RESEARCH ARTICLE

Highly Nested Diets in Intrapopulation Monkey–Resource Food Webs

WESLEY DÁTTILO1, JUAN CARLOS SERIO-SILVA2*, COLIN A. CHAPMAN3,4, AND VÍCTOR RICO-GRAY1

1Instituto de Neuroetología, Universidad Veracruzana, Xalapa, Veracruz, Mexico
2Red de Biología y Conservación de Vertebrados, Instituto de Ecología A.C., Xalapa, Veracruz, Mexico
3Department of Anthropology & McGill School of Environment, McGill University, Montreal, Quebec, Canada
4Wildlife Conservation Society, Bronx, New York

Recently several studies have focused on the structure of ecological networks to provide insights into ecological and coevolutionary dynamics of interacting species. However, rarely have the tools of ecological networks been used to understand how feeding relationships vary among individuals of the same population. Here we use 7 years of data and network analysis to examine the intrapopulation diet variation in a group of howler monkeys (Alouatta palliata). We show that individual monkey–resource food webs are nested, but not modular and the stability of these patterns is independent of time of day or season. Our findings indicated that individuals do not forage randomly when compared to null models and that the diets of more selective monkeys represent subsets of the diets of other individuals. Moreover, there are no subgroups that eat a particular set of available plant species more frequently than other sets, suggesting that the spatial strategy of group foraging plays an important role in the feeding ecology of each group given that individuals of the same group tend to share similar resources while the group remains at a feeding site. Since the diets of more selective individuals are a subset of other monkeys, we suggest that more selective monkeys are able to outcompete others for preferred foods. Additionally, we did not observe differences in nutritional content or spatial abundance of more frequently eaten plant species when compared with less frequently eaten species, but in most cases, the more frequently eaten plant species were Ficus (Moraceae). This reinforces the important role that Ficus trees play in howler monkey feeding ecology, likely due to its year-round availability. Am. J. Primatol. 76:670–678, 2014. © 2014 Wiley Periodicals, Inc.

Key words: complex networks; intrapopulation variation; modularity; nestedness; social animals

INTRODUCTION

Trophic interactions affect all attributes of ecosystems and play an important role in the stability and diversity of communities and populations in space and time [O’Gorman & Emmerson, 2009]. Despite this, few studies have evaluated how feeding relationships vary within populations [Bolnick et al., 2003; Inger et al., 2006], but see studies on Oreochromis aureus [Gu et al., 1997], Epipedobates flavopictus [Biavati et al., 2004], Gracilinanus microtarsus [ Martins et al., 2006], and Procolobus rufomitratus [Chapman et al., 2002]. These studies have shown that there can be wide variation in rates of resource consumption by individuals in a population [Bolnick et al., 2003; Shine et al., 2002]. For example, a species of intertidal snail (Nucella melones) consumes 21 prey taxa, but any one consumer consumes only one to five of these taxa, ignoring prey species eaten by others. In the case of gray-cheeked mangabeys (Lophocebus albigena) and redtail monkeys (Cercopithecus ascanius), high ranking females use agonism to monopolize sodium rich bark [Chancellor & Isbell, 2009; Rode et al., 2006; Rothman et al., 2012]. Thus, group members may exhibit alternative feeding strategies. The little evidence available to date suggests that some individuals are more selective (concentrate their feeding efforts on a small number of foods), while others are more opportunistic [ Araújo et al., 2010; Bolnick et al., 2002; Pires et al., 2011].

Several studies have recently used tools derived from network analysis to describe the dietary variation found in a population [Araújo et al., 2010;
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Cantor et al., 2013; Pires et al., 2011; Tinker et al., 2012]. A network analysis uses a set of mathematical abstractions to identify and connect links that represent interactions; in this case among individuals in a group characterized by different feeding patterns [Bondy & Murty, 1976]. Using this type of analysis, data on sea otters, didelphid marsupials, frogs, and lizards have shown that intrapopulation food webs share non-random structural patterns [reviewed in Pires et al., 2011]. One of the main characteristics of these food webs is that they are highly nested [Araújo et al., 2010; Cantor et al., 2013; Pires et al., 2011], indicating that there are group members that only eat a subset of items consumed by other group members, signifying that individuals differ in their foraging strategies [Araújo et al., 2010; Cantor et al., 2013; Pires et al., 2011]. One possibility is that the individuals that eat a smaller subset of items are being more selective (i.e., choosing the more nutritious or advantageous items) and represent dominant animals that can monopolize these items [Janson & van Schaik, 1988; Snaith & Chapman, 2007], individuals with specific dietary needs [e.g., lactating females with higher protein requirements; Hinde & Mulligan, 2011], or lower ranking individuals who are excluded from preferred feeding sites.

In its typical ecological application, nestedness is a measure of order in a system and the more nested a system is the more organized it is. Here, nestedness is used to describe the organization of a population’s niche breadth, in which more nested food webs tend to have higher niche overlap (e.g., individuals making similar dietary selections); thus, more nestedness represents similar dietary choices. Moreover, it also has been shown that some individuals can feed more frequently on a specific plant species and generate highly modular or compartmentalized food webs [Araújo et al., 2008]. Classic examples of a modular system are pollination systems where species co-evolve so that the pollinator and the flower converge on a correlated suite of traits (e.g., birds with long curved bills pollinate large flowers where the nectar is deep within the flower; Olesen et al., 2007; Dáttilo et al., 2013a, 2014). However, it is unclear whether both nestedness and modularity also are found in intrapopulation food webs of group-living species.

For animals, such as primates, it is argued that one nutritional strategy is focused on regulating nutrient intake to obtain a sufficient amount of protein, lipids, and carbohydrates, while avoiding secondary compounds [Chapman & Chapman, 2002; Milton, 1979, 1998; Rothman et al., 2012; Simmen et al., in press]. Specifically primates may use information on the color and size of food resource in assessing the nutritional and chemical content of foods [Domjan, 2009; Mishkin, 1982; Thompson, 1982]. A strategy based on collective decisions can have important consequences on feeding behavior within a population [Clark & Mangel, 1986; Garber, 2004; Garber et al., 2009; Krause & Ruxton, 2002; Vickery et al., 1991]. Therefore, evaluating intrapopulation variation in feeding behavior in social animals may reveal new insights into the ecological and evolutionary dynamics of consumer–resource relationships. In addition to food quality, food items abundance plays a large role in selection, with patches with abundant food items attracting more individuals [Hanya & Chapman, 2013; Snaith & Chapman, 2005]. In addition, in species in which individuals forage in widely scattered subgroups subgroup spread may aid individuals in more easily locating feeding sites already encountered by conspecifics [Garber et al., 2009; Krishna et al., 2008].

In this study, we used network analysis to investigate intrapopulation dietary variation over 7 years for a group of howler monkeys (Alouatta palliata). In these networks, plant species and monkeys are depicted as nodes and their interactions are depicted by links describing the use of plant species by individuals. Specifically, we were interested in determining if intrapopulation monkey–resource food webs are nested, modular, or both, and describing the patterns in which different group members feed. Finally we also evaluated how the abundance and nutritional content of plant species structure food webs. The use of network analysis allows us to describe more clearly different patterns of interactions among trophic levels and to detect non-random patterns of monkey–resource interactions. This approach identifies the role of each monkey within a food web based on the roles of all individuals within a group, which provides a benchmark to test against random null models.

METHODS

Study Site

We conducted our fieldwork on Agaltepec Island (8.3 ha) in Lake Catemaco, Veracruz, Mexico (18°27‘N, 95°02‘W; elevation <400 m). The climate is warm and humid with an annual rainfall of approximately 2,000 mm. Most rain occurs between June and February, with May being the driest month. Mean temperature is 24°C, with a mean maximum and minimum of 36.5 and 11°C, respectively. Tropical deciduous forest is the main vegetation on the island, complemented by riparian vegetation, secondary vegetation, and grassland [Serio-Silva et al., 2002].

Behavioral Data

At least every 2 weeks between November 1989 and December 1996, we conducted two weeks long surveys of a group of howler monkeys (A. palliata) released on the island (October 1988–April 1989). The initial group composition was one adult male, eight adult females, and one immature, and the sex–
age composition at the end was eight adult males, 12 adult females, and nine immatures. Monkeys were systematically observed using focal animal sampling over the day, and individuals observed 1 day and was not observed again until all the others had been observed. We alternated the behavioral sampling each day (±8–12 days every 2 weeks depending on weather conditions or other variables) between 06:00–12:00 and 12:00–18:00 for a total of 3,663 hr of observation (2,303 hr of feeding behavior; 916 hr in the dry season and 1387 hr in the wet season). When possible, each focal animal session lasted at least 6 hr, and we attempted to sample equally all sex–age individuals across all seasons and times of day (AM or PM). Additional details of feeding behavior and daily activity patterns are reported in Serio-Silva [1997]. Our study was conducted in accordance with laws and protocols on animal research of Mexico and adheres to American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

Data Analyses

We used network analysis because it allows us to study non-random patterns of interactions in complex systems where different trophic levels can interact (e.g., monkey–plant food webs) and test the significance of the patterns found against specific null models of interactions [Lange et al., 2013]. Moreover, network analysis permits a very rich and detailed graphical visualization of large-scale datasets. Using traditional methods, it would be very difficult to find non-random patterns of interactions, since the behavior of a complex system is the sum of its different levels. We initially defined each consumer–resource network as an adjacency matrix $A$, where $a_{ij} = 1$ if the consumption of a resource from a plant species $j$ by the individual monkey $i$ was recorded, and zero otherwise [Bascompte et al., 2003]. Specifically, we recorded the plant species eaten by an individual during a day independent of the part of the plant (fruits or leaves). In our adjacency matrix, columns are plant species and rows are individual monkeys. We used an approach where the matrices had 0 and 1 values due to the difficulty of accurately measuring the difference in the frequency of feeding on leaves compared to fruits, this approach decreases the probability of under- or over-estimating the amount of leaves consumed due to the difficulty of identifying correctly the amount of ingested leaves by monkeys.

Our study area has very well defined wet and dry seasons, which directly affect food availability and the feeding ecology of monkeys [Dias, 2002; Serio-Silva et al., 2002]. Thus, to evaluate the effect of resource/seasonality on monkey–resource food webs, we initially built three different food webs according to season: wet season, dry season, and total period. Despite the fact that our database considers more than 7 years, there is a difference in the number of hours sampled between months. To decrease the bias generated by this difference, we combined years according to the season, therefore, for each of the seasonal food webs we included 7 years of observation.

Several studies have shown that there is a large difference in the foraging pattern of monkeys in relation to time of day [Chapman & Chapman, 1991; Milton, 1980]. For instance, monkeys can substantially change their diet between the morning and afternoon [Yamagiwa & Mwanza, 1994], which could lead to differences in the topology of food webs. Thus we built three resource–consumer food webs to evaluate within-population diet variation during the day: morning (between 06:00 and 12:00), afternoon (between 12:01 and 18:00), and total day (between 06:00 and 18:00). In total, we evaluated nine monkey–resource food webs: three based in seasons (wet, dry, and total sampling period), and for each of the three seasons, we built three food webs based on foraging time: morning, afternoon, and whole day.

We used “nestedness” to evaluate whether the diets of more selective monkeys represent subsets of the diets of monkeys that consumed a broader based diet. We term these opportunist monkeys. We computed the degree of nestedness of each network using the nestedness based on overlap and decreasing fill metric (NODF) [Almeida-Neto et al., 2008] in ANINHADO [Guimarães & Guimarães, 2006]. The values of this metric range from 0 (non-nested) to 100 (perfectly nested). When compared with other metrics, the NODF metric is better at calculating nestedness and is less prone to type-I errors [Almeida-Neto et al., 2008]. In addition, we tested whether within each network there were groups of individuals strongly associated with a particular set of plant species. For this we used the modularity index ($M$) based on simulated annealing (SA) (range 0–1) [Guimerà et al., 2004] using the software MODULAR [Marquitti et al., 2013]. High values of $M$ index indicate the presence of groups of monkeys and plants that generate modules that are semi-independent of other interactions within the network [Olesen et al., 2007]. Although this index $M$ is used for unipartite food webs, our null models control any potential effects of bipartite structure on modularity (interactions only occur between monkey and plant species) [Pires et al., 2011]. The $M$ index is calculated as follows:

$$M = \sum_{s=1}^{N_m} \left[ \frac{L - \left( \frac{d_s}{2L} \right)^2}{L} \right],$$

where $N_m$ is the number of modules, $L$ is the total number of links in the network, $l_s$ is the number of links between species in module $s$, and $d_s$ is the sum of
the degrees of all species in module s [Olesen et al., 2007].

To verify the significance of nestedness and modularity, we tested the empirical values against null distributions of these values. For this, we computed 1,000 food webs generated by Null Model II (CE) [Bascompte et al., 2003]. In this null model, the probability of an interaction occurring is proportional to the number of interactions of both monkeys and plants. Despite the possibility of having one individual used more than once within the same network, our null model controls the potential effects of this type of sampling bias [Bascompte et al., 2003]. We used these food webs descriptors (nestedness and modularity) and the null model because they characterize the organization of these networks in a way that allows direct comparison with previous work on intrapopulation food webs [Araújo et al., 2010; Cantor et al., 2013; Pires et al., 2011; Tinker et al., 2012].

We also tested if the plants more frequently eaten by monkeys are the most abundant plant species and/or with better nutritional content. To identify the more or less frequently eaten plant species, we first initially defined core or peripheral plant species components of the food webs using: 

$$G_c = \frac{(k_i - k_{\text{mean}})}{z}$$

[Dáttilo et al., 2013b], where $k_i$ = mean number of links for a given plant species, $k_{\text{mean}}$ = mean number of links for all plant species in the network, and $z$ = SD of the number of links for plant species. $G_c > 1$ (generalist core): are plant species with the largest proportion of interactions in relation to other plant species, and therefore, are plant species more frequently eaten by monkeys. $G_c < 1$ (periphery of food webs): are plant species with the lowest proportion of interactions in relation to other plant species, and therefore, are plant species less eaten by monkeys. We then collected samples of all plant species consumed by the howlers, concentrating on those plant parts most frequently consumed (i.e., young and mature leaves, mature fruits) in both wet and dry seasons (between 1994 and 1997) to determine the amount of plant nutrients (e.g., water, ash, fiber, protein, carbohydrates, lipids) [for these methods, see Serio-Silva et al., 2002]. To summarize the amount of plant nutrients inserted on the core or periphery of food webs, we ordered the similarity between points using non-metric multidimensional scaling (NMDS) and tested the difference of two categories (core and periphery) through a permutation test (10,000 permutations) based on an analysis of similarities (ANOSIM) using the quantitative Bray–Curtis’s index. We performed this procedure separately for each season. Additionally, to evaluate

Fig. 1. Pattern of interactions between monkeys (right) and plant species (left) according to season: (A) wet season, (B) dry season, and (C) total sampling period. Each circle represents one monkey or plant species, which are represented by gray and white colors, respectively. Lines represent monkey–plant interactions. Food webs above are represented as bipartite food webs ordered for nestedness, where the resources consumed by selective individuals are a subset of generalist individuals that feed on more plant species. Food webs below were represented as an energy two-mode graph (Kamada–Kawai free method). Both networks were built using the program Pajek.
whether the level of generalization of plant species is proportional to their abundances, we initially ranked the plant species by their abundances, and correlated the position of each species with the rank position of plant in the ordered matrix for nestedness using a Spearman correlation test. To obtain the information of spatial abundance of plant species collected independently, we used the database in which each individual plant (dbh >30 cm, and >5 m in height) was numbered and mapped [Rodríguez-Luna et al., 1993]. We performed Spearman correlations and NMDS using the R-software version 2.13.1 [R Development Core Team, 2012].

RESULTS

Over a 7-year period, A. palliata individuals fed on 40 plant species, representing 65% of all available species (Appendix A). Among the 40 species used, 38 were used in the wet season and 30 in the dry season. The mean number of species on which each monkey fed was higher in the wet (n = 4.58 interactions or links) than dry season (n = 3.81). Similarly, the number of interactions or links per plant species was higher in the wet (n = 28.45) than dry season (n = 12.57; statistics are in Table I). This is likely due to the fact that in the wet season monkeys feed on a greater number of plant species. Given limitations in our data, we were not able to determine how age and sex affected monkey–resource interactions.

Regardless of the season, when we analyzed the temporal variation in the food webs, we found more monkey–resource interactions in the morning (wet: 614; dry: 207) than afternoon (wet: 467; dry: 170). This may result from the fact that the monkeys tended not to feed intensively during afternoon periods, causing a higher rate of feeding in the morning. During both seasons, both monkeys and plants also show the highest number of interactions in the morning (wet season—monkeys: 3.18, plants: 18.61; dry season—monkeys: 2.56, plants: 8.63) compared to the afternoon (wet season—monkeys: 3.03, plants: 15.06; dry season—monkeys: 2.50, plants: 8.10). Moreover, we also observed that there were more monkey–resource interactions in the wet season than in the dry season regardless of time of day (statistics are in Table I).

We found a significant nestedness value in all nine food webs studied, regardless of time of day, season, or sampling period (mean ± SD: 22.33 ± 4.14; range: 16.64–29.48; all P < 0.05). In contrast, we did not find a significantly modular pattern of interactions in any of the nine food webs (mean ± SD: 0.479 ± 0.055; range: 0.405–0.549; all P > 0.05), indicating that monkey–resource food webs did not contain subgroups of individuals that feed more strongly on a particular group of plant species (Table I). Moreover, the number of individuals that feed on more species did not vary over time (n = 3 or 4 for all food webs).

We found that the number and identity of the plant species most frequently eaten by monkeys (Bursera simaruba, Ficus cotinifolia, Ficus maxima, and Ficus pertusa) did not differ throughout the day. On the other hand, when we focused on seasonal variation, we observed a 25% change in the identity of the plant species most frequently eaten by monkeys between the wet and dry seasons. In the wet season the core plant species were: B. simaruba, F. cotinifolia, F. maxima, and F. pertusa. However, F. maxima was not present in the monkeys’ diet in the dry season. It was replaced as a core species by Andira galleottiana.

Independent of season, the nutritional content of plants of these core species was not different from those in the periphery of the food webs (wet: NMDS, followed by ANOSIM; P = 0.682; dry: NMDS, followed by ANOSIM; P = 0.961). We also observed this

### Table I. Network Attributes of Individual Monkey–Resource Interactions Recorded Between November 1989 and December 1996, on Mexican Howler Monkeys Alouatta palliata mexicana Living in Agaltepec Island, in the Municipality of Catemaco, Veracruz, Mexico

<table>
<thead>
<tr>
<th>Network attributes</th>
<th>Wet season</th>
<th>Dry season</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Morning</td>
<td>Afternoon</td>
<td>All day</td>
</tr>
<tr>
<td>No. of interactions</td>
<td>614</td>
<td>467</td>
<td>1081</td>
</tr>
<tr>
<td>Number of focal-animal samples</td>
<td>193</td>
<td>154</td>
<td>236</td>
</tr>
<tr>
<td>Mean no. of interactions or links</td>
<td>3.18</td>
<td>3.03</td>
<td>4.58</td>
</tr>
<tr>
<td>per monkey</td>
<td>33</td>
<td>31</td>
<td>38</td>
</tr>
<tr>
<td>Mean no. of interactions or links</td>
<td>18.61</td>
<td>15.06</td>
<td>28.45</td>
</tr>
<tr>
<td>per plant species</td>
<td>19.41</td>
<td>16.64</td>
<td>24.92</td>
</tr>
<tr>
<td>Nestednessa</td>
<td>0.489</td>
<td>0.513</td>
<td>0.421</td>
</tr>
<tr>
<td>Modularityb</td>
<td>0.489</td>
<td>0.513</td>
<td>0.421</td>
</tr>
</tbody>
</table>

aAll networks were significantly nested (P < 0.05).
bNo networks showed a modular pattern of interaction (P > 0.05).
same pattern for the total sampling period (NMDS, followed by ANOSIM; \( P = 0.734 \)). In addition, the plant species more frequently eaten by monkeys were not the plant species spatially more abundant in the nine food webs studied (Spearman rank correlation test: all \( P > 0.05 \)).

**DISCUSSION**

Several studies have shown that at the community level species interactions (e.g., seed dispersal, pollination, and protective networks) represent nested patterns that are an intrinsic property of an ecological network [Bascompte et al., 2003; Hagen et al., 2012; Vázquez et al., 2009]. However, it is only in the past 5 years that such nested patterns have been reported in consumer–resource food webs at the intrapopulation level [Araújo et al., 2008, 2010; Cantor et al., 2013; Pires et al., 2011]. Here we show that nestedness is also a property of the within-group food webs of animals with complex group social organization such as nonhuman primates. Our results indicate that some monkeys eat a subset of items consumed by other individuals in the group. Several possibilities exist to explain the mechanisms that generate a nested pattern in food webs use at the group level. These include optimal diet theory, phenotypic variation, age, or sex-based differences in behavioral strategies and dietary needs, and shared preferences models [Araújo et al., 2008, 2010; Cantor et al., 2013; Pires et al., 2011]. Each of these possibilities contain the basic premise that individual variation within a population is due to differences in individual physiology and/or differences in the ability to access resources or avoid predators [Bolnick et al., 2003; Svanbäck & Bolnick, 2005].

For monkeys, it is possible that the spatial strategy of group foraging may be an important factor structuring the nested pattern in monkey–resource food webs. Unlike animals that forage individually, monkeys have been shown to employ a complex strategy of foraging that involves spatial memory regarding the location, quality, and abundance of food resources, as well as sensory mechanisms to minimize exposure to plant toxins [Bonnell et al., 2013; Deneubourg & Goss, 1989; Garber, 2004; Garber et al., 2009; Serio-Silva et al., unpublished data]. Thus, we propose that if the mobility or spatial positioning of individuals within a group varies, a nested pattern of resource use could emerge [Bonnell et al., 2013]. Individuals that range across a larger area may have a higher probability of finding alternative resources and potentially have broader diets. We expected a highly stable dietary pattern among group members because when a group of howler monkeys visits a feeding site, all individuals tend to consume the resource (although this may not be the case for primates that forage on solitary insects) [Hare & Kwetuenda, 2010]. Therefore, more selective individuals (e.g., dominant individuals or individuals with particular dietary needs) are likely to fall within a subset of all individuals. One possibly is that more selective monkeys are able to outcompete other individuals when feeding and consume the more nutritional resources [Janson & van Schaik, 1988; Snaith & Chapman, 2007], or particular individuals may have specific dietary needs [e.g., lactating females with higher protein requirements; Hinde & Mulligan, 2011]. Such possibilities remain to be tested.

Additionally, supporting other studies conducted in intrapopulation food webs in plant–animal systems [Cantor et al., 2013; Pires et al., 2011], we did not find evidence of modularity or compartmentalization in our monkey–resource food webs. These findings indicate that despite the difference in selective foraging among individuals within a monkey population which may include differences in the exploitation of mature versus immature leaves, rates of food intake, or the ingestion of particular invertebrate and vertebrate species, there are no subgroups of monkeys that consumed a specific subgroup of available plant species more frequently. We observed a higher frequency of monkey–resource interactions in the wet season possibly because the monkeys invested in higher rates of food selection during periods of increased availability of a larger number of plant species [Youlatos, 1998]. A study conducted by Dias [2002] showed that in the wet season agonistic encounters among males in our study group decreased compared to the dry season. This could reflect increased aggression during periods of food scarcity or be associated with seasonal patterns of female receptivity and mating competition. Pires et al. [2011] recently stated that when a resource is scarce, the asymmetry caused by the nested pattern could generate highly competitive interactions. For social animals where the dominance hierarchy is well-defined, competitive interactions within the group could lead to individual differences in the number of plant species consumed [Hinde, 1976]. In this context, competitively superior individuals could control access to preferred resources and result in socially submissive individuals to develop alternative or less efficient foraging strategies [Barta & Giraldeau, 1998; Gemmill & Gould, 2008].

We observed that the frequency of monkey–resource interactions (feeding events: amount of food consumed) was higher in the morning in all food webs regardless of season. Consistent with these results, we suggest that the seasonal availability of food shapes the intrapopulation monkey–resource food webs [Dammhahn & Kappeler, 2009], since the food web size and heterogeneity of interactions can change over time, and consequently, these network attributes also can affect the structure of such food webs.

Species abundance is one of the most fundamental criteria shaping ecological networks [Krishna et al., 2008]. In this case, under conditions when plant
foods are equal in their nutritional content and ease of acquisition, foragers should interact more frequently with abundant species than with less abundant species [Vázquez et al., 2007]. However, we did not find a relationship between the spatial abundance of plant species and its level of consumption. The ability of primates to encode and recall the spatial location of a large number of food patches may enable howler monkeys to efficiently relocate previously visited food patches [Chapman, 1988; Serio-Silva et al., unpublished data]. In addition, we did not find differences between the nutritional contents of more frequently and less frequently eaten plant species (based on number of visits to that species). A study conducted by Serio-Silva et al. [2002] on the same mantled howler study group illustrated that fig trees accounted for almost 64% of howler feeding time over the course of 85 months. Our results reinforce observations that Ficus trees are a critical resource for monkeys in Central and South America [Felton et al., 2013], and Alouatta in particular. This is, due to the fact that figs produce an enormous fruit crop, fruit asynchronously, and therefore are often availability during periods when fruit availability in the forest is otherwise limited [Altmann, 1989; Serio-Silva et al., 2002, but see Chapman et al., 2005].

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APPENDIX. Percentage of the Occurrence of Plant Species in the Diet of Howler Monkeys Alouatta palliata in Wet and Dry Seasons on an Island in Southern Veracruz, Mexico

<table>
<thead>
<tr>
<th>Species or morphospecies (family)</th>
<th>Wet (%)</th>
<th>Dry (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ficus pertusa (Moraceae)</td>
<td>18.1</td>
<td>24</td>
</tr>
<tr>
<td>Bursera simaruba (Burseraceae)</td>
<td>9.5</td>
<td>9.3</td>
</tr>
<tr>
<td>Ficus cotinifolia (Moraceae)</td>
<td>7.9</td>
<td>8.9</td>
</tr>
<tr>
<td>Ficus maxima (Moraceae)</td>
<td>6.7</td>
<td>5.3</td>
</tr>
<tr>
<td>Chlorophora tinctoria (Moraceae)</td>
<td>5.7</td>
<td>1.2</td>
</tr>
<tr>
<td>Gliricidia sepium (Fabaceae)</td>
<td>5.6</td>
<td>3.7</td>
</tr>
<tr>
<td>Spondias mombin (Anacardiaceae)</td>
<td>5.2</td>
<td>2.4</td>
</tr>
<tr>
<td>Masticodendron capiri (Sapotaceae)</td>
<td>5.1</td>
<td>7.7</td>
</tr>
<tr>
<td>Ficus obtusifolia (Moraceae)</td>
<td>4.8</td>
<td>3.3</td>
</tr>
<tr>
<td>Astronium graveolens (Anacardiaceae)</td>
<td>4.0</td>
<td>2.4</td>
</tr>
<tr>
<td>Ficus insipida (Moraceae)</td>
<td>3.8</td>
<td>2.0</td>
</tr>
<tr>
<td>Protium copal (Burseraceae)</td>
<td>3.7</td>
<td>5.3</td>
</tr>
</tbody>
</table>

(Continued)

REFERENCES


