suggested that not all leaves and fruit are palatable between and within tree species and that the apparent abundance of food may be offset by a lack of nutrients or the presence of secondary compounds. The current results suggest that when preferred diet items are isolated for food abundance estimates, howler densities are strongly related to food abundance (see also Stoner, 1996).

4.3. Spider monkeys

Densities of spider monkeys in relatively intact forest were much higher than in other sites of similar age. One explanation is that spider monkey densities may still be influenced by hunting pressure that occurred over 25 years ago. Hunting pressure may have been lower in the undisturbed forests than the rest of the park, which would explain the large difference in current densities. Many studies have suggested that historical hunting pressure strongly influences Ateles densities (Freese et al., 1982; Chapman et al., 1989).

Fig. 3. a. Density (± SE) of howler monkeys (Alouatta palliata) along a regeneration gradient. Density in site F may be inflated by a large number of residual fruiting trees relative to site G. The majority (90%) of sightings in site H were within two areas of older forest (70–90 years old). b. Howler density (± SE) vs. howler food biomass. The food biomass and howler density in site F was higher than site G due to residual fruiting trees. The majority (90%) of sightings in site H were within two areas of older forest (70–90 years old) which probably had higher food biomass/ha.
The upper limits of primate density, but not the lower limits, are set by the food abundance of primate habitats (Butynski, 1990). This appeared particularly true for spider monkeys (see also Coelho et al., 1976). Densities were positively correlated with food abundance; however, some sites with high food abundance had very low spider monkey densities. Spider monkey densities may respond to food availability on a larger spatial scale (entire forest stands) than that sampled by transects. Similarly, spider monkeys may use foraging routes more consistently than the other two monkey species, and therefore may be less likely to find newly regenerated resources.

Monkey species returned to the abandoned pastures in the following order: capuchins (14–25 years), howlers (30–60 years), and spider monkeys (60–80 years). These results support predictions that large body size, large home range size, the proportion of fruit in the diet, diet specialization, and slow reproduction are negatively associated with tolerance for habitat disturbance (see also Branch, 1983).

4.4. Comparative density estimates

The most important benefit of transect methods for density estimates is that they provide a rigorous and objective method to compare the relative abundance of multiple species in a variety of habitats. However, there are several drawbacks to using transect methods. The accuracy of the estimate is highly dependent on the estimate of transect width ($\mu$), on the accuracy of distance measurements, and on the interest of the observer.
Fig. 5. a. Fruit biomass of capuchin food (items > 1.9% of diet) along a regeneration gradient. The food biomass in site F was higher than site G due to residual fruiting trees. b. Biomass of howler food (items > 1.9% of diet) along a regeneration gradient. The food biomass in site F was higher than site G due to residual fruiting trees. c. Biomass of spider monkey food (items > 1.9% of diet) along a regeneration gradient. The food biomass in site F was higher than site G due to residual fruiting trees.
Whether or not the density estimate is representative of a larger area also depends on how much of the study area is sampled by the transect. A \( 600 \times 50 \) m transect only samples 9% of a 35 ha forest patch.

Unfortunately, in wild populations there rarely are ‘true’ or ‘accurate’ densities to compare with any method. Unless monkeys spend all of their time uniformly over all of the study area, different methods will result in different estimates. Skorupa (1987) found that transect methods have equal probabilities of over- (8–50%) or underestimating (7–46%) densities compared to home range methods. Fedigan et al. (1996, 1998) calculated ecological densities from total abundance in the park divided by the area of suitable habitat (evergreen and mixed deciduous forest). Their results suggest overall ecological densities of 7.5/km\(^2\) for capuchins and 7.9/km\(^2\) for howlers in Santa Rosa in 1992. Other studies have found much higher densities within smaller areas of the park using home range methods (19.2–91.8 howlers/km\(^2\); Larose, 1996) and transect methods (19–33 capuchins/km\(^2\) and 19–28 howlers/km\(^2\); Chapman et al., 1988; 61 ± 14 capuchins/km\(^2\) and 85 ± 19 howlers/km\(^2\); maximum in current study). Clearly, density estimates are highly dependent on temporal and spatial scales.

### 4.5. Management implications

Management plans must account for resource shortages over the short term and the long term. Resource limitation may only be operating during the dry season (Terborgh, 1986; Dobson and Lyles, 1989) when fruit, leaf, and water resources are reduced (Chapman and Chapman, 1990; Chapman and Balcomb, 1998) and ecological roles are most sharply defined (Terborgh, 1986). In the dry season, monkeys may spend more time in older forests where there are more large evergreen trees and consequently more leaf food sources, more shade and lower temperatures to avoid dehydration, and more tree holes with drinking water. In the future, additional variation in monkey densities should be examined by correlating monkey densities with food abundance within each season (Sorensen, in preparation).

Although absolute numbers of a species are the foremost concern for conservation, viable population compositions are equally important. There is growing evidence that the proportions of immature capuchins and howlers are increasing within the park over time as the forest regenerates (Fedigan et al., 1996, 1998), as well as along a regeneration gradient within the park at a given point in time (Sorensen, 1998). Similarly, ratios of immature to adult spider monkeys are higher in the latest surveys (0.57) compared to surveys in 1972 (0.33, Freese, 1976). However, our ratios are still well below those in Tikal, Guatemala where the forests are much less recently disturbed (1.00–1.08; Coelho et al., 1976; Heltne and Thorington, 1976; Cant, 1978). Sex ratios for both howling (0.43) and spider monkeys (0.55) are within the range reported in the literature (0.31–0.82 for howlers; Clarke et al., 1986; Stoner, 1994; 0.45–0.57 for spider monkeys; Coelho et al., 1976; Cant, 1978).

The results indicate that regenerating habitat cannot be expected to contain densities of these three monkey species similar to those found in undisturbed forest. Only undisturbed forests older than 150–180 years old contained maximum densities of capuchin and spider monkeys. There is, however, potential for the use of regenerating forest to complement, but not replace, protected undisturbed forest in habitat management plans (Bearder, 1991). One example would be a buffer area adjacent to protected parks in which the majority of the forest was maintained at a mid- to mature regeneration state (70–100 years old) through long return intervals for clear-cutting or through low intensity selective harvesting.

It appears that both forest age and food abundance influence the density and group compositions of these monkeys. Managers may be able to increase the densities of capuchins and howlers in disturbed forests by managing the forest for higher monkey food biomass (Terborgh, 1986; Bearder, 1991; Johns, 1992) such as in site F. Residual fruiting trees increased the abundance of food and primate densities above what would be expected by forest age alone. Many researchers have emphasized the importance of protecting species such as figs that provide the ‘base-line’ food even during periods of food scarcity such as the dry season (Terborgh, 1986; Bearder, 1991; Whitmore, 1991; Frumhoff, 1995). These food trees constitute a small proportion of the trees and wood volume of the forest, and could be left during logging operations with minimal cost (Terborgh, 1986). Unfortunately spider monkey densities were not strongly correlated with food biomass and thus management of food biomass may have little impact on spider monkey densities. Areas of undisturbed forest must be protected to conserve spider monkey populations.

The most successful management strategies for tropical dry forest will probably incorporate a variety of land-use and protection policies. The importance of large areas of undisturbed ‘pristine’ habitat has been stressed for years and there is little argument (Johns, 1985); however, managers are beginning to obtain the tools to manage primate populations in selectively logged, fragmented, and regenerating habitats (Wilson and Wilson, 1975; Bernstein et al., 1976; Wilson and Johns, 1982; Johns, 1985, 1986, 1988; Lovejoy et al., 1986; Skorupa, 1986; Weisenseel et al., 1993; Estrada and Coates-Estrada, 1996). Management of primates in these disturbed areas should not replace the protection of undisturbed forest, but rather work in addition to conservation areas. This study suggests that a portion of
the monkey population may be maintained by protecting relatively small, but connected, patches of mature forest in a disturbed landscape.

Acknowledgements
We wish to thank the National Parks Service of Costa Rica for permission to conduct research in Santa Rosa National Park. We thank Roger Blanco-Segura and his staff for logistic support and interest in the research. Jan Murie was also very generous with his time, supervision, and encouragement for the research. We thank Monica Sorensen, Craig Sheerba, David Benitez, and Hugo Guadamuz-Rogas for assistance in data collection. We especially thank Brian Enquist and Roberto Espinoza-Obando for their plant identification work and Brian’s allometric growth models to age the forest patches. Daniel Janzen was extremely helpful in establishing study sites and providing forest histories. We would like to thank Susan Hannon, Mark Dale, and Susan Crites for their time and comments on earlier drafts of this manuscript. This research was funded by a NSERC Undergraduate Summer Scholarship, a University of Alberta Graduate Teaching Assistantship, a J. Gordin Kaplan Graduate Student Award, and a NSERC operating grant of L.M. Fedigan.

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