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Do Forest Composition and Fruit Availability Predict Demographic Differences Among Groups of Territorial Owl Monkeys (*Aotus azarai*)?

Griëtte van der Heide · Eduardo Fernandez-Duque · David Iriart · Cecilia Paola Juárez

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Abstract Small-scale ecological variables, such as forest structure and resource availability, may affect primate groups at the scale of group home ranges, thereby influencing group demography and life-history traits. We evaluated the complete territories of 4 groups of owl monkeys (*Aotus azarai*), measuring and identifying all trees and lianas with a diameter at breast height ≥10 cm (n=7485). We aimed to determine all food sources available to each of those groups and to relate food availability to group demographics. For analyses, we considered the core areas of the home range separately from the 80% home range. Our results showed that groups occupy territories that differ in size, species evenness, stem density, and food species' stem abundances. The territories differed in the availability of fruits, flowers, and leaves, and most fruit sources were unevenly distributed in space. Differences among territories were more pronounced for the whole range than they were for the core areas. Despite marked differences among territories in structure and food availability, the number of births and age at natal dispersal were quite similar, but 1 group had a consistently lower group size. Our results suggest that owl

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G. van der Heide (✉) · E. Fernandez-Duque · C. P. Juárez
Fundación ECO, Formosa, Argentina
e-mail: griette.vanderheide@gmail.com

E. Fernandez-Duque
CECOAL-Conicet, Corrientes, Argentina

E. Fernandez-Duque
Department of Anthropology, University of Pennsylvania, Philadelphia, PA, USA

D. Iriart
Universidad Nacional del Nordeste, Corrientes, Argentina

Present Address:
G. van der Heide
15801 Chase Hill Boulevard, Apartment 515, San Antonio, TX 78256, USA

monkey groups occupy territories of different structure and composition and food availability, yet ones that contain similar quantities of, mostly, dry season fruit sources. We propose that groups inhabit these territories to overcome food shortages safely during limiting periods, specifically the dry season, in this markedly seasonal forest. The occupancy and defense of territories with strict boundaries may therefore be associated with food resources available during limiting seasons that may be the ones influencing life history patterns and demographics.

Keywords *Aotus azarai* · Demography · Food availability · Forest structure and composition · Life history

Introduction

Primate populations experience temporal and spatial fluctuations in abundance and density that occur on large ecological scales in response to natural disasters, historical events, or climatic patterns (Kay *et al.* 1997; Reed and Bidner 2004; Wiederholt and Post 2010). Niche diversification, interspecific competition, predator pressure, disease, parasites, and habitat contraction and expansion are additional factors that can influence primate population dynamics (Fleagle and Reed 1996; Holzmann *et al.* 2010; Isbell *et al.* 2009; Rudran and Fernandez-Duque 2003; Struhsaker 2008). Sometimes, several factors can influence a population simultaneously, such as habitat contraction and variations in interspecific competition (Vitazkova and Wade 2007). The existence of possible past covarying factors represents a challenge when attempting to explain contemporary population distributions that were influenced by historical variables.

There are also factors that influence primate populations at a smaller ecological scale. For example, the plant community structure influences primate abundance and distribution through the availability of valuable resources, such as sleeping sites, cover from heat and predators, pathways to range, water, and food (Anderson 1998; DeGama-Blanchet and Fedigan 2006; Janson and Chapman 1999; Stevenson 2001). Understanding how these resources vary over time and across space, and which of them are essential to any particular population or species, is important in comprehending life-history evolution, population dynamics, and directing conservation strategies (Marshall *et al.* 2009; Struhsaker 2008; Wieczkowski 2004).

Socioecological theory has been developed starting from the premise that the distribution and abundance of food is intimately related to the distribution of females. Over the years, numerous studies have shown that variations in food source availability influence primate abundance, behavior, and life history (Chapman and Chapman 2000; Di Bitetti and Janson 2000; Poulsen *et al.* 2001; Pruetz and Isbell 2000; Wrangham 1980). For example, fallback foods, keystone resources, top diet species, protein/fiber ratios, and fruit macronutrient content have been associated with life-history traits, density, and behavior (Chapman *et al.* 2002; Felton *et al.* 2009; Janson and Chapman 1999; Marshall *et al.* 2009; Savini *et al.* 2009). However, most of the studies that examined fluctuations in the availability of food sources across space and time focused on an ecological scale that was also likely influenced by uncontrolled confounding factors such as the presence of potential

predators and parasites, climatic variables, isolation, phylogenetic constraints, and local traditions (Chapman and Rothman 2009; Marshall *et al.* 2010; Moura 2007; Vitazkova and Wade 2007) .

Confounding factors are related to both the dependent and the independent variables, obscuring the real relationship between those. A failure to restrict the number of confounding factors or to exclude known ones in analyses (Marshall *et al.* 2010) can lead to erroneous results and conclusions. Unfortunately, confounding factors are often too numerous to recognize when working in natural systems, and, when recognized, it is usually extremely difficult to control for them. Small-scale studies that can help identify and control some of those confounding factors are scarce. Moreover, our knowledge of which environmental factors are important at a local level is limited (Butynski 1990; Chapman and Chapman 2000; Potts *et al.* 2009; Rovero and Struhsaker 2007), especially at the scale of neighboring group home ranges (Curtis and Zaramody 1998; Harris and Chapman 2007; Savini *et al.* 2008). At a small scale, we can reasonably expect that common confounding variables, such as climate and predator presence, are constant and therefore ineffective at affecting relationships between variables of interest.

The Azara owl monkeys (*Aotus azarai azarai*) of the Argentinean Chaco offer a suitable model for examining certain aspects of socioecological theory at a small scale. Their territoriality and monogamous social system constitute a relatively simple system on which to investigate the relationship between forest structure and composition, food availability, life-history traits, and demography. First, groups include 1 pair of adults and a few young that exploit a range of foods (Arditi 1992; Giménez 2004; Wright 1985). Fruits are consumed year round, representing as much as 84% of the dry season and 97% of the wet season diet (Arditi 1992; Giménez 2004). Leaves and leaf buds are consumed more frequently in the dry season, whereas flowers and flower buds are preferred during the spring (Arditi 1992). Although owl monkeys have been observed eating insects, there are no quantitative estimates of this. Second, in the Argentinean Province of Formosa, owl monkeys inhabit small, slightly overlapping territories of 4–10 ha in a semideciduous low-diversity subtropical forest (Placci 1995). Their territoriality reduces the confounding factor of intergroup competition in overlapping portions of neighboring home ranges (Harris 2006). Third, the relatively small size of their territories makes it possible to obtain complete determination of food source distribution and abundance, instead of sampling only a portion of their ranges with the subsequent uncertainty regarding the extent to which the sample actually represents the available food (Chapman *et al.* 1994; Hemingway and Overdorff 1999; Miller and Dietz 2004). Fourth, the relatively small monogamous groups minimize the complexities inherent to characterizing the effects of food abundance on intragroup competition, compared to the difficulties of studying these relationships in, e.g., fission–fusion societies (Wallace 2008). Finally, although changes in group composition through the replacement of adults may occur (Fernandez-Duque *et al.* 2008), the size and location of territories have not changed over a 10-yr period (Fernandez-Duque, *unpubl. data*). This enduring spatiotemporal stability that is, apparently, independent of group composition makes it reasonable to consider territories as representative units of resources available to owl monkey groups.

We present here the results of a study that examined the relationships of small-scale ecological variables with owl monkey life-history parameters. Focusing on 4 neighboring owl monkey territories and groups, we investigated the spatial variation in forest structure and composition and potential food availability throughout the year. Within the framework of socioecological theory, we hypothesized that females in a monogamous system are distributed in space in a manner that allows them to maximize their reproductive success given the distribution and availability of resources. In other words, it is expected that the reproductive histories of social groups and their subsequent demographic characteristics will be determined by access to resources, which in turn is directly influenced by resource availability (Clutton-Brock 1989; Emery Thompson and Wrangham 2008). In this theoretical context, we first predicted that there would be no significant differences among territories in the spatial distribution and abundance of food resources. Second, we predicted that there would be a relatively even distribution of food in space that prevents the formation of multifemale groups and leads to socially monogamous ones. Third, if territories were similar in quality, we predicted that the number of offspring produced in each territory over a 10-yr period should not differ much. This prediction is formulated under the assumption that the number of offspring produced is intimately related to the nutritional status of females, which is related to available food. Fourth, if territories had similar amounts of resources, we expected that they should support similar numbers of individuals, which would be reflected in similar group sizes. Fifth, assuming that the age when individuals disperse from their natal groups could be partially influenced by competition for resources within the group (Fernandez-Duque 2009), we predicted that the ages at dispersal would not be very different if territories were similar.

Methods

Site and Focal Groups

The study site is located in the cattle ranch Estancia Guaycolec (58°13′W, 25°54′S; Fig. 1) in the humid portion of the Argentinean Chaco, a habitat that includes pastures, palm savannas, patches of dry forest, and continuous gallery forest along the Pilagá River (Placci 1995). The gallery forest in the ranch has been relieved from logging, hunting, and grazing pressures for >10 yr and includes 4 main types of forests: flooded, high and low *albardón* (a Spanish word used to refer to riverine forests situated on lateral, sandy-silt, deposits from the riverbeds), and Austro-Brazilian transitional forest (Neiff 2004; Placci 1995). The floodable forest is a relatively open and low habitat dominated by a few exclusive tree species that is found on a 20–100 m wide belt along the margins of the Pilagá River. The other 3 forest types are more floristically diverse, higher (± 15 m with emergent trees of 25 m), and constitute a botanical gradient of decreasing altitude, utilizable soil layer depth, and water holding capacity from the river to the savannah. Certain species exclusively or preferentially grow on specific parts of the gradient and typify the 3 forest types accordingly. A system of intersecting transects at 100-m intervals covers *ca.* 300 ha of the various forest types.

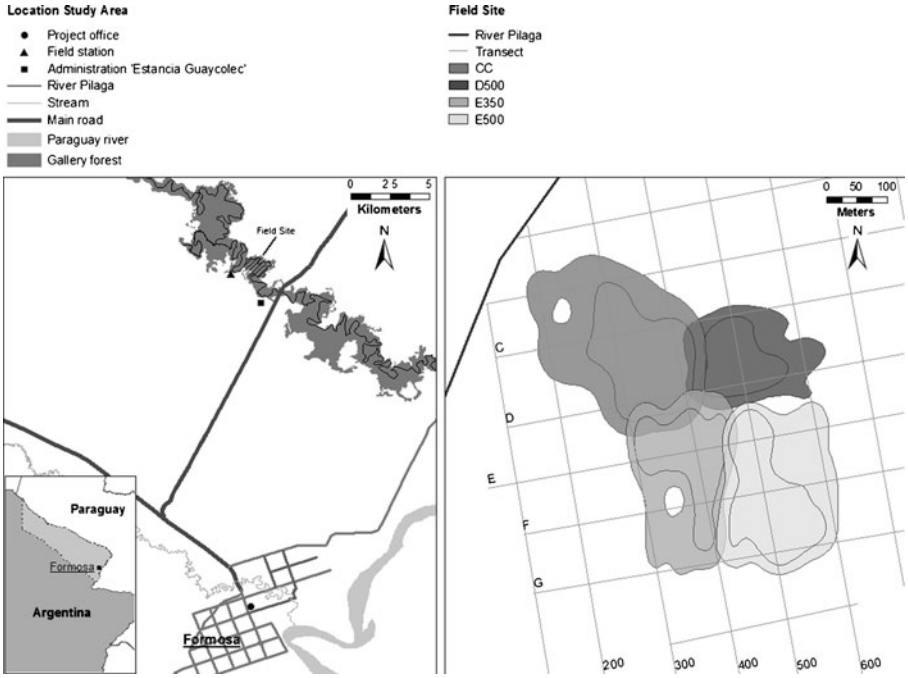

Fig. 1 Map of the field site and territories of the 4 owl monkey groups. The inner isoclines represent the 50% core areas and the outer isoclines represent the 80% home ranges.

Mean monthly temperature and annual precipitation in the area are 22.3°C and 1466 mm, respectively. Monthly mean rainfall varies significantly during the year, with 2 rain peaks in April and November, and it reaches a low (<100 mm) during June–August (Fernandez-Duque 2009). Monthly mean temperatures are 11°C lower in April–August than in December–March. Extreme low and high temperatures are frequent.

Owl monkeys in the area are sympatric with only 1 other primate species (*Alouatta caraya*), but they might also compete for food with coatis (*Nasua nasua*) and frugivorous birds such as toucans (*Toco toucan*: Arditi 1992; Hirsch 2009; van der Heide *pers. obs.*). For our study we focused on 4 groups intensively studied since 1997: CC, D500, E350, and E500. These groups included 3–5 individuals during 2008 and 2009. In the text we use CC, D500, E350, and E500 to refer to a group of monkeys or the territory they occupy.

Home Ranges and Demography

We contacted the 4 focal groups to collect demographic data at least weekly. We collected data on group composition, encounter time, dominant behavioral state of the group, and location of the group relative to the transect system when encountered and when left. A more detailed description of demographic data collection was provided by Fernandez-Duque (2009).

To estimate home range size and location, we used 500 randomly selected group locations recorded during 1998–2008 for each group. On average, we recorded 78, 89, 75, and 74 locations per year for the CC, D500, E350, and E500 groups,

respectively (ranges, CC: 11–166, D500: 29–180, E350: 0–218, E500: 16–237). About 60% of the group yearly totals consisted of >50 locations, and we missed data only for E350 in the year 2002.

To obtain 50% and 80% probability areas we used the fixed Kernel density estimator with an automated smoothing parameter (h=0.346) with biased-cross validation in ArcGIS 9.1 (Wartmann *et al.* 2010). The 50% area identifies a core area that was used intensively and almost exclusively (Fig. 1). The 80% home range areas are approximately twice as large and show some overlap (Fig. 1). We chose an 80% home range because it was the largest area that was not influenced by group locations associated with nonforaging events, e.g., predispersing juvenile exploring the area, intergroup encounters. Computation of the Swihart and Slade and the Schoener indices to assess the autocorrelation of data points (Swihart and Slade 1985; Wartmann *et al.* 2010) indicated that the data used for the home range estimates of E350 did not autocorrelate; the data of CC and D500 showed some acceptable levels of autocorrelation (S&S: 0.67 and 0.66, Schoener's: 1.55 and 1.37), whereas the E500 data autocorrelate only according to the Schoener index (1.58).

Forest Composition and Structure

To characterize the gallery forest and to compare specific aspects of forest structure, composition, and food availability among territories, we collected ecological data from the 16.25 ha that roughly corresponded to the 80% home ranges of the 4 focal groups (Fig. 1). We subdivided the 16.25 ha in quadrants of 25×25 m to facilitate data collection on the ground. We collected data from the D500 territory between 2002 and 2004 and in the other 3 territories in 2007. For the comparisons of forest structure and food availability among territories we used information of the Kernel density estimates of core areas and home ranges to choose the corresponding subset of 25×25 m quadrants.

We measured the diameter at breast height (DBH), identified the species, and tagged the stem for further reference of all trees and lianas with a DBH (1.3 m above ground) ≥10 cm. We collected botanical specimens of each species and of ambiguous cases for identification and vouchering. In case of bifurcated trees, we measured the DBH of the thickest stem. We did not measure hemiepiphytic figs when still present as lianas on host trees or when aerial roots did not encircle the entire host trunk at breast height. We mapped trees with a DBH ≥30 cm and all trees belonging to 15 species known to be important as elements of the forest, or as owl monkey food species, with reference to the transect system (Arditi 1992; Giménez 2004; Placci 1995).

Annual Changes in Food Availability

To characterize the general annual phenological patterns of owl monkey food sources we used monthly data on the timing, duration, and intensity of tree and liana phenophases of individuals located in 30 50×10 m plots randomly placed within the area of study between February 2003 and September 2009 (Fernandez-Duque 2003). Until 2008, the monthly sample included 272 trees belonging to 51 species; in 2009 we increased the sample to 441 trees. We collected categorical data recording which percentage of the tree crown showed the particular phenophase

(leaves: 0–1, 1–5, 5–10, 10–25, 25–50, 50–75, 75–100%; flower buds and flowers: 0–25, 25–50, 50–75, 75–100%). We calculated fruit loads of immature, intermediate, mature, overmature fruits, and fruits of unknown maturity counting all fruits in a visible portion of the crown and multiplying by the total number of even-sized portions with fruits in the crown.

Territory Differences in Food Availability

We used stem abundances and total basal areas (TBAs; see section on data analyses) of all the species known to be part of the owl monkey's diet to produce estimates of food availability in the 4 territories throughout the year. The approach assumes that each territory has an inherent food resource potential, represented by all trees and lianas that could serve as a food source. We included in the estimation all tree and liana species mentioned by the 3 studies reporting data on the diet of *Aotus azarai* in the Chaco (Arditi 1992; Giménez 2004; Wright 1985), and unpublished data from our project. We classified food resources as consumed during the dry (winter) or wet season (summer, spring, autumn) or both.

Data Analyses

Forest Composition and Structure To characterize the structure and composition of the forest we calculated the abundance and density (stems/ha) of each species, as well as Simpson's indices of diversity and evenness. To estimate stand basal area (SBA, m^2/ha) we used DBH to estimate, first, individual basal area (IBA, m^2; cross-sectional area of a trunk), then summed across individuals of each species to produce total basal area (TBA, m^2), and then divided the total by the sampled area. We calculated the Simpson's index of diversity (D) as $D = \sum (n_i(n_i - 1)/N(N - 1))$ wherein N is the total number of individuals and n_i is the number of individuals of the ith species. We derived Simpson's evenness index $E_{1/D}$ from Simpson's index D ($E_{1/D}$=(1/D)/S; Magurran 2004). This index is insensitive to species richness. It approaches 0 when many individuals belong to a few species and 1 when species show equal abundances.

Annual Changes in Food Availability To characterize annual fluctuations in phenological patterns, we analyzed the phenological data collected from food species between January 2003 and September 2009. To account for the loss of trees due to death, limited visibility, and the increase in the sample size of monitored trees during the 7-yr period, we adjusted the monthly fruit count, per species, using the following equation:

$$Adjusted\ F_{a,I} = \left(F_{a,I}/TBA_{a,I}\right) \times SBA_a$$

wherein $F_{a,\ I}$ is the total fruit count and $TBA_{a,\ I}$ the TBA of species a in month I. SBA_a is the stand basal area of species a, an estimate of the presence of the species in the 16.25-ha area (electronic supplementary material [ESM] Table SI, in cm^2/ha). We averaged monthly fruit loads across years to obtain a mean species-specific monthly fruit load. To obtain the mean monthly fruit availability, we summed species-specific monthly means across species. We made these estimates for each of the fruit maturation states.

To summarize flowering and leaf burst patterns, we took the midpoint of the proportion category used and multiplied it by the corresponding IBA, an approach that accounts for tree-size effects. For example, to calculate an index of available new leaves (*Index NL*), we used the following equation:

$$Index\ NL = \left(\sum\nolimits_i \left(pNL_{a,i} \times IBA_{a,i}\right)\right) / TBA_a$$

wherein $pNL_{a\ i}$ is the proportion (categorical midpoint) of new leaves on tree i of species a, $IBA_{a,i}$ is the basal area of individual i of species a, and TBA_a is the total basal area of species a in the phenology sample for that month. We averaged monthly proportions across years and subsequently multiplied these by the species-specific SBA to obtain a monthly mean species-specific projected basal area flowering. Per month, we summed all edible species and divided this by the SBA of all species to obtain the proportion of basal area of all trees in a hectare flowering. We followed the same procedure for estimating the availability of flower buds (*Index FlB*) and flowers (*Index Fl*).

Size, Structure, and Forest Composition of Territories To compare forest structure and composition among 50% core and 80% home range areas, we used the same methods as described in the preceding text for the characterization of the forest. We compared species, stem abundance, SBA, and stem densities among territories. We examined the differences among territories statistically using χ^2 goodness of fit tests.

Food Availability in Territories To estimate food availability, we obtained the abundance and TBA per species and territory. We performed species abundance analyses without correcting for territory size, thereby comparing total food availability among territories. We examined statistical differences in species abundance among territories using χ^2 goodness of fit tests.

Group Demography and Life-History Traits To evaluate the relationship between the characteristics of the territories and life-history traits, we examined the monthly demographic records of the groups to summarize information on infant production, infant mortality, age of natal dispersal, and group size. We examined differences in birth numbers among groups with a χ^2 goodness of fit test. We used a Kruskal-Wallis test to analyze differences among groups in age at natal dispersal. We analyzed group size differences using a Friedman test for repeated measures and executed this test with half-year mean group sizes.

We ran all statistical tests using PASW 18.0 (SPSS Inc. 2009) and we set α=0.05 when reporting 2-tailed test results.

Results

Forest Composition and Structure

The area was botanically diverse (Simpson's index of diversity, D=0.06) and showed an uneven distribution of individuals across species (Simpson's evenness

index, $E_{1/D}$=0.26). For comparison, a recent study in Indonesia reported some "high species richness" sampling sites with a mean of 27 species, D=0.05 and $E_{1/D}$=0.73, whereas sites with similar number of species (26) but an "unevenly distributed, species-rich vegetation" had D=0.15 and $E_{1/D}$=0.26 (Hamard *et al.* 2010). We recorded 7485 individuals belonging to 65 species, 59 plant genera, and 30 plant families (ESM Table SI). Most species were trees (n=43), some were small trees (treelets) or shrubs (n=14), a few were lianas (n=5), one was a palm, one was a cactus, and one was a hemiepiphyte.

Half of the species accounted for almost 95% of the individuals, and 7 species accounted for *ca.* 50% of the individuals. The 3 species with the most individuals were *Gymnanthes discolor*, *Chrysophyllum gonocarpum*, and *Trichilia catigua*, and those with the highest TBA were *Calycophyllum multiflorum*, *Patagonula americana*, and *Phytolacca dioica*. Most individuals (60%) had a DBH of 10–20 cm and few (8%) had a DBH >50 cm. The surveyed area had an all-species TBA of 478 m^2, an all-species SBA of 29.4 m^2/ha, and a mean density of 461 stems/ha.

Potential owl monkey food sources were very abundant. Eighty-four percent of individuals (n=6290, 41 spp.), representing 89% (424 m^2) of all-species TBA, produced potential owl monkey food. Fruit sources accounted for 67% (n=4978, 25 spp.) of individuals and 59% (283 m^2) of all-species TBA.

Annual Changes in Food Availability

The forest showed a strong seasonal pattern in the production of leaves, flowers, and fruits (Fig. 2). *Phytolacca dioica* and *Myrcianthes pungens*, the latter with a tendency to fruit supra-annually in the area, contributed significantly to a high peak of fruits in November–December (monthly mean=86,922 fruits/ha). Mature edible fruits were available primarily from November to March and relatively scarce from April to September. The low availability of mature fruits in the dry period was reflected not only in the amount of fruit, but also in the number of species producing them (dry season: 7–9 spp., wet season: 11–14 spp.).

The availability of new leaves also increased considerably after the dry season (Fig. 2b). New leaf availability fluctuated between 2.8% and 4.5% of all-species SBA from December to April and reached a minimum in July (1.9%). The amount of flowers and flower buds also showed an oscillating pattern with a maximum of 1.6% of all-species SBA flowering during July–August (Fig. 2b).

Size, Structure, and Forest Composition of Territories

There were marked differences among groups in the size of their core areas and 80% home ranges (core area: CC=2.7, D500=1.3, E350=1.8, E500=2.4 ha; home range: CC=6.1, D500=2.9, E350=4.1, E500=4.8 ha; Fig. 1). The 4 territories also varied slightly in forest composition and structure (Table I). The larger territories (CC, E500) included more species, more individuals, i.e., abundance, and a higher all-species TBA than the smaller ones. However, estimates of density and all-species SBA were similar among all 4 territories. The pattern of differences, or lack of them, was similar for the 50% core and 80% home range areas.

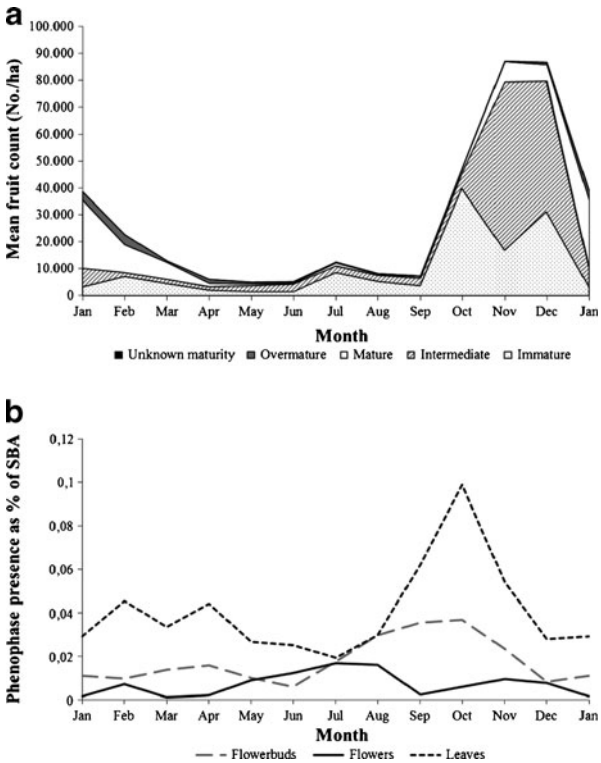

Fig. 2 Monthly changes in the phenology of owl monkey food sources. (**a**) Mean fruit count per hectare. (**b**) Leaf flushing and flowering as percentage of SBA.

There were also differences among territories in the distribution of stems in the various diameter classes. For both the 50% core and 80% home range areas, D500 had fewer trees in the smaller diameter classes (<50 cm DBH), whereas the differences among the territories were smaller in the higher diameter classes (≥50 cm DBH, Table I).

Food Availability in Territories

Fruit availability, as estimated from TBA, was highly variable among the 80% home range areas. The CC territory had the most fruit available (103.4 m^2), with more than double the availability present in the D500 territory (44.1 m^2, Table II). The high amount of fruit in CC territory was due to having the highest TBA in a large number of species (14 out of 25 for the 80% territories), whereas the D500 territory had the highest TBA for only 1 fruit source (*Diplokeleba floribunda*). Most fruit sources were also unevenly distributed among territories with respect to counts of individuals (Table II). However, 6 fruit sources for the 80% territories were evenly available in all 4 territories, e.g., *Cecropia pachystachya*, *Guazuma ulmifolia.*

The territories also differed in the availability of flowers, leaves, and other edible vegetative parts (Table III). CC territory was again the one with the highest TBA in 10 out of 18 possible species. CC territory also had species (*Tabebuia heptaphylla*) that were entirely absent from the D500 and E350 territories. With respect to abundant leaf sources, the CC territory had more *Patagonula americana*, and the

Table I Forest composition and structure in owl monkey territories (50% core and 80% home range areas)

	80% territory						50% territory					
	Group				Chi-square		Group				Chi-square	
Forest variable	CC	D500	E350	E500	χ^2	*p*	CC	D500	E350	E500	χ^2	*p*
Species (*n*)	63	53	53	57	1.19	0.76	54	46	48	52	0.80	0.85
Abundance (*n*)	2740	1175	1982	2164	622.51	<0.01	1210	538	877	1178	309.90	<0.01
Total basal area (m^2)	174	81	122	136	34.50	<0.01	79	34	53	72	20.66	<0.01
Density (ind./ha)	457	409	496	468	8.62	0.03	450	411	485	495	9.45	0.02
Stand basal area (m^2/ha)	29	28	31	29	0.16	0.98	29	26	29	30	0.32	0.96
Stems (*n*):												
DBH 10–20 cm	1647	671	1185	1263	405.84	<0.01	741	301	541	704	210.56	<0.01
DBH 20–30 cm	447	195	347	380	99.64	<0.01	197	110	140	207	39.32	<0.01
DBH 30–40 cm	245	126	187	204	38.45	<0.01	96	52	86	108	20.34	<0.01
DBH 40–50 cm	170	69	110	145	46.78	<0.01	71	23	49	70	28.71	<0.01
DBH 50–60 cm	110	57	80	88	17.16	<0.01	40	27	32	45	5.39	0.15
DBH 60–70 cm	61	25	39	38	16.41	<0.01	32	10	14	21	14.48	<0.01
DBH 70–80 cm	35	23	20	31	5.31	0.15	20	12	7	13	6.62	0.09
DBH >80 cm	25	9	14	15	8.51	0.03	13	3	8	10	6.24	0.10
Simpson's Diversity Index (1-D)	0.93	0.93	0.95	0.94			0.92	0.93	0.94	0.94		
Simpson's Evenness Index ($E_{1/D}$)	0.23	0.28	0.38	0.30			0.22	0.29	0.36	0.30		

Included are the results of uncorrected χ^2 tests for variables representing counts

E500 territory offered more *Albizia inundata*. Three nonfruit sources were present in similar quantities among 80% home ranges.

Differences in fruit availability among the core areas were not as pronounced (Table II). Although the CC territory still had the highest TBA for most species (n=9), the other groups had the highest TBA for 8 (E350), 6 (E500), and 1 species (D500). Some dry season fruit sources (*Chrysophyllum gonocarpum*, *Guazuma ulmifolia*) occurred mostly in the E500 territory. Five fruit sources were similarly present in all 4 territories, including important fruit sources such as *Ficus* spp., *Inga uraguensis*, *Phytolacca dioica*, and *Sideroxylon obtusifolium.*

Seven nonfruit sources showed similar, but overall low, abundances among core areas (Table III).

Group Demography and Life-History Traits

There were no significant differences in infant production among groups (Table IV, Chi-square test, χ^2=1.387, df=3, p=0.71). Three groups had infants in 75% of the years (CC, E500, and D500: 9 infants in 12 yr) and E350 had 5 infants in 7 yr (71%). Infant mortality did not differ much among groups either (CC: 11%; D500:

Table II Availability of fruit sources in the 80% and 50% territories

		80% territory						50% territory					
		Individuals (TBA (m^2))				Chi-square		Individuals (TBA (m^2))				Chi-square	
Species	Food item	CC	D500	E350	E500	χ^2	p	CC	D500	E350	E500	χ^2	p
Cecropia pachystachya	FR, FL	**22 (0.7)**	9 (0.3)	12 (0.6)	15 (0.6)	6.41	0.09	**20 (0.6)**	5 (0.1)	11 (0.6)	9 (0.4)	10.73	0.01
Celtis iguanaea	FR, L	2 (0.0)	1 (0.0)	**6 (0.1)**	6 (0.1)	5.53	0.14*	1 (0.0)	1 (0.0)	**3 (0.1)**	3 (0.0)	2.00	0.57*
Chrysophyllum gonocarpum	FR	158 (7.7)	80 (3.9)	178 (10.7)	**210 (12.6)**	58.65	<0.01	86 (4.3)	38 (2.1)	70 (4.9)	**131 (7.5)**	55.32	<0.01
Crateva tapia	FR, FL	**62 (2.2)**	30 (1.1)	45 (1.6)	28 (1)	18.10	<0.01	**25 (0.9)**	10 (0.2)	15 (0.3)	13 (0.5)	8.41	0.05
Diplokeleba floribunda	FR	2 (0.6)	**3 (1.5)**		1 (0.0)				**2 (0.3)**				
Enterolobium contortisiliquum	FR, FL	**6 (2.2)**	1 (0.3)	9 (2.0)	5 (1.3)	6.24	0.10	1 (0.7)		2 (0.4)	**4 (1)**		
Eugenia moraviana	FR, FL, L	17 (0.2)	14 (0.2)	**27 (0.3)**	28 (0.3)	6.93	0.07	3 (0.0)	9 (0.1)	**20 (0.2)**	15 (0.1)	13.85	<0.01
Eugenia sp.	FR, FL, L	95 (1.4)	60 (1.1)	**173 (2.8)**	160 (2.7)	70.64	<0.01	17 (0.2)	33 (0.7)	**130 (2.1)**	115 (2.0)	132.16	<0.01
Eugenia uniflora	FR, FL, L	**37 (0.6)**	11 (0.2)	2 (0.0)	9 (0.2)	47.78	<0.01	**5 (0.1)**	5 (0.1)	3 (0.0)			
Ficus spp.	FR, L	**34 (6.2)**	14 (2.1)	22 (3.8)	27 (3.3)	8.77	0.03	10 (1.8)	7 (0.5)	**14 (2.8)**	16 (1.4)	4.15	0.25
Gleditsia amorphoides	FR, L	**111 (16.6)**	44 (6.1)	63 (6.6)	57 (6.7)	37.36	<0.01	**53 (8.5)**	18 (2.2)	19 (1.5)	33 (4.4)	26.04	<0.01
Guazuma ulmifolia	FR, FL	24 (0.8)	22 (1.2)	14 (1.3)	**24 (1.9)**	3.24	0.36	24 (0.8)	13 (0.7)	**12 (1.1)**	9 (0.5)	8.90	0.03
Gymnanthes discolor	FR	**547 (7.1)**	231 (2.9)	189 (2.5)	330 (4.2)	236.36	<0.01	**284 (3.8)**	116 (1.5)	56 (0.8)	182 (2.4)	179.38	<0.01
Inga uraguensis	FR, FL	45 (4.2)	39 (4.7)	56 (5.4)	**77 (8.7)**	15.46	<0.01	23 (2.1)	24 (2.5)	32 (2.6)	**40 (5.6)**	6.35	0.10
Maclura tinctoria	FR, FL	**2 (0.3)**	1 (0.0)		2 (0.2)			**1 (0.3)**	1 (0.0)		1 (0.2)		
Myrcianthes pungens	FR, FL, L	**166 (10.2)**	37 (2.9)	75 (4.1)	76 (4.8)	101.66	<0.01	**65 (5)**	12 (0.9)	14 (0.5)	40 (2.4)	57.24	<0.01
Ocotea diospyrifolia	FR, L	88 (8.2)	60 (5.2)	97 (10.0)	**102 (11)**	12.16	<0.01	32 (1.9)	26 (2.4)	**58 (6.2)**	50 (5.2)	16.27	<0.01
Opuntia schulzii	FR	**2 (0.1)**		1 (0.0)	1 (0.0)								
Phyllostylon rhamnoides	FR	**148 (16.7)**	25 (2.8)	35 (2.5)	38 (3.2)	163.72	<0.01	**49 (7.1)**	14 (1.3)	21 (1.5)	14 (1.5)	34.00	<0.01
Phytolacca dioica	FR	33 (8.8)	20 (5.1)	**63 (14.4)**	50 (11.2)	25.76	<0.01	15 (4.7)	13 (3.3)	18 (4)	**26 (6)**	5.44	0.14
Psidium kennedyanum	FR	18 (0.2)	7 (0.1)	**28 (0.4)**	16 (0.2)	12.91	<0.01	2 (0.0)	3 (0.1)	**17 (0.2)**	8 (0.1)	18.80	<0.01

Table II (continued)

Species	Food item	80% territory						50% territory					
		Individuals (TBA (m^2))				Chi-square		Individuals (TBA (m^2))				Chi-square	
		CC	D500	E350	E500	χ^2	*p*	CC	D500	E350	E500	χ^2	*p*
Rollinia emarginata	FR, FL	6 (0.1)	5 (0.1)	**12 (0.2)**	5 (0.1)	4.86	0.18	2 (0.0)	1 (0.0)	**10 (0.2)**	3 (0.0)	18.80	<0.01
Sideroxylon obtusifolium	FR	**21 (4.4)**	5 (0.5)	11 (1.0)	15 (3.0)	10.46	0.02	6 (2.1)	3 (0.4)	5 (0.3)	**11 (2.6)**	5.56	0.14
Syagrus romanzoffiana	FR, FL	**43 (1.6)**	20 (0.8)	19 (0.7)	42 (1.5)	17.10	<0.01	20 (0.7)	10 (0.4)	5 (0.1)	**21 (0.8)**	13.00	<0.01
Trichilia catigua	FR, FL	**153 (2.3)**	59 (1.0)	120 (1.6)	113 (1.8)	40.92	<0.01	**79 (1.3)**	21 (0.3)	36 (0.4)	69 (1.1)	43.57	<0.01
Total fruits		**1842 (103.4)**	798 (44.1)	1257 (72.7)	1437 (80.6)	421.37	<0.01	**823 (47.1)**	385 (20.4)	568 (31)	816 (45.7)	207.44	<0.01

Abundances with TBA within brackets are reported. Values in **bold** represent the territories with the highest TBA per food species. Results of the uncorrected χ^2 tests performed on species abundances are provided. Statistically nonsignificant results are underlined. *Based on χ^2 test with ≥1 expected count of <5

Table III Availability of nonfruit sources in the 80% and 50% territories

			80% territory						50% territory					
			Individuals (TBA (m^2))				Chi-square		Individuals (TBA (m^2))				Chi-square	
	Species	Food item	CC	D500	E350	E500	χ^2	*p*	CC	D500	E350	E500	χ^2	*p*
Flowers	*Peltophorum dubium*	FL	**22 (5.0)**	5 (0.9)	6 (3.1)	11 (2.1)	16.55	<0.01	9 (2.2)	2 (0.8)	**4 (2.8)**	5 (0.8)	5.20	0.16
	Pisonia aculeata	FL, L	**86 (1.2)**	37 (0.6)	78 (1.1)	70 (1.1)	20.50	<0.01	**53 (0.8)**	19 (0.3)	28 (0.4)	28 (0.4)	20.06	<0.01
	Pisonia zapallo	FL, L	1 (0.0)	1 (0.0)	**2 (1.2)**					1 (0.0)	**1 (0.2)**			
	Pouteria gardneriana	FL	37 (4.7)	20 (2.4)	**46 (5.9)**	45 (4.8)	11.73	<0.01	13 (1.9)	16 (1.7)	**31 (3.7)**	32 (2.8)	12.78	<0.01
	Pouteria glomerata	FL, L	**36 (1.0)**	18 (0.4)	21 (0.7)	31 (0.7)	8.04	0.05	4 (0.1)	5 (0.1)	9 (0.3)	**12 (0.3)**	5.47	0.14
	Serjania sp.	FL	4 (0.0)	2 (0.0)	**6 (0.1)**	7 (0.1)	3.11	0.38*	1 (0.0)	1 (0.0)	2 (0.0)	**3 (0.0)**	1.57	0.67*
	Tabebuia heptaphylla	FL	**4 (0.6)**			2 (0.2)			**2 (0.2)**			1 (0.1)		
	Terminalia triflora	FL	**32 (1.7)**	11 (1.5)	11 (1.1)	7 (1.2)	25.23	<0.01	5 (0.5)	2 (0.1)	**8 (0.9)**	4 (0.3)	3.95	0.27*
Leaves	*Albizia inundata*	L	9 (2)	6 (1.3)	5 (2.2)	**18 (5.4)**	11.05	0.01	3 (1.3)		3 (0.8)	**9 (2.1)**		
	Caesalpinia paraguariensis	L	**2 (1.0)**											
	Patagonula americana	L	**81 (15.0)**	36 (9.1)	49 (8.9)	39 (6.6)	24.83	<0.01	**29 (6.0)**	23 (4.5)	13 (2.4)	20 (3.0)	6.25	<0.01
	Randia armata	L	1 (0.0)		**1 (0.0)**							**1 (0)**		
Other/ Unknown	*Banara arguta*	U	**5 (2.0)**	6 (0.5)	4 (1.0)	4 (0.1)	0.58	0.90*	**3 (1.0)**	2 (0.0)	3 (1.0)	1 (0.1)	1.22	0.75*
	Calycophyllum multiflorum	O	**128 (14.5)**	100 (10.8)	34 (3.5)	92 (10.9)	52.83	<0.01	**56 (7.5)**	29 (2.9)	10 (1.4)	31 (4.5)	33.94	<0.01
	Fagara hyemalis	O	3 (0.1)		6 (0.4)	6 (0.2)			2 (0.1)			**3 (0.1)**		
	Fagara rhoifolia	O	1 (0.0)	**1 (0.1)**										
	Ruprechtia laxiflora	U	**42 (4.7)**	21 (3.8)	15 (1.7)	24 (3.8)	15.88	<0.01	**12 (2.0)**	9 (1.8)	8 (1.1)	9 (1.8)	0.95	0.81
	Sorocea sprucei	U	7 (0.2)	**5 (0.2)**	6 (0.1)	2 (0.1)	2.80	0.42	2 (0.0)	**3 (0.2)**	5 (0.1)	1 (0.0)	3.18	0.36*
	Total other food items		**500 (54.1)**	270 (31.7)	289 (31.0)	359 (37.2)	92.02	<0.01	**194 (23.6)**	112 (12.5)	125 (14.7)	160 (16.2)	27.65	<0.01

Abundances with TBA within parentheses are reported. Values in **bold** represent the territories with the highest TBA per food species. Results of the uncorrected χ^2 tests performed on species abundances are provided. Statistically nonsignificant results are underlined. *Based on χ^2 test with ≥1 expected count of <5

Table IV Differences between groups in demographic parameters (n=4 groups, 1998–2009)

Variable	Group						
	CC	D500	E350	E500	Test	Statistic	p
Birth (n)	9	9	5	8	χ^2	1.387	0.71
Infant mortality (%)	11 (1/9)	11 (1/9)	14 (1/7)	11 (1/9)			
Age at natal dispersal (y)	3.1 (2.1–4.4)	3.1 (1.8–4.9)	3 (2.0–3.9)	3.4 (2.9–4.0)	K-W	1.497	0.68
Average group size (n)	4.01 (2–6)	3.8 (3–6)	3.12 (2–4)	3.88 (2–6)	Friedman	21.881a	<0.01

The number of infants produced is compared with a χ^2 test, the mean age at dispersal with a Kruskal-Wallis test, and the mean group size with a Friedman test for repeated measures

[a] For half-year means per group. We excluded 1 case (second half of 2002) from analyses because of insufficient data for E350

11%; E350: 14%; E500: 11%). In all groups, 1 infant disappeared when it was <6 mo old and it could be reasonably presumed dead. Median age at natal dispersal was also similar among groups (Kruskal-Wallis test, χ^2=1.497, df=3, p=0.68) and so was the range of ages at dispersal. All groups had some individuals that tended to disperse relatively early (*ca.* 2 yr) and those that did relatively late (*ca.* 4 yr). The E350 group was consistently smaller than the other groups (Friedman test, χ^2=21.881, df=3, p<0.01) and never had >4 individuals, whereas all the other groups had at some point as many as 6 individuals.

Discussion

Size, Structure, Composition, and Food Availability of Territories

We found significant ecological differences in forest structure and composition among territories. General indicators such as species composition, diversity indices, and SBA showed that owl monkey territories were similar in terms of some broad characteristics; e.g., most plant species were present in all territories and most rare plant species tended to be rare in all territories. However, species evenness and stem density suggested clear differences among territories in forest physiognomy. More specific factors, such as stems per diameter class or per food species, were all highly variable both for the 50% core and the 80% home range areas. Thus, our prediction that there would be no significant differences among territories in the spatial distribution and abundance of food resources does not hold with respect to the general structure, composition, and food resources of these territories.

Those differences notwithstanding, we found some clear similarities among territories in potential food availability. For example, among the 80% home ranges, *Cecropia pachystachya* and *Guazuma ulmifolia* were found in similar quantities, while *Sideroxylon obtusifolium*, *Phytolacca dioica*, *Inga uraguensis*, and *Ficus* spp. were similarly present among the 4 50% core areas. *Phytolacca dioica* is a tree species with dark, dense foliage (Peña-Chocarro *et al.* 2006) regularly infested with lianas (60% of population in Atlantic forest, Argentina: Campanello *et al.* 2007),

which offers the owl monkeys a hidden cool sleeping site during the hot summer months (Aquino and Encarnación 1986; Puertas *et al.* 1995). Although the monkeys eat fruits and leaf buds from this tree (Arditi 1992; Giménez 2004), it is possible that the importance of this species is more related to sleeping habits than feeding given that owl monkeys have a narrow thermoneutral zone and might experience metabolically challenging conditions when confronted with high temperatures (Fernandez-Duque 2003). Sleeping sites are often characterized by specific ecological traits, and confer often underappreciated benefits to individuals (Anderson 1998; Fan and Jiang 2008). For example, among pair-living nocturnal Milne Edward's sportive lemurs, territoriality was intimately related to typical sleeping sites (Rasoloharijaona *et al.* 2003).

Particular food species were also present in different amounts in the various territories, but in high quantities in all of them. Among these were species recorded as food by most studies in the Chaco discussing owl monkey diet: *Chrysophyllum gonocarpum*, *Myrtaceae* spp., *Ocotea diospyrifolia*, and *Trichilia catigua*. These species did not show equal distributions over territories, but given that they were present in such large quantities, the differences among territories may have been over a threshold that satisfied the owl monkey needs. Addressing the amount of energy funneled from these food sources to the owl monkey groups could provide meaningful information about their importance in owl monkey ecology.

In spite of remarkably similar abundances of some food species, e.g., *Guazuma ulmifolia*, in all 4 territories, CC was qualitatively different. It exhibited the highest general species richness, highest plant food species richness, and the highest overall availability of resources. A particularly high-quality territory may alleviate the effects of asynchronous fruiting phenologies by decreasing the possibility of severe seasonal shortages and increasing the chance of year-round fruit production. Higher plant species richness can also reduce the risk of trace mineral, amino acid, or other deficiencies. For example, *Tabebuia* contains 6 amino acids in their flowers that are essential to humans (Milton 1999). *Tabebuia heptaphylla* is available only to groups CC and E500, and could therefore be disproportionately significant, even when in low numbers. In view of the particular characteristics of the CC territory, one could expect that it would be associated with the most successful group in terms of reproduction.

There are several possible explanations for the large differences in forest structure and potential food availability among territories. First, a twofold size difference existed between the smallest and largest territory of the 4 neighboring groups, although home-range sizes of our focal groups still fitted well into the range reported for *Aotus* spp. (0.33–12 ha: Fernandez-Duque 2011). Second, microsite availability leads to distinct spatial mosaics of tree communities in this forest (Barberis *et al.* 2002; Placci 1995) and dispersal limitations might in addition lead to clumped patterns of tree species abundance in dry tropical forests (Murphy and Lugo 1986). Indeed, differences in forest structure between nearby home ranges, or study sites, are not uncommon in primate studies (Balko and Underwood 2005; Potts *et al.* 2009). For example, in Kibale, Uganda, the densities of important food trees for red colobus (*Procolobus tephrosceles*) varied by a factor of 7 between nearby sites (Chapman and Chapman 1999). Finally, some differences could have been caused by natural and anthropogenic edge effects. In the past, loggers may have

preferentially cut trees that were easy to access. Territories located near the border of the gallery forest with the palm-savanna, such as E350 and E500, may thus have exhibited a higher stem density with overall smaller diameters due to recent regeneration after past selective logging events (Murphy and Lugo 1986; Placci 1995). Natural edge effects such as the higher occurrence of wind-throw, or generally smaller-statured trees due to higher desiccation rates or different phylogenies, could also have played a role in changing some territories and not others (Lehman *et al.* 2006; Placci 1995).

Forest Structure, Food Availability, Demographic Parameters, and Life-History Traits

We predicted that territories, irrespective of size, would offer similar types and amounts of resources and consequently support socially monogamous owl monkey groups with similar life histories. This prediction was not supported with respect to overall forest structure and food availability of most food sources. That is, our demographic analyses indicated that group sizes, birth rates, infant mortality, and age at natal dispersal were mostly similar among these 4 socially monogamous groups, while the territory characteristics were not. The only marked demographic difference among groups was that the group E350 was smaller than the others and never had >4 individuals. Over a 12-yr period, 1 riverside group, CC, and 2 landlocked groups, D500 and E500, were the same size. The benefit, if any, to the owl monkeys of specifically inhabiting a riverside territory, as suggested by a previous study of owl monkey demography (Fernandez-Duque *et al.* 2001), remains elusive. We can only speculate about factors that would lead to D500 having a larger group size than E350, when the former occupies the smallest territory that offers the fewest resources. The territory of E350 exhibited a higher stem density and relatively, but marginally, more tree individuals in smaller size classes. Such factors could lead to 1) smaller patch sizes sustaining consistently smaller groups, which would typically lead to fission in fission–fusion species (Balko and Underwood 2005; Chapman *et al.* 1995), or 2) fewer trees that produce fruits, or trees that produce smaller fruit crops, leading to a lower carrying capacity in general (Janson and Chapman 1999). Both propositions can be tested only by measuring phenology, and patch size, of food trees within several territories during complete years (Marshall *et al.* 2009; Miller and Dietz 2004).

The CC and E500 groups, with the "better territories," did not seem to derive benefits from access to improved food resources. Some primate species can clearly take advantage of additional resources, in space or time, such as red-tailed guenons (*Cercopithecus ascanius*) in Uganda (Chapman and Chapman 2000). When resource-related variables were equal among groups, ursine colobus monkeys (*Colobus vellerosus*) could still increase their group size, but this occurred concurrently with increases in home range, day range length, and time spent feeding (Teichroeb and Sicotte 2009). Species showing more demographic similarities to the owl monkeys also exist; in Western Madagascar, 9 groups of pair-living *Eulemur mongoz* had similar small group sizes, at least during 1 yr, and 2 neighboring groups had territories of comparable size and quality (Curtis and Zaramody 1998). In a study of flexible pair-living white-handed gibbons (*Hylobates lar*), it was likewise found that no differences existed in most measures of gibbon reproductive

performance, or among the little-overlapping home ranges in overall food production (Savini *et al.* 2008). Offspring mortality was the only factor that did differ in 1 home range, which was attributed to the higher incidence of falling as a result of longer travel distances in the larger home range. Although a similar effect of large territories did not occur in our study, other factors relating to forest structure, food availability, or other resources, e.g. sleeping sites, might have caused the lower size of group E350. It is also plausible that other external factors were limiting fluctuations in demographic parameters. A recent evaluation of the females' reproductive cycle in the seasonal environment of the Argentinean Chaco suggested that females may be cycling at times when they never conceive (Fernandez-Duque *et al.* in press). Moreover, although the seasonality of births in the region sometimes gets extended to late spring, it never starts before October; further reinforcing the notion that some constant abiotic factor, i.e. photoperiod, may be a major factor limiting an increase of female reproduction (Fernandez-Duque *et al.* 2002).

It is most likely not coincidental that other pair-living primates with stable home ranges, like our focal species, show similar demographics among their groups (Curtis and Zaramody 1998; Savini *et al.* 2008). Responses in group size or behavioral changes can strongly correlate with primate social structure and the ecological conditions under which it evolved and persists, which is linked to the form of competition within and among groups (Chapman and Rothman 2009; Marshall *et al.* 2009; Wrangham 1980). We suspect that the characteristics of some predominant or similarly available owl monkey food species relate to the ecological conditions under which owl monkeys' social system most likely evolved.

Seasonality and Fruiting Phenology

The seasonal availability of food sources seems to play a prominent role in the Azara's owl monkey ecology and behavior. For example, they reproduce seasonally (Fernandez-Duque *et al.* 2002), and they also disperse from their natal groups in a fairly seasonal manner (Fernandez-Duque 2009). For some primate species, the relationships among phenological patterns of species-specific foods, limiting seasons, and weaning or birthing periods can be very important (Brugiere *et al.* 2002; Ganzhorn 2002; Goldizen *et al.* 1988; Marshall and Leighton 2006; Potts *et al.* 2009). For this reason, researchers often include information about dietary flexibility or dietary preferences, e.g., annually most consumed species, fallback foods, in food availability indices (Potts *et al.* 2009; Savini *et al.* 2008). With our exceptionally complete but simple food availability measurements (stem counts, TBA), we principally come to the conclusion that territories are broadly different, especially when considering all foods as equally important. This somewhat simplistic conclusion might shift if we take into account the behavioral and phenological characteristics of owl monkeys and owl monkey foods. For example, when considering owl monkey fruit sources according to the season in which they predominantly provide fruit, we observed that some abundant wet season fruit sources (*Inga uraguensis*, *Phytolacca dioica*, *Sideroxylon obtusifolium*) were similarly available to the 4 groups. Three out of 6 strictly dry season fruit sources (*Guazuma ulmifolia*, *Cecropia pachystachya*, *Enterolobium contortisiliquum*) were evenly available among territories as well. The latter finding implies that especially dry season resources might support owl

monkey groups with similar life histories. We also found a similar presence among territories of individuals of *Ficus* spp.; these species can fruit at any time of the year and are potentially a rich source of protein (Felton *et al.* 2009). These findings partially support the prediction that there would be a relatively even distribution of food in space; food sources were evenly distributed in space, just not all food sources. Our findings also provide support for our last 3 predictions concerning demographic parameters; similarities among some food sources appear to be reflected in similar group sizes, births, and ages at natal dispersal.

Sources that reliably produce food and, in addition, provide edible fruits during the period of preferred foods scarcity can function as fallback foods (Lambert 2009; Marshall and Leighton 2006). Even though there has been considerable debate about the definition of fallback foods (Marshall *et al.* 2009), we consider that *Chrysophyllum gonocarpum*, *Guazuma ulmifolia*, and figs could function as fallback foods, while figs could also be preferred foods during certain times (Felton *et al.* 2008). Fruits of *Chrysophyllum gonocarpum* appear occasionally as early as April and can persist until December (Fernandez-Duque *et al.* 2002; Peña-Chocarro *et al.* 2006), resulting in an asynchronous but prolonged fruiting pattern similar to the dry season food resource *C. boivinianum* eaten by ruffed lemurs (*Varecia variegata*: Balko and Underwood 2005). *Guazuma ulmifolia* produces an annual fruit crop with peak production occurring around July (Fernandez-Duque *unpubl. data*; Peña-Chocarro *et al.* 2006). An ongoing study of the abundance of dry season foods and foraging will allow an examination of the importance that dry season foods may have on nutrition and reproduction of owl monkeys.

In contrast to *Guazuma ulmifolia* and *Inga uraguensis*, figs exhibit inter- and intraspecific asynchronous fruiting patterns (Fernandez-Duque *unpubl. data*; Janzen 1979). Although figs yield large fruit crops and show low interannual variations in fruit production (Janzen 1979; O'Brien *et al.* 1998), they can be a predictable year-round fruit source, from an owl monkey's perspective, only if they occur in such high numbers that there will always be a fruiting individual in the territory. Preferentially occupying a spatiotemporally fixed territory with sufficient, often ephemeral, figs might be difficult for the owl monkeys because this largely depends on host availability (Janzen 1979). However, in the Atlantic forest of Argentina, large percentages (83–96%) of the populations of *Chrysophyllum gonocarpum*, *Holocalyx balansae*, *Ocotea diospyrifolia*, *Ruprechtia laxiflora*, as well as *Patagonula americana* were infested with lianas (Campanello *et al.* 2007). These tree species were also well represented at our study site, offering opportunities for figs to germinate, establish, and persist. As demonstrated by our food availability data, the core areas offered similar quantities of stems of *Ficus* spp. The owl monkeys may thus preferentially occupy forest parts containing liana infestation-prone species, thereby ensuring a certain amount of figs, and possibly other lianas, e.g., for hidden sleeping sites, into their territories.

Fruits of *Inga uraguensis* are produced annually with a peak around March during the wet season and may also possibly play an important role during the period of lactation and subsequent weaning (Fernandez-Duque *unpubl. data*). Members of the genus *Inga* are widely dispersed, show regular annual fruiting patterns (Norden *et al.* 2007), and their typical fruit pods are consumed by many primate species (*Alouatta caraya*: Arditi 1992; *Cebus apella*: Galetti and Pedroni 1994; *Lagothrix lagotricha*:

Di Fiore 2003; *Aotus azarai*: Giménez 2004; *Ateles chamek*: Felton *et al.* 2008; *Alouatta guariba* and *Brachyteles arachnoides*: Martins 2008). The abundances, distributions, and phenological patterns of *Inga uraguensis*, *Chrysophyllum gonocarpum*, *Guazuma ulmifolia*, and *Ficus* spp. will thus require more detailed examinations in the future given their potentially important roles in the owl monkey's diet and socio-ecology.

Conclusion

We evaluated territory-wide species-specific abundances, TBAs, and demographic parameters of 4 neighboring groups of owl monkeys over 12 yr, and investigated how ecological factors relate to demography and life history. We did not reveal causal mechanisms underlying relationships, but developed hypotheses based on coincidences between qualitative predictions and the data. However, we clearly demonstrated that owl monkeys occupy territories that are different in size, structure, and potential food availability, although they had similar abundances of some wet season foods and most typical dry season foods. We also demonstrated that owl monkey groups have similar demographic characteristics. Our findings imply that group demographics and social systems of primate species might be closely linked to specific resources that are available to groups during certain limiting times of the year. An evaluation of the phenology and utilization, e.g., dietary preferences, by owl monkeys of food species over several complete years, and especially during the dry season, could clarify which roles plant species exactly play in owl monkey ecology and socio-ecology. Such an evaluation could also shed light on the underlying causes of plant distributions over territories. We expect to see greater life-history differences in owl monkey groups living in edge, fragmented, or drier environments. The Argentinean Chaco offers a notable comparative framework for a study in which the ecological limits of Azara's owl monkey can be examined.

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