



Distribution and Diversity of Primates in Guyana: Species-Area Relationships and Riverine Barriers

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Species-area relationships predict that there is a positive relationship between the number of species and the size of an area. It has been suggested that species richness will covary with area because larger areas have a greater diversity of habitats. Moreover, habitat diversity may operate in conjunction with riverine barriers to influence primate biogeography. Few studies have determined if and how these hypotheses relate to primate diversity in Guyana. To test these biogeographic hypotheses, I used data from 1,725 km of primate surveys I conducted in Guyana. I estimated geographic ranges for each of the 8 primate species via a GIS system. Geographic range size is a major determinant of the number of sightings of the 8 primate species. Primate species diversity is strongly negatively correlated with the number of rivers crossed moving in a clockwise pattern from eastern to NW Guyana. Interfluvial and habitat areas influence primate species diversity in Guyana. However, my data on primate biogeography in Guyana do not support the hypothesis that habitat diversity within the interfluvial areas effects primate diversity. Although the species-area relationship is considered the closest thing to a rule in ecology, researchers should be wary of too readily applying and accepting the model at all scales in biogeographic studies.

KEY WORDS: Biogeography; abundance; surveys; GIS; rivers; habitat use; diet; niche.

INTRODUCTION

The effect of area on species richness is an integral part of studies of species diversity (Rosenzweig, 1995). Species-area relationships predict that

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there is a positive relationship between the number of species and the size of an area (MacArthur and Wilson, 1967; Preston, 1962; Williams, 1964). This relationship is expressed as the equation $S = CA^z$, where S is species richness, C is a fitted constant that varies among taxa and types of ecosystems, and z is a constant that tends to range from 0.1 to 0.5. Species-area relationships have been documented in birds, reptiles, amphibians, and mammals (Bates *et al.*, 1998; Hill *et al.*, 1994; Plotkin *et al.*, 2000; Rafe *et al.*, 1985; Ron, 2000; Thiollay, 1994; Yiming *et al.*, 1998). For example, in a biogeographic study of primate diversity, Reed and Fleagle (1995) documented a high correlation ($R^2 = 0.87$) between the number of primate species and the area of rain forest for major continents (South America, Africa, and SE Asia) and large islands (Madagascar, Borneo, Sumatra, and Java). In another example, Peres and Janson (1999) found a significant positive relationship between local density and geographic range size for ecospecies of platyrrhine primates.

There are several ecological factors used to explain species-area relationships; rainfall, habitat diversity, and latitude (Arita *et al.*, 1990; Bates *et al.*, 1998; Cowlshaw and Hacker, 1997; Eeley and Laws, 1999; Fleagle and Reed, 1996; Kay *et al.*, 1997; Reed and Fleagle, 1995; Stevens, 1989). At the regional level, the habitat diversity hypothesis is one of the most readily accepted theories used to explain species-area relationships (Hill *et al.*, 1994). In this hypothesis, specific richness increases with an increase in area because larger areas have a greater diversity of habitats.

Most studies of species-area relationships in primates were focused on total forest cover within or between continents (Cowlshaw and Hacker, 1997; Eeley and Laws, 1999; Fleagle and Reed, 1996). However, tropical forests are characterized by diversity of habitat types for primates (Cowlshaw and Dunbar, 2000). In Guyana, biogeographers have described and mapped a total of 34 distinct habitat types (Huber *et al.*, 1995). There tends to be a positive relationship between primate species richness and habitat heterogeneity (Ganzhorn, 1994; Skorupa, 1986). This relationship is thought to be driven by the greater number of ecological niches in diverse habitats (Rosenzweig, 1995). Many Neotropical primate species are highly selective in their habitat use. For example, spider monkeys (*Ateles* sp.) and bearded sakis (*Chiropotes* sp.) tend to avoid flooded forests (Johns and Skorupa, 1987; Lehman *et al.*, in press; Peres, 1990; Robinson and Bennett, 2000). Recent studies have shown a link between local and regional patterns of primate diversity in primates (Eeley and Laws, 1999; Laws and Eeley, 2000). Therefore, it is possible that the species-area relationship may function at the habitat level for primates in biogeographic regions characterized by continuous but diverse forests.

Habitat diversity may operate in conjunction with riverine barriers to influence primate biogeography. Many Amazonian primate species are

bounded in at least part of their geographical range by a river (Ayres and Clutton-Brock, 1992; Bennett *et al.*, 2001; Colyn, 1988; Cropp *et al.*, 1999; Da Silva and Oren, 1996; Hershkovitz, 1963, 1968, 1977; Iwanaga and Ferrari, 2002; Peres, 1993; Peres *et al.*, 1996; Wallace *et al.*, 1996). Ayres and Clutton-Brock (1992) conducted a preliminary biogeographic survey of the distribution of Amazonian primates and found that species diversity is strongly effected by rivers acting as barriers to gene flow. There is also a negative correlation between the distance from the headwaters of the Amazon River and the similarity of primate species between its banks. The body mass and foraging behavior of a primate may be 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 mass 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. It has been assumed that differential abilities to cross a river may occur because the larger the primate, the greater its chances of surviving rafting or swimming across a river, though this has not been systematically studied.

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. Generalized foragers should be most likely to survive such crossings because they are not limited in their dietary requirements. Based on this hypothesis, it is not surprising that the South American primates with the most generalized habitat requirements (capuchins, howlers, and squirrel monkeys) have the widest geographical distributions (Peres and Janson, 1999). Although Hershkovitz (1977), Norconk *et al.* (1997), and Cropp *et al.* (1999) have suggested that rivers may have acted as barriers to primate dispersal in Guyana, supporting quantitative data have not been presented.

Interfluvial regions are also characterized by habitat variability. Typically, riparian forests border the banks of large rivers (Ayres and Clutton-Brock, 1992; Salo *et al.*, 1986). The riparian forests are often backed by a variety of woodland habitats (e.g., moist forest, seasonally flooded black water swamp forest, woodlands, or grassland habitats, scrub, wooded grassland, grassland). Primate diversity and abundance can vary considerably between neighboring habitats; such as between non-flooded moist forest and flooded forests (Lehman *et al.*, in press). Thus, it is theoretically possible that habitat heterogeneity may effect primate diversity at two biogeographic levels: regional (across Guyana) and interfluvial (between major rivers in Guyana). However, there are few data on the relationship of primate diversity with habitat heterogeneity in interfluvial areas.

Of the 9 primate species in Guyana (Table I), only 3—red howlers, wedge-capped capuchins, and white faced sakis—are found throughout the

Table I. Primate species in Guyana

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

^aNot used in analyses due to lack of data on distribution or density.

country (Lehman, 1999). The other 6 species live in only some parts of Guyana. There are few variations in primate diversity for conspecifics in Suriname, French Guiana, eastern Venezuela, and northern Brazil. I aimed to determine the ecological correlates to patterns of primate diversity in Guyana. Specifically, I address the following questions about the biogeography of Guyanese primates: (1) do species-area relationships operate at the regional or habitat or both levels, (2) do riparian barriers effect primate diversity, and (3) does habitat diversity in interfluvial areas covary with primate diversity?

METHODS

Location and Climate

The data set is derived from 1,725 km of surveys that I conducted in Guyana, a small country of 215,000 km² situated on the northeastern coast of South America, between 56°20' and 61°23' West and 1°10' and 8°35' North (Fig. 1). The climate is tropical with a high mean daily temperature of 25.7 °C (ter Steege, 1993b). Temperatures are highest in September and October and are lowest in December and January. Mean annual precipitation is between 2,000 and 3,400 mm and is neither evenly distributed throughout the year nor throughout the country (ter Steege, 1993b). There are generally 2 wet seasons and 2 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 extends to November or December. It is characterized by monthly rainfall of <200 mm. The short dry season is usually from February to April.

The 9 primate species in Guyana are arboreal and diurnal. There are unconfirmed reports of night monkeys (*Aotus trivirgatus*) in Guyana (Lehman,

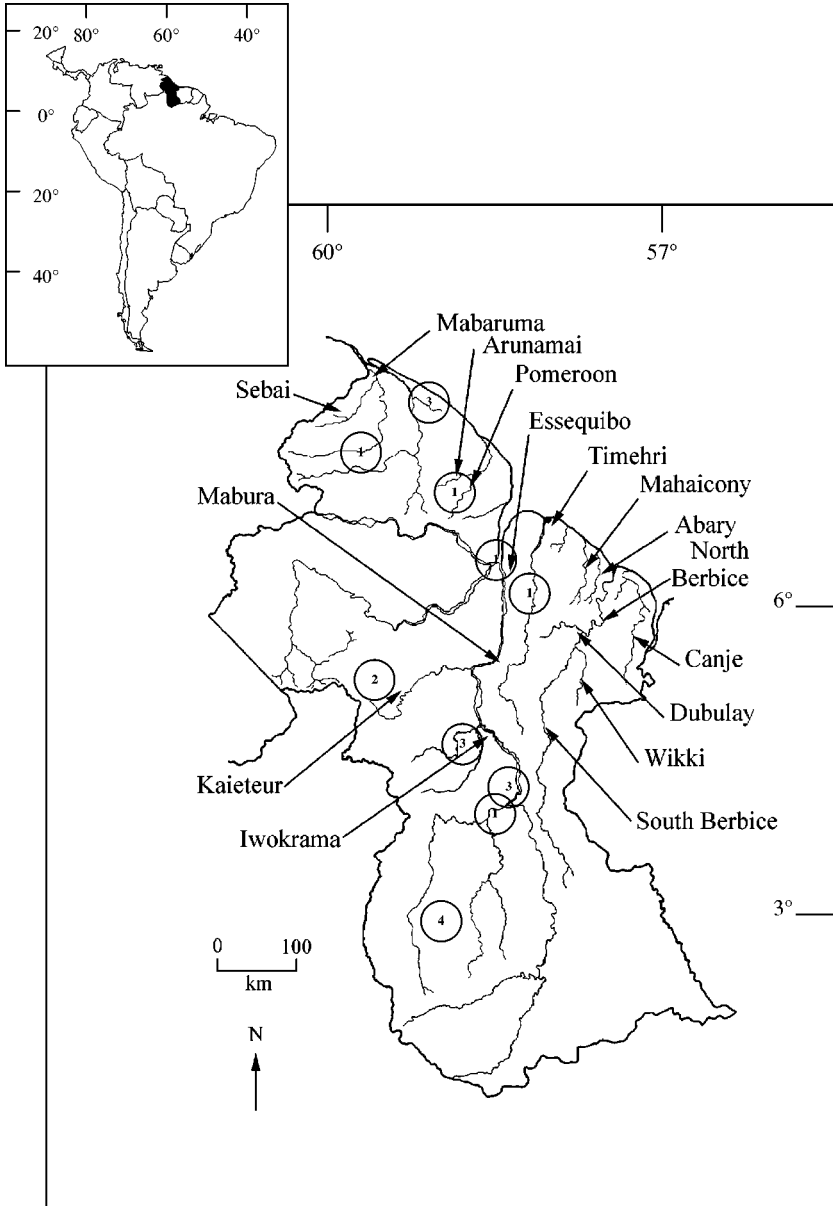


Fig. 1. Locations of Guyana and of 16 survey sites censused. Numbers in circles represent locations of other surveys used to estimate primate distributions (1 = Muckenhirn *et al.* 1975; 2 = Barnett *et al.*, 2000; 3 = Sussman and Phillips-Conroy, 1995; 4 = Parker *et al.*, 1993).

1999; Sussman and Phillips-Conroy, 1995). Because there are few data on the biogeography of white-fronted capuchins in Guyana (Barnett *et al.*, 2000), I excluded them from analyses.

Survey Data

I surveyed the distribution and diversity of primates in forests and along rivers at 16 sites (Fig. 1). Lehman (1999, 2000) provides complete descriptions of each site. Survey data are from 3 periods: (1) November 1994 to June 1995, (2) September 1995 to June 1996, and (3) June to August 1997. These data cover all 4 seasons. I surveyed throughout the day from 0500 to 1900 h.

When surveying forests, I used randomly selected and predetermined transect lines. Although most studies of the distribution of animals use only random selection of transects (Anderson *et al.*, 1979; Buckland *et al.*, 1993; Krebs, 1989), 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. I walked slowly at 1.0 km/h, stopping every 10 min to listen for the sounds of movement in the forest. I measured and marked transects every 10 m with numbered blocks or flagging tape before surveys.

I surveyed rivers by paddling slowly (1.5–2.0 km/h) along riverbanks, either alone or with local guides, during river surveys, I randomly selected areas on each bank for land surveys. I used non-linear transect lines in the forest because travel costs are very high in Guyana. It was cost prohibitive to cut and mark trails when only 2–4 weeks were available for data collection. Furthermore, in protected areas, such as Kaieteur Falls National Park, Mabura Hill Forest Reserve, and Iwokrama Forest Reserve, it is illegal to cut trails. I used established trails in the protected areas.

The location of primate groups was determined by trail markers, LANDSAT-5 satellite photographs, 1:50,000 topographic maps of the region, and/or a Magellan NAV 5000D GPS (Global Positioning System; Magellan, Inc., San Demas, CA). I took GPS readings during all river sightings and verified them on 1:50,000 topographic maps.

Forest Habitats

Unlike many tropical countries, Guyana retains *ca.* 86% of its original rain forest (Huber *et al.*, 1995). High levels of endemism characterize the forests of Guyana, Suriname, and French Guiana. For example, de Granville (1988) conducted a preliminary study of the distribution of

8 groups of vascular plants in the forest regions of the Guianas. Of the 251 plant species surveyed in South America, 35% ($N = 88$) were endemic to the Guianas.

There are 5 main biogeographic regions in Guyana: (1) coastal plain; (2) white sand area; (3) interior rain forest; (4) highlands; and (5) the Rupununi and intermediate savannas (Boggan *et al.*, 1997). The coastal plain is a strip of land ranging from 16 to 60 km in width along the ocean. Most of the plain lies 1.2–1.5 m below sea level at high tide. An extensive series of sea walls, dikes, and drainage canals have been built along the coast to prevent flooding. More than 90% of Guyanese live in the coastal plain, and most of the farming (rice and sugar cane) is done here. There are numerous small patches of seasonally flooded swamp forest in the region. The forest is dominated by corkwood (*Pterocarpus* sp.) and white cedar (*Tabebuia insignis*).

The white sand region extends from the southern limit of the coastal plain 200 km into the interior of the country. Small black water creeks drain the region. The main vegetation in the white sands region is dry evergreen forest, dominated by wallaba (*Eperua* sp.) in excessively drained areas and It palm (*Mauritia flexuosa*) in poorly drained areas (ter Steege, 1993b).

The interior rain forest lies south of the white sands region and it runs diagonally from the NW to the SE. Tropical rain forest covers *ca.* 80% of Guyana (ter Steege, 1993b). It is characterized as tall (20–40 m), evergreen lowland forest dominated by kakaralli (*Eschweilera* sp.), kabukalli (*Goupia glabra*), kautabali (*Licania* sp.), baromalli (*Castostemma* sp.), and greenheart (*Chlorocardium rodiei*).

The highlands are located along the Pakaraima and Merume Mountains in western Guyana, near the border with Venezuela and Brazil (Maguire, 1972; Maguire *et al.*, 1953). Other highland areas, similar in general floristic composition, are found in the Kanuku, Kamoia, and Amuku Mountains in southern Guyana. The flora of the regions is characterized as having extremely high specific diversity and abundance (Henkel, 1994; Hoffman, 1992; Maguire, 1972; Maguire *et al.*, 1953).

The Rupununi savannas are in SW Guyana along the Brazilian border, and the intermediate savannas are located near the lower portions of the Berbice and Canje Rivers. They are dominated by lowland macrothermic shrubs and grasses (Eden, 1964).

Geographic Information System

I analyzed location data on primate sightings, i.e., latitude and longitude coordinates and georeferenced them via ArcView 3.1 (Environmental

Systems Research Institute, Inc., Redlands, CA). Using my survey data and data from other primate surveys in central and SW Guyana (Barnett *et al.*, 2000; Muckenhirn *et al.*, 1975; Parker *et al.*, 1993; Sussman and Phillips-Conroy, 1995), I produced detailed maps of the geographic range of each species. I estimated the geographic range size for each primate species via ArcView (Figure 2). Using published descriptions of habitat and altitudinal preferences for each species (Fleagle and Mittermeier, 1980; Mittermeier, 1977; Rowe, 1996), I excluded habitats deemed unsuitable for Guyanese primates from estimates of range size: savannas and meadows, montane shrublands, high-tepui forests, upper montane forests, lakes, mining areas, and urban centers. I determined primate habitats via a vegetation map of Guyana (Huber *et al.*, 1995). I reclassified each of the 34 forest types on the map into one of 13 mutually exclusive molar habitat categories suitable for use by primates based on data collected during my surveys and published information on primate habitat use in the Guianas (Comiskey *et al.*, 1993; Kinzey *et al.*, 1988; Muckenhirn *et al.*, 1975). I included similar habitats in different geographic areas in range estimates only if there were primate sightings in both habitats and if there was no variation in altitude between the habitats. Production of species-specific range maps necessarily required assuming that primate distributions do not vary between geographically isolated survey sites that contain conspecific primate populations, irrespective of potential barriers to dispersal, e.g., rivers. Moreover, no survey datum is available for SE Guyana (New River Triangle). The Government of Guyana has not allowed research in the area because of a long-standing border dispute with Suriname.

Ecological Variables

I reclassified land area into interfluvial regions using the major rivers in Guyana as boundaries (Figure 3) in order to determine if primate specific diversity is correlated with the subareas between rivers, i.e., interfluvial habitat sizes. I used environmental data—river discharge and catchment area—from the literature (ter Steege, 1993b; UNESCO, 1985) and from international monitoring bodies, such as the Global Runoff Data Centre in Germany, that house and maintain internet accessible databases on global environmental conditions.

I used two characteristics of habitat type during analyses of habitat diversity in each interfluvial area: number of habitat types and total number of habitats. Number of habitat types refers to single counts of each habitat type within an interfluvial area. Total habitat types refers to the running sum of all habitat types within an interfluvial area, i.e., multiple counts of similar habitats.

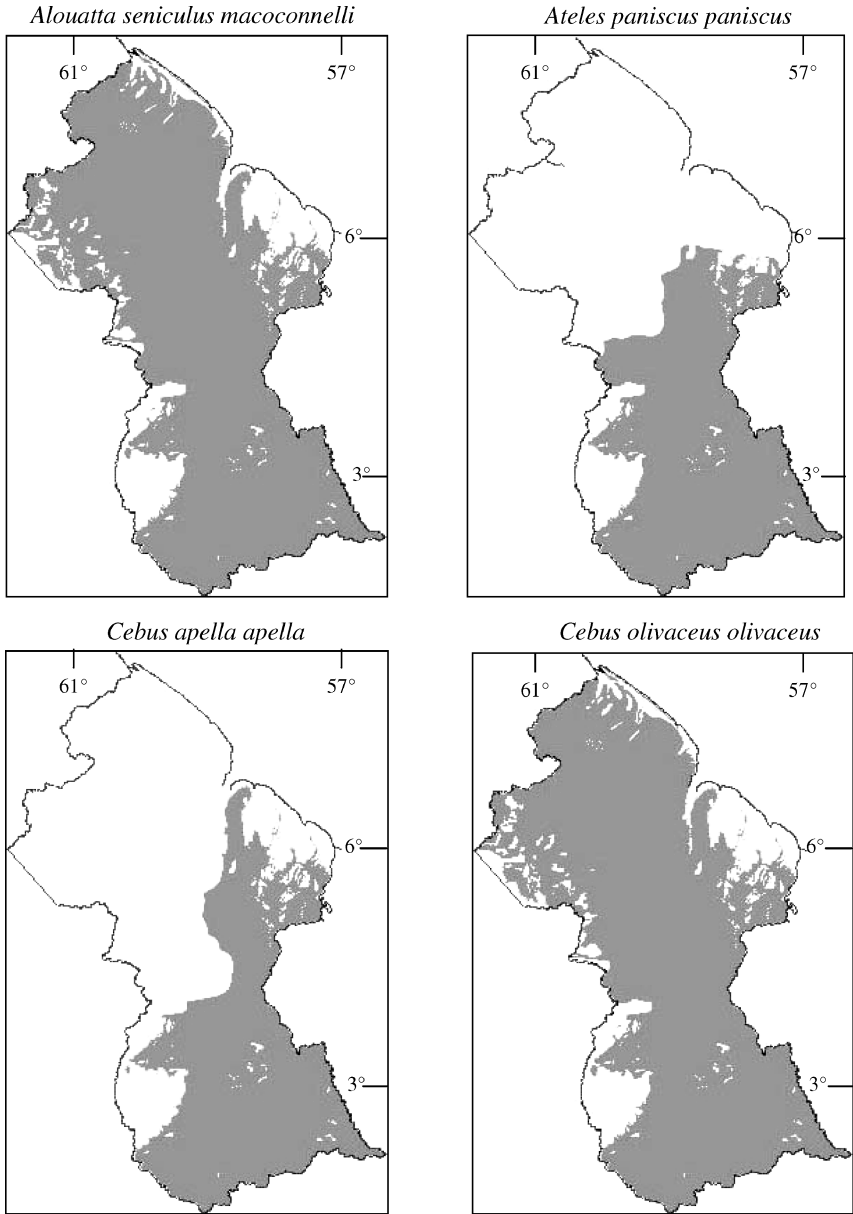


Fig. 2. Distribution of primate species in Guyana based on surveys and habitat use.

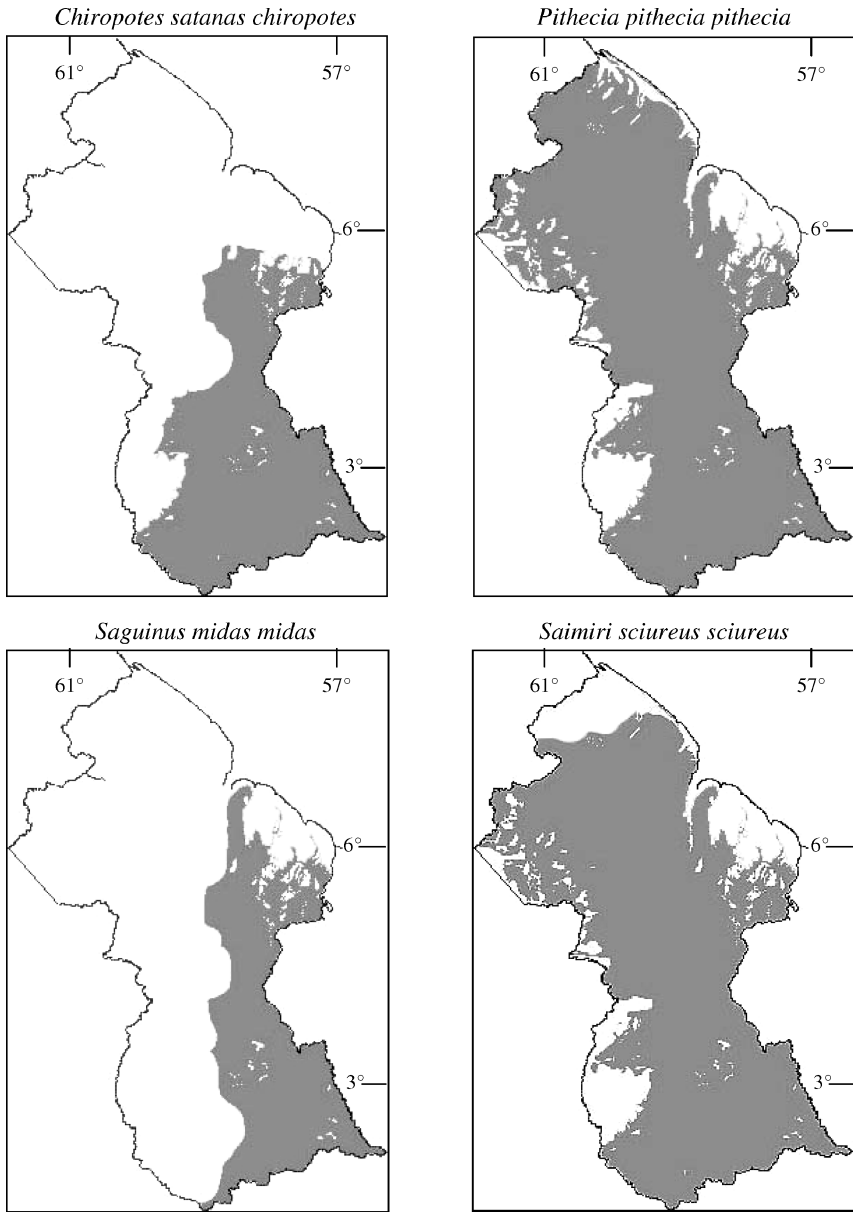


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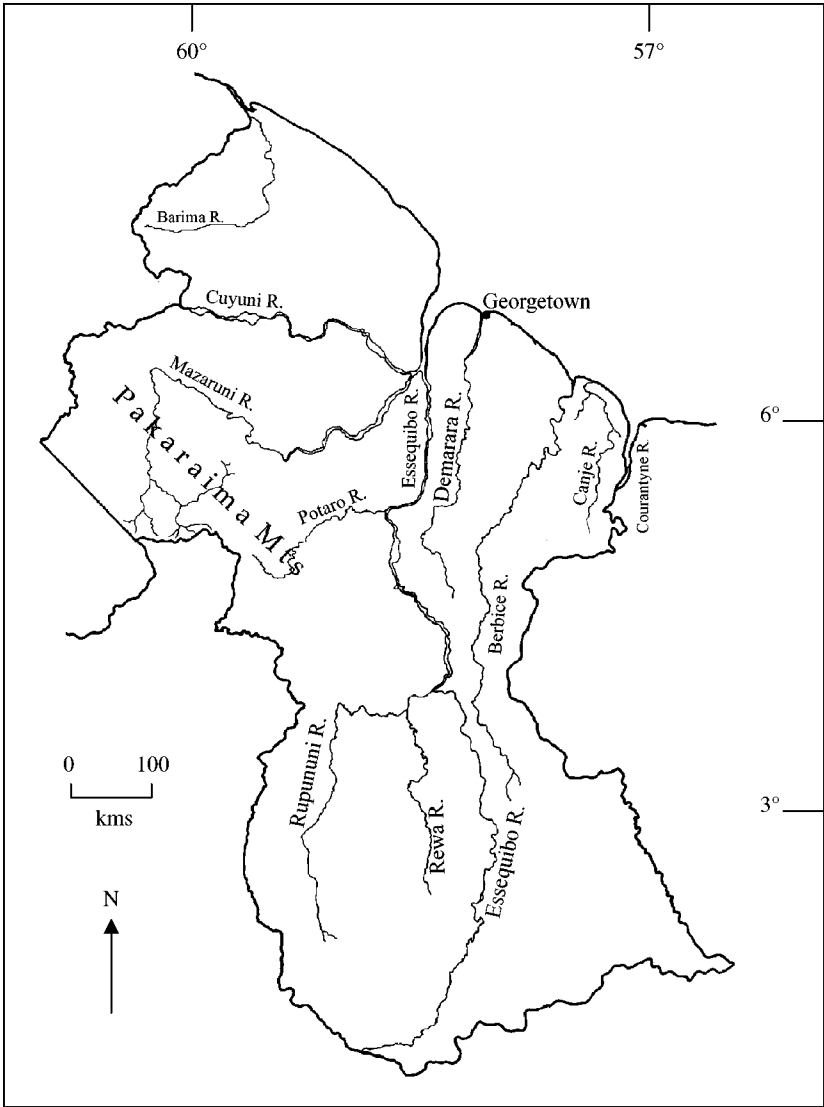


Fig. 3. Locations of major rivers tested for relationship to variations in primate diversity in Guyana.

Statistics

I used a sighting rate of the number of groups censused per 100 km surveyed (Peres, 1997, 1999). Following Peres and Janson (1999), I used published accounts (Muckenhirn *et al.*, 1975; Parker *et al.*, 1993; Sussman and Phillips-Conroy, 1995) and my data on the number of survey sites where each species has been surveyed as the dependent variable in analyses of species-area relationships. I conducted linear regression analyses using species counts as the dependent variable and geographic range and habitat area as independent variables. I transformed habitat area and species counts to natural logarithms. I run stepwise regression analyses using specific diversity as the dependent variable and the following independent variables: geographic area of interfluvial regions, habitat diversity, total number of habitats, and various fluvial characteristics. I tested statistical significance of the variance within the populations via a one-way ANOVA. I conducted statistical analyses via SPSS 10.0. The alpha level is 0.05 for all analyses.

RESULTS

The number of sites at which each primate species has been seen and the estimated geographic range size for the 8 primate species in Guyana are in Table II. Red howlers squirrel monkeys, wedge-capped capuchins, and white-faced sakis have been surveyed at many sites, and they have large geographic ranges. Brown capuchins have neither a large geographic area nor occur at many sites. Spider monkeys, brown bearded sakis, and golden-handed tamarins have small geographic ranges and occur at few sites. Geographic range size is a major determinant of the number of sightings of

Table II. Number of total sites where each species has been sighted, sighting frequency, and geographic range size in Guyana

Species	Total number of sites at which species has been sighted	Sighting frequency (# groups/100 km) ^a	Geographic range (km ²)
<i>A. seniculus</i>	26	3.30	177,139
<i>A. paniscus</i>	9	0.35	70,433
<i>C. apella</i>	12	1.74	80,120
<i>C. olivaceus</i>	20	1.51	177,139
<i>C. satanas</i>	9	0.29	62,911
<i>P. pithecia</i>	15	1.22	177,139
<i>S. midas</i>	9	0.81	47,794
<i>S. sciureus</i>	23	3.54	174,394
Total	123	3.30	

^aFrom Lehman (1999).

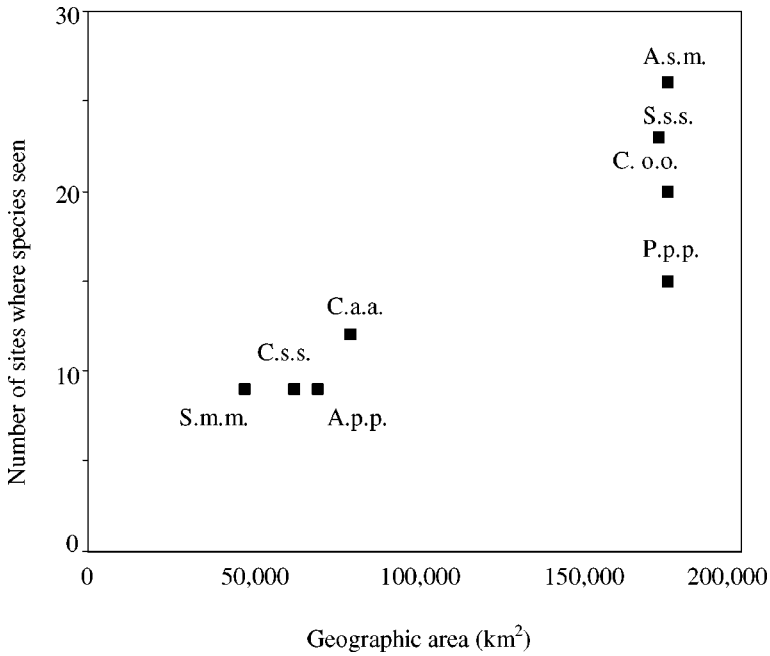


Fig. 4. Relationship between the geographic range size of 8 primates species and the number of sites at which each species occurs in Guyana. (A.s.m. = *Alouatta seniculus macoconnelli*, A.p.p. = *Ateles paniscus paniscus*, C.a.a. = *Cebus apella apella*, C.o.o. = *Cebus olivaceus olivaceus*, C.s.c. = *Chiropotes satanas chiropotes*, P.p.p. = *Pithecia pithecia pithecia*, S.m.m. = *Saguinus midas midas*, S.s.s. = *Saimiri sciureus sciureus*).

the 8 primate species ($R = 0.885$, ANOVA $F_{0.003[1,6]} = 21.682$), explaining 78% of the variation in the number of sites at which the occurred (Fig. 4). However, visual inspection of the data reveals that the population is not normally distributed and that a confounding variable may be affecting the population.

The geographic area for primate habitats and the number of primate species within each habitat are in Table III. Habitat area is correlated with the number of primate species that range into each habitat ($R = 0.796$, ANOVA $F_{0.001[1,10]} = 19.0$), explaining 63% of the variation in the dependent variable (Fig. 5).

Table IV shows the fluvial characteristics for the main rivers in Guyana. Mean monthly discharge varied considerably between the rivers (Fig. 6). The primate community also varied between rivers. Primate species diversity is strongly negatively correlated with the number of rivers crossed moving in a clockwise pattern from eastern to NW Guyana ($R = 0.947$,

Table III. Habitat type, habitat area, and number of primate species located in each habitat type

Habitat	Total area (km ²)	Primate species diversity (no. of species in habitat)
Rain forest	46,369.8	8
Southern hill forest	41,950.6	8
Mora forest	22,241.9	8
Premontane forest	13,655.3	6
Lower montane forest	12,927.5	4
Wallaba forest	11,996.9	8
Kanuku seasonal forest	8,112.2	6
SE Seasonal forest	6,884.0	8
Swamp forest	6,267.0	4
Low seasonal forest	4,447.4	6
Swamp woodland	1,236.3	3
Mazaruni Wallaba forest	641.1	4
Palm marsh woodland	409.0	3
Total	177,139	

slope = -0.602 , ANOVA $F_{0.0018[1,3]} = 54.34$). I did not survey golden-handed tamarins, brown bearded sakis, or brown capuchins west of the Essequibo River. I saw no squirrel monkey in forests west of the Barima River. The similarity of primate species on opposite riverbanks is correlated with both river discharge ($R = 0.902$, ANOVA $F_{0.05[1,2]} = 18.466$) and river length/discharge ($R = 0.912$, ANOVA $F_{0.045[1,2]} = 20.648$). The body masses of primates stopped by a river are correlated with river discharge ($R = 0.955$, ANOVA $F_{0.023[1,2]} = 42.052$) and river length/discharge ($R = 0.958$, ANOVA $F_{0.021[1,2]} = 45.345$).

Table V shows the results of stepwise regression analyses on primate species diversity and interfluvial area and habitat diversity. The stepwise model eliminated number of habitat types ($R = 0.086$, $t = 0.173$, $p = 0.8$) and total number of habitats ($R = 0.30$, $t = 0.631$, $p = 0.563$) from the model. Interfluvial area is the strongest correlate to primate specific diversity ($R = 0.916$, ANOVA $F_{0.04[1,5]} = 26.0$).

DISCUSSION

Geographic range size is a major determinant of primate diversity in Guyana. Furthermore, specific diversity is highest in large habitats, such as rain forest and southern hill-land forest, and lowest in small habitats, such as palm marsh and swamp woodlands. My data corroborate analyses of species-area relationships at continental and global levels in primates (Fleagle and

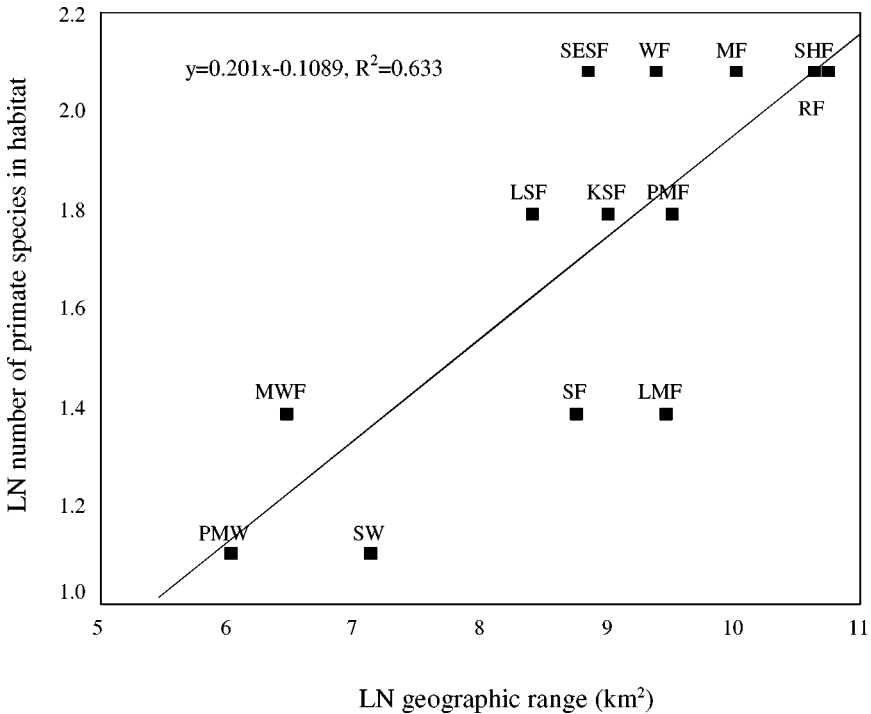


Fig. 5. Relationship between the geographic area of habitats and the number of primate species in each habitat in Guyana. Best-fit line calculated via least-squares linear regression. Habitat descriptions are from Huber *et al.*, 1995. (RF = rain forest, SHF = southern hill-land forest, MF = Mora forest, PMF = premontane forest, LMF = lower montane forest, WF = wallaba forest, KSF = kanuku seasonal forest, SESF = SE seasonal forest, SF = swamp forest, LSF = low seasonal forest, SW = swamp woodland, MWF = mazaruni Wallaba forest, PMW = palm marsh woodland).

Reed, 1996; Peres and Janson, 1999; Reed and Fleagle, 1995). However, visual inspection revealed that the data on geographic area is not normally distributed. Thus, there may be abiotic factors other than geographic area influencing habitat variation and primate specific diversity in Guyana. Rainfall has a unimodal relationship with primate species richness, tree species richness, and plant productivity in South American rain forests (Kay *et al.*, 1997). Although there are few data on rainfall variation within Guyana, there appears to be considerable variation in rainfall amounts throughout the country (ter Steege, 1993b). Longitudinal data on geographic variation in rainfall are needed to document the relationship between abiotic factors and primate diversity in Guyana.

Table IV. Guyanese rivers, their annual discharge, and body mass of the largest primate species whose range was terminated by the river

River	Discharge (10 ⁶ m ³ /yr)	Length/ Discharge (km/m ³ /yr) ^a	No. of species halted	Total combined mass of species halted (kg) ^b	Species halted
Essequibo	2261.00	2.88	4	13.32	<i>C. satanas</i> , <i>C. apella</i> , <i>S. midas</i> , <i>A. paniscus</i>
Cuyuni	1102.30	2.52	0	—	
Mazaruni	805.90	1.62	0	—	
Rupununi	81.30	0.26	2	3.65	<i>C. satanas</i> , <i>C. apella</i>
Demarara	71.10	0.25	0	—	
Rewa	54.30	0.24	1	0.57	<i>S. midas</i>
Berbice	48.80	0.10	0	—	
Canje	2.80	0.02	0	—	
Barima	2.80	0.02	1	0.86	<i>S. sciureus</i>
Siparuni	2.32	0.02	0	—	
Potaro	N/A	N/A	1	9.11	<i>A. paniscus</i>

^aRiver length is a straight line from the approximate location of the headwaters to the mouth via 1:250,000 Guyana Topographic Maps.

^bBody masses from Smith and Jungers (1997).

Although brown capuchins have one of the widest geographic distributions among South American primates (Rowe, 1996; Wolfheim, 1983), they do not range further north than the riverbanks of the Rupununi River in SW Guyana (Figure 2). Although I lack data on the feeding ecology of capuchins in Guyana, I posit a hypothesis to be tested in future field studies. Terborgh and Janson (1986) noted that brown capuchins rely on a few keystone resources (palms) that are available during periods of food shortage. Moreover, the density of palms is positively correlated with the abundance of brown capuchins in Peruvian tropical rain forests (Janson, 1987; Terborgh, 1983). Perhaps the small geographic range of brown capuchins may result from a lack of keystone resources in western and NW Guyana. Abundant palm species, particularly *Astrocaryum* sp. (39 trees/ha at Manu) and *Attalea* sp. (25 trees/ha at Manu), represent a critical food resource for brown capuchins during the dry season when fruit is scarce (Terborgh, 1983; Kiltie, 1980). Habitats in western and NW Guyana are characterized by having some of the lowest densities of palm species (4.6 trees/hectare) in South America (Davis and Richards, 1934; Terborgh and Andresen, 1998). *Astrocaryum* sp., such as *A. aculeatum*, are common in SW Guyana (Clarke *et al.*, 2001; Parker *et al.*, 1993) and the eastern half of the country (ter Steege, 1993a, 1993b), where brown capuchins are abundant. *Astrocaryum aculeatum*, called *warau* by the local people, produces fruit with a fleshy, edible mesocarp *ca.* 0.3 cm thick that is eaten by many primate species, such as brown capuchins, in the Guianas (van Roosmalen, 1985b; Lehman, pers. obs.). Based on >100 years

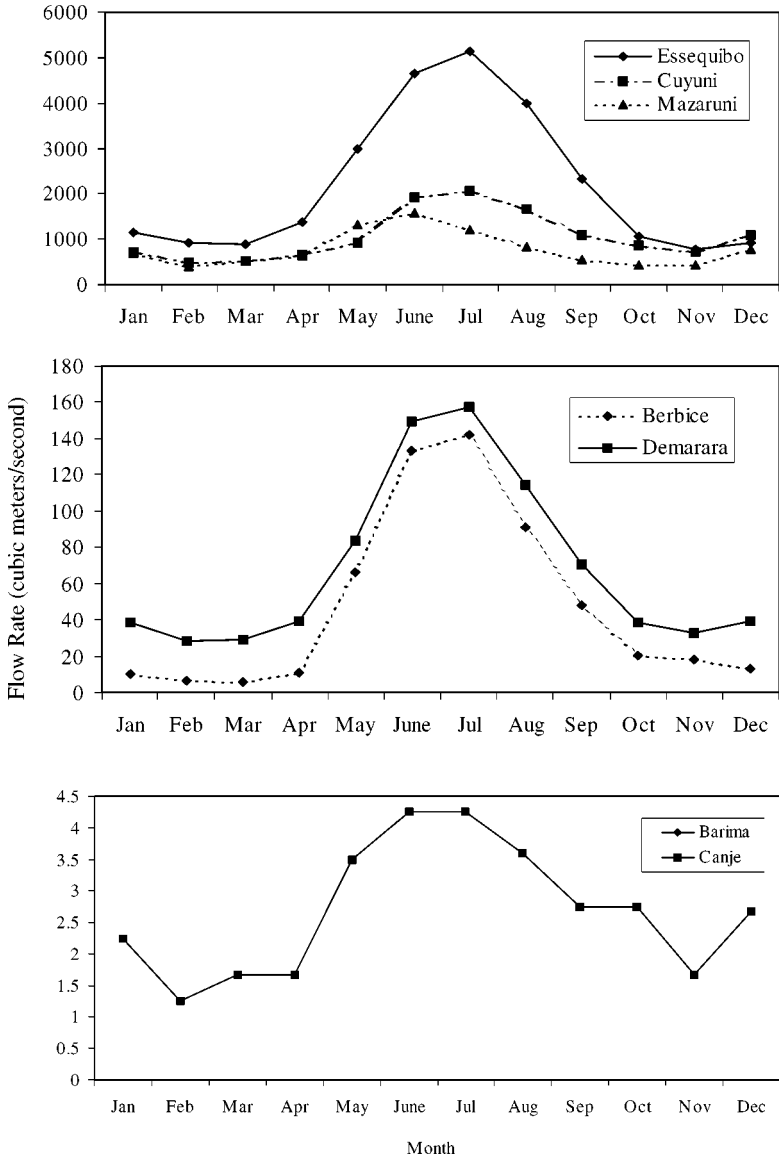


Fig. 6. Monthly flow rates for 7 major rivers in Guyana.

Table V. Stepwise regression analyses of primate species diversity and various habitat characteristics for seven interfluvial regions in Guyana

Independent variable	Beta ln	<i>t</i>	<i>p</i>	Correlation
Interfluvial area	0.001	5.105	0.004	0.916
Number of habitats	0.044	0.173	0.871	0.086
Total number of habitats	0.365	0.631	0.301	0.301

of phenological data collected in Guyana, fruits of *Astrocaryum aculeatum* are most abundant during June–July, when few other trees are producing fruits (ter Steege, 1993b).

Another species of palm (*Attalea maripa*), known locally as *kokerite*, may also be a keystone resource for primates, such as brown capuchins, in Guyana. *Attalea maripa* produce a large crop of fruit with a fleshy, edible endocarp 0.3–0.5 cm thick (van Roosmalen, 1985a). Anecdotal observations I made during periods of low fruit abundance in forests along the Berbice, Canje, and Essequibo Rivers indicate that *Attalea maripa* is an important resource for primates. It and other *Attalea* spp. are absent from forests north of the Rupununi River in Guyana (Clarke *et al.*, 2001). Therefore, I suggest that the distribution of brown capuchins may be limited by the availability of keystone palm plants in NW Guyana.

There is a significant reduction in primate diversity moving in a clockwise direction from eastern Guyana up through NW Guyana, which supports the hypothesis that rivers act as barriers to primate dispersal in Guyana. River discharge and river length/discharge are correlated with similarity of primate species between rivers in Guyana, as they are for Amazonian primates (Ayres and Clutton-Brock, 1992). Large rivers limit the distribution of most Guyanese primates, but small rivers did not limit the distribution of large-bodied primates. My results support predictions on the biogeography of Amazonian primates made by Ayres (1986) and Ayres and Clutton-Brock (1992). There are differences between my findings and those of Ayres and Clutton-Brock (1992). In Guyana, rivers with headwaters in mountainous or savanna habitats or both—Essequibo, Rupununi, Rewa, and Potaro—impede the dispersal of monkeys. For rivers whose headwaters do not originate in impassable habitats, primates can disperse along the river and reach the opposite bank either by crossing at the headwaters or via intertwined tree branches. However, the Barima River may limit the distribution of squirrel monkeys in Guyana despite originating in the NW swamp forests. Because there are few data on the ecology of primates in NW Guyana, it is difficult to determine if the Barima River is only spuriously correlated with distribution patterns of squirrel monkeys. My data do

not support the hypothesis that habitat diversity within the interfluvial areas affects primate diversity. Thus, habitat diversity may only affect primate diversity at the regional level in Guyana.

The distribution and diversity of Guyanese primates are related to both historical and ecological biogeographic processes. Historical processes, such as riverine barriers to dispersal have influenced and continue to influence the dispersal of primates into certain regions of the country. Ecological processes, such as the size and diversity of habitats, influence the biogeography of primates in Guyana.

There may be other variables affecting primate biogeography in Guyana. For example, metapopulation dynamic models predict that locally common species become widely distributed because of their low extinction rates and high colonization abilities (Hanski *et al.*, 1993). However, such data, particularly extinction rates, are difficult to collect on primates in the field. Future studies of Guyanese primates should attempt to document at least some patterns of colonization ability via genetic analyses.

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