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Biogeography of the Primates of Guyana: Effects of Habitat Use and Diet on Geographic Distribution

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Species that exploit a wide range of resources or habitats (generalists) tend to be widely distributed, whereas species that exploit a narrow range of resources or habitats (specialists) often have a limited distribution. The distribution patterns are thought to result from specialists using relatively smaller habitats than those exploited by generalists. I used data from 1,725 km of primate surveys that I conducted in Guyana to test these hypotheses. Habitat breadth is the total number of different habitat types occupied by each species. I used the total number of different food categories exploited by each species to measure dietary breadth. Geographic range size is correlated with habitat breadth but not with dietary breadth or body size for the 8 primate species in Guyana. Habitat generalists—red howlers and wedge-capped capuchins—range into all habitats. Habitat specialists—spider monkeys, brown bearded sakis, and golden-handed tamarins—range only into large habitats. Habitat generalists tend to be dietary type specialists in Guyana. I suggest that only habitat generalists can subsist on the low-quality foods in small habitats in Guyana. Conversely, habitat specialists tend to be dietary type generalists in Guyana. They must feed on a variety of food types in large habitats. However, using the number of food categories exploited as a measure of dietary breadth may be only a weak aspect of multidimensional niche. Researchers testing biogeographic hypotheses associated with dietary breadth should consider including multivariate indicators of both the types of food categories eaten and the number of plant species exploited.

KEY WORDS: biogeography; range size; ecological specialization; niche; generalists; specialists; Guyana.

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INTRODUCTION

Species that exploit a wide range of resources or habitats—generalists—tend to be widely distributed, whereas species that exploit a narrow range of resources or habitats—specialists—often have a limited distribution (Brown, 1984; Hanski, 1982; Hanski and Gyllenberg, 1997). According to Hanski and Gyllenberg (1997), the biogeographic distribution patterns of specialists are the result of their using relatively smaller habitats than those exploited by generalists. Studies of ecological correlates to primate distributions at continental and global levels have provided conflicting results (Arita *et al.*, 1990; Dobson and Yu, 1993; Eeley and Foley, 1999; Harcourt *et al.*, 2002; Jones, 1997; Peres and Janson, 1999). At the global level, Wright and Jernvall (1999) found a remarkably linear relationship between the geographic range of primates and habitat breadth, but not dietary breadth. Conversely, Harcourt *et al.* (2002) found that both habitat breadth and dietary breadth covaried with rarity in primate genera in South America, Africa, and Asia. Eeley and Foley (1999) documented positive relationships between range size and both habitat breadth ($r = 0.851$) and dietary breadth ($r = 0.634$) in African anthropoid primates. However, there are few data on how interspecific variations in habitat breadth and dietary breadth relate to the distribution of platyrrhines at biogeographic scales below that of the continental level.

Biogeographic patterns are best understood as a function of scale because organisms are spatially distributed within their environment (Rosenzweig, 1995). Alpha diversity and beta diversity are two principal scales used in biogeographic studies (Cox and Moore, 1993). Alpha diversity refers to measures of species richness within a single community or site. Beta diversity is a measure of species richness across communities or sites or both. The ecological biogeography of tropical organisms should incorporate data from both alpha and beta diversities (Huston, 1996; Myers and Giller, 1988; Schoener, 1988). Therefore, it is useful to ask biogeographic questions in one subregion of a taxon's distribution (Laws and Eeley, 2000), such as the Guianas (northern Brazil, eastern Venezuela, Suriname, French Guiana, and Guyana). The Guianas are characterized by high levels of floral endemism. For example, de Granville (1988) found that 35% ($N = 88$) of the vascular plants surveyed in South America were endemic to the Guianas. Within the Guianas, Guyana is unique in that it retains *ca.* 86% of its original rain forest (Huber *et al.*, 1995). Unlike studies at continental and global levels, in Guyana primate diversity does not covary with latitude (Lehman, 1999). Thus, biogeographic studies of primates in Guyana are free of conflicting variables such as forest loss, forest fragmentation, latitudinal effects, and edge effects.

Table I. Primate species found in Guyana

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

[a]Not used in further analyses due to lack of data on distribution and density.

Of the 9 primate species in Guyana (Table I), only 3—red howlers, wedge-capped capuchins, and white faced sakis—occur throughout the country (Lehman, 1999). The other 6 species live in only some parts of Guyana, though they range throughout the forested areas of Suriname, French Guiana, northern Brazil, and eastern Venezuela (Rowe, 1996). Moreover, this geographic variation in primate diversity 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 (Rowe, 1996). The question arises then as to how patterns of diet and habitat use relate to the geographic distribution of primates in Guyana?

I aimed to determine ecological correlates to patterns of primate distribution in Guyana. Specifically, I address the following questions: (1) how do dietary breadth and habitat breadth relate to the geographic distribution of primates in Guyana and (2) do specialists use relatively smaller habitats than those exploited by generalists? My data reveal that habitat breadth is strongly correlated with geographic range size for primates in Guyana. However, I documented that specialists are absent from small habitats.

METHODS

Location and Climate

The data derived from 1,725 km of surveys I conducted in Guyana, a small country of 215,000 km^2 on the northeastern coast of South America, between 56° 20′ and 61° 23′ W and 1° 10′ and 8° 35′ N (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. Mean annual precipitation is 2,000–3,400 mm,

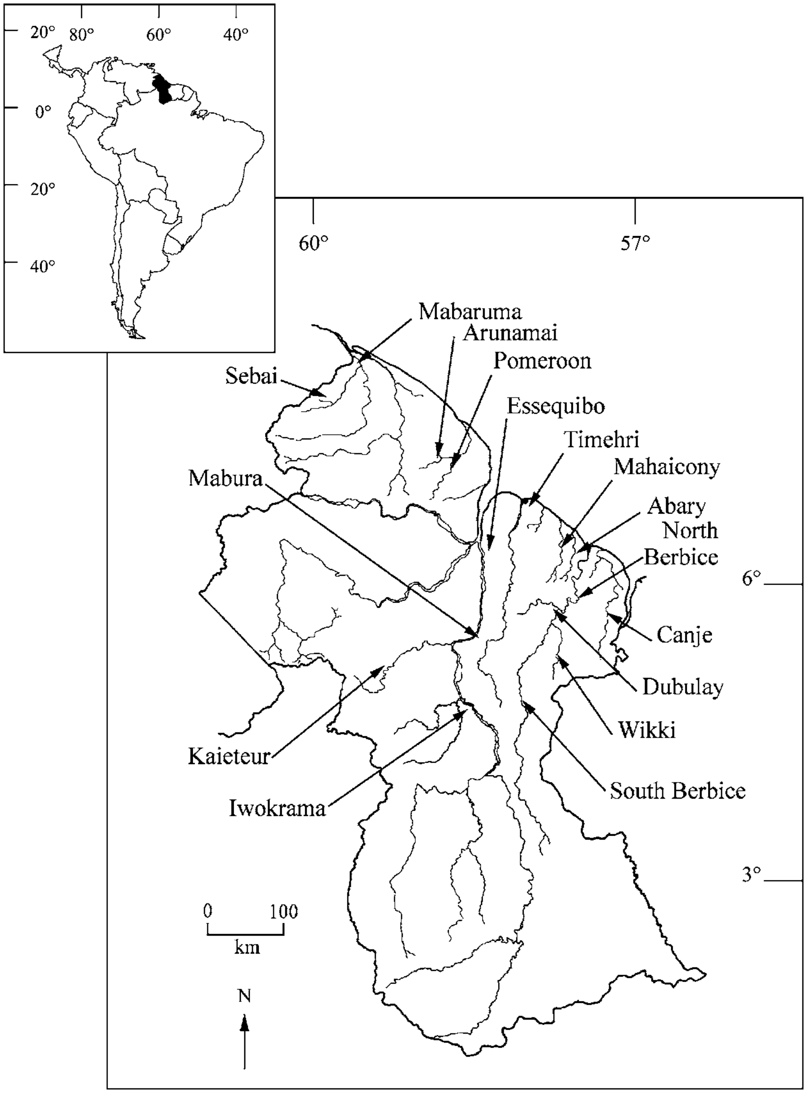

Fig. 1. Location of Guyana and location of 16 survey sites censused.

and is neither evenly distributed throughout the year nor throughout the country (ter Steege, 1993). 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 runs through to November or December. It is characterized by monthly rainfall of <200 mm. The short dry season is usually from February to April.

Each of the 9 primate species in Guyana 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.*, 2000), I omitted them from the analyses.

Survey Data

I surveyed the distribution and diversity of primates in forests and along rivers at 16 sites in Guyana (Fig. 1). Complete descriptions of forest structure and composition for each site were published by Lehman (1999, 2000). I collected survey data during 3 periods: (1) November 1994 to June 1995, (2) September 1995 to June 1996, and (3) June to August 1997. They 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 along transects lines at a rate of 1.0 km/h, stopping every 10 min to listen for the sounds of movement in the forest. I measured transects and marked them every 10 m with numbered blocks or flagging tape before the 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 chose 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 to 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. Thus, I used established trails in the protected areas.

I determined the location of primate groups 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). I took GPS readings during all river sightings and later verified them on 1:50,000 topographic maps. I analyzed and georeferenced the data and data from other primate surveys in the country

(Barnett *et al.*, 2000; Comiskey *et al.*, 1993; Muckenhirn *et al.*, 1975; Parker *et al.*, 1993; Sussman and Phillips-Conroy, 1995) via ArcView 3.1 (Environmental Systems Research Institute, Inc., Redlands, CA) to produce detailed maps and geographic range sizes for each primate species in Guyana (Lehman, in press; Lehman *et al.*, in press). I then determined the presence or absence of each species in a habitat via the GIS database on primate distribution and a digitized version of a vegetation map of Guyana (Huber *et al.*, 1995).

Ecological Variables

Habitat breadth is the total number of different habitat types occupied by each species (Eeley and Foley, 1999; Harcourt *et al.*, 2002; Wright and Jernvall, 1999). Following Eeley and Foley (1999), I used the total number of different food categories exploited by each species as a measure of dietary breadth: fruits, leaves, seeds, pith, insects, nectar, gum, invertebrates, vertebrates, and flowers. Because there are few data on the feeding ecology of Guyanese primates, I used dietary data collected on conspecifics in Venezuela and Suriname (Braza *et al.*, 1981; Eisenberg, 1989; Julliot and Sabatier, 1993; Julliot and Simmen, 1998; Kessler, 1995; Kinzey and Norconk, 1993; Miller, 1997; Mittermeier and van Roosmalen, 1981; Norconk, 1997; Norconk *et al.*, 1998; Packa *et al.*, 1999; Simmon and Sabatier, 1996; van Roosmalen, 1985b, 1987; Youlatos, 1998). The dietary categorization does not discriminate between dietary type breadth—number of food categories exploited—and dietary species diversity: number of plant species exploited. For example, a hypothetical primate species could be a dietary type specialist if it exploited only 2 food categories, e.g., fruits and leaves, but a dietary species generalist if it exploited hundreds of plant species within each of the 2 food types. Primate diversity refers to the number of primate species in a geographic area.

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 have been surveyed as the dependent variable in analyses of species-area relationships. I conducted linear regression analyses via species counts as the dependent variable and geographic range as the independent variable. I tested statistical significance of the variance within the populations via a one-way ANOVA. I used Spearman rank correlations (r_s) to determine ecological, biogeographic, and body size correlates to geographic distribution. I included mean body mass for each species by sex in the analyses as additional measures of resource requirements (Harcourt *et al.*, 2002; Smith and Jungers, 1997). I conducted statistical analyses via SPSS 10.0. The alpha level is 0.05 for all analyses.

RESULTS

Table II shows the number of sites where I saw each primate species and the estimated geographic range size for 8 primate species in Guyana. Red howlers squirrel monkeys, wedge-capped capuchins, and white-faced sakis occur at many sites and they have large geographic ranges. Brown capuchins have neither a large geographic area nor a high number of sites where they were sighted. Spider monkeys, brown bearded sakis, and golden-handed tamarins have small geographic ranges and low numbers of sites where they were sighted. Geographic range size is a major determinant of the number of sightings of 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 species occurred (Fig. 2). However, visual inspection of the data reveals that the population is not normally distributed and that a confounding variable may be affecting the population.

Tables III and IV contain data on habitat size, primate diversity by habitat use, and dietary breadth. Habitat size is positively correlated with the diversity of primate species in Guyana ($r_s = 0.75$, $N = 13$, $p = 0.004$). Red howlers and wedge-capped capuchins range into all habitat types in

Table II. Number of total sites at which each species has been sighted, sighting frequency, and geographic range size for 8 species in Guyana

Species	Total # sites at which species sighted[a]	Sighting frequency (# groups/100 km)[a]	Geographic range (km^2)
Alouatta seniculus	26	3.30	177,139
Ateles paniscus	9	0.35	70,433
Cebus apella	12	1.74	80,120
Cebus olivaceus	20	1.51	177,139
Chiropotes satanas	9	0.29	62,911
Pithecia pithecia	15	1.22	177,139
Saguinus midas	9	0.81	47,794
Saimiri sciureus	23	3.54	174,394
Total	123	3.30	

[a]From Lehman (1999).

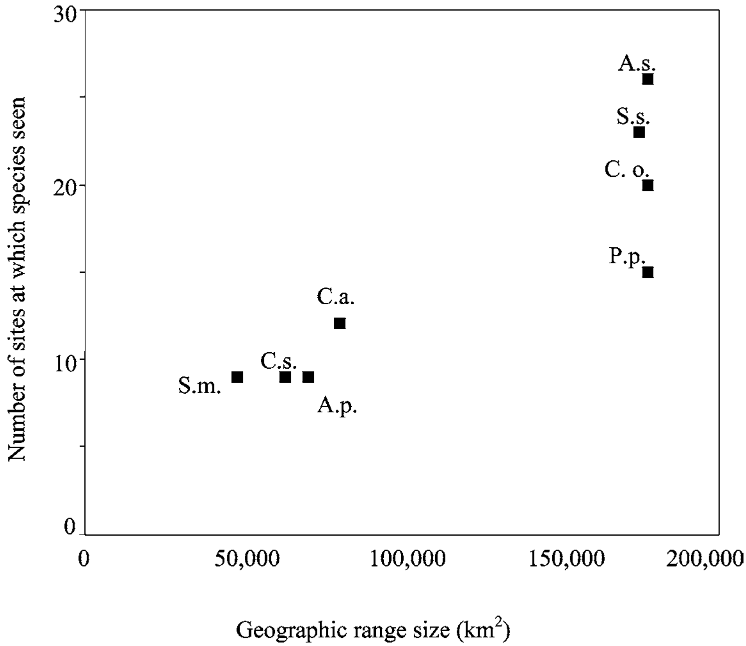

Fig. 2. Relationship between the geographic range size of 8 primates species and the number of sites at which each species was seen in Guyana. (A.s. = *Alouatta seniculus*, A.p. = *Ateles paniscus*, C.a. = *Cebus apella*, C.o. = *Cebus olivaceus*, C.s. = *Chiropotes satanas*, P.p. = *Pithecia pithecia*, S.m. = *Saguinus midas*, S.s. = *Saimiri sciureus*).

Guyana. Brown capuchins and golden-handed tamarins tend to range in the larger habitats (i.e., total area 4,447 km^2). Spider monkeys and bearded sakis only range into large habitats. Habitat selection varies for white-faced sakis and squirrel monkeys. Red howlers and wedge-capped have the highest habitat breadth scores. Golden-handed tamarins, spider monkeys, and bearded sakis have the lowest habitat breadth scores. Table IV shows the dietary components that I used to estimate dietary breadth. Dietary breadth scores are lowest for red howlers and highest for brown capuchins and golden-handed tamarins (Table V).

Table VI shows the correlations between ecological and biogeographic variables for 8 primate species in Guyana. There is no significant correlation between body mass by sex and any of the ecological or biogeographic variables. Geographic range size is significantly correlated with habitat breadth ($r_s = 0.924$, $N = 8$, $p = 0.001$) but not with dietary breadth ($r_s = -0.443$, $N = 8, p = 0.27$) for 8 primate species in Guyana (Fig. 3).

Table III. Habitat use by 8 species in Guyana

Habitat[a]	Total area (km^2)	*Alouatta*	*Ateles*	*Chiropotes*	*Cebus apella*	*C. olivaceus*	*Pithecia*	*Saguinus*	*Saimiri*	Total
Rain forest	46,370	x	x	x	x	x	x	x	x	8
Southern forest	41,951	x	x	x	x	x	x	x	x	8
Mora forest	22,242	x	x	x	x	x	x	x	x	8
Premontane forest	13,655	x	x	x	x	x	x	–	–	6
Lower montane forest	12,928	x	–	–	x	x	x	–	–	4
Wallaba forest	11,997	x	x	x	x	x	x	x	x	8
Kanuku forest	8,112	x	x	x	x	x	x	–	–	6
SE Seasonal forest	6,884	x	x	x	x	x	x	x	x	8
Swamp forest	6,267	x	–	–	x	x	–	–	x	4
Low seasonal forest	4,447	x	–	–	x	x	x	x	x	6
Swamp woodland	1,236	x	–	–	–	x	–	–	x	3
Eastern Wallaba forest	641	x	–	–	–	x	x	–	x	4
Marsh woodland	409	x	–	–	–	x	–	–	x	3
Total	177,139	13	7	7	10	13	10	6	10	

[a]x = present in that habitat, – = not found in that habitat.

Table IV. Dietary breadth in 8 species of primates in Guyana (Dietary data from Braza *et al.*, 1981; Eisenberg, 1989; Julliot and Sabatier, 1993; Julliot and Simmen, 1998; Kessler, 1995; Kinzey and Norconk, 1993; Miller, 1997; Mittermeier and van Roosmalen, 1981; Norconk, 1997; Norconk *et al.*, 1998; Packa *et al.*, 1999; Simmon and Sabatier, 1996; van Roosmalen, 1985b, 1987; Youlatos, 1998)

Diet type[a]	*Alouatta*	*Ateles*	*Chiropotes*	*Cebus apella*	*C. olivaceus*	*Pithecia*	*Saguinus*	*Saimiri*
Fruits	x	x	x	x	x	x	x	x
Leaves	x	x	x	–	–	x	–	–
Seeds	–	–	x	x	x	x	x	–
Pith	–	–	–	x	–	–	–	–
Insects	–	x	x	–	x	–	–	x
Nectar	–	–	–	x	x	–	x	x
Gum	–	–	–	–	–	–	x	–
Invertebrates	–	–	–	x	–	x	x	–
Vertebrates	–	–	–	x	x	–	x	x
Flowers	x	x	x	–	–	x	–	–
Total	3	4	5	6	5	5	6	4

[a]x = eaten, – = not eaten.

DISCUSSION

My biogeographic data support a correlation between geographic range size and habitat breadth rather than dietary breadth in the primates of Guyana. In this model, red howlers and wedge-capped capuchins are habitat generalists because they are widely distributed and range into all habitat types. The following species tend to be habitat specialists: spider monkeys, brown bearded sakis, and golden-handed tamarins. My data differ from studies of other primate communities in that the researchers reported a positive correlation between range size and dietary breadth (Eeley and Foley, 1999; Harcourt *et al.*, 2002; Jones, 1997). Contrary to theoretical

Table V. Habitat breadth, dietary breadth, and body mass by sex for 8 species in Guyana

Species	Habitat breadth	Dietary breadth	Mean male body weight (kg)[a]	Mean female body weight (kg)[a]
Alouatta seniculus	13	3	6.69	5.21
Ateles paniscus	7	4	9.11	8.44
Cebus apella	10	6	3.65	2.52
C. olivaceus	13	5	3.29	2.52
Chiropotes satanas	7	5	2.90	2.58
Pithecia pithecia	10	5	1.94	1.58
Saguinus midas	6	6	0.51	0.57
Saimiri sciureus	10	4	0.78	0.66

[a]From Smith and Jungers (1997).

Table VI. Spearman rank correlations (r_s) between ecological and biogeographic variables for 8 primate species in Guyana

Variables	No. of sightings	Sighting rate	Geographic range	Habitat breadth	Dietary breadth	Mean male body weight	Mean female body weight
No. of sightings	—	**0.878**	**0.850**	**0.886**	−0.544	0.073	−0.049
Sighting rate	0.004	—	0.610	0.704	−0.309	−0.024	−0.252
Geographic range	0.008	0.108	—	**0.924**	−0.443	0.244	0.110
Habitat breadth	0.003	0.051	0.001	—	−0.404	0.346	0.193
Dietary breadth	0.163	0.457	0.272	0.321	—	−0.432	−0.527
Mean male body weight	0.863	0.955	0.560	0.401	0.285	—	**0.922**
Mean female body weight	0.908	0.548	0.795	0.648	0.178	0.001	—

Note. Numbers above the diagonal refer to correlation values. Numbers below the diagonal refer to associated significance levels. Sample size of 8 for all results. Significant correlations ($P < 0.05$) are highlighted in bold text.

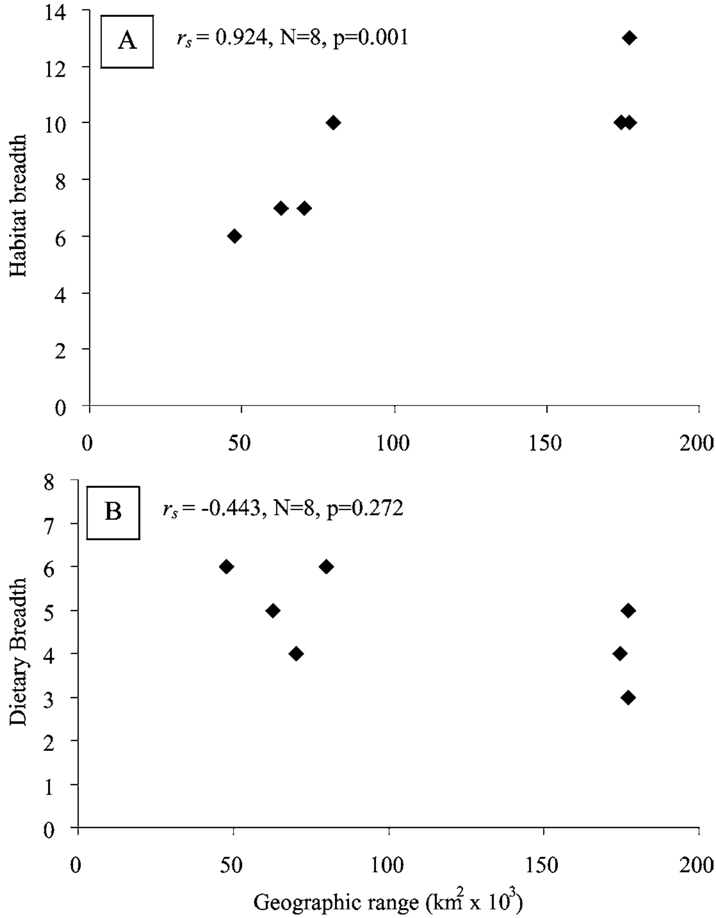

Fig. 3. Correlations between geographic range and habitat breadth (A) and dietary breadth diversity (B) for 8 primate species in Guyana.

work by Hanski and Gyllenberg (1997), I found that only generalists range into small habitats such as swamp woodlands.

The reason for a generalist-specialist reversal for habitat use is likely due to low nutrient levels and plant diversity in Guyana. The tropical forests of Guyana are under extremely tight nutrient budgets because they rest upon nutrient-poor soils (Gibbs and Barron, 1993; ter Steege, 1993). Concomitantly, forests in Guyana contain few plant families that are valuable food resources for primates (Comiskey *et al.*, 1993; Ek, 1997; Lehman, 2000; Terborgh and Andresen, 1998; ter Steege, 1993). For example, Terborgh and Andresen (1998) analyzed floristic patterns in tree plots at 29 sites in South America. They found very few trees of Palmae and Moraceae in *terra firme* plots in Guyana. The 2 families contain tree species that are critical food resources during periods of low resource abundance for many platyrrhines (Pontes, 1997; Terborgh, 1983; van Roosmalen, 1985a). Small habitats—such as swamp and palm marsh woodlands—tend to contain fewer fruiting plant species eaten by primates than *terra firme* forests do in the Guianas (Teunissen, 1993). Moreover, fruits and leaves in swamps and other inundated forests are often low in protein and readily digestible carbohydrates and rich in fiber and plant secondary compounds (Kathiresan and Ravikumar, 1995; Simmen and Sabatier, 1996). The geographic and habitat variations in fruit quality and abundance are important because each of the 8 primate species in Guyana eat at least some fruits, and 3 of them—spider monkeys, bearded sakis, and white-faced sakis—are among the most frugivorous of all South American primates (Kinzey and Norconk, 1993; Norconk, 1997; van Roosmalen, 1985b). Spider monkeys, bearded sakis, brown capuchins, and white-faced sakis do not range into swamp forests, swamp woodlands, or palm marsh woodlands in Guyana. Conversely, I found that habitat generalists that are folivore-frugivores (red howlers), omnivores (wedge-capped capuchins), or insectivores (squirrel monkeys) range into small habitats such as swamp forests. Furthermore, wedge-capped capuchins may forage in small habitats to avoid competition with congenera during periods of food scarcity. I documented that the low plant productivity in Guyanese forests may reduce the abundance of food resources and result in scramble competition between wedge-capped and brown capuchins (Lehman, 2000). Thus, some habitat specialists, such as brown capuchins and bearded sakis, tend to be dietary type generalists. They must feed on a variety of food types in large habitats. Conversely, some habitat generalists, such as red howlers and squirrel monkeys, tend to be dietary type specialists. Only habitat generalists can subsist on the few edible, low-quality foods found in small habitats in Guyana. Therefore, I hypothesize that small habitats do not contain enough high-quality fruit resources to support habitat specialists, which tend to be highly frugivorous primate species in Guyana.

Primate body size is not correlated with any of the ecological variables used in my study. Body size is associated allometrically with metabolic rate, energetic demands, and physical performance in animals (Schmidt-Nielsen, 1997). In terms of energetic demands and body size, large animals tend to require larger home ranges and feeding areas than those of small animals (Calder, 1984). Thus, it has been hypothesized that small body size is associated with high species diversity (Brown, 1995). However, few data support the body size-diversity hypothesis because species may inherit features from a common ancestor rather than evolve them independently (Harvey and Pagel, 1991). For example, Gittleman and Purvis (1998) found no relationship between body size and species diversity in primates at the global level. In another example, Peres and Janson (1999) found that body size is a poor predictor of geographic range size in 21 ecospecies of South American primates. Ultimately, the lack of relationship between body size and species diversity may be a consequence of the conservative phylogenetic and dietary patterns in primates generally, and those in South America in particular (Fleagle and Reed, 1996; Gittlemann and Purvis, 1998; Wright and Jernvall, 1999).

There may be 2 reasons for the differences between my biogeographic data on the primates of Guyana and those from other studies: (1) dietary breadth as a weak indicator of multidimensional niche and (2) variations in sample sizes. First, the measure of dietary breadth that I used may be only a weak aspect of multidimensional niche (Hutchinson, 1957). The multidimensional niche concept is a theoretical explanation of how different environmental factors limit abundance and distribution. Because each species has a range of tolerances and preferences along every niche axis (habitat, diet, rainfall, etc.), a species can only live in areas where niche axes are within ranges of tolerance. Population growth rates are highest where the greatest number of niche axes is closest to most optimal conditions (Brown, 1995). We should employ the most precise measures of niche possible to determine ecological correlates to biogeographic patterns. For example, red howlers having a low niche breadth of 3 dietary categories, i.e., dietary type specialists. However, there is considerable diversity in the number of plant species exploited within each of the 3 food categories because red howlers are highly selective in the plant species they exploit. Julliot and Sabatier (1993) found that red howlers consume plant materials from 195 plant species in French Guiana. Thus, red howlers are both dietary type specialists and dietary species generalists. Conversely, food categories for some monkeys are dominated by only 1–2 plant species. For example, only 2 plant species (*Pradosia caracasana* and *Oryctanthus alveolatus*) account for 53% of the total annual diet of bearded sakis (Norconk, 1997; Peetz, 2001). Consequently, bearded sakis are dietary type generalists and may be dietary species specialists. Therefore, researchers testing biogeographic hypotheses associated with dietary breadth should consider including multivariate indicators of both the types of food categories eaten and the number of plant species exploited, e.g., Shannon-Weiner diversity and Simpson's dominance indices.

Secondly, my regional sample size of 8 primate species is low versus studies on global or continental levels (Arita *et al.*, 1990; Eeley and Foley, 1999; Harcourt *et al.*, 2002). Small sample sizes often include only a truncated distribution of relative abundances, and they also tend to favor the most common species (Hubbell, 2001). Small samples are also very sensitive to outliers, which can be particularly problematic in statistics because one sample point can have a disproportionately large effect on the slope of the correlation equation. Because generalist species tend to be represented more in surveys, a positive correlation between habitat breadth and geographic range may occur simply as a by-product of sampling (Vazquez and Simberloff, 2002).

I found that geographic range size correlates only with habitat breadth and that specialists tend to range into large rather than small habitats in Guyana. I hypothesize that low tree species diversity and abundance and low fruit production may influence biogeographic patterns in the primates in Guyana. Researchers interested in studying ecological correlates to biogeographic patterns in primates should consider employing more robust indices of dietary breadth.

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