

RESEARCH ARTICLE

Terrestrial Activity in Pitheciins (*Cacajao*, *Chiropotes*, and *Pithecia*)

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Neotropical monkeys of the genera *Cacajao*, *Chiropotes*, and *Pithecia* (Pitheciidae) are considered to be highly arboreal, spending most of their time feeding and traveling in the upper canopy. Until now, the use of terrestrial substrates has not been analyzed in detail in this group. Here, we review the frequency of terrestrial use among pitheciin taxa to determine the ecological and social conditions that might lead to such behavior. We collated published and unpublished data from 14 taxa in the three genera. Data were gleaned from 53 published studies (including five on multiple pitheciin genera) and personal communications of unpublished data distributed across 31 localities. Terrestrial activity was reported in 61% of *Pithecia* field studies (11 of 18), in 34% of *Chiropotes* studies (10 of 29), and 36% of *Cacajao* studies (4 of 11). Within *Pithecia*, terrestrial behavior was more frequently reported

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Received 6 November 2011; revised 27 June 2012; revision accepted 2 July 2012

DOI 10.1002/ajp.22068

Published online xx XXXX xxxx in Wiley Online Library(wileyonlinelibrary.com).

in smaller species (e.g. *P. pithecia*) that are vertical clingers and leapers and make extensive use of the understory than in the larger bodied canopy dwellers of the western Amazon (e.g. *P. irrorata*). Terrestrial behavior in *Pithecia* also occurred more frequently and lasted longer than in *Cacajao* or *Chiropotes*. An apparent association was found between flooded habitats and terrestrial activity and there is evidence of the development of a “local pattern” of terrestrial use in some populations. Seasonal fruit availability also may stimulate terrestrial behavior. Individuals also descended to the ground when visiting mineral licks, escaping predators, and responding to accidents such as a dropped infant. Overall, the results of this review emphasize that terrestrial use is rare among the pitheciins in general and is usually associated with the exploitation of specific resources or habitat types. *Am. J. Primatol.* 00:1–22, 2012. © 2012 Wiley Periodicals, Inc.

Key words: behavior; pitheciids; primates; terrestrial

INTRODUCTION

While some extinct New World primates may have been exclusively, predominantly, or partially terrestrial [Rosenberger et al., 2009], all living Neotropical species are highly adapted for an arboreal lifestyle [Heymann, 1998]. Nevertheless, there are examples of terrestrial use among several platyrrhines suggesting that coming to the ground is a response to specific local environmental factors. Potential causes for such interpopulational differences include habitat fragmentation [*Cebus olivaceus*: Fragaszy, 1986], specialized foraging adaptations [*Cebus apella*: Haugaasen & Peres, 2009; *Cebus libidinosus*: Spagnoletti et al., 2009], use of mineral licks [e.g. *Ateles belzebuth*: Link et al., 2011a,b], co-foraging with other (primarily terrestrial) mammals [e.g. *Cebus apella* and *Nasua nasua*: Haugaasen & Peres, 2008], and the relaxation of predation pressure [*Brachyteles hypoxanthus*: Mourthé et al., 2007; *Ateles* spp.: Campbell et al., 2005].

In other Neotropical primate populations, terrestrial activity may be an established, but infrequent element of the behavioral repertoire, and is almost invariably related to the execution of three main activities—the retrieval of food items [*Cebus apella* and *Saimiri sciureus*, Silva & Ferrari, 2009], movement between discontinuous substrates [*Alouatta caraya*, Bicca-Marques & Calegari-Marques, 1995; *Brachyteles arachnoides*: Dib et al., 1997], and specific social behaviors, such as play and resting [*Brachyteles hypoxanthus*: Tabacow et al., 2009]. The use of terrestrial mineral licks is a characteristic of the behavior of many Amazonian atelids, for example [Campbell et al., 2005; Link et al., 2011a,b], and the retrieval of arthropod prey from the leaf litter is a typical behavior in callitrichids [e.g. Garber, 1992; Yoneda, 1984]. With the exception of retrieving food items and minerals from the ground, some terrestrial activities are associated with changes in habitat structure or plant community composition due to human activities. As a result, these changes may be relatively recent [see Tabacow et al., 2009].

The subfamily Pitheciinae encompasses three genera of medium-sized platyrrhines (adult body

weight range 2–4.5 kg). Collectively known as “pitheciins,” these primates are extremely (*Cacajao* and *Chiropotes*), or quite strongly (*Pithecia*), specialized dentally for the predation of immature seeds [Kinzey, 1992; Norconk et al., 2009; Rosenberger, 1992; Teaford & Runestad, 1992]. The larger-bodied genera, *Cacajao* (uacaris) and *Chiropotes* (bearded sakis or cuxiús, hereafter “cuxiús” giving preference to the local common name throughout much of the geographic range of this genus: Barnett et al., in press-a), tend to inhabit the middle to upper strata of the forest, through which they move using a mixture of quadrupedal climbing and leaping along horizontal substrates [Walker, 1996, 2005]. A key difference between the genera is the occupation of flooded forest ecosystems by many uacari populations, which may place additional limitations on the potential for terrestrial behavior. The smallest sakis (*Pithecia pithecia*) typically use lower to middle strata when traveling, which may be related to their morphological specializations for vertical clinging and leaping [Walker, 2005]. Other *Pithecia* species (e.g. *P. albicans*, *P. irrorata*, *P. monachus*) occupy higher forest canopy levels, are more quadrupedal, and more often leap and land horizontally (Janice Chism, unpublished data *vide* Swanson-Ward and Chism, 2003; Anthony Di Fiore and Eduardo Fernandez-Duque, unpublished data *vide* Di Fiore et al., 2007). With the possible exception of *P. irrorata*, which may feed predominantly on hard fruits [Palminteri, 2010], sakis tend to have a more diverse diet that includes a higher proportion of ripe fruit and young leaves than uacaris and cuxiús [Norconk, 2011].

In addition to their tendency to occupy the middle and upper forest strata, the dietary preference of pitheciins for immature seeds may also reduce their potential for terrestrial behavior, given that immature fruit are much less likely to fall to the ground than ripe fruit. Furthermore, a number of recent studies have shown that pitheciins are more flexible in both behavioral [Barnett, 2010; Boyle & Smith, 2010; Thompson & Norconk, 2011; Veiga, 2006] and ecological terms [Boyle et al., 2009, 2012; Norconk, 1996; Port-Carvalho & Ferrari, 2004; Silva &

Ferrari, 2009] than previously thought [e.g. Johns & Ayres, 1987]. As such, the exploitation of terrestrial resources, and moving between fragmented habitats, may contribute to an increase in the probability of terrestrial activity. It is therefore possible that, within the studied genera, those who spend more time in strata closer to the ground may be those that are also more terrestrially active.

While raptors appear to be the principal threat to platyrrhines in trees [Barnett et al., 2011; Ferrari, 2009; Hart, 2007], attacks by ground-based, scansorial, predators (e.g. ocelots, jaguars, tayras) have been documented [see Bezerra et al., 2011; Bianchi & Mendes, 2007; Olmos, 1994; Peetz et al., 1992]. Furthermore, Matsuda and Izawa [2008] witnessed predation by jaguars on spider monkeys when they were on the ground. Thus, risk of predation may reduce the incidence of coming to the ground for arboreal platyrrhines. Indeed, foraging [Ferrari, 2009; Stone, 2007], diurnal resting [Wright, 1998], and frequency of terrestrial play [Tabacow et al., 2009] have been shown to be sensitive to the perceived level of predation risk. Terrestrial activity may therefore be expected to occur more often in areas where predators are either naturally infrequent, or reduced because of human impacts such as hunting or habitat modification. Other limiting factors may include habitat structure and the spatial distribution of resources.

Though specialists in immature seeds, pitheciins track the availability of food resources and may switch to other food classes as the availability of fruit fluctuates (e.g. flowers, insects, or leaves: Norconk, 2011; Veiga & Ferrari, 2006). In other primates, dietary transitions are often accompanied by a shifting to habitats that are not usually frequented or by processing foods differently [e.g. Furuichi et al., 2001; Marshall et al., 2009]. Such items are often termed fall-back foods [Lambert, 2010], and though not necessarily nutritionally poor [Hanya et al., 2006], are generally used when phenological gaps result in an absence of more typical dietary items [Wrangham et al., 1998]. Marked temporal changes in food availability are especially common in areas where rainfall is strongly seasonal. Since fallen fruit may persist on the ground long after it is available in trees [e.g. Forget, 1992], it is possible that terrestrial behavior in pitheciins may peak in the dry season and/or when few other food resources are available.

Although terrestrial activity in pitheciines is frequently observed in captivity (Fig. 1), it is rarely observed in the wild. To investigate why, we extracted behavioral data from pitheciine field studies to obtain an overview of the patterns of terrestrial behavior in this platyrrhine group. On the basis of the arguments presented above, we predicted terrestrial behavior would be:

(1) More common in species spending more time in the lower strata of the forest canopy.



Fig. 1. Pitheciines can engage in terrestrial activity, but do so rarely in the wild (Photo: L.C. Marigo, *Cacajao calvus rubicundus* semicaptive at Amazon Ecopark, Manaus, Brazil).

- (2) Observed more commonly in habitats with fewer predators.
- (3) Recorded more frequently during seasons when the availability of preferred or standard dietary components (fruits and leaves on trees) is restricted.

METHODS

We collated data on 14 pitheciin taxa from 31 study sites (Fig. 2), and grouped terrestrial activities noted during these studies into the following categories: feeding, drinking, play, nonplay social behavior, antipredator behavior, and dispersal.

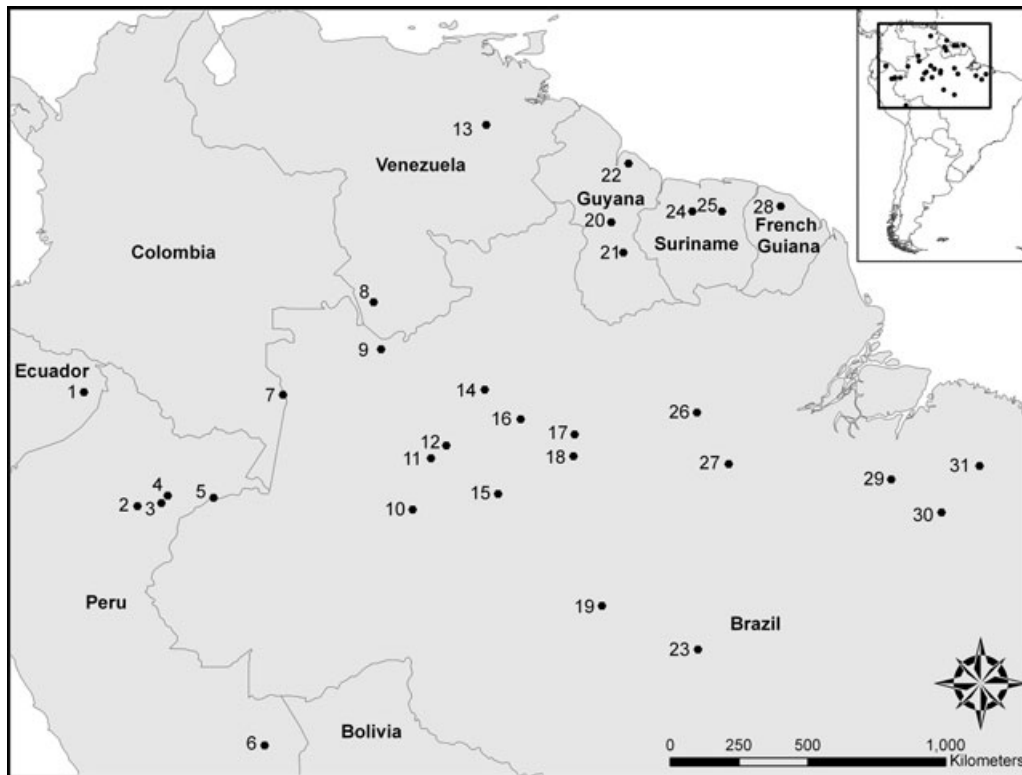


Fig. 2. Map of the 31 study sites represented in this review: (1) Yasuní National Park, Napo Province, Ecuador; (2) Pacaya Smiria National Reserve, Loreto Peru; (3) Quebrada Blanca Biological Station, Ucayali, Peru; (4) Tamshiyacu-Tahuayo Area of Regional Communal Conservation, Ucayali, Peru; (5) Lago Preto, Río Yavari, Ucayali, Peru; (6) Los Amigos Conservation Concession, Madre de Dios, Peru; (7) Mosiro Itajura (Caparú) Biological Station, Río Apaporis, Vaupés, Colombia; (8) Río Pasimoni, Amazonas, Venezuela; (9) Bebedor, Pico da Neblina National Park, Amazonas, Brazil; (10) Upper Urucu River, Amazonas, Brazil; (11) Teiú Lake, Mamirauá, Solimões, Amazonas, Brazil; (12) Amaná Lake, Amaná Sustainable Reserve, Solimões, Amazonas, Brazil; (13) Lago Guri, Bolívar, Venezuela; (14) Barcelos region of middle Rio Negro, Amazonas, Brazil; (15) Uauaçú Lake, Rio Purus, Brazil; (16) Rio Jaú, Jaú National Park, Amazonas, Brazil; (17) Biological Dynamics of Forest Fragments Project, Amazonas, Manaus, Brazil; (18) Bosque de Ciências and INPA campus, Manaus, Amazonas, Brazil; (19) Rio Aripuanã, Tapajós, Pará, Brazil; (20) Turtle Mountain, Iwokrama, Essequibo, Guyana; (21) Upper Essequibo Conservation Concession, Guyana; (22) Timehri District, Guyana; (23) Cristalino Private Reserve, Brazil; (24) Raleighvallen-Voltzberg Nature Reserve, Sipaliwini District, Suriname; (25) Brownsberg Nature Park, Brokopondo District, Suriname; (26) Saracá-Taquera National Forest, Pará, Brazil; (27) Tapajós, Rio Tapajós National Forest, Pará, Brazil; (28) Barrage de Petit-Saut, Sinnamary river basin, Saint-Élie, French Guiana; (29) Tucuruí Hydroelectric Dam Lake, Pará, Brazil; (30) Fazenda Martirinho, Maranhão, Brazil; and (31) Gurupí Biological Reserve, Maranhão, and eastern Pará, Brazil (a complex of five sites in the region).

Because many uacaris inhabit flooded forests, we included activities that involve contact with the surface of groundwater, such as the retrieval of floating fruits and drinking while suspended pedally from branches. Falling to the ground was not included because it is not considered an intentional act.

As none of the studies focused specifically on terrestrial behavior, procedures varied considerably, which impeded statistical analysis. However, to allow comparison among similar studies [i.e. Campbell et al., 2005], we calculated hourly rates of terrestrial behavior whenever possible or appropriate. When examining the likely factors responsible for the observed frequency of terrestrial activity at each site, we considered dry season intensity, hunting pressure, and level of habituation. However, these variables had not always been quantified by the investigators and, when they had, very different methodologies had been used. In consequence, we relied on

qualitative estimates of these three factors made by the researchers for each of their respective study localities. Though clearly less desirable than quantified bases, we consider it an improvement on both no estimates and on collating post-hoc quantifications, the second of which would have provided only an illusory level of accuracy.

As terrestrial activity is rarely reported in published studies, the current review relies on a considerable amount of unpublished data collected during studies from which other results have already been published. Such data are cited as “[unpublished data, *vide* Author’s name, year]”.

Taxonomic note: The Latin name for *Cacajao* species follows Hershkovitz [1987], since the precise appellation for some members of the genus is currently disputed [*vide* Boubli et al., 2008; Ferrari et al., 2010]. The intrageneric taxonomy of *Chiropotes* is also in flux: though it is clear that there

are different taxa east and west of the Rio Branco, Roraima State, Brazil, the correct names for them continue to be debated [compare Bonvicino et al., 2003 with Silva Jr. & Figueiredo, 2002 and Veiga et al., 2008]. Here, we denote populations west of the Rio Branco with a dagger (†) in the text and tables, while populations east of the Rio Branco are marked with an asterisk (*). This research adhered to the American Society of Primatologists ethical principles for the study of primates.

RESULTS

Uacaris (*Cacajao* spp.)

Uacaris are unique among the platyrrhines in their degree of preference for flooded forests, although many populations inhabit terra firme forests seasonally or year round [see Heymann & Aquino, 2010]. Despite this, available data (Table I) suggest a tendency for uacaris occupying terra firme forests to be less terrestrial than those in seasonally flooded habitats. Of these cases, six were observations of animals in contact with aquatic substrates.

The lack of published records of terrestrial use for the Peruvian red uacari, *Cacajao calvus ucayalii* (Table I) is reemphasized by personal communications from Sara Bennett, Richard Bodmer, and Pablo Puentes, who have all conducted many years of fieldwork within its range, and have never encountered these animals on the ground, although R. Bodmer [personal communication] received a report from a student who had observed an animal coming to the ground to escape an agonistic encounter with a conspecific. As if to further emphasize the lack of terrestrial behavior in this species, Bowler and Bodmer [2011] regularly observed *Cebus albifrons* and *Saimiri sciureus*—but never *Cacajao c. ucayalii*—descending to the ground at Lago Preto, Peru, to retrieve fallen *Mauritia flexuosa* (Arecaceae) fruits, even when the uacaris were part of the same mixed-species group. Nearby on the Rio Tahuayo, Janice Chism [unpublished data] also noted uacaris remaining in trees while syntopic *Saimiri* descended to the ground to forage. Similarly, in an 18-month field study in igapó, terra firme, and caatinga habitats the Pico de Neblina region of northeastern Brazilian Amazonia, Jean-Philippe Boubli [unpublished data, *vide* Boubli, 1997] did not observe terrestrial activity by either uacaris or cuxiús.

During the only long-term study of white uacari (*Cacajao c. calvus*), Ayres [1986] recorded monkeys coming to the ground during periods of fruit scarcity (the low water season) to feed on germinating seeds. However, Helder Queiroz [personal communication] has conducted some 30 months of fieldwork in the same area (Mamirauá), and has never witnessed terrestrial behavior in these uacaris. Similarly, João Valsecchi and Nayara Cardoso have surveyed both

C. c. calvus and *C. c. rubicundus* extensively in Mamirauá and neighboring areas since 2001 [e.g. Vieira et al., 2009], and have never observed terrestrial behavior, although most of these surveys were conducted during high water, and on unhabituated animals.

In contrast, there are several records of terrestrial behavior in the golden-backed uacari, *Cacajao melanocephalus ouakary* (Table I). Barnett [2010] observed the predation of germinated seeds of four tree species (*Eschweilera tenuifolia*, Lecythidaceae; *Leopoldinia pulchra*, Areceae; *Pouteria elegans*, *Pouteria* sp., Sapotaceae) at low water, a behavior apparently similar to that recorded by Ayres [1986]. *Eschweilera tenuifolia*, a high-ranked uacari food [Barnett, 2010], was the most commonly eaten diet item. The uacaris were extremely wary when on the ground, and almost invariably retired to perch on a branch or buttress root to process the food. Delfer [2004] has observed similar behavior in Colombia (Fig. 2). Barnett [2010] also observed uacaris retrieving *Aldina heterophylla* fruits from the surface of a river while suspended from overhanging branches by their rear legs during periods of high water. Bruna Bezerra [unpublished data, *vide* Bezerra et al., 2011] observed uacaris drinking water in the same fashion and, on another occasion, an animal was forced to swim to safety after the branch supporting it broke. Marcela Oliveira [unpublished data, *vide* Barnett et al., in press-b] did observe this species briefly on the ground. Barnett [2005] reported that uacaris raid turtle nests at low water on the Rio Negro. In summary, most references to terrestrial use by uacaris are related to seasonal shortages of arboreal foods (or possibly changes in food preferences?). There was only one observation of terrestrial behavior related to social avoidance. None of the uacari studies took place on island habitats where predation pressure might be different from mainland habitats. The rate of terrestrial use in the single uacari study that directly recorded terrestrial use was 0.102 events/hour.

Bearded Sakis or Cuxiús (*Chiropotes* spp.)

Records of systematic terrestrial behavior are restricted to *Chiropotes chiropotes**, *Chiropotes satanas*, and *Chiropotes utahickae* (Table II).

At Tucuruí, cuxiús dispersed distances of up to 400-m across land bridges during low water periods [Liza M. Veiga, unpublished data, *vide* Veiga, 2006], or moved terrestrially between trees on a small island [Suleima Silva, unpublished data]. *Chiropotes satanas* also has been observed to descend haltingly to the ground to retrieve fallen *Attalea* fruits [Marcio Port-Carvalho, unpublished data], and such terrestrial fruit collection also occurred relatively frequently during polyspecific associations with tufted capuchins (*Cebus apella*) and squirrel

TABLE 1. Behavioral Studies of Uacaris (*Cacajao* spp.) Analyzed in This Review

Taxon	Site number and name (Fig. 2)	Habitat	Hunting pressure (none, minimal, frequent, intense)	Study duration	Level of habituation (1 = low, 4 = high)	Terrestrial behavior (n. events)	Dry season intensity (1 = low, 4 = high, ND = no data)	Observer (Reference)
<i>C. calvus calvus</i>	11: Teiú Lake, Mamirauá (Brazil)	Seasonally-flooded várzea	Low	21 months	1	Foraging (n/a)	3	Ayres [1986]
<i>C. calvus ucayalii</i>	3: Quebrada Blanca (Peru)	Primary terra firme forest, palm swamp	Formerly frequent, now low	10 + years	2	None	1	E.W. Heymann [unpubl. Data: <i>vide</i> Heymann, 1990]
	4: Tamshiyacu-Tahuayo Area of Regional Communal Conservation (Peru)	Flooded and terra firme forest, and palm swamp	Low	10 years	4	None	—	J. Chism [<i>vide</i> Swanson-Ward and Chism, 2003]
	5: Lago Preto (Peru)	Primary terra firme forest, palm swamp	Minimal	28 months	1	None	1	M. Bowler [Bowler, 2007; Bowler & Bodmer, 2009; 2011; unpublished data.]
<i>C. melanocephalus</i>	8: Río Pasimoni (Venezuela)	Seasonally flooded igapó	Minimal	3 weeks	1	None	ND	S. Lehman [<i>vide</i> Lehman and Robertson, 1994]
	9: Pico da Neblina National Park (Brazil)	Terra firme and caatinga	Low	18 months	2	None	—	J-P. Boubli
<i>C. m. ouakary</i>	12: Amanã Lake, Amanã Sustainable Reserve (Brazil)	Seasonally flooded igapó	Medium	12 months	2	Dispersal (1)	—	[unpublished data: <i>vide</i> Boubli, 1997]
	16: Jau National Park (Brazil)	Seasonally flooded igapó	None	15 months	2	Foraging (11)	3	M. Oliveira [unpublished data, <i>vide</i> Barnett et al., in press]
	16: Jau National Park (Brazil)	Seasonally flooded igapó	None	11 months	2	Dispersal (1), drinking (1)	—	Barnett [2010]
								Bezerra et al. [2011]

TABLE II. Behavioral Studies of Cuxiús (*Chiropotes spp.*)^a Analyzed in This Review

Taxon	Site number and name (Fig. 2)	Habitat	Hunting pressure (none, minimal, frequent or intense)	Study duration	Level of habituation (1 = low, 4 = high)	Terrestrial behavior (n. events)	Dry season intensity (1 = low, 4 = high, ND = no data)	Observer (Reference)
<i>C. albinasus</i>	19: Rio Aripuanã (Brazil)	Primary <i>terra firme</i> forest	Minimal	12 months	1	None	ND	Ayres [1981]
	23: Cristalino Private Reserve (Brazil)	Primary <i>terra firme</i> forest	None	6 months	4	Falling (1)	—	Soares da Silva [2011]
<i>C. chiropotes</i> † (west of the Rio Branco)	27 Tapajós National Forest (Brazil)	Primary <i>terra firme</i> forest	Minimal	11 months	2	Infant retrieval (1)	—	Pinto [2008]
	13: Danto Manchado, Lago Guri (Venezuela)	<i>Terra firme</i> forest (reservoir island, 180 ha)	None	15 months	4	None	—	A. Peetz [unpubl. data, <i>vide</i> Peetz, 2001]
	13: Danto Manchado, Lago Guri (Venezuela)	<i>Terra firme</i> forest (reservoir island, 180 ha)	None	17 months	4	None	—	Norconk (1996)
	13: Danto Manchado, Lago Guri (Venezuela)	<i>Terra firme</i> forest (reservoir island, 180 ha)	None	6 months	4	None	—	Norconk and Kinzey [1994]
<i>C. chiropotes</i> * (east of the Rio Branco)	17: Biological Dynamics of Forest Fragments Project (Brazil)	<i>Terra firme</i> forest (continuous and fragments)	Minimal	17 months	2	None	—	Boyle and Smith [2010]
	17: Biological Dynamics of Forest Fragments Project (Brazil)	Primary <i>terra firme</i> forest	Minimal	12 months	1	None	—	Fração [1992]
	20: Turtle Mountain, Iwokrama International Centre, Guyana	Primary <i>terra firme</i> forest at reservoir	None	11 months	2	None	—	Wright et al. [2009]
21: Upper Essequibo Conservation Concession, Guyana	Conservation Concession, Guyana	Primary <i>terra firme</i> forest at reservoir	None	570 hr	1	Between-group aggressive interactions (3); Foraging for insects (3); Play (1); Predator escape (1)	4	Shaffer [2012]
		Primary <i>terra firme</i> forest	Frequent	6 months	1	None	ND	S. Lehman [<i>vide</i> Lehman, 2004a, 2004b]

TABLE II. Continued.

Taxon	Site number and name (Fig. 2)	Habitat	Hunting pressure (none, minimal, frequent or intense)	Study duration	Level of habituation (1 = low, 4 = high)	Terrestrial behavior (n. events)	Dry season intensity (1 = low, 4 = high, ND = no data)	Observer (Reference)
	24: Raleighvallen-Voltzberg Nature Reserve (Suriname)	Primary <i>terra firme</i> continuous forest	Minimal	14 months	4	Potentially foraging (2)	ND	Phillips <i>vide</i> Phillips, 2008]
	24: Raleighvallen-Voltzberg Nature Reserve (Suriname)	Primary <i>terra firme</i> continuous forest	Minimal	18 months	4	Foraging (1), Play (1)	-	Vreedzaam <i>vide</i> Boinski et al., 2005]
	24: Raleighvallen-Voltzberg Nature Reserve (Suriname)	Primary <i>terra firme</i> continuous forest	Minimal	28 months	1	None	-	van Roosmalen et al. [1988]
	24: Raleighvallen-Voltzberg Nature Reserve (Suriname)	Primary <i>terra firme</i> continuous forest	None	6 months	3.4	None	4	Norconk and Kinzey [1994]
	25: Brownsberg Nature Park (Suriname)	Primary <i>terra firme</i> continuous forest	Minimal	13 months	3.5	None	4	Gregory [2011]
	25: Brownsberg Nature Park (Suriname)	Primary <i>terra firme</i> continuous forest	Minimal	6 months	3.5.	None	4	Gregory [2006]
	25: Brownsberg Nature Park (Suriname)	Primary <i>terra firme</i> continuous forest	Minimal	12 weeks	3.5	Foraging (1); Other (1)	4	Norconk et al. [2006]
	26: Saracá-Taquera National Forest (Brazil)	Primary <i>terra firme</i> continuous forest	Minimal	1107 obs. hr.	3	Within-group chases (4); Foraging (1); Nuisance-avoidance (1); Uncertain cause (1)	3	Melo et al. [2010]
<i>C. satanas</i>	29: Base 4, Tucuruí (Brazil)	Primary <i>terra firme</i> forest fragment (1,300 ha)	Minimal	7 months	4	Foraging (4); Accidents: falling (3)	3	A.C.P. Guimarães, <i>vide</i> Guimarães, 2011]
	29: Base 4/Su Island Tucuruí (Brazil)	Primary <i>terra firme</i> forest (fragment 1,300 ha/island 16 ha)	Minimal (base4), frequent (Su Is.)	6 months	Well (base 4), not (Su Is.)	Dispersal (2: Su Is.), foraging (1: Base 4)	3	Silva & Ferrari [2009]

TABLE II. Continued.

Taxon	Site number and name (Fig. 2)	Habitat	Hunting pressure (none, minimal, frequent or intense)	Study duration	Level of habituation (1 = low, 4 = high)	Terrestrial behavior (n. events)	Dry season intensity (1 = low, 4 = high, ND = no data)	Observer (Reference)
	29: Base 4, Tucuruí (Brazil)	Primary <i>terra firme</i> forest fragment (1,300 ha)	Minimal	12 months	4	Accident – (falling, 1); foraging (12)	3	Veiga [2006]
	29: Base 4, Tucuruí (Brazil)	Primary <i>terra firme</i> forest fragment (1,300 ha)	Minimal	8 months	2	Drinking (1)	—	Santos [2002]
	29: João Island, Tucuruí (Brazil)	Primary <i>terra firme</i> forest (island 19 ha)	Minimal	12 months	4	Dispersal via land bridges (2); infant retrieval (1); foraging (1); Foraging (1)	3	Veiga [2006; Veiga & Ferrari, in press]
	30: Fazenda Martininho	<i>Terra firme</i> forest	High	12 months	1	Foraging (1)	3	M. Port-Carvalho [vide Port-Carvalho & Ferrari, 2004]
	31: Gurupí Biological Reserve, western Maranhão and eastern Pará states (Brazil)	Five sites varying from highly disturbed and fragmented forest to undisturbed continuous <i>terra firme</i> forest	None to frequent	48 months	1–2	None	—	M.A. Lopes [vide Lopes & Ferrari, 2000]
<i>C. utahickae</i>	29: Ilha Germoplasma, Tucuruí (Brazil)	Primary <i>terra firme</i> forest (reservoir island, 129 ha)	Minimal	6 months	4	Foraging (3)	3	Vieira [2005]
	29: Ilha Germoplasma, Tucuruí (Brazil)	Primary <i>terra firme</i> forest (reservoir island, 129 ha)	Minimal	8 months	3	Foraging (1), dispersal (1)	3	Santos [2002]

^aFor cuxiús north of the Amazon River, Silva Jr. and Figueiredo [2002] proposed that individuals east of the Rio Branco should be called *Chiropotes sagulatus* (Trail, 1821) and those to the west of that river, *C. chiropotes*, while Bonvicino et al. [2003] separated them into *C. chiropotes* and *C. israelita*, respectively. Despite the uncertainties over the species name, supporting evidence shows there are two distinct populations of cuxiús north of the Amazon River: a tawny to brown backed from the Rio Branco to the west (¹) and a reddish backed from the Rio Branco to the east (*). Because of this, we have distinguished them in this table.

monkeys, *Saimiri sciureus* [Guimarães, 2011; Veiga & Ferrari, in press]. Vieira [2005] observed *Chiropotes utahickae* coming to the ground to retrieve *Endopleura uchi* (Humiriaceae) and *Annona tenuipes* (Annonaceae) fruits, the latter sometimes occurring during associations with capuchins and squirrel monkeys. While retrieval of fruits accounted for most of the observations of *C. satanas* and *C. utahickae* on the ground, both species also have been seen eating “geniparana” (*Gustavia augusta*: Lecythidaceae) and drinking lake water while suspended by their feet in a manner similar to that observed in *Cacajao* [Ricardo Santos, unpublished data, *vide* Santos, 2002; Suleima Silva, unpublished data, Liza Veiga, unpublished data, *vide* Veiga, 2006]. At Saracá-Taquera National Park, Pará, Thiago Alvim and colleagues [Melo et al., 2010] recorded seven instances of terrestrial activity in *Chiropotes chiropotes**. During a foraging bout, a group of seven adults (2M, 5F) and a juvenile were recorded foraging on the ground for more than 15 min, for immature *Duckesia verrucosa* (Humiriaceae) fruits (the monkeys’ previous foraging activities in the parent tree having caused the fruit to fall to the forest floor). The single-seeded fruits of *D. verrucosa* are some 6-cm long and have seeds protected by a sclerotized endocarp, implying extended processing time for each fruit. During the 15-min terrestrial foraging bout, animals spent 10–20 sec selecting a fruit from the ground, retreating to a branch to process it, and then repeating the process. Three examples of within-group aggression were also recorded: in one, a male and female chased another male to the ground and proceeded to bite him for over a minute. The male ran 20 m along the ground with an open wound on his foot, being chased by the male and female. The event lasted 6 min and 35 sec. In the second, the observer encountered two animals, clearly in an aggressive interaction, running on the ground 4 m apart. After the aggressor returned to the trees, the other 10 members of the subgroup descended to within 2 m of the ground and vocally mobbed the aggressed animal (an adult female). Two other events involved a single animal running along the ground (for a distance of 10 m and 30 m) following aggressive interactions in the canopy. In a third event, an adult was seen running along the ground for some 10 m: although the cause was unknown the many vocalizations in the canopy indicated an aggressive interaction may recently have occurred. During a 15-min intergroup encounter, two adult males attacked an adult female who ran 30 m along the ground before climbing a tree. The seventh event involved a nest of bees that the group accidentally disturbed while foraging. This generated many alarm calls and animals could be seen manually fanning their faces to ward off the insects. One individual avoided them by jumping to the ground and running there for some 20 m.

At Cristalino Nature Private Reserve, Matto Grosso, Brazil, Rafaela Soares was observing a 9-strong group of *C. albinasus* (3 M/4 F/1 YF-young female/1 FF-female with baby) feeding on seeds of an understory Bignoniaceae, when two adult males who had been playing together fell from 5 m, sat on the ground hugging each other for a few seconds and then walked quickly along the ground for a minute before ascending a liana, rejoining the group and beginning to feed [Soares, unpublished data; *vide* Sasaki et al., 2010; Soares, 2011]. This does not fit the definition of terrestrial activity used in this paper. However, as the study area is strictly protected, hunting unrecorded in recent times and the animals highly habituated by dint of ecotourist activity, this example is therefore included to show that true terrestrial activity in this species appears to be genuinely rare. That the population at Crisalino appears to strongly avoid terrestrial activity is underscored by observations that, while in mixed groups with *Cebus apella*, red-nosed cuxiús will use the lower strata of the forest, but a female *C. albinasus* did not retrieve a fallen infant from the ground even though it was barely yet capable of independent locomotion.

At Brownsberg Nature Park, Suriname, Katherine MacKinnon [unpublished data, *vide* Norconk et al., 2006] twice observed *Chiropotes chiropotes** on the ground. Once four animals were observed eating fallen fruit, most likely naturally *Byrsonima crassifolia* (Malpighiaceae). On the second occasion, 2+ *C. chiropotes* were present on the ground, but ran up a tree as soon as they perceived the human observer. The animals on the ground had been silent, and remained so as they fled. Other troop members gave a whistle alarm call, and remained silent as they ascended. At nearby Raleighvallen-Voltzberg Nature Reserve, Carson Phillips [*vide* Phillips, 2008] observed two instances of *Chiropotes chiropotes** on the ground. This dry season observation occurred while a lone male was travelling with a group of *Saimiri sciureus*. The association lasted for a week. As the *S. sciureus* foraged for insects in dry bamboo leaves the male *C. chiropotes* was observed on two occasions to accompany them, though it was not clear if he also foraged. As part of an extended study of *Saimiri* and *Cebus* at the same site [unpublished data, *vide* Ehmke, 2004; Kauffman, 2004], Arioene Vreedzaam encountered lone juvenile male *Chiropotes chiropotes** who travelled with mixed *S. sciureus*-*C. apella* group (some 50 individuals of each species) for 2 days and accompanied them in their terrestrial activities. Bouts of terrestrial activity up to 10-min long were recorded. These included both foraging and play, in the latter case the young *C. chiropotes* attempted to engage even though it was some three times larger than the *Saimiri*. Diet items eaten by the *Chiropotes* were not recorded, but, like *C. apella*

and *S. scuireus*, *C. chiropotes* was seen to rummage among dry fallen leaves.

At the Upper Essequibo Conservation Concession, Guyana, Chris Shaffer [unpublished data, *vide* Shaffer, 2012] recorded 8 instances of terrestrial behavior in *C. chiropotes**. Three were quite brief (some 10–15 sec) and occurred during agonistic interactions between two or three adult males of the same group. In these, one male was chased down the trunk of the tree onto the ground, and along the ground, and then up another tree. No physical contact was observed. In one case, a male intervened during a copulation between another male and a female, then proceeded to chase the male who had been copulating. Similar chasing was observed during an intergroup encounter. In this case, three males from one group chased a single male from another group. The chasing lasted for more than 15 min, with repeated bouts of terrestrial behavior. It was preceded by alarm calling as the groups approached each other. A fourth instance occurred during an attempted attack by a harpy eagle (*H. harpyja*). As the eagle swooped down, all of the cuxiús jumped to lower vertical strata while alarm calling. Most group members settled into dense vegetation in the understory, remaining there for 8 min before returning to canopy.

In all of the instances reported above, the individuals appeared to go to the ground as a last resort, in an attempt to escape. However, Shaffer also recorded four cases where individuals appeared comfortable on the ground. In one of these, a female and juvenile playing in the lower canopy, ran down a tree to the ground some 3 m away from the observer, and continued playing on the ground for 6 min, before returning to the canopy. Three instances of terrestrial insectivory also were observed. One of these involved nine individuals who searched through dead leaves and bark from fallen trees for 15 min. Another involved four individuals for 10 min, and the third two individuals for 5 min. In all cases, the terrestrial individuals represented only a small portion of the group, almost all of whom were foraging for insects. Shaffer noted that the terrestrial animals appeared to use foraging techniques similar to those used by the other individuals in the group who were foraging in the understory.

Martins et al. [2005] observed *C. utahickae* descending to the ground to avoid an attack by a harpy eagle, *Harpia harpyja*. The only terrestrial behavior observed in the other *Chiropotes* species was the retrieval of an infant by its mother, seen once each in *C. albinasus* and *C. satanas* (Table II). This can be considered a random event, however, rather than a systematic behavior.

As in some uacari reports, cuxiús at two sites have been observed remaining in the trees even though capuchins and squirrel monkeys in the same mixed-species groups retrieved fruits from the ground (*Attalea* and *Orbygnia*) [Santos, 2002; Silva

& Ferrari, 2009], and these fruits represented a dietary staple for cuxiús. At a third site [Boyle & Smith, 2010], *Chiropotes chiropotes** did not come to the ground to forage or disperse, even though sympatric capuchins (*Cebus apella*) and tamarins (*Saguinus midas*) did so. On the rare occasions when *Chiropotes* has been observed coming to the ground to forage, the behavior involves extreme caution and almost invariably, a rapid retreat to a higher perch. Overall, while terrestrial activity does occur in *Chiropotes*, it does not appear to have any major ecological role.

In summary, terrestrial activities in cuxiú were related to retrieving food and for purposes of dispersal, with the proviso that both populations inhabited artificial islands or peninsulas in the Tucuruí reservoir. The cuxiús were well habituated to human observers, although Boyle's study groups also were well habituated and some of her study groups inhabited forest fragments. She, however, did not observe terrestrial habitat use. Neither it was observed by Soares in her well-habituated group (even to the extent of not retrieving a fallen infant), nor it was clearly very rare in *Chiropotes* at Raleighvallen. As in the case of uacaris, wild cuxiús appear to be more reticent to come to the ground for food than capuchins and squirrel monkeys; even where human hunting is not known to occur (e.g. Shaffer's site in Guyana). The rate of terrestrial use in cuxiús studies ranged from 0.002 to 0.111 events per hour, with a mean rate of 0.034 events per hour.

Sakis (*Pithecia* spp.)

The data on sakis (Table III) indicate that terrestrial behavior was recorded in more than half of the studies. *Pithecia pithecia* is clearly the best-studied pitheciin species, and the fact that a third of field studies failed to record terrestrial behavior suggests that the absence of records for some species (Table III) may be partly related to duration of study, degree of habituation, and site-specific characteristics (e.g. mineral licks, insect eating, island habitats). Thus, while a long-term study of *P. monachus* [Soini, 1986] did not record terrestrial use (Table III), Happel [1982] observed *P. monachus* (identified in litt. as *P. hirsuta*) visiting a terrestrial mineral lick during her much briefer fieldwork.

Three studies [Di Fiore et al., 2005; Harrison, 1998; Suzanne Palminteri, unpublished data] have reported terrestrial foraging for insects (Fig. 2). In *P. aequatorialis* [A. Di Fiore and E. Fernandez-Duque, unpublished data: *vide* Di Fiore et al., 2005], and *P. irrorata* (Fig. 3), the preys were army ants themselves (Ectoninae) rather than any insects or small vertebrates that the ants had disturbed. This contrasts with the pattern typically reported in calitrichids [e.g. Rylands et al., 1989] and formicariid birds [Willis & Oniki, 1978]. Di Fiore et al. [2005]

TABLE III. Behavioral Studies of Sakis (*Pithecia* spp.) Analyzed in This Review

Taxon	Site number and name (Fig. 2)	Habitat	Hunting pressure (none, minimal, low frequent or intense)	Study duration	Level of habituation (1 = low, 4 = high)	Terrestrial behavior (n. events)	Dry season intensity (1 = low, 4 = high ND = no data)	Observer (Reference)
<i>P. aequatorialis</i>	1: Yasuni National Park (Ecuador)	<i>Terra firme</i> forest	ND	6+ years	ND	Insect foraging (>10)	No	A. Di Fiore and E. Fernandez-Duque [unpublished data; <i>vide</i> Di Fiore et al., 2007]
	4: ACR Tamshiyacu-Tahuayo (Peru)	<i>Terra firme</i> forest, palm swamp	Minimal	6 seasons	2	None	—	J. Chism [unpublished data, <i>vide</i> Frisoli et al., 2009]
<i>P. albicans</i>	10: Rio Urucu (Brazil)	<i>Terra firme</i> forest, seasonally flooded	ND	19 months	ND	None	—	Peres [1993]
	15: Rio Purus, Brazil	<i>Terra firme</i> forest	Low	2+ years	3	Aggressive inter-species chasing (2)	n/a	T. Haugaasen [unpublished data, <i>vide</i> Haugaasen & Peres, 2008]
<i>P. irrorata</i>	6: Los Amigos Conservation Concession (Peru)	<i>Terra firme</i> forest	Low	3000 hr	3	Insect foraging (7), play (1)	No	S. Palminteri [Palminteri, 2010]
<i>P. monachus</i>	2: Pacaya Samiria National Reserve, Peru.	<i>Terra firme</i> , swamp forests	ND	13 months	ND	None	—	Soimi [1986]
	4: ACR Tamshiyacu-Tahuayo (Peru)	<i>Terra firme</i> forest, palm swamp	Minimal	6 seasons	3	None	—	J. Chism [unpublished data, <i>vide</i> Frisoli et al., 2009]
<i>P. pithecia</i>	13: Isla Redonda, Lago Guri (Venezuela)	<i>Terra firme</i> forest (reservoir islands)	Minimal	546 hr	4	Foraging (32)	Yes	S. Walker-Pacheco [<i>vide</i> Walker, 2005]
	13: Isla Redonda, Lago Guri (Venezuela)	<i>Terra firme</i> forest (reservoir island)	Minimal	950 hr	4	Insect foraging (156), foraging (1)	No	A. Harrison-Levine [Harrison-Levine et al., 2003]
	13: Danto Machado, Lago Guri (Venezuela)	<i>Terra firme</i> forest (reservoir islands)	Minimal	15 months	4	None	—	I. Homburg, unpublished data [<i>vide</i> Homburg, 1998]
	13: Isla Redonda, Lago Guri (Venezuela)	<i>Terra firme</i> forest (reservoir islands)	Minimal	20+ years	4	Foraging (occasionally)	Possibly	M.A. Norconk [<i>vide</i> Norconk, 1996]

TABLE III. Continued.

Taxon	Site number and name (Fig. 2)	Habitat	Hunting pressure (none, minimal, low frequent or intense)	Study duration	Level of habituation (1 = low, 4 = high)	Terrestrial behavior (n. events)	Dry season intensity (1 = low, 4 = high ND = no data)	Observer (Reference)
17: Biological Dynamics of Forest Fragments Project (Brazil)		Primary <i>terra firme</i> forest	Minimal	500 hr	2	Play (106), gap crossings (2), movement between fragments (various), accidental falling (2), fallen fruit retrieval (1),	Yes	E. Setz [vide Setz, 1993]
17: Biological Dynamics of Forest Fragments Project (Brazil)		Primary <i>terra firme</i> forest	Low	6 months	3	None	-	JMS Oliveira et al. [1985]
18: INPA, Bosque de Ciências, Manaus, (Brazil)		Urban forest fragment	Minimal	60 days	4	Play, social intecations	2	L. Rodrigues da Silva [vide Rodrigues da Silva, 2007]
20: Iwokrama International Centre, Guyana		Primary <i>terra firme</i> forest at reservoir	Low	11 months	2	None	-	K. Wright [vide Wright et al., 2009]
22: Timehri District, Guyana		Various	Frequent	186 days	1	Dispersal (1)	ND	S. Lehman [vide Lehman, 2004a.b]
25: Brownsberg Nature Park (Suriname)		Primary <i>terra firme</i> continuous forest	Low	17 months	Highly (3.5)	Play (5); Foraging (4); Within-group chases (2); Predator-threat response (2)	3	Thompson and Norconk [2011]
25: Brownsberg Nature Park (Suriname)		Primary and secondary <i>terra firme</i> forest	Minimal	129 hr	4	Play (22)	3	M.A. Norconk [vide Norconk et al., 2006]
28: Petit Saut reservoir (French Guiana)		Artificially flooded <i>terra firme</i> forest	ND	1600 hr	ND	Foraging (1), social interaction (1), predator avoidance (1)	4	Vié et al. [2001]



Fig. 3. Terrestrial foraging by *Pithecia irrorata*, southern Amazonian Peru (Photos: Edgard Collado).

observed that insect-feeding bouts could last for more than an hour, with the sakis spending much of their time close to the ground and making brief terrestrial forays to capture the ants. In *P. pithecia* [Harrison-Levine et al., 2003] the prey were large acridid grasshoppers (*Tropidacris* spp.), and this behavior represented the single most frequent record of terrestrial behavior in the pitheciins, a total of 126 events. The sakis spent an average of 8.8 sec on the ground to capture each grasshopper, but invariably ascended to branches above 3 m from the ground to consume their prey [Harrison-Levine et al., 2003].

Retrieval of fruits or seeds from the forest floor was observed in a number of *P. pithecia*, studies, and, as in the other genera, the pattern of behavior was a rapid retreat to a high branch for processing. Walker [2005] observed *P. pithecia* feeding extensively on fallen *Capparis muco* (Cappariaceae) and *Chrysophyllum* (Sapotaceae) fruits, which contributed 2.5% of total feeding records. This species also has been observed feeding extensively on fallen *Licania* (Chrysobalanaceae) *discolor* fruits at the same site [Harrison, 1998; Norconk, 1996], and in

French Guiana [Vié et al., 2001]. The study sites in Venezuela and French Guiana were islands surrounded by water, the result of inundation during dam creation. In the Colosso forest fragment in the BDFFP (Biological Dynamics of Forest Fragments Project) near Manaus, Brazil, Eleonore Setz [unpublished data, *vide* Setz, 1993] observed a male *P. pithecia* coming to the ground to retrieve a *Duguetia latifolia* (Annonaceae) fruit dropped by the adult female.

Other isolated cases of terrestrial behavior in *P. pithecia* include locomotion between fragments of forest [Shawn Lehman, unpublished data, *vide* Lehman, 2004a, 2004b], drinking at the edge of a reservoir [Harrison, 1998], the avoidance of an attack by a harpy eagle, and an agonistic encounter with conspecifics [Vié et al., 2001]. In a long-term study on a small BDFFP fragment, E. Setz [unpublished data] observed juveniles falling to the ground on two occasions, while the mother watched, but did not descend to assist. On a number of occasions, the same study group also crossed at least 300 m of shrub-filled pasture to move between fragments. On two other occasions, a juvenile, unable to cross a gap in the canopy by leaping, called for assistance and, when none arrived, descended to the ground to move between trees. A subadult male of this same group was observed following the group on the ground during two consecutive days [A.M. Calouro, personal communication], and was presumed to be sick or injured. It did not rejoin the group and presumably died.

In *P. albicans*, one animal was observed briefly chasing another to the ground from the lower canopy, where further chasing and a brief fight occurred before both returned to the canopy [Torbjørn Haugaasen, unpublished data, *vide* Haugaasen & Peres, 2005]. Chases in which individuals descended to the ground (i.e. chased to the ground or fell from a tree and ran along the ground) during territorial encounters also were observed in *P. pithecia* in both Venezuela (Lago Guri) [Norconk, 2011] and Suriname (Brownsberg) [Norconk, unpublished data: *vide* Norconk et al., 2006].

Social interactions on or near the ground involving play were documented in two *P. pithecia* studies. In *P. pithecia*, E. Setz [unpublished data: *vide* Setz, 1993] recorded 106 play events—including chasing and slapping hands on the ground—during 500 hr of monitoring. At Brownsberg Nature Park, Suriname, 8 of 30 bouts of juvenile play in 2007 occurred on the ground [K. Talbot and M. Norconk, unpublished data]. Bouts lasted up to 33 min (mean 21 min) and were significantly longer than the more numerous arboreal play bouts (mean 9.3 min). Cynthia Thompson [unpublished data, *vide* Thompson & Norconk, 2011] also observed play in *P. pithecia* at this site. The play would entail locomoting and hopping on the ground between small trees (where they clung in a posture typical of a Vertical Clinger and Leaper,

sensu Napier, 1967), "pinning" their playmate to the ground, and "wrestling" (for lack of better descriptors). Such bouts lasted between 5 and 20 minutes. Thompson's study group would regularly reuse-specific travel paths, and would predictably locomote on the ground when crossing the same paths. In addition, a juvenile was observed to take cover on the ground under some brush when a hawk was sighted and alarm calls were given by other group members. On another occasion an adult male was seen running on the ground from a predator threat, and two terrestrial chasing events were seen as a result of intergroup encounters. Thompson twice observed feeding on the seeds of *Vouacapoua americana* (Fabaceae) the ground. Feeding on this species initially occurred in trees only, but appeared to switch to ground foraging later in the feeding season when more of the fruits had dropped to the ground (and presumably, fewer were left still on the tree, though quantitative data on this was not collected). Bouts involved the entire group and lasted some 10 minutes. Thompson also observed *P. pithecia* feeding on fruits and flowers of Passifloraceae vines located at or near the ground.

In *P. irrorata*, Palminteri [unpublished data, *vide* Palminteri, 2010] recorded a single bout of terrestrial play that lasted approximately 10 min. This is the only example of this behavior in any of the other four saki species.

At other sites, however, terrestrial use is either absent or so rare as to be unrecorded. For example, at Iwokrama International Centre, Guyana, where *Alouatta macconnelli* and *Ateles paniscus* have both been observed crossing open savannah between forested areas [B. and K. Wright, unpublished data, *vide* Wright et al., 2009], sympatric *Pithecia* have never been seen on the ground.

In summary, among pitheciins, sakis provide the most extensive and diverse information on use of terrestrial habitats, with terrestrial activity reported most consistently in *P. pithecia*. Several characteristics of saki species and the habitats in which they live may have influenced terrestrial activities. First, among *Pithecia* species, *P. pithecia* uses the lowest strata of the forest extensively [Norconk, 2011; Walker, 1996]. Second, two studies (Lago Guri, Venezuela, and a BDFFP fragment, Brazil) took place in small forest islands or fragments. The social groups in these two studies were very well habituated and were the subjects of long-term studies. Third, the Lago Guri study took place in a strongly seasonal habitat that resulted in periods of strong food- and water-shortage [Cunningham & Janson, 2007; Norconk, 1996]. Additionally, the animals clearly could not easily leave the islands and so may have been forced to adopt other foraging strategies. The very sparse information from other *Pithecia* species, even when they are well habituated (e.g. Di Fiore and Palminteri studies), suggests that their

TABLE IV. Mean per Hour Rate of Terrestrial Activity Observed

Species	Study	Mean per hourly observation rate ^a
<i>Cacajao m. ouakary</i>	Barnett [2010]	0.102
<i>Chiropotes albinasus</i>	Pinto [2008]	0.002
<i>Ch. chiropotes</i>	Melo et al. [2010]	0.0072
<i>Ch. chiropotes</i>	Shaffer [2012]	0.014
<i>Ch. satanas</i>	Guimarães [2011], mainland group	0.010
<i>Ch. satanas</i>	Veiga [2006], mainland group	0.111
<i>Ch. satanas</i>	Veiga [2006], island group	0.004
<i>Ch. utahickae</i>	Vieira [2005]	0.008
<i>Pithecia irrorata</i>	Palminteri [2010]	0.003
<i>P. pithecia</i>	Thomson and Norconk [2011]	0.0046
<i>P. pithecia</i>	Walker [2005]	0.058
<i>P. pithecia</i>	Norconk [<i>vide</i> Norconk et al, 2003]	0.062
<i>P. pithecia</i>	Vié et al. [2001]	0.002
<i>P. pithecia</i>	Harrison [1998]	0.165
<i>P. pithecia</i>	Setz [<i>vide</i> Setz, 1993]	0.220

^aNumber of events divided by the number of observation hours.

preference for higher forest strata limits their access to (and possibly interest in) the ground. Furthermore, the finding of frequent play activities on the ground in free-ranging sakis of Brownsberg Nature Park in Suriname (a continuous habitat), suggests that forest fragmentation is not a necessary criterion for the observation of terrestrial behavior in this species. Fourth, the rate of terrestrial use in saki studies ranges from 0.003 to 0.22 events/hour, average 0.0845 (Table IV). However, this figure does not take into account the fact that typical contact with the ground is brief and entails picking up an insect or a brief tussle during play.

Because of differing methods used by authors in studying pitheciin species, it was only possible to calculate hourly rates of terrestrial behavior for a small subset of the studies analyzed here (Table IV). Assuming a daily activity period of 12 hr, an hourly rate of 0.083 events would represent an average rate of terrestrial behavior of once per day per group. This, value was surpassed in only four studies, suggesting that terrestrial behavior is neither a common nor a regular occurrence in pitheciins. This is especially so given that it was extremely rare for all group members to be on the ground at the same time, and that most bouts of terrestrial behavior were brief and highly context specific.

TABLE V. Concordance of Results and Predictions

Prediction	Concordance
Terrestriality will be more common in species that spend more time in the lower strata of the forest canopy.	Some firm support: High canopy sakis (e.g. <i>P. irrorata</i>) engaged in terrestrial activity, as did <i>Cacajao</i> spp. and <i>Chiropotes</i> spp. However, the greatest number of terrestrial behavior events was recorded for <i>P. pithecia</i> , the pitheciine that spends more time in lower strata than any other. In this species there may be a predisposition to regard the ground as a supplementary feeding source.
Terrestriality will be observed more commonly in habitats where there were fewer predators.	Equivocal support: Terrestriality was regularly observed at sites where predator pressure was presumed low (forest fragments, islands in dam-created lakes), <i>but</i> actual predator densities were not quantified, so terrestriality may have been due to other factors (e.g. food availability). Also, terrestrial behavior (including both foraging and play) was recorded in primary habitats where predator densities expected to be high.
Terrestriality will be recorded more frequently in seasons when the availability of the standard components of the diet were limited (effectively that terrestriality occurs when species descend to the ground to access fall-back foods).	Some firm support: It may be the case for <i>Cacajao</i> feeding on germinating seedlings, and <i>Pithecia</i> feeding on seeds from fallen fruits; however, the latter was recorded most frequently in environments (such as artificially created islands) where food availability may be highly restricted in some months due to the reduced tree diversity. Seasonality does not appear to explain the insectivory recorded in three saki species. This foraging appears to be purely opportunistic, taking advantage of a protein source whenever it occurs.

Meeting Predictions

We found some support (Table V) for the predictions that terrestriality will occur more frequently in: (1) species spending more time in lower forest strata; (2) habitats with fewer predators; and (3) seasons when the availability of standard dietary components are limited.

DISCUSSION

Terrestrial behavior is rare in pitheciins, and even when contact with the ground occurs, it is usually brief. It has been recorded in all three genera, but not in all species, and in fewer than half the studies analyzed here. Nevertheless, it seems reasonable to assume that the lack of records for some species was the result of relatively few, or short, studies, rather than systematic interspecific variation in behavior. This observation is supported by the data on *P. pithecia* (Table III), in which terrestrial behavior was unusually common at some sites, but not observed at others, even under ostensibly similar ecological conditions.

Where terrestrial behavior was observed, most studies recorded a very small number of events, suggesting that the probability of recording the behavior in a given study was, to some degree, a chance event.

Certainly, the overall pattern was distinct from the one observed by Campbell et al. [2005] for *Ateles*, in which terrestrial behavior was recorded in all studies, albeit at relatively low rates (0.01–0.05 events per hour). Hourly rates higher than those reported for spider monkeys were recorded in four pitheciins, whereas in all other studies for which it was possible to calculate a rate, values were well below 0.02 events/hour (Table IV).

Even when they did come to the ground, pitheciins normally spent a very limited amount of time there. Even during the play bouts observed in some *P. pithecia* groups, individuals were on the ground for only a matter of seconds. The aversion of pitheciins to terrestrial activity is emphasized by a number of aspects of their foraging behavior, such as the removal of terrestrially retrieved items to perches for processing, accessing ground-level water by pedal suspension, and a reluctance to accompany to the ground the foraging primates with which they were associating. Similarly, while many Amazonian spider (*Ateles*), and howler (*Alouatta*) monkeys visit terrestrial mineral licks regularly [Link et al., 2011a,b], pitheciins appear to prefer arboreal sources, such as termite nests [Ferrari et al., 2008; Setz et al., 1999; but see Happel, 1982]. Given the circumstances of most observations, it seems unlikely that the avoidance of terrestrial activity is a predator-avoidance

strategy directed toward human observers [Gautier et al., 1999], although this may have been a factor in some cases [e.g. Peres, 1993].

In *Cacajao* and *Chiropotes*, terrestrial activities other than dispersal were observed so infrequently that it is inappropriate to infer causal relationships from any inter-site differences in frequencies. In *Pithecia*, by contrast, terrestrial activity was recorded in more than half the study sites, with foraging being the most common behavior. For *P. pithecia*, terrestrial foraging was most commonly observed when the availability of ripe fruit and young leaves was low (Table III). In this regard, ground-retrieved resources may be considered fallback foods for sakis [Marshall & Wrangham, 2007 for topic review]. Furthermore, sites where habituated *Pithecia* study groups terrestrial have not been observed to exhibit terrestrial behavior (e.g. Quebrada Blanca, and rios Tahuayo and Yavarí, Peru), have a very attenuated dry season [Goulding et al., 2003], while at Guri Lake, and terrestrially active sakis studied by Harrison-Levine, Norconk, and Walker-Pacheco, lived on islands that had a strong and prolonged dry season [Norconk, 1996] and a depauperate plant community. However, seasonal food dearth is unlikely to be the sole explanation, since in *Pithecia* populations south of the Amazon, observed terrestrial behavior did not coincide with times of low fruit and young leaf availability (e.g. the ant feeding observed by S. Palminteri in *P. irrorata* [Fig. 3], and for *P. aequatorialis* by A. Di Fiore et al. occurred at various times of the year, not just when fruits and leaves were least available, Table III). In addition, while the forests around Manaus have a pronounced dry season [Ribeiro et al., 1999], terrestrial foraging in by pitheciins there remains unreported. This is understandable for the urban *P. pithecia* studied by Rodrigues da Silva [2007] because their forests, which contained horticultural resources, allowed them to supplement their diet with non-native, dry-season fruiting species (e.g. bananas). However, studies in unmanaged nearby terra firme forests [e.g. Setz, 1993; E. Oliveira et al., 1985] did not record terrestrial foraging. Thus, while there may be a causal connection with duration and/or intensity of reduced dry season food availability for some populations, the link is far from clear-cut and terrestrial use appears to involve a number of factors.

A cautious overview of the data points suggest that three factors underpin the observed pattern of terrestrial behavior in the Pitheciinae: (1) the ecological division between the more dietary generalist *Pithecia* and the more specialized seed predators, *Cacajao* and *Chiropotes*, (2) an apparent association between flooded habitats and terrestrial activity, and (3) the development of a “local behavioral pattern” in some populations. Methodological variables, such as the level of study population habituation, also may be important.

In addition to the quantitative differences (Tables I–III), the sakis presented two behavioral patterns—insect foraging and play—only once recorded on the ground for the other pitheciins. Both behaviors are more typical of callitrichids than pitheciins, and may represent specific local circumstances (see below). Such differences between sakis and uacaris/cuxiús may at least partly be accounted for by the ecological divergences between the two groups, in particular the preference of *P. pithecia* for lower forest strata and a tolerance for more disturbed habitats [Norconk, 2011]. This explanation does not hold for such saki species as *P. irrorata*, which spends most of its time in high canopy [vide Palminteri, 2010], and descends to lower layers only to practice myrmecophagy.

Overall, 13 of the 30 studies in which terrestrial behavior was recorded were conducted in the context of flooded habitats, although this parameter is inflated by the fact that nearly half of these studies took place at two sites, Tucuruí (Brazil) and Guri Lake (Venezuela), with recently created fragments. In the specific case of the uacaris, the ability to exploit ground-based resources, in particular, would likely be an important attribute for populations inhabiting seasonally flooded várzeas and igapós, where resource availability may show very strong seasonal variation, with fruit being scarce for long periods. In such circumstances, the only available fruits may be on the ground. By contrast, no terrestrial behavior has been observed in studies of *Cacajao c. ucayalii* and *Cacajao m. melanocephalus* conducted primarily in unflooded habitats (Table I). A similar pattern can be observed in *Chiropotes*—only three events were recorded at sites other than Tucuruí, and one of these was the retrieval of an infant, which is an *extrematis* event. This is consistent with observations of cuxiús at most sites, where they tend to occupy the highest strata of terra firme forests [Bobadilla & Ferrari, 2000; Norconk, 2011]. Predation risk may also be important: in five forest fragments studied by Port-Carvalho and Ferrari [2004], *C. satanas* was active on the ground at only those sites where *Panthera onca* and *Puma concolor* were least likely to have occurred. In addition, human hunting levels may be significant, since the only site at which *Chiropotes* were observed to both play and engage in protracted terrestrial insectivory was at the Shaffer’s Essequeibo site in Guyana, where the nearest village is 80 km away (and its animistic residents of the Macushi and Wapishana tribal groups do not hunt monkeys). As noted above, even in an area with no recently recorded hunting, a well-habituated group of *C. albinasus* were not seen to forage or play on the ground in over a year of field observation (though the risk of higher predation from non-human predators at such a site is a consideration). At Raleighvallen, terrestrial activity (especially

foraging) in *Saimiri sciureus* and in *Cebus apella* was so common as to be unremarkable [Erin Ehmke, Laurie Kauffman, unpublished data: *vide* Ehmke, 2004; Kauffman, 2004; Phillips, 2008; Vath, 2008], but any *Chiropotes* or *Pithecia* that were associating with them were never recorded as participating.

The evidence in *Pithecia* is less conclusive, and is more consistent with the greater propensity of this genus for terrestrial behavior, which, as argued above, may reflect the broader ecological differences between the three genera. In this case, half of the studies in which terrestrial behavior was recorded were conducted at reservoir sites (Guri Lake and Petit Saut). In addition, play was more frequent at non-reservoir sites (though insect foraging was well represented at both reservoir and non-reservoir sites).

Considering the third possibility, the development of a “a locally occurring behavior pattern” [“a local tradition” *sensu* Huffman & Hirata, 2003] in some populations, it should be noted that in the case of a *Brachyteles hypoxanthus* population in southeastern Brazil, the evolution of a terrestrial tradition appears to have been reinforced by factors such as habitat fragmentation and reduced terrestrial predator pressure (including human hunters) [Tabacow et al., 2009]. While habitat fragmentation is relatively accentuated at some of the analyzed sites, predation pressure is unlikely to have declined significantly in any area. On the contrary, Camargo and Ferrari [2007] suggested that the high population densities and isolation of one site (Germoplasma Island in Tucuui) might have contributed to increased vulnerability of the island’s primates to *Eira barbara*, a scanorial predator known to hunt terrestrially [Presley, 2000]. In this context it is interesting to note that, for *P. pithecia*, I. Homburg [unpublished data, *vide* Homburg, 1998] recorded no terrestrial activity in fifteen months in 1991–1992 while working on exactly the same small island where Harrison [1998] and Harrison-Levine et al. [2003] later recorded substantial terrestrial foraging activity in this species. The rise of a local tradition (or, at least, locale-specific patterns of behavior) at this site seems plausible (perhaps following increasing impoverishment of food resources). However, it is possible (though difficult to prove) that increased familiarity with observers between 1992 and 1998 resulted in *Pithecia* feeling more confident in their presence and simply exhibiting more frequently the already present high-risk behavior of terrestrial foraging.

Population specific behaviors (“local traditions” to some authors) may be a possible explanation for interpopulational differences in other genera. While, for example, *Cacajao m. ouakary* was observed exploiting germinating *Eschweilera* seeds at Jaú [Barnett, 2010], it was not seen doing so at Amanã, some 150 km to the west, despite the availability of the resource [M. Oliveira, personal communication], and the near-identical nature of the habitats. Similarly,

while some cuxiús groups at Tucuui often came to the ground to retrieve fruit, others were clearly reluctant to do so [Santos, 2002; Silva & Ferrari, 2009; Veiga, 2006; Vieira, 2005], even though they inhabited areas with apparently identical resource profiles. Terrestrial insect foraging and play are also risk-sensitive behaviors, which may require a learning component. However, any such conclusions are speculative, given the limited time scale of most of the available data.

Overall, data presented in this review suggests that pitheciins may be the least terrestrial of the platyrrhines, but engage in this behavior in response to the particular ecological contexts, for example retrieval of specific high-yield resources, such as insects or germinating seeds. However, the rate and persistence of this activity appears to differ greatly among populations and species. One question raised by these data is that terrestrial behavior among pitheciins may be increasing in response to anthropogenic disturbance that alters forest structure and modifies resource availability, and may necessitate that animals engage in relatively risky activities, such as terrestrial behavior. This may represent an additional cause for concern for the long-term survival of impacted populations, especially if such actions are combined with increased hunting (e.g. Peres, 2001). Hopefully this, and other aspects, will be clarified as an expanded database is accumulated through ongoing and future field studies. We also recommend the use of more detailed sampling protocols for the study of terrestrial behavior in Neotropical primates.

ACKNOWLEDGMENTS

The following colleagues generously shared unpublished data indicating the absence of pitheciin terrestrial use in their primate study populations: Sara Bennett, Bruna Bezerra, Richard Bodmer, Jean-Philippe Boubli, Nayara Cardoso, Erin Ehmke, Eckhard Heyman, Tremaine Gregory, Marcelo Gordo, Ingo Homburg, Laurie Kauffman, Maria Aparecida Lopes, Marcela Oliveira, Angela Peetz, Leila Porter, Pablo Puertas, Helder Queiroz, João Valsecchi, Carrie Vath, Robert Wallace, Barth W. Wright, and Kristin A. Wright. Elena Cunningham provided useful comments and Caroline Ross greatly improved an early draft of the manuscript. This is Contribution No. 1 from the Pitheciine Action Group.

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