Chapter 2
Diets of Howler Monkeys

Pedro Américo D. Dias and Ariadna Rangel-Negrín

Abstract Based on a bibliographical review, we examined the diets of howler monkeys to compile a comprehensive overview of their food resources and document dietary diversity. Additionally, we analyzed the effects of rainfall, group size, and forest size on dietary variation. Howlers eat nearly all available plant parts in their habitats. Time dedicated to the consumption of different food types varies among species and populations, such that feeding behavior can range from high folivory to high frugivory. Overall, howlers were found to use at least 1,165 plant species, belonging to 479 genera and 111 families as food sources. Similarity in the use of plant taxa as food sources (assessed with the Jaccard index) is higher within than between howler species, although variation in similarity is higher within species. Rainfall patterns, group size, and forest size affect several dimensions of the dietary habits of howlers, such that, for instance, the degree of frugivory increases with increased rainfall and habitat size, but decreases with increasing group size in groups that live in more productive habitats. Moreover, the range of variation in dietary habits correlates positively with variation in rainfall, suggesting that some howler species are habitat generalists and have more variable diets, whereas others are habitat specialists and tend to concentrate their diets on certain plant parts. Our results highlight the high degree of dietary flexibility demonstrated by the genus *Alouatta* and provide new insights for future research on howler foraging strategies.

Resumen Con base en una revisión bibliográfica, examinamos las dietas de los monos aulladores para describir exhaustivamente sus recursos alimenticios y la diversidad de su dieta. Asimismo, analizamos los efectos de la pluviosidad, tamaño grupal y tamaño del bosque en que viven los grupos sobre la variación en su dieta. Los monos aulladores consumen casi todas las partes vegetales presentes en sus hábitats. El tiempo dedicado al consumo de diferentes tipos de alimentos varía entre especies y poblaciones, de tal manera que la conducta alimenticia de los monos aulladores puede ser altamente folívora o frugívora. Los monos aulladores usan como recurso alimenticio al menos 1,165 especies de plantas, pertenecientes a 479 génerosya 111

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familias. La similitud (medida con el índice de Jaccard) en el uso de taxa de plantas como alimento es mayor dentro que entre especies, aunque la variación en los índices de similitud es mayor dentro de una misma especie que entre diferentes especies. La pluviosidad, el tamaño grupal y el tamaño del bosque afectan diversas dimensiones de la conducta alimenticia de los monos aulladores, de tal modo que, por ejemplo, la frugivoría incrementa de manera directamente proporcional con la pluviosidad y el tamaño del bosque, pero disminuye en grupos grandes que viven en hábitats más productivos. Por otra parte, el rango de variación en los hábitos alimenticios se correlaciona positivamente con la variación en la pluviosidad, sugiriendo que algunas especies de monos aulladores son generalistas de hábitat y tienen dietas más variadas, mientras que otras son especialistas de hábitat y tienden a concentrar sus dietas en ciertas partes vegetales. Nuestros resultados subrayan el notable grado de flexibilidad alimenticia del género *Alouatta* y aportan nuevas perspectivas hacia futuras investigaciones sobre las estrategias de forrajeo de los monos aulladores.

Keywords *Alouatta* • Cross-species comparisons • Dietary diversity • Herbivory patterns

2.1 Introduction

In the 80 years following the pioneering study by C.R. Carpenter on the behavior of mantled howler monkeys (*Alouatta palliata*) of Barro Colorado Island in Panama, our knowledge of the howler diet has increased substantially. Current data provide evidence that members of the genus *Alouatta* are eclectic herbivores and present a very selective foraging profile combined with a highly diverse diet. This dietary pattern, a number of behavioral adaptations and digestive flexibility, allows howlers to efficiently solve the basic problem of meeting their nutrient requirements each day while staying below their maximum threshold for toxins. In this chapter we build on previous reviews of the diets of howlers (Crockett and Eisenberg 1987; Neville et al. 1988; Bicca-Marques 2003; Di Fiore and Campbell 2007; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Chaves and Bicca-Marques 2013) to better understand variation across species and populations for two main topics: (1) the food types and food taxa selected by howlers and (2) the extent and overall diversity of the howler diet. Additionally, we examine how the diet of howlers may vary throughout a gradient of high folivory to high frugivory as a function of rainfall, group size, and the size of the forests they inhabit. These three factors have been described as important determinants of the food habits of howlers, as: (1) rainfall is associated with habitat productivity and seasonality, and therefore, food availability (e.g., Dunn et al. 2010; Palma et al. 2001); (2) group size may affect within-group scramble competition for food, so that larger groups deplete food patches faster (e.g., Arroyo-Rodríguez et al. 2011); (3) forest size correlates positively with the number of food sources available for howler monkeys (e.g., Arroyo-Rodríguez and Dias 2010). Finally, we analyze the influence of rainfall, group size, and forest size on the dietary breadth (i.e., the patterns of plant species and plant family use) of howlers.

2.2 Literature Review

2.2.1 Database and Analyses

We reviewed all published articles, book chapters, and unpublished dissertations available on ProQuest Dissertations &Theses Database (ProQuest LLC, Ann Arbor, MI, USA) as well as those in digital libraries of Latin-American universities up to January 2012 that focused on the diet of *Alouatta*. When data from a thesis were published, we only used information presented in the publication. In this chapter we follow the howler taxonomy proposed by Cortés-Ortiz et al. (2003).

From each study, we extracted the following information for each sampled howler group: (1) the proportion of daily activity time spent feeding; (2) the proportion of feeding time dedicated to eat leaves (both mature and young leaves), fruits, flowers, and other food items (OFI); (3) the number of plant species and families used as food sources. Data on plant taxonomy were homogenized using relevant taxonomic literature and online databases (Tropicos, IPNI, ILDIS) by checking for synonyms and misspellings. The taxonomic treatment of plant families follows the Angiosperm Phylogeny Group II classification (APG 2003); (4) percentage of total feeding time dedicated to the top five plant species; (5) the number of plant species comprising >50 % of total feeding time; (6) the number of plant species used as sources of leaves and the number of plant species used as sources of fruits; (7) group size, calculated as the mean number of individuals present in each group during the sampling period; (8) average annual rainfall (in mm) at each study site. When this information was not provided by the authors, we consulted it at WorldClim (Hijmans et al. 2005); (9) forest size (in ha), calculated as the amount of continuous habitat available to each group.

To reduce the influence of seasonality, variation in study duration and differences in study design on our results, in analyses of the use of food items and similarity in the use of plant taxa as food sources, we only used studies that: (1) included ≥9 months and ≥140 h of observations; (2) included data collected in both wet and dry seasons; (3) sampled feeding behavior using focal or scan sampling methods. To analyze variation in dietary breadth (defined as the number of plant species and families used as sources of food), we similarly used studies with a duration ≥9 months and that sampled feeding behavior with focal or scan sampling, but divided the number plant species and families by the number of observation hours to obtain a measure of breadth that could be directly compared among studies with different observation effort.

We used paired *t*-tests to compare the proportions of time dedicated to consume different plant parts and one-way ANOVA to compare: (1) dietary variables among howler species (followed by LSD post hoc tests); (2) the number of plant species used as sources of leaves and the number of plant species used as sources of fruits. We used Pearson correlations to analyze associations between: (1) the proportion of time dedicated to the consumption of different plant parts; (2) the number of plant species included in the diet and the percentage of total feeding time dedicated to the top five plant species; (3) the number of plant species comprising >50 % of total

feeding time and the time dedicated to the consumption of different plant parts. To explore variation in the howler diet (higher folivory to higher frugivory) as a function of rainfall, group size, and forest size, we first used a PCA to combine data on the proportion of feeding time dedicated to eat fruits with the proportion of feeding time dedicated to eat leaves in a single variable that could be used to describe the dietary habits of howlers. From this analysis we obtained a component that explained 88.4 % of the total variance in both variables (eigenvalue = 1.8). This component (dietary habits hereafter) correlated positively ($r = 0.94$) with fruit consumption and negatively with leaf consumption ($r = -0.94$). Values of this component ≥ 1 indicate a mainly frugivorous diet (i.e., >50 % of feeding time dedicated to fruits). Second, we used a backward stepwise regression analysis to predict variation in dietary habits as a function of rainfall, group size, and forest size. Third, to further understand the relationships between the predictive variables that were included in the stepwise analysis and dietary habits, we performed piecewise regressions. These regressions allowed identifying discontinuities in the relationships between each predictive variable and dietary habit by determining breakpoints. A new stepwise regression was then calculated for each slope defined by the breakpoints, in which we again included all predictive variables. To normalize distributions and homogenize variances, in these analyses percentage data was converted to proportions and proportions were transformed using the square root of the arcsine; and rainfall, group size, and forest size were log transformed.

We used backward stepwise regressions to predict variation in the proportion of time dedicated to consume flowers and OFI, as well as in the dietary breadth of howlers as a function of rainfall, group size, and forest size. In these analyses the proportions of time dedicated to feeding and the rates of consumption of plant species and families were transformed using the square root of the arcsine; and rainfall, group size, and forest size were log transformed.

We analyzed intra- and interspecific similarity in the use of plant taxa with the Jaccard's coefficient: S_{ij} = number of taxa consumed in both sites i and j/total number of taxa consumed in either site i or j. Similarity was calculated at the family, genus, and species level.

2.2.2 Sample Characteristics

The majority of studies (55.8 %) that have addressed topics related to the diet of howler monkeys have been conducted with groups living in Brazil and México, whereas in Ecuador, Peru, and Surinam, respectively, only a single study related to the howler diet could be found (Fig. 2.1). For Bolivia, Guiana, Paraguay, and Uruguay, countries where howler monkeys also occur, we could not find any dietary studies. *Alouatta palliata* has been the most thoroughly studied species, followed by *A. pigra* and *A. guariba*. Among the least studied species are *A. belzebul* and *A. macconnelli*, and no studies could be found on the diet of *A. nigerrima* and *A. sara* (Table 2.1).

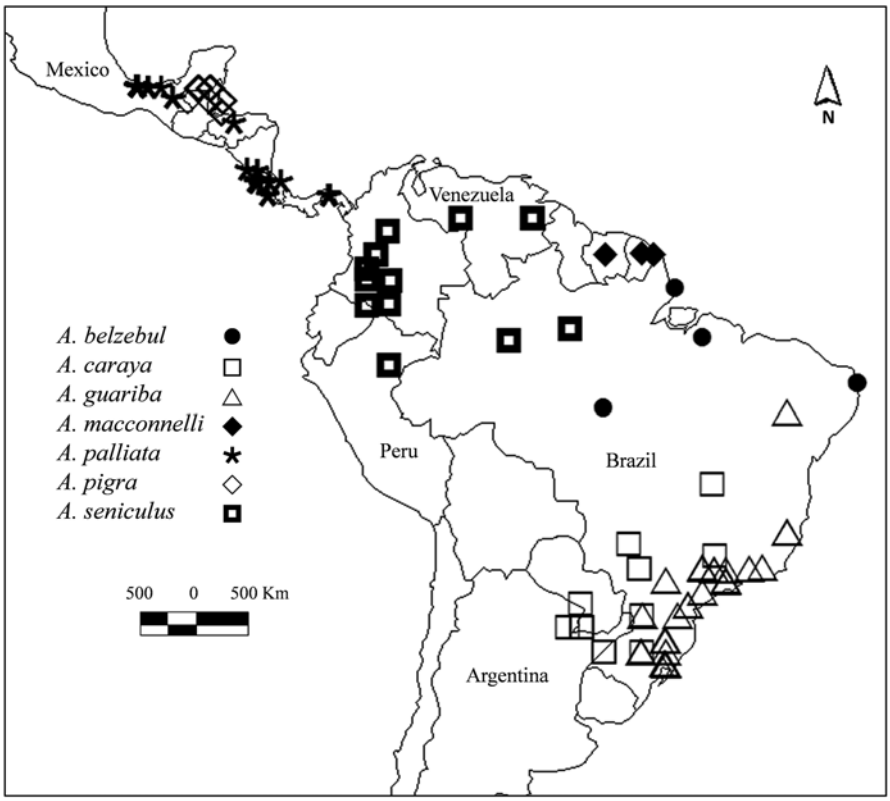

Fig. 2.1 Sites where the diets of howlers have been studied

More than half of all studies have been conducted with groups living in tropical dry forests (58.3 %; i.e., rainfall <2,000 mm), followed by groups in wet forests (27 %; i.e., rainfall >2,700 mm) and groups in moist forests (14.7 %; i.e., rainfall 2,000–2,700 mm). At the species level, all *A. belzebul* groups have been observed in moist forest, whereas all *A. caraya* and *A. guariba*, as well as the majority of *A. pigra* groups, live in dry forest. Conversely, the majority of *A. macconnelli*, *A. palliata,* and *A. seniculus* groups have been studied in wet forests. A similar number of groups have been studied in protected and unprotected forests (i.e., conservation status assigned by country's government), although most studies have been conducted in small forests: 47.1 % of studies were carried out in forests ≤100 ha, whereas only 18.5 % were carried out in forests ≥10,000 ha.

The diet of howler monkeys has been studied using a variety of different sampling methods. Most studies (98.2 %) relied on direct observations of the behavior of individuals within a discrete howler group or groups, and among these, the majority (72.4 %) used focal or scan sampling (Altmann 1974). Variation in the duration of studies is impressive, ranging from 1 week to 74 months and from 31 to 2,303

Table 2.1 Studies on the diet of howlers

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)[a]	Plant items in diet (%)					No. species	No. families	%TFS[b]	>50 % TFT[c]	Sources fruits	Sources leaves	References[d]
									Fruits	Leaves		Flowers	OFI[e]							
										All[f]	Young									
A. belzebul	Pacatuba, MG, Brazil	1985–1986	14/–	Scan	7	2,176	271	6.5	59.0	13.3	6.0	27.6	0.2	47	21	–	–	38	6	1
A. belzebul	Pacatuba, MG, Brazil	1998–1999	11/–	Scan	–	2,176	271	12.3	20.1	46.1	6.2	11.6	–	–	–	–	–	–	–	2
A. belzebul	Estação Científica Ferreira Penna, PA, Brazil	1997–1998	10/–	Scan	9	2,250	33,000	31.4	35.1	60.5	–	4.4	–	–	–	–	–	–	–	3
A. belzebul	Paranaíta, MT, Brazil	1999–2000	10/–	Scan	8	2,174	10,000	20	55.6	25.6	19.8	5.7	13.2	67	24	38.0	10	35	27	4
A. belzebul	Cauaxi, PA, Brazil	2000	10/1, 203	Scan	6	2,000	20,000	18.8	43.4	45.0	–	11.3	0.4	–	–	–	–	–	–	5
All *A. belzebul*[g]					7.5 (6–9)	2,155.2 (2,000–2,250)	12,708.4 (271–33,000)	17.8 (6.5–31.4)	42.6 (20.1–59)	38.1 (13.3–60.5)	10.7 (6–19.8)	12.1 (4.4–27.6)	4.6 (0.2–13.2)	57 (47–67)	22.5 (21–24)	38	10	36.5 (35–38)	16.5 (6–27)	
A. caraya	Parque Nacional de Brasília, BSB, Brazil	1984	4/–	–	–	1,520	30,000	–	–	–	–	–	–	12	11	–	–	2	11	6
A. caraya	Ribeirão Preto, SP, Brazil	1980–1983	26/480	–	16	1,400	8.8	–	38.7	52.7	–	8.7	–	32	15	–	–	11	19	7
A. caraya	Riachuelo River, Corrientes, Argentina	1994–1995	2/200	Ad libitum	6	1,200	10	–	–	–	–	–	–	–	–	–	–	–	–	8
A. caraya	Riachuelo River, Corrientes, Argentina[‡]	1981–1982	15/528	Focal	7	1,200	7, 10, 12	–	29.0	71.0	–	–	–	23	17	~93	2	11	17	9
A. caraya	Isla Guáscara, Corrientes, Argentina[‡‡]	1981	3/58	Focal	10	1,200	40	–	–	–	–	–	–	12	10	–	–	5	12	10
A. caraya	El Piñalito, Misiones, Argentina*	2006–2007	12/734	Scan	10.8	1,952	3,796	–	19.0	64.0	25.0	6.0	10.0	56	–	40.4	9	7	9	11

A. caraya	Estabelecimento N.S[h] Conceição, RS, Brazil	2005–2006	12/699	Scan	13	1,500	0.7	14.9	12.3	82.4	–	2.7	2.6	14	13	61.7	2	9	12	12
A. caraya	Estância Casa Branca, RS, Brazil	1989–1990	12/745	Scan	16	1,500	2	–	28.9	60.9	15.6	2.7	7.5	27	18	77.4	3	20	18	13
A. caraya	Several locations in RS, Brazil	1989–1990/ 2005–2007	36/ 2,274	–	–	1,500	–	–	–	–	–	–	–	–	–	–	–	–	–	14
A. caraya	Isla Brasilera, Argentina*	1998–2000	17/ 1,680	Scan	18.5	1,230	141	18.9	19.0	64.0	13.0	12.0	5.0	22	13	–	–	17	12	15
A. caraya	San Cayetano, Corrientes, Argentina‡	2005–2008	–	Focal/ scan	6.75	1,230	–	–	–	–	–	–	–	–	–	–	–	–	–	16
A. caraya	Ilha Mutum, PR, Brazil	2004–2005	12/306	Scan	10	1,250	1,050	–	24.0	65.0	–	10.0	1.0	18	14	79.5	2	9	14	17
A. caraya	Rancho Praia Grande, PR, Brazil	2004–2005	12/288	Scan	12	1,250	–	–	46.0	49.0	–	4.0	1.0	18	11	84.4	3	9	13	18
A. caraya	N. Esperança and N. Querência, MS, Brazil	2002–2003	15/–	Scan	6	1,250	6,267	14.7	35.5	51.7	3.7	12.9	–	–	–	–	–	–	–	19
A. caraya	Corrientes, Argentina	–	–	–	6	1,200	12	15.2	26.7	70.5	–	0.8	2.0	–	–	–	–	–	–	20
A. caraya	Rancho Guaycolec, Formosa, Argentina	1988–1989	–	–	–	1,300	300	13.3	21.2	72.8	–	2.7	3.3	–	–	–	–	–	–	21
A. caraya	Tupanciretã, RS, Brazil	2006–2007	12/830	Scan	4.5	1,700	0.3	19	2.0	85.0	–	11.0	2.0	17	13	95.5	1	6	15	22
A. caraya	Corrientes, Argentina	1992–1993	20/421	Ad libitum	8.5	1,645	15	–	43.5	50.5	26.0	5.3	0.6	–	–	–	–	–	–	23
All *A. caraya*					10.1 (4.5 –18.5)	1,390.4 (1,200–1,952)	2.974.5 (0.3–30,000)	16 (13.3–19)	26.6 (2–46)	64.6 (49–85)	16.7 (3.7–26)	6.6 (0.8–12.9)	3.5 (0.6–10)	22.8 (12–56)	13.5 (10–18)	73.2 (40.4 –95.5)	3.1 (1–9)	9.6 (2–20)	13.8 (9–19)	
A. guariba	El Piñalito, Misiones, Argentina*	2006–2007	12/660	–	7.5	1,952	3,796	–	24.0	62.0	24.0	6.0	7.0	40	–	50.0	5	7	9	24
A. guariba	Montes Claros, MG, Brazil	1983–1984	10/–	Scan	7	1,250	970	15.6	15.6	70.6	18.0	8.4	5.4	–	–	–	–	–	–	25

(continued)

Table 2.1 (continued)

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)[a]	Plant items in diet (%)					No. species	No. families	%TFS[b]	>50 % TFT[c]	Sources fruits	Sources leaves	References[d]
									Fruits	Leaves		Flowers	OFI[e]							
										All[f]	Young									
A. guariba	Cantareira, SP, Brazil	1979	–	–	–	1,400	5,400	–	29.4	70.6	–	–	–	13	9	–	–	4	11	26
A. guariba	Sta. Genebra, SP, Brazil	1991–1992	12/718.5	Scan	6	1,366	250	18.5	5.0	76.0	59.0	12.0	8.0	68	30	49.3	6	12	60	27
A. guariba	Sta. Genebra, SP, Brazil	1988–1991	45/–	Allocurrence	–	1,366	250	–	15.0	75.0	–	10.0	–	52	24	37.0	9	18	42	28
A. guariba	Montes Claros, MG, Brazil	2003	6/–	Ad libitum	8	1,250	970	–	–	–	–	–	–	–	–	–	–	–	–	29
A. guariba	Mata Doralice, PR, Brazil†	2001–2002	12/122	Ad libitum	4.33	1,148	170	–	47.9	50.3	–	1.4	0.3	42	21	60.4	4	11	5	30
A. guariba	Fazenda Barreiro Rico, SP, Brazil	2001–2002	12/–	Scan	6	1,284	1,450	–	8.0	80.7	–	7.5	3.7	–	–	–	–	–	–	31
A. guariba	Parque Estadual Itapuã, RS, Brazil	–	–	–	8.5	1,200	35	20	36.0	54.0	27.0	10.0	0.0	45	–	–	6	32	37	32
A. guariba	Aracuri, RS, Brazil	1993–1994	13/765	Ad libitum	6	1,200	70	19	29.0	59.0	26.0	12.0	–	43	–	–	4	–	–	33
A. guariba	Fazenda Rio Claro, SP, Brazil	1992–1993	12/408	Scan	3.5	1,385	165	10	21.0	76.0	10.0	0.0	–	34	18	46.2	6	11	31	34
A. guariba	Floresta Nacional de Três Barras, SC, Brazil	–	–	–	7	1,300	4,458.5	19	34.0	38.0	–	–	–	–	–	–	–	–	–	35
A. guariba	Mata Boa Vista, RJ, Brazil	1993–1994	17/700	Scan	4	1,400	80	13	12.0	72.0	–	10.0	6.0	–	–	–	–	–	–	36
A. guariba	Ribeirão Cachoeira, SP, Brazil	1995–1996	12/228	Scan	8	1,409	234	16	12.0	74.0	–	9.0	6.0	–	–	–	–	–	–	37
A. guariba	Parque Estadual Intervales, SP, Brazil	1998–1999	12/918.3	Allocurrence	6	1,707	49,888	17	23.0	74.0	37.0	1.0	2.0	95	–	–	5	34	72	38
A. guariba	Chácara Payquerê, PR, Brazil*	2003–2004	12/393	Ad libitum	5	1,600	700	–	–	–	–	–	–	–	–	–	–	–	–	39

A. guariba	Chácara Payquerê, PR, Brazil	2002–2003	12/76.5	Scan	6	1,600	700	–	41.0	57.0	–	1.7	0.3	34	20	–	–	20	21	40
A. guariba	Floresta da Cicuta, RJ, Brazil‡	2002	5/165	Allocurrence	5.75	1,600	131	–	7.0	81.0	–	2.0	10.0	–	–	–	–	–	–	41
A. guariba	Montes Claros, MG, Brazil	1983	2/100	–	–	1,250	880	–	5.0	88.0	–	–	–	–	–	–	–	–	–	42
A. guariba	Sapiranga, RS, Brazil	1981	–/–	–	–	1,300	–	–	–	–	–	–	–	13	10	–	–	10	8	43
A. guariba	Fontes do Ipiranga, SP, Brazil	–	44/–	Feces	–	1,368	526.4	–	–	–	–	–	–	76	34	–	–	52	2	44
A. guariba	Morro da Extrema, RS, Brazil	2002–2003	12/609	Scan	12	1,300	27	12	19.0	66.0	–	4.0	–	–	–	–	–	–	–	45
A. guariba	Morro da Extrema, SP, Brazil	1998–1999	7/454	Scan	9.5	1,310	27	28.2	28.3	57.6	31.5	6.4	3.9	35	21	54.7	6	11	30	46
A. guariba	Lami, SP, Brazil	1998–1999	7/415	Scan	8.5	1,310	12	34.5	40.4	46.1	21.6	8.3	2.6	26	19	65.2	3	11	20	46
A. guariba	Campo de Instrução de Sta. Maria, RS, Brazil	2005	12/654	Scan	7	1,700	1.8	–	17.8	67.0	41.9	7.8	–	52	–	47.7	6	8	44	47
A. guariba	Campo de Instrução de Sta. Maria, RS, Brazil	2005	12/623	Scan	6	1,700	20	–	35.3	58.8	44.3	5.2	–	48	–	60.1	3	5	42	47
A. guariba	Campo de Instrução de Sta. Maria, RS, Brazil	2005	12/577	Scan	5	1,700	977	–	8.8	78.3	51.1	10.0	–	48	–	51.5	5	14	42	47
A. guariba	Barra do Ribeiro, RS, Brazil	2007	5/243	Focal	6.5	1,350	5	17.1	34.3	53.3	–	12.2	–	38	24	56.1	5	10	32	48
A. guariba	Ipê, RS, Brazil	2007–2008	12/636	Scan	6	1,900	2.2	20	15.0	78.0	–	2.0	5.0	42	22	56.0	4	13	41	49
A. guariba	Cantareira, SP, Brazil	–	–	–	9	1,400	7,900	21	15.0	55.0	50.0	29.0	–	41	–	–	6	–	–	50
A. guariba	Camaquã, RS, Brazil	2004/2005	13/–	Focal	5	1,200	10	30	29.5	70.5	38.9	–	–	–	–	–	–	–	–	51
All *A. guariba*					6.7 (3.5 –12)	1,426 (1,148–1,952)	2,670.2 (1.8–49,888)	19.4 (10–34.5)	22.5 (5–47.9)	66.3 (38–88)	34.3 (10–59)	7.7 (0–29)	4.3 (0–10)	44.3 (13–95)	21 (9–34)	52.9 (37 –65.2)	5.2 (3–9)	15.7 (4–52)	30.5 (2–72)	

(continued)

Table 2.1 (continued)

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)[a]	Plant items in diet (%)					No. species	No. families	%TFS[b]	>50 % TFT[c]	Sources fruits	Sources leaves	References[d]
									Fruits	Leaves		Flowers	OFI[e]							
										All[f]	Young									
A. macconelli	Petit Saut hydro-eletric dam, French Guiana	–	<1/70	Scan	5	2,600	–	26	–	55.0	–	–	45.0	–	–	–	–	–	–	52
A. macconelli	Les Nourages, French Guiana	1989	6/–	Feed frecuency	6	3,125	100,000	–	42.0	56.9	55.7	0.7	0.5	77	27	–	–	43	29	53
A. macconelli	Les Nourages, French Guiana	1988–1990	19/ 1,540	Feed frecuency	6	3,125	100,000	–	25.5	57.0	54.0	12.6	4.9	195	47	16.5	~40	97	96	54
A. macconelli	Saut Pararé, French Guiana	1977–1985	21/–	Stomachconts.	–	3,125	100,000	–	45.8	53.4	–	0.4	0.5	–	–	–	–	–	–	55
A. macconelli	Raleighvallen-Voltzbert Reserve, Surinam	1976–1977	12/–	–	–	2,375	56,000	–	69.0	28.6	14.3	2.4	–	–	–	–	–	–	–	56
All *A. macconnelli*					5.7 (5–6)	2,870 (2,375 –3,125)	89,000 (56,000–100,000)	26	45.6 (25.5–69)	50.2 (28.6–57)	41.3 (14.3–55.7)	4 (0.4–12.6)	12.7 (0.5–45)	136 (77–195)	37 (27–47)	16.5	~40	70 (43–97)	62.5 (29–96)	
A. palliata	Isla Agaltepec, VER, Mexico	1989–1990	10/ 1,500	Focal	18	2,029	8.3	24	59.0	28.9	–	–	12.1	28	15	60.4	3	–	–	57
A. palliata	Isla Agaltepec, VER, Mexico	1989–1996	74/ 2,303	Focal	19.5	2,029	8.3	27	39.5	29.4	–	–	31.1	36	15	66.0	3	18	32	58
A. palliata	Isla Agaltepec, VER, Mexico	1989–1990	10/ 1,500	Focal	10	2,029	8.3	22.7	52.5	26.6	–	–	20.9	32	15	61.6	4	–	–	59
A. palliata	Isla Agaltepec, VER, Mexico	1997	10/630	Focal	57	2,029	8.3	16.9	31.0	33.0	–	–	37.0	30	13	45.9	6	–	–	59
A. palliata	Isla Agaltepec, VER, Mexico	1997–1998	11/300	Focal	59	2,029	8.3	29	21.4	57.1	48.5	5.3	16.3	56	23	43.2	7	15	52	60
A. palliata	Playa Escondida, VER, Mexico	1997–1998	11/300	Focal	7	3,500	40	25.9	57.3	36.9	32.6	0.2	5.6	49	26	66.8	3	22	42	60

A. palliata	Arroyo de Lisa, VER, Mexico	2000–2001	11/300	Focal	6	3,500	1.3	24.2	51.2	36.6	33.5	2.1	10.0	35	19	62.2	3	17	29	60
A. palliata	Barro Colorado Island, Panama	1932	5/–	Ad libitum	–	2,730	1,600	–	–	–	–	–	–	56	29	–	–	20	29	61
A. palliata	Barro Colorado Island, Panama	1974–1976	14/480	Scan	11	2,730	1,600	16.2	36.9	53.4	–	9.3	–	73	32	43.7	7	25	59	62
A. palliata	Barro Colorado Island, Panama	1974–1976	14/540	Scan	11	2,730	1,600	16.2	46.7	43.6	–	9.6	–	73	32	63.9	3	22	58	62
A. palliata	Hacienda La Pacifica, Costa Rica	1972–1973	14/ 2,078	Focal	13	1,431	9.9	21.3	12.5	63.6	44.2	18.2	5.7	62	25	44.7	6	15	51	63
A. palliata	Hacienda La Pacifica, Costa Rica	–	–/–	–	–	1,431	9.9	–	–	–	–	–	–	–	–	–	–	–	–	63
A. palliata	Sta. Rosa, Costa Rica	1983–1985	17/393	Focal	40	1,527	10,800	15.7	28.5	49.0	17.4	22.5	–	11	4	64.9	3	5	5	64
A. palliata	Sta. Rosa, Costa Rica	1996–1998	18/ 1,380	Scan	7.5	1,527	10,800	11.6	28.6	41.5	27.6	29.5	0.4	37	18	64.3	3	17	27	65
A. palliata	Refugio de Fauna Silvestre Curu, Costa Rica	1990	1/31	–	–	2,738	60	–	0.0	94.2	0.0	5.8	0.0	–	–	–	–	–	–	66
A. palliata	Barro Colorado Island, Panama§§	1966–1968	14/–	–	–	2,730	1,600	–	62.8	27.4	21.2	5.9	–	27	13	–	–	20	9	67
A. palliata	Barro Colorado Island, Panama**	1967–1968	6/407	Scan	–	2,730	1,600	21.6	38.8	53.7	–	5.6	1.8	–	–	–	–	–	–	68
A. palliata	Isla Ometepe, Nicaragua	1999	4/350	Focal/scan	7.1	1,550	4	21.5	11.0	54.0	–	33.0	–	–	–	–	–	–	–	69
A. palliata	Yumká, Tabasco, Mexico	2000–2001	7/302	Focal	28	2,159	33	13.2	15.0	72.0	38.0	13.0	–	21	13	–	3	5	20	70
A. palliata	Rancho Huber, Veracruz, Mexico	2003–2004	12/–	–	–	3,800	244.1	14	46.0	49.0	–	5.0	0.0	–	–	–	–	–	–	71
A. palliata	Montepío-G3, Veracruz, Mexico	2003–2004	12/–	–	–	3,800	63.8	14	23.0	77.0	–	0.0	0.0	–	–	–	–	–	–	71
A. palliata	Ruiz Cortinez, VER, Mexico	2003–2004	12/–	–	–	3,800	7.2	22	40.0	60.0	–	0.0	0.0	–	–	–	–	–	–	71

(continued)

Table 2.1 (continued)

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)[a]	Plant items in diet (%)					No. species	No. families	%TFS[b]	>50 % TFT[c]	Sources fruits	Sources leaves	References[d]
									Fruits	Leaves		Flowers	OFI[e]							
										All[f]	Young									
A. palliata	Flor de Catemaco, VER, Mexico	2004–2005	8/400	Focal	4	3,500	90	25.6	41.0	55.0	10.0	–	1.0	26	16	79.5	2	–	–	72
A. palliata	Montepío-T1, VER, Mexico	2002–2003	11/140	Focal	10	3,800	63.8	8	16.0	81.0	–	–	–	14	11	86.0	2	–	–	73
A. palliata	Montepío-T2, VER, Mexico	2002–2003	11/176	Focal	19	3,800	63.8	9	18.0	80.0	–	–	–	19	9	73.4	3	–	–	73
A. palliata	Sta. Martha, VER, Mexico	1986–1987	12/–	Focal	10	3,800	10	28	30.0	–	–	–	–	7	–	98.8	1	–	–	74
A. palliata	Sta. Martha, VER, Mexico	1996–1997	12/–	Focal	22	3,800	8	40	13.0	61.0	–	26.0	–	40	18	56.4	5	–	–	75
A. palliata	Rancho Huber, VER, Mexico	2006–2007	13/480	Focal	9	4,900	244	24.2	49.4	48.3	32.8	1.0	1.3	–	–	–	–	–	–	76
A. palliata	Ruiz Cortinez, VER, Mexico	2006–2007	13/480	Focal	8	4,900	7.2	17.9	39.1	58.3	49.6	2.2	0.4	–	–	–	–	–	–	76
A. palliata	EBT Los Tuxtlas, VER, Mexico	1977–1982	12/–	–	16	4,500	700	–	–	–	–	–	–	19	11	–	–	19	–	77
A. palliata	EBT Los Tuxtlas, VER, Mexico	1977–1978	12/883	Focal	14	4,500	700	–	51.0	49.3	39.3	0.2	–	27	16	79.6	2	12	24	78
A. palliata	EBT Los Tuxtlas, VER, Mexico	–	–	Focal	16	4,500	700	–	53.0	46.0	36.0	–	1.0	–	–	–	–	–	–	79
A. palliata	La Venta, TAB, Mexico	2001	5/448.5	Focal	15	1,800	6	–	19.0	76.0	57.0	5.0	–	31	17	57.5	4	9	30	80
A. palliata	F1, Los Tuxtlas, VER, Mexico	1994–1995	7/~840	Focal	6	4,900	3.7	12	29.0	65.0	56.0	0.4	6.0	44	19	82.8	3	–	–	81
A. palliata	F1, Los Tuxtlas, VER, Mexico	1999–2000	7/~840	Focal	6	4,900	2.2	13	20.0	80.0	78.0	0.1	0.1	33	17	82.4	2	–	–	81

A. palliata	F1, Los Tuxtlas, VER, Mexico	1999	6/–	Focal	5	4,900	3.2	24.3	1.9	98.1	81.9	0.0	0.0	–	–	–	–	–	–	82
A. palliata	F2, Los Tuxtlas, VER, Mexico	1999	6/–	Focal	7	4,900	35	16.4	44.1	45.2	34.2	10.7	0.0	–	–	–	–	–	–	82
A. palliata	F3, Los Tuxtlas, VER, Mexico	1999	6/–	Focal	8	4,900	250	28	71.8	23.5	22.5	4.7	0.0	–	–	–	–	–	–	82
A. palliata	Sta. Rosa, Costa Rica	1991–1992	11/577	Focal	5.7	1,527	10,800	23	14.3	58.5	31.8	27.3	–	37	16	74.9	3	5	25	83
A. palliata	Sta. Rosa, Costa Rica	1991–1992	11/532	Focal	11.7	1,527	10,800	23	18.0	63.0	33.8	19.0	–	30	18	71.7	3	17	28	83
A. palliata	Sta. Rosa, Costa Rica	1991–1992	11/628	Focal	20	1,527	10,800	24	22.3	58.0	36.3	19.8	–	29	18	72.2	3	7	25	83
A. palliata	Sta. Rosa, Costa Rica	1992	7/193	Focal	6	1,527	10,800	24	23.5	50.0	24.5	26.5	–	35	21	55.6	4	8	30	83
A. palliata	Cuero y Salado, Honduras	2000–2001	12/81	Focal	7	3,050	8,615.75	36.1	13.9	82.8	64.2	3.3	–	15	12	79.7	2	3	15	84
A. palliata	Cuero y Salado, Honduras	2000–2001	12/32.9	Focal	6	3,050	8,615.75	39.4	13.0	81.1	59.2	5.9	–	14	13	72.7	3	3	14	84
A. palliata	Finca La Luz, Mombacho, Nicaragua	1999–2000	14/396	Focal	25.9	1,490	650	11.1	29.0	58.0	19.0	10.0	3.0	50	~17	55.5	5	17	34	85
A. palliata	Finca La Luz, Mombacho, Nicaragua	1999–2000	14/451	Focal	15.3	1,490	650	13.5	42.0	50.0	22.0	5.0	3.0	43	~14	67.3	3	14	33	85
A. palliata	Finca La Luz, Mombacho, Nicaragua	1999–2000	14/461	Focal	20.2	1,490	650	15.4	34.0	56.0	38.0	8.0	2.0	45	~15	70.4	2	13	30	85
A. palliata	F1, Los Tuxtlas, VER, Mexico	–	12/–	Focal	7	4,900	3.6	17	38.0	62.0	–	1.0	–	–	–	–	–	–	–	86
A. palliata	La Selva, Heredia, Costa Rica	1991–1992	15/140	Scan	22	3,962	46,000	25	17.0	72.0	57.0	11.0	–	95	42	42.9	7	32	75	87
A. palliata	La Selva, Heredia, Costa Rica	1991–1992	15/208	Scan	12	3,962	46,000	27	29.0	65.0	57.0	6.0	–	65	36	67.3	2	24	49	87
A. palliata	Montepío 2, VER, Mexico	2009–2010	12/207	Focal	16	4,900	100	14.8	15.9	39.7	–	0.5	–	–	–	–	–	–	–	88

(continued)

Table 2.1 (continued)

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)[a]	Plant items in diet (%)					No. species	No. families	%TFS[b]	>50 % TFT[c]	Sources fruits	Sources leaves	References[d]
									Fruits	Leaves		Flowers	OFI[e]							
										All[f]	Young									
A. palliata	Balzapote, VER, Mexico	2009–2010	12/197	Focal	10	4,900	10	20.2	25.6	39.4	–	0.3	–	–	–	–	–	–	–	88
A. palliata	Chomes, Puntareas, Costa Rica	2005	6/–	Scan	8	1,725	–	27.7	26.0	39.8	31.5	29.0	5.1	19	8	65.7	3	4	16	89
A. palliata	Parque Nacional Palo Verde, Costa Rica	2005	6/–	Scan	38	1,725	19,804	35.7	26.0	45.0	41.5	28.0	0.2	24	9	70.8	3	6	22	89
All *A. palliata*					15.2 (4–59)	3,066.9 (1,431 –4,900)	3,911.3 (1.3–46,000)	21.3 (8–40)	31.1 (0–71.8)	55.5 (23.5–98.1)	38.7 (0–81.9)	9.9 (0–33)	5.9 (0–37)	36.5 (7–95)	18.2 (4–42)	66.2 (42.9 –98.8)	3.5 (1–7)	14.1 (3–32)	32 (5–75)	
A. pigra	El Tormento, CAM, Mexico*	2002	10/360	Focal	–	1,380	500	32.6	42.2	42.0	–	6.3	4.5	24	17	59.2	4	12	20	90
A. pigra	Cockscomb Basin Wildlife Sanctuary, Belize‡	1994	12/ 1,540	–	–	2,420	40,000	18	34.0	58.0	29.0	6.0	3.0	20	12	54.6	5	13	16	91
A. pigra	Tikal, Guatemala	1974	<1/84	Scan	7	1,350	56,700	22	–	–	–	–	–	7	6	96.5	1	4	7	92
A. pigra	Tikal, Guatemala	1973	3/1,147	–	–	1,350	56,700	–	–	–	–	–	–	2	1	–	1	2	1	93
A. pigra	Monkey River, Belize‡	2000–2001	8/368	Focal	–	2,500	52	17.5	38.8	56.7	25.8	4.5	–	28	21	59.2	4	7	25	94
A. pigra	Monkey River, Belize§	2002	4/149	Focal	–	2,500	52	15.3	0.0	99.7	85.3	0.3	–	15	10	83.9	2	0	15	94
A. pigra	Monkey River, Belize‡	2004	6/290	Focal	2	2,500	52	18	37.0	59.0	20.0	3.0	1.0	12	10	84.8	2	–	–	95
A. pigra	Monkey River, Belize	2004	6/290	Focal	3	2,500	52	20	22.0	70.0	27.0	7.5	0.5	11	9	81.2	3	–	–	95
A. pigra	Monkey River, Belize	2004	6/290	Focal	6	2,500	52	13	32.5	65.0	32.5	2.5	0.5	10	8	88.9	2	–	–	95
A. pigra	Monkey River, Belize	2004	6/290	Focal	4	2,500	52	15	67.0	29.0	24.0	3.5	0.5	12	9	83.6	2	–	–	95

A. pigra	Monkey River, Belize†	1999	2.5/ 125.7	Focal	10.7	2,500	52	16.3	68.0	30.0	–	2.0	–	21	16	64.0	4	11	15	96
A. pigra	Monkey River, Belize††	1999–2001	11/662	Focal	6.6	2,500	52	18.6	40.2	59.9	–	–	–	35	–	60.5	4	–	–	97
A. pigra	Baboon Santuary, Belize**	1999	12/–	Scan	6	1,650	1.25–75	–	–	–	–	–	–	–	–	–	–	–	–	98
A. pigra	Baboon Santuary, Belize**	1994–1995	12/ 1,160	Focal	5.9	1,955	25–50	24.4	40.8	45.1	37.2	10.2	3.4	74	10	42.8	7	19	20	99
A. pigra	Baboon Santuary, Belize	1995–1996	12/252	Scan	5	1,988	83	–	24.0	52.0	–	24.0	–	43	18	54.1	5	11	34	100
A. pigra	Baboon Santuary, Belize	1995–1996	12/252	Scan	7	1,988	24	–	20.0	68.0	–	11.0	–	44	–	64.3	3	17	36	100
A. pigra	Baboon Santuary, Belize	1995–1996	12/216	Scan	5	1,988	3.5	–	33.0	54.0	–	13.0	–	37	–	77.4	3	10	33	100
A. pigra	Baboon Santuary, Belize	1995–1996	12/264	Scan	5	1,988	1.25	–	34.0	57.0	–	9.0	–	51	–	65.3	4	19	39	100
A. pigra	Baboon Santuary, Belize	1995–1996	12/204	Scan	8	1,988	4.5	–	36.0	62.0	–	2.0	–	43	–	55.1	5	12	38	100
A. pigra	Baboon Santuary, Belize	1995–1996	12/216	Scan	6	1,988	121	–	63.0	33.0	–	4.0	–	32	–	85.1	1	8	24	100
A. pigra	Leona Vicario, Balancán, Mexico	2002–2003	12/499	Focal	9	1,906	0.2	19.6	17.4	55.7	49.2	5.3	21.6	15	8	65.8	4	7	13	101
A. pigra	Calakmul, CAM, Mexico†	2003	8/ ~201.6	Scan	6.3	1,750	147,915	–	–	–	–	–	–	10	8	96.3	1	–	–	102
A. pigra	Ejidos near Calakmul, CAM, Mexico*	2003	8/ ~134.4	Scan	6	1,750	12.8	–	–	–	–	–	–	16	13	80.6	3	–	–	102
A. pigra	Calakmul, CAM, Mexico	2001–2002	4/1,752	Feed.bouts	9	1,750	147,915	23	78.0	16.8	–	1.9	3.3	–	–	–	–	–	–	103
A. pigra	Calakmul, CAM, Mexico	2001–2002	4/1,752	Feed.bouts	10	1,750	147,915	23.2	62.0	20.0	–	18.0	–	–	–	–	–	–	–	103

(continued)

Table 2.1 (continued)

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)[a]	Plant items in diet (%)					No. species	No. families	%TFS[b]	>50 % TFT[c]	Sources fruits	Sources leaves	References[d]
									Fruits	Leaves		Flowers	OFI[e]							
										All[f]	Young									
A. pigra	Calakmul, CAM, Mexico	2001–2002	4/1,752	Feed.bouts	3	1,750	147,915	22.5	59.0	39.4	–	1.6	–	–	–	–	–	–	–	103
A. pigra	C G27 Calakmul, CAM, Mexico	2006	2/103	Focal	9	1,300	147,915	17.2	79.1	19.6	17.3	0.0	1.2	11	7	–	2	–	–	104
A. pigra	C G9 Calakmul, CAM, Mexico	2006	2/103	Focal	5	1,300	147,915	23.5	58.1	39.9	39.1	1.6	0.4	17	9	–	2	–	–	104
A. pigra	A GAA Álamo, CAM, Mexico	2005	2/103	Focal	4	1,400	96	21.6	0.0	72.8	51.3	2.4	24.7	34	21	–	3	–	–	104
A. pigra	A GR Álamo, CAM, Mexico	2005	2/103	Focal	7	1,400	96	22.1	13.1	77.0	69.3	4.5	5.4	24	13	–	4	–	–	104
A. pigra	Subestación, CAM, Mexico	2005	2/103	Focal	6	1,400	5.78	9.5	13.1	16.1	12.8	68.6	2.3	12	9	–	3	–	–	104
A. pigra	Oxcabal, CAM, Mexico	2006	2/103	Focal	5	1,400	7.99	16.3	62.5	24.7	24.2	0.9	11.9	12	8	–	2	–	–	104
A. pigra	Atascadero, CAM, Mexico	2005	1/103	Focal	4	1,400	1.14	7.2	0.0	100.0	100.0	0.0	0.0	14	9	–	3	–	–	104
A. pigra	Chilar, CAM, Mexico	2006	2/103	Focal	8	1,400	<1	10.5	41.7	37.8	28.3	19.7	0.8	4	2	–	1	–	–	104
All *A. pigra*					6.2 (2–10.7)	1,873.2 (1,300–2,500)	33,621.4 (0.2–147,915)	18.6 (7.2–32.6	38.5 (0–79.1)	50.4 (16.1–100)	39.6 (12.8–100)	8.3 (0–68.6)	5 (0–24.7)	23 (2–74)	10.6 (1–21)	71.6 (42.8–96.5)	3 (1–7)	10.1 (0–19)	22.4 (1–39)	
A. seniculus	Finca Merenberg, La Plata, Colombia	1976	10/340	Focal	9	1,942	270	12.7	42.3	52.0	44.5	5.4	0.1	33	17	73.1	4	12	28	105
A. seniculus	Hato El Frío, Apure, Venezuela	1975–1976	13/–	Dissection/ scan	7.5	1,424	1,000	21.8	–	–	–	–	–	40	18	–	–	–	–	106
A. seniculus	Fazenda Esteio, AM, Brazil	1984–1985	5/491	Scan	8	2,900	13	22	13.5	56.0	39.0	4.0	27.0	93	30	–	–	22	93	107

A. seniculus	Río Peneya, Colombia	1971–1994	–	Ad libitum	–	3,000	1,000	–	–	–	–	–	–	–	–	–	–	–	–	108
A. seniculus	Tiputini, Orellana, Ecuador	2005–2008	–	Cameratraps	–	2,800	1,700,000	–	–	–	–	–	–	–	–	–	–	–	–	109
A. seniculus	Isla Iguana, Lago Guri, Venezuela	1999–2001	9/325	Allocurrence	6	1,100	0.6	–	2.0	73.0	52.0	14.0	11.0	–	–	–	–	–	–	110
A. seniculus	Isla Danto Machado, Lago Guri, Venezuela*	1999–2001	9/347	Allocurrence	6.5	1,100	190	–	22.0	55.0	26.0	18.0	5.0	–	–	–	–	–	–	110
A. seniculus	Tinigua, Meta, Colombia	1990–1991	13/672	Focal/scan	–	2,604	500	23	39.0	51.0	–	4.0	7.0	–	–	–	–	–	–	111
A. seniculus	Otún-Quimbaya, Colombia	2001	6/119.4	Scan	5	2,712	489	–	25.4	57.3	–	17.3	–	21	11	67.4	4	8	17	112
A. seniculus	Otún-Quimbaya, Colombia	2001	6/136.4	Scan	10	2,712	489	–	36.7	59.2	–	4.0	–	27	11	63.4	3	6	22	112
A. seniculus	Otún-Quimbaya, Colombia	2001	6/132	Scan	8	2,712	489	–	65.5	34.5	–	0.0	–	12	10	96.0	1	3	11	112
A. seniculus	Mamirauá, AM, Brazil	–	–	–	8	2,300	1,240,000	6	47.0	46.0	20.0	2.0	5.0	26	–	–	2	8	20	113
A. seniculus	A0 Yotoco, Valle del Cauca, Colombia	2004–2005	12/–	Focal	8	1,500	559	22.1	30.1	67.0	59.7	–	2.9	–	–	–	–	–	–	114
A. seniculus	A9 Yotoco, Valle del Cauca, Colombia	2004–2005	12/–	Focal	5	1,500	559	23.1	13.3	82.9	76.7	–	3.8	–	–	–	–	–	–	114
A. seniculus	Hacienda San Juan del Carare, Colombia	2008–2009	9/~475	Scan	–	3,496	65.87	7	35.1	61.4	22.8	0.8	2.5	–	–	–	–	–	–	115
A. seniculus	Estación Biológica de Cahuana, Peru[§§]	1979–1992	–/–	Ad libitum	5.5	3,000	720	–	40.0	53.0	–	6.0	–	–	–	–	–	–	–	116
All *A. seniculus*					7.2 (5–10)	2,300.1 (1,100–3,496)	184,146.5 (0.6–1,700,000)	17.2 (6–23.1)	31.7 (2–65.5)	57.6 (34.5–82.9)	42.6 (20–76.7)	6.9 (0–18)	7.1 (0.1–27)	36 (12–93)	16.2 (10–30)	75 (75–96)	2.8 (1–4)	9.8 (3–22)	31.8 (11–93)	
All *Alouatta*					9.9 (2–59)	2,211.4 (1,100–4,900)	30,596.4 (0.2–1,700,000)	19.7 (6–40)	31.4 (0–79.1)	56.7 (13.3–100)	36.2 (0–100)	8.4 (0–68.6)	5.6 (0–45)	35 (2–195)	16.4 (1–47)	65.6 (16.5–98.8)	3.6 (1–10)	14.7 (0–97)	27.8 (1–96)	

(continued)

Table 2.1 (continued)

[a]% Time feeding = proportion of daily activity time dedicated to feeding
[b]%TFS = percentage of feeding time dedicated to feed from top five plant species
[c]>50 % TFT = number of plant species contributing >50 % of total feeding time
[d]References: 1. Bonvicino (1989); 2. Camargo et al. (2008); 3. de Souza et al. (2002); 4. Pinto (2002), Pinto and Setz (2004); 5. Pinto et al. (2003); 6. Lindberg and Santini (1984); 7. Alves and Guix (1992); 8. Bravo and Zunino (2000); 9. Rumiz et al. (1986); 10. Rumiz et al. (1986); 11. Agostini et al. (2010); 12. Prates (2007), Prates and Bicca-Marques (2008); 13. Bicca-Marques and Calegaro-Marques (1994a, b, c); 14. Bicca-Marques et al. (2009); 15. Bravo and Sallenave (2003); 16. Pavé et al. (2009); 17. Ludwig et al. (2008); 18. Ludwig et al. (2008); 19. Rímoli et al. (2008); 20. Zunino (1986, 1989); 21. Arditi (1992); 22. Muhle (2008); 23. Giudice and Mudry (2000); 24. Agostini et al. (2010); 25. Mendes (1989); 26. Silva (1981); 27. Chiarello (1993), (1994); 28. Galetti et al. (1994); 29. Almeida-Silva et al. (2005); 30. Aguiar et al. (2003); 31. Martins (2008, 2009); 32. Cunha (1994); 33. Biedzicki de Marques (1996); 34. Martins (1997); 35. Pérez (1997); 36. Limeira (1997); 37. Gaspar (1997); 38. Steinmetz (2000, 2001); 39. Miranda et al. (2005); 40. Miranda and Passos (2004); 41. Alves and Zaú (2007); 42. Young (1983); 43. Chitolina and Sander (1981); 44. Kuhlmann (1975); 45. Koch and Bicca-Marques (2007); 46. Fialho (2000); 47. Fortes (2008); 48. Pereira (2008); 49. Guzzo (2009); 50. Lunardelli (2000); 51. Damé (2006); 52. de Thoisy and Richard-Hansen (1997); 53. Simmen and Sabatier (1996); 54. Julliot and Sabatier (1993), Julliot (1996); 55. Guillotin et al. (1994); 56. Mittermeier and van Roosmalen (1981); 57. Serio-Silva (1995); 58. Serio-Silva et al. (2002); 59. Rodríguez-Luna et al. (2003); 60. Asensio-Herrero et al. (2007); 61. Carpenter (1934); 62. Milton (1980); 63. Glander (1978b, 1981); 64. Chapman (1987a, b, 1988); 65. Welker (2004); 66. Tomblin and Cranford (1994); 67. Hladik and Hladik 1969); 68. Smith (1977); 69. Devos (1999); 70. García del Valle et al. (2001), Muñoz et al. (2002); 71. Hervier (unpublished data *in* Cristóbal-Azkarate and Arroyo-Rodríguez 2007); 72. Sedden-González and Rodríguez-Luna (2010); 73. Bravo-Xicoténcatl (2003); 74. Jiménez-Huerta (1992); 75. García-Orduña (2002); 76. Dunn et al. (2009, 2010); 77. Estrada and Coates-Estrada (1984), Estrada et al. (1984); 78. Estrada (1984); 79. Estrada and Coates-Estrada (1986); 80. Fuentes et al. (2003); 81. González-Picazo et al. (2001); 82. Juan et al. (2000); 83. Larose (1996); 84. Snarr (2006); 85. Williams-Guillén (2003); 86. Juan et al. (1999), Ortiz-Martínez et al. (1999); 87. Stoner (1996); 88. Cuende-Fanton (2010); 89. Martínez-Esquivel (2010); 90. Barrueta (2003); 91. Silver and Marsh (2003); 92. Schlichte (1978); 93. Coelho et al. (1976); 94. Behie and Pavelka (2005); 95. Bridgett (2006); 96. Loudon (2000); 97. Pavelka and Knopff (2004); 98. Marsh and Loiselle (2003); 99. Silver et al. (1998); 100. Marsh (1999); 101. Pozo-Montuy and Serio-Silva (2006, 2007); 102. Rivera and Calmé (2006); 103. Rizzo (2004); 104. Coyohua-Fuentes (2008); 105. Gaulin and Gaulin (1982); 106. Braza et al. (1983); 107. Neves and Rylands (1991); 108. Izawa (1975); 109. Blake et al. (2010); 110. López et al. (2005); 111. Stevenson et al. (2000, 2002); 112. Giraldo et al. (2007); 113. Queiróz (1995); 114. Palma et al. (2011a, b); 115. Aldana-Saavedra (2009); 116. Soini (1992)
[e]OFI = other food items
[f]All = includes mature and young leaves, leave buds, bracts, petioles, pulvini, and tendrils
[g]Averages and ranges for each species and for the genus
[h]Length = months, observation hours
*Averages for two groups; [†]Averages for three groups; [‡]Averages for four groups; [§]Averages for five groups; **Averages for six groups; [††]Averages for eight groups; [‡‡]Averages for ten groups; [§§]Averages for an unspecified number of groups

observation hours. However, the majority of studies (57.8 %) have included >300 h of observations, and 12.9 % had an observation effort >1,000 h. Finally, the majority of groups (65.1 %) were studied for ≥9 months, which allows controlling for and assessing the effects of seasonality on the diet.

2.3 Results

2.3.1 Howler Foods

Overall, howlers spend on average (±SD) approximately 19.7 ± 6.9 % of their daily activity time feeding, and time spent feeding does not vary significantly between species ($F_{5,49} = 0.891$, $p = 0.494$). As expected for an arboreal primate that occupies primarily the upper and middle portions of the canopy, howlers spend the majority of their feeding time (82 ± 17.1 %) consuming food items from trees.

Howlers consume both ripe and unripe fruits. Sometimes, they select and eat specific parts of fruits, such as seeds or arils (see Arroyo-Rodríguez et al. 2014). A significant proportion of the range of variation in time spent consuming fruits is shared by all howler species (Fig. 2.2a). This is particularly marked in species that

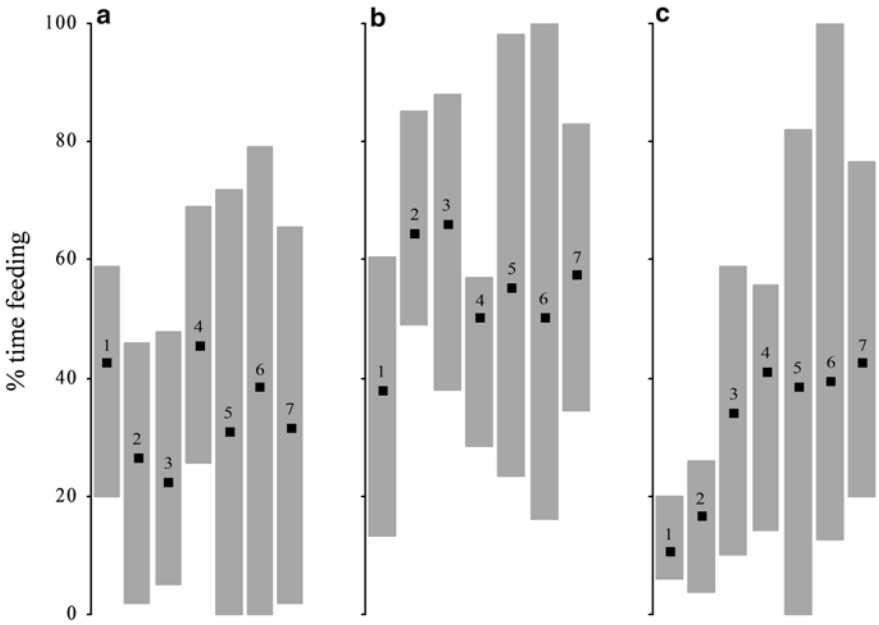

Fig. 2.2 Range (*gray columns*) and average (*black squares*) proportion of feeding time dedicated to the consumption of fruits (**a**), leaves of all ages (**b**) and young leaves (**c**). 1 = *A. belzebul*; 2 = *A. caraya*; 3 = *A. guariba*; 4 = *A. macconnelli*; 5 = *A. palliata*; 6 = *A. pigra*; 7 = *A. seniculus*

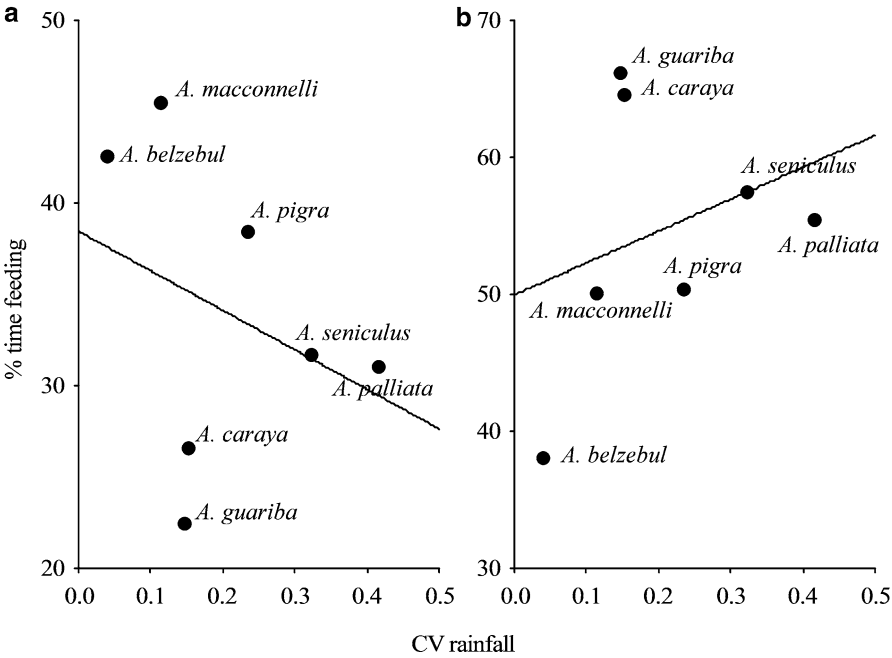

Fig. 2.3 Relationship between variation (CV = coefficient of variation) in rainfall and the proportion of time dedicated to the consumption of fruits (**a**) and leaves of all ages (**b**)

occupy a wider range of forest types (as assessed by variation in rainfall levels; Fig. 2.3a), such as *A. palliata*, *A. pigra,* and *A. seniculus*. In contrast, howler species that live in forests with low variation in rainfall levels (*A. belzebul* and *A. macconnelli*), and forests that are also more seasonal (*A. caraya* and *A. guariba*), present the highest and lowest values for fruit consumption, respectively.

Howlers eat young and mature leaves, leaf petioles, pulvini, and leaf buds. In contrast to fruit consumption, which for some species ranges from zero (e.g., *A. palliata*), howlers at all study sites always eat at least some leaves. As in the case of fruits, some howler species show higher variation in leaf consumption (including young leaves), which encompasses the range of other species (e.g., *A. palliata*; Fig. 2.2b, c). Species that are found in forests with low variation in rainfall tend to spend the highest (e.g., *A. caraya*) or lowest (e.g., *A. belzebul*) proportion of time consuming leaves, whereas species that live in more diverse forests in terms of rainfall levels (e.g., *A. palliata*) show intermediate proportions (Fig. 2.3b).

Besides fruits, leaves, and flowers, howlers consume lesser amounts of a variety of OFI. These include: other plant items, such as bark, gum, decayed and live wood, pine cones, pods, pseudobulbs (from epiphytes), roots, stems (including twigs) and herbs; chicken eggs; honey; insects (eggs, larvae, and adults); lichens; mushrooms; nectar; soil; and termitaria. Concerning the ingestion of insects, howlers inadvertently eat Hymenoptera (e.g., Blastophaga), Diptera, and Coleoptera (e.g., Curculionidae)

(Hladik and Hladik 1969; Milton 1980; Gaulin and Gaulin 1982; Alves and Guix 1992; Serio-Silva 1995; Bravo and Zunino 1998) that infest fruits, and these insects may be an important source of vitamins, minerals, and amino acids that can only be obtained from animal source foods (Urquiza-Haas et al. 2008).

Howlers have been observed ingesting soil from the forest floor (from "barreiros" or "salados": Izawa 1993; Stevenson et al. 2000, 2002; Blake et al. 2010), bird nests (Bicca-Marques and Calegaro-Marques 1994a, b, c), and termitaria (Julliot and Sabatier 1993; de Souza et al. 2002). It has been suggested that the main function of geophagy is as a digestive aid (e.g., detoxification of secondary compounds). This suggestion is supported by the observation that, in some howler populations, geophagy is positively correlated with leaf consumption, usually during the dry season (Julliot and Sabatier 1993; de Souza et al. 2002). Specifically, some soils consumed by howlers are rich in organic matter and clay, which may help to absorb secondary metabolites of plants, such as tannins, alkaloids, and terpenoids, and balance gastric acidity (Hirabuki and Izawa 1990; de Souza et al. 2002). Alternative explanations for geophagy by howlers include mineral supplementation (Izawa 1993) and to combat to endoparasite infestations (Bicca-Marques and Calegaro-Marques 1994a), although currently there is only very scarce data addressing both hypotheses.

The low proportion of time (<1 %) howlers dedicate to drinking water indicates that they acquire most water from their foods. However, howlers have been observed drinking rainwater accumulated in flowers, epiphytic bromeliads (Bonvicino 1989; Steinmetz 2000, 2001; Miranda et al. 2005), pools and holes in trunks (Glander 1978a; Silver et al. 1998; Giudice and Mudry 2000; Fialho 2000; Miranda et al. 2005; Pozo-Montuy and Serio-Silva 2006, 2007; Snarr 2006), as well as from ponds and rivers (Gilbert and Stouffer 1989; Almeida-Silva et al. 2005; Miranda et al. 2005). In several howler species (e.g., *A. guariba*, *A. palliata*, *A. pigra*), drinking is negatively correlated with precipitation, temperature, and fruit consumption and/or positively related to the consumption of mature leaves (Glander 1978a; Gilbert and Stouffer 1989; Bonvicino 1989; Steinmetz 2001; Miranda et al. 2005; Dias et al. 2014). Therefore, drinking water by howlers seems to relate to hydration when the climate is dryer or foods rich in water (i.e., new leaves, fruits) are unavailable.

Howlers consume significantly more leaves than fruits ($t_{71}=7.86$, $p<0.001$), and significantly more young leaves than mature leaves ($t_{37}=2.47$, $p=0.018$; Table 2.1). At the species level, *A. caraya* ($t_8=4.53$, $p=0.002$), *A. guariba* ($t_{11}=11.72$, $p<0.001$), *A. palliata* ($t_{30}=4.15$, $p<0.001$), and *A. pigra* ($t_9=2.58$, $p=0.003$) consume significantly more leaves than fruits, and only in *A. caraya* ($t_3=4.08$, $p=0.027$) and *A. palliata* ($t_{17}=4.26$, $p<0.001$) is the consumption of young leaves significantly higher than that of mature leaves. There are differences between species in the proportions of time dedicated to consume fruits ($F_{5,66}=4.77$, $p<0.001$), leaves ($F_{5,66}=7.70$, $p<0.001$), and young leaves ($F_{5,32}=5.94$, $p<0.001$), but not flowers ($F_{5,53}=0.67$, $p=0.649$) or OFI ($F_{5,33}=0.85$, $p=0.527$). These differences are determined by (LSD tests $p<0.05$): (1) higher consumption of fruits by *A. belzebul* than by *A. caraya* and *A. guariba*; (2) higher consumption of fruits by *A. palliata* and *A. pigra* than by *A. guariba*; (3) lower consumption of leaves in *A. belzebul* than by all other species; (4) higher consumption of leaves by *A. guariba* and *A. caraya* than

in *A. palliata* and *A. pigra*; (5) lower consumption of young leaves in *A. belzebul* and *A. caraya* than all other species, except for each other. Time spent eating fruits correlates negatively with the consumption of leaves ($r=-0.77$, $n=72$, $p<0.001$) and flowers ($r=-0.27$, $n=59$, $p=0.034$).

Dietary habits of howlers are significantly predicted ($R^2=0.22$, $F_{3,63}=5.81$, $p=0.001$) by rainfall ($\beta=0.50$, $t=3.09$, $p=0.003$), group size ($\beta=0.25$, $t=2.81$, $p=0.007$), and the interaction between rainfall and group size ($\beta=0.22$, $t=2.78$, $p=0.007$). These results suggest that overall howlers tend to be more frugivorous when living in larger groups that occupy habitats with more rainfall (Fig. 2.4a, b). A piecewise regression of rainfall levels on the dietary habits of howlers resulted in a highly explicative model ($R^2=0.81$), which defined a breakpoint at 2,287.2 mm. For groups living in habitats with rainfall <2,287.2 mm ($R^2=0.40$, $F_{3,45}=9.84$, $p<0.001$), again rainfall was the most explicative variable, indicating that frugivory increases with increasing rainfall (rainfall $\beta=0.59$, $t=5.06$, $p<0.001$; group size $\beta=0.21$, $t=1.79$, $p=0.081$; forest size $\beta=0.17$, $t=1.48$, $p=0.146$; Fig. 2.4c). For rainfall >2,287.2 mm ($R^2=0.27$, $F_{1,16}=5.99$, $p=0.026$), dietary habits tend to frugivory as group size decreases (group size $\beta=-0.52$, $t=2.45$, $p=0.026$; Fig. 2.4d). Concerning group size, a piecewise regression identified a breakpoint at 11.9 individuals ($R^2=0.64$). For groups <11.9 individuals, dietary habits were significantly predicted ($R^2=0.15$, $F_{2,43}=3.74$, $p=0.032$) by rainfall ($\beta=0.47$, $t=3.32$, $p=0.001$) and forest size ($\beta=0.20$, $t=1.44$, $p=0.156$), indicating that, at these group sizes, howler diets are more frugivorous in larger forests that receive more rainfall (Fig. 2.4e, f). For larger groups (i.e., >11.9 individuals) no model could be defined by the stepwise regression. Time dedicated to flower consumption is significantly predicted by rainfall and forest size ($R^2=0.30$, $F_{2,51}=10.78$, $p<0.001$). Specifically, howlers spend more time consuming flowers when they live in larger habitats ($\beta=0.30$, $t=2.51$, $p=0.015$) that receive less rain ($\beta=-0.43$, $t=3.68$, $p<0.001$). The consumption of OFI is significantly predicted by group size and forest size ($R^2=0.34$, $F_{2,32}=8.09$, $p=0.001$). Howlers spend more time consuming OFI when living in larger groups ($\beta=0.41$, $t=2.83$, $p=0.008$) and smaller forests ($\beta=-0.35$, $t=2.43$, $p=0.021$).

2.3.2 Dietary Diversity

Combined data show that howlers consume a total of 1,165 plant species, belonging to 479 genus and 111 families. If plant morphotypes are included in these calculations and we assume that no morphotypes are shared between studies, howlers consume 1,665 or more plant species. [A complete list of the plants used by howlers as food sources per study group and the plant parts used is available at http://goo.gl/F3ysf.] Fabaceae (200 species), Moraceae (104), Sapotaceae (56), and Bignoneaceae (53) are the families showing the highest number of plant species in the howler diet: together, these four families represent 35.5 % of all species consumed. At the genus level, *Ficus* and *Inga* are the taxa represented by more species in the howler diet, with 65 and 31 species, respectively. However, the majority of genera (ca. 50 %)

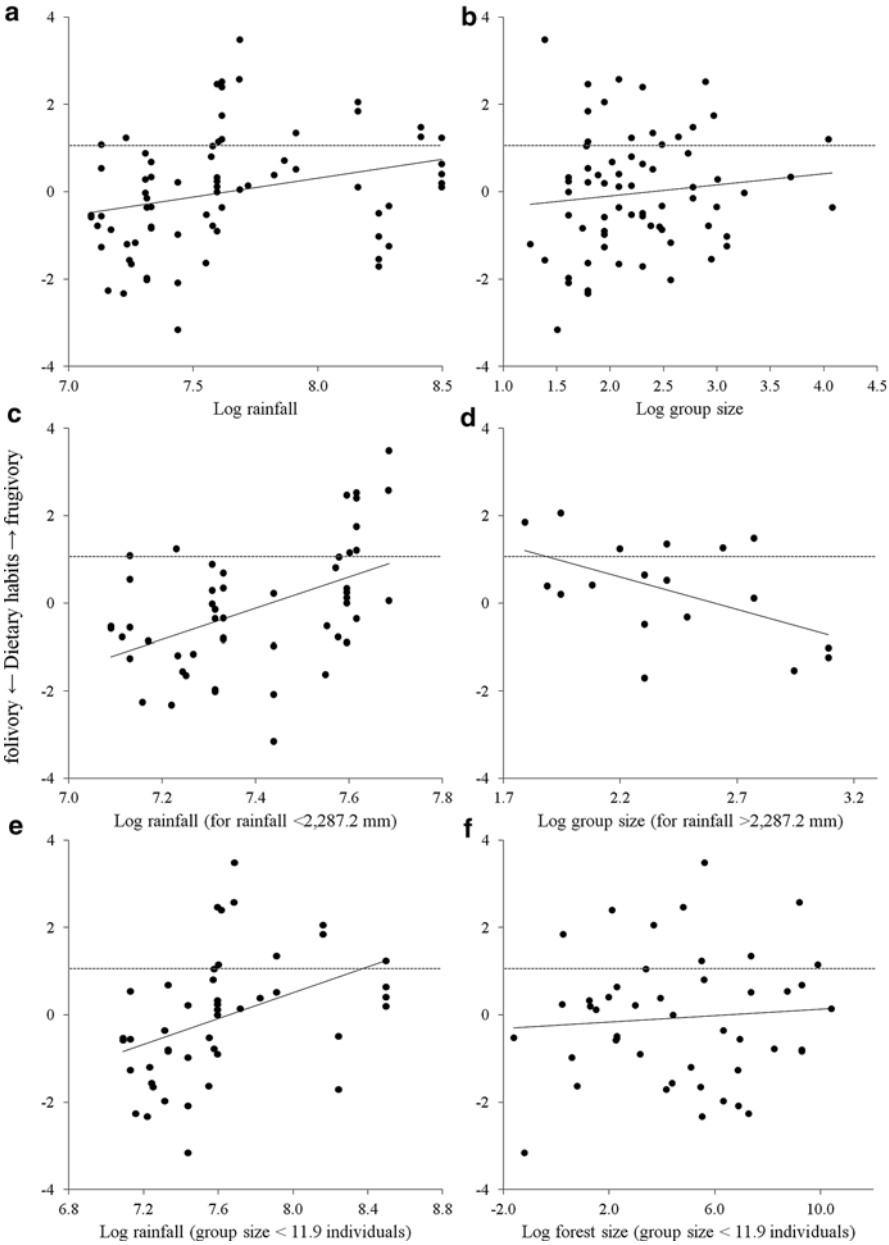

Fig. 2.4 Variation in the dietary habits of howlers as a function of: rainfall (**a**); group size (**b**); rainfall in groups that live in habitats that receive less than 2,287.2 mm of rainfall per year (**c**); group size in groups that live in habitats that receive more than 2,287.2 mm of rainfall per year (**d**); rainfall in groups with less than 11.9 individuals (**e**); forest size in groups with less than 11.9 individuals (**f**). The *dotted line* represents threshold for a balanced diet (i.e., equal amounts of time dedicated to consume fruits and leaves). Values higher than this threshold represent a mainly frugivorous diet, whereas lower values represent a mainly folivorous diet

are represented in the diet of howlers by only 1–3 species, and 78 % are represented by ≤10 species. Among known plant species used as food sources, 47 % are sources of fruit (548 species, 80 families), 64.8 % (754 species, 98 families) are sources of leaves, and 21.2 % (247 species, 59 families) are sources of flowers. The majority (>50 % of species) of fruits consumed by howlers belong to the Moraceae (83 species), Fabaceae (62), Sapotaceae (43), Myrtaceae (31), Urticaceae (24), Lauraceae (18) and Anacardiaceae (16) families; and to the genera *Ficus* (53 species), *Inga* (19), *Pouteria* (14), *Eugenia* (13), and *Cecropia* (11). The majority of leaves consumed by howlers belong to the Fabaceae (160 species), Moraceae (66), Bignoneaceae (36), Malvaceae (29), Sapotaceae (28), Myrtaceae (24), Lauraceae (19), and Chrysobalanaceae (18) families; and to the genera *Ficus* (41), *Inga* (23), *Protium* (13), *Licania* (11), *Eugenia* (10), *Lonchocarpus* (10), *Machaerium* (10), and *Pithecellobium* (10). Flowers are mainly consumed from the families Fabaceae (81), Bignoniaceae (29), and Malvaceae (14); 42 genera account for the majority of plant species serving as sources of flowers, led by *Inga*, which contributes 14 species.

Thirty-two percent of the plant families used as food sources are exclusively exploited by a single howler species, whereas 7 families (6.3 % of the total number of families utilized), Anacardiaceae, Bignoneaceae, Fabaceae, Malvaceae, Moraceae, Sapotaceae, and Urticaceae, are used by all howler species for which feeding data are currently available. At the genus level, the number of plant taxa used exclusively by a single howler species increases nearly twofold with respect to the previous taxonomic level, to 57 %, and only 4 genera are shared by all howler species (0.8 %; *Cecropia*, *Ficus*, *Inga,* and *Tabebuia*). At the species level, 81.5 % of all taxa are used by a single howler species, and no plant species is used by all howler species. Two plant species (0.2 %) are shared by five howler species, namely *Brosimum guianense* (Aubl.) Huber (*A. belzebul*, *A. guariba*, *A. macconnelli*, *A. pigra* and *A. seniculus*) and *Ficus insipida* Willd (*A. caraya*, *A. guariba*, *A. palliata*, *A. pigra* and *A. seniculus*). Interestingly, these two species are very different in terms of light requirements for their germination, as the first is shade-tolerant (i.e., typical of mature forests), whereas the second is a light-demanding species.

2.3.2.1 Similarity in the Use of Plant Taxa

Average similarity (as assessed by the Jaccard index) among howler species in the use of plants is low (Table 2.2) at the family, genus, and species level. Overall, *Alouatta pigra* shows the highest average similarity with other species, particularly with *A. palliata*; *A. caraya* and *A. guariba* show the highest similarity between each

Table 2.2 Similarity (*J* index) in the consumption of plant taxa between and within howler species

	Interspecific			Intraspecific		
Plants	Mean	SD	Range	Mean	SD	Range
Family	0.38	0.05	0.22–0.55	0.43	0.18	0.05–0.88
Genus	0.16	0.02	0.08–0.31	0.29	0.19	0.04–0.91
Species	0.04	0.007	0.007–0.16	0.22	0.19	0–0.93

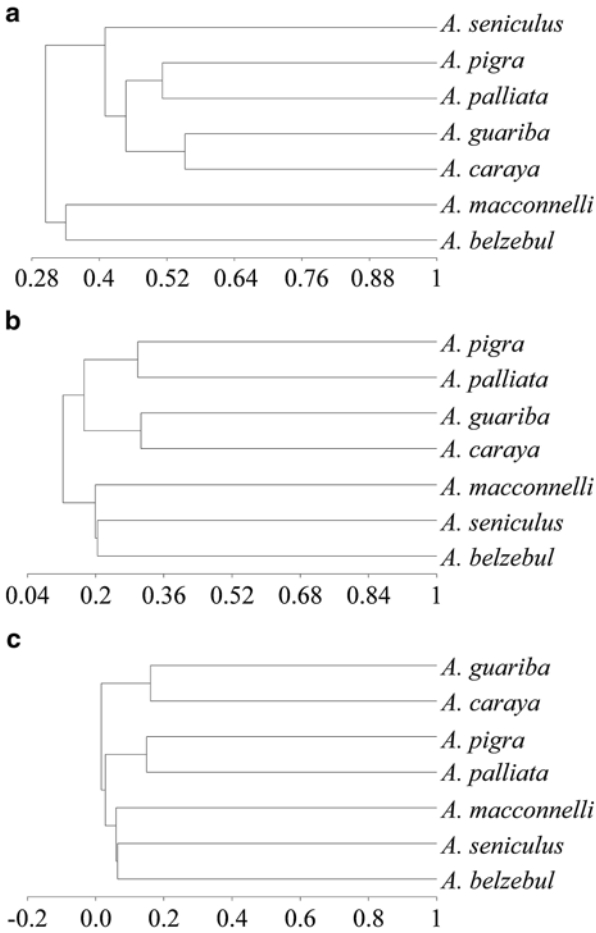

Fig. 2.5 Interspecific similarity (Jaccard's index) in the use of plant families (**a**), genus (**b**), and species (**c**)

other than any other pair of species; and *A. belzebul* and *A. macconnelli* have the lowest average similarity with other species (Fig. 2.5). As expected by the distributional ranges of howler species, three major groupings may be identified in terms of similarity in the use of plant species, genus, and families as food sources: (1) trans-Andean howlers; (2) howlers from Amazonia and northern South America; (3) howlers from Chaco, Cerrado, and Atlantic forest. As an exception to this relationship between distributional range and use of similar plant taxa, *A. seniculus* groups with the first two groups at the plant family level. Average dietary similarity is higher intraspecifically than interspecifically (Table 2.2). Nevertheless, variation in similarity is higher within species than between species, particularly at the plant species level. In general, higher ($J > 0.75$) similarity levels are found between: (1) different groups of the same species living in the same (e.g., Refs. 85, 95 and 112 in Table 2.1) or different forests (e.g., Refs. 82 and 100 in Table 2.1) observed in the same study; (2) a single group observed at different moments (e.g., Ref. 78 vs. 79 in Table 2.1; Ref. 57 vs. 58 in Table 2.1).

2.3.2.2 Dietary Breadth

The average (±SD) rate of use of plant species and families as food resources by howler groups is 0.12 ± 0.1 and 0.06 ± 0.08 families/h, respectively. Plant species and families use is significantly predicted by rainfall and forest size (species: $R^2 = 0.26$, $F_{3,51} = 5.83$, $p < 0.001$; families: $R^2 = 0.32$, $F_{3,38} = 5.85$, $p < 0.002$). In both models rainfall (species: $\beta = 0.34$, $t = 2.80$, $p = 0.007$; families: $\beta = 0.34$, $t = 2.51$, $p = 0.017$), forest size (species: $\beta = 0.28$, $t = 2.29$, $p = 0.026$; families: $\beta = 0.33$, $t = 2.39$, $p = 0.022$), and group size (species: $\beta = -0.19$, $t = 1.59$, $p = 0.117$; families: $\beta = -0.22$, $t = 1.63$, $p = 0.112$) were included in the stepwise regression, but only the first two variables had significant effects, indicating that howlers use more plant species and families in extensive forests that receive more rainfall. The proportion of feeding time dedicated to top food species (TFS) varies significantly between howler species ($F_{5,44} = 2.74$, $p = 0.031$), a result that is mainly due to *Alouatta caraya* groups concentrating more feeding time to TFS than *A. belzebul*, *A. guariba,* and *A. palliata* (LSD tests $p < 0.05$). Time dedicated to the consumption of TFS increases when howlers use fewer plant species ($r = -0.68$, $n = 50$, $p < 0.001$). The number of plant species contributing >50 % of feeding time is negatively correlated with the percentage of time dedicated to consume fruits ($r = -0.20$, $n = 43$, $p = 0.05$), suggesting that higher fruit consumption is associated with a decrease in the use of plant species. Finally, howlers use significantly more plant species as sources of leaves than fruits ($t_{47} = 7.76$, $p < 0.001$) in a ratio of approximately 2:1 (Table 2.1).

2.4 Perspectives on the Diets of Howlers

The results from this review support previous classifications of howlers as folivore–frugivore primates, whose diets vary both inter- and intraspecifically. Furthermore, our analyses reveal several patterns in the diets of howlers that suggest that their degree of dietary variation is affected by both environmental (i.e., rainfall, forest size) and social (i.e., group size) factors.

Rainfall is a critical factor underlying variation in the diets of howlers. Water availability, through its limiting effects on plant physiology, determines the establishment of plant communities and their phenologies. Tropical forests with annual rainfall lower than 2,000–2,500 mm tend to be drier, more seasonal, and have lower fruit availability than forests with higher rainfall (van Schaik et al. 1993; Kay et al. 1997; Dirzo et al. 2011). Across the genus, howlers that live in wetter habitats have more frugivorous diets, consume fewer flowers, and show more diverse diets than those in drier habitats, although they concentrate a higher percentage of their total feeding time on a lower number of species. In particular, frugivory increases steadily with increasing rainfall up to the level of ≈2,200 mm and up to group sizes of ≈12 individuals; 47 % of all studied howler groups live under these circumstances. Furthermore, frugivory increases with increasing forest size (a proxy for availability of food sources: Arroyo-Rodríguez and Dias 2010) in groups with less than ≈ 12 individuals.

In habitats with rainfall higher than ≈2,200 mm, frugivory decreases with increasing group size, suggesting that in more productive habitats fruit sources are depleted faster. Therefore, overall and temporal fruit availability and perhaps indirect scramble competition for food (Sterck et al. 1997) in larger howler groups (Knopff and Pavelka 2006; Arroyo-Rodríguez et al. 2011) explain how the dietary habits of howlers vary throughout the folivore–frugivore gradient.

At the species level, howler species that are distributed exclusively in drier forests (*A. caraya* and *A. guariba*) show the highest consumption of leaves and lowest consumption of fruits across the genus. They also show a number of additional dietary similarities, including the use of many of the same plant taxa as food sources. Howlers that live in less seasonal moist forests (*A. belzebul* and *A. macconnelli*) are in turn the most frugivorous and least folivorous species and also share other features of their diets, such as the use of more plant species as sources of fruits than leaves. Contrasting with these habitat specialists, the remaining howler species occupy a large array of habitat types, and as a result, their dietary habits are more variable. Still, even among these species, rainfall patterns consistently explain variation in the consumption of leaves and fruits. Therefore, our analyses suggest that, although at the genus level howlers are primarily folivorous, their dietary habits range from higher folivory to higher frugivory depending on the rainfall patterns, group size, and forest size that a particular species or population faces. The fact that despite these differences time dedicated to feeding is not significantly variable across species supports previous suggestions that howlers' time-budgets are either phylogenetically or metabolically constrained (Bicca-Marques 2003; Pavelka and Knopff 2004). It is interesting to observe that similarity in dietary habits seems to parallel proximity in geographic distributions more than phylogenetic relationships within the genus (e.g., Cortés-Ortiz et al. 2003; Gregorin 2006).

As discussed above, in addition to rainfall, group size and habitat size explain variation in several traits of howler diets. Across the genus, larger groups spend more time eating fruits and OFI. Furthermore, frugivory increases steadily with increased group size up to the level of ≈12 individuals per group. This suggests that larger groups deplete patches of preferred foods faster and increase the consumption of alternative food sources. At the species level, however, the relationship between fruit consumption and group size stands only for *A. palliata*, probably because this is the species with the highest mean group size, and in which some groups eat fruits more intensively (only second to *A. pigra*). This result coincides with previous evidence that some *A. palliata* populations experience reduced access to food sources when living in large groups (Arroyo-Rodríguez et al. 2011). In other species, the effects of group size on the consumption of seasonal plant items are more variable, probably because the interaction among dietary preferences, availability of seasonal foods, and food-patch depletion varies within and between species as a function of habitat characteristics. Among these, habitat size is particularly important as it is positively related to food availability throughout the forests occupied by howlers; small forests have less food sources that are additionally smaller (Arroyo-Rodríguez and Dias 2010). As a consequence, howlers eat less fruits, more flowers, and OFI, and their diets are less diverse. As discussed elsewhere, these relationships have

important consequences for the conservation of howlers in disturbed habitats (Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Arroyo-Rodríguez and Dias 2010).

Howlers have a number of anatomical and physiological adaptations that enable the use of leaves as a primary food resource. In addition to dental morphology and other craniomandibular features (e.g., Anapol and Lee 1994), the caecum and proximal colon of howlers are enlarged (Fooden 1964; Milton 1998) and harbor extensive communities of symbiotic microorganisms that degrade the structural components of plant cell walls through fermentation (Milton and McBee 1983). Due to the slow transit and long retention times of digesta associated with the kinetics of caeco-colic fermentation (Crissey et al. 1990; Milton 1998; Edwards and Ullrey 1999), and an important dependence on fermentation end products to meet daily energy requirements (Milton and McBee 1983), the ability of howlers to exploit non-leaf foods is probably limited. However, all species of howlers consume some non-leaf foods which, in some cases, may represent their main food resource (e.g., *A. belzebul*). In fact, it has been demonstrated that howlers prefer eating fruits when these are available (e.g., Silver et al. 1998; Stevenson et al. 2000; Palma et al. 2001), and our own data indicates that during peak fruiting *A. pigra* may spend up to 95 % of their feeding time consuming fruits for at least two week periods and may consume no leaves at all up to 3 consecutive days. Data from a reduced number of captive *A. caraya*, *A. palliata,* and *A. seniculus* individuals suggests that, independent of fiber concentrations in the diet, digestive capabilities vary among howler species (Edwards and Ullrey 1999). Therefore, it is possible that interspecific variation in feeding behavior results from differences in the interplay between food availability and digestive capabilities. In the future it will be interesting to compare the digestive flexibility of howlers that tend to be more highly frugivorous with those showing stronger folivorous tendencies.

In summary, howlers exploit some proportion of nearly all types of plant parts that are available in their habitat and their diets tend to be highly diverse. In the present study we concentrated on the description of the dietary habits of howlers and on analyzing the influences of rainfall, group size, and forest size on its variation. However, in a broader context, the feeding behavior of howlers is part of a foraging strategy that essentially relies on an intricate interplay between food availability and nutrient requirements that vary individually (e.g., Dias et al. 2011), a relatively non-specialized digestive tract and a number of mechanisms that allow behavioral modulation of their active metabolism (e.g., Milton 1998). This set of interaction has seldom been modeled, and its understanding continues to be among the major challenges we face in future howler research.

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