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Research paper

How does a howler monkey *Alouatta pigra* choose what to eat and where to sleep during the day?

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Abstract

How does a howler monkey Alouatta pigra *choose what to eat and where to sleep during the day?* Studies of primate behavior have focused on animals independently of their interactions with their environment, ignoring critically important interactions with plants other than feeding. Black howler monkeys *Alouatta pigra* spend up to 60 % of their diurnal time resting, but structure and mechanisms of monkey-plant interactions associated with resting still need to be better understood. In this study, we assessed how plant characteristics influence howler monkeys' interactions with plants they use for feeding and diurnal resting over three seasons in southeast Mexico. Inter-individual preferences and plant feeding patterns were also examined, and we conducted phenological surveys to determine how availability influences feeding interactions. We found a high diversity of monkey-plant interactions, a nested network (when specialists can only interact with subset of the species generalists interact with) pattern invariant of seasonality, and a higher level of specialization for feeding networks compared to diurnal resting networks. We observed that monkeys preferred large trees for diurnal resting sites and repeatedly selected the same species, resulting in less specialization for resting than feeding. By using an interaction network approach, our study represents a valuable conservation tool for this endangered primate because they highlight the importance of identifying essential species for feeding and diurnal resting.

Key words: Ecological networks, Monkeys, Behavior, Habitat fragmentation, Mexico

Introduction

Quantifying the relationship between primates and fruiting trees shows that these organisms are involved in complex interactions (Chapman and Onderdonk 1998). Monkeys typically depend on plants for two essential interactions: resting and feeding; however, most research focuses only on feeding. Even though howler monkeys can spend more than 60 % of the day resting (Garber and Jelinek 2006, Knopff and Pavelka 2006, Di Fiore and Campbell 2007). Recent studies in primates described how howler monkeys act key agents to disperse the seeds and keep the diversity of several hot spots in the Atlantic Forest of South America (Bufalo et al 2016). Their diet generally varies according to the available food supply, with increased leaf consumption occurring during periods of scarcity. As a result of this high leaf consumption (with limited easily digestible energy), this genus has slower behavior than other primates, with low percentages of time spent traveling between food sources and diurnal rest as their main activity (Stevenson et al 2000). Nonetheless, the structure and mechanisms of monkey-plant interactions associated with resting remain poorly understood and that void leads to two of our main questions: How do the structures of monkey-plant interactions differ concerning feeding and resting, and which factors influence these interactions?

Interactions

These questions can be analyzed using interaction networks, valuable tools for quantifying population-level patterns (Bascompte and Jordano 2008, Pires et al 2011,

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Vidal et al 2013). Network theory allows us to clearly describe patterns of interactions and detect non-random patterns of monkey-resource interactions (Dáttilo et al 2014). This approach also identifies the role of each individual in the environment with all individuals within a group (Benitez-Malvido et al 2016). To our knowledge, only a few studies have quantified monkey-plant interaction networks (Albert et al 2013, Dáttilo et al 2014, Benitez-Malvido et al 2016, Bufalo et al 2016) and only two of these projects used network analysis to answer ecological questions at the population level. Similarly, Benitez-Malvido et al (2016) evaluated the role of inter-individual variation in monkey-plant networks by comparing differences in fragmented and continuous forests and found that the diets of more selective monkeys represent subsets of the diets of other individuals (i.e., a nested pattern of monkey-plant interactions), specifically, the high selectivity of immatures, who fed on a subset of plants eaten by adults. However, the authors did not consider how phenology or tree characteristics influence the architecture of the networks. Moreover, we have limited knowledge of how seasonal changes in the traits of the trees shape the way plants and monkeys interact between them (Allesina 2011, Eklöf et al 2013). However, we know that howler monkeys are strongly influenced by seasonality and fruit availability (Estrada and Coates-Estrada 1985, Chapman 1988, Julliot and Sabatier 1993, Stevenson et al 2000, Pavelka and Knopff 2004). For example, howler monkeys focus their diet exclusively on fruit during the peak season, and this species can spend weeks feeding primarily on fruits (Dias and Rangel-Negrín 2015). Therefore, knowing how and why ecological networks from diurnal rest and feeding sites are organized could improve our understanding of the dynamics of plant-monkey interactions and their role in maintaining ecosystem function.

Although feeding preferences and resting-site selection in howler monkeys have been widely documented, most previous studies have analyzed these behaviors independently or through species-level summaries, implicitly assuming that interactions occur in isolation (Anderson 1998). However, animals simultaneously interact with multiple resources and individuals, generating complex interaction systems whose organization cannot be captured using traditional frequency-based or univariate approaches (Dáttilo et al 2014, Martínez-Falcón et al 2019). Ecological network analysis provides a framework to integrate all individual-resource interactions within a single analytical structure, allowing the detection of emergent properties such as nestedness, specialization, and interaction heterogeneity that arise from the collective behavior of individuals rather than from isolated observations (Benitez-Malvido et al 2016). By explicitly quantifying how individuals share or partition resources, network approaches enable the identification of structural patterns linking behavior, resource availability, and population-level organization (DaRocha et al 2016). Consequently, applying a network perspective does not simply describe what monkeys eat or where they rest, but reveals how interaction patterns are organized across individuals and seasons, offering mechanistic insight into resource use and potential system vulnerability that would remain hidden under traditional analyses.

An additional factor that could influence the network's organization is the intraspecific variation within populations. For individual-resource networks, this variation, in turn, may be translated into the properties of networks that depict interactions among individuals and the food resources they consume (Pires et al 2011). Specific attributes may cause this variation, such as the individual physiological requirements, the ability to reach resources, the need to avoid predation risk, and the differences in resource availability through time and space (Boinski 1988, Chaves et al 2012, Cantor et al 2013). Moreover, an individual's rank preferences for alternative resources likely reflect a complex interaction between resource traits, resource abundance, and the individual's phenotype (Bolnick et al 2002). In this study, we consider these issues using a bipartite network analysis structured with the partitions of plant species and age and sex categories of *A. pigra*. As this genus behaves as a cohesive social unit (Garber and Jelinek 2006), we expect this will be reflected in the network patterns. On the one hand, Chapman studies with the genus *Alouatta* showed inter-population shifts in diet preferences (Chapman and Onderdonk 1998), although the specific items used for feeding are unknown. On the other hand, resting sites protect animals from extreme rainfall, wind, and temperature conditions, and to reduce energetic expenses, primates tend to select high trees with a wide tree crown (Anderson 1998, Seiler et al 2013). The traits that likely influence diurnal resting site selection include tree height, DBH (diameter at breast height), GTB (ground to branching distance), and the diameter of the tree crown.

Here, we used interaction networks as an analytical tool to investigate the difference between feeding and diurnal rest interaction patterns during three seasons with six groups of black howler monkeys *A. pigra* in southeastern Mexico. In these networks, plant species and individuals (age-sex representatives) are depicted as nodes, and their interactions are shown as links describing the use of plants by individuals. Specifically, we postulated that monkey individuals should be more selective (based on their physiological needs) in their choice of plants to eat compared to plants for resting, where the whole group would be expected to rest together. This selective behavior should generate differences in the structural properties of feeding and diurnal rest interaction networks involving black howler monkeys and plants. Moreover, we also postulated that the selection of food resources varies among sex-age categories due to the individual specialization (i.e., non-overlapping diets) previously observed in howler monkeys. Moreover, we evaluated how the phenology and tree characteristics influence the feeding and resting interactions by monkeys, respectively. Our results are a valuable tool for conservation planners because we highlight the importance (how and why) of identifying plant species important for feeding and the species monkeys appear to require for resting during the day in a highly fragmented landscape, where original floodplain forests have undergone severe degradation, losing around 80 % of their original cover due to human activities including livestock areas, farmland and perturbed forest, with the presence of domestic animals like pigs, goats, sheep, cows and dogs (Hernández-Rodríguez et al 2019).

Material and methods

Study area

Fieldwork was conducted in six sites (from 1 to 3 ha) in a fragmented habitat with grassland and forest remnants of evergreen rainforest in southeast Mexico (17° 46' 30.51" N, 91° 29' 49.31" W, 10 m.a.s.l). Each site had one monkey group, and the distance between fragments was approximately two kilometers. The sites had distinct vegetation: one site had secondary vegetation but was protected from tree cutting (SVUC), three areas had secondary vegetation with constant disturbance (e.g., logging and livestock feeding) (SVCD), and two areas had riparian secondary vegetation (RSV). There are three distinct seasons: a rainy season from May to October with an average rainfall of 1,780 mm, a 'nortes' season characterized by strong winds from the North from November to January and an average rainfall of 1,370 mm, and a dry season from February to April with an average rainfall of 570 mm. and involved 648 contact hours.

Data collection - Records of plant-monkey interactions and characteristics of trees and their phenology

We considered feeding interaction every time a monkey ate a plant item (1 min to 1 hr.) diurnal rest longer than 10 minutes. The group size averaged six individuals. We made continuous observations for 1 hour per individual and observed the group for 12 h (06:00 hr. to 18:00 hr.). We switched among age and sex per hour, considering adult females (AF), adult males (AM), juvenile females (JF), juvenile males (JM), infant females (IF), and infant males (IM). Registrations of trophic interactions were estimated in minutes, and food items considered included: young leaves (YL), mature leaves (ML), leave buds (LB), flower bottoms (FB), flowers (FL), immature fruits (IFR) and mature fruits (MFR). We have four measurements to evaluate the trees' characteristics and explain the preferences for diurnal rest interactions: 1. Height (using Nikon® Forestry Pro Laser RangeFinder 10 - 500 Meter, 3 Point Measurement), 2. DBH, 3. GTB (ground to branch distance), 4. Standardized diameter of the crown (SDC), using a tape measure. GTB and SDC are measurements designed for this study. SDC has two dimensions in meters: polar = a; and equatorial = b; being categorized as small (a < 12.9 and b < 11.9 m), medium (a: from 13 to 14.9 m and b: from 12 to 13.9 m), large (a > 15 and b >14 m), to standardize those categories we obtained the previous measurement of trees used for phenology and systematized *in situ* each tree used for resting. These categorical data have been established in several studies of 'roosting' or sleeping trees used by several species of primates for nocturnal rest records (Chapman et al 1989, Liu and Zhao 2004, Teichroeb et al 2012), however we do not, include any data from nocturnal rest.

To quantify the food availability, we chose 40 trees/sites of species reported as part of the usual diet of monkeys in this region (Ramírez-Julián 2010, Aristizabal 2013) and monitored their phenophases for nine months (young leaves, mature leaves, leave buds, flower bottoms, flowers, immature fruits, and mature fruits). Each plant part's abundance was estimated at 0 to 100% at the beginning of each month (García-Vettorazzi et al 2015).

Data Analyses

For each kind of interaction (diurnal rest and feeding), we built two kinds of interaction matrices for each site: a qualitative (presence/absence) and a quantitative matrix (data of interaction intensity or interaction strength) for each season. The matrices were built to compare the pattern and structure for each kind of interaction. We counted all feeding and diurnal resting interactions per species to determine the primary plants used for those activities.

The following parameters were calculated for each period and each activity: nestedness, specialization, diversity of interactions, and links per individual, to characterize the temporal variation and the differences between diurnal rest and feeding in network parameter values. *Nestedness* was calculated with the NODF estimator (Almeida-Neto et al 2008) using ANINHADO software (Guimarães and Guimarães 2006), which is a measure describing the organization of niche breadth in which more nested networks tend to have the highest niche overlap. A network is considered nested if a central core of species (generalists) has many interactions among themselves, peripheral species with few interactions (specialists) interact with subsets of the central core of generalists, and few interactions occur among the specialists (Guimarães and Guimarães 2006, Bascompte and Jordano 2008). Monkey intra-population network analysis followed this premise that the monkeys' diets are selective monkeys and represent subsets of those that consumed a broader diet (Benitez-Malvido et al 2016). *Specialization* (H_2') measures niche segregation between plant species based on the deviation between the absolute number of species interactions and the total number of expected interactions for a network. This index assumes that all species interact with their mutualistic species at the observed rates. *Diversity of interactions* (based on the Shannon diversity index) and *Links per monkey* (average interactions per individual in each site for the season). Network parameters and plots were obtained with the *bipartite* package (Dormann et al 2023) in R-software version 2.08. It is essential to mention that in this research, we considered the same concepts for those four parameters. Still, regarding the concept of intra-population specialization, we replace specialist and generalist species with specialist and generalist individuals. To evaluate the differences between diurnal rest and feeding, we used *t* paired test comparing the mean of the four network parameters (nestedness (NODF), network-level specialization (H_2), diversity of interactions, and links per monkey) per study area in each season. We used a graphical representation of the results through a non-metric multidimensional scaling (NMDS) ordination with a significance analysis of similarity (ANOSIM) to determine if the plant species for feeding were the same for diurnal rest. To carry out the analysis and ordination, the six samplings were ordered by the Bray-Curtis index, implementing a multivariate variance analysis using the distance between matrices (species composition dissimilarities in each sampling), from which probabilistic significance is obtained through 462 permutations (Anderson 2017). For finding temporal (seasonal) influences in those four indices, we compared network parameters among climatic seasons using the

Kruskal-Wallis test where the season is the independent variable and the indices are the dependent variable N = 18 (three-season repetitions, six of each study area) and we performed this procedure separately for each season. We performed NMDS and ANOSIM using the R-software version 2.13.1 and PRIMER- software version 6.

We used generalized linear models (GLM's) to evaluate the relationship between feeding interactions and the phenology of the trees. Every season we did phenological transects in our 6 study sites observing each one of the 160 trees of 31 species with binoculars where we registered the percentage of young leaves, mature leaves, flower bottoms, flowers, immature fruits, mature fruits per tree to be able to calculate an average per species during the season. The percentage of each phenophase per plant species was contrasted that with the number of monkey-plant interactions for that plant species in the three seasons. For each season, we performed different models with no significant correlation between variables: in the rainy season, we used two models with a Gamma error distribution, the first using the variables (young leaves, mature leaves, immature fruits); and the second (mature fruits, flower bottoms, and mature leaves); in *nortes* season we counted data with a Normal error distribution and an identity link function using the variables (young leaves, leave buds, flower bottoms, and immature fruits) and Gamma error distribution and an Identity link function using the variables (mature leaves, flowers, and mature fruits); and in the dry season we counted data with a Normal error distribution and an Identity link function using the variables (young leaves, mature leaves, flowers, and mature fruits) and Gamma error distribution and an Identity link function using the variables (mature leaves, leave buds and immature fruits). We also used GLMs for counting data with a Normal error distribution and an Identity link function to identify which characteristics have the trees with more interactions, contrasting DBH, height, GTB, and the standardized diameter of the crown vs. the number of interactions per tree species. Finally, to find the resource preferences of each age/sex class, we analyzed the percent of feeding items for age/sex class. We complemented this with a correspondence analysis where biplot ordination corresponds to individuals vs. items (minutes). We performed GLM analysis using STATISTICA-software version 7.0 and a Correspondence analyses plot ordination using the R-software version 2.13.1.

Results

We recorded 1,038 interactions of 43 individuals of *A. pigra* (12 adult females, ten adult males, five juvenile males, six juvenile females, seven infant males, and three infant females), with 417 plant individuals used for feeding and 621 for diurnal rest. Thirty plant species were used for feeding and 21 plants spp. for diurnal rest, of 32 different species. Of the 48 networks obtained, only seven exhibited significant nestedness (mean ± SD: 51.27 ± 64.11; range: 19.22-83.33; all $P < 0.05$); however, the six total networks showed a nested pattern (fig. 1).

Feeding and rest interactions

Nineteen plant species were used both for feeding and diurnal rest, and 11 species were used just for feeding. The eight plant species that were used by the primates for feeding during all three seasons were, in order of importance: *Pithecellobium lanceolatum* (Fabaceae), *Maclura tinctorea* (Moraceae), *Haematoxylon campechianum* (Fabaceae), *Albizia leucocaly* (Fabaceae), *Guazuma ulmifolia* (Malvaceae), *Inga edulis* (Fabaceae), *Sabal mexicana* (Arecaceae), and *Syngonium podophyllum* (Araceae). Other plant species fed on represented 24 % of the total records (table 1).

The howler monkeys had diurnal rest interactions with 21 plant species. Nineteen species were used both for feeding and diurnal rest, and two species were just for diurnal rest: *Nectandra salicifolia* and *Bucida buceras*. The five plant species observed in the three seasons for diurnal rest were, in order of importance: *Lysiloma microphyllum*, *Tabebuia rosea*, *Pithecellobium lanceolatum*, *Guazuma ulmifolia*, and *Enterolobium cyclocarpum*. The other plants used for diurnal rest accounted for 11.27 % of the total records (table 1).

Network parameters

The means of nestedness for feeding and diurnal rest interactions are different just in the *nortes* season when the diurnal rest were more nested (59.02 ± 19.12) (mean ± standard deviation) than feeding interactions in the same season (32.68 ± 20.01) (table 2). In the three seasons combined, the specialization values for feeding were significantly more nested than resting interactions (table 2).

The diversity of interactions and the links per individual did not differ among seasons for diurnal rest and feeding interactions. The season did not influence nestedness, specialization, species diversity of interactions, or links per individual (Kruskal-Wallis, feeding: nestedness; H = 1.29, df = 2, $P = 0.52$, diversity of interactions; H = 1.28, df = 2, $P = 0.52$, specialization; H = 3.52, df = 2, $P = 0.17$. diurnal rest: nestedness; H = 1.06, df = 2, $P = 0.93$, diversity of interactions; H = 0.081, df = 2, $P = 0.95$, specialization; H = 0.14, df = 2, $P = 0.17$). The composition of tree communities for feeding and diurnal rest by monkeys were similar in rainy and *nortes*, but not during dry season (rainy: R global = 0.195, $P = 0.05$; *nortes*: R global = 0.251, $P = 0.05$; dry: R global 0.066, $P = 0.28$).

Factors explored to explain feeding and diurnal rest interactions

Feeding interactions were a function of phenological changes in feeding trees. Feeding was related to availability; for rainy season, immature fruits (IFR) and mature fruits (MFR) were significant (GLM IFR: Wald Chi-square = 4.35; $df = 1$; $P = 0.03$; GLM MFR: Wald Chi-square = 4.19; $df = 1$; $P = 0.04$), for *nortes* season leave buds (LB) and mature leaves (ML) were significant (GLM LB: Wald Chi-square = 6.11; $df = 1$; $P = 0.01$; GLM ML: Wald Chi-square = 6.28; $df = 1$; $P = 0.01$) and for dry season young leaves (YL) and leave buds (LB) were significant (GLM YL: Wald Chi-square = 5.62; $df = 1$; $P = 0.01$; GLM LB: Wald Chi-square = 6.96; $df = 1$; $P = 0.008$). Individual diets were mostly folivores for all individuals: 51 %-73 % young leaves, 21 %-12 % mature fruits, 7 %-13 % mature leaves, 8 %-15 % immature fruits, and flowers or floral bottoms, 3 %.

For the characteristics of trees and diurnal rest interactions the principal characteristics influencing monkey

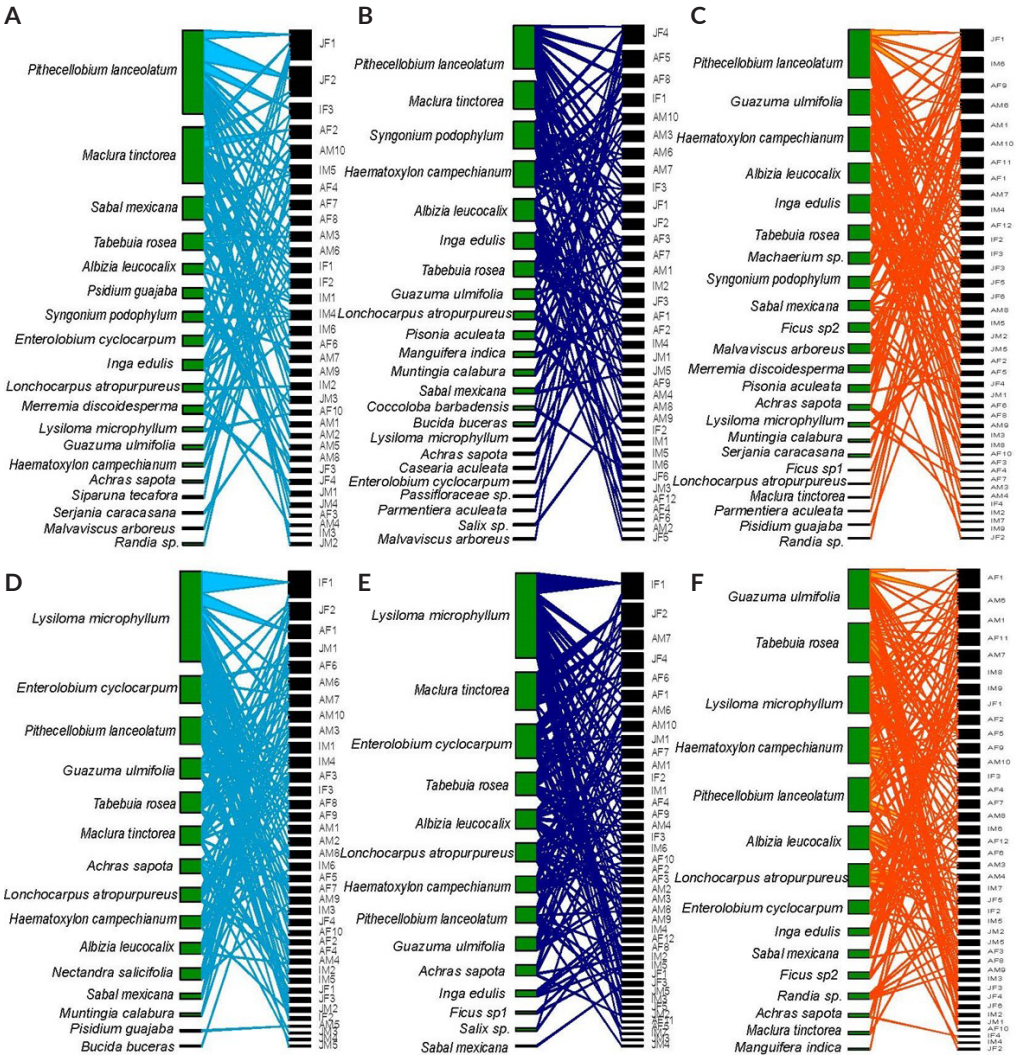

Fig. 1. Interaction Networks between *A. pigra* monkeys (right) and 41 plant species (left). Each black line represents one monkey, and each green line represents one plant species. The kind of interactions are shown for feeding networks in A, B, and C, respectively and for diurnal rest networks in D, E, and F. Lines represent monkey-plant interactions according to seasons in colors: rainy season (light blue), nortes season (dark blue) and dry season (orange). Food webs above are represented as bipartite webs ordered for preferences, where the most consumed species of plants are above the network, with the wider green squares.

tree to choose were the DBH: (GLM: F = 17.03; *P* = 0.022) and the diameter of the crown: (GLM: F = 11.46; *P* < 0.001) (table 3).

Discussion

Using network analysis to examine the associations between vertebrates and their environment is a relatively novel and underused approach. Nevertheless, the application of this framework to the seasonal interactions between howler monkeys and their arboreal resources yields significant insights. We found a high diversity of monkey-plant interactions and a nested network pattern invariant of seasonality. Phenological changes influence feeding interactions, and each individual has their specific preferences of food items but feeds on the same plant species. For diurnal rest, monkeys preferred large trees, and individuals selected the same tree species as the remainder of the group, resulting in less specialization for resting than feeding.

Our results highlight why a network framework provides insights beyond traditional descriptions of diet composition or resting-site use. Previous studies have successfully identified preferred food items and resting trees in howler monkeys, yet such approaches do not reveal how resource use is structured across individuals or how interactions are distributed within the population (Anderson 1998). By analyzing monkey-plant relationships as interaction networks, we were able to demonstrate differences in specialization, nested organization, and resource sharing between feeding and resting behaviors, revealing collective patterns emerging from individual decisions. These structural properties help explain how populations maintain flexibility under seasonal varia-

Table 1. Plant species used for feeding and diurnal rest, percent of interactions and main season for consumption.

Plant species used for feeding (Family)	Number of interactions	Main season of consumption	Total percent of interactions
Pithecellobium lanceolatum (Fabaceae)	94	Dry and rainy	21.9%
Maclura tinctorea (Moraceae)	41	Rainy and nortes	9.8%
Haematoxylon campechianum (Fabaceae)	31	Dry	7.43%
Albizia leucocalyx (Fabaceae)	29	Dry	6.95%
Syngonium podophyllum (Araceae)	28	Nortes	6.71%
Tabebuia rosea (Bignoniaceae)	26	(3 seasons equal)	6.23%
Inga edulis (Fabaceae)	25	Dry	5.9%
Guazuma ulmifolia (Malvaceae)	24	Dry	5.75%
Sabal mexicana (Arecaceae)	21	Rainy	5.03%
24 Other sp.	26	Nortes	6.23%
	32	Rainy	7.6%
	45	Dry	10.79%
Plant species used for diurnal rest	**Number of interactions**	**Main season of usage**	**Total percent of interactions**
Lysiloma microphyllum (Fabaceae)	154	Dry, nortes	24.80%
Tabebuia rosea (Bignoniaceae)	61	Dry	9.82%
Pithecellobium lanceolatum (Fabaceae)	57	Dry	9.18%
Guazuma ulmifolia (Malvaceae)	55	Dry	8.86%
Enterolobium cyclocarpum (Fabaceae)	52	Rainy, nortes	8.37%
Haematoxylon campechianum (Faba-ceae)	48	Dry	7.73%
Maclura tinctorea (Moraceae)	43	Nortes	6.92%
Lonchocarpus atropurpureus (Faba-ceae)	41	Dry	6.60%
Albizia leucocalyx (Fabaceae)	40	Dry	6.44%
11 Other sp.	26	Rainy	4.19%
	18	Nortes	2.90%
	2	Dry	4.19%

tion and allow the identification of key plant species that disproportionately support the interaction system. Therefore, the network approach transforms behavioral observations into a system-level understanding of ecological organization, linking individual choices to population stability and conservation relevance.

As expected, we found that specialization for feeding was higher than resting in all seasons, thus, monkeys were more selective when choosing to feed than resting species. The howler monkeys followed a typical collective behavior (Garber and Jelinek 2006), choosing larger trees for diurnal rest, indicating that more locations could be used for resting than feeding. Nonetheless, individuals made different choices for feeding, likely due to individual needs and preferences (Boinski 1988, Bolnick et al 2002, Pires et al 2011, Benitez-Malvido et al 2016). The monkeys were more selective of feeding sites; thus, diurnal rest networks overlap more species than feeding networks. On the other hand, the difference in specialization and, consequently, nestedness was higher in the dry season. In the dry season, more fruits and young leaves are available (Aristizabal 2013), allowing individuals to be more selective in feeding interactions (specialist). This suggests that high food diversity leads to specializations, and animals are generalists when food availability is low. Our findings support several previous studies where the diet in the *Alouatta* genus is strongly influenced by seasonality, availability, and the species they prefer (Stevenson et al 2000, Pavelka and Knopff 2004, Pinto and Setz 2004, Dias and Rangel-Negrín 2015). However, seasonal changes did not affect the choice of resting trees, as they have a wider range individual trees suitable for resting and their characteristics are mostly independent of climate (DBH, crown diameter, height, GTB (ground to branching)). This is complementary with the similarity analysis (ANOSIM), as in the dry season, the community of trees used for feeding and diurnal rest differ, while in the rainy and *nortes* seasons, the monkeys

Table 2. Comparison of the values obtained for feeding networks and diurnal rest networks in the three seasons for network parameters. N, nestedness; S, specialization; LM, Interaction per monkey; DI, diversity of interactions.

		Feeding	Diurnal rest	t	p
Rainy					
	N	47.69 ± 17.11	55.44 ± 11.9	-1.08	0.33
	S	0.55 ± 0.10	0.28 ± 0.16	2.54	**0.05
	LM	46.2 ± 17.11	55.94 ± 11.48	-0.21	0.84
	DI	2.54 ± 0.58	2.68 ± 0.62	-0.53	0.62
Nortes					
	N	32.68 ± 20.01	59.02 ± 19.12	-3.5	**0.02
	S	0.55 ± 0.07	0.25 ± 0.14	4.49	***0.006
	LM	3.39 ± 1.29	3.32 ± 0.86	0.16	0.87
	DI	2.54 ± 0.56	2.71 ± 0.55	-2.1	0.08
Dry					
	N	47.69 ± 27.56	62.82 ± 16.10	-1.38	0.23
	S	0.41 ± 0.13	0.25 ± 0.14	40.6	***0.0001
	LM	3.39 ± 1.29	3.32 ± 0.86	0.15	0.87
	DI	2.87 ± 0.29	2.90 ± 0.25	0.23	0.83

Table 3. GLM analyses. The DBH and crown diameter are related to daytime resting interactions.

GLM	F	DF	*P*
DBH	17.03	1	**0.0022
Diameter of the crown	11.46	1	**0.001
Height	0.85	1	0.35
GTB	0.76	1	0.38

choose similar trees for feeding and diurnal rest and are thus more generalist. This variation suggests that *A. pigra* is changing its pattern of feeding interactions depending on the season, which agrees with previous studies in the same site (Pozo-Montuy and Serio-Silva 2006).

We also found that feeding interactions vary due to phenological changes (Glander 1981, Brockman and Van Schaik 2005). Some species, like *Maclura tinctoria* and *Guazuma ulmifolia* have fruiting peaks that occur with the rains (Ramírez-Julián 2010, Aristizabal 2013), and the feeding interactions occur at this time. In *nortes* season, mature leaves were selected, probably because other food options were unavailable. We also observe a seasonal effect on the nestedness pattern and specialization of feeding interactions. For instance, dominant nodes in the network analysis symbolize plant species used more for feeding. If those dominant plants were not available, the monkeys would eat a greater variety of species, rendering more nodes to the network and 'spreading out' the interactions, thereby reducing the nestedness in the whole network. We saw this phenomenon in the *nortes* season, where the standard deviation of nestedness decreased significantly for feeding interactions (table 1). Another explanation for the decline in nestedness of feeding interactions in the *nortes* season may be the heavy rains. Rainfall reduced the time the animals spent feeding, explaining day-to-day differences in activity budgets (González-Zamora et al 2011, Giné et al 2012). At this time, the monkeys selected fewer trees for feeding and had more diurnal resting interactions.

We found that certain age/sex classes have preferences for specific items. For instance, immature males had the highest percentage of young leaves (73 % in their interactions). Juvenile females preferred mature fruits, which constituted 21 % of their diet, much high than the percentage for other sex-age classes. This is similar to other individual-based monkey-plant networks (Dáttilo et al 2014, Benitez-Malvido et al 2016), confirming the importance of potential attributes like individual physiological capacities, the ability to search for resources and avoid predators and the differences between habitats in their resource availability through time and space in individual choice (Boinski 1988, Pires et al 2011, Cantor et al 2013).

As expected, we observed howler monkeys prefer large trees for diurnal resting. Anderson (1998) and Seiler et al (2013) showed that primates tend to select tall trees for resting with a wide tree crown to reduce energetic expenditure. Additionally, comparing continuous and fragmented forests emphasized the preference for trees with greater DBH and wider crown for resting reducing the distance to feeding sites. Several studies of sleeping tree selection confirmed our results (Chapman et al 1989, Liu and Zhao 2004, Albert et al 2011, González-Zamora et al 2011, Teichroeb et al 2012). Consequently, we determine that DBH and crown diameter are essential factors when a howler monkey chooses a tree for diurnal rest.

Ecological network analysis allowed us to quantify community-level interactions. It was a starting point for understanding that the entire system shows properties beyond the sum of its parts (emerging properties) (Solé and Bascompte 2006, Jordano et al 2009). Although primates are a very well-studied taxonomic group, to our knowledge, there are just two previous studies that focus specifically on monkey-plant interactions using a network approach (Dáttilo et al 2014, Benitez-Malvido et al 2016), and this is the first study directly assessing the structure of diurnal rest and feeding interactions in a complex network to understand interactions in terms of phenology, inter-individual diets, and traits of trees. We believe it will prove valuable to test these new sampling methods in monkey-plant interactions in other sites, for other species of primates, and in different circumstances to obtain comparable data. Finally, these results represent a valuable tool for conservation, mainly because we identify priority plant species that can be implemented in a restoration plan that considers the importance of crucial feeding species and species used for diurnal resting.

References

Albert A, Savini T, Huynen MC, 2011. Sleeping site selection and presleep behavior in wild pigtailed macaques. *American Journal of Primatology* 73, 1222-1230. DOI: 10.1002/ajp.20993

Albert A, Savini T, Huynen MC, 2013. The role of Macaca spp. (Primates: Cercopithecidae) in seed dispersal networks. *Raffles Bulletin of Zoology* 61, 423-434.

Allesina S, 2011. Predicting trophic relations in ecological networks: a test of the allometric diet breadth model. *Journal of Theoretical Biology* 279, 161-168. DOI: 10.1016/j.jtbi.2010.06.040

Almeida-Neto M, Guimarães P, Guimarães PR, Loyola RD, Ulrich W, 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117, 1227-1239. DOI: 10.1111/j.0030-1299.2008.16644.x

Anderson JR, 1998. Sleep, sleeping sites, and sleep-related activities Awakening to their significance. *American Journal of Primatology* 46, 63-75. DOI: 10.1002/(SICI)1098-2345(1998)46:1<63::AID-AJP5>3.0.CO;2-T

Anderson MJ, 2017. Permutational multivariate analysis of variance (PERMANOVA). *Wiley StatsRef: Statistics Reference Online* 1-15. DOI: 10.1002/9781118445112.stat07841

Aristizabal J, 2013. Estrategias de forrajeo y características nutricionales de la dieta del mono aullador negro (*Alouatta pigra*) en un ambiente fragmentado. Tesis de maestría, Instituto de Ecología. A.C., (INECOL) Xalapa, Veracruz. Mexico.

Bascompte J, Jordano P, 2008. Redes mutualistas de especies. *Investigación y Ciencia* September 50-59.

Benitez-Malvido J, Martínez-Falcón AP, Dáttilo W, González-DiPierro AM, Estrada RL and Traveset A, 2016. The role of sex and age in the architecture of intrapopulation howler monkey-plant networks in continuous and fragmented rain forests. *PeerJ* 4, e1809. DOI: 10.7717/peerj.1809

Boinski S, 1988. Sex differences in the foraging behavior of squirrel monkeys in a seasonal habitat. *Behavioral Ecology and Sociobiology* 23, 177-186. DOI: 10.1007/BF00300352

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML, 2002. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* 161, 1-28. DOI: 10.1086/343878

Brockman DK, Van Schaik CP, 2005. *Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge Studies in Biological and Evolutionary Anthropology*, (Vol. 44). Cambridge and New York: Cambridge University Press.

Bufalo FS, Galetti M, Culot L, 2016. Seed Dispersal by Primates and Implications for the Conservation of a Biodiversity Hotspot, the Atlantic Forest of South America. *International Journal of Primatology* 37, 333-349. DOI: 10.1007/s10764-016-9903-3

Cantor M, Pires MM, Longo GO, Guimarães PR, Setz EZF, 2013. Individual variation in resource use by opossums leading to nested fruit consumption *Oikos* 122, 1085-1093. DOI: 10.1111/j.1600-0706.2012.00070.x

Chapman CA, 1988. Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica *Behaviour* 105, 99-116. DOI: 10.1163/156853988X00467

Chapman CA, Onderdonk DA, 1998. Forests without primates: primate/plant codependency. *American Journal of Primatology* 45, 127-141. DOI: 10.1002/(SICI)1098-2345(1998)45:1<127::AID-AJP9>3.0.CO;2-Y

Chapman CA, Chapman LJ, McLaughlin RL, 1989. Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites *Oecologia* 79, 506-511. DOI: 10.1007/BF00378668

Chaves ÓM, Stoner KE, Arroyo-Rodríguez V, 2012. Differences in diet between spider monkey groups living in forest fragments and continuous forest in Mexico *Biotropica* 44, 105-113. DOI: 10.1111/j.1744-7429.2011.00766.x

Dáttilo W, Serio-Silva JC, Chapman CA, Rico-Gray V, 2014. Highly nested diets in intrapopulation monkey-resource food webs. *American Journal of Primatology* 76, 670-678. DOI: 10.1002/ajp.22261

Di Fiore A, Campbell CJ, 2007. The Atelines: variation in ecology, behavior, and social organization. En: *Primates in perspective*: 155-185 (CJ Campbell, A Fuentes, KC MacKinnon, M Panger, SK Beader Eds). New York: Oxford University Press, Oxford.

Dias PAD, Rangel-Negrín A, 2015. Diets of howler monkeys. En: *Howler Monkeys: Behavior, Ecology and Conservation*: 21-56 (MM Kowalewski, PA Garber, L Cortes-Ortiz, B Urbani, D Youlatos Eds). New York: Springer.

Dormann C, Fruend J, Gruber B, 2023. Package "bipartite": Visualizing bipartite networks and calculating some (ecological) indices, R Package version 2.18. Available online at: https://CRAN.R-project.org/package=bipartite (Accessed on 14 November 2023).

Eklöf A, Jacob U, Kopp J, Bosch J, Castro-Urgal R, Chacoff NP, Dalsgaard B, de Sassi C, Galetti M, Guimaraes PR, Lomascolo SB, Martın-Gonzalez AM, Pizo MA, Rader R, Rodrigo A, Tylianakis JM, Vazquez DP, Allesina S, 2013. The dimensionality of ecological networks. *Ecology Letters* 16, 577-583. DOI: 10.1111/ele.12081

Estrada A, Coates-Estrada R, 1985. A preliminary Study of resource overlap between howling monkeys *Alouatta palliata* and other arboreal mammals in the tropical rain forest in Los Tuxtlas, Mexico. *American Journal of primatology* 9, 27-37. DOI: 10.1002/ajp.1350090104

Garber PA, Jelinek PE, 2006. Travel patterns and spatial mapping in Nicaraguan mantled howler monkeys (*Alouatta palliata*). En: *New Perspectives in the Study of Mesoamerican Primates. Developments in Primatology: Progress and Prospects*: 287-309 (A Estrada, PA Garber, MSM Pavelka, L Luecke Eds). Boston, MA: Springer.

García-Vettorazzi MG, González-Castillo VR, Yaxcal-Ochoa PE, Herrera PJ, 2015. Levantamiento y evaluación de la línea base para el monitoreo de los efectos del cambio climático en la fenología reproductiva de especies vegetales de importancia ecológica en la Reserva de Biosfera Maya. Centro de Estudios Conservacionistas, Facultad de Ciencias Químicas y Farmacia, Universidad de San Carlos de Guatemala. Consejo Nacional de Ciencia y Tecnología. Guatemala.

Giné GAF, Duarte JMB, Motta TCS, Faria D, 2012. Activity, movement, and secretive behavior of a threatened arboreal folivore, the thin-spined porcupine, in the Atlantic Forest of southern Bahia, Brazil. *Journal of Zoology* 286, 131-139. DOI: 10.1111/j.1469-7998.2011.00855.x

Glander KE, 1981. Feeding patterns in mantled howling monkeys. En: *Foraging behavior: Ecological, Ethological, and Psychological Approaches*: 231-257 (A Kamil, TD Sargent Eds). New York: Garland Press.

González-Zamora A, Arroyo-Rodríguez V, Chaves OM, Sánchez-López S, Aureli F, Stoner KE, 2011. Influence of climatic variables, forest type, and condition on activity patterns of geoffroyi's spider monkeys throughout Mesoamerica. *American Journal of Primatology* 73, 1189-1198. DOI: 10.1002/ajp.20989

Guimarães PR, Guimarães P, 2006. Improving the analyses of nestedness for large sets of matrices. *Environmental Modelling and Software* 21, 1512-1513. DOI: 10.1016/j.envsoft.2006.04.002

Hernández-Rodríguez D, Vásquez-Aguilar A, Serio-Silva J, Rebollar E, Azaola A. 2019. Molecular detection of Bifidobacterium spp. in faeces of black howler monkeys (Alouatta pigra). *Journal of Medical Primatology* 48, 99-105. DOI: 10.1111/jmp.12395

Jordano P, Vazquez D, Bascompte J, 2009. Redes complejas de interacciones mutualistas planta-animal. En: *Ecología y Evolución de Interacciones Planta-Animal*: 17-41 (R Medel, MA Aizen, R Zamora Eds). Santiago de Chile: Editorial Universitaria.

Julliot C, Sabatier D, 1993. Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. *International Journal of Primatology* 14, 527-550. DOI: 10.1007/BF02215446

Knopff KH, Pavelka MSM, 2006. Feeding competition and group size in *Alouatta pigra*. *International Journal of Primatology* 27, 1059-1078. DOI: 10.1007/s10764-006-9060-1

Liu ZH, Zhao QK, 2004. Sleeping sites of *Rhinopithecus bieti* at Mt. Fuhe, Yunnan. *Primates* 45, 241-248. DOI: 10.1007/s10329-004-0091-y

Martínez-Falcón AP, Martínez-Adriano CA, Dáttilo W, 2019. Redes complejas como herramientas para estudiar la diversidad de las interacciones ecológicas, La biodiversidad en un mundo cambiante: fundamentos teóricos y metodológicos para su estudio. In: Moreno C, ed. La Biodiversidad En Un Mundo Cambiante: Fundamentos Teóricos Y Metodológicos Para Su Estudio. Ciudad de México: Universidad Autónoma del Estado de Hidalgo/Libermex.

Pavelka MSM, Knopff KH, 2004. Diet and activity in black howler monkeys (*Alouatta pigra*) in southern Belize: Does degree of frugivory influence activity level? *Primates* 45, 105-111. DOI: 10.1007/s10329-003-0072-6

Pinto LP, Setz EZ, 2004. Diet of *Alouatta belzebul discolor* in an Amazonian rain forest of Northern Mato Grosso State, Brazil. *International Journal of Primatology* 25, 1197-1211. DOI: 10.1023/B:IJOP.0000043958.75534.7f

Pires MM, Guimarães PR, Araújo MS, Giaretta AA, Costa JCL, dos Reis SF, 2011. The nested assembly of individual-resource networks. *Journal of Animal Ecology* 80, 896-903. DOI: 10.1111/j.1365-2656.2011.01818.x

Pozo-Montuy G, Serio-Silva JC, 2006. Comportamiento alimentario de monos aulladores negros (*Alouatta pigra* Lawrence, Cebidae) en hábitat fragmentado en Balancán, Tabasco, México. *Acta Zoologica Mexicana* 22, 53-66. DOI: 10.21829/azm.2006.2232023

Ramírez-Julián R, 2010. *Respuestas conductuales de monos aulladores negros Alouatta pigra, viviendo en remanentes de vegetación entre pastizales, Balancán, Tabasco, México*. Tesis de maestría, Instituto de Ecología. A.C., (INECOL), Xalapa, Veracruz. México.

DaRocha WD, Neves FS, Dáttilo W, Delabie JH, 2016. Epiphytic bromeliads as key components for maintenance of ant diversity and ant-bromeliad interactions in agroforestry system canopies. *Forest*

Ecology and Management 372, 128-136.
Seiler M, Holderied M, Schwitzer C, 2013. Effects of Habitat Alteration on Resting Behaviour of the Sahamalaza Sportive Lemur in Northwest Madagascar. En: *Primates in Fragments: Complexity and Resilience*: 259-271 (Marsh LK, CA Chapman Eds). Berlin: Springer-Verlag Berlin.
Solé RV, Bascompte J, 2006. *Self-Organization in Complex Ecosystems.* En: Serie: Monographs in Population Biology -Vol. 42: 384 (Levin SA, RM Pringle, CE Tarnita Eds). Princeton University Press.
Stevenson PR, Quiñones MJ, Ahumada J, 2000. Influence of fruit availability on ecological overlap among four neotropical primates at Tinigua National Park, Colombia. *Biotropica* 32, 533-544. DOI: 10.1111/j.1744-7429.2000.tb00499.x
Teichroeb JA, Holmes TD, Sicotte P, 2012. Use of sleeping trees by ursine colobus monkeys (*Colobus vellerosus*) demonstrates the importance of nearby food. *Primates* 53, 287-296. DOI: 10.1007/s10329-012-0299-1
Vidal MM, Pires MM, Guimarães PR, 2013. Large vertebrates as the missing components of seed-dispersal networks. *Biological Conservation* 163, 42-48. DOI: 10.1016/j.biocon.2013.03.025

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Author contributions
NX Sánchez-Garzón: experimental work, formal analysis, manuscript writing, review, and editing; **W Dáttilo:** experimental work, methodology, formal analysis; **CA Chapman:** conceptualization, methodological supervision, experimental design, formal analysis, manuscript writing; **JC Serio-Silva:** conceptualization, methodological supervision, experimental design, supervision, review, and editing.

Conflicts of interest
The author(s) declare no potential conflicts of interest with respect to the research, authorship, or publication of this article.

Ethics statement
All necessary permits were obtained, and our research was conducted with the approval of the Graduate Program Academic Committee of Instituto de Ecología AC (INECOL). Behavioral sampling was obtained by permit number [SEMARNAT: SGPA/DGVS/05938/08] provided by Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT), and we follow the International Primatological Society ethical guidelines for the ethical treatment of non-human primates.

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