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Abstract Limited food resource availability during yearly dry seasons can influence population dynamics and direct life-history evolution. We examined actual food production during two dry seasons and its relationship to feeding, life history, and demography in territorial, monogamous, and pair-living owl monkeys (*Aotus azarae azarae*). To quantify food availability in 16.25 ha of gallery forest in the Argentinean Chaco, we collected phenological data, from dry season fruit sources (N=894), twice a month, during July and August of 2008 and 2009. At the same time, we collected feeding data from the four groups (N=1448 h) inhabiting that forest portion. We also examined demographic data on births, natal dispersal, and group size. Our data show that owl monkeys occupy territories, and core areas, that produce food consistently, even during harsh times. Following the 2009 drought, less fruit was available than in 2008, but the 50 % core areas produced fruit amounts comparable to the 80 % territories. Owl monkeys showed dietary flexibility; fruits were the most frequent food item in 2008, whereas all groups increased their consumption of leaves in 2009. Infant production was lower in 2008 than after the drought of 2009. Interbirth intervals between the 2 yr were longer than the mean for the population, and more individuals dispersed in 2008 than in 2009. Our study suggests that owl monkeys occupy territories that provide similar amounts of reliable dry season foods within the core areas. Although access to these core areas may allow them to overcome severe dry seasons, our findings underscored the

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difficulties of understanding the potential causal relationships between ecological factors and demographic and life-history parameters.

Keywords Foraging · Monogamy · Phenology · Reproduction · Resource availability · Seasonality

Introduction

The tropical forests where most primates live are a complex habitat with a diverse and changing local environment (Chapman *et al*. 1997). In that environment, resources such as sleeping sites, cover from heat and predators, pathways to range and disperse, water, and food all influence primate abundance and distribution (Anderson 1998; DeGama-Blanchet and Fedigan 2006; Janson and Chapman 1999; Stevenson 2001). Understanding spatiotemporal changes in these resources, and which of them are essential to any particular population or species, is important for understanding feeding behavior, life history, and demography, and for directing conservation strategies (Marshall *et al*. 2009; Struhsaker 2008; van der Heide *et al*. 2012; Wieczkowski 2004).

Food sources in particular constitute an ecological factor that is strongly related to primate abundance, behavior, social systems, life history, and demography (Chapman and Chapman 2000; Di Bitetti and Janson 2000; Poulsen *et al*. 2001; Pruetz and Isbell 2000; Wrangham 1980). But in attempting to understand those relationships, it is necessary that food sources as a category are carefully deconstructed and contextualized. Considerations of what food sources are need to be specific to the taxon and the habitat under consideration, and then even a simple description of them is seldom accomplished fully. For example, seasonal forests are marked by extended periods of fruit scarcity and strong resource fluctuations (Murphy and Lugo 1986; van Schaik *et al*. 1993). In those habitats, populations are not always regulated by the overall level of productivity, but rather by the lowest level of food availability in an annual or supra-annual cycle (Lambert 2007; Marshall and Leighton 2006; Potts *et al*. 2009). Thus, to understand the influence of food resources on primate populations, it is necessary to examine the availability of foods at the limiting times because the carrying capacity of the habitat is likely controlled by the quality and/or quantity of food available during the period of food scarcity (Brugiere *et al*. 2002; Di Bitetti 2001; Fernandez-Duque *et al*. 2002; Marshall and Leighton 2006; Peres 1994). This insight has led to an increasing literature on the significance of fallback foods and on the relations among fallback foods; prolonged resource deprivation; and behavior, life history, and population dynamics (Altmann 2009; Chapman *et al*. 2010; Lambert 2009; Marshall *et al*. 2009).

When carefully examining relevant food sources, it is also necessary to consider spatiotemporal fluctuations. Frequently, the relationship between food and primate population biology is assessed at a spatiotemporal scale that makes it difficult to control for confounding factors such as the presence of potential predators and parasites, climate, isolation, phylogenetic constraints, or local traditions (Chapman and Rothman 2009; Marshall *et al*. 2010; Moura 2007; Vitazkova and Wade 2007). Even more importantly, too frequently the relationship is not described through the analyses of actual food available. For example, the estimation of fruit abundance using sampling transects or sampling plots does not tell us the actual food available, but gives us an estimate of the potentially available food. For many primate taxa, the complexity inherent in characterizing highly diverse forests, combined with relatively large home range sizes, makes it impossible to quantify the actual amount of food available to any given social group. Thus, it is only for an extremely small number of forests and primate taxa that the adequacy of the sample size or the adequacy of the proxies used for estimating food abundance in relation to home range size have been evaluated (Miller and Dietz 2004; Savini *et al*. 2008).

The territorial, pair-living and monogamous Azara's owl monkeys (*Aotus azarae azarae*) offer a suitable model for investigating the relationships among actual food availability, foraging, and reproduction. In the Argentinean Province of Formosa, owl monkeys inhabit subtropical, semideciduous, seasonally dry forests that are typically less productive and diverse than tropical rain forests (Placci 1995; van der Heide *et al*. 2012). Groups include one pair of adults and a few young who exploit a range of food resources distributed in small, slightly overlapping territories that range in size between 4 and 11 ha (Fernandez-Duque *et al.* 2011). Their territoriality reduces the confounding factor of intergroup competition in overlapping portions of neighboring home ranges (Harris 2006), whereas the presence of relatively small monogamous groups, as opposed to fission–fusion societies (Wallace 2008), minimizes the complexities inherent to characterizing the effects of food abundance on intragroup competition.

We recently completed an evaluation of the forest composition and structure of four owl monkey territories (van der Heide *et al*. 2012) that examined the relationships between potential food sources, female reproductive parameters, and group demography. The relatively small territory sizes allowed us to accomplish a complete characterization of forest structure and potential food availability, thus removing any potential problems associated with sampling (Chapman *et al*. 1994; Hemingway and Overdorff 1999; Miller and Dietz 2004). We found that the territories differ in size, species evenness, stem abundance and density, total basal area, and food species' stem abundances (van der Heide *et al*. 2012). Still, despite those differences, there were no marked differences among groups in some demographic parameters expected to be associated with territory quality: group sizes, birth rates, age at natal dispersal, and infant mortality were mostly similar among them. In other words, we did not find a strong relationship between *potential* territory quality and long-term demography when considering the whole territory and all of the foods available across the year.

To explore further the relationship between pair-living, monogamy, and territory quality, we present the results of a study that examined actual food production during two dry seasons and its relationship to feeding, life history, and demography. Given that the potential food available during the dry season tends to be similar (van der Heide *et al*. 2012), our hypothesis is that groups inhabit territories that allow them to overcome food shortages during the limiting dry season and that the demographic characteristics of the four groups are determined primarily by access to those dry season resources. To evaluate the hypothesis, we addressed the following questions: Are there differences among territories, both 50 % core areas and 80 % home ranges (following van der Heide *et al*. 2012), in the amount of fruit produced during the dry season? Do owl monkeys exhibit behavioral adjustments to cope with seasonality and/or changes in the spatial distribution of foods? Are dry season resources related to demographic and reproductive events in owl monkey groups? We predicted that there would be no marked differences among territories in fruit load during the dry season. If the dry season acts as a bottleneck, we expected owl monkeys to occupy areas that will provide enough food even during the harshest times. Regarding behavioral adjustments, if the amount and spatial distribution of preferred foods changed during harsh times, we would expect the animals to adjust accordingly. Finally, if the dry season resources were critical, we would predict that fruit load during that time would be related to aspects of owl monkeys' demography and life history. For example, we anticipated that the amount of fruit in the core and/or 80 % territories would be positively related to infant production (Clutton-Brock 1989; Savini *et al*. 2008).

Methods

Site and Focal Groups

We worked in the humid Argentinean Chaco, a habitat that includes pastures, palm savannas, patches of dry forest, and continuous gallery forest along the Pilagá River (Placci 1995). The study site is located in the cattle ranch "Estancia Guaycolec" (58°l3′W, 25°54′S), 25 km away from the city of Formosa in Formosa Province.

The study took place in a portion of gallery forest that has been relieved from logging, hunting, and grazing pressures for more than 15 yr and established as the Reserva Mirikiná in 2006. The forest, which is botanically diverse, including 65 species, 59 plant genera, and 30 plant families, shows a strong seasonal pattern in the production of leaves, flowers, and fruits (van der Heide *et al*. 2012). A system of intersecting transects at 100-m intervals covers *ca*. 300 ha of various forest types (Placci 1995; van der Heide *et al*. 2012).

The mean annual precipitation was 1536 mm (± 291, 1977–2010). Monthly mean rainfall varies significantly during the year, with two rain peaks in April (220±179 mm) and November (204±126 mm), and a low (53±53 mm) during June–August (Fernandez-Duque 2009). Monthly mean temperatures are lowest between May and August (16–18°C) and highest between October and March (23–27°C). Extreme low and high temperatures are also frequent. Daily minimum temperatures <10°C occur between April and September, whereas maximum daily temperatures >33°C are concentrated between September and March (Fernandez-Duque *et al*. 2002). A La Niña period, and associated weather conditions, were noticeable in Northern Argentina during 2008 and the first part of 2009, while El Niño weather started to gain momentum from June 2009 onward (Peterson and Baringer 2009; Alexander *et al*. 2010).

The owl monkey population in the gallery forest has been monitored demographically since 1997 (Fernandez-Duque 2009; Fernandez-Duque *et al*. 2001). For this study, we focused on four groups of known composition and demographic history (CC, D500, E350, and E500) that have been studied since 1997 (Fernandez-Duque et al. 2011). The territories of these groups have been fully characterized regarding the structure and composition of the forest (van der Heide *et al*. 2012). The four territories vary in the size of their 50 % core areas (1.3, 1.8, 2.4, and 2.7 ha) and 80 % home ranges (2.9, 4.1, 4.8, and 6.1 ha), as well as in the forest composition and structure, although certain potential food sources occurred in similar quantities (van der Heide *et al*. 2012). Owl monkeys might compete for food with sympatric howler monkeys

(*Alouatta caraya*), coatis (*Nasua nasua*), and frugivorous birds, e.g., *Toco toucan* (Arditi 1992; Hirsch 2009; van der Heide, *pers. obs*.), as they use some of the same food sources.

Data Collection

Dry Season Phenology Surveys To quantify food availability, we collected phenological data, twice a month, from the predominant owl monkey dry season fruit sources during July–August of 2008 and 2009 (van der Heide *et al*. 2012): *Chrysophyllum gonocarpum*, *Guazuma ulmifolia*, *Ficus* spp., and *Syagrus romanzoffiana*. In addition, we included the trumpeter flower tree *Tabebuia heptaphylla* for their importance as a flower (protein) source, and *Enterolobium contortisiliquum* in 2009 for their fruits, as these were observed to be heavily foraged in 2009, but not in 2008. In total, we monitored 894 individuals belonging to the six species within the 16.25 ha that encompass the four territories. For all species, except *Chrysophyllum gonocarpum* in 2009, we monitored all individuals present in the area surveyed; for *C. gonocarpum* in 2009 we randomly monitored 197 individuals of the 583 present in the area. Individuals of *Chrysophyllum gonocarpum* flowered for only *ca*. 2 wk in February and March 2009 (*unpubl. data*) because of a drought (0 mm of rain in both March and April), and at the beginning of the 2009 dry season we did not detect any fruits on them, nor did we observe owl monkeys feeding on fruits of *C. gonocarpum*; therefore *C. gonocarpum* was not systematically monitored in 2009.

We collected categorical data on leaf, flower, and flower bud phenophases (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 %), recording which percentage of the tree crown showed the particular phenophase. 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 (van der Heide *et al*. 2012).

Dry Season Feeding To describe owl monkey feeding patterns during the dry season, we collected feeding data during July–August of 2008 and 2009, simultaneously with the dry season phenology surveys described earlier. We collected feeding data during 46 full-day (≥10 h) and 29 half-day (3 to 10 h) follows in 2008, and during 59 full-day and 19 half-day follows in 2009. We observed the four groups during 696 h in 2008 (CC: 191 h, D500: 183 h, E350: 165 h, E500: 157 h), and during 752 h in 2009 (CC: 201 h, D500: 189 h, E350: 66 h, E500: 196 h). Thus, the total 1448 h of observations were relatively well-balanced across the two study periods and groups.

During each follow we collected feeding data at instantaneous focal points every 2 min and every time a feeding bout occurred. We defined a feeding bout as the period between the time when we observed a group member first feeding from a new plant individual, e.g., liana, tree, and the time when we observed the last individual finish feeding from the same plant individual. For each feeding bout, we recorded the start and end time, tree number, plant part eaten, and maximum number of individuals feeding. We marked all untagged food trees for later identification and measurement. We recorded the following plant parts as eaten: fruit, flower, new leaf, mature leaf, other, or unknown. When the monkeys were eating from vines, epiphytes, or lianas, we recorded the type of life form and species if known. When a hemi-epiphyte was recorded as the life form, we assigned it to the genus *Ficus*, as no other hemi-epiphytes occur in the area (van der Heide *et al*. 2012). The unknown plant individuals were identified afterward by the field manager or a local long-term field assistant/botanist. A small percentage of total feeding bout time (*ca*. 4 %) could not be linked to the food source. Most of these bouts involved short feeding periods, during which the observer did not have enough time to gather accurately all necessary information about the food source. For analyses we classified all those undetermined cases as "unidentified."

Demography and Life-History Events Most focal groups in the population have been contacted at least once a month to collect demographic data since 1997, and the four focal groups were usually contacted weekly since then. We contacted the groups during active periods that take place early in the morning (05:00–09:30 h) and late in the afternoon (16:00– 19:30 h) given the cathemeral habits of the species (Fernandez-Duque *et al*. 2010). When we contacted a group, we observed it for ≥15 min and collected data on group composition, encounter time, behavioral state, and position of the group relative to the transect system. A more detailed description of demographic data collection is presented elsewhere (Fernandez-Duque 2009).

Data Analyses

Dry Season Fruit Availability To examine fruit availability, we limited our analyses to maturation states known to be eaten by owl monkeys in the area based on our own observations and published studies (Arditi 1992; Wright 1985). For *Enterolobium contortisiliquum* we included only overmature, black fruit pods, whereas for *Guazuma ulmifolia* we excluded overmature black fruits. For *Syagrus romanzoffiana* we included only fruits ripened to a fleshy, yellow state. For *Ficus* spp. and *Chrysophyllum gonocarpum* we considered all maturation states. Of the *Chrysophyllum gonocarpum* trees sampled in 2009, 100 showed no phenological activity, 12 had a mean of 9 fruits, and the remaining ones had only new leaves as phenological activity. From these data we produced fruit estimations of *Chrysophyllum gonocarpum* for every territory in 2009, by calculating the mean number of fruits per tree and multiplying by the number of trees of *C. gonocarpum* in a territory.

We summed all fruit counts of edible maturation states per survey (two in July, two in August), per year, per species, and per territory. We compared overall differences in fruit production during the 2 yr with a Mann–Whitney *U*-test and we computed an estimator of effect size r for the test as Z/Sqrt (N). The differences among territories within a year were evaluated statistically with a Friedman test for repeated measures. Because there is no standard effect size estimator for the Friedman test, we calculated the effect sizes for each of the *post hoc* pairwise comparisons.

Dry Season Feeding We compared the percentage feeding time (% FT) spent on each food item per group and year and analyzed the use of species and life forms. Feeding time is defined as the total minutes spent feeding in the 2-mo period as determined by feeding bout durations. Group dietary differences between years were analyzed using χ^2 goodness of fit tests treating percentages as counts. We estimated r, the effect size for a goodness of fit test, as Sqrt ($\chi^2/(N)(c - 1)$), where N is the total sample size (total number of feeding bouts considered) and c is the number of categories considered (four groups).

Demography and Life-History Events To evaluate the relationship between dry season food availability and life-history traits, we examined the monthly demographic records of the groups to summarize information on infant production, mortality, age at natal dispersal, group size, and group composition between October 2007 and March 2010. This is a period that encompasses the infants born in 2007 whose survival could have been influenced by the dry season of 2008, as well as infants born in 2008 and 2009.

Results

Dry Season Fruit Availability

The 80 % home range of D500 produced the fewest fruits, whereas the other three home ranges were more similar in their productions (Fig. 1a). The differences among groups were not statistically significant for *Chrysophyllum gonocarpum* (χ^2=3.60, df=3, P=0.31), *Ficus* spp. (χ^2=7.15, df=3, P=0.07), or *Guazuma ulmifolia* (χ^2=5.40, df=3, P=0.15).

Among 50 % core areas, CC offered most fruits, especially of *Chrysophyllum gonocarpum* (Fig. 1a,b). Differences among the 50 % core areas were statistically significant for *Ficus* spp. (χ^2=9.90, df=3, P=0.02), with effect sizes for differences between pairs of groups ranging between 0.2 and 0.6, but were not statistically significant for *Chrysophyllum gonocarpum* (χ^2=3.60, df=3, P=0.31) or *Guazuma ulmifolia* (χ^2=5.10, df=3, P=0.17).

Mean fruit production in the 2009 dry season was a third of that in the 2008 dry season for both the 80 % home range (2008: 20,267±5353; 2009: 7271±1820, z=−2.31, P=0.02, r=−0.82) and the 50 % core areas (2008: 10,886±3578; 2009: 4822±1162, z=−2.31, P=0.02, r=−0.82; Fig. 1a,b). The differences were due primarily to the nonfruiting of individuals of *Chrysophyllum gonocarpum* in 2009, whereas the productivity of *Guazuma ulmifolia* was similar in both years and the productivity of *Ficus* spp. was higher in 2009 than in 2008 (Fig. 1a,b).

Absolute differences among 80 % territories were small in 2009 (Fig. 1a,b). There was a statistically significant difference in the production of *Enterolobium contortisiliquum* (χ^2=12.00, P=0.01), but not in the production of *Guazuma ulmifolia* (χ^2=6.30, P=0.10) or *Ficus* spp. (χ^2=7.50, P=0.06).

In 2009, absolute differences among the 50 % core areas were also relatively small. The core areas had no statistically significant differences in the availability of *Ficus* (χ^2=0.030, P=0.96), whereas their production of *Guazuma ulmifolia* and *Enterolobium contortisiliquum* differed significantly (*G. ulmifolia*, χ^2=11.10, P=0.01; *E. contortisiliquum*. χ^2=10.03, P=0.02).

Dry Season Feeding

The groups had very different diets in 2008 and 2009 (Fig. 2). Fruits were the most frequent food item in 2008, and there were no statistically significant differences

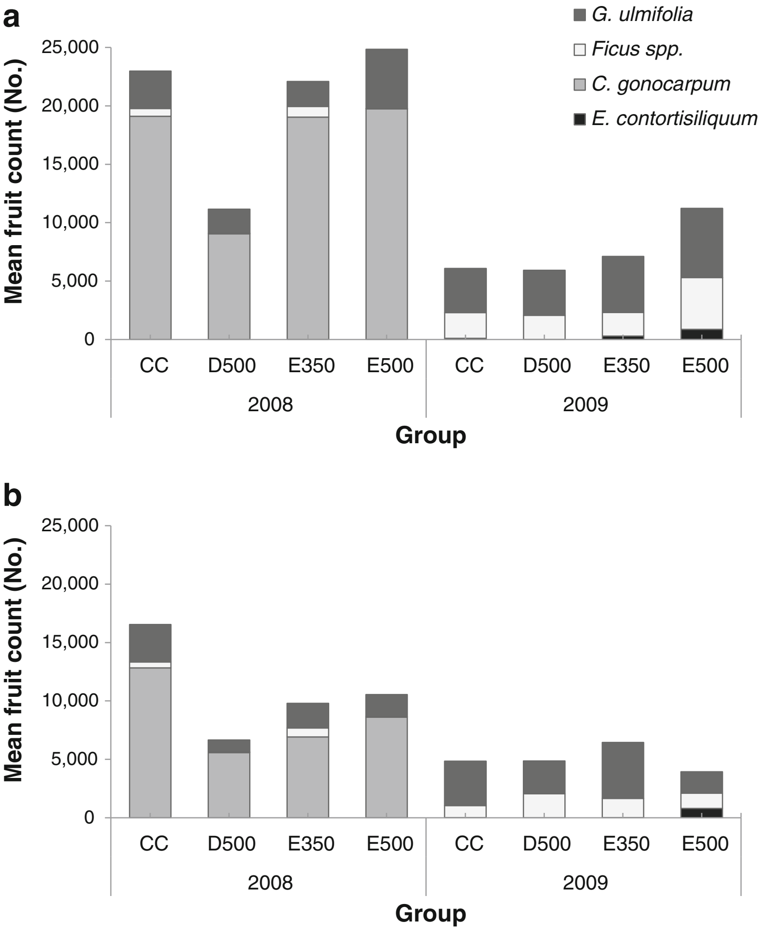

Fig. 1 Mean July–August fruit counts for each group territory of *Aotus azarae* in the ranch Estancia Guaycolec of Argentina during the dry seasons of 2008 and 2009. **(a)** 80 % home range areas. **(b)** 50 % core areas.

among groups in the percentage of feeding time spent on them (χ^2=1.1, df=3, *P*=0.77; Fig. 2a). In 2009, fruits were a less frequent food item, and group differences in the percentage of time devoted to feeding on them were statistically significant (χ^2=8.4, df=3, *P*=0.04, *r*=0.13; Fig. 2b). By contrast, the percentage time spent feeding on leaves was higher in 2009 than it was in 2008. The differences among groups in percentage time spent feeding on leaves were more pronounced in 2008 than 2009 (Fig. 2a,b), although neither was statistically significant (χ^2=7.3, df=3, *P*=0.06; 2009, χ^2=6.4, df=3, *P*=0.10).

In 2008, the groups did not differ in the percentage of time spent feeding from *Chrysophyllum gonocarpum* (Table I; χ^2=1.6, df=3, *P*=0.66). *Ficus* spp. were also an important food source that year, with all groups spending a similar percentage of time feeding from it (χ^2=3.3, df=3, *P*=0.34, *r*=0.13). The epiphytes *Rhipsalis* sp. and *Phoradendron* sp. were additional important food items; their use showed more variation among the groups but the differences did not reach statistical significance

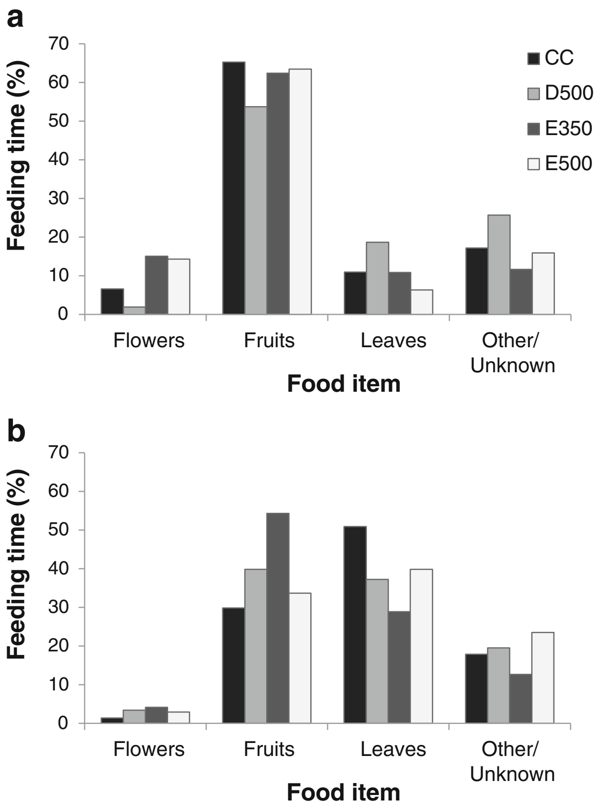

Fig. 2 Percentage of feeding time spent by each group of *Aotus azarae* in the ranch Estancia Guaycolec of Argentina on the different food items. **(a)** Dry season 2008. **(b)** Dry season 2009.

Table I Percentage of feeding time, per group, allocated to seven species or growth forms that were in one or both dry seasons among the top three of at least one of the groups

	2008						2009					
	Group						Group					
Species	CC	D500	E350	E500	Mean	SD	CC	D500	E350	E500	Mean	SD
Chrysophyllum gonocarpum	26.5	26.0	19.5	25.1	24.3	3.3	0.2	0.7	3.8	3.1	1.9	1.7
Citrus sp.	0.0	0.0	14.9	7.3	5.6	7.1	0.0	5.2	5.7	2.4	3.3	2.7
Epiphyte	17.8	11.5	6.4	15.9	12.9	5.1	0.0	4.7	3.4	1.9	2.5	2.0
Ficus spp.	19.8	17.0	10.2	16.8	16.0	4.1	17.7	35.5	46.5	30.2	32.5	11.9
Guazuma ulmifolia	10.9	5.7	23.3	3.9	10.9	8.7	25.8	17.4	16.1	12.2	17.9	5.7
Liana	1.1	0.4	0.2	0.5	0.6	0.4	18.1	5.4	13.3	11.6	12.1	5.3
Vine	0.2	2.3	0.0	0.4	0.7	1.1	10.1	12.3	4.2	4.2	7.7	4.1
Total	76.3	63.0	74.4	70.0			71.9	81.2	92.9	65.6		

The top three species for every group and for both years are underlined.

(χ^2=6.8, df=3, P=0.08, r=0.21). However, there were statistically significant differences in the percentage of time the groups spent feeding on *Guazuma ulmifolia* (χ^2=19.8, df=3, P<0.01, r=0.39).

The groups had qualitatively different diets in 2009 (Table I). They spent barely any time feeding on *Chrysophyllum gonocarpum*, and instead spent 18–46 % of the feeding time feeding on *Ficus* spp. and 12–26 % on *Guazuma ulmifolia*. The differences among groups in the time they spent feeding on *Guazuma ulmifolia* were not statistically significant (χ^2=5.9, df=3, P=0.12), but were significant for the time spent feeding on *Ficus* spp. (χ^2=12.6, df=3, P=0.01, r=0.18). Lianas and vines, which were hardly included in the groups' diets in 2008, were an important food source in 2009 when the groups fed heavily on the leaves of these life-forms (vines, χ^2=6.8, df=3, P=0.08; lianas, χ^2=7.2, df=3, P=0.07).

Demography and Life-History Events

Infant production was lower in 2008 (one of four groups) and higher in 2009 (three of four groups) than the historical population mean (56 %, 15 birth seasons, Fernandez-Duque, *unpubl. data*). The three groups that did not have infants in 2008 had them in 2009, whereas the only group that had an infant in 2008 did not give birth again in the following year. Thus, the interbirth interval for the four groups was ≥2 yr.

All groups changed in composition and size during 2008 and 2009 owing to births, disappearances, presumed deaths, and evictions of resident adults (Table II).

Discussion

Dry Season Fruit Availability

Our data show that owl monkeys occupy territories, and, more importantly, core areas, which produce food even during harsh dry seasons. After the 2009 drought, the

Table II Group size and composition of the four study groups during the dry seasons of 2008 and 2009

Group	Year	Group size	Birth	Death	Dispersal	Replacement
CC	2008	4/5	No	No		
	2009	4	Yes	No	Cata (August 3)	
D500	2008	4	No	No	Diáfano (September 26)	Dinamita (September 3)
	2009	3	Yes	No		
E350	2008	3/4	No	(Emilia)	Emilia (June 29)	
	2009	3	Yes	Eros (October 15)		
E500	2008	3	Yes	Inf07	Emma (January 15)	
	2009	4	No	No		

Demographic events during the years 2008 and 2009 are also presented. AM=adult male >48 mo; AF=adult female >48 mo; SA=subadult >24–48 mo; Juv=juvenile >6–24<mo

50 % core areas of CC, D500, and E350 produced very similar fruit amounts, in absolute terms, compared to the 80 % territories. Core areas of exclusive use were thus more productive in this harsh dry season than the rest of the territories. Three tree species were crucial in providing resources during the dry season: *Chrysophyllum gonocarpum*, *Guazuma ulmifolia*, and *Ficus* spp.

Chrysophyllum gonocarpum fruits with a prolonged but asynchronous pattern (Fernandez-Duque *et al*. 2002; Peña-Chocarro *et al*. 2006), as does its congeneric *C. bolivinianum* (Balko and Underwood 2005). In the Argentinean Chaco, El Niño and La Niña weather oscillations are usually associated with unusually wet and dry years, respectively (Barros *et al*. 2008; Fernandez-Duque *et al*. 2002). Phenophase abundance in this gallery forest fluctuates accordingly, with maturation of fleshy fruits usually higher after a rainy April (Placci 1995). Maturation of fruits of *Chrysophyllum gonocarpum* occurred successfully after average rainfall (mean rainfall February–April=123 mm) in early 2008, but failed to fruit after several dry months in late 2008 (mean rainfall September–December=74 mm) and early 2009 (0 mm).

The increase in the percentage of time the groups spent feeding on *Guazuma ulmifolia* and figs during the harsh dry season of 2009 (Table I) suggests that these species may be filler fallback foods (Marshall *et al*. 2009), albeit this does not necessarily imply a mixed or high-quality fallback strategy (Lambert 2007; Marshall *et al*. 2009). *Guazuma ulmifolia* produces a consistent fruit crop every year (Fig. 3 in Peña-Chocarro *et al.* 2006). Figs also produce very large fruit crops with low interannual variation, but these characteristics contrast with their unpredictable asynchronous intra- and interspecific fruiting patterns (Fernandez-Duque, *unpubl. data*; Janzen 1979; O'Brien *et al.* 1998). As demonstrated by the potential (van der Heide *et al*. 2012) and actual (this study) dry season food availability, as well as the feeding data, all the core areas offered important quantities of stems and/or fruits of *Ficus* spp. These results suggest that owl monkeys are able to occupy territories with similar amounts of this ephemeral food source.

Dry Season Feeding

During the harsh dry season of 2009 all groups incorporated more leaves into their diet, obtained mainly from vines and lianas, possibly to counteract fruit scarcity. These life forms are fairly abundant in the South American Chaco and other tropical forests (Campanello *et al*. 2007; Lorea and Brassiolo 2007; Schnitzer and Bongers 2002) and lianas in particular tend to be more abundant in drier, more seasonal tropical forests (DeWalt *et al*. 2010) and can therefore constitute an important, but poorly studied, primate food resource. Primate species that have generalized, flexible diets are regularly shown to be resilient in fruit-scarce years or seasons (Curtis and Zaramody 1998; Peres 1994; Tutin *et al*. 1997). In the Argentinean and Paraguayan Chaco, Azara's owl monkeys also inhabit xerophytic forest islands (Giménez 2004; Wright 1985), where they regularly consume more leaves, confirming the dietary flexibility observed in our study system (Ganzhorn and Wright 1994; Giménez 2004; Wright 1985). Leaves are protein-rich organs, compared to most fruits, even though the protein can be less accessible in leaves (Janson and Chapman 1999). Fruits of neotropical plant taxa, however, are generally richer in protein than fruits from paleotropical taxa (Ganzhorn *et al*. 2009). Few studies have been conducted on macronutrient optimization by primates (Rothman *et al*. 2011), and at least one study by Felton *et al*. (2009b) showed that foraging efforts of *Ateles chamek* in the lowlands of Bolivia were strictly regulated by the availability of protein-rich foods. In the future, the analysis of macronutrient content of owl monkey foods during key owl monkey life-history events will provide greater insight into the significance of fruit and leaf consumption for these primarily frugivorous primates (Chapman *et al*. 2003; Felton *et al*. 2009a; Worman and Chapman 2005).

Demography and Life-History Events

There is abundant evidence in support of the effects of seasonal factors on the biology of owl monkeys in the forests of the Argentinean Chaco. Azara's owl monkeys have seasonal patterns of activity (Erkert *et al*. 2012), give birth during a short period in the spring (October–December), have short mating seasons in the fall (Fernandez-Duque *et al*. 2011), and seasonal peaks in natal dispersal (Fernandez-Duque 2009). Given estimates of gestation length in the population (Fernandez-Duque *et al*. 2011), we can assume that females usually conceive at the beginning of the dry season (June–July). If the dry season were an energetic bottleneck, then adverse conditions right before or during it could impede reproduction by limiting conceptions, or result in miscarriages because of suboptimal nutritional conditions. Alternatively, conceiving at the beginning of the dry season may be the consequence of females taking advantage of the prior wet season to improve their energetic status (Savini *et al*. 2008).

Our results on infant production are interesting in an unexpected manner. Infant production in the four groups that we studied was not representative of population-wide patterns. Although only one group in our study had an infant, a population-wide analysis of habituated and nonhabituated groups conducted in 2008 (Fernandez-Duque, *unpubl. data*) suggests higher than average infant production that year (17 of 23 groups produced infants). Conversely, although three of the study groups produced offspring in 2009, fewer than half of the monitored groups in the population (10/23) had infants that year. During the study, the four groups also experienced interbirth intervals that were longer than the median interbirth intervals of 370 d for the population (Fernandez-Duque *et al*. 2002). Given that the birth season is usually limited to October and November, and only rarely extends into December or January, there may not be enough temporal flexibility to extend the interbirth interval. In other words, in this seasonal environment there may be a short timeframe for conception; if conception is delayed past a critical time, reproduction may not occur in that year at all. The consequence is that the length of the interbirth interval ranges between 12 and14 mo, or is longer than 2 yr.

The careful examination of group dynamics and female life history characteristics, e.g., age, may contribute to explaining the observed patterns of female reproduction. With regard to the lower than average reproduction in 2008, one of the females had a late birth in 2007 (November 30), which may have affected her resumption of cycling in 2008. The female from D500, evicted in September 2008, may have been pregnant at the time. The third female, which did not produce young in 2008, was relatively old and had given birth in 4 of the 5 previous yr (2003, 2004, 2005, and 2007). In the population-wide poor birth season of 2009, one of the births was by the new female, which had evicted the resident adult in D500; this young female may have been energetically able to bear a pregnancy during a time of limited resources. A second female that gave birth conceived in mid-August (Fernandez-Duque *et al*. 2011) for a birth late in the season (December 22, 2009), suggesting possible energetics limitations during the normal mating season of May–June. The other relatively old female may have recovered energetically after not giving birth in 2008.

Even after an apparently harsh period experienced during early 2009, females were able to restore body reserves, presumably past a certain threshold level, and resume ovarian cycling (Bercovitch and Strum 1993; Koenig *et al*. 1997; Takahashi 2002). Thus, our results suggest that costs of lactation, weaning, and ovarian cycling resumption; social dynamics; resource availability; and environmental cues are likely factors determining the timing of mating and birth seasonality in owl monkeys, like in other primate species (Di Bitetti and Janson 2000; Fernandez-Duque *et al*. 2002; Goldizen *et al*. 1988; Tecot 2010). We suggest that the ecological dry season bottleneck period may not be the predominant period during which an energetic bottleneck period occurs for Azara's owl monkeys. Reproduction depends on the costs incurred by both adults during the period of lactation and carrying (Rotundo *et al*. 2005), in combination with the quantity and quality of resources after weaning and during the mating period. For example, the likelihood that Verreaux's sifaka (*Propithecus verreauxi verreauxi*) give birth was positively related to their mating season body mass (Lewis and Kappeler 2005).

It is currently unknown whether the dry season adversities can have delayed effects on dispersal and mortality. Juveniles and subadults may be forced to disperse as a result of decreased food resources (Fernandez-Duque 2009), and then be challenged with relatively higher costs of dispersal. The effects of decreased resources within territories might therefore not be incurred at a group level, but rather on a population level by the dispersing individuals that function as floaters for a while. Such effects are often not accounted for in primate studies. For example, in a study of ring-tailed lemurs (*Lemur catta*), >80 % of the males disappeared after a drought period, but the fates of these males were unknown (Gould *et al*. 1999).

An Owl Monkey Perspective on Monogamy, Territoriality, and Foraging Ecology

Owl monkeys are one of very few socially and genetically monogamous mammal taxa that show a prolonged and essentially exclusive mating relationship between one male and one female, territoriality, and extensive male involvement in offspring care (Fernandez-Duque *et al*. in prep.). Traditional socioecological models have hypothesized that monogamy is a system imposed on males when either the spatial or temporal distribution of females makes it difficult for single males to simultaneously defend access to more than one mate (Dunbar 1995; van Schaik and van Hooff 1983). Under this hypothesis, females should be distributed in space, matching the availability of food, which is evenly distributed in relatively small patches that cannot support more than one female, while those patches should also be far enough from each other to prevent males from monitoring more than one female. Although we have not yet evaluated the patchiness of owl monkey food sources or the temporal distribution of reproductive females (Fernandez-Duque *et al*. 2011), our data agree well with the prediction that females are distributed in space matching the total availability of fruit, particularly during the dry season. Previous research suggests that at least some subadults (24–48 mo old; Huck *et al*. 2011) disperse during or shortly after the dry season, possibly as a result of increased resource competition (Fernandez-Duque 2009). In view of these findings, it is plausible that territories do not provide sufficient foods to support additional individuals attaining adult weight (*ca*. 1 kg at 24 mo; Huck *et al*. 2011), let alone multiple pregnant or lactating females. Territorial primate species have fewer or no options to track resources outside their normal home range, which contrasts with nonterritorial or semiterritorial species that sometimes track transient and/or distant resources in times of food scarcity (Di Bitetti 2001; Peres 1994). For example, capuchins (*Cebus apella*) tracked the palm *Syagrus romanzoffiana* at Iguazú National Park, Argentina (Di Bitetti 2001). Fighting, chasing, and voicing resonant whoops at territory borders are an indication that tracking resources, or finding mates, outside one's own territory can be very costly (Fernandez-Duque 2009; van der Heide, *pers. obs*.). The fact that only two individual trees were shared by two groups during these two dry seasons, and were visited on different days, indicates that the only resources available to an owl monkey group are those within its territorial borders. This interlocked system of spatiotemporally fixed territories (Wartmann and Fernandez-Duque, *unpubl. data*) also makes it potentially difficult for floaters to obtain food.

In light of their monogamous mating systems, territoriality, i.e., spatiotemporally fixed home ranges, and expected high costs of reproduction, i.e., necessitating paternal care (Rotundo *et al*. 2005), Azara's owl monkeys may include sufficient, and similar, quantities of filler fallback foods in their territory to guarantee survival and reproduction at a steady rate. Our findings parallel the suggestion by Marshall *et al*. (2009) that primate species ensuring survivorship are adapted to and regulated by fallback foods, whereas primates with faster life-histories are adapted to the availability of preferred foods. It is therefore not surprising that owl monkey groups occupying territories of various sizes, but with equal food quantities during the harsh dry season, show similar demographic parameters leading to comparable life histories.

In conclusion, we thoroughly evaluated fruit production of four territories during two consecutive dry seasons, as well as the feeding patterns and demographic parameters of the four groups occupying those territories. Bearing in mind that the observational data we presented are not enough to reveal the causal mechanisms underlying the relationships examined (Taborsky 2008), we demonstrated that owl monkeys occupy territories that provide similar amounts of dry season foods. Our study also supports the notion that the spatial and temporal components of resource abundance should be investigated concurrently and preferably during a simultaneous study of primate foraging behavior and dietary choices. Even then, our findings underscored the difficulties of understanding the potential causal relationships between ecological factors and demographic and life-history parameters.

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