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Primate Community Structure in Guyana: A Biogeographic Analysis

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Studies of primate community structure increase our understanding of behavior, adaptation, and evolution. However, there are few biogeographic data on specific composition and association patterns in primate communities. I conducted a biogeographic analysis of the community structure of primate species at 16 sites in Guyana. I used data from 1725 km of line-transect censuses to determine specific composition and association patterns of 220 primate groups . Of the 18 polyspecific groups, 94.1% (N = 16) included squirrel monkeys. There was an overall trend towards positive specific associations among Guyanese primates. The only species that exhibited a negative pattern of interspecific associations were brown and wedge-capped capuchins. The sighting rate for wedge-capped capuchins at sympatric sites was particularly depressed compared to that for brown capuchins. Low plant productivity in Guyanese forests may reduce the diversity of feeding niches and result in a low incidence of polyspecific associations and scramble competition between wedge-capped and brown capuchins.

KEY WORDS: community structure; biogeography; specific composition; surveys; association patterns; Guyana.

INTRODUCTION

Studies of community structure are important to understand behavior, adaptation, and evolution because they enable us to formulate and to test

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hypotheses on patterns of competition, predation, and extinction (Schoener, 1988; Putman, 1994; Jernvall and Wright, 1998; Losos *et al.,* 1998). The behavior and ecology of primate species living in a single community has been investigated extensively by Chivers (1980), Mittermeier and van Roosmalen (1981), Terborgh (1983), Bourliere (1985), Soini (1986), Waser (1986), Pontes (1997), Tutin *et al.,* (1997), and Davies *et al.* (1999). Researchers have also focused on comparing and contrasting primate communities within or between continents and large islands (Terborgh and van Schaik, 1987; Fleagle and Reed, 1996; Kappeler and Heymann, 1996; Ganzhorn, 1997; Eeley and Lawes, 1999; Peres and Janson, 1999). However, few data exist on the community structure of primate species within one biogeographic region, notable exceptions being those of Mittermeier (1977), Johns and Skorupa (1987), and Peres (1988, 1990, 1993a, 1993b, 1997). Most researchers emphasized anthropogenic disturbance (Johns and Skorupa, 1987; Peres, 1990). Thus, little attention has been placed on documenting biogeographic differences in primate species composition and abundance in undisturbed habitats.

A primary component of analyses of community structure is testing interspecific associations (Ludwig and Reynolds, 1988), which may be absent, positive, or negative. The presumed benefits of positive associations are greater foraging efficiency and predator avoidance (Terborgh, 1983; Norconk, 1990b, 1990a; Terborgh, 1990). In negative associations, it is assumed that ecologically similar species cannot co-exist because of competition for food resources (Lotka, 1925; Gause, 1934; Connell, 1961). Interspecific competition may be particularly intense between species that mutually exploit similar keystone resources (Tutin *et al.,* 1997). Although sympatric species employ different dietary strategies and modes of habitat use to avoid interspecific competition (Fleagle and Mittermeier, 1980; Mittermeier and van Roosmalen, 1981), evidence still exists for negative association patterns (Rodman, 1973; Terborgh, 1983; Peres, 1993b). For example, in a 3-km^2 area of Borneo Rodman (1973) found negative association patterns for 6 of 10 possible specific pairs among the 5 primate species in the survey area (*Macaca nemestrina, M. fascicularis, Pongo, Hylobates,* and *Presbytis aygula*).

There are few data on the dynamics of negative association patterns and whether these patterns hold throughout the geographic ranges of sympatric primate species. However, Hall (1965) and Dunbar and Dunbar (1974) suggested that greater ecological overlap between species can occur in terrestrial habitats that are relatively richer in food resources than others. Species in habitats with low levels of food resources may not be able to tolerate polyspecific associations due to increased competition for food. Few studies have determined if these patterns hold for primates in Neotropical rain forests.

Studies of primate community structure, association patterns, and habitat diversity have been conducted in French Guiana, Suriname, and northern Amazonia by Mittermeier (1977), de Granville (1988), Pontes (1997), Julliot and Simmen (1998), and Youlatos (1998). Only recently have studies been conducted on the primates of Guyana (Muckenhirn *et al.,* 1975; Sussman and Phillips-Conroy, 1995; Lehman, 1999). Many of the primate species in French Guiana, northern Amazonia, and, to a lesser extent, Suriname form positive polyspecific associations. Forests in Guyana are characterized by extremely low soil quality and relatively low tree species diversity and abundance compared to forests in Suriname and French Guiana (ter Steege, 1993; Terborgh and Andresen, 1998). There have been few reports on how these regional differences in soil properties and floristic characteristics affect primate community structure. I documented patterns of primate specific composition and associations in Guyana and compared them with data from studies conducted in Suriname, French Guiana, and northern Amazonia.

METHODS

Site and Species Descriptions

The data are from 1725 km of surveys I conducted in Guyana, a small country of 215,000 km^2 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, 1993). Temperatures are highest in September and October and are lowest in December and January (Fig. 2). Mean annual precipitation is between 2,000 and 3,400 mm (Fig. 2); it is neither evenly distributed throughout the year nor 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 extends to November or December. It is characterized by monthly rainfall < 200 mm. The short dry season is usually from February to April.

Unlike many tropical countries, Guyana retains approximately 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.

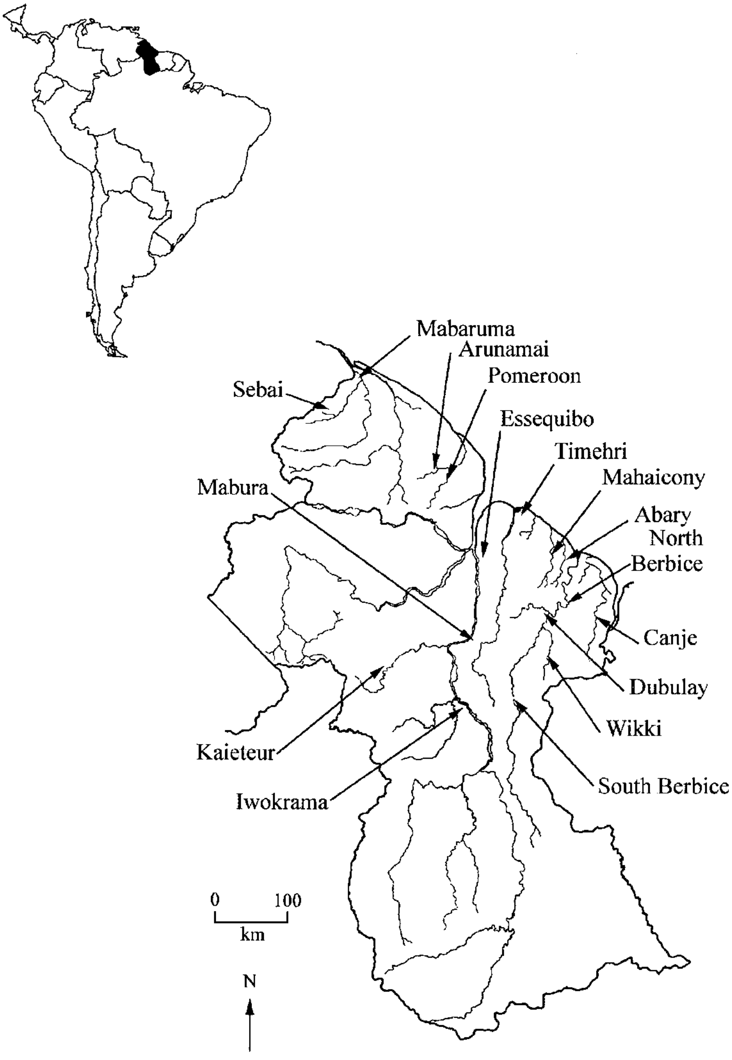

Fig. 1. Locations of Guyana and the 16 survey sites.

I surveyed the distribution and diversity of primates in forests and along rivers at 16 sites in Guyana (Fig. 1). Brief characterizations of them are in Table I. The survey data are from three periods: (1) November 1994 to June 1995, (2) September 1995 to June 1996, and (3) June to August 1997. They cover all four seasons. I conducted surveys throughout the day from 0500 to 1900 hours.

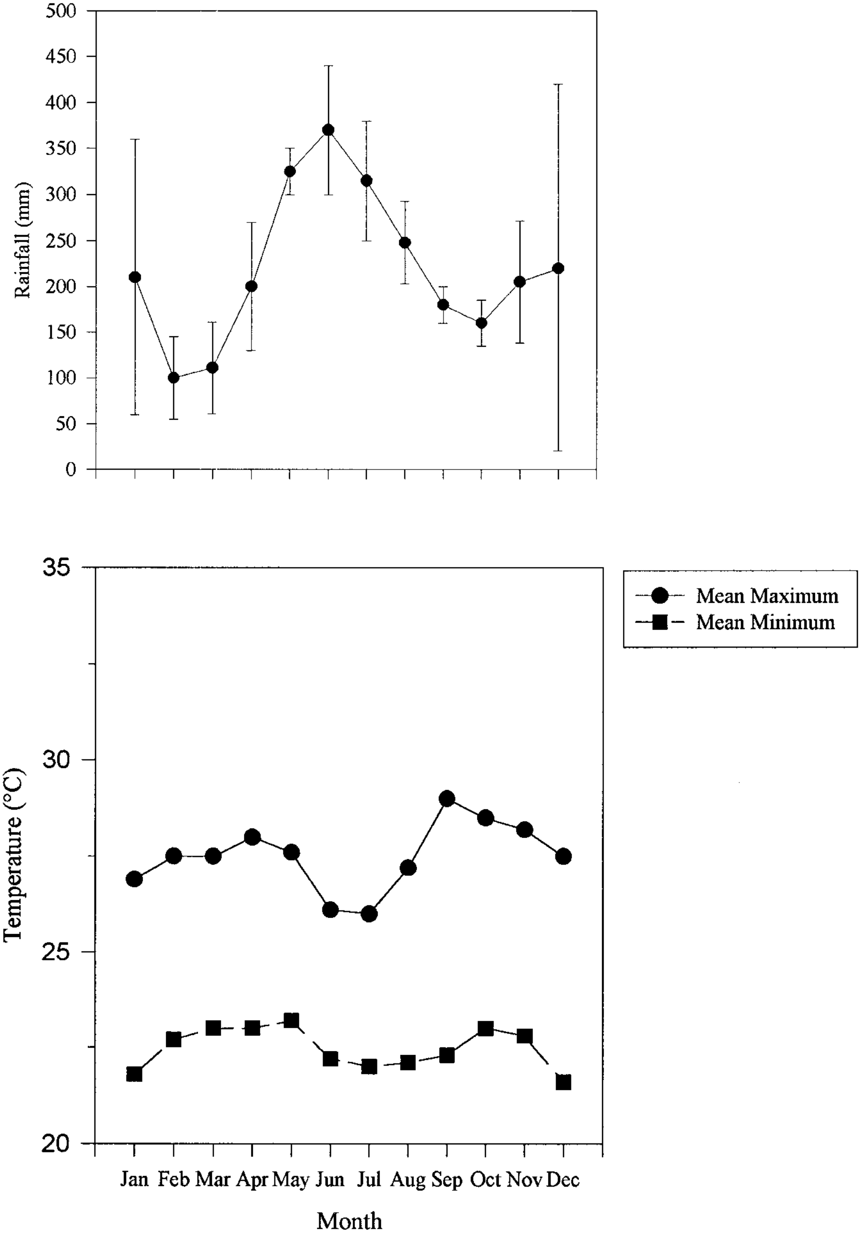

Fig. 2. Annual variations in mean temperature and mean precipitation (±1 SD) in central Guyana during 1994–1996.

Table I. Description of 16 survey sites in Guyana

Site	Latitude, longitude	Habitat	Key sources of disturbance[a]	Hunting/trapping pressures[b]	Census distance (km)
1 Essequibo	6°17′N, 58°32′W	Evergreen, nonflooded rain forest	L(l)	–	80
2 Timehri	6°29′N, 58°13′W	Seasonally flooded swamp forest	F (m), BW (m), A (h)	L–M	147
3 Mahaicony	6°16′N, 57°53′W	Seasonally flooded swamp forest	F (l), BW (l)	L	108
4 Abary	6°16′N, 57°53′W	Seasonally flooded swamp forest	F (h), BW (h)	L	37
5 North Berbice	5°41′N, 57°51′W	Riparian forest	F (l), L (l), A (m)	M	120
6 Canje	5°42′N, 57°31′W	Riparian forest	F (l), L (l), A (l)	M–H	127
7 Dubulay	5°41′N, 57°31′W	Riparian forest	F (l)	–	162
8 Wikki	5°25′N, 57°47′W	Riparian forest	F (m), L (l)	L	51
9 South Berbice	5°4′N, 58°,13′W	Evergreen, nonflooded rain forest	–	L	136
10 Mabura	5°9′N, 58°42′W	Evergreen, nonflooded rain forest	–	–	178
11 Iwokrama	4°31′N, 58°41′W	Evergreen, nonflooded rain forest	–	L	45
12 Kaieteur	5°10′N, 59°29′W	Basimontane forest	–	L	129
13 Sebai	7°50′N, 59°52′W	Seasonally flooded swamp forest	BW (m), A (l)	L	256
14 Mabaruma	8°12′N, 59°29′W	Seasonally flooded swamp forest	BW (m), L (m)	L	32
15 Arunamai	7°7′N, 58°57′W	Seasonally flooded swamp forest	BW (m)	L–M	12
16 Pomeroon	7°9′N, 58°55′W	Seasonally flooded swamp forest	BW (m), A (l)	H	105

[a] Indicates most important sources of natural or anthropogenic sources of forest disturbance: (F) prolonged seasonal flooding, (BW) backwater palm swamps, (L) selective logging, (A) agriculture. Classes of intensity are: none (−), light (l), moderate (m), and heavy (h).

[b] Classes of hunting/trapping pressures are: (−) none, (L) light, (M) moderate, and (H) heavy.

There are at least 9 primate species in Guyana: red howlers (*Alouatta seniculus macoconnelli*), Guianan black spider monkeys (*Ateles paniscus paniscus*), whitefronted capuchins (*Cebus albifrons*), brown capuchins (*Cebus apella apella*), wedge-capped capuchins (*Cebus olivaceus olivaceus*), bearded sakis (*Chiropotes satanas chiropotes*), white-faced sakis (*Pithecia pithecia pithecia*), golden-handed tamarins (*Saguinus midas midas*), and common squirrel monkeys (*Saimiri sciureus sciureus*). All nine species are arboreal and diurnal. There are unconfirmed reports of night monkeys (*Aotus trivirgatus*) in Guyana (Sussman and Phillips-Conroy, 1995; Lehman, 1999). Because there are few data on the biogeography of white-fronted capuchins in Guyana (Barnett *et al.,* in press), I did not use them in the analyses.

Line-Transect Censuses

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; Burnham *et al.,* 1980; 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 along transects lines at a rate of 1.0 km/h, stopping every 10 min to listen for movements in the forest. Before the surveys, I had measured and marked transects every 10 m with numbered blocks or flagging tape.

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

During surveys, I recorded data on: (1) primate species; (2) time of day; (3) weather; (4) vegetation height; (5) general height of group; (6) number of monkeys in group; (7) cue by which monkeys were detected; (8) activity; (9) perpendicular distance from the transect [meters]; (10) sighting angle; and (11) habitat type. When I saw a primate group, I spent a standardized time of 10 min observing the behavior of individuals in the group. I also collected notes *ad libitum* on behavior, obvious individual physical characteristics, and vocalizations.

I determined the location of primate groups during surveys via 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). GPS readings provide location data within 10 m of the actual site, depending on the selective availability limit. The GPS could pinpoint the location of an encounter within 3–4 min, and <65% forest cover (Lehman, unpublished data). GPS readings were made during all river sightings and later verified on 1:50,000 topographic maps.

I used two association types in my analysis of primate community structure: polyspecific associations and site associations. Polyspecific groups are ≥2 groups of different species feeding or traveling ≤20 m of each other (Chapman and Chapman, 1996). This definition has been used in previous studies of mixed-species groups of primates by Oates and Whitesides (1980) and Chapman and Chapman (1996). The association had to occur for ≥10 min to be scored as a polyspecific group. Following Schluter (1984), I analyzed a site association for ≥2 species if they were observed during the same census of a transect line at a site. I used site associations to produce association indices. This methodology has been used successfully to measure strength of associations in communities by Peet and Loucks (1977) and Wolda *et al.* (1983).

Statistical Analyses

I used a null association model which employs a variance ratio (VR) to test for significant associations between species pairs (Schluter, 1984). The variance ratio is given by

$$VR = S_T^2/\sigma_T^2$$

wherein S_T^2 is the total sample variance for the occurrences of the S species in the sample and σ_T^2 is the variance in total species number. If $VR > 1$, then the species exhibit a positive association. If $VR < 1$, then a negative net association is suggested. I computed a statistic (W) to determine if deviations from 1 were significant. This statistic is given by

$$W = (N)(VR)$$

If, for example, the species are not associated, then there is a 90% probability that W lies between limits given by the following chi-square distribution:

$$\chi^2_{.05,N} < W < \chi^2_{.95,N}$$

Following Ludwig and Reynolds (1988), I used the Ochiai index (O_i) to measure the degree of association between pairs of species (Ochiai, 1957). In this analysis, a presence–absence matrix is computed for each specific pair at each survey site. Then I used a chi-squared test statistics to test the null hypothesis of independence in a 2 × 2 table. I calculated a Yate's correction to avoid biased values resulting from low cell expectations.

Following Peres (1997), I used a sighting rate of the number of groups censused per 10 km walked/paddled. I computed another sighting rate using only transect distances for sites where each species was censused. Use of both rates controls for overall differences in sampling effort and for variations in geographic range. I computed a Spearman correlation coefficient (r_s) for monthly data on polyspecific groups and fruiting records via SPSS 8.0 statistical software. Data on fruiting records are based on 100 years of phenological data collected in Guyana (ter Steege, 1993). I used an alpha level of $p < 0.05$ for all tests.

RESULTS

I censused a total of 220 primate groups during surveys at the 16 sites (Table II). Squirrel monkeys were common, accounting for 27.7% (N = 61) of the total number of primate groups censused. Red howlers also are frequent in the censuses (26% of total groups, N = 57). Squirrel monkeys and red howlers had similar sighting rates. I also sighted brown capuchins (13.6% of total groups, N = 30), wedge-capped capuchins (11.8% of total

Table II. Frequency and sighting rates of primate groups observed during surveys in Guyana

Species	No. of groups censused	Percentage	Sighting rate[a] (groups/10 km)	Adjusted sighting rate[b] (groups/10 km)
Alouatta seniculus macoconnelli	57	26.0	0.33	0.33
Ateles paniscus paniscus	6	2.7	0.03	0.08
Cebus apella apella	30	13.6	0.17	0.39
Cebus olivaceus olivaceus	26	11.8	0.15	0.15
Chiropotes satanas chiropotes	5	2.3	0.03	0.05
Pithecia pithecia pithecia	21	9.5	0.12	0.12
Saguinus midas midas	14	6.4	0.08	0.12
Saimiri sciureus sciureus	61	27.7	0.35	0.41
Total	220	100	1.26	1.65

[a] Rate estimated using total survey distance for study.
[b] Rate estimated using survey distance at sites where species present.

groups, $N = 26$), and white-faced sakis (9.5% of total groups, $N = 21$) frequently in the survey areas. The total sighting rate for brown capuchins (0.17 groups/10 km) is only slightly higher than the rate for wedge-capped capuchins (0.15 groups/10 km). White-faced sakis have a total sighting rate of 0.12 groups/10 km. Golden-handed tamarins account for 6.4% ($N = 14$) of the total number of groups censused, and their sighting rate is 0.08 groups/10 km. Of the 220 primate groups censused, only 2.7% ($N = 6$) are spider monkeys (sighting rate = 0.03 groups/10 km) and 2.2% ($N = 5$) are bearded sakis (sighting rate = 0.03 groups/10 km). The total primate sighting rate is 1.26 groups/10 km.

I observed 18 polyspecific groups during surveys (Table III), resulting in a sighting rate of 0.10 polyspecific groups/10 km. I documented only one instance in which three primate species—squirrel monkeys, brown capuchins, and howlers—formed a polyspecific group. The remaining groups involved only two species. Squirrel monkeys formed polyspecific groups more often than the other species, accounting for 94.1% ($N = 16$) of total associations. Squirrel monkeys formed polyspecific groups with four primate species: brown capuchins ($N = 10$), red howlers ($N = 3$), wedge-capped capuchins ($N = 2$), and white-faced sakis ($N = 1$). The only polyspecific group not involving squirrel monkeys was one between red howlers and wedge-capped capuchins. There is no correlation between monthly patterns of sightings of polyspecific groups and fruit abundance ($r_s = -0.175$, $p = 0.587$).

Table IV shows interspecific association indices for 28 pairwise combinations of primate species in Guyana. There is a significant trend towards positive specific associations for primates at the 16 survey sites (Schluter's variance test for overall association, $V = 3.56$, $W = 56.96$, $p = 0.001$). Four primate specific pairs show significant positive patterns of interspecific associations. The highest degree of positive association ($O_i = 1.00$) is between spider monkeys and bearded sakis, which were always at the same survey sites. Golden-handed tamarins and squirrel monkeys also show a strong degree of positive association ($O_i = 0.79$). Brown capuchins formed positive associations with both bearded sakis ($O_i = 0.77$) and spider monkeys ($O_i = 0.77$).

The only species that exhibited a significant negative pattern of interspecific association were brown and wedge-capped capuchins. The total average sighting rate for brown capuchins at the four sites—Wikki River, South Berbice, Canje River, and Dubulay Ranch—where they were observed, but where wedge-capped capuchins were absent, is 0.35 groups/10 km (Table V). The mean sighting rate for wedge-capped capuchins at 10 allopatric sites—Timehri, Mahaicony River, Abary River, Essequibo River, Iwokrama Rain Forest Reserve, Kaieteur Falls National Park, Pomeroon

Table III. Patterns of polyspecific groups observed during surveys at 16 survey sites in Guyana[a]

Species	*A. s. macoconnelli*	*A. p. paniscus*	*C. a. apella*	*C. o. olivaceus*	*C. s. chiropotes*	*P. p. pithecia*	*S. m. midas*	*S. s. sciureus*
A. s. macoconnelli		0	0	1	0	0	0	3
A. p. paniscus	0		0	0	0	0	0	0
C. a. apella	0	0		0	0	0	0	10
C. o. olivaceus	5.8	0	0		0	0	0	2
C. s. chiropotes	0	0	0	0		0	0	0
P. p. pithecia	0	0	0	0	0		0	1
S. m. midas	0	0	0	0	0	0		0
S. s. sciureus	17.7	0	58.8	11.8	0	5.8	0	

[a] Numbers above the diagonal refer to frequency of association. Numbers below the diagonal refer to frequency as percentage of total associations.

Table IV. Interspecific association indices and test statistics between 8 primate species at 16 sites in Guyana[a]

Species pair	Association type[a]	Chi-square[b]	Yate's chi-square[b]	O_i[c]
A. s. macoconnelli & A. p. paniscus	+	0.85	0.01	0.48
A. s. macoconnelli & C. a. apella	+	2.73	1.07	0.67
A. s. macoconnelli & C. o. olivaceus	+	0.14	0.14	0.80
A. s. macoconnelli & C. s. chiropotes	+	0.85	0.01	0.48
A. s. macoconnelli & P. p. pithecia	+	3.69	1.64	0.78
A. s. macoconnelli & S. m. midas	−	0.01	0.60	0.50
A. s. macoconnelli & S. s. sciureus	+	0.41	0.00	0.68
A. p. paniscus & C. a. apella	+	8.12*	4.66*	0.77
A. p. paniscus & C. o. olivaceus	+	0.58	0.04	0.41
A. p. paniscus & C. s. chiropotes	+	16.00*	10.11*	1.00
A. p. paniscus & P. p. pithecia	+	0.41	0.00	0.41
A. p. paniscus & S. m. midas	+	2.16	0.60	0.52
A. p. paniscus & S. s. sciureus	+	0.41	0.00	0.41
C. a. apella & C. o. olivaceus	−	4.75*	7.85*	0.26
C. a. apella & C. s. chiropotes	+	8.12*	4.66*	0.77
C. a. apella & P. p. pithecia	+	2.29	1.02	0.71
C. a. apella & S. m. midas	+	2.80	1.19	0.60
C. a. apella & S. s. sciureus	+	2.29	0.00	0.47
C. o. olivaceus & C. s. chiropotes	−	0.14	1.23	0.33
C. o. olivaceus & P. p. pithecia	+	1.33	0.33	0.71
C. o. olivaceus & S. m. midas	−	0.87	2.42	0.39
C. o. olivaceus & S. s. sciureus	−	0.00	0.33	0.61
C. s. chiropotes & P. p. pithecia	+	0.41	0.00	0.41
C. s. chiropotes & S. m. midas	+	2.16	0.60	0.52
C. s. chiropotes & S. s. sciureus	+	0.16	0.06	0.38
P. p. pithecia & S. m. midas	+	1.33	0.33	0.53
P. p. pithecia & S. s. sciureus	+	1.00	0.25	0.63
S. m. midas & S. s. sciureus	+	7.27*	4.65*	0.79

[a] Sign indicates direction of the species association (+, pair of species occurred together more often than expected if independent; −, pair of species occurred together less often than expected if independent).

[b] Asterisk indicates significance at $p < 0.05$ and df = 1.

[c] Ochiai's index of association.

Table V. A comparison of sighting rates for *Cebus* at sympatric and allopatric sites in Guyana

Species	Sighting rate (number of groups/10 km) Allopatric sites	Sighting rate (number of groups/10 km) Sympatric sites
Cebus apella apella	0.35 (*N* = 4)	0.43 (*N* = 2)
Cebus olivaceus olivaceus	0.25 (*N* = 10)	0.06 (*N* = 2)

River, Arunamai River, Mabaruma, and Sebai—is 0.25 groups/10 km. The average sighting rate of brown capuchins (0.43 groups/10 km) at the two sympatric sites—North Berbice and Mabura—is >7 times greater than that of wedge-capped capuchins (0.06 groups/10 km).

DISCUSSION

Of the 220 primate groups in my surveys, 8.2% ($N = 18$) involved polyspecific associations. Mittermeier (1977) observed a higher proportion of polyspecific groups during his census work in Suriname (16.4% of total groups sighted, $N = 114$). In my study, squirrel monkeys were the most common primate seen during surveys and they had the highest incidence of polyspecific associations. The most common association was between brown capuchins and squirrel monkeys ($N = 10$, 58.8% of total associations). There is, however, no significant associative pattern between brown capuchins and squirrel monkeys. The Ochiai index did not reach significance for them because of differences in geographic distribution. Although squirrel monkeys range throughout most of the country, brown capuchins live only in eastern and SW Guyana (Lehman, 1999).

My data are similar to those of primate researchers in other regions of South America (Thorington, 1968; Klein and Klein, 1973; Mittermeier, 1977; Terborgh, 1983; Pontes, 1997), in which, squirrel monkeys were most likely to be in the company of other species and their most common association was with brown capuchins. My data corroborate those of Mittermeier (1977) in that spider monkeys, white-faced sakis, and golden-handed tamarins rarely form polyspecific groups. However, brown bearded sakis associated with brown capuchins and squirrel monkeys in Suriname, whereas no polyspecific associations were observed for brown bearded sakis in Guyana. Differences in association patterns for brown bearded sakis between the studies conducted in Suriname and Guyana may be due to low sighting rates in Guyana. I saw only five groups of brown bearded sakis. In Guyana, red howlers associated with squirrel monkeys ($N = 3$, 17.7% of total associations), but they formed no polyspecific group in Suriname (Mittermeier, 1977).

The combined effects of low-quality soils and low plant specific diversity in Guyana may influence patterns of polyspecific associations in primates. Polyspecific groups in Guyana accounted for a smaller proportion of total group sightings compared to surveys conducted in Suriname, where soils are richer and plant diversity is greater (Mittermeier, 1977). Mendes Pontes (1996) found that all primate species (*Alouatta seniculus, Ateles belzebuth, Cebus apella, C. olivaceus,* and *Saimiri sciureus*) formed polyspecific groups at the Maracá Ecological Station in northern Amazonia. Furthermore, forest habitats at Maracá with low density and diversity of food trees supported few polyspecific groups. One hypothesized benefit of polyspecific associations is increased foraging efficiency during periods of minimum fruit abundance (Janson *et al.,* 1981; Terborgh, 1983; Podolsky, 1990; Pontes, 1997). During periods of low resource availability, mixed-species groups forage for fruits from large tree species in plant families such as Moraceae, Sapotaceae, and Palmae (Terborgh, 1983; Mendes Pontes, 1997). However, I found no correlation between fruiting abundance and polyspecific groups in Guyana. Mixed-species groups formed during both the dry and wet seasons. The question arises then as to why the primates of Guyana do not form polyspecific groups during periods of low fruit abundance? The answer to this question may lie in the abundance of certain plant species and families. Tropical forests in Guyana have low levels of floral diversity and abundance of plant families that are valuable food resources for primates (Comiskey *et al.,* 1993; ter Steege, 1993; Ek, 1997; Terborgh and Andresen, 1998). For example, Terborgh and Andresen (1998) analyzed floristic patterns in tree plots at 29 sites in South America. They found that plots in Guyana had the lowest abundance of trees in the plant families Palmae and Moraceae, which contain many tree species that are critical food resources during periods of low resource abundance for polyspecific groups of primates (Terborgh, 1983; Mendes Pontes, 1997).

Forest habitats in Guyana may not contain a high enough abundance of large fruiting trees to support polyspecific groups during periods of fruit scarcity. Therefore, the potential benefits of increased foraging efficiency may be outweighed by the high costs of low resource availability.

Despite reports that brown and wedge-capped capuchins compete with each other (Eisenberg, 1979) and that they are morphologically, ontogenetically, and behaviorally similar (Moynihan, 1976; Terborgh, 1983; Eisenberg, 1989; Ford and Hobbs, 1994), they are sympatric at some sites in Guyana (Muckenhirn *et al.,* 1975; Sussman and Phillips-Conroy, 1995), Suriname (Mittermeier, 1977), French Guiana (Simmon and Sabatier, 1996; Youlatos, 1998), and northern Amazonia (Pontes, 1997). Before my study in Guyana, both species were known to co-occur at only one site, Apoteri, in central Guyana (Muckenhirn *et al.,* 1975; Sussman and Phillips-Conroy, 1995). Sussman and Phillips-Conroy (1995) hypothesized that where the two species co-occur, wedge-capped capuchins may live at lower densities than brown capuchins. Although I found that brown and wedge-capped capuchins co-occur at two sites (Berbice River and Mabura Hill), analyses of specific composition across all 16 survey sites indicate that they have a negative pattern of interspecific association. Sighting rates of wedge-capped capuchins were lower at sites where they were sympatric with brown capuchins (Table V). Thus, as predicted by Sussman and Phillips-Conroy (1995), wedge-capped capuchins may be sensitive to the presence of a congener.

My biogeographic study of the community structure of Guyanese primates indicates that a negative pattern of interspecific association exists between wedge-capped capuchins and brown capuchins. Furthermore, the sighting rate for wedge-capped capuchins was reduced in areas of sympatry compared to allopatric areas. Although I lack data on dietary patterns of capuchins in Guyana, I posit a hypothesis to be tested in future field studies. Given that Guyanese forests are characterized by low plant specific diversity and abundance and that I saw relatively fewer polyspecific primates groups in Guyana compared to neighboring countries, there may be interspecific competition between wedge-capped and 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 and Janson, 1986; Janson and van Schaik, 1987; van Schaik and van Noordwijk, 1988).

Intergroup contest competition involves direct interactions, such as intergroup aggression. This form of competition has been observed rarely between wedge-capped capuchins and brown capuchins in French Guiana, Suriname, or Guyana by Muckenhirn *et al.* (1975), Mittermeier (1977), Simmon and Sabatier (1996), Youlatos (1998), and Lehman (1999). Intergroup scramble competition results in resource depression or depletion (Janson and van Schaik, 1987).

Scramble competition may have a negative impact on primate densities because of low food availability, which may be particularly pronounced in Guyana because the forests are characterized by low fruit and leaf production compared to other sites in South America (ter Steege, 1993; Chale, 1996; Zagt *et al.,* 1997; Terborgh and Andresen, 1998; Toriola *et al.,* 1998). A recent study of primate species richness in South America by Kay and coworkers (1997) indicates that plant productivity is the ecological variable most strongly correlated with primate species richness. Thus, low plant productivity in Guyanese forests may reduce the abundance of food resources and result in scramble competition between wedge-capped and brown capuchins. However, there are limits to behavioral interpretations drawn from survey data. Long-term behavioral data on habituated study groups of each species of capuchins are needed to fully test any competitive hypotheses.

Low tree specific diversity and abundance and low fruit and leaf production may influence patterns of polyspecific association among primates in Guyana. My biogeographic data on community structure provide some support to the theory that species in habitats with low levels of food resources cannot support numerous polyspecific associations due to increased competition for food (Hall, 1965; Dunbar and Dunbar, 1974). Despite the overall pattern of positive association patterns among the 8 primate species, brown capuchins and wedge-capped capuchins may be experiencing scramble competition for food resources. Studies of their diet and habitat use are needed to test this hypothesis. Furthermore, surveys should be conducted in the remote regions of the country for which we have few data on primate distributions and community structure, e.g., SE Guyana and the western highlands.

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