

# Insectivory and prey foraging techniques in *Callicebus* – a case study of *Callicebus cupreus* and a comparison to other pitheciids

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## Introduction

For primates, animal prey and leaves represent alternative sources of protein, and no primate species combines large amounts of prey and leaves in the diet (Chivers & Hladik 1980; Martin 1990). These alternative dietary strategies can be explained by body-size constraints on the efficiency of prey foraging and by physiological constraints imposed on the digestion of leaves (Terborgh 1992). The absolute amount of obtainable prey does not increase with body size, thus making prey foraging unprofitable for large primate species, unless prey occurs in large clusters (like ant or termite mounds) (Terborgh 1983). The digestion of leaves through bacterial fermentation requires large amounts of space, which is not available in animals of small body size (Martin 1990). Consequently, primate diets show a predictable relationship with body mass (Martin 1990): while most extant primate species actually include fruit pulp in their diet, smaller species (below ca. 1–2 kg) usually supplement their diet with animal prey, while larger species (above ca. 1–2 kg) supplement with leaves (Harding 1981; Terborgh 1992). Additional factors such as the quality of leaves in the habitat or prey capture efficiency may, however, determine whether prey or leaves are used as source of protein. Kinzey (1978, 1997) compared the diets of two species of titi monkeys, and attributed the comparatively high amount of prey in the diet of *Callicebus lucifer* to leaves being very sclerophyllous and not readily available as a source of protein in its white-sand habitat, while very low capture efficiency was assumed to limit the amount of prey in *Callicebus brunneus*. He also suggested that “a ‘critical function’ ... such as reducing the dietary protein source” (Kinzey 1978, p. 383) influences the molar structure of these otherwise basically frugivorous titi monkey species (Rosenberger & Kinzey 1996). Similarly, Rosenberger (1992) and Lambert (2007) emphasized that behavioral, morphological and physiological adaptations to the acquisition and consumption of minor food categories which may be vital for

supplying certain essential nutrients, either throughout the year or as a fallback resource during critical periods of food scarcity, may be under strong selective pressure.

Members of the Pitheciidae feed either principally on fruit pulp (titi monkeys) or seeds (sakis and uacaris), and are classified as “sclerocarpic frugivores” (Kinzey 1981; Norconk 2011; Rosenberger 1992). Neither fruit pulp nor seeds usually provide significant amounts of protein, so pitheciids have to exploit either prey or leaves to obtain proteins. In light of Kinzey’s (1978, 1997) hypothesis on the source of interspecific variation in prey consumption in titi monkeys, it is thus timely to review the available evidence for insectivory in the Pitheciidae. In this chapter we therefore examine (a) the contribution of prey to the diet and (b) the prey spectrum and prey foraging techniques, and analyze (c) whether a relationship exists between body mass and the contribution of prey to the diet, as predicted from theory. As a starting point for these comparisons and analyses, we provide detailed information on prey foraging in red titi monkeys, *Callicebus cupreus*.

## Methods

The data on prey foraging in *C. cupreus* stem from a study by the second author on two groups of this species at the Estación Biológica Quebrada Blanco (EBQB) in northeastern Peru (Nadjafzadeh 2005). Detailed information on study methods are provided by Nadjafzadeh and Heymann (2008). While Nadjafzadeh (2005) and Nadjafzadeh and Heymann (2008) reported data for the two study groups separately, for the purpose of this chapter we combined these data, as the two groups did not differ in any respect.

For the comparison with other Pitheciidae, we searched the literature for data on the amount of prey in the diet (in terms of feeding time or of stomach contents), prey spectrum, prey search and capture techniques, and body mass. The relationship between body mass and feeding time on prey was examined through regression analyses with Statistica 6.0.

## Animal prey in the diet of *Callicebus* and other pitheciids

### *Callicebus cupreus*

The two study groups of *Callicebus cupreus* at EBQB dedicated between 11.7% and 14.8%, respectively, of feeding time on prey. These values fall into the range of these values from two earlier studies at EBQB which reported 11.1% and 18.0% (Table 19.1).

### Comparison with other pitheciids

Based on evidence from direct feeding observations or on the examination of stomach contents, all other titi monkey species except for *Callicebus personatus* also include prey in their diet (Table 19.1). The proportion of time spent consuming prey varies between 0.3% in *Callicebus melanochir* and 22% in *Callicebus oenanthe*. Notably, proportions are similarly high in the closely related *C. cupreus* and *discolor* and in *C. brunneus*, very divergent for the closely related *C. lucifer* and *lugens*, and similarly low in the closely related *C. personatus*, *C. melanochir* and *nigrifrons*. Proportions of time spent consuming prey by eastern Brazilian species of *Callicebus* (*C. personatus*, *C. melanochir*, *C. nigrifrons*) are more similar to other pitheciids, where the proportion varies between 0.4% in *Pithecia albicans* and 5.2% in *Cacajao calvus calvus* (Table 19.1). *Pithecia irrorata* in southeastern Peru “fed extensively on invertebrates” (Palminteri *et al.* 2005, p. 157), but quantitative data are not available.

*Callicebus cupreus* exploited prey from at least five orders of insects and from the Araneida; almost half of all prey feeding corresponded to Hymenoptera, mainly socially living ants

(Figure 19.1). Unidentified prey mainly involved small items that were grabbed and directly put into the mouth, without providing the observers an opportunity for identification. This unidentified portion probably includes tiny hymenopterans, small enough to be put straight into the mouth without further handling. The detection of residuals of small hymenopterans in feces supports this assumption (Nadjafzadeh 2005).

In other species of *Callicebus* and in the pitheciines, animal prey also comprises diverse orders of insects, and spiders (Table 19.1). Ants are the prey category that is exploited by the majority of species and populations, followed by caterpillars, beetles and orthopterans (katydids and grasshoppers). Except for a single observation of a *C. nigrifrons* feeding on a pigeon egg (Neri 1997) and very sporadic bird egg consumption by *P. pithecia* (0.4% of prey feeding time; Homburg 1998), there is a notable absence of predation on vertebrates. Prey consumed by *Callicebus* and other pitheciids includes both taxa that live socially (many ant species) or can be found in large aggregations (many caterpillars), and taxa that usually occur solitarily (e.g. orthopterans).

Quantitative data on the amount of different prey taxa are lacking for other *Callicebus* species, but are available for some pitheciines. The prey spectrum of *Chiropotes satanas* is dominated by caterpillars, which represented 70% of all prey in a group of *C. s. chiropotes* studied by Peetz (2001), and 60.5% and 25.2%, respectively, in two groups of *C. s. satanas* studied by Veiga (2006) and Veiga and Ferrari (2006). Caterpillars also dominate in the prey spectrum of *C. c. calvus* and *Cacajao melanocephalus* as determined from stomach contents (Ayres 1986). Termites represented more than 50% of prey feeding records in *Pithecia pithecia*, with ants ranking second (Homburg 1998). However, termites were only taken on two observation days during their mass swarming.



**Photo 19.1** *Callicebus cupreus* grooming. Photo: Mirjam Nadjafzadeh. (See color plate section.)

**Table 19.1** Contribution of prey to the diet (as % of feeding time or % of stomach content) and prey items of *Callicebus* and other pitheciids.

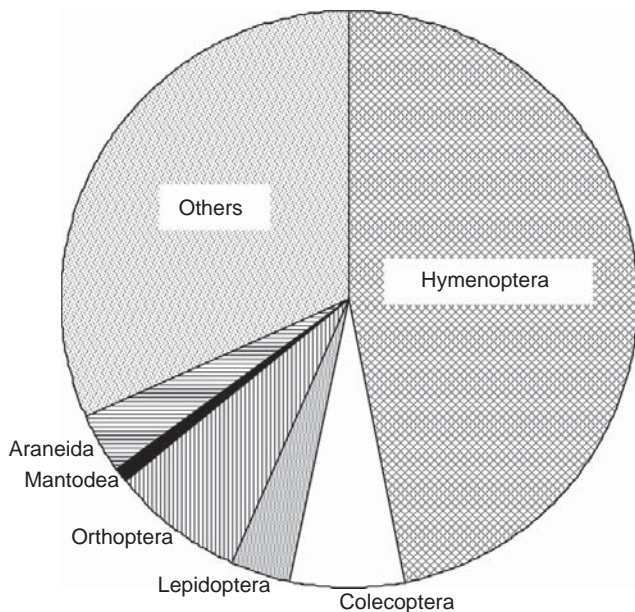
Species	Prey in diet (%)	Prey items	Data type	Reference
<i>Callicebus brunneus</i>	< 1	n.a. <sup>a</sup>	o <sup>b</sup>	Kinzey 1978
<i>Callicebus brunneus</i>	(~15%) <sup>c</sup>	Moths, caterpillars, chrysalises, ants, beetles, grasshoppers, katydids, larvae, spiders	o	Wright 1985, 1986
<i>Callicebus brunneus</i>	8.0	n.a.	o	Lawrence 2007
<i>Callicebus brunneus</i>	11.0	Spiders, caterpillars, moths, butterflies, ants	o	Crandlemire-Sacco 1988
<i>Callicebus cupreus</i>	11.1	Ants, katydids	o	Tirado Herrera & Heymann 2004
<i>Callicebus cupreus</i>	18.0	Ants, katydids, spiders, mantis, butterflies, termites	o	Pérez Yamacita 2010
<i>Callicebus cupreus</i> , Group W Group N	11.7 14.8 <sup>d</sup>	Ants, beetles, katydids, grasshoppers, caterpillars, wasps, mantis, spiders	o	Nadjafzadeh 2005
<i>Callicebus discolor</i>	13.0	n.a.	o	Youlatos & Pozo Rivera 1999
<i>Callicebus lucifer</i>	n.a.	Orthopterans, hymenopterans, beetles	sc <sup>e</sup>	Izawa 1975
<i>Callicebus lucifer</i>	20.0 <sup>f</sup>	Ants, insect galls, beetles, hymenopteran larvae	o	Kinzey 1978
<i>Callicebus lucifer</i>	15.8	Grasshoppers, praying mantis, spiders, larvae	o	Easley 1982
<i>Callicebus lugens</i>	n.a.	Caterpillars, wasps, ants, beetles, flies	sc	Milton & Nessimian 1984
<i>Callicebus lugens</i>	3.4 <sup>g</sup>	Ants and other hymenopterans, beetles, orthopterans, spiders, galls	o	Palacios <i>et al.</i> 1997
<i>Callicebus lugens</i>	19.5 <sup>h</sup>	Katydids, ants, spiders	o	Alvarez & Heymann 2009
<i>Callicebus melanochir</i>	0.0	–	o	Müller 1996
<i>Callicebus melanochir</i>	0.3	n.a.	o	Heiduck 1997
<i>Callicebus oenanthe</i>	22.0	Ants, spiders, cicada, grasshoppers, butterflies, beetles, bees/wasps, caterpillars, walking sticks, galls, unidentified small flying insects	o	DeLuycker 2007, 2009
<i>Callicebus ornatus</i>	n.a.	Beetles, orthopterans	sc	Hernández Camacho & Cooper 1976
<i>Callicebus ornatus</i>	9.4	n.a.	o	Polanco 1992 quoted in Defler 2004
<i>Callicebus nigrifrons</i>	3.4	Caterpillars, galls, chrysalises, bird eggs	o	Neri 1997
<i>Callicebus nigrifrons</i>	10.0	n.a.	o	Souza <i>et al.</i> 1996
<i>Callicebus personatus</i>	0.0	–	o	Kinzey & Becker 1983
<i>Callicebus personatus</i>	0.0	–	o	Price & Piedade 2001
<i>Cacajao calvus calvus</i>	5.2	Caterpillars, orthopterans, beetles, spiders, butterflies, flies, cicadas, homopteran nymphs	o sc	Ayres 1986, 1989

**Table 19.1** (cont.)

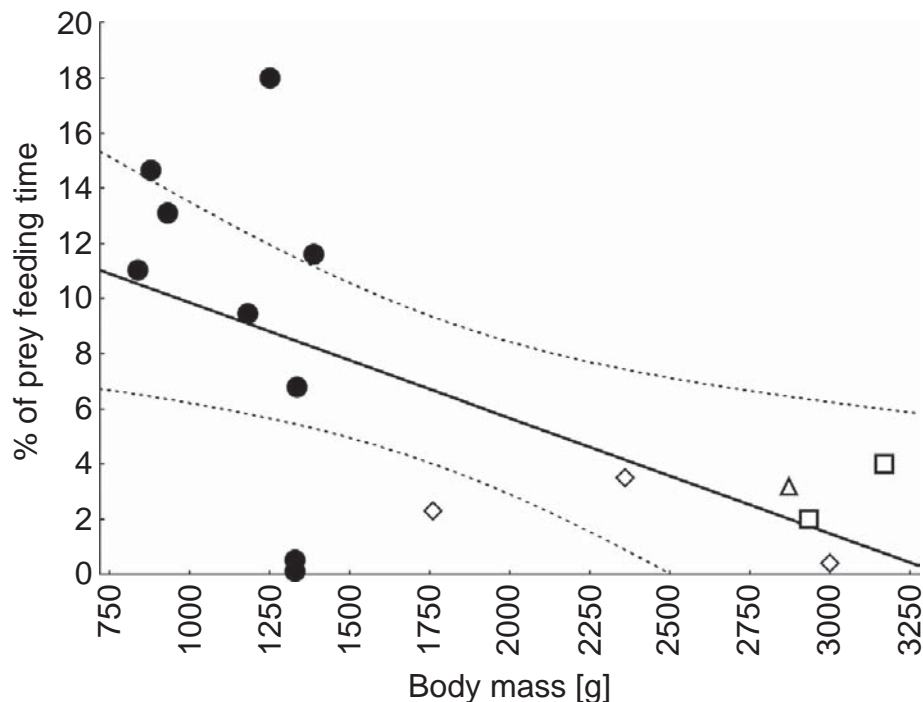
Species	Prey in diet (%)	Prey items	Data type	Reference
<i>Cacajao calvus ucayalii</i>	2.8	Ants, caterpillars, termites, mantids, katydids		Bowler 2007
<i>Cacajao melanocephalus melanocephalus</i>	2.0	Ants, spiders, grasshoppers, katydids, roaches	o	Boubli 1999
<i>Cacajao melanocephalus ouakari</i>	n.a.	Caterpillars, hymenopterans, beetles, cicadas, orthopterans, spiders	sc	Ayres 1986, 1989
<i>Cacajao melanocephalus ouakari</i>	n.a.	Wasps	o	Barnett <i>et al.</i> 2005
<i>Chiropotes albinus</i>	n.a.	Unidentified larvae(?)	o	Ayres 1981
<i>Chiropotes satanas chiropotes</i>	n.a.	Caterpillars, ants, beetles	sc	Ayres & Nessimian 1982
<i>Chiropotes satanas chiropotes</i>	n.a.	Ants, flies, beetles	sc	Mittermeier <i>et al.</i> 1983
<i>Chiropotes satanas chiropotes</i>	n.a.	Caterpillars, ants, beetles	sc	Frazão 1991
<i>Chiropotes satanas chiropotes</i>	0.5	Caterpillars	o	Kinzey & Norconk 1993; Norconk 1996
<i>Chiropotes satanas chiropotes</i>	3.9	Caterpillars, cicadas, ants, orthopterans, hymenopterans (nests, galls), spiders	o	Peetz 2001
<i>Chiropotes satanas satanas</i> , mainland group	4.6	Caterpillars, hymenopterans, termites, cicadas, beetles, spiders	o	Veiga 2006; Veiga & Ferrari 2006
<i>Chiropotes satanas satanas</i> , island group	3.7			
<i>Pithecia albicans</i>	n.a.	Caterpillars, spiders, hymenopterans	sc	Johns 1986
<i>Pithecia albicans</i>	0.4	n.a.	o	Peres 1993
<i>Pithecia irrorata</i>	n.a. <sup>i</sup>	n.a.	o	Palminteri <i>et al.</i> 2005
<i>Pithecia monachus</i>	n.a.	Ants, butterflies	sc	Izawa 1975
<i>Pithecia monachus</i>	~3.5 <sup>j</sup>	Ants	o	Soini 1987
<i>Pithecia pithecia</i>	2.3	Ants, spiders, caterpillars	o	Kinzey & Norconk 1993; Norconk 1996
<i>Pithecia pithecia</i>	3.7	Ants, caterpillars, termites, hymenopterans, orthopterans	o	Homburg 1998
<i>Pithecia pithecia</i>	1.8	n.a.	o	Norconk & Conklin-Brittain 2004
<i>Pithecia pithecia</i>	<1	n.a.	o	Norconk & Setz (Chapter 25)

<sup>a</sup> n.a.: no information available. <sup>b</sup> o: direct observation. <sup>c</sup> Estimated from figure 3b in Wright (1986), includes search time. <sup>d</sup> Rainy season only. <sup>e</sup> sc: stomach content. <sup>f</sup> Different figures are provided in Kinzey (1977: 14%) and Kinzey *et al.* (1977: 16%). <sup>g</sup> During period of low fruit and leaf abundance. <sup>h</sup> During period of high fruit and leaf abundance. <sup>i</sup> "extensively" (Palminteri *et al.* 2005, p. 157). <sup>j</sup> Calculated from data in Soini (1987).

These findings suggest that for *Callicebus* and the other pitheciids it may be profitable to exploit prey that occurs in larger patches (social ants, caterpillars, swarming termites). However, on a cautionary note, it must be taken into consideration that feeding on prey in larger patches – which can involve all or most of the group members – may be more conspicuous and thus be more easily recorded than feeding on solitary prey items that is done individually.



**Figure 19.1** The proportion of different prey taxa in the diet of *Callicebus cupreus* (from data in Nadjafzadeh 2005 Nadjafzadeh & Heymann 2008).



**Figure 19.2** The proportion of feeding time on prey in *Callicebus* (●), *Pithecia* (◇), *Chiropotes* (△) and *Cacajao* (□) in relation to body mass. —: regression line (% prey feeding time =  $14.045 - 0.004 * \text{body mass}$ ); .....: 95% confidence intervals. For body mass, midpoints of values for males and females were calculated from data in Smith and Jungers (1997), Hernández Camacho and Defler (1985, for *C. lugens*), Hershkovitz (1990, for *C. discolor* and *C. ornatus*), and Bicca-Marques et al. (2002, for *C. cupreus*). Body mass data from *C. personatus* were used for *C. melanochir* and *C. nigrifrons*, since head–body length data in Hershkovitz (1990) indicate similar size. If more than one data point was available for the proportion of feeding time on prey for one species (see Table 19.1), the midpoint of values was calculated, except for *C. brunneus* (values provided by Kinzey [1978] and Wright [1985] for this species were not used because the former was based on a very small observation time, and the latter included search time).

## Prey capture techniques

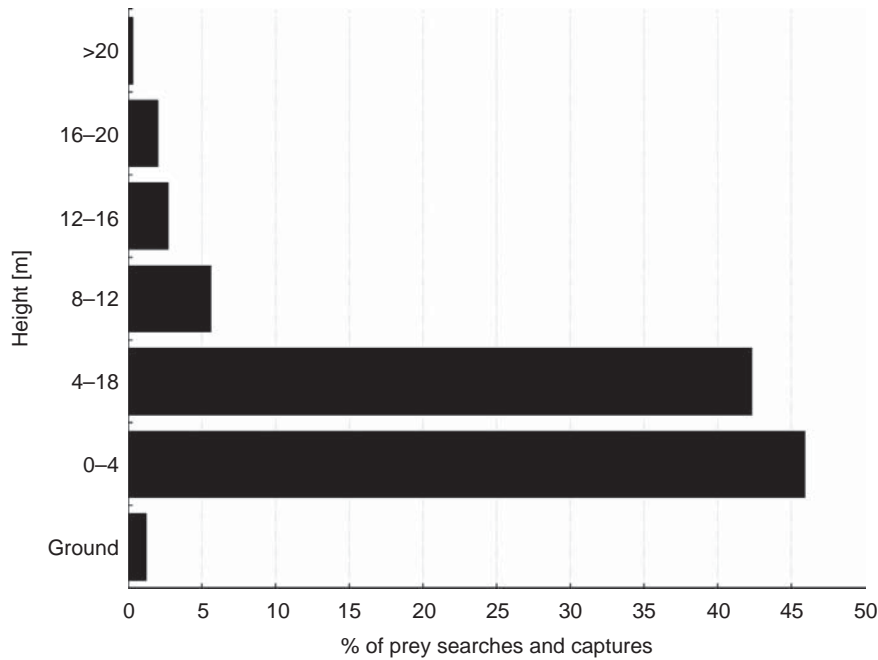
### *Callicebus cupreus*

Red titi monkeys mainly forage for prey in the lower strata of the forest (Figure 19.3), and occasionally obtain prey even from the ground. While searching and capturing prey they are usually sitting or standing on branches (48.6% of records) or lianas (28.6%), but also clinging to trunks (19.8%); other substrates like palm leaves, epiphytes and ground are only sporadically used. Red titi monkeys are positioned on horizontal (0–15°) and diagonal (15–75°) supports during 40.6% and 36.4% of prey searches and captures, respectively, while 23% take place while the titi monkeys are positioned on a vertical substrate (75–90°) (Nadjafzadeh 2005).

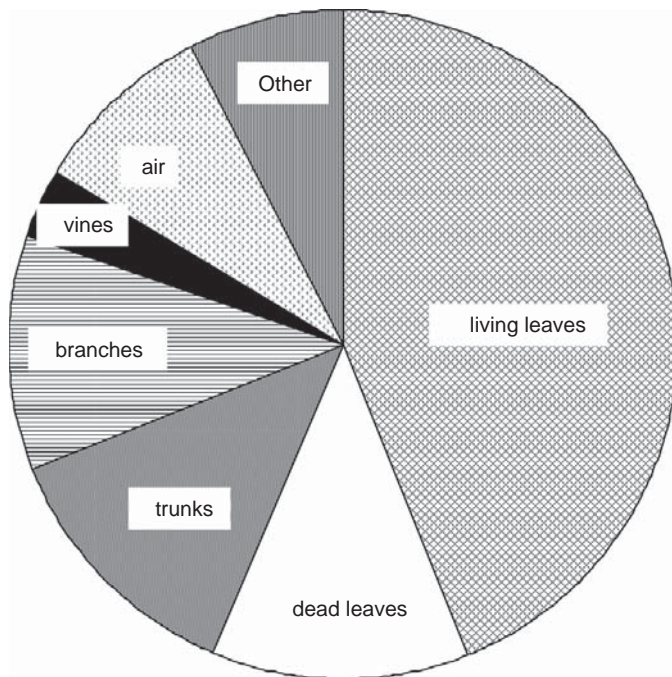
Red titi monkeys search and find prey most often on living leaves. Dead leaves, trunks, branches, and gleaning insects from the air are used with more or less similar frequencies (Figure 19.4). Open microhabitats (i.e. microhabitats where prey items are exposed to view) account for 81.8% of all prey searches and captures. From these open microhabitats prey is grabbed directly with one or both hands, or is first fixed with the hand(s) and subsequently transferred to the mouth. Closed microhabitats that require slight manipulation comprise enrolled leaves, mainly dead, but also living. Only on four occasions was extractive foraging in microhabitats observed that require intensive manipulation (bark, dead branch).

### Comparison with other pitheciids

Information provided by Alvarez and Heymann (2009), DeLuycker (2007), Easley (1982), Kinzey (1977), Neri (1997) and Wright (1985) indicate that *C. oenanthe*, *C. brunneus*,



**Figure 19.3** Height use during prey search and capture by *Callicebus cupreus* (mean values for two study groups, total  $N = 938$  records) (from data in Nadjafzadeh 2005 Nadjafzadeh & Heymann 2008).



**Figure 19.4** Microhabitats on which prey is searched and captured by *Callicebus cupreus* (from data in Nadjafzadeh 2005 and Nadjafzadeh & Heymann 2008).

*C. lucifer*, *C. lugens* and *C. nigrifrons* search for and capture prey on trunks and branches, unroll dead and green leaves, grab flying insects, but do not to tear open bark or branches, or grab into holes. This coincides with observations on *C. cupreus*, although it remains to be determined for most pitheciids

whether different microhabitats are also used to the same or similar degree to obtain prey (but see Alvarez & Heymann 2009 for comparative quantitative information on *C. lugens*).

*Chiropotes* locates prey on living leaves and dry fruits. They also extract prey from dead branches, and have been observed to strip off bark and search beneath (Peetz 2001; Veiga 2006; Veiga & Ferrari 2006). *Cacajao calvus ucayalii* search on dead and living leaves, they split open the end of branches that contained chambers with ants, and were once seen to capture termites on the wing (Bowler 2007). *Cacajao melanocephalus* unrolls dry leaves, strips off bark from dead branches, and scrapes ant nests off trees (Boubli 1999). Similar to titi monkeys, they capture flying insects directly from the air (Boubli 1999). *Pithecia pithecia* also unrolls dry leaves, and from the descriptions in Homburg (1998) it can be deduced that prey is also commonly taken from open microhabitats such as leaf surfaces or branches.

There is also some evidence for “indirect prey foraging”, i.e. uptake of insects infesting the fruit pulp or seeds, in *C. c. calvus* (Ayres 1989) and possibly *C. lugens* (Alvarez Vargas 2007).

## Animal prey and body size in pitheciids

Nutritional ecology theory predicts that the amount of prey in the diet should decrease with increasing body mass (Chivers & Hladik 1980; Martin 1990; see “Introduction” above). Examination of the proportion of feeding time on prey in *Callicebus* and other pitheciids in relation to body mass reveals a significant negative correlation ( $r = -0.61$ ,  $R^2_{\text{adj}} = 0.33$ ,  $F_{1,13} = 7.83$ ,  $p < 0.05$ ; Figure 19.2). This correlation is likely to be biased because no phylogenetic correction was applied. Nevertheless,

it indicates that the difference in the amount of time dedicated to prey consumption between *Callicebus* as a genus on the one hand and *Pithecia*, *Chiropotes* and *Cacajao* on the other hand might be accounted for by differences in body size. However, there is considerable intrageneric variation in *Callicebus* that cannot be explained by body-size differences. The highest (17.9%) and lowest (0%) proportions of feeding time on prey are found in the larger *Callicebus* species (Figure 19.1). Potentially, this variation may represent biases arising from different lengths of study periods, from the coverage of different seasons, or from group idiosyncrasies. Nadjafzadeh (2005) noted that there was no difference in the amount of prey between wet and dry season in *C. cupreus*. However, for the same species, there was some variation between studies made at different times and of different duration (Perez Yamacita 2010; Tirado Herrera & Heymann 2004; see Table 19.1). In contrast, two independent studies of *C. melanochir* in subsequent years consistently reported very little or no prey consumption (Heiduck 1997; Müller 1996). Highly contrasting proportions of feeding time on prey were found in two groups of *C. lugens*: one studied during the period of low fruit and leaf abundance showed low proportions of prey in the diet (Palacios *et al.* 1997), the other during the period of high fruit and leaf abundance high proportions (Alvarez Vargas 2007; Alvarez & Heymann 2009). Lawrence (2007) reported little overall variation (6–11%) between groups of *C. brunneus*, but marked seasonal variation, with higher proportions of insect consumption during the season with low fruit availability. The available data do not allow drawing a conclusion on what is causing variation within the genus *Callicebus*.

## Conclusions and perspectives

It is clear from our review that animal prey is an integral component of the diet of almost all *Callicebus* and most other pitheciids, although the proportion of prey varies considerably. For some of the *Callicebus* species, time spent feeding on prey matches or even exceeds values from other Platyrrhines that are often classified as frugivores–insectivores or gummivores–insectivores, like the callitrichids (e.g. Digby *et al.* 2007). All pitheciid species studied so far exploit a variety of behaviors to search for and capture prey. From the available descriptions, these behaviors seem to be relatively uniform within *Callicebus* and mainly involve the search for and capture of prey exposed to view, being superficially similar to many tamarins (see Garber 1993), while *Chiropotes* and *Cacajao* also employ “destructive” foraging in the sense of Terborgh (1983). The difference between foraging techniques of *Callicebus* and the other pitheciids, along with the relationship between body mass and time spent feeding on insects, support Terborgh’s (1983) considerations on the role of body size for prey foraging and consumption.

Red titi monkeys differ in their prey foraging techniques and consequently in prey spectrum from sympatric tamarin monkeys: while tamarins (*Saguinus mystax*, *Saguinus*

*fuscicollis*) mainly capture prey that is occurring solitarily, *C. cupreus* mainly takes prey living socially (Nadjafzadeh 2005; Nadjafzadeh & Heymann 2008). Given the almost complete lack of quantitative data on foraging techniques and prey spectrum in other *Callicebus* and in pitheciine species, it is unclear at the moment how far they differ from or overlap with other sympatric insect-feeding primates such as *Cebus*, *Saimiri*, *Saguinus* or *Callimico*. Quantitative analysis of patterns of prey foraging will help to define the feeding niches of pitheciids in more detail and to understand whether and how far prey foraging contributes to niche differentiation and the avoidance of interspecific competition, as suggested by Terborgh (1983). The inclusion of prey foraging techniques in interspecific comparisons will also allow obtaining a deeper understanding of the evolution of feeding niches in platyrrhines in general (Rosenberger 1992).

It is unclear for the moment whether the interspecific variation of the amount of prey within *Callicebus* relates to species-specific traits (e.g. dental, postcranial or gut morphology) or population/habitat-specific factors such as the temporal and spatial availability and distribution of prey. Interestingly, Kinzey’s (1978) hypothesis on dental differences between *C. brunneus* and *C. lucifer* does not hold up in light of the available data. Kinzey had argued that a longer shearing blade (crisid oblique) in the former species and a larger crushing and grinding surface (taloid basin) in the latter is related to their different emphasis on leaves and insects, respectively, as sources of protein. Nevertheless, given the nutritional importance of protein, foraging for and consumption of animal prey must be taken into consideration in the interpretation of the feeding adaptations – be they morphological, behavioral, or physiological – of *Callicebus* and the other pitheciids.

## Note added in proof

After the manuscript had been accepted for publication, additional information on prey feeding in *Callicebus* emerged.

In a 1-year study, a group of *Callicebus coimbrai* included 2.6% insects in its diet (Souza-Alves *et al.* 2011). Prey consumption peaked in the dry season months November–December, when the titi monkeys fed on agglomerations of the caterpillar *Pseudosphinx tetrio* (Lepidoptera: Sphingidae). Other prey items were Phasmatodea and Homoptera.

In a 9-month study, a group of *Callicebus nigrifrons* included 11% insects in its diet (Barbosa Caselli & Setz 2011).

In a 4-month study (March–June, the end of the rainy season) of two groups of *Callicebus cupreus* at EBQB, Kulp (2011) reported 8.0% and 8.1% of prey in the diet, respectively.

The general conclusions of the chapter are not altered by this additional information.

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