

RESEARCH ARTICLE

Geographic Comparison of Plant Genera Used in Frugivory Among the Pitheciids *Cacajao*, *Callicebus*, *Chiropotes*, and *Pithecia*

SARAH A. BOYLE^{1*}, CYNTHIA L. THOMPSON², ANNEKE DELUYCKER³, SILVIA J. ALVAREZ⁴, THIAGO H.G. ALVIM⁵, ROLANDO AQUINO⁶, BRUNA M. BEZERRA⁷, JEAN P. BOUBLI⁸, MARK BOWLER⁹, CHRISTINI BARBOSA CASELLI¹⁰, RENATA R.D. CHAGAS¹¹, STEPHEN F. FERRARI¹², ISADORA P. FONTES¹³, TREMAINE GREGORY¹⁴, TORBJØRN HAUGAASEN¹⁵, STEFANIE HEIDUCK¹⁶, ROSE HORES¹⁷, SHAWN LEHMAN¹⁸, FABIANO R. DE MELO¹⁹, LEANDRO S. MOREIRA²⁰, VIVIANE S. MOURA²¹, MARIANA B. NAGY-REIS²², ERWIN PALACIOS²³, SUZANNE PALMINTERI²⁴, CARLOS A. PERES²⁵, LILIAM PINTO²⁶, MARCIO PORT-CARVALHO²⁷, ADRIANA RODRÍGUEZ²³, RICARDO R. DOS SANTOS^{28,29}, ELEONORE Z.F. SETZ²², CHRISTOPHER A. SHAFFER³⁰, FELIPE ENNES SILVA³¹, RAFAELA F. SOARES DA SILVA³², JOÃO P. SOUZA-ALVES¹¹, LEONARDO C. TREVELIN³³, LIZA M. VEIGA^{33†}, TATIANA M. VIEIRA³¹, MARY E. DUBOSE¹, AND ADRIAN A. BARNETT³⁴

¹Department of Biology, Rhodes College, Memphis, Tennessee

²Department of Biomedical Sciences, Grand Valley State University, Allendale, Michigan

³Smithsonian-Mason School of Conservation, Front Royal, Virginia

⁴Department of Biology, University of Maryland, College Park, Maryland

⁵Research Support Foundation, Universidade Federal de Goiás, Jataí, Goiás, Brazil

⁶Universidad Nacional Mayor de San Marcos, Lima, Peru

⁷Department of Zoology, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

⁸University of Salford, Manchester, United Kingdom

⁹San Diego Zoo Global Institute for Conservation Research, San Diego, California

¹⁰Department of Biological Sciences, Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brazil

¹¹Department of Systematics and Ecology, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil

¹²Department of Ecology, Universidade Federal de Sergipe, São Cristóvão, Sergipe, Brazil

¹³Municipal Environment Secretariat, Aracaju, Sergipe, Brazil

¹⁴Center for Conservation Education and Sustainability, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC

¹⁵Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

¹⁶Deutsches Primatenzentrum, Göttingen, Germany

¹⁷Department of Anthropology, Southern Illinois University, Carbondale, Illinois

¹⁸Department of Anthropology, University of Toronto, Toronto, Ontario, Canada

¹⁹Biological Sciences Program, Universidade Federal de Goiás, Jataí, Goiás, Brazil

²⁰Center of Ecological and Environmental Education Studies, Carangola, Minas Gerais, Brazil

²¹Program in Ecology and Conservation, Universidade Federal de Sergipe, São Cristóvão, Sergipe, Brazil

²²Biology Institute, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil

²³Conservation International Colombia, Bogotá D.C., Colombia

²⁴RESOLVE, Washington, DC

²⁵School of Environmental Sciences, University of East Anglia, Norwich, United Kingdom

²⁶National Center for Amazonian Biodiversity Research and Conservation, Chico Mendes Institute for Biodiversity Conservation, Manaus, Amazonas, Brazil

²⁷São Paulo Forestry Institute, São Paulo, Brazil

²⁸Centre for Agrarian and Environmental Sciences, Universidade Federal de Maranhão, Chapadinha, Maranhão, Brazil

²⁹Center for Geospatial Research, University of Georgia, Athens, Georgia

³⁰Department of Anthropology, Grand Valley State University, Allendale, Michigan

³¹Mamirauá Institute for Sustainable Development, Tefé, Amazonas, Brazil

³²Program in Zoology, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil

³³Department of Zoology, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil

³⁴Biodiversity Unit, National Institute for Amazonian Research, Manaus, Amazonas, Brazil

Pitheciids are known for their frugivorous diets, but there has been no broad-scale comparison of fruit genera used by these primates that range across five geographic regions in South America. We compiled 31 fruit lists from data collected from 18 species (three *Cacajao*, six *Callicebus*, five *Chiropotes*, and four *Pithecia*) at 26 study sites in six countries. Together, these lists contained 455 plant genera from 96 families. We predicted that 1) closely related *Chiropotes* and *Cacajao* would demonstrate the greatest similarity in fruit lists; 2) pitheciids living in closer geographic proximity would have greater similarities in fruit lists; and 3) fruit genus richness would be lower in lists from forest fragments than continuous forests. Fruit genus richness was greatest for the composite *Chiropotes* list, even though *Pithecia* had the greatest overall sampling effort. We also found that the *Callicebus* composite fruit list had lower similarity scores in comparison with the composite food lists of the other three genera (both within and between geographic areas). *Chiropotes* and *Pithecia* showed strongest similarities in fruit lists, followed by sister taxa *Chiropotes* and *Cacajao*. Overall, pitheciids in closer proximity had more

similarities in their fruit list, and this pattern was evident in the fruit lists for both *Callicebus* and *Chiropotes*. There was no difference in the number of fruit genera used by pitheciids in habitat fragments and continuous forest. Our findings demonstrate that pitheciids use a variety of fruit genera, but phylogenetic and geographic patterns in fruit use are not consistent across all pitheciid genera. This study represents the most extensive examination of pitheciid fruit consumption to date, but future research is needed to investigate the extent to which the trends in fruit genus richness noted here are attributable to habitat differences among study sites, differences in feeding ecology, or a combination of both. *Am. J. Primatol.* © 2015 Wiley Periodicals, Inc.

Key words: bearded saki; diet; saki; titi; uacari

INTRODUCTION

The composition of primate diets can be attributed to body size, gut morphology, group size, and home range size, as well as the spatial distribution, quality, and availability of food resources [Garber, 1987; Hemingway & Bynum, 2005; Robbins & Hohmann, 2006]. Dietary differences occur between primate taxa and between geographic locations [Chapman et al., 2002a; Porter, 2001; Wahungu, 1998; Zhou et al., 2009]. Previous studies have identified several factors that appear to strongly influence diet differences, such as niche partitioning and competition [Harcourt & Nash, 1986; Hadi et al., 2012], forest composition and seasonal fluctuations in fruit availability [Brugiere et al., 2002; Stevenson et al., 2000], habitat differences associated with temperate or cool habitats [Agetsuma & Nakagawa, 1998], and plant and soil chemistry [Fashing et al., 2007]. Given the extent of diet variability in primates, the goal of our study was to investigate the degree of similarity in frugivory for the four genera of pitheciid primates (*Cacajao*, *Callicebus*, *Chiropotes*, and *Pithecia*) across geographic regions.

Primates that specialize on ripe fruit encounter periods when fruit availability declines because of seasonal variation in fruit production [Peres, 1994a]. During such times of fruit scarcity, some primates use alternative resources, such as leaves and flowers [González-Zamora et al., 2009; Marshall et al., 2009; Stevenson et al., 2000], but many frugivorous primates maintain a fruit-rich diet throughout the year [Boyle et al., 2012; Chapman, 1988; Wich et al., 2006]. Pitheciids eat fruit primarily, including seeds [Norconk et al., 2013]. Flowers, leaves, bark, and invertebrates are also included as minor components of their diets [Barnett et al., 2013a,b; Boubli, 1999; Boyle et al., 2012; Norconk & Setz, 2013; Palacios & Rodríguez, 2013]. Because pitheciids consume both ripe and unripe fruits, they can use fruit resources throughout the year [Boyle et al., 2012; Norconk & Veres, 2011], thereby buffering periods of severe fruit scarcity [Palminteri et al., 2012]. Whole fruits and fruit parts comprise more than 85% of the diet of *Cacajao*, with many foods that are eaten unripe [Barnett, 2010; Boubli, 1999; Bowler & Bodmer, 2011]. In *Chiropotes* [Boyle et al., 2012; Gregory,

2011; Kinzey & Norconk, 1990; Shaffer, 2013] and *Pithecia* [Norconk & Conklin-Brittain, 2004; Palminteri et al., 2012], fruits have been documented to constitute up to 95% of the monthly diet. *Callicebus* diets include a lower proportion of fruits than other pitheciids, but fruits still account for more than half (50–82%) of the diet [Alvarez & Heymann, 2012; Caselli & Setz, 2011; Palacios et al., 1997; Palacios & Rodríguez, 2013; Souza-Alves et al., 2011]. Overall, pitheciids eat fruits at relatively high frequencies year-round, and these fruits are generally ones that most other frugivorous primates cannot access or do not exploit [Ayres & Prance, 2013; Norconk et al., 2013].

Specialized dentition (i.e., hypertrophied procumbent incisors; robust canines; dished, cusplless molars) and robust, strongly fused mandibles enable pitheciids to process mechanically protected fruit [Kinzey, 1992; Norconk et al., 2009; Kay et al., 2013] and gain access to seeds. The masticatory systems of *Cacajao* and *Chiropotes* are very similar and highly derived, and permit sclerocarpic foraging on mechanically resistant foods to a greater degree than *Callicebus* [Kinzey, 1992; Norconk et al., 2009, 2013; Rosenberger, 1992], while *Pithecia* is intermediate in dental and dietary specialization [Kinzey, 1992]. These morphological adaptations enable pitheciids to consume a range of fruit parts and species.

Pitheciids diverged from the other platyrrhines approximately 22 million years ago [Schrage, 2007]. *Callicebus* diverged from the other pitheciids 16 million years ago, followed by *Pithecia* 9 million years ago, and the *Chiropotes* and *Cacajao* lineages diverging 5 million years ago [Schrage, 2007].

†In memoriam.

*Correspondence to: Sarah A. Boyle, Rhodes College, Department of Biology, 2000 North Parkway, Memphis, TN 38112. E-mail: sarahannboyle@gmail.com

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Because primates that are phylogenetically closer frequently have been found to share more similar diets than primates that are more distantly related [Porter et al., 2014], our first aim was to test whether the diets of *Chiropotes* and *Cacajao* are more similar to each other than either is to *Pithecia* and *Callicebus*.

The geographic distribution of the pitheciids covers 600 million ha in 10 South American countries [Boyle, 2014; IUCN, 2013]. Among pitheciids, *Cacajao* has the smallest total geographic range and *Callicebus* the largest, and the range of *Callicebus* extends beyond that of other pitheciids in approximately 25% of its geographic range (i.e., southern Bolivia, Paraguay, southwestern Brazil, Atlantic Forest of Brazil) [Boyle, 2014; IUCN, 2013]. Pitheciid distribution can be divided into five geographic regions—Guiana Shield, Western Amazon, Central Amazon, Eastern Amazon, and Atlantic Forest—corresponding to the canonical divisions of Neotropical biogeography [Ribeiro et al., 2009;]. In a comparison of plots from the three Amazon regions and the Guiana Shield, tree alpha-diversity was greatest in Western and Central Amazon and lowest in Eastern Amazon and the Guiana Shield [ter Steege et al., 2000]. The Atlantic Forest is geographically distant and distinct from the Amazon and the Guiana Shield, separated by the Brazilian Caatinga and Cerrado, and by the Paraguayan, Argentinian, and Bolivian Chaco [Oliveira-Filho & Fontes, 2000]. Of the 20,000 plant species in Brazil's Atlantic Forest, 40% are endemic [Forzza et al., 2012;]. Thus, given the large geographic range of the pitheciids and the differences in plant composition across the major geographic regions, our second aim was to determine if similarities in fruit genera used by the pitheciids correlated with the geographic regions inhabited by the pitheciid genera.

Within the geographic range of the pitheciids, 5% of the forest was lost from 2000 to 2012, and the greatest extent of deforestation occurred in the southern portion of the Central Amazon, the Eastern Amazon, Paraguayan Chaco, and western portion of the Western Amazon [Boyle, 2014]. In addition, approximately 88–92% of the original Atlantic Forest has been deforested, and much of the remaining forest consists of fragments <250 ha [Myers et al., 2000; Ribeiro et al., 2009]. Forest fragmentation greatly affects plant communities in both the Atlantic Forest [Oliveira et al., 2004] and the Amazon [Laurance et al., 2011]. Forest fragments can experience an increase in tree mortality, an increase in the prevalence of pioneer species, and changes in tree recruitment patterns [Laurance et al., 2011], which could limit the plant taxa available as food for primates. Given that some pitheciids living in heavily modified or fragmented habitats use a different set of plant taxa as food than do conspecific populations living in continuous forest

[Boyle et al., 2012; Heiduck, 2002; Souza-Alves, 2013], our third aim was to determine if pitheciids in continuous forest used more fruit genera than pitheciids in forest fragments.

In this study we investigated patterns in fruit consumption across pitheciid genera and across the geographic regions they inhabit. We hypothesized that the particular fruits included in the diet vary by primate taxon and geographic location. Specifically, we tested these three predictions:

1. Given their similarities in mandibular and dental morphology [Kinzey, 1992; Norconk et al., 2009, 2013; Rosenberger, 1992], and their closer phylogenetic distances [Perez & Rosenberger, 2014; Schrago, 2007], *Cacajao* and *Chiropotes* would share more similarity in fruit genera used than either of them would share with *Pithecia* or *Callicebus*.
2. Given the floristic differences in habitats between the Guiana Shield and Amazon Basin [ter Steege et al., 2000], and the high level of plant endemism in the Atlantic Forest [Forzza et al., 2012; Myers et al., 2000], pitheciids living in closer geographic proximity would share more similarity in fruit genera used.
3. Given that forest fragmentation can greatly influence tree assemblages and lead to increased tree mortality [Laurance et al., 2011; Oliveira et al., 2004], pitheciid populations in forest fragments would have diets with lower richness in fruit genera than populations in continuous forest.

Here we use pitheciids as a case study to examine to what extent the set of fruit genera used by different members of a primate clade correspond with phylogenetic and geographic similarity. Similar examinations could be completed in the future with other primate families to add to the understanding of how primates differ in diet across their geographic ranges. Although dietary richness and variation have been examined in Neotropical primates at the primate species level (e.g., *Ateles geoffroyi* [González-Zamora et al., 2009]), genus level (e.g., *Ateles* [Russo et al., 2005]), or more generally at the family level (e.g., comparing *Lagothrix lagotricha cana* from one site in the Brazilian Amazon to other atelids [Peres, 1994b]), our study is unique in its extent of the analysis at the primate family level across a continent.

METHODS

Assembling Site-Specific and Regional Fruit Lists

We compiled 31 “fruit lists” for 18 pitheciid species at 26 study sites by combining information

TABLE I. Characteristics of the 31 Fruit Lists Analyzed

Fruit list no.	Pitheciid ^a	Site ID ^b	Site name	Forest extent ^c	Fruits used ^d			Contact hours	Source ^e
					Families	Genera	Species		
1	<i>Cacajao</i>	12 CA	Mamirauá, Brazil	Cont.	30	55	75	834	Ayres [1986] Silva [unpublished]
2	<i>C. calvus calvus</i>	7 WA	Tamshiyacu-Tahuayo, Peru	Cont.	21	33	44	115	Aquino & Encarnación [1999], Hores [unpublished]
3	<i>C. c. ucayalii</i>	8 WA	Rio Yavari, Peru	Cont.	33	69	100	945	Bowler & Bodmer [2011]
4	<i>C. melanocephalus</i>	11 CA	Pico de Neblina National Park, Brazil	Cont.	30	68	105	120	Boubli [1999]
5	<i>C. ouakary</i>	14 CA	Jau National Park, Brazil	Cont.	35	72	103	108	Barnett & Bezerra [unpublished]
6	<i>Callitcebus</i>	21 AF	Fazenda Trapsa, Brazil	14 ha (F)	26	39	54	1203	Souza-Alves et al. [2011]
7	<i>C. coimbrai</i>	22 AF	Mata do Junco Wildlife Refuge, Brazil	522 ha (F)	25	33	37	654	Souza-Alves & Chagas [unpublished]
8	<i>C. lugens</i>	9 WA	Mosiro Itajura (Caparú), Colombia	Cont.	24	37	52	240	Alvarez & Heymann [2012]
9	<i>C. melanochir</i>	23 AF	Lemos Maia Biological Station, Brazil	80 ha (F)	26	44	60	460	Heiduck [1997]
10	<i>C. nigrifrons</i>	24 AF	Campinas, Brazil	24 ha (F)	28	50	61	547	Nagy-Reis [unpublished]
11	<i>C. nigrifrons</i>	25 AF	Serra do Japi Municipal Ecological Reserve, Brazil	Cont.	34	53	68	983	Caselli & Setz [2011], Caselli [unpublished]
12	<i>C. nigrifrons</i>	26 AF	Cantareira State Park, Brazil	Cont.	8	13	15	13	Trevelin et al. [2007]
13	<i>C. oenanthe</i>	5 WA	Bosque Azungue, Moyobamba, Peru	3 ha (F)	23	26	32	884	DeLuycker [2007]
14	<i>C. torquatus</i>	9 WA	Mosiro Itajura (Caparú), Colombia	Cont.	25	46	66	564	Palacios & Rodríguez [2013]
15	<i>Chiropotes</i>	17 EA	Tapajós National Forest, Brazil	Cont.	34	62	86	449	Pinto [2008]
16	<i>C. albinasus</i>	18 EA	Cristalino Private Reserve, Brazil	Cont.	17	25	32	154	Soares da Silva [2013]
17	<i>C. chiropotes</i>	1 GS	Guri Lake, Venezuela	365 ha (I)	27	62	68	765	Kinzey & Norconk [1993]; Norconk [1996]; Norconk et al. [1998]; Norconk & Veres [2011]
18	<i>C. sagulatus</i>	2 GS	Upper Essequibo Conservation Concession, Guyana	Cont.	37	86	123	560	Shaffer [2013]
19	<i>C. sagulatus</i>	3 GS	Raleighvallen-Voltzberg Nature Reserve, Suriname	Cont.	16	26	37	150	Kinzey & Norconk [1990]; Norconk & Kinzey [1994]; Norconk et al. [2009]; Norconk & Veres [2011]
20	<i>C. sagulatus</i>	4 GS	Brownsberg Nature Park, Suriname	Cont.	26	51	65	540	Gregory [2011]
21	<i>C. sagulatus</i>	15 CA	Biological Dynamics of Forest Fragments Project, Brazil	Cont., 100 ha (F), 10 ha (F)	47	112	240	388	Boyle et al. [2012, 2013]
22	<i>C. sagulatus</i>	16 EA	Saracá-Taquera National Forest, Brazil	Cont.	41	92	153	1514	de Melo [unpublished]
23	<i>C. satanas</i>	19 EA	Tucuruí, Brazil	Cont., 19.4 ha (I)	38	108	179	1206	Santos [2002] Veiga [2006]
24	<i>C. satanas</i>	20 EA	Celmar plantation complex, western Maranhão, Brazil	63 ha (F)	19	31	47	16	Port-Carvalho & Ferrari [2004]
25	<i>C. utahickae</i>	19 EA	Tucuruí, Brazil	129 ha (I)	38	87	129	631	Santos [2002]; Santos et al. [2013] Vieira [2005]
	<i>Pithecia</i>								

TABLE I. Continued

Fruit list no.	Pitheciid ^a	Site ID ^b	Site name	Forest extent ^c	Fruits used ^d				Contact hours	Source ^e
					Families	Genera	Species	hours		
26	<i>P. albicans</i>	13 CA	Upper Rio Uruçu, Brazil	Cont.	22	39	60	56	Peres [1993]	
27	<i>P. aequatorialis</i>	6 WA	Alto Itaya River, Peru	Cont.	22	31	35	41	Aquino et al. [2013]	
28	<i>P. irrorata</i>	10 WA	Los Amigos Conservation Concession, Peru	Cont.	46	91	127	3100	Palminteri et al. [2012]	
29	<i>P. pithecia</i>	1 GS	Guri Lake, Venezuela	15-70 ha (I)	26	44	54	1125	Kinzey & Norconk [1993]; Norconk [1996]; Norconk & Conklin-Brittain [2004]; Norconk & Veres [2011]	
30	<i>P. pithecia</i>	4 GS	Brownsberg Nature Park, Suriname	Cont.	37	69	102	3051	Norconk & Veres [2011]; Gregory & Norconk [2013]; Norconk & Setz [2013]; Thompson [2011]	
31	<i>P. pithecia</i>	15 CA	Biological Dynamics of Forest Fragments Project, Brazil	10 ha (F)	31	54	83	268	Setz [1993]	
	<i>C. melanocephalus</i>	d* CA	Amazonas region along Río Pasimoni, Venezuela	Cont.	2	2	2	1	Lehman & Robertson [1994]	
	<i>C. moloch</i>	e* CA	Lower Rio Purus, Brazil	Cont.	1	1	1	0.1	Haugaasen [unpublished]	
	<i>C. sagulatus</i>	c* GS	Iwokrama and Berbice, Guyana	Cont.	3	3	3	0.5	Lehman [unpublished]	
	<i>P. albicans</i>	e* CA	Lower Rio Purus, Brazil	Cont.	3	3	3	0.3	Haugaasen [unpublished]	
	<i>P. pithecia</i>	a* GS	Maburuma, Guyana	Cont.	1	1	1	0.25	Lehman [unpublished]	
	<i>P. pithecia</i>	b* GS	Mahaicony and Ebini, Guyana	Cont.	6	6	7	2	Lehman [unpublished]	
	<i>P. pithecia</i>	c* GS	Iwokrama and Berbice, Guyana	Cont.	2	2	2	1.5	Lehman [unpublished]	

^aTaxonomy follows Silva Júnior et al. [2013].

^bStudy sites and regions (GS: Guiana Shield; WA: Western Amazon; EA: Eastern Amazon; AF: Atlantic Forest) are mapped in Fig. 1.

^cForest extent details whether the forest was continuous (Cont.), a forest fragment (F) of a given size, or a forested island (I) of a given size. In our analyses we classified a forest fragment as a patch of forest ≤ 1000 ha.

^dNumber of families, genera, and species take into account only identified specimens verified by The Plant List. Therefore these numbers may be less than numbers in the cited publications.

^eSources without a date indicate that the data presented in the analyses have not been published prior to this analysis. Some of the sources have been updated with additional diet items when research continued post-publication of the listed source.

^fData not included in the main analysis of fruit richness in the lists for each study site. Data used only for general comparisons because the location of the surveys represented areas that were not represented by the longer-term pitheciid studies.

from published and unpublished data sets (Table I, Fig. 1). A given fruit list began with all known records of fruit species used by a given primate species at that site. To avoid unintentionally inflating fruit lists with synonyms, we checked the names of all plant species in the fruit lists using The Plant List [2013] and The Taxonomic Name Resolution Service [2013] to determine the currently accepted taxonomy and to identify synonyms (if any) for each plant species. If a fruit list provided only the genus, we listed the item using its genus; however, multiple items from the same genus (e.g., *Inga edulis*, *Inga* sp.1) counted as a single listing (*Inga*) for the genus. We did not include vague morphospecies (e.g., Unknown sp.1) in the genus tally because of the lack of taxonomic resolution associated with such entries.

We then condensed each fruit list to represent only plant genera because of the very large number of fruit species involved and because 17% of the fruit samples had been identified by the various researchers only to the genus level. A fruit list sometimes represented multiple studies or multiple groups of the same species at the same study site (Table I). We further collapsed the site-specific fruit lists into five geographic areas for regional comparisons (i.e.,

Guiana Shield, Western Amazon, Central Amazon, Eastern Amazon, and Atlantic Forest; Fig. 1). We also amassed data from several short-term surveys [Lehman & Robertson, 1994; Lehman, unpublished data; Haugaasen, unpublished data; Table I]. We used these data only to determine if the short-term studies included genera that were not part of the 31 fruit lists derived from more in-depth studies because these short-term surveys occurred in areas that were not represented by the longer-term primate studies in our analysis (Table I). The inclusion of the short-term studies thus enabled us to assemble the most complete list of fruit taxa possible for each pitheciid genus. Although we included studies that varied in both duration (Table I) and in data collection methods (including opportunistic sightings and scan samples at short intervals), wide-scale analyses of dietary data, such as ours, can be successful in illustrating large-scale patterns [Hawes et al., 2013].

Analysis

The “completeness” of fruit taxa inventories can be examined with accumulation curves, which are most likely to approach an asymptote when sampling

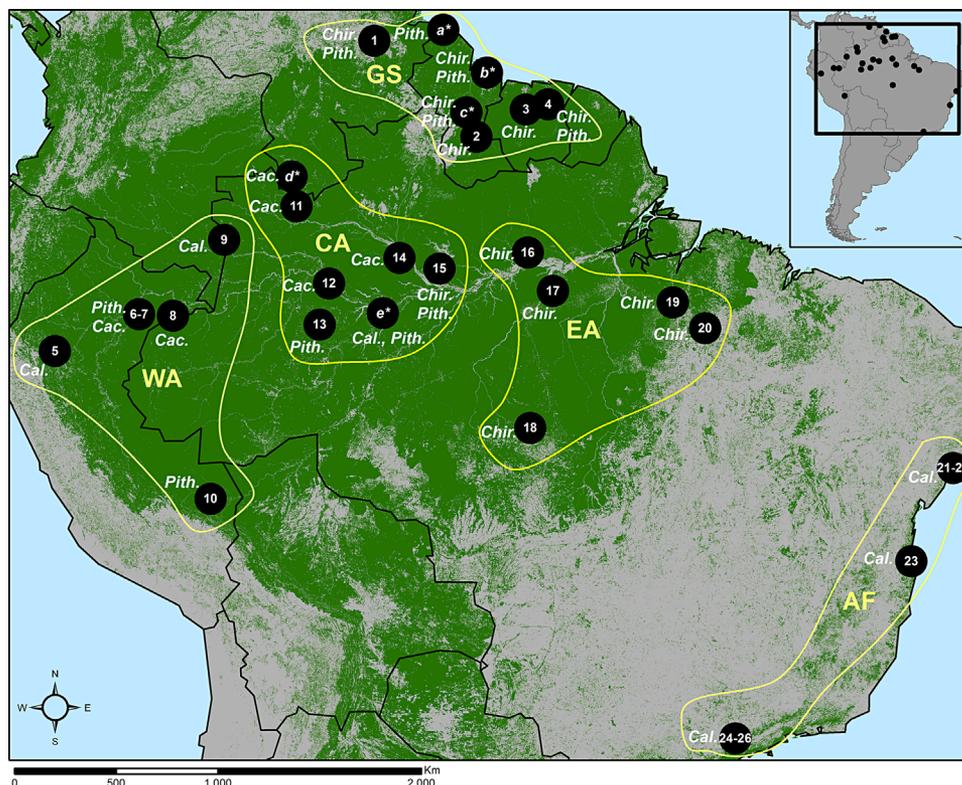


Fig. 1. Distribution of the *Cacajao* (*Cac.*), *Callicebus* (*Cal.*), *Chiropotes* (*Chir.*), and *Pithecia* (*Pith.*) fruit lists analyzed, overlaid on forest cover data and grouped by 26 study sites (listed in Table I). Lettered sites with an asterisk represent locations with additional fruit data. However, these lists were not used in analysis because of limited observation time. Forest cover data [GlobCover, 2009] represent consolidated forest cover classes. Yellow outlines specify ecogeographic regions (GS: Guiana Shield; WA: Western Amazon; CA: Central Amazon; EA: Eastern Amazon; AF: Atlantic Forest).

effort is high [Hawes & Peres, 2014]. We constructed accumulation curves for the total dataset (all fruit lists combined), the four pitheciid genera, and the five geographic regions. We constructed these curves by plotting the studies' cumulative contact hours (sorted from shortest to longest duration) against the cumulative number of fruit genera. Because some studies used in the current analysis did not include fruiting phenology data, we did not assess feeding selectivity.

We analyzed all data at the plant genus level. We first tested for differences in fruit genus richness among the four pitheciid genera with a non-parametric Kruskal–Wallis analysis of variance. We used this test because the data did not satisfy the assumption of homogeneity of variances necessary for a parametric procedure.

To compare dietary similarity with phylogenetic relatedness, we first computed dietary similarity (Sørensen similarity index [Magurran, 2004]) for each pair of pitheciid genera using each genus' composite fruit list as the input data. We then evaluated the correlation between matrices of dietary similarity and matrices of phylogenetic distance, which we measured as divergence times as reported by Schrago [2007]. We ran a Mantel test with 10,000 permutations for the matrix comparison.

To test whether a relationship existed between the similarity (Sørensen similarity index [Magurran, 2004]) of the composite fruit lists for each of the five geographic regions and the geographic proximity of the five geographic areas to each other, as measured by the Euclidean distance between the centroid of the location of the study sites within each geographic region, we ran a Mantel test with 10,000 permutations. The centroid and distance were determined using ArcGIS 10.1. We further calculated Sørensen similarity indices for pairwise comparisons of fruit lists of pitheciid genera within each geographic region, as well as pairwise comparisons of fruit lists for each pitheciid genus between geographic regions. We then repeated the Mantel analyses (with 10,000 permutations) to compare matrices for each pitheciid genus within and between geographic regions.

Lastly, we compared fruit genus richness in continuous versus fragmented forests with a *t*-test. We defined fragments as any patch of forest ≤1000 ha, whether surrounded by water or non-primary forest habitat. For all analyses, we set a two-tailed significance at $P \leq 0.05$. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

RESULTS

The 31 fruit lists represented the four pitheciid genera *Cacajao* ($n = 5$ lists), *Callicebus* ($n = 9$), *Chiropotes* ($n = 11$), and *Pithecia* ($n = 6$), and were distributed across the Guiana Shield ($n = 6$), Western

Amazon ($n = 7$), Central Amazon ($n = 6$), Eastern Amazon ($n = 6$), and Atlantic Forest ($n = 6$; Table II). In total, the pitheciid fruit lists contained records of 1189 plant species from 455 genera and 96 families. Of the seven short-term datasets (Table I), no additional genera contributed to the 455 total genera from the 31 fruit lists. None of the pitheciid genera and none of the five geographic regions had accumulation curves that reached an asymptote (Fig. 2).

Of the 455 fruit genera identified in the current study (Sup. Table I), 12% ($n = 55$) were present in fruit lists representing all four pitheciid genera, 8% ($n = 36$) were present in fruit lists across all five geographic regions, and 7% ($n = 32$) were present in fruit lists from all four pitheciid genera and all five geographic areas. Forty percent ($n = 180$) of the genera were on only one of the 31 fruit lists (Sup. Table I). The most common fruit genus was *Inga* (Fabaceae), found in 94% ($n = 29$) of the fruit lists, followed by *Brosimum* (Moraceae) and *Pouteria* (Sapotaceae), both occurring in 74% ($n = 23$) of the fruit lists.

The number of plant genera in the fruit lists varied considerably, with the highest values being recorded for *Chiropotes* (284 genera) and the Central Amazon (220 genera; Table II), but there were no statistical differences in the number of plant genera recorded *per fruit list* among the four pitheciid genera (Kruskal–Wallis: $X^2 = 6.21$, $df = 3$, $P = 0.1$,

TABLE II. Characteristics of the 31 Fruit Lists across the Four Pitheciid Genera and Five Geographic Areas*

Pitheciid genus or geographic area	No. of fruit lists	No. of fruit genera (mean ± SE)
<i>Cacajao</i>	5	177 (59.4 ± 7.2)
<i>Callicebus</i>	9	198 (37.9 ± 4.2)
<i>Chiropotes</i>	11	284 (67.6 ± 9.5)
<i>Pithecia</i>	6	189 (54.5 ± 9.0)
Guiana Shield	6	198 (56.2 ± 8.5)
<i>Chiropotes</i>	4	155 (56.3 ± 12.5)
<i>Pithecia</i>	2	103 (56.0 ± 12.0)
Western Amazon	7	190 (47.6 ± 9.0)
<i>Cacajao</i>	2	82 (51.0 ± 18.0)
<i>Callicebus</i>	3	83 (36.3 ± 5.8)
<i>Pithecia</i>	2	111 (61.0 ± 30.0)
Central Amazon	6	220 (66.7 ± 10.2)
<i>Cacajao</i>	3	144 (65.0 ± 5.1)
<i>Chiropotes</i>	1	112
<i>Pithecia</i>	2	77 (46.5 ± 7.5)
Eastern Amazon ^a	6	205 (67.8 ± 13.7)
<i>Chiropotes</i>	6	205 (67.8 ± 13.7)
Atlantic Forest ^a	6	148 (38.7 ± 5.9)
<i>Callicebus</i>	6	148 (38.7 ± 5.9)

*Geographic areas are mapped in Fig. 1.

^aValues for the geographic region and the pitheciid genus are identical because there was only one pitheciid genus represented for the Eastern Amazon and Atlantic Forest.

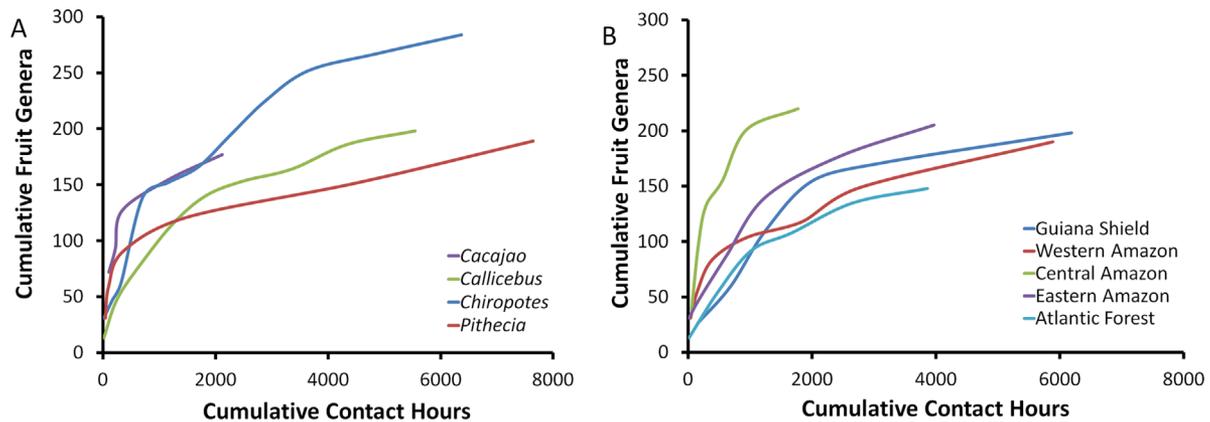


Fig. 2. Accumulation curves for the fruit genera within each of the four pitheciid genera (A) and fruit genera across the five geographic areas (B), with the x-axis indicating the cumulative number of contact hours represented by each fruit list.

$n = 31$) or the five geographic areas (Kruskal–Wallis: $X^2 = 5.56$, $df = 4$, $P = 0.2$, $n = 31$).

Similarity Comparisons

Similarities in fruit genera were greatest between the composite fruit lists for *Chiropotes* and *Pithecia* (Sørensen similarity index: 0.59) and lowest between *Cacajao* and *Callicebus* (Sørensen similarity index: 0.40; Table III). Overall, pairwise comparisons between *Callicebus* and the other three pitheciid genera were the lowest of all the pairwise comparisons. There was no correlation between the

phylogenetic distance among the four pitheciid genera and similarities in the fruit genera used (Mantel test: $r = -0.76$, $n = 6$, $P = 0.11$). Therefore, we did not find support for the first prediction that *Cacajao* and *Chiropotes* would share more similarity in fruit genera with each other than with either *Pithecia* or *Callicebus*.

The composite fruit lists for each of the five geographic regions indicated that the greatest similarity occurred between the Guiana Shield and Eastern Amazon fruit lists, closely followed by fruit lists from the Central Amazon and Eastern Amazon, Guiana Shield and Central Amazon, and the

TABLE III. Pairwise Comparisons of Genera Similarities (Sørensen Similarity Index^{*}) in Pitheciid Fruit Lists

Pitheciid Genera ^a				Geographic Area ^b				
	<i>Cal.</i>	<i>Chir.</i>	<i>Pith.</i>		WA	CA	EA	AF
<i>Cac.</i>	0.40	0.53	0.51	GS	0.52	0.56	0.59	0.39
<i>Cal.</i>		0.41	0.49	WA		0.56	0.52	0.35
<i>Chir.</i>			0.59	CA			0.57	0.34
				EA				0.33
Pitheciid Genera in Guiana Shield				<i>Cacajao</i> between Geographic Areas				
	<i>Pith.</i>			CA				
<i>Chir.</i>	0.47			WA	0.43			
Pitheciid Genera in Western Amazon				<i>Callicebus</i> between Geographic Areas				
	<i>Cal.</i>	<i>Pith.</i>		AF				
<i>Cac.</i>	0.32	0.44		WA	0.29			
<i>Cal.</i>		0.35						
Pitheciid Genera in Central Amazon				<i>Chiropotes</i> between Geographic Areas				
	<i>Chir.</i>	<i>Pith.</i>		CA	EA			
<i>Cac.</i>	0.45	0.39		GS	0.44	0.54		
<i>Chir.</i>		0.46		CA		0.51		
				<i>Pithecia</i> between Geographic Areas				
				WA	CA			
				GS	0.42	0.41		
				WA		0.46		

^{*}Values range from 0.0 to 1.0, with larger numbers indicating greater similarities.

^aPitheciid genera are abbreviated as *Cac.* (*Cacajao*), *Cal.* (*Callicebus*), *Chir.* (*Chiropotes*), and *Pith.* (*Pithecia*)

^bFig. 1 defines the five geographic areas: Guiana Shield (GS), Western Amazon (WA), Central Amazon (CA), Eastern Amazon (EA), and Atlantic Forest (AF). There are no pairwise comparisons between pairs of pitheciid genera in EA or AF because these two geographic areas had one pitheciid genus represented by the fruit lists.

Western Amazon and Central Amazon (Table III). The lowest similarity was between the Eastern Amazon and Atlantic Forest, and all comparisons between the Atlantic Forest and the other four geographic regions resulted in the lowest similarity values. Pairwise comparisons of fruit lists in the five geographic regions indicated that geographic regions in closest geographic proximity had the highest Sørensen similarity index for diet (Mantel test: $r = -0.81$, $n = 10$, $P = 0.015$).

When we compared each pitheciid genus by geographic region (using one composite fruit list for each geographic region), similarity indices were relatively comparable for all pitheciid genera (Table III), with the exception of *Callicebus*. The similarity value between *Callicebus* fruit lists from the Western Amazon and the Atlantic Forest was 0.29, while the similarity values for all geographic comparison of the other three pitheciid genera ranged from 0.41 to 0.54 ($n = 7$).

When we examined the fruit lists at a finer scale, the four pitheciid genera did not exhibit the same patterns in fruit list similarities between and within geographic regions. Pairwise comparisons of fruit lists for each pitheciid genus indicated that for both *Callicebus* and *Chiropotes* fruit lists, lists from sites in closest geographic proximity had the highest Sørensen similarity index (Mantel test: $r = -0.55$, $n = 36$, $P < 0.001$; $r = -0.48$, $n = 55$, $P < 0.001$, respectively), but we did not observe this trend in *Cacajao* (Mantel test: $r = -0.29$, $n = 10$, $P = 0.41$) or *Pithecia* (Mantel test: $r = -0.16$, $n = 15$, $P = 0.59$). Therefore, we found support for the second prediction that there would be greater similarities in fruit genera used by pitheciids living in closer geographic proximity, but only for overall region-wide comparisons and only for two genera (*Callicebus* and *Chiropotes*).

Furthermore, when we separated *Callicebus* fruit lists by geographic location (Western Amazon and Atlantic Forest), the fruit lists in closest geographic proximity had the highest Sørensen similarity index for both the Western Amazon (Mantel test: $r = -0.99$, $n = 3$, $P < 0.001$) and Atlantic Forest (Mantel test: $r = -0.65$, $n = 15$, $P = 0.001$). The six *Chiropotes* fruit lists from the Eastern Amazon exhibited a similar pattern as the *Callicebus* lists (Mantel test: $r = -0.57$, $n = 15$, $P = 0.03$). However, the four *Chiropotes* lists from the Guiana Shield did not fit this pattern (Mantel test: $r = -0.83$, $n = 6$, $P = 0.1$).

Diets in Fragmented Forests

Fruit lists from study sites with forest fragments or islands had $57.6 \pm \text{SE } 8.5$ ($n = 12$) fruit genera, while fruit lists from continuous forest sites had 53.6 ± 5.3 ($n = 19$) fruit genera. These values for forest type were not significantly different (t-test:

$t = 0.42$, $\text{df} = 29$, $P = 0.68$). Therefore, we did not find support for the prediction that pitheciids in forest fragments would have lower richness in fruit genera used than populations in the continuous forest.

DISCUSSION

Pitheciid genera consume fruit from a large number of plant genera, which is to be expected given the large geographic ranges of the four genera [Boyle, 2014], the diversity of habitats found within these ranges [Silva Júnior et al., 2013], and the morphological adaptations that allow pitheciids to consume ripe and unripe fruit parts [Kinzey, 1992; Norconk et al., 2009]. We found that 1) *Chiropotes* and *Pithecia* fruit lists were the most similar to each other and *Callicebus* fruit lists were the least similar to the fruit lists of the other genera; 2) overall, and for *Callicebus* and *Chiropotes*, fruit lists from locations in close proximity had greater similarities than lists from study sites that were further apart; and 3) fruit lists from forest fragments and continuous forest did not differ in the number of fruit genera used by the pitheciids.

Pitheciids use more plant genera than do most catarrhines and prosimians [Tutin et al., 1997; Norconk et al., 2013]. Hawes & Peres [2014] found that pitheciid genera as well as *Alouatta*, *Ateles*, *Lagothrix*, *Cebus*, *Sapajus*, and *Saguinus* have a higher degree of fruit genus richness in their diets than *Aotus*, *Leontopithecus*, and *Mico*. Furthermore, when Hawes & Peres [2014] standardized sampling effort across taxa, they found that pitheciids use the greatest richness of fruit genera. In our study, fruit lists for each of the four pitheciid genera contained between 177 (*Cacajao*) and 284 (*Chiropotes*) genera (Table II). At a finer taxonomic scale, in comparisons across other platyrrhine genera of the number of plant species used [González-Zamora et al., 2009; Peres, 1994b; Russo et al., 2005], our results suggest that the four pitheciid genera appear to be comparable to frugivorous *Ateles* and *Lagothrix*. Furthermore, the mean number of fruit genera on the individual fruit lists in this study (Table II) was comparable to the number of fruit genera in a study of *Gorilla* and *Pan* [Yamagiwa & Basabose, 2006].

It is likely that our totals for plant genera and species used are underestimates, given that none of the pitheciid genera had accumulation curves that reached an asymptote in the number of fruit genera used. Diet richness typically increases with sampling time and rarely do accumulation curves for primate diets reach an asymptote [Hawes & Peres, 2014]. Our findings indicate that although the true extent of fruit genera used is underestimated for all pitheciid genera in this analysis, fruit lists for some genera (i.e., *Cacajao*) are less complete than others based on the slope of the accumulation curve (Fig. 2). This

result is likely due to the small number of studies and an incomplete geographic coverage (*Cacajao*: 5 fruit lists for the entire geographic range).

Fruit Genus Richness Across Pitheciid Genera

The composite fruit list for *Chiropotes* had the greatest number of fruit genera and the composite fruit list for *Cacajao* had the lowest. When the fruit lists were examined individually, the mean number of fruit genera recorded was smallest for *Callicebus* and greatest for *Chiropotes* (Table II), but these findings did not differ statistically and so there were no differences among the four pitheciid genera in the richness of fruit genera used. These findings were not primarily a result of sampling effort because *Pithecia* had a greater sampling effort (measured in contact hours) than did the other three genera (Fig. 2).

Fruit List Similarities, Pitheciid Morphology, and Phylogenetic Distances

Although the pitheciids had similar richness in their fruit lists, the level of similarity between lists varied. We predicted that, given the similarities in mandibular and dental morphology [Kinzey, 1992; Norconk et al., 2009, 2013; Rosenberger, 1992] and the close phylogenetic distances [Perez & Rosenberger, 2014; Schrago, 2007], *Cacajao* and *Chiropotes* would share more fruit genera with each other than either would share with *Pithecia* or *Callicebus*. However, there was no correlation between phylogenetic distance (measured by divergence time) and similarity of fruit lists. The greatest relative similarity was between *Chiropotes* and *Pithecia*, both overall and within the geographic regions (Table III), but the similarity between *Cacajao* and *Chiropotes* was nearly at the same level, as was the similarity between *Cacajao* and *Pithecia*. Because these values were close it is possible that with increased sampling (given that the accumulation curve for *Cacajao* indicated the least amount of completeness) this pattern could change with diet data from additional field studies. Alternatively, there may not be such a pattern: Porter et al. [2014] found that while primates from sites in Malaysia, Suriname, Uganda, and Ivory Coast with closer phylogenetic distances had more similar diets than primates that are more distantly related, such a pattern was not present for primates at Manú National Park, Peru.

Even though there were no overall patterns between phylogenetic distance and fruit genera similarities, *Callicebus* had the lowest similarity indices when we conducted pairwise comparisons of the 1) composite fruit list for *Callicebus* with the fruit lists for the three other genera and 2) composite fruit list for *Callicebus* in the Western Amazon with the composite fruit lists from *Cacajao* and *Pithecia* in

this region (Table III). These differences between *Callicebus* and the three other pitheciid genera may be because of morphological differences, given that *Cacajao*, *Chiropotes*, and *Pithecia* are more specialized for sclerocarpic foraging than *Callicebus* [Kay et al., 2013; Kinzey, 1992; Norconk et al., 2009, 2013]. It is likely that some of these differences are related to compositional differences of the plant assemblages in the Atlantic Forest, Guiana Shield, and Amazon regions, but when fruit lists for *Cacajao*, *Callicebus*, and *Pithecia* in the Western Amazon were compared, *Callicebus* continued to be the least similar.

In summary, Neotropical primate lineages differentiated early and are strongly separated by their dietary specializations [Kay, 2015; Rosenberger, 1992; Rosenberger & Tejedor, 2013], and there are strong links between morphology and diet within the platyrrhines [Marroig & Cheverud, 2005; Rosenberger, 1992]. However, behavioral flexibility is a notable primate characteristic, and it is common for primates to have diets that include components for which they do not appear to be morphologically specialized [Barnett et al., 2013a; Marshall et al., 2009]. Consequently, geographically distinct populations may exist in very different habitats [Ayres, 1989; Heymann & Aquino, 2010] and have very different resource bases and suites of potential competitors, but display little morphological divergence [Albrecht & Miller, 1993; Kamilar 2006], and hence display little of the character displacement seen in other vertebrate groups [Grant & Grant, 2006; Schluter & McPhail, 1992].

Fruit List Similarities: Geographic Comparisons

We found support for the prediction that there would be greater similarities in fruit genera used by pitheciids living in closer geographic proximity: the Guiana Shield and Eastern Amazon fruit lists were most similar, followed closely by comparisons of the Central and Eastern Amazon, Central and Western Amazon, and Guiana Shield and Western Amazon. The Western and Eastern Amazon were the most different within the Amazon comparisons, and all pairwise comparisons with the Atlantic Forest had relatively low similarity values. When we examined each pitheciid genus, *Chiropotes* and *Callicebus* groups living in closer proximity had greater similarities in their fruit lists than did groups that were geographically more distant. Similar findings were also noted in studies of *Alouatta* spp. [Chaves & Bicca-Marques, 2013; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007]. However, *Cacajao* and *Pithecia* did not fit this pattern in our study, and the factors contributing to this discrepancy are not clear.

Given the range of forest habitats (e.g., *terra firme*, *várzea*, *igapó*) represented by the five *Cacajao* fruit lists [Aquino & Encarnación, 1999; Ayres, 1986;

Barnett, 2010; Boubli, 1999; Bowler & Bodmer, 2011], with most of the *Pithecia* and *Chiropotes* fruit lists coming from *terra firme* habitats, it was not possible to test a prediction examining similarities of fruit lists based on habitat type due to the small sample size for the non-*terra firme* habitats. In the future the importance of floristic differences between forest types should be investigated to determine whether diet similarity scores are *primarily* influenced by geographic proximity, habitat type, niche partitioning, or dental and mandibular morphology.

Fruit Lists and Forest Fragments

While anthropogenic factors can affect the composition of primates' diets [Boyle et al., 2012; Heiduck, 2002; Souza-Alves, 2013], we did not find support for the prediction that pitheciid populations in forest fragments would have lower richness in fruit genera used than populations in continuous forest. Instead, pitheciids living in heavily modified habitats can have distinct diets in comparison with their counterparts living in continuous forest [Boyle et al., 2012; Heiduck, 2002; Souza-Alves, 2013]. Given that *Callicebus*, *Chiropotes*, and *Pithecia* have used forest fragments at multiple study sites [Boyle, 2014], the ability of pitheciids to use the fruits of a wide range of plant genera may allow these populations to obtain sufficient resources to live in disturbed habitats.

Insights Into Primate Frugivory

Primates can be important seed dispersers and influence the structure of forest communities [Chapman & Russo, 2006]. Although pitheciids are considered seed predators (with *Callicebus* to a lesser extent than the other three genera), they can also facilitate epizoochory and germination [Barnett et al., 2012; Norconk et al., 1998]. If pitheciids use a diverse array of plants, with little overlap among pitheciid genera or sites, then pitheciid population declines could affect plant demography as well as community composition and diversity, as has shown to be the case with peccaries, a terrestrial Neotropical seed predator that may play a large role in plant community regulation [Beck, 2006].

When making generalizations about the plant taxa that are most commonly used by primates, it is necessary to have long-term studies covering multiple groups from a variety of habitats [Chapman et al., 2002a,b]. Although this study represents the most extensive examination of the richness of fruit consumption by pitheciids to date, there are still gaps in our knowledge. Much of what we know for the pitheciids is based on studies lasting less than 18 months and there are major geographic gaps (Fig. 1) where few or no data have been collected on pitheciid diet. Lastly, more than half of

the recognized pitheciid species could not be included in this analysis due to lack of studies, and others (e.g., *Callicebus moloch*, *Chiropotes chiropotes*, *Pithecia aequatorialis*) are only minimally represented. We acknowledge the difficulties in making comparisons across dozens of studies that vary in sampling effort and methods, but compilations of this type are important for understanding continental-scale patterns in diet [Hawes et al., 2013].

We suggest that future analyses include comparisons among the plant taxa in the pitheciids' diets with data on their relative abundance in study areas, given the potential implications of this parameter for the composition of the diet [Boyle et al., 2012; Peres, 1993]. In the future we plan to evaluate the significance of the characteristics (e.g., height, seed size, pericarp hardness, fruit color) of the plant species exploited, as well as expanding the analysis to include folivory and florivory. More detailed analyses on the characteristics of the particular fruit species used will allow us to address questions specifically related to pitheciid morphology and diet, as well as diet selectivity in the various habitats. This further work will be essential to understanding whether the trends in dietary richness observed here across the five general geographic regions are simple reflections of well-established patterns in botanical diversity [e.g., Stevenson, 2001; ter Steege et al., 2000, 2003] or of specific adaptations in the feeding ecology of the primates involved.

In summary, our examination of fruit genera used by pitheciids demonstrates that broad, continental-scale analyses of primate diet are important for understanding both the variety of plant genera used by primates and the extent to which there are similarities across primates and geographic regions. Examining regional patterns in primate plant use can provide preliminary findings from which to base more-detailed analyses of the local flora, because it may be that patterns in plant genera use by primates are more generalizable by habitat type or biogeography instead of by larger geographic regions. Lastly, it may be that the primary variables influencing primate diet differ across primate taxa.

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