

CHAPTER TWO

Nested Distribution Patterns and the Historical Biogeography of the Primates of Guyana

S. M. Lehman

ABSTRACT

I investigated if primate species assemblages exhibit nestedness in Guyana. In a nested pattern, individual species have a strong tendency to be present in all assemblages of equal or greater size than the smallest one in which they occur. I conducted 1,725 km of surveys to determine primate species composition and distribution patterns at sixteen survey sites in Guyana. The resulting dataset showed a strong pattern of nestedness in the distribution of Guyanese primates, and differed significantly from random species assemblages generated using Monte Carlo simulations. Species similarities between sites was significantly but weakly negatively correlated with distance between sites. These assemblage patterns may be due to interspecific variations in the ability of some primate species to cross rivers as well as to species extirpations in western Guyana. The absence of wedge-capped capuchins at four sites, which the model predicted should be occupied by this species, may be due to interspecific competition with brown capuchins.

S. M. Lehman • Department of Anthropology, University of Toronto, Toronto, Ontario, Canada M5S 3G3

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INTRODUCTION

Numerous studies have revealed that variations in species assemblages can reflect nested distribution patterns at the landscape level (Cook and Quin, 1995, 1998; Boecklen, 1997; Ganzhorn, 1998; Hansson, 1998; Wright *et al.*, 1998; Yiming *et al.*, 1998; Bruun and Moen, 2003; Heino and Soininen, 2005; Sada *et al.*, 2005). In a nested pattern, individual species have a strong tendency to be present in all assemblages of equal or greater size than the smallest one in which they occur (Atmar and Patterson, 1993). Nestedness results from selective extirpations such that species will disappear from different habitats in roughly the same order (Patterson, 1991). Conversely, Cook and Quin (1995) suggested that nested patterns represent differential colonization abilities of species. For example, Ganzhorn (1998) documented that species-poor lemur communities represent nested subsets of species-rich communities in both eastern humid and western dry forests in Madagascar. However, there was a distance effect of species similarity only for lemur communities in western Madagascar. Ganzhorn (1998) suggested that this pattern of differential colonization reflected selective species extinctions from a common species pool in eastern Madagascar. In western dry forests, lemurs dispersed north and south from the SW part of the island. Subsequent genetic and biogeographic analyses of mouse lemurs supports a north-south pattern of speciation and dispersal in western dry forests (Yoder *et al.*, 2000). Thus, nestedness models can provide important information on both ecological and historical biogeographic processes. However, no studies have investigated nestedness as a model for primate assemblages in South America.

Although nestedness has been detected in numerous species assemblages (e.g., Fernandez-Juricic, 2000; Puyravaud *et al.*, 2003; Greve *et al.*, 2005), there tends to be some species that are either present at sites not predicted by the model or absent at sites where they are predicted to exist (Cook and Quin, 1998; Wright *et al.*, 1998; Puyravaud *et al.*, 2003). Four ecological mechanisms are responsible for these species-specific departures from the model predictions (Atmar and Patterson, 1993). First, postisolation immigration of new species into the site may generate idiosyncratic distributions. Second, these distributions may also be the result of competitive exclusion. For example, generalist primates may be excluded from larger sites dominated by competitively superior

Table 1. Primate species found in Guyana

Species	Common name	Local name(s)
<i>Alouatta seniculus</i>	Red howler monkey	Baboon
<i>Ateles paniscus</i>	Guianan red-faced spider monkey	Kwatta
<i>Cebus albifrons</i> ^a	White-fronted capuchins	Unknown
<i>Cebus apella</i>	Brown capuchin	Blackjack, corn monkey
<i>Cebus olivaceus</i>	Wedge-capped capuchin	Ring tail
<i>Chiropotes satanas</i>	Brown bearded saki	Besa
<i>Pithecia pithecia</i>	White faced saki	Moon monkey, hurawea
<i>Saguinus midas</i>	Golden handed tamarin	Marmoset
<i>Saimiri sciureus</i>	Common squirrel monkey	Monkey-monkey, squirrel

^a Not used in further analyses due to lack of data on distribution or density.

specialists (Thiollay, 1994; Ganzhorn, 1997). These generalist species may then be relegated to small peripheral sites. Third, the distributions may result from the presence of a fundamental disjunction in the historical evolution of community structure. Last, the presence of unique ecogeographic features, such as rivers, in the region of some sites may influence species closely associated with such features.

The primates of Guyana represent a unique opportunity to test the nestedness model. Of the nine primate species in Guyana (Table 1), only three—red howler monkeys, wedge-capped capuchins, and white faced sakis—are found throughout the country (Muckenhirn *et al.*, 1975; Sussman and Phillips-Conroy, 1995; Norconk *et al.*, 1997; Lehman, 2004b). The other six species are found in only some parts of Guyana. This biogeographic pattern is remarkable given that some primate species, such as brown capuchins (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*), with limited distributions in Guyana are amongst the widest ranging of all platyrrhines (Thorington, 1985; Eisenberg, 1989; Brown and Zunino, 1990; Wallane *et al.*, 1996).

In this paper I investigate if primate species assemblages reflect nestedness in Guyana. Specifically, I address the following questions: (1) if patterns of nestedness do occur, are they the result of primate extirpations or colonization and (2) how do the observed distribution patterns of Guyanese primates relate to historical biogeographical processes?

METHODS

Guyana is a small country of 215,500 km² situated on the northeastern coast of South America, between 56° 20' and 61° 23' west and 1° 10' and 8° 35'

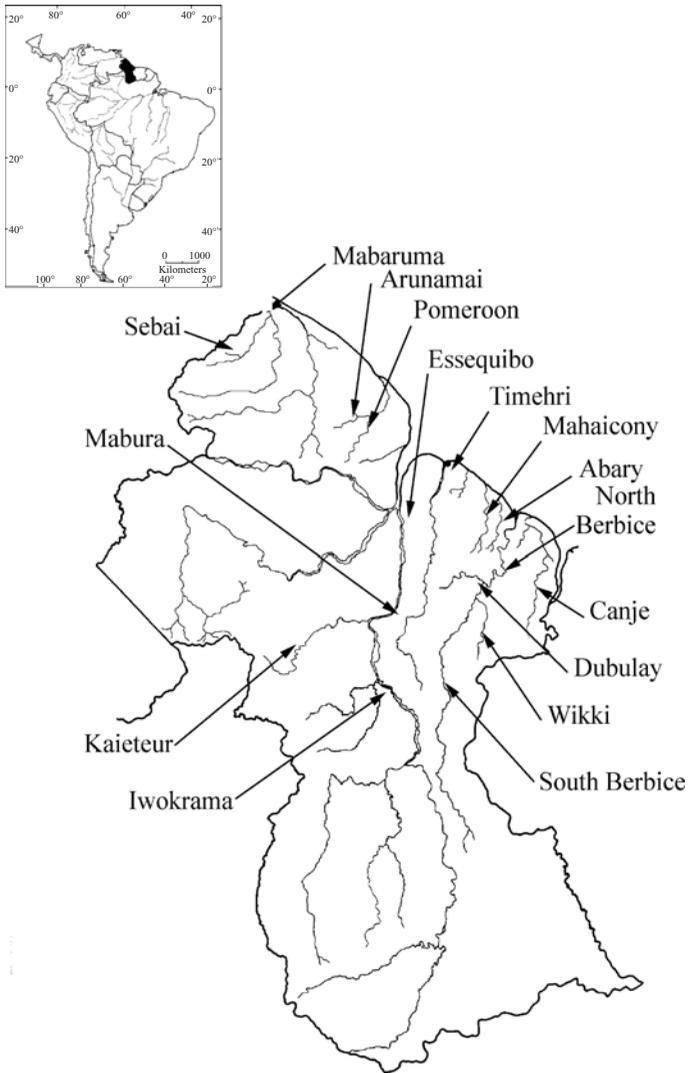


Figure 1. Location of study sites used in the analyses of nested subsets for primates in Guyana.

north (Figure 1). The climate is tropical with a high mean daily temperature of 25.7 °C (ter Steege, 1993). Temperature is highest in September and October and is lowest in December and January. Mean annual precipitation is between 2,000 and 3,400 mm, and is neither evenly distributed throughout the year or throughout the country (ter Steege, 1993). There are generally two wet seasons and two dry seasons. Much of the annual rainfall comes during the

summer rainy season, from May to mid-August. There is a shorter rainy season from November to January. The long dry season begins in mid-August and runs through to November or December. This season is characterized by monthly rainfall of less than 200 mm. The short dry season is usually from February to April.

I surveyed the distribution and diversity of primates in forests and along rivers at sixteen sites in Guyana (Figure 1). Complete description of each site can be found in Lehman (1999, 2000, 2004b). Survey data were collected during three periods: (1) November 1994 to June 1995, (2) September 1995 to June 1996, and (3) June to August 1997. These periods cover all four seasons in Guyana. Surveys were conducted throughout the day from 0500 to 1900 hours.

While surveying forests, I used randomly selected and predetermined transect lines. Although most studies on the distribution of animals use only random selection of transects (e.g., Anderson *et al.*, 1979; Krebs, 1989; Buckland *et al.*, 1993), I also used predetermined transect lines to ensure that biogeographic features, such as rivers that may be barriers to dispersal, were included in the data set (Peres, 1999). Predetermined transect lines often ran along paths in the forest to maximize survey time in remote areas. Transects were measured and marked every 10 m with numbered blocks or flagging tape before surveys were conducted. Two types of surveys were conducted: (1) unique and (2) repeat. Unique surveys were made along transects, such as trails or riverbanks, where one to two transits were made during a census. During repeat surveys, I conducted more than two transits of a transect line. Repeat surveys were conducted along paths at five locations: (1) Timehri; (2) Dubulay Ranch; (3) Kaieteur Falls National Park; (4) Mabura Hill Ecological Reserve; and (5) Sebai River. I walked slowly along transects at a rate of 1.0 km/h, stopping every 10 min to listen for the sounds of movement in the forest. I also surveyed riparian forests by paddling slowly (1.5–2.0 km/h) along riverbanks, either alone or with the assistance of local guides. Randomly selected areas were chosen on river banks for land surveys. However, it is illegal to cut trails in protected areas (e.g., Kaieteur Falls National Park, Mabura Hill Forest Reserve, and Iwokrama Forest Reserve). Thus, established trails were used in these protected areas.

During surveys, data were recorded on: (1) primate species; (2) time of day; (3) weather; (4) vegetation height; (5) general height of group; (6) number of animals in group; (7) cue by which animals detected; (8) activity; (9) perpendicular distance from the transect [meters]; (10) sighting angle; and (11) habitat

type. When a primate group was seen, a standardized time of 10 min was spent observing the behavior of individuals in the group. *Ad libitum* notes on behavior, obvious individual physical characteristics, and vocalizations were also collected. The location of primate groups seen during surveys was determined using LANDSAT-5 satellite photographs, 1:50,000 topographic maps of the region, and a Magellan NAV 5000D GPS. Habitat descriptions were made using soil features, a vegetation map (Huber *et al.*, 1995), various monographs on Guyanese flora (van Roosmalen, 1985; de Granville, 1988; Mennega *et al.*, 1988; Lindeman and Mori, 1989; ter Steege, 1990; Comiskey *et al.*, 1993; ter Steege, 1993), and LANDSAT-5 satellite imagery of survey areas.

I created a presence–absence dataset of primate species composition in Guyana. Because there are few data on the biogeography of white-fronted capuchins in Guyana (Barnett *et al.*, 2000), they were not used in further analyses. Following Atmar and Patterson (1993), if two sites contained similar species composition, the one site was removed from the dataset to avoid unnecessary duplication of biogeographic data (i.e., South Berbice, Wikki). Thus, presence–absence data were taken from 14 sites in eastern ($N = 8$) and western ($N = 6$) Guyana. NESTCALC software was used to sort the dataset from high to low for site diversity (top to bottom) and species diversity (left to right). NESTCALC also calculates a statistical test value T of the order (nestedness) or disorder (lack of nestedness) in the dataset (Atmar and Patterson, 1993). The test value T ranges from 0 (complete order) to 100 (complete disorder). In an ordered dataset, every site contains a proper subset of the species at all of the sites above it. As T increases, complete disorder approaches and the biogeography of the sites or species in question become unpredictable. The observed T value was then compared to a distribution of values generated by Monte Carlo simulations (Atmar and Patterson, 1993). Every program was run 1000 times to generate 1000 random primate faunas.

A geometric extinction line, which represents the line of smoothest transition (Figure 2), was calculated for the dataset. This line separates the occupied area of the dataset from the unoccupied area. Species absence above the line is defined as unexpected, as is a species presence below the line (Atmar and Patterson, 1993).

NESTCALC was then used to calculate idiosyncratic T values by site and by species (Atmar and Patterson, 1993). Unexplained species presence or absence lead to specifically higher T values than the complete dataset. Such elevated T values may indicate that the species in question was influenced by a

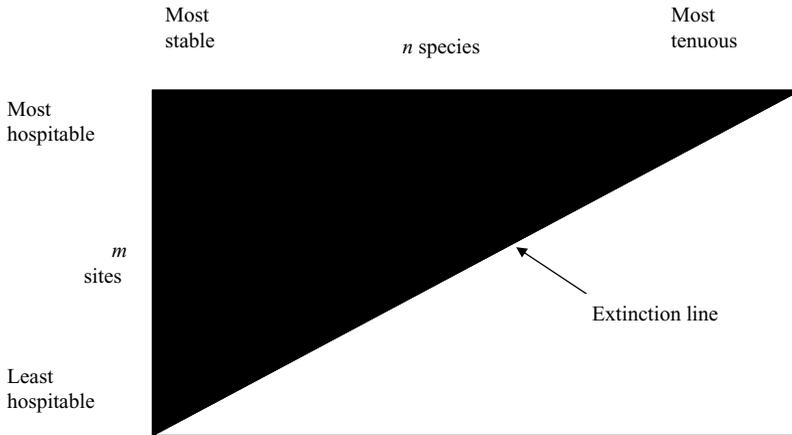


Figure 2. Example of a perfectly nested (ordered) dataset.

biogeographic event different from that affecting the other species. Following Ganzhorn (1998), pairwise similarities of species composition between sites were described using Jaccard's index (J). This index is given by

$$J = \frac{t}{a + b - t}$$

where t is the number of species occurring in both sites, a is the number of species at site A and b is the number of species at site B.

Spearman rank correlations (r_s) were used to determine the relationship between species similarities and intersite distance. Statistical analyses were conducted using SPSS 11.5 and the alpha level was set at 0.05 for all analyses.

RESULTS

Figure 3 shows the dataset and idiosyncratic temperatures for eight primate species at 14 sites in Guyana. The dataset has a T value of 14.04, indicating a pattern of nestedness in the distribution of Guyanese primates. The observed dataset differs significantly from random species assemblages generated using Monte Carlo simulations (mean T of 1000 simulations = 44.61 ± 8.51 , $p = 0.0001$). One primate species (*C. olivaceus*) and four sites (Canje, Dubulay, Timehri, and Abary) exhibited T values that departed from the total metric for the dataset.

Communities of primates at all sites in Guyana exhibited similarities between 0 and 100% (mean and SD of Jaccard's index: 0.48 ± 0.22 ; $N = 98$). Figure 4

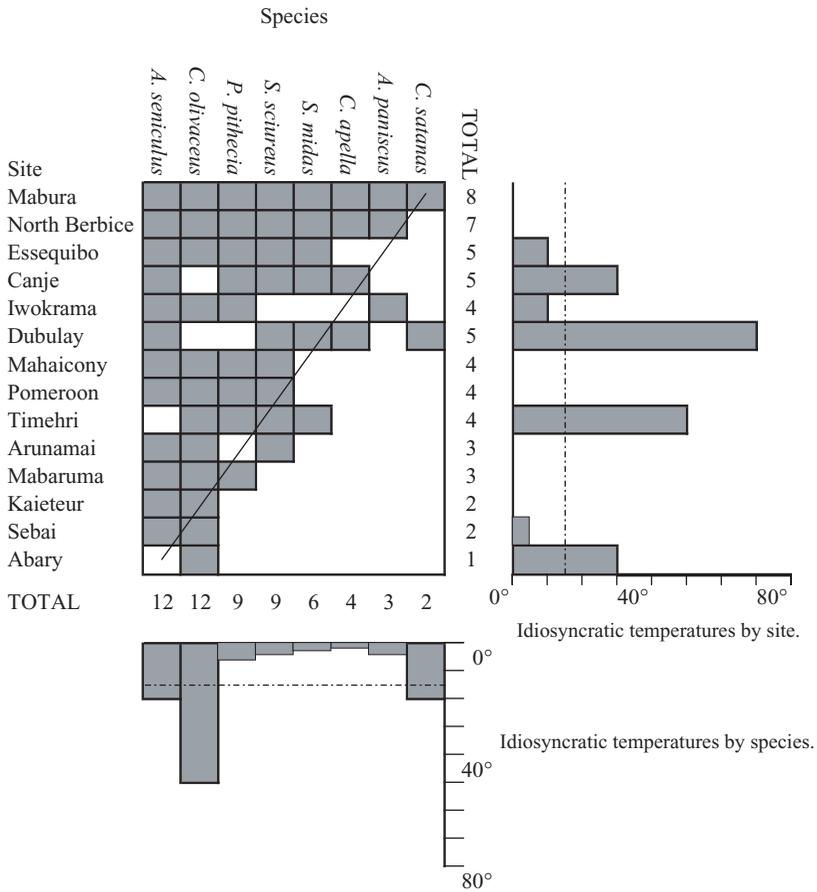


Figure 3. Nested patterns and idiosyncratic temperatures for eight primate species at fourteen sites in Guyana.

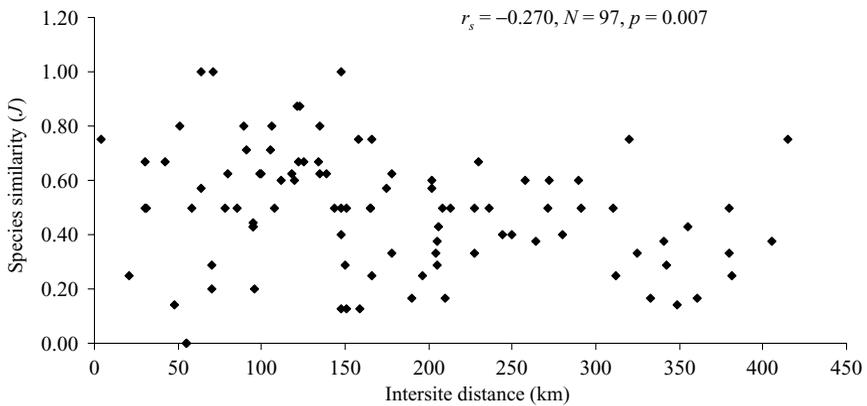


Figure 4. Correlation between Jaccard's index for similarity of species composition and intersite distance for sixteen sites in Guyana.

shows the relationship between community structure and distance between sites in Guyana. Species similarities was negatively correlated with distance between sites in Guyana ($r_s = -0.270$, $N = 97$, $p = 0.007$).

DISCUSSION

The primates of Guyana exhibit a strong pattern of nestedness, which may be the result of habitat characteristics. Specifically, eastern and western Guyana contained all species of the common species pool (i.e., eight species) but sites in western Guyana began losing species. Climatic fluctuations may also relate to species extirpations in western Guyana. Reduced rainfall and lower world temperatures occurred during the last glacial period (Colinvaux, 1987; Colinvaux *et al.*, 1996). Palynological studies by van der Hammen and colleagues (van der Hammen, 1963; Wijmstra and van der Hammen, 1966; van der Hammon and Absy, 1994) found that coastal areas of northern Guyana and Suriname were covered with dry grass savanna during the Pleniglacial period (ca. 21,000–14,000 year B.P.). Models of rainfall and forest area during this period indicate that large tracts of rain forest existed only in extreme NW Guyana and the middle section of eastern Guyana (Figure 5). Despite the presence of a forest refuge in NW Guyana, it is unlikely that most primates could have existed in the area. This refuge may have been flooded swamp forest and swamp woodlands, as it is today. Few primates in NE South America exist in these habitats (Mittermeier and van Roosmalen, 1981; Eisenberg, 1989; Lindeman and Mori, 1989). Thus, the forest refuge in eastern Guyana may be the site in which primates survived climatic fluctuations during the Pleniglacial period.

The statistically significant but weak distance effect on species similarities indicates that there may have been colonization of some sites in Guyana from a species pool (i.e., forest refuge) in the eastern portion of the country. Primates may have dispersed into Guyana from areas outside the country, such as northern Brazil (Lehman, 1999). Despite the possibility for recolonization of sites in western Guyana from the refuge in eastern Guyana and from northern Brazil, rivers may have limited the colonization abilities of many primate species. Rivers have an important role in delimiting the distribution of primates in Guyana (Lehman, 2004b). Primates dispersing out of eastern Guyana would have been faced with a series of large rivers (e.g., Essequibo, Rupununi,



Figure 5. Location of heaviest rainfall and approximate rain forest in Guyana during Pleistocene period (based on van der Hammen and Absy, 1994).

and Mazaruni) that must be crossed to recolonize western Guyana. The body weight and foraging behavior of a primate are important factors influencing its ability to cross a river. Ayres (1986) found a positive correlation between the size of a river and the maximum body weight of the largest primate whose

distribution was limited by a river. Thus, large rivers can limit the distribution of all primates, but small rivers may not limit the distribution of large-bodied primates. Once a river has been crossed successfully, a primate must also be able to cope with a variety of vegetation types within the new region. Although forest habitats in eastern Guyana tend to be similar across major rivers, there is considerable habitat variation between river banks in western Guyana (ter Steege, 1993; Funk, 1995; Huber *et al.*, 1995; Ek, 1997; Barnett *et al.*, 2000). These habitat variations are due to elevational changes that occur from SW Guyana up through the Pakaraima Mountains and then down into the alluvial floodplains of NW Guyana. Generalized foragers should be most likely to survive river crossings into western Guyana because they are not limited in their dietary requirements (Ayres and Clutton-Brock, 1992; Goodman and Ganzhorn, 2003; Lehman, 2004b). Therefore, primate species with most generalized diets are found throughout much of the country (e.g., *A. seniculus* and *S. sciureus*) whereas primates with more specialized dietary and habitat requirements have a smaller geographic distribution limited to eastern Guyana (e.g., *S. midas* and *C. satanas*).

Other biogeographic factors relate to differences in primate assemblages between western and eastern Guyana. Reduced rainfall during the Pleniglacial period may have enlarged savannas in present-day western Guyana (Rupununi and Pakaraima savannas). Eastern Guyana contains fewer and smaller savanna regions. Furthermore, western Guyana is considerably more mountainous than eastern Guyana. High montane habitats (500–800 m elevation) and shrubland/scrub habitats (1000–2400 m elevation) in this region support few primates (Lehman, 1999). These habitats may have expanded downslope as the climate dried during the Late Pleistocene, further reducing forest areas in western Guyana. The stochastic fluctuation of rain forest and monkey populations in western Guyana may have resulted in local extirpations and brought about the present pattern of discontinuous primate distribution in this country. This scenario is supported by the fact that in western Guyana, species diversity decreases northward, with only three species (red howler monkeys, wedge-capped capuchins, and white faced sakis) surviving in the extreme northwest region of the country (Lehman, 1999). Therefore, climatic variation during the Pleistocene may have reduced forest habitats in Guyana and ultimately reduced the number of primate species found in the western half of the country. Climatic change during the Pleniglacial period described herein has been cited as a significant force in the biogeography of primate taxa in South America,

Africa, Asia, and Madagascar (Froehlich *et al.*, 1991; Brandon-Jones, 1996; Ganzhorn, 1998; Jablonski, 1998). For example, Brandon-Jones (1996) analyzed the biogeography of Asian colobines and concluded that Quaternary climatic change played an essential role in delimitating primate populations in this region.

Despite the strong nestedness for primate assemblages in Guyana, there was an unexplained absence for wedge-capped capuchins at four sites (Dubulay Ranch, Canje River, Timehri, and Abary River). It is doubtful that the absence of wedge-capped capuchins from these sites was the result of postisolation immigration or disjunct historical evolution. Forests in some parts of eastern Guyana were not adversely effected by Quaternary climatic changes. In fact, the four survey sites where wedge-capped capuchins were absent are located near to the proposed eastern forest refuge (Figure 5). Thus, it is doubtful that wedge-capped capuchins would be absent from regions that experienced the least forest disturbance since the Quaternary. Unique ecogeographic features, such as rivers, are also unlikely to have caused the observed idiosyncratic temperatures. Wedge-capped capuchins are found in forests bordering rivers, such as the Essequibo River, that are much larger than the Berbice River, where it is absent. Moreover, survey results are unlikely to be related to sampling error (i.e., animals present but not seen). I conducted repeat surveys at two of the sites (Timehri and Dubulay Ranch). Furthermore, other researchers have noted the absence of wedge-capped capuchins at these sites (Sussman and Phillips-Conroy, 1995). Instead, the unexpected absence of wedge-capped capuchins from sites in eastern Guyana may be due to competitive exclusion. My data on the community ecology of the primates of Guyana indicate that a negative pattern of interspecific association exists between wedge-capped capuchins and brown capuchins (Lehman, 2000). Furthermore, sighting rates for both species were reduced in areas of sympatry compared to allopatric areas Lehman *et al.* (this volume). Therefore, the absence of wedge-capped capuchins may be the result of interspecific competition with brown capuchins.

If wedge-capped capuchins and brown capuchins are competing at sympatric sites, then the question arises as to which competitive process, contest or scramble, is involved (Terborgh, 1986; Janson, 1987; van Schaik and van Noordwijk, 1988). Contest competition typically involves agonistic interactions over access to scarce food resources (Koenig *et al.*, 1998; Ganzhorn, 1999; Iwanaga and Ferrari, 2002). This form of competition has been observed rarely between wedge-capped capuchins and brown capuchins in French Guyana, Surinam,

and Guyana (Muckenhirn *et al.*, 1975; Mittermeier, 1977; Sussman and Phillips-Conroy, 1995; Simmon and Sabatier, 1996; Lehman, 1999). Between group scramble competition results in resource depression or depletion (Janson and van Schaik, 1988). Scramble competition may have a negative impact on primate densities because of low food availability. This impact may be particularly pronounced in the Guianas because the forests are located on nutrient poor soils (ter Steege, 1993). As a result, the forests are characterized by low plant species diversity as well as low fruit and leaf production compared to other sites in South America (ter Steege, 1993; Chale, 1996; Terborgh and Andresen, 1998; Tori-ola *et al.*, 1998). A recent study of primate species richness in South America by Kay *et al.* (1997) found that plant productivity was the ecological variable most strongly correlated with primate species richness. Thus, low plant productivity in Guyanese forests may reduce the diversity of feeding niches and result in scramble competition between wedge-capped and brown capuchins. Further studies of the diet and habitat use of these capuchins are needed to test this hypothesis.

SUMMARY

The primates of Guyana exhibit a strong pattern of nestedness. Specifically, individual species are present in all assemblages of equal or greater size than the smallest one in which they occur. This nestedness may be the result of species extirpations in western Guyana during the last Pleniglacial period (ca. 21,000–14,000 year B.P.). Colonization may have occurred for primates dispersing from eastern to western Guyana. However, large rivers and montane habitats would have limited primate dispersal to generalized foragers (e.g., *A. seniculus* and *S. sciureus*) in western Guyana. The unexpected absence of wedge-capped capuchins from sites in eastern Guyana may be due to competitive exclusion by brown capuchins.

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