Quantifying Primate Food Distribution and Abundance for Socioecological Studies: An Objective Consumer-centered Method

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Abstract Food abundance and distribution have played a central role in the conceptual theory of primate socioecology. This theory predicts that agonistic (contest) competition should occur when food is distributed in discrete, defensible patches; in contrast, when food sources are distributed uniformly or randomly, nonagonistic (scramble) competition is expected. Primatologists usually measure resource density and patchiness from a botanical perspective, without an explicit link to the biology of the animal being studied. Such an approach may be irrelevant to how the animals view the dispersion of resources. For studies related to feeding competition, we suggest the use of a method that provides a consumer-based index of food distribution. We then describe such an approach and apply it to understand agonistic behavior in white-faced capuchins (*Cebus capucinus*), at Lomas Barbudal. Instead of choosing sample plots at random, we use each actual feeding tree of a group as the center of a sample plot and we use the monkey species' average group spread as the sampling area. This focal tree method allows us to evaluate the resource availability both within and outside of the feeding tree during a particular feeding bout. To summarize the spatial distribution of food at the level of a foraging group, we define and use an extension of Lloyd's Dispersion Index, Lloyd's Extended Index (LEI), designed to allow the inclusion of resources of diverse sizes and species in a single measure. We evaluate if LEI can be used to predict the frequency of aggression, if changing the area of the plot alters these results, and if calculating LEI based on fruit abundance or fruit biomass better predicts the frequency of aggression in this population of capuchins. In support of socio-ecological predictions, our results show that the frequency of agonism in a focal tree

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declines as LEI increases. This relationship is significant when LEI is calculated using a 20-m plot size and weighting tree size by fruit counts, but not when using larger plot sizes, unweighted tree counts, or weighting by fruit biomass. Our approach demonstrates the importance of carefully considering plot size and different measures of food availability when testing socioecological models relating resource distribution and quality to aggression in nonhuman primates.

Introduction

The study of primate socioecology assumes that most social behavior is influenced by an animal's ecological conditions. Socioecological theory assumes that resources that are spatially clumped are more worth defending. If resources limit reproductive success and can be defended, intragroup contest competition is expected and selection should favor the formation of formal dominance hierarchies and potentially, nepotistic coalitions (Isbell 1991; Koenig 2002; Sterck *et al.* 1997; van Schaik 1989). Thus, the distribution of food resources, often referred to as patchiness, is one of the many variables proposed to explain patterns of agonism in primates.

In the ecological literature, the concept of patchiness has a simple meaning (Krebs 1999; Stephens and Krebs 1986). Individuals of a given species are clumped (underdispersed) if they have more conspecific neighbors than would be expected if the locations of neighbors were randomly chosen within the study site. They are evenly distributed (overdispersed) if they have fewer neighbors than expected. The difficulty is applying this concept to food sources in a way that is relevant to explaining resource defense by animals. Should patchiness be measured using the individual tree, the spread of the foraging group, individual food items, or some animal-dependent other measure?

Various studies focusing on the effect of food resource patchiness on aggression have defined food dispersion quite differently, making cross-study comparisons difficult. For example, Shopland (1987, p. 151) defined a resource as clumped "if it was distributed in patches that could accommodate several baboons but not the whole group, and within which the density of food units is high." Isbell *et al.* (1998) defined clumped foods as those that are monopolizable by dominants, quantified as the dominant individuals obtaining more food per resource than do lower ranking individuals. Pruetz and Isbell (2000) defined a patch as an area in which a monkey could move and feed continuously and measured patchiness using both a sample point and a plot system in an area based on the size of the monkey's home range. Whitten (1983) and many others have used standard botanical methods to derive quantitative indexes of patchiness of individual trees for various species of primate foods.

This discrepancy in definitions has led to consequent confusion as to the role food resources play in primate social behavior. For example, increased agonism has been associated with food resources that are scarce (Gore 1993; Hanya 2009; Janson 1985a,b, 1986, 1988a,b; Vogel and Janson 2007), abundant (Hall 1963; Southwick

1967; Rosenblum *et al.* 1969), more clumped (Barton and Whiten 1993; Koenig *et al.* 1998; Southwick *et al.* 1976; van Schaik and van Noordwijk 1988; Whitten 1983), or less clumped (Gore 1993). These discrepancies may be present because different authors choose different units for analysis (food items vs. food trees), they employ different methods to assess patchiness, or because the scale that was used to measure the availability of resources was not relevant to how the feeding monkeys perceive them (See Isbell *et al.* 1998; Koenig and Borries 2004 for detailed discussions).

Often, researchers have taken a botanical approach to measure the patchiness of resources used by primates without necessarily taking into account the behavior of the focal species (reviewed in Vogel 2004). Such methods, including both individual-based methods (Cottam and Curtis 1956; Shopland 1987) and plot-based methods (Doran *et al.* 2002; Janson 1987; Kinnaird 1992; McFarland-Symington 1988; Nunes 1995; Robinson 1986), may be irrelevant for studying intraspecific food competition because the plot size or foraging scale chosen may not be biologically meaningful to the species under investigation. In addition, there is often a temporal mismatch between when the plots are monitored and the occurrence of the aggressive interactions (Vogel and Janson 2007). Although some researchers have addressed the former issue by modifying plot sizes to scales that are relevant to the species under investigation (Janson 1987; Koenig *et al.* 1998), few have taken into account temporal and spatial scales of food availability when examining the ecological basis of aggression (*cf.* Chapman *et al.* 1995; Isbell and Enstam 2002; Isbell *et al.* 1998; Janson and Vogel 2006; Pruetz and Isbell 2000; Saito 1996; Vogel 2005; Vogel and Janson 2007). To deal with the problem of temporal mismatch between behavioral and ecological observations in socioecological studies of agonism, we employed the focal tree method (Vogel 2005; Vogel and Janson 2007; Vogel *et al.* 2007). Because a more appropriate spatial scale of patchiness is needed, we define and apply here a consumer-oriented index of resource availability, Lloyd's Extended Index (LEI), that can be compared across studies intended to measure the effect of food resource distribution, e.g., spatial dispersion, and abundance, e.g., biomass or quantity of food, on primate social behavior (Vogel 2004; Vogel and Dominy 2010). Unlike the traditionally used dispersion indices applied to plot-based methods, e.g., Morisitas's Index (Morisita 1959), our method uses the feeding tree as the basis of the sampling plot and thus does not consider empty plots as meaningful data in calculating dispersion. The benefits of using LEI instead of the original index proposed by Lloyd (1967) is that our extended index incorporates food tree qualities into Lloyd's patchiness index, and thus a small or unproductive food tree is not considered equally valuable as a large or productive one.

Before discussing this index, one must consider under what conditions aggression is expected to occur among gregarious foraging animals (Vahl *et al.* 2007). This question has been addressed in producer-scrounger models of foragers employing hawk-dove strategies (DuBois and Giraldeau 2003; DuBois *et al.* 2003). They predict that aggressive contests are more likely 1) when feeding sites contain many items (because scroungers are more likely to show up the longer the producer feeds at a site), and 2) when the density of feeding sites decreases (because each site has a higher value given that fewer alternative feeding sites would be available). Although these models make assumptions that are not entirely consistent with the more flexible dominance-structured kleptoparasitism usually

found in primates (Di Bitetti and Janson 2001), our data on brown capuchins (*Cebus apella*) and white-faced capuchins (*Cebus capucinus*) concur with these predictions (Janson 1985b, 1986, 1987; Vogel and Janson 2007; Vogel *et al.* 2007). Most tests of the effect of resource distribution on agonism in captive or semi-free-ranging animals use resources of constant nutritional quality. However, in the wild, food quality will vary across sites both within and between species (Chapman *et al.* 2003). If a consumer has a choice to consume, and contest access to, many food species during a single foraging bout, then food availability should be measured across all available food species, not within each food species separately. Thus, we include all plant food resources available to the focal individuals in a focal tree sample in our calculation of resource distribution. However, it is also important to recognize that certain tree species may be characterized by higher rates of aggression, presumably because the resources in these trees have greater value to the foraging monkeys relative to the alternatives available nearby. Our studies on *Cebus apella* and *C. capucinus* support this finding (Janson 1988a; Vogel 2005; Vogel and Janson 2007), and therefore we examine the distribution of resources on a species by species basis. Further, availability must be assessed only in the area over which a foraging individual will travel to use them. Although this area is typically not known, for social foragers it probably is reasonably approximated by the spatial spread of the foraging group (Vogel and Janson 2007), as moving further away from the group may be associated with increased costs including increased risk of predation and intergroup aggression.

Our purpose here is to define an index of dispersion, LEI, that takes into account the variation in richness —food abundance and distribution— of the available resources. We then apply this index to data from Costa Rican *Cebus capucinus* to test whether LEI can be used to predict the frequency of food-related aggression in this species. If the spatial distribution and biomass of fruit are important, then a decrease in clumping should result in a decrease in the amount of aggression within a given feeding tree. This trend is predicted because as the availability of alternative resources increases outside of the focal tree, group members can spread out among these resources, avoiding the costs associated with aggression (Vogel and Janson 2007). Using this method, as the amount of available biomass outside of the focal tree increases (LEI increases), the frequency of aggression within the focal tree was predicted to decrease.

Methods

Study Site

E. R. Vogel studied *Cebus capucinus* in Lomas Barbudal Biological Reserve, the surrounding Instituto para Desarollo Agricultura Property, and the adjacent Finca El Pelón de la Bajura. Lomas Barbudal Biological Reserve, hereafter referred to as Lomas, is a 2279-ha reserve located in the northwest of Costa Rica, in Guanacaste Province (10°30′N and 85°22′W). The forest of Lomas is generally classified as a tropical deciduous forest. More than 200 tree species have been identified in the reserve (Frankie, *unpubl. data*), 120 of were used for food by the monkeys during the study period (Vogel 2004, 2005; Vogel and Janson 2007).

Subjects

Cebus capucinus are primarily arboreal monkeys that live in mixed-sex cohesive groups of 15–33 individuals with a male-to-female ratio close to 1:2.3 (Fedigan 1984; Fedigan *et al.* 1985; Oppenheimer 1968; Vogel 2005). All individuals, both males and females, formed a linear dominance ranking system in the 3 focal groups (Perry 1996, 1997; Vogel 2005; Vogel and Janson 2007; Vogel *et al.* 2007), and adult males are dominant over females, except for the alpha female in some cases (Fedigan 1993; Perry 1997; Vogel 2005). E. R. Vogel observed 3 groups of *Cebus capucinus*, composed of 29–31 individuals, from December 1999 until August 2002. Data collection for this study started in December 2000 and ended July 2002. E. R. Vogel studied the AA and RR groups from December 2000 to August 2001, and the QQ group from December 2001 to August 2002, for a total of 4134 contact hours. Home ranges of the focal groups during the study period extended over 2.76–4.40 km² and overlapped from 0.25 to 0.42 km² with those of other groups of *Cebus capucinus* (Vogel 2004). Most data collection took place during the dry season, although it did carry over a few months into the rainy season.

Focal Tree Method

We developed the the focal tree method to measure the costs and benefits of food related aggression within fruiting trees in groups of white-face capuchins. This method is described in detail elsewhere (Janson and Vogel 2006; Vogel 2005; Vogel and Janson 2007); however, we briefly summarize it here. Two or more observers are required for this method. One observer, the primary observer, moved to the front of the group and stood under a feeding tree that the group was likely to visit, particularly ones used in the recent past. The primary observer recorded the time and identification of first arrival, each successive arrival, and time and identification of each departing monkey from the tree. The secondary observer recorded the number, identification, activity, and relative position of all monkeys in the tree at 2.5-min intervals. If there were not too many individuals feeding in the tree, the primary observer also collected these data. At the time of an aggressive interaction, the number and identity of all monkeys within the feeding tree are known. We collected data until the last group member left the tree.

At the time of an aggressive interaction, the primary observer recorded the individuals involved and the proximity of all visible monkeys in the tree to the interacting individuals. The primary observer recorded data on who won the interaction, if the aggressor(s) started feeding at the site of the interaction, and continued recording data on all arrivals and departures. The secondary observer followed the displaced monkey and noted the distance traveled from the focal tree and the time that it resumed feeding (minutes lost feeding; Janson 1985a; Vogel and Janson 2007).

Minutes lost feeding is one estimate of the opportunity cost of contesting access to a feeding tree (Janson 1985a). A measure of the opportunity cost that does not rely on the behavior of the displaced monkey is based on the availability of alternative food trees outside a focal feeding tree. For each focal tree, we recorded all alternative resources used by the monkeys at that time of year that lie within their

average group spread of the focal tree. In this study, we determined average group spread to be *ca.* 0.5 ha for all focal groups; thus we recorded all trees ≤40 m of the focal tree (Vogel and Janson 2007). For each alternative resource we measured the following variables: fruit crop size and the distance and direction of the alternative resource to the focal tree. We located alternative feeding trees by splitting the circle surrounding the focal tree into quarters and systematically moving through each of the 4 areas starting at the 0–90° quarter. We estimated fruit crop size of individual trees by measuring diameter at breast height (DBH) and crown volume using the equation for an ellipsoid (Chapman *et al.* 1992; Zhang and Wang 1995). In addition, we visually estimated the fruit crop using binoculars, according to the following categories, which follow a logarithmic scale: 1=1–9 fruits, 2=10–99, 3=100–999, 4= 1000–9999, 5=10,000–99,999 and 6 = >999,999 (Janson and Chapman 1999; Stevenson *et al.* 1998). For large trees with many small fruits that were difficult to count, we used an additional method of estimation. We selected 5 1-m^3 areas of the crown on an *ad libitum* basis, spreading the samples throughout the tree crown, and then we counted the number of fruits within this area (Chapman *et al.* 1992). We calculated the mean of these counts and multiplied the mean by the crown volume. Finally, for trees with few large fruits, we simply counted the number of fruits in the tree.

Because it is too difficult to gather the ecological data while taking behavioral observations, we marked the focal tree during a feeding bout, and the following day one observer, in this case the same throughout the entire study, recorded the alternative resource tree data. To calculate grams of dry pulp-mass/fruit, we collected fruit samples for all fruit items consumed by the monkeys. We collected only fruits that were similar in size and maturation stage to fruits selected by the capuchins during the feeding bout. We weighed all samples, divided them into components (seed, husk, and pulp), weighed them again, and then dried the samples until they maintained a constant weight (Hladik 1977). For all species, we collected ≥2 samples for a total of 200 samples.

We quantified resource dispersion using LEI as follows:

$$LEI = \frac{\sum_j \sum_i \left(s_{ij} \sum_{k \neq i} s_{kj} \right)}{\sum_j \sum_i s_{ij}} * \frac{n}{\sum_j \sum_i s_{ij}}$$

where s_{ij} = size of the ith food tree in the jth plot, k = is an index of all potential food trees other than the focal tree within a plot, and n = number of quadrats or plots. Any constant scaling factor, e.g., using m instead of cm, or joules instead of calories, applied to all s_{ij} leaves the index unchanged. The first term in the equation is the equivalent to Lloyd's index of crowding. The part in parentheses sums the amount of food available in all food trees outside of each potential feeding tree in a plot, then weights this alternative food availability by the food available in the potential feeding tree. The purpose is to characterize how much alternative food is available per unit of food available in a focal tree; small focal trees should count less toward an evaluation of overall availability of alternative foods because small focal trees necessarily provide less food and feeding time to the focal individuals. We summed

the term in parentheses for all potential focal trees in the plot, then summed across all plots, and finally divided by the total size of all focal trees to produce an average alternative food availability, in absolute size units, per unit of food available in a focal tree per plot. Alternative food trees in LEI explicitly include all food species, not just trees of the same species as the focal tree. Because the average alternative food availability would increase simply with greater average food density per plot, the second term in the formula corrects for this effect by dividing the first term by the mean food density per plot. In addition, food tree size could mean physical size, i.e., a correlate of productivity (Chapman *et al.* 1992); actual or estimated edible biomass of food; or nutritional value, i.e., energy content or mass of a particular nutrient. If s_{ij} is defined to be 1.0 for all individuals, then tree productivity is removed from the calculation and LEI yields precisely the same result as Lloyd's index of patchiness, which is analogous to more traditional measures of clumping such as Morisita's index (Morisita 1959) when applied to food sources of all species.

Lloyd's index, whether extended or not, has a scale from 0 —perfectly uniform dispersion wherein each focal tree is surrounded by no alternative neighbors— to potentially near infinity —clumped, wherein each focal tree occurs in a single plot with all the other fruiting trees of all species in the population. The regular Lloyd's index (LI) reaches a value of 1.0 when individual trees are randomly dispersed across plots. For the LEI, it is not clear what random means, as individual units of size —biomass, fruit numbers, protein concentration, DBH, or other scaling— are not independent of each other. However, the interpretation of LEI remains the same as the regular index: it is the amount of neighboring size units per average resource individual per plot, divided by the level expected if dispersion were random. Thus, an LEI of 2.5 would indicate that the summed productivity or size of neighboring individuals per focal plant per plot is 2.5 times that expected if productivity or size were randomly divided across all plots.

Data Analyses

We calculated LI and LEI for a total of 646 focal trees from 35 tree species (Table I). We calculated LEI from all alternative resources for each species using either fruit abundance (FC) or fruit biomass (FM) as a proxy for tree productivity (s_{ij}). We then compared these 2 measurements to determine which one best predicts frequency of aggression in *Cebus capucinus*. For comparison, we also calculated LI, which weights all alternative trees equally regardless of fruit abundance. We chose 3 different plot areas for comparison to test how sensitive LEI is to differences in group spread: 0.5 ha (radius of 40 m), which is the average group spread for *Cebus capucinus* in these focal groups (Vogel 2004), 0.283 ha (radius of 30 m), and 0.125 ha (radius of 20 m). Thus, we used the same focal plots for all calculations, but for the smaller areas we included only the alternative trees that fell ≤30 or 20 m of the focal tree.

For our analyses, we used a Poisson Generalized Linear Model (GdLM) with a logarithmic link function. This type of linear model is more flexible than conventional General Linear Models (GLM) in that it allows the dependent variable to possess a distribution other than the Normal distribution and to be linked as a nonlinear function of a linear combination of the independent variables. We applied

Table I Number of plots/focal species and average number of alternative trees outside of the focal tree for all species used in the analysis of the predicting the amount of aggression from LEI

Focal tree species	Focal tree species code	Total number of focal tree plots			Mean number of alternative trees/plot		
		r=40 m	r=30 m	r=20 m	r=40 m	r=30 m	r=20 m
Anacardium excelsum	AE	4	3	3	3.75	3.33	1.33
A. occidentalis	AO	62	62	62	14.84	12.56	7.89
Ardisia revoluta	AR	14	14	12	8.21	5.86	5.67
Brosimum alicastrum	BA	3	3	3	2.33	2.33	2.33
Bursera simaruba	BS	52	46	42	4.83	3.89	2.31
Curatella americana	CA	9	8	9	10.33	8.88	5.00
Cocolobo sp.	CO	7	7	6	3.71	3.00	2.33
Casearia slyvestris	CS	2	2	1	3.00	2.50	2.00
Diospyros nicaraguensis	DN	2	1	1	4.50	3.00	2.00
Erthroxylum havanense	EH	3	3	2	8.00	7.33	7.00
Ficus sp.	FI	23	23	22	2.43	1.91	1.27
Genipa americana	GA	31	30	23	2.87	2.40	1.30
Garcinia edulis	GE	9	9	9	3.22	2.67	1.89
Guazuma ulmifolia	GU	4	4	4	6.00	5.25	3.25
Inga vera	IV	5	5	5	2.80	2.80	2.40
Spondias purpurea	JO	7	7	7	5.86	3.00	1.29
Luehea speciosa	LS	33	29	29	7.61	6.17	2.97
Miconia argentea	MA	6	6	4	4.67	3.33	3.00
Mangifera indica	MG	87	86	70	3.84	2.90	2.04
Muntingia calabura	MU	30	18	18	5.57	6.39	3.44
Byrsonima crassifolia	NA	34	32	30	4.15	3.75	2.47
Quercus oleoides	OK	2	2	2	5.00	3.00	1.00
Prockia crucis	PC	8	5	5	5.00	6.00	4.20
Sterculia apetala	PN	5	4	4	2.00	1.75	1.25
Cochlospermum vitifolium	PO	7	6	6	5.71	6.50	4.83
Doliocarpus dentatus	RB	13	13	12	3.92	3.00	2.17
Randia subcordata	RS	2	2	2	12.00	9.00	6.50
Sciadodendron excelsum	SE	20	18	16	1.55	1.56	1.13
Simaruba glauca	SG	17	15	14	4.65	3.73	2.93
Casearia arguta	SQ	7	7	7	3.71	3.43	3.14
Sloanea terniflora	ST	111	105	88	3.63	2.68	1.74
Tabebuea ochracea	TO	4	4	4	9.25	7.75	6.00
Psychotria pubescens	UR	4	4	4	7.00	3.75	2.75
Ximenia americana	XA	10	10	10	8.50	6.60	4.00

We calculated LEI for 3 different plot size (radius of 20, 30, and 40 m) for each focal tree species.

the Poisson model because the dependent variable, the number of aggressive interactions, had a Poisson distribution (Vogel and Janson 2007). We used the logarithmic link function to allow for possible nonlinearities in the relationship of agonism to the independent variables. For all of the statistical analyses, we controlled for the duration of the feeding bout and the average number of individuals in the focal tree by including these variables in the GdLM, as both of these variables

predict the frequency of aggression in this species (Vogel and Janson 2007). We used a total of 9 models (3 measures of food tree dispersion at each of 3 plot sizes). We applied a Bonferroni correction to the results of the 9 tests to account for multiple comparisons. In addition, to evaluate the relative power of the different measures of LI and LEI, we performed a global test with all 3 measures entered into a single model.

In calculations of LEI using fruit biomass, a single exceptionally productive tree can strongly influence the value for the entire species, producing an LEI that does not represent the trend for most focal trees of that species. We excluded any tree from the calculation of the LEI for a given species if it resulted in the index becoming an outlier relative to all other species' LEI (using this criterion resulted in excluding 1 focal tree in the sample). Because we examined the relationship between the amount of aggression and LEI/LI in different tree species instead of variation in aggression among feeding trees regardless of species (Vogel and Janson 2007), different species necessarily contributed different sample sizes of focal trees, depending on the seasonal diet of the focal population. Therefore, we weighted each tree species in the analyses by the total number of plots in our sample for that species, as data values —LEI, frequency of aggression— should be estimated more reliably for species with more focal tree follows. We used a log transformation for all independent variables except the log-scaled fruit abundance. We consider here only aspects of alternative resource abundance, although other measures —minutes lost feeding by displaced individual, distances to alternative resources, energy gain rate and hunger levels— may be important and can be included in the regression analysis (Vogel 2004; Vogel and Janson 2007; Vogel et al. 2007). We conducted all statistical procedures in JMP-SAS 8.0®. All probability levels are 2-tailed and we set significance for all tests at $\alpha \leq 0.05$.

Results

The LI and LEI values for the most common tree species used by this population of *Cebus capucinus* are given in Table II. For all plot sizes and both weighting methods (fruit count vs. biomass), LEIs ranged from very even (nearly 0.0) to markedly clumped (values≥2.0).

For a given tree species, LEI could vary markedly depending on the plot size used, although there was not a clear pattern across species (Fig. 1). For instance, for *Sloanea terniflora,* LEI weighted by fruit count ranged from 1.5 to 0.49 depending on the size of the plot used, whereas for *Anacardium occidentalis* plot size did not affect LEI except at the smallest plot size (Fig. 1). Similarly, there were sometimes large differences between LI and LEI weighted by either fruit count or mass for a given tree species. In the case of *Sloanea terniflora*, LI results in a random distribution while LEI weighted by fruit mass results in a more clumped distribution for a plot size of 0.283 ha (Fig. 2). Factors affecting the variation shown in Figs. 1 and 2 are 1) the diameter of the plot relative to the crown size of the focal tree (small plots with large trees will contain few other potential food trees), 2) different species-typical tendencies for trees to clump near each other in plots, and 3) sometimes large species differences in the numbers or mass of fruits per tree. For instance, there is a marked difference in LEI for *Sloanea terniflora* depending on whether fruit count or

Table II LEI and LI calculated for all tree species using 3 different sized plots

Species	Radius = 40			Radius = 30			Radius = 20		
	LI	LEI-FC	LEI-FM	LI	LEI-FC	LEI-FM	LI	LEI-FC	LEI-FM
AE	0.924	0.194	0.217	2.340	0.228	0.058	0.375	0.122	0.010
AO	1.076	0.001	0.009	1.086	0.001	0.008	1.213	0.108	0.438
AR	1.148	0.035	0.001	1.083	0.014	0.039	1.054	1.075	0.001
BA	0.735	0.824	0.824	0.735	0.824	0.824	0.735	0.824	0.824
BS	2.559	0.932	0.948	2.531	1.091	1.208	1.830	1.084	0.589
CA	2.054	1.893	1.127	1.829	1.504	0.893	2.072	1.337	0.138
CO	0.953	0.838	0.792	0.889	0.361	0.643	0.918	0.017	0.470
CS	0.667	1.028	0.070	0.640	0.374	0.014	0.250	0.238	0.238
DN	0.889	0.088	0.058	0.667	0.374	0.460	0.500	0.498	0.498
EH	1.236	1.243	1.233	1.322	1.333	1.326	0.939	1.052	0.741
FI	2.294	0.987	0.653	2.450	1.195	1.381	1.827	0.376	0.897
GA	1.502	1.511	3.314	1.436	1.498	3.249	0.474	0.060	0.803
GE	0.827	0.085	0.097	0.851	0.015	0.052	0.633	0.004	0.012
GU	1.035	1.194	0.735	1.052	1.231	0.623	0.994	0.646	0.910
IV	1.319	0.402	0.642	1.319	0.402	0.642	1.400	0.407	0.582
JO	0.973	0.519	0.222	0.762	0.538	0.543	0.346	1.334	1.334
LS	1.478	2.893	8.633	1.598	2.109	10.551	1.307	1.708	0.917
MA	0.857	0.471	0.001	0.789	0.448	0.001	0.778	0.311	0.000
MG	1.299	1.947	2.333	1.303	1.848	2.330	1.012	1.654	1.952
MU	1.470	0.826	1.616	1.368	0.752	1.127	1.016	0.386	1.632
NA	1.080	2.845	2.835	1.051	2.529	2.534	1.298	2.660	2.656
OK	0.790	0.685	0.717	0.778	0.461	0.444	0.000	0.000	0.000
PC	1.463	3.692	3.692	1.620	2.511	2.511	1.468	2.689	2.689
PN	0.864	0.613	1.700	0.889	0.669	1.754	0.349	0.037	0.022
PO	1.290	0.000	0.142	1.271	0.000	0.141	1.156	0.000	0.082
RB	1.050	0.895	0.620	1.178	1.301	2.060	1.000	1.408	2.069
RS	0.924	0.676	0.462	0.901	0.384	0.281	0.994	1.059	0.731
SE	0.832	0.122	0.693	1.157	0.120	0.643	0.568	0.110	0.671
SG	1.519	1.769	3.011	0.110	0.067	1.367	1.319	0.056	0.074
SQ	1.169	0.001	0.002	1.217	0.000	0.001	1.238	0.000	0.000
ST	1.171	0.750	2.711	1.070	0.494	3.725	0.876	1.515	2.501
TO	2.267	1.522	1.453	2.006	1.524	1.470	1.958	1.716	1.672
UR	1.010	0.600	1.020	0.818	0.311	0.249	0.793	0.566	0.326
XA	2.947	1.618	1.673	3.609	0.065	0.010	3.063	0.028	0.003

LI Lloyd's Index; *LEI-FC* Lloyd's Extended Index weighted by fruit count; *LEI-FM* Lloyd's Extended Index weighted by fruit mass. See Table I for species codes.

fruit mass is used as a measure of size. This large change is due to the fact that *Sloanea* overlaps spatially and fruits during the same period as *Anacardium occidentalis* and *Mangifera indica*, which have few fruits, so LEI-FC is low, but very heavy ones, so LEI-FM is large.

Fig. 1 LEI weighted by fruit count for the top 4 most commonly used focal tree species ($n>50$) calculated for 3 different circular plot areas: 0.125 ha (radius of 20 m), 0.283 ha (radius of 30 m), and 0.5 ha (radius of 40 m). Tree species abbreviations correspond with Table I.
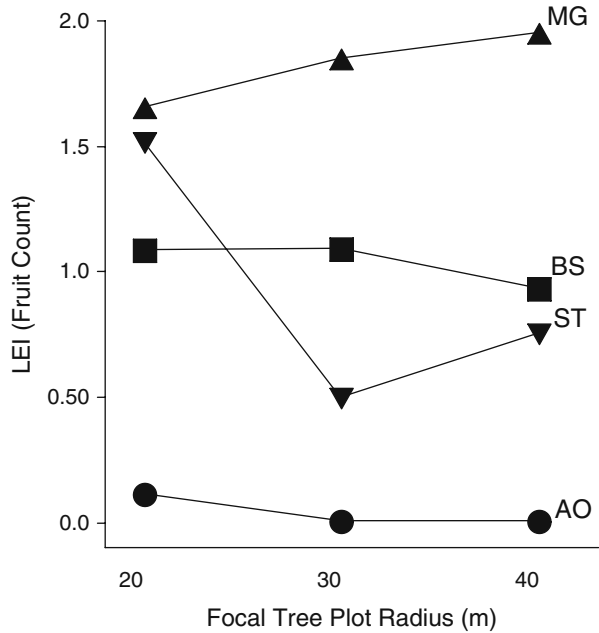
We predicted that as the relative amount of alternate food resources available to group members outside of the focal tree increases, individuals would spread out to use them and avoid aggression with more dominant group members. Thus, we expected a negative relationship between the frequency of aggression in focal trees of a given species and LEI, which indexes the amount of alternative food available per focal tree used of a given species relative to the amount of food in the focal tree. Controlling for feeding bout length and the number of feeding individuals in the tree,

Fig. 2 LI and LEI weighted by fruit count (LEI-FC) and by fruit mass (LEI-FM) for the top 4 most commonly used focal tree species ($n>50$). Indices were calculated for a plot area of 0.283 ha (radius of 30 m). Tree species abbreviations correspond with Table I.
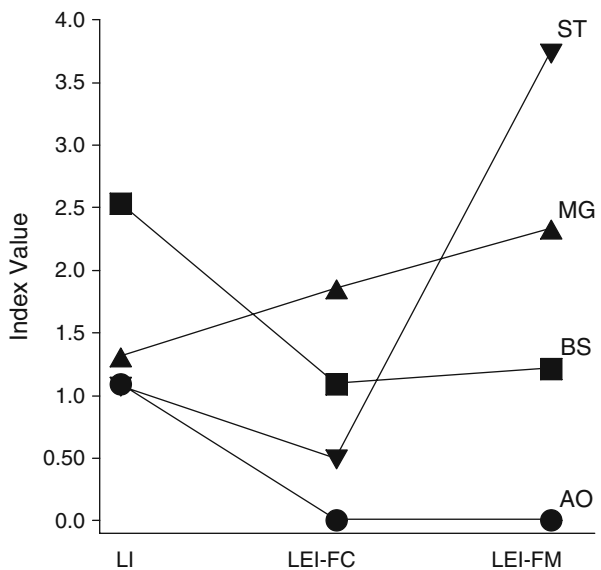
we found a significant negative relationship for LEI based on fruit counts with a plot size of $r=20$ ($F_{1,33}=6.96$, $p=0.01$), and a nonsignificant trend for LEI based on fruit mass with plot sizes of $r=20$ and $r=30$ ($F_{1,33}=3.70$, $p=0.06$ and $F_{1,33}=3.26$, $p=0.08$). There is no relationship between the original version of LI and the frequency of aggression for any of the plot sizes analyzed (Table III). We confirmed these results by entering all measures of LEI and LI into one Generalized Linear Model, which was highly significant ($r_{adj}^2=0.40$, $F_{9,33}=3.45$, $p=0.0073$). The significance of this model was largely driven by the relationship between the frequency of aggression and LEI based on fruit counts for a plot size of $r=20$ ($\beta=-2.27$, $p=0.008$).

Discussion

Previous attempts at predicting the frequency of food-related aggression in *Cebus capucinus* in individual feeding trees using measures of alternate resource availability and opportunity costs on a scale that is relevant to the focal individuals have not been successful, e.g., Alternative resource score, Minutes lost feeding (Vogel and Janson 2007; Vogel *et al.* 2007). Thus, whether the focal individuals respond most readily to patchiness measured at the scale of entire trees, counts of fruit, fruit biomass, and energy availability remained unclear. Using the same data set, we could predict the frequency of aggression during a feeding bout by our species-level LEI when weighted by fruit count per tree at the 20 m radius. Whether this difference with prior analyses is a result of the smaller plot sized used in our LI calculations, the species level LEI, or a combination of these 2 factors remains an avenue for future investigation. There was also a trend in the predicted direction with LEI weighted by fruit mass at the smaller plot size; however, the frequency of aggression does not correlate well with the unweighted LI. Thus, it appears that for this population of capuchins, the number of fruits available outside the focal tree was

Table III Predicting the frequency of aggression within a focal tree from LEI and LI using 3 different radii, while holding the duration of the feeding bout and for the average number of individuals in the focal tree constant

Independent variable	Plot radius (m)	Resulting effect	SS	DF	*F*	*p*-level
LEI fruit count	40	+	0.00	1	0.00	0.98
LEI fruit mass	40	−	10.0	1	2.17	0.15
LI	40	+	0.90	1	0.18	0.67
LEI fruit count	30	+	2.49	1	0.51	0.48
LEI fruit mass	30	−	14.6	1	3.26	0.08
LI	30	+	2.02	1	0.41	0.52
LEI fruit count	20	−	28.2	1	6.96	0.01*
LEI fruit mass	20	−	16.4	1	3.7	0.06
LI	20	−	0.65	1	0.13	0.72

Dependent variable: Standardized frequency of aggression

The results for the 3 different plot sizes (radius of 20, 30, and 40 m) for each focal tree species are reported. An asterisk (*) indicates a significant result.

most important for predicting the amount of aggression in the focal tree, but the biomass of fruits may also contribute to whether the capuchins contest the resource. Other measures, such as available total digestible energy per tree, could also be incorporated into the LEI. For our focal population, fruit biomass, but not total energetic value, per focal tree was a significant correlate of agonism (Vogel and Janson 2007); thus we did not incorporate energetic value into our calculation of LEI. Studies for other populations and species should ideally test explicitly for the effects of nutrient composition on the predictive power of LEI.

The LEI predicted rates of aggression in our example at the 20-m-radius plot size, and there was a trend for the 30-m-radius plot size. This was not an expected outcome, as it would seem logical that a displaced monkey could look for alternative food sources anywhere within the 40-m radius of the focal tree, while staying within the group spread and avoiding additional costs associated with predation and becoming separated from the group. However, it is possible that an individual's willingness to fight to remain in a focal tree responds mostly to the availability of alternative resources that are within visible range of that tree. Detection distances by *Cebus apella* in a subtropical forest were <20 m based on platform experiments (Janson 1996; Janson and DiBitetti 1997). Although the forest types are different, we predict that detection distances in the dry forest of Lomas Barbudal are unlikely to be as large as 40 m. An alternative yet not mutually exclusive explanation is that individuals may be less willing to move away from the majority of the feeding group because of potential predation pressure. Several researchers have shown that individuals prefer more central positions in groups, potentially to reduce predation pressure (Hall and Fedigan 1997; Janson 1990a; Ron *et al.* 1996), although this may only apply to juveniles (Janson 1990b).

Our results suggest that the larger the plot size surrounding the focal tree, the weaker is the relationship between the number of aggressive interactions and the patchiness index based on fruit count. If this relationship is general, it has several important implications. First, large phenological plots that have sometimes been used in primate studies may be too large to estimate a relevant measure of clumping for a given species. The same sampling effort might be better spent on a greater number of smaller plots. Second, it is important to take data on alternative resource availability in such a way that different spatial scales, up to the total group spread, can be analyzed after the fact. The total group spread provides a likely maximum scale of analysis, as it is implausible that individuals would consider the alternative food source that lay outside the group spread from the focal feeding tree as being available when deciding to contest food in a given focal tree. Although capuchins can incorporate the location and value of future food sources in group foraging decisions (Janson 2007), we suspect that such group level decisions will more likely affect whether or not a group visits a given focal tree at all, instead of an individual's decision to contest food within the focal tree given that it is visited. However, we do not know the degree to which individuals prefer closer feeding alternatives over more distant ones, and such a preference could shrink the effective radius of the plot size needed to predict rates of aggression. Depending on the species under investigation, the observer may also want to use maximum group spread. However, given that we found that smaller plot sizes were better predictors of the frequency of aggression for *Cebus capucinus*, using average group spread may give similar results

as using maximum group spread. Third, the better predictive power of the 20-m radius plots vs. larger plot sizes suggests that LEI may allow for some error when estimating total or maximum group spread without sacrificing the ability to predict rates of aggression. However, we suggest that average group spread should be calculated several times throughout the year, in case major changes occur that should be incorporated into the focal tree method. Likewise, any intergroup differences in group spread should be applied in the calculation of LEI using the focal tree method.

We did not account for the actual area an individual can defend in our calculation of patchiness. For example, the dominant's effect on feeding success of subordinates vanishes by 10 m in *Cebus apella* (Janson 1996), and *C. capucinus* tend to defend food that is ≤4 m of the focal individual (Vogel and Janson 2007). Thus, a single tree may have >1 feeding site (Leighton and Leighton 1982), whereas here we have assumed that a feeding tree is a single feeding site. For example, if a tree has a spherical crown with a radius of 15 m (crown volume of 14,137 m^3), for *Cebus apella* there could be ≤3 feeding sites within this tree (radius of 10 m = crown volume of 4188 m^3), whereas for *C. capucinus* there could be up to *ca.* 50 feeding sites (radius of 4 m = crown volume of 268 m^3). Therefore, although we have presented a way to determine resource distribution that is relevant to the subjects, future analysis should take into account tree size relative to the potential area an individual can defend when determining the number of feeding sites within the average group spread surrounding the focal feeding tree (Hanya 2009; Leighton and Leighton 1982; Vogel and Janson 2007). For *Cebus capucinus* in Guanacaste, this may not be an issue because most feeding trees in our analysis were <7 m in radius (Vogel and Janson 2007). However, for primate species that feed on large fruit trees, the area that an individual can defend should be considered when determining patchiness relative to food-related aggression. In addition, the defendable area will probably vary across species, with small species typically defending smaller areas than large ones. Therefore, the same tree could represent a very different competitive regime to tamarin monkeys at 300 g than to spider monkeys at 9000 g.

The focal tree method combined with LEI may be difficult to apply in all types of forests and focal species. The method may require modification based on the plant and primate species under investigation. For example, for species that use forage in smaller subgroups, e.g., *Ateles sp.* (McFarland-Symington 1988), the spatial spread of the subgroup may be the more relevant unit for examining food competition. On the other hand, if a particular species spreads out over an area that is too large to monitor alternative resources with the available personnel, researchers can fall back on traditional fixed-plot methods, but with some important guidelines: 1) make the plot size roughly equal to the spread of the focal group(s); and 2) use LEI (or at least LI) to calculate clumping. This method was developed primarily to quantify the distribution of resources for a primarily frugivorous primate species to test predictions of the socioecological model (Sterck *et al.* 1997; van Schaik 1989). For folivorous primates with lower levels of direct (contest) competition and higher levels of indirect (scramble) competition, other methods may be more appropriate and less labor intensive (Borries *et al.* 2008; Snaith and Chapman 2005). Likewise, because insect encounters by primates are generally unpredictable in space and time, this method would not be appropriate to study insect foraging unless applied to social insects as prey. However, for both leaves and insects, the use of LEI on

resource availability in randomly chosen plots of a size commensurate with a primate group's spread would provide relevant data on resource patchiness for comparison with results of the focal tree method used here to assess the patchiness of fruit availability.

The advantage of LEI over conventional botanical indexes of clumping such as Morisita's index is that the latter consider empty plots as meaningful data, whereas LI or LEI require ≥1 focal tree of a species to be present for a plot to contribute to the index of crowding. Clearly, from the point of feeding competition in fruit or leaf trees, a plot with no feeding tree provides no data about feeding competition and thus should not contribute to a monkey-based measure of food clumping. LI or LEI has this characteristic, whereas standard botanical indexes of clumping, designed to examine relationships among plants, not between plants and monkeys, do not. In addition, most standard botanical indexes of dispersion measure spatial distribution of a single plant species, but LI or LEI as used here specifically requires the integration of resource availability across all the potential food resources in a focal tree plot, both of the same and of different species as the focal tree. If the focal tree method cannot be applied because of logistical difficulties, we encourage researchers to combine LEI with a plot-based method while using a plot size that is biologically relevant to the study species under investigation and the study question being asked. Traditional plot-based methods focusing on resource density and phenology are also indispensable to monitor habitat-wide fruit availability if researchers are interested in examining primate behavior in relation to general food availability. We encourage field biologists to modify the focal tree method as necessary to fit their focal species but urge them always to measure resource availability from the focal individual's point of view.

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