



Initial effects of fragmentation on the density of three neotropical primate species in two lowland forests of Colombia

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ABSTRACT: Fragmentation and habitat destruction are 2 factors driving the current decline of mammal populations. Spider monkeys *Ateles* spp. are some of the first neotropical mammals to go extinct after fragmentation, as they (1) are large-bodied, specialized frugivores that require large areas to subsist, (2) are preferred targets for local hunters, (3) have slow reproductive cycles, and (4) rarely move between adjacent forest fragments. Brown spider monkeys *A. hybridus* are Critically Endangered, and most of their historical habitat has either been cleared or is seriously fragmented. We conducted census surveys at 2 areas in Colombia (Las Quinchas and San Juan) in order to compare the population density of brown spider monkeys, red howler monkeys *Alouatta seniculus*, and white-fronted capuchins *Cebus albifrons* in both continuous forest and recently fragmented forest in each of these 2 areas. We found a higher density of brown spider monkeys and red howler monkeys in recent fragments at both sites, while differences were not consistent for white-fronted capuchins. We suggest that these patterns could be explained by the constrained ability of spider monkeys and howler monkeys to move between forest fragments and to exploit impacted or degraded areas. In the absence of hunting, the immediate effects of fragmentation on spider monkeys seem to lead to a sudden increase in population density as a result of a decreasing forested area, while maintaining population numbers relatively stable. Longer-term research will lead to the identification of the proximate factors leading to the generalized pattern of local extinction of spider monkey populations in small isolated fragments.

KEY WORDS: *Ateles hybridus* · Endangered species · Fragmentation · Line transects · Population density

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INTRODUCTION

Habitat destruction is among the main factors driving the rapid decline of a large number of plants and animals in most of the planet's ecosystems (Fahrig 2002). The loss of natural habitats as well as their frag-

mentation is exposing wildlife to rapidly emerging challenges, particularly for migratory species and those with large home ranges or 'specific' ecological requirements (Andrén 1994). The genetic and demographic consequences associated with these isolation processes have been described using the island bio-

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geographical theory (MacArthur & Wilson 1967, Lovejoy et al. 1986, Soulé et al. 1988, Newmark 1996, Sih et al. 2000). Furthermore, as fragmentation increases and more areas become accessible and exposed to anthropogenic activities, wild populations become more vulnerable, especially when activities such as hunting (Michalski & Peres 2005) or increased exposure to diseases (Chapman et al. 2006, Goldberg et al. 2008) have a direct and negative effect on their members. Although several studies have found support for the idea that fragmentation, in the long run, increases the probability of local extinctions for many birds and mammals (Andrén 1994, Fahrig 2002 and references therein), there is still a knowledge gap regarding the proximate factors driving these extinction processes.

Neotropical primates (infraorder Platyrrhini) are characterized as having evolved physical and behavioral adaptations for arboreality (Hershkovitz 1977), and all extant New World monkeys spend all or at least most of their time above ground on shrubs, trees, and lianas. For those species that occasionally do come to the ground for feeding or traveling, even subtle fragmentation can isolate previously neighboring individuals or groups (Chiarello & de Melo 2001). Most New World monkeys rely on fruits, seeds, leaves, gum, and other plant parts as the most important items in their diets, and thus are directly affected when deforestation and habitat loss take place, causing resources to become scarce (Cowlshaw & Dunbar 2000). As a result, arboreal primates are particularly vulnerable to local extinction as a result of fragmentation and habitat loss (Cowlshaw 1999).

Different primate species may adapt or respond differently to habitat loss and other anthropogenic interventions (Michalski & Peres 2005). Large-bodied frugivorous primates are among the most vulnerable guilds when exposed to habitat disturbances and fragmentation, not only because they usually require large areas in order to meet their nutritional requirements, but also because given their large size, they are often preferred targets for hunters. Of neotropical primates, spider monkeys *Ateles* spp. are among the most fragile taxa, as they prefer undisturbed forests, are preferred hunting targets (Peres 2000, Peres & Lake 2003), and are among the first animals to go locally extinct under such hunting pressure (Franzen 2006).

Spider monkeys also have additional biological characteristics that restrict their potential flexibility to adapt to habitat loss and fragmentation. First, their long reproductive cycles are only comparable to those of hominoids, after controlling for body size (Di Fiore & Campbell 2007). Females first reproduce at approximately 7 to 9 yr of age, and they have long average inter-birth intervals of 3 yr (Symington 1988). Thus,

their populations are unable to recover in the short term from rapid population declines, especially if hunters target adult females, given their large body size (in comparison to most other primates) and the possibility of capturing offspring as pets (Cowlshaw & Dunbar 2000, Duarte-Quiroga & Estrada 2003, Franzen 2006). Second, spider monkeys are among the largest neotropical primates (ca. 8 kg) and are ripe-fruit specialists (Dew 2005, Di Fiore et al. 2009), requiring large areas to obtain these resources. Thus, habitat fragmentation and habitat loss pose a significant challenge for these primates.

Folivorous and omnivorous primates are expected to cope better with habitat disturbance and fragmentation, as leaves and insects are more evenly distributed resources in tropical forests. Also, primates that are able to move between isolated forest fragments, crossing through disturbed areas (e.g. pastures or regenerating vegetation), are expected to be less affected by fragmentation processes. Howler monkeys *Alouatta* spp. are large folivorous primates found throughout the Neotropics, in both large and fragmented habitats (Di Fiore & Campbell 2007). Capuchin monkeys *Cebus* spp. are omnivorous primates that include a large proportion of invertebrates and vertebrates in their diets and show ample resilience to habitat disturbance (Michalski & Peres 2005).

The Inter-Andean lowland rainforests of Colombia have been exposed to human intervention for centuries. Nonetheless, the late twentieth century was marked by an accelerated process of habitat loss as forests were increasingly cut and transformed into pastures for extensive cattle ranching and agriculture (Vargas et al. 1998). In fact, Morales-Jimenez (2004) estimated that only 18% of the potential distribution of the forests where brown spider monkeys once lived still persists, and only 9% remains in large tracts of continuous forest. The increasing destruction of Inter-Andean forests is likely to drive the extinction of many taxa whose distribution is mostly limited to these forests, including the blue-billed curassow *Crax alberti* and the silvery-brown tamarin *Saguinus leucopus* and other endemic taxa, in addition to brown spider monkeys *Ateles hybridus*.

Currently, brown spider monkeys are considered Critically Endangered primates by the International Union for the Conservation of Nature and Natural Resources (IUCN: www.iucnredlist.org). Brown spider monkeys came to be considered a distinct primate species (Collins & Dubach 2000) only about a decade ago, and almost no information existed on the ecology and social behavior of these endangered primates.

Although many studies have attempted to describe the behavioral changes or ecological strategies of pri-

mates living in altered and fragmented habitats (Johns & Skorupa 1987), few have assessed the effects of fragmentation on demography and population density. Several methods to estimate primate population densities have been developed and implemented, but there is still no consensus on which method provides the most accurate results (Marshall et al. 2008 and references therein). Accurate results have only been attained through direct counts (Defler & Pintor 1985), but these methods are too costly to be implemented in large-scale studies. Thus, other methods such as home range analyses or line transect methods have been used more frequently. Home range analyses require enormous effort to obtain a sample size large enough (several overlapping groups) to be accurately extrapolated to the population level (Fashing & Cords 2000), and most studies have relied on small samples to estimate 'real' population densities (Hassel-Finnegan et al. 2008). Within the wildlife biology literature, there is ample debate on the accuracy and precision of line transect methods due to the practical difficulties to comply with all required assumptions (Marshall et al. 2008). Nevertheless, line transect methods still remain the most used techniques for assessing primate population densities. Independent of their accuracy, these methods can be used to compare relative differences in population densities between different areas (assuming a similar precision in data collection).

The main objective of this study was to assess the initial effects of fragmentation and habitat loss on the population densities of brown spider monkeys *Ateles hybridus*, red howler monkeys *Alouatta seniculus*, and white-fronted capuchins *Cebus albifrons* in 2 lowland forests in Colombia. We evaluated the effects of fragmentation on primate population densities in a continuous forest and a recently fragmented forest in each of 2 areas within the Magdalena River Valley in Colombia. We describe differences in population density for 3 primate species in the initial phase of habitat reduction (soon after fragmentation took place) in order to build on our current knowledge of how fragmentation affects primate populations, and we discuss the potential factors that lead to the local extinction of primate populations in small isolated patches in the long run.

MATERIALS AND METHODS

Study sites. We collected data at 2 study areas characterized by a mosaic of forest fragments around larger patches of continuous forests: Serranía de Las Quinchas (hereafter 'Quinchas') and Hacienda San Juan de Carare (hereafter 'San Juan') (Fig. 1). The sites are ca. 75 km apart and comprise some of the

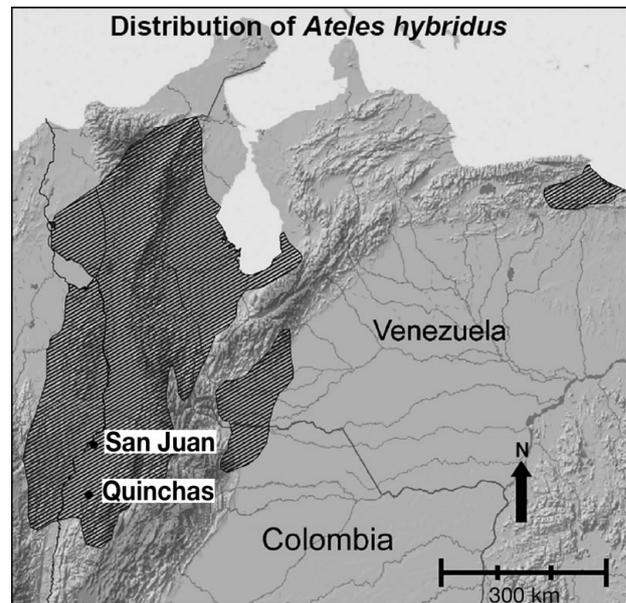


Fig. 1. Location of the 2 study sites in Colombia (San Juan and Quinchas). The shaded area represents the probable distribution of the brown spider monkey as published by the IUCN (2010)

last remains of lowland Inter-Andean rainforests in the Colombian Magdalena River valley region (Fig. 1). In each site, we conducted line transect surveys to estimate population densities of primates in one relatively large and continuous forest and another forest fragment that had recently been exposed to fragmentation and selective logging. We focused on surveying all diurnal primates in the region: brown spider monkeys, red howler monkeys, and white-fronted capuchins; grey-legged night monkeys *Aotus griseimembra* are present in the area but were not included in this study.

At Quinchas, we conducted census surveys at a fragmented forest within the private natural reserve 'El Paujil' (referred to here as 'Quinchas Fragment') owned by Fundacion ProAves, where we have been studying brown spider monkeys since 2005, and at a section of a continuous private forest at Vereda La Guinea (referred to here as 'Quinchas Continuous'). Both sites are on the western slope of the eastern Andes and are situated approximately 7 km from each other. At the time of the study, both sites had been exposed to selective logging. Although hunting of brown spider monkeys had been prohibited in the region, it still occurs at a very low frequency. The terrain of the region is characterized by narrow ridges intersected by steep riverine valleys. A trail system was established at each site and was mapped and marked every 25 m with flagging tape. Annual rainfall averaged 3544 ± 336 mm ($n = 3$; 2006 to 2008) with few

months receiving less than 100 mm (3 out of 36). The dry season occurs during the months of December to February.

Quinchas Fragment, La Reserva (06° 03' N, 74° 16' W), is located at Puerto Pinzon, Boyacá Department, and comprises 2 adjacent forest fragments of 20 and 60 ha that were isolated for several years from an adjacent ca. 300 ha fragment by a road. The fragments have recently been reconnected with the larger fragment at ca. 5 points through natural 'bridges' in the canopy that allow spider monkeys to cross the road and move between fragments. The site is located in the north-western part of Serranía de Las Quinchas between 200 and 350 m a.s.l. Selective logging was widespread around a decade ago, but since 2003 the site has been owned by Fundación ProAves and has been protected from logging and hunting.

Quinchas Continuous, La Guinea (06° 01' N, 74° 12' W), is located in a central part of the Serranía de Las Quinchas at Bolivar, Santander, between 200 and 700 m a.s.l., and access to the forest is restricted to mules or trekking due to the rough terrain. At the time of the study, the area was privately owned and part of it had been transformed into pastures for cattle ranching. Nonetheless, the study area was connected to a large and continuous forest of ca. 80 000 ha that was experiencing selective logging of hardwoods.

At Hacienda San Juan de Carare, we conducted census surveys at a fragmented seasonally flooded forest patch (referred to hereafter as 'San Juan Fragment') where we have been studying brown spider monkeys since 2007, and in a larger forest fragment (referred to hereafter as 'San Juan Continuous') that consists of a mosaic of terra-firme forest and seasonally flooded forests. The sites are approximately 3 km apart and the terrain is relatively flat. San Juan is located near the Magdalena River in the middle of the Magdalena valley between the eastern and central Andes of Colombia. Mean rainfall is 2070 mm (IDEAM 2008), and average temperature oscillates around 28°C.

San Juan Fragment (06° 43' N, 74° 09' W) is a thin, riverine forest fragment of roughly 70 ha that runs along the San Juan River and was recently (ca. 3 yr ago) fragmented in the northern and southernmost part of the current forest by man-made pastures. Natural flooded savannas in the west and the San Juan River in the east also define the forest fragment. Selective logging has occurred in the fragment, although large emergent trees (e.g. *Ficus insipida*) are still present.

San Juan Continuous (06° 42' N, 74° 08' W) is one of the largest forest patches in the region, comprising ca. 1500 ha. The area has recently been exposed to selective logging and is surrounded by pastures for cattle ranching and natural savannas.

Demographic data. We habituated and studied the only group of brown spider monkeys living at Quinchas Fragment from January 2006 onwards; the 2 social groups of spider monkeys in San Juan Fragment have been habituated and studied since September 2007. Demographic, ranging, and other ecological data have been systematically collected over approx 485 h of behavioral 'follows' in San Juan, and 847 h at Quinchas. Spider monkeys from these 3 social groups have been individually identified based on differences in their facial and ano-genital patterns. Births, disappearances, and emigration events have been monitored during this time.

Primate density. Population density surveys were calculated following the line transect method and following the recommendations suggested by Peres (1999). Data were collected during approximately 8 d each month from August 2007 to August 2008 for a total of 954.24 km walked during 239 walks. Sampling at San Juan was somewhat less intensive than sampling at Quinchas, as the region had extended periods of floods that prevented us from doing the surveys. Transects were walked from 06:00 to 10:00 h at a speed of approximately 1 km h⁻¹ stopping every 100 m and waiting 5 min in silence looking for any animal that could be resting over the transect, and trying to detect any movement or sound. In the case of rain, censuses were interrupted until the weather allowed us to continue. Upon detecting a primate group, we waited from 5 to 10 min in order to increase the chance of detecting all members of the group. When a group of primates was encountered, we recorded the time, number of individuals, the perpendicular distance of the group's center to the transect, the location, and the sex-age category of each individual if possible. Cluster size represents the number of individuals in a group or subgroup of primates that were detected during census surveys. For howler monkeys, cluster size represents the size of the social groups (which are cohesive), while for spider monkeys it represents the size of traveling or foraging subgroups (given their fission-fusion grouping patterns). For capuchins, it attempts to represent the size of the social group, but given the large group spread in this taxon, data presented here were taken on subgroups of capuchins.

We calculated primate density and cluster size from line transect data for each species separately, using different analytical methods: (1) Distance 5.0 (Thomas et al. 2006), (2) the Kelker method based on perpendicular distances, and (3) the King estimator (Leopold 1933). For the Distance method, we used the distance sampling function of the program, testing 5 candidate models in the program for fit to the distribution of transect data, including the default half-normal key with cosine polynomial expansion, uniform key with

cosine polynomial expansion, uniform key with simple polynomial expansion, half-normal key with hermite polynomial expansion, and hazard-rate key with the cosine polynomial expansion. We selected the model with the lowest Akaike's information criterion (AIC) value (Buckland et al. 2001). The cluster size was calculated using the cluster size-biased regression method unless warnings indicated the need to use the mean of the observed clusters. For Distance-based analyses, we truncated 5% of the data as suggested by Buckland et al. (2001) to exclude potential outliers.

For the Kelker method, we used the equation:

$$D = n/2La \quad (1)$$

where D is the density of individuals or groups per unit area, n is the number of individuals or groups along the transect, L is the total length of the transect, and a equals half the effective strip width.

To obtain the species-specific strip width by the Kelker method, the cutoff point was determined by analyzing the distribution of perpendicular distances as described by Hassel-Finnegan et al. (2008) and Marshall et al. (2008). We selected the histogram used for each analysis on the basis of which block width resulted in the clearest detection cutoff point up to where we assumed that the probability of detection was 1. We included all sightings up to the cutoff point, but excluded sightings beyond the cutoff point for analyses.

When using the King estimator, we used the same density formula as in the Kelker method; however, the effective strip width was calculated as the average perpendicular distance recorded for a given species at each site. For both the Kelker and King methods, the mean subgroup size was calculated based on all groups observed within the effective strip width, using the maximum number of individuals measured for all calculations.

Finally, in the San Juan Fragment, we were able to directly count all individual spider monkeys living in the fragment and were thus able to compare the results of the density estimates obtained through the different methods to the 'real' density of spider monkeys in the fragment. To estimate the accuracy of the different methods, we estimated the deviation from the results obtained from each method to the known density of spider monkeys at San Juan Fragment. We used the following equation:

$$\text{Deviation between methods} = (|Dt - Dr|/Dr) \times 100 \quad (2)$$

where Dt = estimated density and Dr = known 'real' density of spider monkeys at San Juan Fragment. All statistical analyses were performed using SPSS 13.0.

RESULTS

Direct counts

From our long-term research at Quinchas and in the San Juan forest fragments, we were able to directly count the number of individuals (through individual identification) living in the groups that overlapped with our census transects. At the time of the study, there was 1 group of 29 spider monkeys at Quinchas and 2 groups of 16 and 14 spider monkeys in the 2 social groups living in the San Juan Fragment. Nevertheless, we were only able to estimate the true density of spider monkeys at San Juan, as the fragment in Quinchas re-connected (after several years of isolation) to adjacent and relatively inaccessible fragments (to observers), and thus our study group expanded its previously restricted home range. The forest fragment at San Juan has an area of 0.70 km² where 30 spider monkeys were living at the time of this study, giving a density of 42.8 ind. km⁻².

Density estimates

We recorded a total of 640 sightings of primates in ca. 954 km of transect surveys at the 4 census surveys included in this study. Overall, white-fronted capuchins were observed most frequently ($n = 264$ encounters), followed by brown spider monkeys ($n = 223$) and red howler monkeys ($n = 153$). The number of censuses and the total sampling effort was unequal for each site, and results are given in Table 1.

At Quinchas, spider monkeys and howler monkeys were more frequently encountered in recently formed fragments (while controlling for sampling effort), while capuchins were more frequently observed in the continuous forests. In a similar pattern, spider monkeys and howler monkeys were much more frequently encountered in the forest fragment at San Juan when compared to the more continuous forests, although capuchins had similar rates of encounter in both forests (Table 1). During census surveys and opportunistic observations, we recorded several groups of night monkeys *Aotus griseimembra*, confirming their presence in all 4 study areas.

Given the low number of sightings of spider monkeys in San Juan Continuous ($n = 6$) and of howler monkeys in Quinchas ($n = 13$) and in San Juan Continuous ($n = 3$) during the census surveys, we were unable to use Distance-based analyses for these taxa at those sites. Thus, we relied on estimating their densities only via the Kelker and King methods using perpendicular distances to the transect (Aldana et al. 2008, Hassel-Finnegan 2008).

Even though there were marked differences in the density estimates of all taxa based on the different methods of data analysis (Table 2), we found a consistent pattern of higher group density for both spider monkeys and howler monkeys in recently fragmented forests than in the more continuous forests at both Quinchas and San Juan (Fig. 2). Differences in the rate of encounter of *Ateles hybridus* and *Alouatta seniculus* between fragmented and continuous forests were more striking at San Juan than at Quinchas. This pattern was not observed for capuchin monkeys, which showed less dramatic differences in group density between recent forest fragments and continuous forests. In fact, at Quinchas, capuchin monkey groups had higher densities in continuous forests, and at San Juan there were no differences in group density between fragmented and continuous forests (Fig. 2).

Table 1. *Ateles hybridus*, *Alouatta seniculus*, and *Cebus albifrons*. Site size, sampling effort, and sightings of brown spider monkeys, red howler monkeys and white-fronted capuchins in a continuous and fragmented forest at Quinchas and San Juan, Colombia. Sightings are total nos. followed by mean per km in parentheses

	Quinchas		San Juan	
	Continuous	Fragment	Continuous	Fragment
Site size (ha)	80 000	~400	~1500	70
Transect distance (km)	4.725	3.825	3.534	3.258
No. of censuses	81	85	31	42
Sampling effort (km)	382.725	325.125	109.554	136.836
Sightings of <i>A. hybridus</i>	75 (0.20)	85 (0.26)	6 (0.05)	57 (0.42)
Sightings of <i>A. seniculus</i>	13 (0.03)	32 (0.10)	3 (0.03)	105 (0.77)
Sightings of <i>C. albifrons</i>	90 (0.24)	47 (0.14)	55 (0.50)	72 (0.53)

Table 2. *Ateles hybridus*, *Alouatta seniculus*, and *Cebus albifrons*. Estimates of population density (ind. km⁻²) of brown spider monkeys, red howler monkeys, and white-fronted capuchins in the 4 forests surveyed and calculated using the 4 methods Distance, Kelker, King and direct counts (see 'Materials and methods; Primate density'). nd: not determined

Method	Quinchas		San Juan	
	Continuous	Fragmented	Continuous	Fragmented
<i>Ateles hybridus</i>				
Distance	12.3	27.1	3.7	21.8
Kelker	12.1	27.0	3.3	25.0
King	26.1	41.1	5.2	33.0
Direct count	nd	nd	nd	42.8
<i>Alouatta seniculus</i>				
Distance	1.9	7.9	1.6	60.2
Kelker	1.8	8.7	1.5	64.0
King	3.7	15.6	2.5	98.3
Direct count	nd	nd	nd	nd
<i>Cebus albifrons</i>				
Distance	29.4	19.6	98.4	116.6
Kelker	29.8	22.9	82.8	56.3
King	59.2	35.9	138.6	130.3
Direct count	nd	nd	nd	nd

Brown spider monkeys were found in subgroups that averaged (\pm SD) 3.9 (\pm 2.9) ind. and ranged from 1 to 17 ind. Howler monkey group size was on average 4.1 (\pm 2.0) ind. and ranged from 1 to 9. White-fronted capuchins had the largest average group size with 5.8 (\pm 4.0) ind., and groups ranged in size from 1 to 21 ind. Spider monkey subgroup size did not differ significantly between sites (Kruskal-Wallis test: spider monkeys $\chi^2 = 0.153$, $n = 205$, $p = 0.985$), but the same was not true for howlers and capuchins. Howler monkeys were found in bigger groups in the Quinchas fragment and small groups in the continuous forests. On the other hand, capuchin clusters contained fewer individuals per group in San Juan continuous forests (Kruskal-Wallis test: howler monkeys $\chi^2 = 25.83$, $n = 146$, $p < 0.001$; capuchins $\chi^2 = 7.82$, $n = 226$, $p = 0.05$). (Fig. 3).

Due to the relatively small differences in group or subgroup size for each primate species across all 4 forests, the results of primate density (ind. km⁻²) are similar to those reported for group density, only scaled up by a factor associated with average cluster size. Spider monkey and howler monkey population densities were higher in fragments than in continuous forests, especially at San Juan (Table 2). On the other hand, capuchins seemed to be responding in a different way to fragmentation, since their densities were very similar between fragments and continuous forests. Moreover, capuchin densities were overall significantly higher in San Juan compared to Quinchas.

When comparing the different line transect methods to the true density of spider monkeys in San Juan Fragment, all methods underestimated the population density of 42.8 ind. km⁻². The density estimated by the King method (33.0 ind. km⁻²) was closest to the direct count, showing an underestimation of 23%. The Kelker and DISTANCE methods yielded very similar results for all species and sites, but underestimated the true population density at San Juan by over 40%. When comparing density estimates between methods, results obtained with the King method were statistically different from those obtained with Kelker and Distance, which on the other hand were not statistically

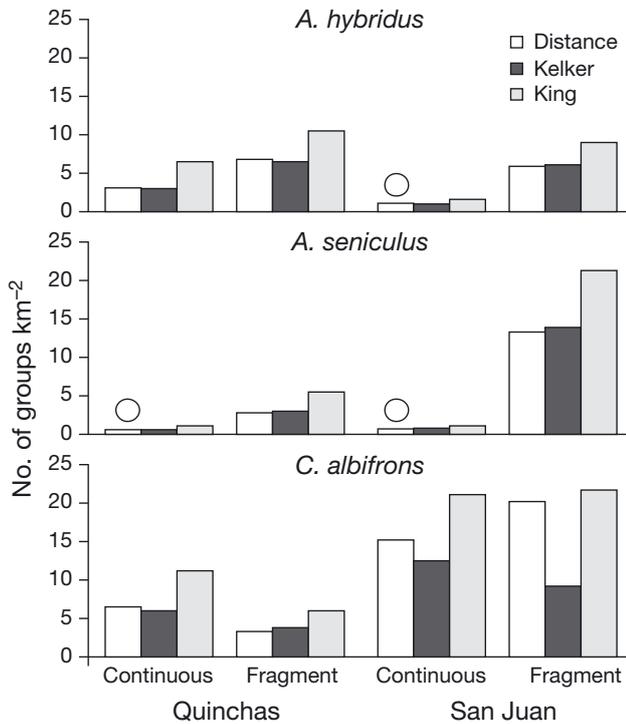


Fig. 2. *Ateles hybridus*, *Alouatta seniculus*, and *Cebus albifrons*. Group densities estimated with 3 different methods for diurnal primates in 4 different forests. Circles represent data obtained with the Distance method using small sample size

different from one another (Wilcoxon signed ranks test: Distance–King $Z = -3.06$, $n = 12$, $p = 0.002$; Kelker–King $Z = -3.06$, $n = 12$, $p = 0.002$; Kelker–Distance $Z = -0.39$, $n = 12$, $p = 0.695$).

DISCUSSION

Our results suggest that primate species differ in their ability to respond to recent fragmentation and habitat disturbance, as has been suggested in previous studies (Cowlshaw & Dunbar 2000 and references therein). As described above, spider monkeys and howler monkeys had higher densities in recent forest fragments compared to continuous forests, while capuchin monkeys showed no marked differences in their population densities between continuous and fragmented areas. The apparently better ability of capuchin monkeys to cope with fragmentation could be related to 2 main factors. First, capuchins are omnivorous primates that rely on a wide variety of food items in their diets, including fruits, seeds, and invertebrate and vertebrate prey (Siemers 2000); thus they can exploit a wider variety of habitats and still find enough food to supply their energetic requirements. Second, capuchins are frequently observed on the ground and have fewer limitations than most other

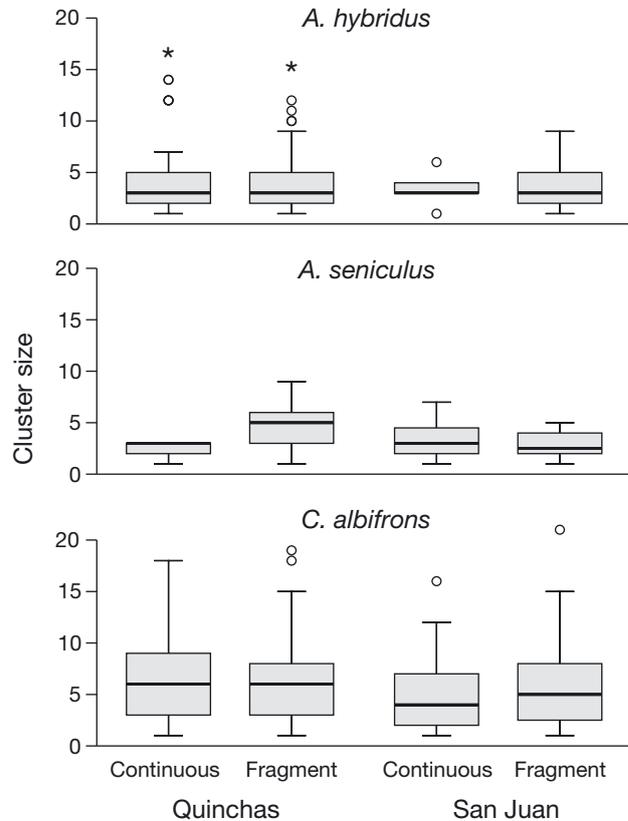


Fig. 3. *Ateles hybridus*, *Alouatta seniculus*, and *Cebus albifrons*. Cluster sizes (no. of individuals) for brown spider monkeys, red howler monkeys, and white-fronted capuchins in the 4 forests. The box plots show the median and 25th and 75th percentiles; whiskers represent all data except extreme values, circles show outliers (1.5 to 3 times the interquartile ranges), and asterisks are data 3 or more times the interquartile range

neotropical primates in their ability to move between nearby forest fragments over small savanna, swamps, or bushy areas or even man-made pastures (Brown & Zunino 1990, Siemers 2000). In fact, capuchin monkeys were found to occupy the largest proportion of forest fragments of different size (range 0.47 to 13 551 ha) from a large set of carnivores and primates in southern Amazonia. Out of 129 forests surveyed, capuchins were only absent in 3 small fragments, but were present in most other fragments, even those as small as <1 ha (Michalski & Peres 2005). These results suggest that capuchins have the ability to cope with fragmentation by using disturbed areas to move among patches of more intact forest and might also be able to exploit food resources in these altered habitats. These facts are consistent with our results showing similar population densities in both continuous forests and forest fragments, suggesting a more homogeneous distribution of the capuchin population in habitats comprised of a mosaic of small forest fragments and larger forests.

Brown spider monkeys and red howler monkeys seemed to be more severely affected by habitat loss and fragmentation. For both taxa, we found higher population densities in the recently fragmented forests, suggesting that the population has been exposed to a reduction of habitat and highlighting the limited dispersal opportunities available for individuals of these taxa. In fact, differences in densities between fragments and continuous forest were more pronounced at San Juan, where the forest fragment has been isolated from all other forests nearby for ca. 3 yr, compared to the Quinchas Fragment that was isolated for several years beginning approximately 10 yr ago and was then re-connected during the study period to an adjacent fragment. Nevertheless, it remains unclear to what extent this isolation affects each species. Long-term surveys are currently underway in order to understand the long-term effects of fragmentation on these primate populations. Thus, continuous monitoring of primate population dynamics after fragmentation is needed to understand why some species such as spider monkeys *Ateles* spp. are absent from most small forest fragments (e.g. Estrada & Coates-Estrada 1996, Cowlshaw & Dunbar 2000, Michalski & Peres 2005)

Folivorous primates are expected to respond better to habitat disturbances than are frugivorous primates, especially to habitat loss or fragmentation (Cowlshaw & Dunbar 2000). Folivorous primates such as howler monkeys have been proposed to 'minimize energy expenditure' (Strier 1992), and have extended periods of rest during which fermentation takes place. Several studies have focused on howler monkeys living in, and able to survive in, small fragments (Estrada & Coates-Estrada 1996). That they can do so is probably due to the fact that leaves (their most important food item) are more readily available and evenly distributed in space and time in tropical forests (Chapman 1988). On the other hand, large-bodied frugivorous primates, such as spider monkeys, have evolved behavioral patterns associated with 'maximizing energy intake' (Strier 1992). Spider monkeys move fast and efficiently over long distances in the forest canopy in order to find spatially clumped but sparse resources. Furthermore, spider monkeys have a specialized digestive system with fast retention times that allows them to process large quantities of fruits in short periods of time (Link & Di Fiore 2006). As ripe fruit specialists and canopy dwellers, spider monkeys have been identified as species strongly affected by habitat fragmentation (Estrada & Coates-Estrada 1996, Cowlshaw & Dunbar 2000).

Our results showing higher densities of *Ateles* spp. and *Alouatta* spp. in fragmented areas seem contradictory at first, as most studies have documented that primate abundance correlates positively with patch

size (Medley 1993, Estrada & Coates-Estrada 1996, Wieczkowski 2004). On the other hand, Lovejoy et al. (1986) proposed that secondary vegetation at forest fragment edges might increase resources available to folivores. Nonetheless, we caution that our results reflect the initial response of primate population density when exposed to fragmentation (same number of primates restricted to smaller areas), and before other direct threats might come into play (e.g. hunting, diseases). This is especially true for spider monkeys that have been found to be among the first species to disappear as fragmentation and habitat disturbance increase (Estrada & Coates-Estrada 1996, Peres & Lake 2003).

The results described in this study showing higher densities of primates soon after fragmentation takes place, coupled with the general pattern of local extinction of spider monkeys in small fragments (Michalski & Peres 2005), sets an initial framework to begin research on the proximate factors that potentially drive the local extinction of vulnerable taxa in fragmented landscapes (Fig. 4). The most relevant potential and non-exclusive factors proposed to influence local extinction of spider monkeys from small fragments are (1) hunting, as fragmentation increases the potential area accessed by hunters (Peres & Lake 2003), (2) a decrease in food availability leading to resource scarcity and intra- and interspecific competition, (3) higher exposure to diseases (Chapman et al. 2006, Goldberg et al. 2008), and (4) genetic inbreeding and loss of population viability.

Most studies involving line transect methods have had to face limitations on the applicability of their results, given their variable accuracy in describing the true densities of wild populations (Marshall et al. 2008). It is difficult to rely on these methods, as most studies have different results supporting different methods as the most accurate. Nevertheless, to date they have been widely used and probably still are con-

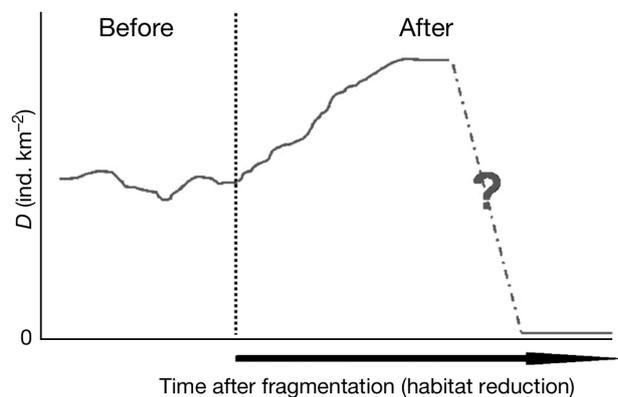


Fig. 4. *Ateles* spp. Effects of fragmentation on the population density (D) of spider monkeys. Factors leading to population declines are still largely unknown

sidered to be the most practical methods to estimate population densities in large areas (Peres 1999). Thus, in our study we have restrained from estimating population numbers in the different areas (even though such information is relevant to the development of conservation action plans), since the differences in density estimates produced by different methods were significant. When comparing the direct count of primates at San Juan fragment with the different population density estimate methods, we found that the King method yielded a somewhat more accurate estimate of the true number of spider monkeys resident in the fragment.

Despite the small sample size, the fact that the pattern of our results is consistent amongst sites in showing larger densities of *Ateles hybridus* and *Alouatta seniculus*, but not of *Cebus albifrons*, in recently fragmented areas allows an initial hypothesis about the effects of fragmentation on these species which will be tested as more data become available.

CONCLUSIONS

This study builds on our current understanding of how primates, in particular Critically Endangered brown spider monkeys, are affected by ongoing habitat loss and fragmentation. This information is of special interest when considering that one of the main causes of this species' disappearance is habitat loss (Urbani et al. 2008). Our results show that the first effect observed on the population densities of primates that are unable to easily move between fragments (e.g. *Ateles hybridus* and *Alouatta seniculus*) and are subject to little hunting pressure, is an increase in population density. Even though the process of logging or habitat destruction might not directly 'kill' the primates present in the area, such activities force them to progressively move to areas with remaining forest cover, thus maintaining the population numbers and territorial behavior in a decreasing forested area. Long-term effects of fragmentation still need to be addressed by long-term studies. Our results will provide the basis for more focused future research on the long-term effects of fragmentation on primate populations as well as on the flexibility of spider, howler, and capuchin monkeys to cope with habitat disturbance. These data will prove useful in the implementation of successful conservation strategies for brown spider monkeys in the fragmented landscapes where they are currently living.

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