ACTA
AMAZONICA

http://dx.doi.org/10.1590/1809-4392202200842

ORIGINAL ARTICLE

Are larger primates less faunivorous? Consumption of arthropods by Amazonian primates does not fulfil the Jarman-Bell and Kay models

Anamélia de Souza JESUS[1,2,3*], Reyna Isabel CASTILLA TORRES[4], Jean Carlo de QUADROS[2], Alisson Nogueira CRUZ[2,5], João VALSECCHI[2,3,6], Hani R. EL BIZRI[2,3,6,7], Pedro MAYOR[1,6,8]

[1] Universidade Federal Rural da Amazônia, Programa de Pós-Graduação em Saúde e Produção Animal na Amazônia, Av. Presidente Tancredo Neves 2501, Bairro Terra Firme, Belém, Pará, Brazil
[2] Instituto de Desenvolvimento Sustentável Mamirauá, Estrada do Bexiga 2584, Bairro Fonte Boa, Tefé, Amazonas, Brazil
[3] Rede de Pesquisa para Estudos sobre Diversidade, Conservação e Uso da Fauna na Amazônia (RedeFauna), Manaus, Amazonas, Brazil
[4] Universidad Nacional Mayor de San Marcos, Facultad de Medicina Veterinaria, Unidad de Postgrado, Maestría en Ciencias Veterinarias, Lima, Peru
[5] Universidade Estadual do Amazonas, Centro de Estudos Superiores de Tefé, Rua Brasília 1217, Bairro Jerusalém, Tefé, Amazonas, Brazil
[6] Comunidad de Manejo de Fauna Silvestre en la Amazonía y en Latinoamérica (ComFauna), Iquitos, Loreto, Peru
[7] University of Salford, School of Science, Engineering and Environment, Newton Building, Crescent, M5 4NT, Salford, United Kingdom
[8] Universitat Autònoma de Barcelona, Departament de Sanitat i d'Anatomia Animals, Edifici V, 08193 Bellaterra (Cerdanyola del Vallès), Barcelona, Spain
* Corresponding author: anaa.sj@gmail.com; https://orcid.org/0000-0001-5551-6707

ABSTRACT

Terrestrial arthropod groups, including insects, spiders, and millipedes, represent an important food resource for primates. However, species consumed and patterns and rates of arthropod-related feeding for most frugivorous primates are still poorly known. We examined stomach contents of 178 Amazonian primate specimens of nine genera and three families obtained from community-based collections voluntarily donated by subsistence hunters. Based on our results, we assessed whether consumption patterns followed the expected negative relationship between arthropod ingestion and body size as postulated in the Jarman-Bell and Kay models. We identified 12 consumed arthropod taxa, including insects (beetles, grasshoppers, ants, flies, caterpillars, praying mantises, and others), spiders and millipedes. Medium and large-bodied primates consumed a greater diversity (measured by Simpson's diversity index) and richness of arthropods, but differed in terms of composition of taxa consumed. *Cacajao, Sapajus* and *Cebus* consumed proportionally more Orthoptera and Coleoptera compared to the other primate genera analyzed. We did not find significant correlations between richness and diversity of arthropods consumed and primate body mass. There was a slight tendency for the decrease in the relative content of arthropods in the diet with increased body mass in medium and large primates, which does not provide full support for the Jarman-Bell and Kay models. The study of arthropod consumption by arboreal primates in the wild remains challenging. Our study suggests that arthropods supply essential nutrients for frugivorous primates, and provides an alternative method to analyse faunal consumption patterns in primates.

KEYWORDS: animal matter, community-based sampling, faunivory, foraging ecology, tropical forests

Primatas maiores são menos faunívoros? Consumo de artrópodes por primatas amazônicos não atende aos modelos de Jarman-Bell e Kay

RESUMO

Grupos de artrópodes terrestres, incluindo insetos, aranhas e milípedes, representam um importante recurso alimentar para muitos primatas. Porém, espécies consumidas e padrões de consumo de artrópodes ainda são pouco conhecidos para a maioria dos primatas frugívoros. Nós examinamos o conteúdo estomacal de 178 espécimes de primatas amazônicos, de nove gêneros e três famílias, provenientes de coletas de base comunitária, doados voluntariamente por caçadores de subsistência. Com base em nossos resultados, avaliamos se os padrões de consumo seguem a relação negativa esperada em relação ao tamanho corporal, conforme postulado nos modelos de Jarman-Bell e Kay. Identificamos 12 *taxa* de artrópodes consumidos, incluindo insetos (besouros, gafanhotos, formigas, moscas, lagartas, louva-a-deuses, entre outros), aranhas e milípedes. Primatas de médio e grande porte consumiram maior diversidade (medida pelo índice de diversidade de Simpson) e riqueza de artrópodes, mas difeririam na composição dos *taxa* consumidos. *Cacajao*, *Sapajus* e *Cebus* consumiram proporcionalmente mais Orthoptera e Coleoptera que os outros gêneros analizados. Não encontramos correlações significativas entre riqueza ou diversidade de artrópodes consumidos e a massa corporal dos primatas. Houve uma leve tendência de diminuição no conteúdo relativo de artrópodes na dieta com o aumento da massa corporal de primatas médios e grandes, o que não fornece suporte completo para os modelos de Jarman-Bell e de Kay. O estudo do consumo de artrópodes por primatas arborícolas na natureza continua sendo desafiador. Nosso estudo sugere que os artrópodes fornecem nutrientes essenciais para primatas frugívoros, e apresenta um método alternativo para estudar padrões de consumo de fauna por primatas.

PALAVRAS-CHAVE: matéria animal, amostragem de base comunitária, faunivoria, ecologia alimentar, florestas tropicais

CITE AS:. Jesus, A.S.; Castilla Torres, R.I.; Quadros, J.C.; Cruz, A.N.; Valsecchi, J.; El Bizri, H.R.; Mayor, P. 2022. Are larger primates less faunivorous? Consumption of arthropods by Amazonian primates does not fulfil the Jarman-Bell and Kay models. *Acta Amazonica* 52: 208-217.

INTRODUCTION

To meet their daily energy, protein, and micronutrient requirements, frugivorous primates in tropical forests consume a variety of non-fruit diet items, including leaves and/or animal matter (Janson and Chapman 1999; Chapman *et al.* 2012). The animal component of the diets of these primates is mostly formed by terrestrial arthropods (i.e., ground- and tree-living arthropods). In forest habitats, such arthropods are widely available, though patchily distributed on the ground and in vegetation, often highly mobile or found embedded in fruits and galls or within wood (Stork and Blackburn 1993; Santos-Barnett *et al.* 2022). For many primates, arthropods represent an important food resource (Redford 1987; Rothman *et al.* 2014). Because of their generally high digestibility, elevated content of lipids, proteins, vitamins, and minerals (Raubenheimer and Rothman 2013; Rothman *et al.* 2014), and their high energy yield per unit mass, terrestrial arthropods may be a significant source of nutrients for frugivorous primates (DeFoliart 1995; Lambert 1998). However, the frequency and importance of arthropod consumption for most frugivorous primates remains poorly known (Rowe *et al.* 2021).

The three families of platyrrhines (Atelidae, Cebidae and Pitheciidae) comprise arboreal species found in the tropical regions of Mexico, Central and South America (Wang *et al.* 2019). The tree-living habit of these primates hinders the collection of information on arthropod consumption, which is often via direct observations, due to the height of the canopies in which these monkeys normally move and feed (Milton and Nessimian 1984; Pickett *et al.* 2012; Nielsen *et al.* 2018). Given how swiftly arthropods can be ingested, and the often opportunistic nature of such encounters, these limitations may considerably underestimate the diversity and relative content of arthropods consumed (Rowe *et al.* 2021).

According to the Jarman-Bell principle (Gaulin 1979), arthropod consumption is generally ecologically related to the nutritional requirements in mammals, and generally inversely correlated with the species' body size. Large animals therefore consume large amounts of lower quality food (e.g., leaves) due to their lower energy requirement per body mass, while smaller species tend to consume mainly high-quality items (e.g., arthropods). For primates, Kay's Threshold hypothesis predicts that significant consumption of animal matter will be typical in primates < 350 g, and consumption of leaves will predominantly occur in primates > 500 g (Kay 1984). Since most frugivorous primates have intermediate body sizes (Gaulin 1979; Kay 1984; Hawes and Peres 2014), leaves may be predicted to be the main complementary food item.

Field observations of frugivorous primates show that rates of arthropod consumption vary significantly, even among species with similar body size. For instance, arthropod consumption in medium-sized (from 2 to 3 kg) platyrrhine primates, such as *Cacajao ouakary* (Barnett *et al.* 2013), *Cebus kaapori* Queiroz, 1992 (Oliveira *et al.* 2014), and *Sapajus apella* Linnaeus, 1758 (Fragaszy *et al.* 2004; Gómez-Posada *et al.* 2019), may range from 3 to 50%, and from 1.3 to 23% in large-sized primates (above 7 kg), such as *Ateles belzebuth* É. Geoffroy Saint-Hilaire, 1806 (Link 2003), and *Lagothrix lagotricha* Humboldt, 1812 (Stevenson *et al.* 1994). More precise information based on large sample sizes is required to adequately assess the importance of arthropod consumption in primates of varying body sizes.

Here, we analysed stomach samples of nine Amazonian primate genera obtained from subsistence hunters who voluntarily donated these organs to our study. By directly examining the contents of ingested food material, it was possible to accurately assess and compare the arthropod richness, diversity, and relative content consumed. This method provided a useful snapshot of foods eaten shortly before collection (Milton and Nessimian 1984), despite the rapid gastrointestinal transit of foods, particularly in frugivorous primates (from 2.5 to 7.2 hours of gastric residence time, Chen *et al.* 2008). Using the data gathered, we also determined whether our observations fit the theoretical predictions established in the Jarman-Bell and Kay models.

MATERIAL AND METHODS

Data collection

Primate stomach samples were collected as part of a community-based effort involving subsistence hunters in three localities in the central and western Amazonia. Hunters voluntarily donated stomachs of a total of 178 specimens of nine primate genera: *Alouatta* Lacépède, 1799 (n = 48); *Ateles* E. Geoffroy, 1806 (n = 6); *Lagothrix* E. Geoffroy, 1812 (n = 30); *Cacajao* Lesson 1840 (n = 38); *Pithecia* Desmarest, 1804 (n = 11); *Cebus* Erxleben, 1777 (n = 9); *Sapajus* Linnaeus, 1758 (n = 29); *Leontocebus* Elliot, 1913 (n = 3); and *Saguinus* Hoffmannsegg, 1807 (n = 4) (Table 1). Biological materials were received from: 1) one community in the upland forest of the Yavarí-Mirín River basin (YMR; 04°S, 71°W) in western Amazonia, northeastern Peru, from 2009 to 2015; 2) five communities in the white-water flooded forest of the Mamirauá Sustainable Development Reserve (MSDR; 2°S, 65°W), in central Amazonia, northern Brazil, from 2002 to 2017; and 3) three communities in the upland forest of the Amanã Sustainable Development Reserve (ASDR; 01°S, 64°W) in central Amazonia, northern Brazil, from 2002 to 2018. All these communities are far from urban centres and, as a result, carry out subsistence activities such as extraction of timber and non-timber forest resources, fishing, hunting, and small-scale agriculture.

All primate stomachs were opportunistically collected during normal hunting activities of the communities' inhabitants. Subsistence hunting was not focused on primates,

Table 1. Number of specimens (N) and mean adult body mass of Amazonian primate taxa analysed for stomach contents. Arthropod frequency of occurrence = percentage of stomachs that contained arthropods; total content mass = mean (± standard deviation) of stomach content biomass; arthropod content mass = mean (± SD) of arthropod stomach content mass; relative content of arthropods = mean (± SD) of the arthropod content mass relative to total stomach content mass; frequency of occurrence of arthropod taxon = percentage of stomachs that contained each arthropod taxon; λ = Simpson' diversity index.

Primate taxa								**Frequency of occurrence of arthropod taxon (%)**													
Family/ Subfamily	**Species**	**N**	**Body mass (kg)**	**Arthropod frequency of occurrence (%)**	**Total content mass (g)**	**Arthropod content mass (g)**	**Relative content of arthropods**	**Hym (Form)**	**Hym (Vesp)**	**Col**	**Ort**	**Dip**	**Hem**	**Lep**	**Man**	**Bla**	**Der**	**Arac**	**Myr**	**NI**	**λ**
Atelidae																					
Alouattinae	*Alouatta juara* Elliot, 1910 *Alouatta seniculus* Linnaeus, 1766	48	6.11	93.7	52.1 ± 38.0	0.01 ± 0.02	0.003 ± 0.004	77.8	4.4	13.3	0	6.7	0	4.4	0	0	0	4.4	0	17.8	0.60
Atelinae	*Ateles chamek* Humboldt, 1812	6	8.80[†]	67	60.0 ± 51.3	0.002 ± 0.004	0.00005 ± 0.0001	50.0	0	0	0	0	0	0	0	0	0	0	0	50.0	0.40
	Lagothrix lagotricha poeppigii Schinz, 1844	30	7.10[‡]	33.3	43.9 ± 34.8	0.1 ± 0.5	0.004 ± 0.02	60.0	0	40.0	10.0	10.0	10.0	0	0	0	10.0	10.0	10.0	0	0.80
Pitheciidae																					
Pitheciinae	*Cacajao ouakary* Spix, 1823 *Cacajao ucayalli* Thomas, 1928	38	3.15[§]	94.7	17.0 ± 13.1	0.9 ± 0.8	0.05 ± 0.04	63.9	11.1	44.4	61.1	2.8	11.1	22.2	5.6	0	0	8.3	0	5.6	0.80
	Pithecia monachus É. Geoffroy, 1812	11	2.35[¶]	45.5	7.1 ± 6.0	0.02 ± 0.03	0.003 ± 0.005	71.4	0	14.3	0	0	14.3	0	0	0	0	0	0	0	0.50
Cebidae																					
Cebinae	*Cebus albifrons* Humboldt, 1812	9	2.9	62.5	8.0 ± 5.5	0.5 ± 0.7	0.05 ± 0.06	40.0	20.0	100	60.0	20.0	0	0	0	0	0	20.0	0	0	0.80
	Sapajus macrocephalus Spix, 1823	29	2.96	69	11.8 ± 13.5	0.4 ± 0.6	0.1 ± 0.2	65.0	25.0	65.0	30.0	5.0	20.0	10.0	0	15.0	0.0	10.0	5.0	0	0.80
Callitrichinae	*Leontocebus nigricollis* Spix, 1823	3	0.35[††]	33.3	0.8 ± 0.9	0.1 ± 0.5	0.0007 ± 0.001	100	0	0	0	0	0	0	0	0	0	0	0	0	0.00
	Saguinus inustus Schwartz, 1951	4	0.4	100	2.6 ± 3.3	0.05 ± 0.03	0.02 ± 0.03	50.0	0	50.0	25.0	0	25.0	0	25.0	0	0	25.0	0	0	0.80

Literature used for body mass of YMR' primates: [†]Smith and Jungers (1997), Rosenberger et al. (2008); [‡]Lu (1999); [§]Ford (1994); [¶]Emmons and Feer (1990); [††]Ravetta (2015). Frequency of occurrence of arthropd taxon (orders and families): Hym (Form) = Hymenoptera (Formicidae); Hym (Vesp) = Hymenoptera (Vespidae); Col = Coleoptera; Ort = Orthoptera; Dip = Diptera; Hem = Hemiptera; Lep = Lepidoptera; Man = Mantodea; Bla = Blattodea (Blattidae); Der = Dermaptera; Arac = Arachnida; Myr = Myriapod (Diplopoda); NI= not identified.

instead they form part of an extensive list of consumed regional mammals. No animals were killed other than those harvested as part of local hunters' usual activities. Samples were identified by a code that included the primate genus and date of hunting, and kept in containers with 4% formaldehyde, following Mayor *et al.* (2017). In ASDR and MSDR, hunters also recorded the animals' body mass (in kg) using a 20 kg Pesola scale (accuracy = ± 0.3%).

The research protocol was approved by the Chico Mendes Institute for Biodiversity Conservation in Brazil (license SISBIO # 29092-1) and by the Research Ethics Committee for Experimentation in Wildlife at Dirección General de Flora y Fauna Silvestre in Peru (license # 0229-2011-DGFFS-DGEFFS). The samples collected in Peru were deposited at the Instituto Veterinario de Investigaciones Tropicales y de Altura of Universidad Nacional Mayor de San Marcos (Peru) and those collected in MSDR and ASDR were deposited in the Scientific Collection of Mastozoology of the Instituto de Desenvolvimento Sustentável Mamirauá (Brazil).

Stomachs were opened at their greatest curvature. The contents were washed over granulometric sieves with different mesh sizes (4.0, 0.6 and 0.075 mm) to retain whole arthropods and their fragments, and the retained material was then dried in an oven at 60 °C for up to 6 h (following Torres *et al.* 2022). Using an Olympus stereoscopic microscope, we isolated all whole and fragmented arthropods found in the sieved contents at 10 to 40X magnification. We weighed the mass of the whole stomach content, and the arthropod content was weighed on a Shimadzu analytical balance (precision: 0.0001 g). Arthropods were identified by the authors of this study with the help of experienced entomologists (see acknowledgements) up to order level and, in a few cases, to family level.

Data analysis

We conducted all primate analyses at genus level by pooling congeneric species into the same taxon. We calculated the relative content of arthropods in each stomach by dividing the arthropod content mass by the total mass in the contents of each stomach, and the frequency of occurrence of each arthropod taxon for each primate genus.

We estimated the diversity of arthropods consumed by each primate genus using the Simpson diversity index (λ), following the equation: $\lambda = 1 - \Sigma(P_i)^2$; where P_i is the frequency of each arthropod taxon in relation to the total richness consumed by each primate genus. When λ values approach 1 (one) they indicate high diversity, and when they approach 0 (zero) they indicate low diversity (Simpson 1949). We produced richness rarefaction curves with 95% confidence intervals using EstimateS 9.1.0 (Colwell and Elsensohn 2014), based on a resampling with 100 permutations of our samples, aiming to reduce the effect of undersampling of some primate genera. We also extrapolated the sample size of each primate genus based on the sample size of the most sampled taxon (*Alouatta*, n = 48) in order to estimate the stabilization of the rarefaction curves and predict the richness of arthropods for each primate genus if sample sizes were equal.

We used a multidimensional analysis (principal coordinates analysis, PCoA), to assess the differences in terms of composition of arthropod taxa (i.e., presence/absence of each arthropod taxa in each primate stomach) consumed by primate genera based on the binomial distance index, using R 3.5.2 (R Core Team 2019). The binomial distance deals with binary presence/absence data and can handle varying sample sizes. As a complementary approach, we performed an analysis of similarity (ANOSIM) to obtain the statistical significance of dissimilarities in arthropod composition between the primate genera obtained by the PCoA.

We performed Pearson and Spearman correlations (according to the normality of the data tested by the Shapiro-Wilk test) to assess the relationship between primate body mass and the contribution of arthropods to their diets in terms of relative content consumed, the Simpson diversity index and estimated richness with extrapolated sample sizes. We tested these correlations in two scenarios. In the first scenario, we considered the nine primate genera evaluated, and in the second, we kept only medium- and large-sized primates and excluded genera with body weights < 500 g (i.e., *Leontocebus* and *Saguinus*), since these could mask the relationships or bias the analysis due to small sample size. We used the mean primate body mass recorded by hunters in the ASDR and MSDR, and from literature information for YMR (Table 1).

RESULTS

We found terrestrial arthropods in the stomachs of all studied primate genera. Overall, we recorded the presence of arthropods in 73% (130/178) of the stomachs, with arthropod frequency of occurrence ranging from 33.3 to 100% among primate genera (Table 1). Mean ingested arthropod content varied from 0.02 - 0.9 g among primate genera, and the relative arthropod content averaged from 0.00005 to 0.1 of the total stomach content mass (Table 1). Arthropod content proportions were higher in *Lagothrix*, *Cacajao*, *Cebus* and *Sapajus* (Table 1), and lower in *Ateles* and *Leontocebus*, though sample sizes for the latter were lowest (Table 1).

We were able to identify 94.6% of the arthropods consumed, classified into 12 taxonomic groups. The most frequent arthropod groups were insects (present in 90% of the stomachs with arthropods), followed by spiders (Arachnida, Araneae, 3.7%) and myriapods (0.8%). Ants (Hymenoptera, Formicidae) accounted for 36.8% of all records, followed by beetles (Coleoptera, 19.4%) and grasshoppers (Orthoptera, 13.6%). The frequency of other arthropods ranged from 0.4% for earwigs (Dermaptera) to 5% for caterpillars (Lepidoptera larvae) and wasps (Hymenoptera, Vespidae).

In terms of arthropod richness, rarefaction curves indicated that our sample size was appropriate for estimating the arthropod richness consumed by most primate taxa, except for *Lagothrix* (n = 30) and *Leontocebus* (n = 3) (Figure 1). The highest richness was observed in *Lagothrix*, *Cacajao* and *Sapajus* (Figure 1), with at least nine arthropod taxonomic groups ingested (Table 1); beetles and ants represented 40-65% of all records, followed by grasshoppers with 10-61%. On the other hand, only ants were found in the three *Leontocebus* specimens, the genus with the lowest richness and a null Simpson diversity index value. Simpson diversity index values of 0.8 indicated the highest arthropod diversity was consumed by *Sapajus*, *Cebus*, *Lagothrix*, *Saguinus* and *Cacajao*, while the lowest index was obtained for *Ateles*, followed by *Pithecia* and *Alouatta*, which tended to have moderate diversity indices (Table 1).

The two PCoA axes explained 76% of the distribution of individuals in the ordination space based on the composition of arthropods in their diet (axis 1: 47%, axis 2: 29%). The composition of arthropods consumed by the different platyrrhines were clearly differentiated (ANOSIM R = 0.21, p < 0.01; Table 2), as data from *Cacajao*, *Cebus*, and *Sapajus* were concentrated on the right side of the first axis (Figure 2). *Cacajao, Cebus* and, to some extent, *Sapajus* are clearly separated from the other genera in their consumption of spiders, bugs, wasps, caterpillars, and, most importantly, beetles and grasshoppers. *Cebus* also differed in consuming less ants than the other genera.

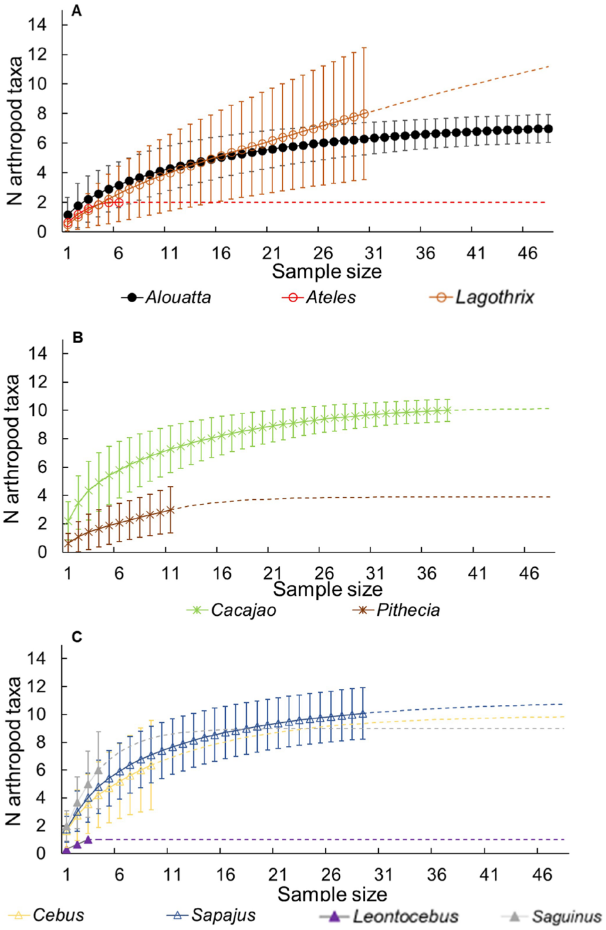

Figure 1. Rarefaction curves showing the observed and predicted ingested arthropod richness for 178 specimens of nine Amazonian primate genera. Predicted values estimated through the extrapolation of sample size up to 48 samples (stomach contents) for each primate taxon. A – Atelidae; B – Pitheciidae; C – Cebidae. This figure is in color in the electronic version.

We did not find any significant association between primate body mass and arthropod consumption in any of the scenarios analyzed (Figure 3). In scenario 1, which included all nine primate genera, the correlation between the relative content of arthropods showed a tendincy to a negative relationship, while the other variables showed a slight tendincy to a positive relationship. In scenario 2, which included only medium and large-sized primates, all variables tended to a negative relationship, as expected in the theoretical models. However, none of the correlations strongly supported the predictions of the Kay and Jarman-Bell models.

DISCUSSION

Platyrrhines in general have frugivorous diets which are supplemented by other foods such as leaves, but also arthropods (Chapman *et al.* 2012; Hawes and Peres 2014). Here, we have shown that arthropods are consumed frequently, but not in large volumes. We found a wide range

Table 2. Correlation coefficients and multiple regression coefficients of determination for arthropod taxa composition (Taxon) in the diet of 178 specimens of nine Amazonian primate genera, showing the loadings of axis 1 and 2 of the principal coordinate analysis (PCoA).

Taxon	Axis 1	Axis 2	R^2	P-value
Hym_Form	-0.45709	-0.88942	0.7794	0.001*
Hym_Vesp	0.4073	-0.9133	0.1739	0.002*
Col	0.95414	0.29937	0.6289	0.001*
Ort	0.89193	-0.45218	0.6071	0.001*
Dip	0.16487	-0.98632	0.0098	0.580
Hem	0.30095	-0.95364	0.1886	0.001*
Lep	0.56702	-0.82371	0.3413	0.001*
Man	-0.99839	-0.05679	0.0242	0.249
Bla_Blat	-0.99821	0.0598	0.0371	0.134
Der	-0.92974	0.36821	0.0113	0.502
Arac	0.75492	-0.65582	0.0252	0.245
Myr_Dipl	0.23721	0.97146	0.0339	0.142

Taxon (arthropod orders and families): Hym_Form = Hymenoptera (Formicidae); Hym_Vesp = Hymenoptera (Vespidae); Col = Coleoptera; Ort = Orthoptera; Dip = Diptera; Hem = Hemiptera; Lep = Lepidoptera; Man = Mantodea; Bla_Blat = Blattodea (Blattidae); Der = Dermaptera; Arac = Arachnida; Myr_Dipl = Myriapoda (Diplopoda). Asterisks (*) indicate statistical significance.

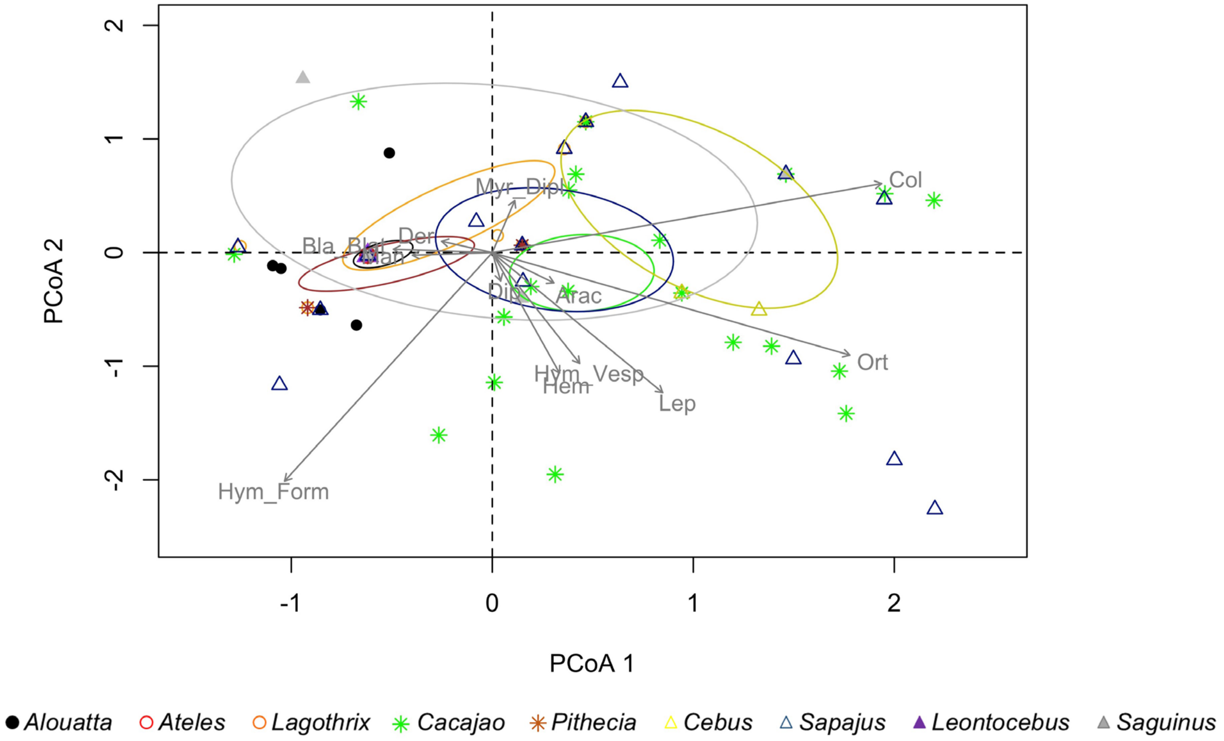

Figure 2. Principal coordinates analysis (PCoA) showing the variation in the composition of arthropod taxa consumed by 178 specimens of nine primate genera based on binomial distance (76% of variance explanation for the two axes, 47% of axis 1 and 29% of axis 2). Abbreviations for arthropod taxa (orders and families): Hym_Form = Hymenoptera (Formicidae); Hym_Vesp = Hymenoptera (Vespidae); Col = Coleoptera; Ort = Orthoptera; Dip = Diptera; Hem = Hemiptera; Lep = Lepidoptera; Man = Mantodea; Bla_Blat = Blattodea (Blattidae); Der = Dermaptera; Arac = Arachnida; Myr (Dipl) = Myriapod (Diplopoda). Some symbols are not clearly distinguishable on the graph due to overlapping of points in the ordination space. This figure is in color in the electronic version.

of arthropods consumed by the platyrrhine genera studied, with differences of up to 2,000 times in the relative content of arthropods consumed among the genera. Although terrestrial arthropod consumption was highest in the Cebidae and Pitheciidae, it was also important for Atelidae, especially for the large-bodied *Lagothrix*. Our findings support direct field observations of intentional consumption of arthropods being typical of cebines *Cebus* and *Sapajus* (e.g., Fragaszy *et al.* 2004; Oliveira *et al.* 2014), the callitrichines *Leontocebus* and *Saguinus* (e.g., Peres 1993), the pitheciids *Pithecia* and *Cacajao* (e.g., Ayres 1989; Heymann and Bartecki 1990; Barnett *et al.* 2013, 2017), and the ateline *Lagothrix* (e.g., Stevenson *et al.* 1994). Although the literature provides some reports of intentional consumption of arthropods by *Ateles* (Link 2003; Santos-Barnett *et al.* 2022), our small sample size for this genus did not allow us to confirm whether the consumption of arthropods in this genus is intentional or not. On the other hand, arthropod frequency and richness in the stomach contents of the more folivorous platyrrhines (e.g., *Alouatta*, Crockett 1998) may indicate that arthropod consumption can be intentional in these primates. Further studies are needed to clarify this issue and to understand the nutritional implications of this ingestion.

The arthropods found most frequently in the stomach contents were insects from the orders Coleoptera, Hymenoptera and Orthoptera, also reported in other studies as the main taxa consumed by primates (McGrew 2014; Rothman *et al.* 2014; Rowe *et al.* 2021). These same taxa represent the PCoA loadings with the greatest effects on the separation of groups in terms of the composition of arthropod taxa consumed. While the frequent consumption of Coleoptera and Orthoptera clustered *Cacajao*, *Cebus* and *Sapajus*, the higher occurrence of Formicidae (Hymenoptera) clustered the other genera. These differences suggest differential strategies among coexisting Amazonian primate taxa to reduce food niche overlap (e.g., Lyke *et al.* 2019) and to seek and acquire prey.

Ants (Hymenoptera, Formicidae) were eaten by all primate genera evaluated, corroborating the recent finding that myrmecovory is widespread among 18 of the 22 platyrrhine genera (Ferreira *et al.* 2021). However, the higher frequency of ants in the diet of the genera furthest to the left-hand side of the PCoA ordination space, particularly *Alouatta* and *Pithecia*, may point to a more opportunistic or accidental consumption of these arthropods. Ants are individually small, but they are extremely abundant and gregarious social insects that can be eaten in large quantities during a single feeding event (Redford 1987; McGrew 2014), or even accidentally eaten with fruits

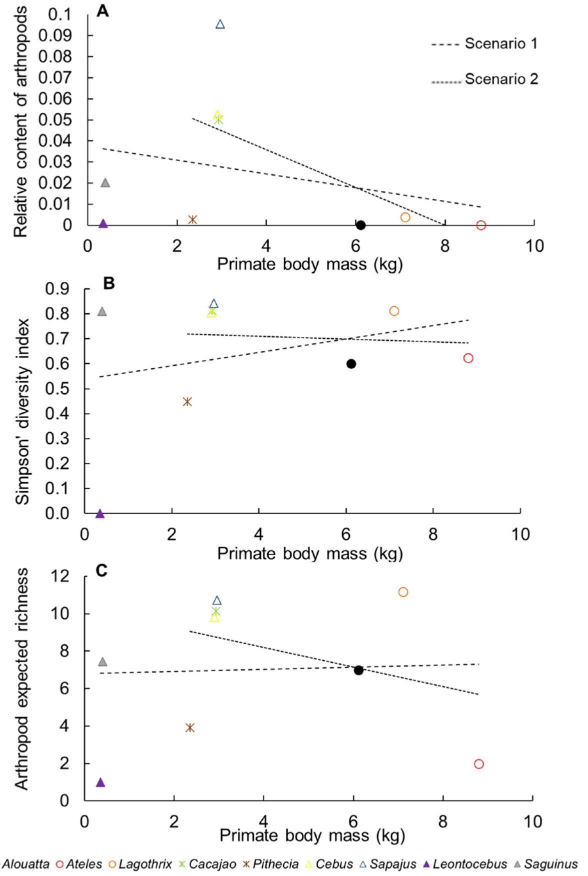

Figure 3. Pearson correlation between the mean body mass of Amazonian primate genera and three arthropod consumption variables for two scenarios: 1) including all nine genera (small-, medium- and large-sized), and 2) including seven genera (medium- and large-sized). A – mean relative content of arthropod in stomach contents (Scenario 1: $r_s = -0.2333$, $p = 0.55$; Scenario 2: $r_s = -0.5357$, $p = 0.22$); B – Simpson diversity index (Scenario 1: $r_s = 0.3051$, $p = 0.42$; Scenario 2: $r_s = -0.0371$, $p = 0.93$); C – estimated richness of consumed arthropods (Scenario 1: $r = -0.0438$, $R^2 = 0.2\%$, $p = 0.93$; Scenario 2: $r = -0.2455$, $R^2 = 6\%$, $p = 0.59$). This figure is in color in the electronic version.

or leaves (e.g., Ayres and Nessimian 1982). On the other hand, the clear separation of *Cacajao*, *Cebus* and *Sapajus* due to the proportionally higher frequency of Coleoptera and Orthoptera in their diet suggests more specifically developed visual and capture capacities, as these insects are fast in flying and jumping (Rothman *et al.* 2014), and are usually large and very active (Ozanne and Bell 2003).

Other arthropods may have only been consumed opportunistically or accidentally, so explaining why they appeared at very low frequencies in the primate stomachs analysed. Flies (Diptera) and fig wasps (Hymenoptera, Vespidae) may be accidentally consumed along with fruits (see Redford *et al.* 1984; McGrew 2014; Lyke *et al.* 2019). Some fly families cause infestations in ripe fruits (e.g., Tephritidae and Lonchaeidae, Souza-Filho 2019) or insect-induced leaf galls (Redford *et al.* 1984; McGrew 2014), and fig wasps' life cycle is mutualistic with figs (*Ficus* spp., Moraceae) (e.g., Weiblen 2004). On the other hand, primates may prefer seeds/fruits infested with arthropods from which they can obtain a mixture of energy and protein (Redford *et al.* 1984), as recorded for *Cacajao ouakary* (Barnett *et al.* 2017), *Ateles chamek* and *A. marginatus* É. Geoffroy, 1809 (Santos-Barnett *et al.* 2022). *Cacajao ouakary* also consumes insects embedded in rotting wood, tearing through dead wood with their canines and extracting insects with their teeth, a behavior pattern very similar to removing seeds from hard-shelled fruits (Barnett *et al.* 2013).

Our results did not statistically support the predictions of the Jarman-Bell and Kay models, either in terms of proportion of stomach content, diversity or richness of arthropods consumed by Amazonian primates in the two scenarios analyzed. Observational studies on congeneric species of small primates (< 500 g, *Saguinus* and *Leontocebus*) show that, contrary to Jarman-Bell and Kay predictions, these primates consume less arthropods than medium and large-sized primates, naturally deviating from the models. Furthermore, despite their small body size, these primates have a large caecum and colon, similar to folivorous species (Ferrari *et al.* 1993), suggesting a lower dependence on faunivory. Even so, arthropods comprise between 5.7 and 12.4% of the diet of *Leontocebus fuscicollis* Spix, 1823 and *Saguinus mystax* Spix, 1823, respectively (Peres 1993). The greater arthropod richness and diversity that we found for *Saguinus* specimens agreed with the greater levels of *Leontocebus* faunivory reported by Peres (1993). The changes in the coefficients of determination of correlations when these genera were excluded are compatible with the abovementioned evidence for lower arthropod consumption in *Leontocebus* and *Saguinus*.

Predictions of models based solely on body mass do not match with the dietary needs and morphological adaptations in platyrrhines, although there is a tendency for an inverse relationship in the relative content of arthropod consumed, providing tentative support for the models for medium- and large-bodied primates. It is likely that these relationships are neither simple nor linear, and other factors are involved in the evolutionary process determining the dietary requirements of primate species. Beyond body mass and morphophysiological digestive adaptations, cognitive skills and the availability of food resources are interrelated factors that are likely to be important in shaping feeding strategies (Hartwig *et al.* 2011; Raubenheimer and Rothman 2013). All these complementary factors need further investigation.

One limitation of our study was that stomach contents may underestimate the relative content and richness of ingested arthropods, as these are the undigested remains of chitinous arthropod structures that allows taxonomic identification only up to order or family level (e.g., Ozanne and Bell 2003). Soft-bodied forms, such as caterpillars and other larvae, as well as aphids, may also be underestimated because they have fewer chitinous body parts. Therefore, the use of stomach content of arthropods as an estimator used in our study likely introduced a bias towards forms with heavily sclerotized exoskeletons in detriment of lightly sclerotized arthropods.

Another limitating factor in the study is the opportunistic sampling by local subsistence hunters, which does not allow to control the number of sampled individuals. In the scenario in which our study was carried out, primate hunting by itself is a seasonal event, which occurs with greater intensity in periods of flooding, when fishing yield (the main source of animal protein in the participant communities) decreases (Endo *et al.* 2016). Thus, our samples are not distributed in a way that allows to control seasonal differences in primate diet due to availability of food resources or the effects of environmental variables. Seasonality effects should be explored in future research, to better understand the consumption of arthropods by frugivorous primates.

Finally, the participation of hunters by donating samples that originate from their usual subsistence activities, allows communities to contribute to research without encouraging any further killing of animals. As such, the use of donated samples can be a useful alternative to study several ecological aspects of wild animals (Mayor *et al.* 2017; Jesus *et al.* 2022), including the diet of hard-to-observe frugivorous arboreal primates.

CONCLUSIONS

We described the patterns of consumption of arthropods in nine frugivorous Amazonian primate genera, as well as the diversity of arthropods in the diet of these species. The frequency, relative content, richness, diversity, and composition of arthropod taxa consumed showed that arthropods are important complementary food items that may allow these species to meet essential nutritional requirements. In this sense, even arthropods consumed accidentally can provide nutritional benefits. Arthropods may also complement the diet when fruit resources are scarce or absent. The study of arthropod consumption by frugivorous arboreal primates remains a challenge, but the use of alternative sampling methods, such as the community-based sampling employed here, in combination with direct observations of primate foraging behavior in the field, have the potential to generate well-grounded knowledge on the feeding ecology of primates.

ACKNOWLEDGMENTS

We sincerely thank all the local communities that permitted the research development in their living areas, and the subsistence hunters of the Mamirauá and Amanã Sustainable Development Reserves and the Yavarí-Mirín River for their collaboration in donating samples, without which this work would not be possible. We thank the institutional support provided by Instituto de Desenvolvimento Sustentável Mamirauá (Brazil) and Instituto de Investigaciones Tropicales y de Altura (Peru), and the support by the entomologists of the Instituto de Investigaciones de la Amazonía Peruana (IIAP) (Peru) in arthropod identification. This research was partially supported by Gordon and Betty Moore Foundation (Grant # GBMF9258). ASJ was supported by a PhD scholarship from the Fundação Amazônia de Amparo a Estudos e Pesquisas (FAPESPA/UFRA - 007/2017) (Brazil), and ANC by Programa Institucional de Bolsas de Iniciação Científica of Conselho Nacional de Desenvolvimento Científico e Tecnológico (PIBIC/CNPq) (Brazil). We are also grateful to Julia E. Fa for the review, comments, and suggestions that improved the manuscript.

REFERENCES

Ayres, J.M. 1989. Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *Journal of Human Evolution,* 18: 697-716.

Ayres, J.M.; Nessimian, J.L. 1982. Evidence for insectivory in *Chiropotes satanas*. *Primates,* 23: 458-459.

Barnett, A.A.; Ronchi-Teles, B.; Almeida, T.; *et al*. 2013. Arthropod predation by a specialist seed predator, the golden-backed uacari (*Cacajao melanocephalus ouakary*, Pitheciidae) in Brazilian Amazonia. *International Journal of Primatology,* 34: 470-485.

Barnett, A.A.; Ronchi-Teles, B.; Andrade, R.; Almeida, T.; Bezerra, B.M.; Gonçalves de Lima, M.; Spironello, W.R.; MacLarnon, A.; Ross, C.; Shaw, P.J.A. 2017. Covert carnovory? A seed-predation primate, the golden backed uacari, shows preferences for insect-infested fruits. *Journal of Zoological Research,* 1: 16-31.

Chapman, C.A.; Rothman, J.M.; Lambert, J.E. 2012. Food as a selective force in primates. In: Call, J.; Kappeler, P.M.; Silk, K.B.; Mitani, J.C.; Palombit, R.A. (Ed.). *The Evolution of Primate Societies*. The University Chicago Press, Chicago, p.149-168.

Chen, E.P.; Doan, K.M.M.; Portelli, S.; Coatney, R.; Vaden, V.; Shi, W. 2008. Gastric pH and gastric residence time in fasted and fed conscious cynomolgus monkey using the Bravo® pH system. *Pharmaceutical Research,* 25: 123-134.

Colwell, R.K.; Elsensohn, J.E. 2014. EstimateS turns 20: statistical estimation of species richness and shared species from samples, with non-parametric extrapolation. *Ecography,* 37: 609-613.

Crockett, C.M. 1998. Conservation biology of the genus *Alouatta*. *International Journal of Primatology,* 19: 549-578.

DeFoliart, G.R. 1995. Edible insects as minilivestock. *Biodiversity and Conservation,* 4: 306-321.

Emmons, L.H.; Feer, F. 1990. *Neotropical Rainforest Mammals: a field guide*. 2nd ed. University of Chicago Press, Chicago, 396p.

Endo, W.; Peres, C.A.; Haugaasen, T. 2016. Flood pulse dynamics affects exploitation of both aquatic and terrestrial prey by Amazonian floodplain settlements. *Biological Conservation,* 201: 129-136.

Ferrari, S.F.; Lopes, M.A.; Krause, A.K. 1993. Gut morphology of *Callithrix nigriceps* and *Saguinus labiatus* from Western

Brazilian Amazonia. *American Journal of Physical Anthropology,* 90: 487-493.

Ferreira, N.I.R.; Verhaagh, M.; Heymann, E.W. 2021. Myrmecovory in Neotropical primates. *Primates,* 62: 871-877.

Ford, S.M. 1994. Evolution of sexual dimorphism in body weight in platyrrhines. *American Journal of Primatology,* 34: 221-244.

Fragaszy, D.; Izar, P.; Visalberghi, E.; Ottoni, E.B.; Oliveira, M.G. 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology,* 64: 359-366.

Gaulin, S.J. 1979. A Jarman/Bell model of primate feeding niches. *Human Ecology,* 7: 1-20.

Gómez-Posada, C.; Rey-Goyeneche, J.; Tenorio, E.A. 2019. Ranging responses to fruit and arthropod availability by a tufted capuchin group (*Sapajus apella*) in the Colombian Amazon. In: Reyna-Hurtado, R.; Chapman, C.A. (Ed.). *Movement Ecology of Neotropical Forest Mammals*. Springer, Cham, p.195-215.

Hartwig, W.; Rosenberger, A.L.; Norconk, M.A.; Owl, M.Y. 2011. Relative brain size, gut size, and evolution in New World monkeys. *The Anatomical Record,* 294: 2207-2221.

Hawes, J.E.; Peres, C.A. 2014. Ecological correlates of trophic status and frugivory in neotropical primates. *Oikos,* 123: 365-377.

Heymann, E.W.; Bartecki, U. 1990. A young saki monkey, *Pithecia hirsuta*, feeding on ants, *Cephalotes atratus*. *Folia Primatologica,* 55: 181-184.

Janson, C.H.; Chapman, C.A. 1999. Resources and primate community structure. In: Fleagle, J.G.; Janson, C.; Reed, K. (Ed.). *Primate communities*. Cambridge University Press, Cambridge, p.237-267.

Jesus, A.S.; Oliveira-Ramalho, M.L.; El Bizri, H.R.; Valsecchi, J.; Mayor, P. 2022. Environmental and biological drivers of prevalence and number of eggs and oocysts of intestinal parasites in red howler monkeys from Central Amazonia. *Folia Primatologica,* 93: 121-138.

Kay, R.F. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Cant, J.; Rodman, P. (Ed.). *Adaptations for foraging in nonhuman primates*. Columbia University Press, New York, p.21-53.

Lambert, J.E. 1998. Primate digestion: Interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology,* 7: 8-20.

Link, A. 2003. Insect-eating by spider monkey. *Neotropical Primates,* 11: 104-107.

Lu, F.E. 1999. *Changes in subsistence patterns and resource use of the Huaorani indians in the Ecuadorian Amazon*. Doctoral thesis, University of North Carolina, USA. 363p.

Lyke, M.M.; Di Fiore, A.; Fierer, N.; Madden, A.A.; Lambert, J.E. 2019. Metagenomic analysis reveal previously unrecognized variation in the diets of sympatric Old World monkeys species. *PLoS ONE,* 14: e0218245.

Mayor, P.; El Bizri, H.R.; Bodmer, R.E.; Bowler, M. 2017. Assessment of mammal reproduction for hunting sustainability through community-based sampling of species in the wild. *Conservation Biology,* 31: 912-923.

McGrew, W.C. 2014. The 'other faunivory' revisited: Insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution,* 71: 4-11.

Milton, K.; Nessimian, J.L. 1984. Evidence for insectivory in two primate species (*Callicebus torquatus lugens* and *Lagothrix lagothricha lagothricha*) from Northwestern Amazonia. *American Journal of Primatology,* 6: 367-371.

Nielsen, J.M.; Clare, E.L.; Hayden, B.; Brett, M.T.; Kratina, P. 2018. Diet tracing in ecology: Method comparison and selection. *Methods in Ecology and Evolution,* 9: 278-291.

Oliveira, S.G.; Lynch Alfaro, J.W.; Veiga, L.M. 2014. Activity budget, diet, and habitat use in the critically endangered Ka'apor capuchin monkey (*Cebus kaapori*) in Pará State, Brazil: A preliminary comparison to other capuchin monkeys. *American Journal of Primatology,* 76: 919-931.

Ozanne, C.M.; Bell, J.R. 2003. Collecting arthropods and arthropod remains for primate studies. In: Setchell, J.M.; Curtis, D.R. (Ed.). *Field and Laboratory Methods in Primatology: A Practical Guide*. Cambridge University Press, Cambridge, p.214-227.

Peres, C.A. 1993. Diet and feeding ecology of saddle-back (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins in an Amazonian *terra firme* forest. *Journal of Zoology,* 230: 567-592.

Pickett, S.B.; Bergey, C.M.; Di Fiore, A. 2012. A metagenomic study of primate insect diet diversity. *American Journal of Primatology,* 74: 622-631.

R Core Team. 2019. *R: A language and environment for statistical computing (version 3.5. 2)*. R Foundation for Statistical Computing, Vienna.

Raubenheimer, D.; Rothman, J.M. 2013. Nutritional ecology of entomophagy in humans and other primates. *Annual Review of Entomology,* 58: 141-160.

Ravetta, A.L. 2015. Avaliação do risco de extinção de *Saguinus fuscicollis fuscicollis* (Spix, 1823) no Brasil. Instituto Chico Mendes de Conservação da Biodiversidade. (https://www.icmbio.gov.br/portal_antigo/biodiversidade/fauna-brasileira/estado-de-conservacao/7236-mamiferos-saguinus-fuscicollis-fuscicollis-sagui-de-cara-suja.html). Accessed on 31 Jul 2022.

Redford, K.H. 1987. Ants and termites as food: Patterns of mammalian myrmecophagy. In: Genowaysm H.H. (Ed.). *Current Mammalogy*. Plenum Press, New York, p.349-399.

Redford, K.H.; da Fonseca, G.A.B.; Lacher, T.E. 1984. The relationship between frugivory and insectivory in primates. *Primates,* 25: 433-440.

Rothman, J.M.; Raubenheimer, D.; Bryer, M.A.; Takahashi, M.; Gilbert, C.C. 2014. Nutritional contributions of insects to primate diets: implications for primate evolution. *Journal of Human Evolution,* 71: 59-69.

Rowe, A.K.; Donohue, M.E.; Clare, E.L.; Drinkwater, R.; Koenig, A.; Zachary, R.M.; *et al.* 2021. Exploratory analysis reveals arthropod consumption in 10 lemur species using DNA metabarcoding. *American Journal of Primatology,* 83: e23256.

Santos-Barnett, T.C.; Cavalcante, T.; Boyle, S.A.; Matte, A.L.; Bezerra, B.M.; Oliveira, T.G.; Barnett, A.A. 2022. Pulp Fiction: Why some populations of ripe-fruit specialists *Ateles chamek* and

A. marginatus prefer insect-infested foods. *International Journal of Primatology,* 43: 384-408.

Simpson, E.H. 1949. Measurement of diversity. *Nature,* 163: 688.

Smith, R.J.; Jungers, W.L. 1997. Body mass in comparative primatology. *Journal of Human Evolution,* 32: 523-559.

Souza-Filho, M.F.; Raga, A.; Azevedo-Filho, J.A.; Strikis, P.C.; Guimarães, J.A.; Zucchi, R.A. 2019. Diversity and seasonality of fruit flies (Diptera: Tephritidae and Lonchaeidae) and their parasitoids (Hymenoptera: Braconidae and Figitidae) in orchards of guava, loquat and peach. *Brazilian Journal of Biology,* 69: 31-40.

Stevenson, P.R.; Quiñones, M.J.; Ahumada, J.Á. 1994. Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at Tinigua National Park, Colombia. *American Journal of Primatology,* 32: 123-140.

Stork, N.E.; Blackburn, T.M. 1993. Abundance, body size and biomass of arthropods in tropical forest. *Oikos,* 67: 483-489.

Torres, R.I.C.; Jesus, A.S.; Loaiza, J.O.; Mayor, P. 2022. Dietas de primatas no humanos del norte amazónico peruano. *Revista de Investigaciones Veterinarias del Perú,* 33: e22159.

Wang, X.; Lim, B.K.; Ting, N.; Hu, J.; Liang, Y.; Roos, C.; Yu, L. 2019. Reconstructing the phylogeny of the new world monkeys (Platyrrhini): Evidence from multiple non-coding loci. *Current Zoology,* 65: 579-588.

Weiblen, G.D. 2004. Correlated evolution in fig pollination. *Systematic Biology,* 53: 128–139.

RECEIVED: 17/03/2022
ACCEPTED: 24/07/2022
ASSOCIATE EDITOR: Paulo D. Bobrowiec