

RESEARCH ARTICLE

Highly Nested Diets in Intrapopulation Monkey–Resource Food Webs

WESLEY DÁTILLO¹, JUAN CARLOS SERIO-SILVA^{2*}, COLIN A. CHAPMAN^{3,4}, AND VÍCTOR RICO-GRAY¹¹Instituto de Neuroetología, Universidad Veracruzana, Xalapa, Veracruz, Mexico²Red de Biología y Conservación de Vertebrados, Instituto de Ecología A.C., Xalapa, Veracruz, Mexico³Department of Anthropology & McGill School of Environment, McGill University, Montreal, Quebec, Canada⁴Wildlife 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 analyzed 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 rufomitratu* [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 individual consumes only one to five of these taxa, ignoring prey species eaten by others. In the case of gray-cheeked mangabeys (*Lophocebus albigena*) and redbelt 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;

Contract grant sponsor: Conselho Nacional de Desenvolvimento Científico (CNPq)

*Correspondence to: Juan Carlos Serio-Silva, Red de Biología y Conservación de Vertebrados, Instituto de Ecología, A.C.—INECOL, Antigua Carretera a Coatepec No. 351, El Haya, Xalapa 91070, Veracruz, Mexico. E-mail: juan.serio@inecol.mx; serioju@yahoo.com

Received 9 September 2013; revised 16 December 2013; revision accepted 11 January 2014

DOI: 10.1002/ajp.22261

Published online 5 February 2014 in Wiley Online Library (wileyonlinelibrary.com).

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 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 others 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:

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

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

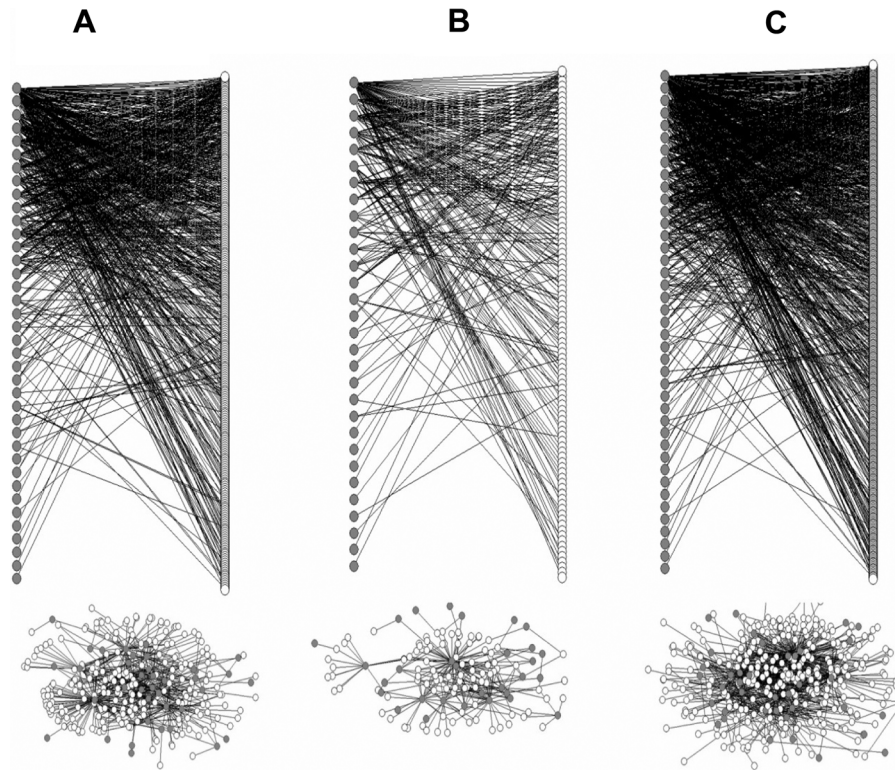


Fig. 1. Pattern of interactions between monkeys (right) and plant species (left) according to season: (A) wet season, (B) dry season, and (C) total sampling period. Each circle represents one monkey or plant species, which are represented by gray and white colors, respectively. Lines represent monkey-plant 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.

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: $G_c = ((k_i - k_{\text{mean}})/z)$ [Dáttilo et al., 2013b], where k_i = mean number of links for a

given plant species, k_{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

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 \pm 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 \pm 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

Network attributes	Wet season			Dry season			Total		
	Morning	Afternoon	All day	Morning	Afternoon	All day	Morning	Afternoon	All day
No. of interactions	614	467	1081	207	170	377	860	632	1492
Number of focal-animal samples	193	154	236	81	68	99	282	220	333
Mean no. of interactions or links per monkey	3.18	3.03	4.58	2.56	2.50	3.81	3.05	2.87	4.48
No. of plant species	33	31	38	24	21	30	37	34	40
Mean no. of interactions or links per plant species	18.61	15.06	28.45	8.63	8.10	12.57	23.24	18.59	36.39
Nestedness ^a	19.41	16.64	24.92	20.07	23.95	29.48	22.05	18.12	26.35
Modularity ^b	0.489	0.513	0.421	0.542	0.549	0.413	0.484	0.513	0.405

^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 possibility 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].

ACKNOWLEDGMENTS

We are grateful to Denise Lange, Pedro Dias, Paul Garber, and two anonymous reviewers for valuable comments on earlier drafts of the manuscript and to Flavia Marquitti for her careful support with modularity analyses. W.D. is grateful for financial support by the Conselho Nacional de Desenvolvimento Científico (CNPq) and Consejo Nacional de Ciencia y Tecnología (CONACYT).

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

Species or morphospecies (family)	Wet (%)	Dry (%)
<i>Ficus pertusa</i> (Moraceae)	18.1	24
<i>Bursera simaruba</i> (Burseraceae)	9.5	9.3
<i>Ficus cotinifolia</i> (Moraceae)	7.9	8.9
<i>Ficus maxima</i> (Moraceae)	6.7	5.3
<i>Chlorophora tinctoria</i> (Moraceae)	5.7	1.2
<i>Gliricidia sepium</i> (Fabaceae)	5.6	3.7
<i>Spondias mombin</i> (Anacardiaceae)	5.2	2.4
<i>Mastichodendron capiri</i> (Sapotaceae)	5.1	7.7
<i>Ficus obtusifolia</i> (Moraceae)	4.8	3.3
<i>Astronium graveolens</i> (Anacardiaceae)	4	2.4
<i>Ficus insipida</i> (Moraceae)	3.8	2
<i>Protium copal</i> (Burseraceae)	3.7	5.3

(Continued)

Species or morphospecies (family)	Wet (%)	Dry (%)
<i>Dendropanax arboreus</i> (Araliaceae)	3.5	3.3
<i>Andira galleottiana</i> (Fabaceae)	2.9	11
<i>Plumeria rubra</i> (Apocynaceae)	1.4	0.4
<i>Nectandra coriacea</i> (Lauraceae)	1.3	0.4
<i>Ficus</i> sp.1 (Moraceae)	1.3	0
<i>Brosimum alicastrum</i> (Moraceae)	1.1	0.8
<i>Cordia dodecandra</i> (Boraginaceae)	1	0.8
<i>Cupania dentata</i> (Sapindaceae)	1	0.4
<i>Erythrina folkersii</i> (Fabaceae)	0.8	2
<i>Cecropia obtusifolia</i> (Cecropiaceae)	0.6	0
<i>Diospyros verae-crucis</i> (Ebenaceae)	0.6	0.4
<i>Chrysophyllum mexicanum</i> (Sapotaceae)	0.6	0
<i>Diospyros digina</i> (Ebenaceae)	0.5	0.4
<i>Scheelea liebmanii</i> (Palmae)	0.5	0
<i>Randia albonervia</i> (Rubiaceae)	0.5	0.4
<i>Tapirira mexicana</i> (Anacardiaceae)	0.3	0
<i>Cedrela odorata</i> (Meliaceae)	0.3	0
<i>Stemmadenia donnell-smithii</i> (Apocynaceae)	0.2	0.4
<i>Ceiba aesculifolia</i> (Bombacaceae)	0.2	0.8
<i>Pachira aquatica</i> (Bombacaceae)	0.2	0
Unidentified sp1 (Compositaceae)	0.2	0.4
<i>Diphysa macrophylla</i> (Fabaceae)	0.2	0
<i>Guarea glabra</i> (Meliaceae)	0.2	0.4
<i>Trichilia havanensis</i> (Meliaceae)	0.2	0
<i>Pisonia aculeata</i> (Nyctaginaceae)	0.2	0
<i>Lonchocarpus cruentus</i> (Fabaceae)	0	1.2
<i>Leucaena glauca</i> (Fabaceae)	0	0.4
<i>Guazuma ulmifolia</i> (Malvaceae)	0	0.4

REFERENCES

- Almeida-Neto M, Guimaraes P, Guimaraes PR, Loyola RD, Ulrich W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239.
- Altmann SA. 1989. The monkey and the fig. *American Scientist* 77:256–263.
- Araújo MS, Guimarães PR, Svanback R, et al. 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. *Ecology* 89:1981–1993.
- Araújo MS, Martins EG, Cruz LD, et al. 2010. Nested diets: a novel pattern of individual-level resource use. *Oikos* 119:81–88.
- Barta Z, Giraldeau LA. 1998. The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype limited producing-scrounging game. *Behavioral Ecology and Sociobiology* 42:217–223.
- Bascompte J, Jordano P, Melián CJ, Olesen JM. 2003. The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America* 100:9383–9387.
- Biavati GM, Wiederhecker HC, Colli GR. 2004. Diet of *Epipedobates flavopictus* (Anura: Dendrobatidae) in a neotropical savanna. *Journal of Herpetology* 38:510–518.
- Bolnick DI, Yang LH, Fordyce JA, Davis JA, Svanback R. 2002. Measuring individual-level trophic specialization. *Ecology* 83:2936–2941.
- Bolnick DI, Svanback R, Fordyce JA, et al. 2003. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* 161:1–29.

- Bondy JA, Murty USR. 1976. Graph theory with applications. New York, NY: Elsevier. 651 p.
- Bonnell TR, Chapman CA, Reyna-Hurtado R, et al. 2013. Emergent group level navigation: an agent-based evaluation of movement patterns in a folivorous primate. *PLoS ONE* 8: e78264.
- Cantor M, Pires MM, Longo GG, Guimarães PR, Setz EZF. 2013. Individual variation in resource use by opossums leading to nested fruit consumption. *Oikos* 122:1085–1093.
- Chancellor RL, Isbell LA. 2009. Food site residence time and female competitive relationships in wild gray-cheeked mangabeys (*Lophocebus albigena*). *Behavioral Ecology and Sociobiology* 63:1447–1458.
- Chapman CA. 1988. Patch use and patch depletion by spider and howling monkeys of Santa Rosa National Park, Costa Rica *Behaviour* 105:99–116.
- Chapman CA, Chapman LJ. 1991. The foraging itinerary of spider monkeys: when to eat leaves? *Folia Primatologica—International Journal of Primatology* 56:162–166.
- Chapman CA, Chapman LJ. 2002. Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. *Comparative Biochemistry and Physiology* 133:861–875.
- Chapman CA, Chapman LJ, Gillespie TR. 2002. Scale issues in the study of primate foraging: red colobus of Kibale National Park. *American Journal of Physical Anthropology* 117: 349–363.
- Chapman CA, Chapman LJ, Zanne AE, Poulsen JR, Clark CJ. 2005. A 12-year phenological record of fruiting: implications for frugivore populations and indicators of climate change. In: Dew JL, Boubli J, editors. *Tropical fruits and frugivores*. New York, NY: Springer Press. p 75–92.
- Clark CW, Mangel M. 1986. The evolutionary advantages of group foraging. *Theoretical Population Biology* 30:45–75.
- Dammhahn M, Kappeler PM. 2009. Females go where the food is: does the socio-ecology model explain variation in social organization of solitary foragers? *Behavioral Ecology and Sociobiology* 63:939–952.
- Dáttilo W, Izzo TJ, Vasconcelos HL, Rico Grat V. 2013a. Strength of the modular patterns in Amazonian symbiotic ant–plant networks. *Arthropod–Plant Interactions* 7:455–461.
- Dáttilo W, Guimarães PR, Izzo TJ. 2013b. Spatial structure of ant–plant mutualistic networks. *Oikos* 122:1643–1648.
- Dáttilo W, Marquitti FMD, Guimarães PR, Izzo TJ. 2014. The structure of ant–plant ecological networks: is abundance enough? *Ecology*. Available online ahead of print: DOI:10.1890/12-1647.1
- Deneubourg JL, Goss S. 1989. Collective patterns and decision-making. *Ethology Ecology & Evolution* 1:295–311.
- Dias PAD. 2002. Alterações na estrutura das relações sociais num grupo de macacos uivadores de manto (*Alouatta palliata mexicana*): estudo dos machos de uma comunidade na Ilha de Agaltepec, Município de Catemaco, Veracruz, México. Dissertation, Universidade Técnica de Lisboa.
- Domjan M. 2009. The principles of learning and behavior. Belmont, CA: Wadsworth Publishing. p 696.
- Felton AM, Felton A, Rumiz DI, et al. 2013. Commercial harvesting of *Ficus* timber—an emerging threat to frugivorous wildlife and sustainable forestry. *Biological Conservation* 159:96–100.
- Garber PA. 2004. New perspectives in primate cognitive ecology. *American Journal of Primatology* 62:133–137.
- Garber PA, Bicca-Marques JC, Azevedo-Lopes MAO. 2009. Primate cognition: integrating social and ecological information in decision-making. In: Garber PA, Estrada A, Bicca-Marques J-C, Heymann E, Strier KB, editors. *South American primates: comparative perspectives in the study of behavior, ecology and conservation*. New York, NY: Springer Press. p 365–385.
- Gemmill A, Gould L. 2008. Microhabitat variation and its effects on dietary composition and intragroup feeding interactions between adult female *Lemur catta* during the dry season at Beza Mahafaly Special Reserve, Southwestern Madagascar. *International Journal of Primatology* 29: 1511–1533.
- Gu B, Schelske CL, Hoyer MV. 1997. Intrapopulation feeding diversity in blue tilapia: evidence from stable-isotope analyses. *Ecology* 78:2263–2266.
- Guimarães PR Jr, Guimarães PR. 2006. Improving the analyses of nestedness for large sets of matrices. *Environmental Modelling & Software* 21:1512–1513.
- Guimerà R, Sales-Pardo M, Amaral LAN. 2004. Modularity from fluctuations in random graphs and complex networks. *Physical Review E* 70:025101.
- Hagen M, Kissiling WD, Rasmussen C, et al. 2012. Biodiversity, species interactions and ecological networks in a fragmented world. *Advances in Ecological Research* 46: 89–210.
- Hanya G, Chapman CA. 2013. Linking feeding ecology and abundance: a review of primate resource limitation. *Ecological Research* 28:183–190.
- Hare B, Kwetuenda S. 2010. Bonobos voluntarily share their own food with others. *Current Biology* 20:230–231.
- Hinde K, Mulligan LA. 2011. Primate milk: proximate mechanisms and ultimate perspectives. *Evolutionary Anthropology* 20:9–23.
- Hinde RA. 1976. Interactions, relationships and social structure. *Man* 11:1–17.
- Inger R, Ruxton GD, Newton J, et al. 2006. Temporal and intrapopulation variation in prey choice of wintering geese determined by stable isotope analysis. *The Journal of Animal Ecology* 75:1190–1200.
- Janson CH, van Schaik CP. 1988. Recognizing the many faces of primate food competition: methods. *Behaviour* 105: 165–186.
- Krause J, Ruxton GD. 2002. *Living in groups*. Oxford, UK: Oxford University Press. 210 p.
- Krishna A, Guimarães PR Jr, Jordano P, Bascompte J. 2008. A neutral-niche theory of nestedness in mutualistic networks. *Oikos* 117:1609–1618.
- Lange D, Dáttilo W, Del-Claro K. 2013. Influence of extrafloral nectary phenology on ant–plant mutualistic networks in a neotropical savanna. *Ecological Entomology* 38:463–469.
- Marquitti FMD, Guimarães PR, Pires MM, Bittencourt LF. 2014. MODULAR: Software for the autonomous computation of modularity in large network sets. *Ecography*. Available online ahead of print: DOI:10.1111/j.1600-0587.2013.00506.x
- Martins EG, Bonato V, Pinheiro HP, Reis SF. 2006. Diet of the gracile mouse opossum (*Gracilinanus microtarsus*) (Didelphimorphia: Didelphidae) in a Brazilian cerrado: patterns of food consumption and intrapopulation variation. *Journal of Zoology* 269:21–28.
- Milton K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *The American Naturalist* 114:362–378.
- Milton K. 1980. *The foraging strategy of howler monkeys. A study in primate economics*. New York, USA: Columbia University Press. 165 p.
- Milton K. 1998. Physiological ecology of howlers (*Alouatta*): energetic and digestive considerations and comparison with Colobinae. *International Journal of Primatology* 19:513–548.
- Mishkin M. 1982. A memory system in the monkey. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 298:85–95.
- O’Gorman EJ, Emmerson MC. 2009. Perturbations to trophic interactions and the stability of complex food webs.

- Proceedings of the National Academy of Sciences of the United States of America 106:13393–13398.
- Olesen JM, Bascompte J, Dupont YL, Jordano P. 2007. The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America* 104:19891–19896.
- Pires MM, Guimaraes PR, Araújo MS, et al. 2011. The nested assembly of individual–resource networks. *The Journal of Animal Ecology* 80:896–903.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria [www document]. Available online at: <http://www.R-project.org> [accessed April 21, 2012].
- Rode KD, Chapman CA, McDowell LR, Stickler C. 2006. Nutritional correlates of population density across habitats and logging intensities in redtail monkeys *Cercopithecus ascanius*. *Biotropica* 38:625–634.
- Rodríguez-Luna E, García-Orduña F, Canales-Espinosa D. 1993. Translocación del mono aullador *Alouatta palliata*: una alternativa conservacionista. In: Estrada A, Rodríguez-Luna E, López-Wilchis R, Coates-Estrada R, editors. *Estudios primatológicos en México*. Xalapa, Mexico: Biblioteca de la Univ. Veracruzana. p 129–177.
- Rothman JM, Chapman CA, van Soest PJ. 2012. Methods in primate nutritional ecology: a user's guide. *International Journal of Primatology* 33:542–566.
- Serio-Silva JC. 1997. Studies of howler monkeys (*Alouatta palliata*) translocated to a neotropical rainforest fragmented. *Laboratory Primate Newsletter* 36:11–14.
- Serio-Silva JC, Rico-Gray V, Hernandez-Salazar LT, Espinosa-Gomez R. 2002. The role of *Ficus* (Moraceae) in the diet and nutrition of a troop of Mexican howler monkeys, *Alouatta palliata mexicana*, released on an island in southern Veracruz, Mexico. *Journal of Tropical Ecology* 18:1–16.
- Shine R, Reed RN, Shetty S, Cogger HG. 2002. Relationships between sexual dimorphism and niche partitioning within a clade of sea-snakes (Laticaudinae). *Oecologia* 133:45–53.
- Simmen B, Taraud L, Marez A, Hladik A. 2014. Leaf chemistry as a predictor of primate biomass and the mediating role of food selection: a case study in a folivorous lemur (*Propithecus verreauxi*). *American Journal of Primatology*. Available online ahead of print: DOI:10.1002/ajp.22249
- Snaith TV, Chapman CA. 2005. Towards an ecological solution to the folivores paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys. *Behavioral Ecology and Sociobiology* 59:185–190.
- Snaith TV, Chapman CA. 2007. Primate group size and interpreting socioecological models: do folivores really play by different rules? *Evolutionary Anthropology* 16:94–106.
- Svanbäck R, Bolnick DI. 2005. Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evolutionary Ecology Research* 7:993–1012.
- Thompson JN. 1982. *Interaction and coevolution*. New York, NY: John Wiley & Sons. 179 p.
- Tinker MT, Guimaraes PR, Novak M, et al. 2012. Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. *Ecology Letters* 15:475–483.
- Vázquez DP, Melián CJ, Williams NM, et al. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116:1120–1127.
- Vázquez DP, Chacoff NP, Cagnolo L. 2009. Evaluating multiple determinants of the structure of mutualistic networks. *Ecology* 90:2039–2046.
- Vickery W, Giraldeau LA, Templeton J, Kramer D, Chapman CA. 1991. Producers, scroungers, and group foraging. *The American Naturalist* 137:847–863.
- Yamagiwa J, Mwanza N. 1994. Day-journey length and daily diet of solitary male gorillas in lowland and highland habitats. *International Journal of Primatology* 15:207–224.
- Youlatos D. 1998. Seasonal variation in the positional behavior of red howling monkeys (*Alouatta seniculus*). *Primates* 39:449–457.