Seasonal Variations in the Diet and Feeding Effort of Two Groups of Howlers in Different Sized Forest Fragments

Jacob C. Dunn · Jurgi Cristóbal-Azkarate · Joaquím J. Veà

Abstract Little is known about how resource limitation affects the feeding ecology of primates in forest fragments. Here, we describe seasonal variation in the diet and feeding effort of 2 groups (RH and RC3) of howlers (*Alouatta palliata mexicana*) living in different sized forest fragments in Los Tuxtlas, Mexico. The RH group, which lived in a larger and more preserved forest fragment, with a higher availability of fruit and *Ficus* trees, had a higher and more constant consumption of fruit throughout the study year. Moreover, this group fed from larger food sources, i.e., trees, lianas, and shrubs, and spent more time feeding from each food source. The feeding effort, defined as the time spent feeding and traveling divided by time spent resting, of the RH group was also significantly lower and more stable than that of the RC3 group throughout the study year. As feeding effort has been positively related to stress in primates, such increases in feeding effort could have negative consequences for howlers in small or degraded forest fragments. Our study suggests that habitat characteristics interact with plant seasonality to determine the diet and feeding effort of howlers in forest fragments and that groups living in small and degraded forest fragments may be particularly vulnerable to years of low fruit production.

Keywords Big trees · Diet · *Ficus* · Howlers · Seasonality

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Introduction

Habitat loss and fragmentation can affect the quantity and quality of food resources available to primates (Arroyo-Rodríguez and Mandujano 2006; Dunn et al. 2009; Medley 1993; Tutin 1999) because passive sampling and edge effects modify plant composition and vegetation structure (Benitez-Malvído and Martínez-Ramos 2003; Hill and Curran 2003). Passive sampling affects the presence and abundance of particular plant species in forest fragments (Connor and McCoy 1974), potentially limiting the availability of preferred resources for primates, while edge effects result in the increased mortality of big trees (Laurance et al. 2000; Malcolm 1994), which produce a greater quantity of food resources (Chapman et al. 1992). Indeed, plant species richness and the density of large trees have both been positively related to the distribution and abundance of primates in forest fragments (Arroyo-Rodríguez and Mandujano 2009; Cristóbal-Azkarate et al. 2005).

Optimal foraging theory (MacArthur and Pianka 1966) predicts that as preferred foods become limited, more less-preferred foods will be included in the diet and food patches will be more depleted (Charnov 1976). Therefore, as mature fruits become scarcer, frugivorous primates are predicted to maintain net energy intake by including less ripe fruit in their diet and by consuming more fruit from each patch. However, as fruit abundance continues to decline, full compensation becomes increasingly difficult and net intake may begin to suffer. In this case, primates may be forced to make adjustments including adapting their activity pattern, switching their diet to fallback foods (for definition see Marshall et al. 2009), moving into a different habitat where resource abundance is higher, or reducing their basal metabolic requirements. Otherwise they may face episodes of generalized famine, which may affect their persistence (van Schaik and Brockman 2005).

Several studies have shown that howlers (*Alouatta*) maximize fruit intake when it is available and that when fruit is scarce they switch to a diet consisting almost entirely of leaves (Estrada 1984; Glander 1981; Milton 1980; Silver et al. 1998). However, despite being one of the most studied primate genera in forest fragments, there are no studies of how their diet varies seasonally in relation to habitat characteristics, and how such variations may affect their activity pattern. Determining this is important, as the regulatory processes controlling wild primate populations are often more notable at certain times of the year, e.g., during periods of fruit scarcity (Milton 1982; van Schaik and Brockman 2005).

In a previous study of 2 groups of Mexican mantled howlers (*Alouatta palliata mexicana*) living in different sized forest fragments with a marked difference in fruit availability in Los Tuxtlas, Mexico, we observed that howlers optimized their foraging when feeding from fruit, as this allowed them to spend less time traveling and feeding and more time resting. This was consistent with the results of previous authors (Asensio et al. 2007; Juan et al. 2000; Rodríguez-Luna et al. 2003; cf. Bicca-Marques 2003; Pavelka and Knopff 2004). Here, we analyzed the seasonal variations in diet and feeding effort (defined as the time spent feeding and traveling divided by time spent resting) of the same 2 groups. If feeding effort is negatively related to fruit consumption, then we may expect that both groups would increase their feeding effort during periods of fruit scarcity. Therefore, we predicted that both groups would increase feeding effort when fruit was reported to be less

available, but that the RH group, with a higher availability of fruit in its home range, would exhibit a lower overall feeding effort than the RC3 group. Understanding how habitat loss and fragmentation interacts with seasonality to affect the feeding ecology of Mexican mantled howlers is central to their conservation as an increasing component of the small remaining population is found in forest fragments, leading to this subspecies recently being listed as critically endangered by the IUCN (Cuarón *et al.* 2009).

Methods

Study Site

We conducted fieldwork in the northern part of the Los Tuxtlas Biosphere Reserve (18°37′–18°35′N, 95°08′–95°05′W; elevation 0–400 m asl) in southeast Veracruz, Mexico. Los Tuxtlas is the northernmost limit for howler populations (Estrada and Coates-Estrada 1988) and represents the most northerly tropical rain forest distribution in the American continent (Dirzo and Garcia 1992). The region has been severely fragmented during the last 60 yr, resulting in a loss of 88.3% of original forest cover (Guevara-Sada *et al.* 2004). As a consequence, the remaining howler population is spread across an archipelago of forest fragments that vary in size, isolation distance, age, and habitat quality (Arroyo-Rodríguez and Mandujano 2006; Arroyo-Rodríguez *et al.* 2008; Cristóbal-Azkarate *et al.* 2005).

Local Climate and Plant Phenology

In Los Tuxtlas the local climate is warm and humid with a mean annual temperature of 25°C and rainfall of 4900 mm (Soto and Gama 1997). Phenological records from the region (Estrada and Coates-Estrada 1991, 2001; Estrada *et al.* 1999; Ibarra-Manríquez and Oyama 1992) show that there are 2 distinct peaks in fruit production: a peak at the end of the dry season–beginning of the rainy season (April–June) and a peak in the wet season (August–October). However, fruit production falls abruptly to very low levels from November to March. Flowers are mainly produced during the dry season (March–May), while young leaf production is year round, but at its greatest during the dry season and beginning of wet season (March–June).

Forest Fragments and Focal Groups

The 2 howler groups observed during the course of this study resided in different forest fragments that were 2.25 km apart, Rancho Huber and Ruiz Cortines 3. Rancho Huber is a 244-ha fragment inhabited by 5 groups of howlers and the total population density is 0.12 ind/ha (Cristóbal-Azkarate *et al.* 2005). Ruiz Cortines 3 is a much smaller forest fragment (7.2 ha) inhabited by only 1 group of howlers (population density=1.11 ind/ha). We studied 1 group from each fragment, the RH group (from Rancho Huber) and the RC3 group (from Ruiz Cortines 3). The groups were similar in terms of age-sex composition (3 adult males, 3 adult females, 2 infants in each group, and 1 juvenile in the RH group: Dunn *et al.* 2009), and have

both been observed almost continuously since 1999 as part of long-term studies (Asensio *et al.* 2009; Cristóbal-Azkarate *et al.* 2005; Dunn *et al.* 2009).

Habitat Characteristics of Home Ranges

In a previous study, we calculated the home range area of the 2 groups from 12 mo of ranging data: the home range area of the RH group was 89.5 ha, and that of the RC3 group was 5.8 ha (Dunn *et al.* 2009). In Los Tuxtlas, home range area is known to be positively related to fragment size, and the average home range area (± SD) is 28.1± 21.7 ha (Cristóbal-Azkarate and Arroyo-Rodríguez 2007). Therefore the RH group's home range area was far larger than average, while the RC3 group's home range was much smaller than average, with potential implications for food availability.

We sampled the vegetation within the home range of each group following a modified Gentry (1982) protocol. We systematically located 40 50×2 m transects, distributing them evenly throughout the home range area of each group, and measured the diameter at breast height (DBH) of all trees ≥10 cm. In a previous study, we demonstrated that this sampling effort was adequate to characterize the vegetation in the home ranges of each group by randomly selecting a subset of 10 transects from each home range 100 times and comparing the mean results with the overall result from 40 transects (Dunn *et al.* 2009). To characterize fruit availability in the home range of each group, we conducted a literature search of all the available studies (published articles, book chapters, and theses) on the diet of *Alouatta palliata mexicana* in Los Tuxtlas (Cristóbal-Azkarate and Arroyo-Rodríguez 2007). We were able to determine the items consumed for 115 trees species, defined as consumable species, of which 69 species are reported as sources of fruit, defined as consumable fruit species (CFS) (Appendix I). We report the species richness, number of stems, and dominance (sum of basal area) of CFS, fig trees, and big trees (defined as those with a DBH >60 cm; Laurance *et al.* 2000) of consumable species in the home range of each group. Determining the availability of fig trees is important, as during periods of fruit scarcity, fig trees (*Ficus*) provide an important source of food resources for many animal species throughout the tropics (Shanahan *et al.* 2001), including primates (Felton *et al.* 2008; Leighton 1993; Milton 1980, Peres 1994). This is as they grow to be large trees, exhibit intraspecific asynchrony in fruit production, and often produce >1 fruit crop per year and large crops of new leaves for most or all of an annual cycle (Milton 1991).

Dietary Composition and Feeding Effort

We organized our sampling sessions throughout 1 complete year (February 2006– February 2007) into 10 periods (termed registration periods in Dunn *et al.*, 2009) of 16 d (8 d/fragment), for a total of 80 nonconsecutive observation days and 480 h/group. To increase independence between records, we alternated days between groups and left a gap of ≥7 d between periods. Although we aimed *a priori* to conduct our observations over 12 monthly periods, instead of 10 periods, we were unable to do so due to bad weather and unforeseen circumstances, which meant that we were unable to complete the 16 d each month. To increase independence between records, we alternated days between groups and left a gap

of ≥ 7 d between periods. The specific dates of the periods were as follows: 1 = February 4–March 2, 2006; 2 = March 10–April 6, 2006; 3 = April 24–May 20, 2006; 4 = May 28–June 14, 2006; 5 = July 12–August 1, 2006; 6 = August 9–August 27, 2006; 7 = September 6–September 26, 2006; 8 = October 7–October 25, 2006; 9 = November 14–December 18, 2006; 10 = January 20–February 9, 2007 (for further details see Dunn et al. 2009).

We broke each day down into 3 focal observation sessions (Altmann 1974), from 0700 to 0900 h, 1000 to 1200 h, and 1300 to 1500 h, during which we recorded the behavior of a single randomly selected adult individual. J. Dunn conducted all observations. We used EZrecord® for Palm Pilot® to record the data and we categorized behavioral observations into the following: resting (sleep or static without interaction), feeding (inspection of food, bringing food to mouth, chewing and swallowing, moving while feeding within a food source), traveling (movement to a new area or food source), and other behavior (remaining activities not categorized as resting, feeding, or traveling). During feeding we recorded the food item consumed: fruits, flowers, leaves, and others (petioles or bark). We report the consumption of food items in terms of total feeding time per period. Finally, we numbered, identified to species level, geo-located, and measured the DBH of each plant used by focal individuals as a food source, i.e., trees, lianas, and shrubs.

Statistical Analysis

We analyzed all the available quantitative data on plant phenology in Los Tuxtlas and calculated the mean percentage of species that contained fruit each month from the studies that presented these data (Estrada and Coates-Estrada 1991, 2001; Estrada et al. 1999; Ibarra-Manríquez and Oyama 1992). We also include data on flushing and flowering from one of these studies (Estrada et al. 1999) and fruit biomass from another (Estrada and Coates-Estrada 2001) (Fig. 1). As no
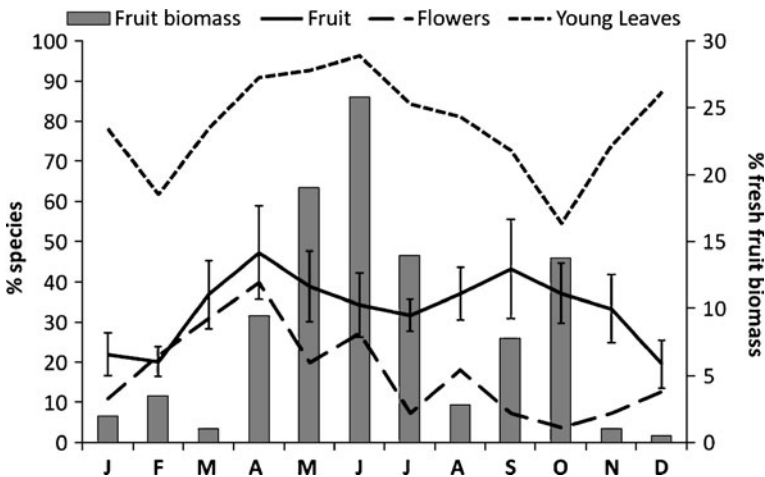

Fig. 1 Plant phenology in Los Tuxtlas. The mean percentage of tree species containing fruit is given from a meta-analysis of several publications (Estrada and Coates-Estrada 1991, 2001; Estrada et al. 1999; Ibarra-Manríquez and Oyama 1992). Data on flushing and flowering (Estrada et al. 1999) and fruit biomass (Estrada and Coates-Estrada 2001) are also presented.

phenological data has been published for the region since 2001, we analyzed climate data from the Los Tuxtlas Biology Field Station of the National Autonomous University of Mexico (*ca*. 5 km from the study site) for 1989–2006. The phenology of tropical forests correlates highly with temperature and rainfall (van Schaik *et al*. 1993) and, therefore, if there are no significant differences in climate between the study period and the years for which we have phenological data, we could reasonably expect few changes in plant phenology. We used Student *t*-tests to compare single observations of maximum and minimum temperature and rainfall in each month of the study period with the mean values from 1989–2006, as well as with the mean values from the years for which we have quantitative data on plant phenology (1991, 1992, 1999, and 2001) (Sokal and Rohlf 1995).

Following Cavigelli (1999), we calculated feeding effort by dividing the time spent feeding and traveling by time spent resting. We used Spearman correlations to examine the relationships between the percentage time spent feeding on different food items per period for each group and also used similar correlations to analyze the relationships between the items consumed and the number of species consumed, the mean DBH of food sources consumed, and feeding effort. We used Mann-Whitney *U* tests to compare diet and feeding effort per period between the 2 groups. We performed all tests with Statistica for Windows, version 5.5 (Anonymous 2000) and we considered $p<0.05$ as significant.

Results

Climate Data

We found no significant differences between the study period and the mean data from 1989–2005 in either maximum temperature or rainfall (Fig. 2). However, minimum temperature was significantly higher than average in October (Fig. 2a; $t=$ 2.4, df=15, $p=0.03$). We found no significant differences in maximum temperature between the study period and the means for the years for which we have quantitative data on plant phenology. However, the minimum temperature was significantly higher in October (Fig. 2a; $t=5.0$, df=2, $p=0.04$), and rainfall was significantly higher in June (Fig. 2b; $t=4.9$, df=2, $p=0.04$) and significantly lower in October (Fig. 2b; $t=-6.6$, df=2, $p=0.02$).

Habitat Characteristics of Home Ranges

The home range of the RH group contained higher species richness, a greater number of stems and higher dominance of CFS, big trees of consumable species, and fig trees than the home range of the RC3 group (Table I).

Diet

The consumption of plant items varied throughout the year (Fig. 3a). Both groups showed a very similar and marked peak in fruit consumption between late April and mid-June (periods 3 and 4), followed by a reduction in fruit consumption in July
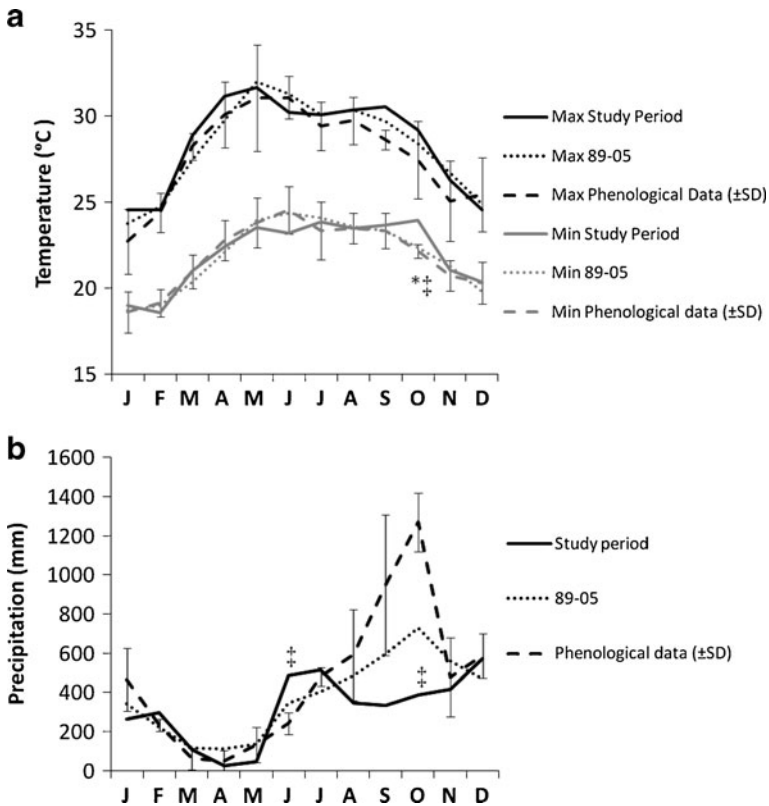
Fig. 2 Maximum and minimum monthly temperature (°C; **a**) and monthly rainfall (mm; **b**) at the Los Tuxtlas Biology Field Station of the National Autonomous University of Mexico during the study period, with mean data from 1989–2005 and mean data from the years from which phenological data is available (1991, 1992, 1999, and 2001). [*]Significant difference ($p<0.05$) between study period and mean from 1989–2005; Students t-test (df=15). [‡]Significant difference ($p<0.05$) between study period and the years from which phenological data are available; Student's t-test (df=2).

Table I General habitat characteristics sampled from 40 50×2 m transects in the home range of 2 groups of Mexican mantled howlers in different forest fragments in Los Tuxtlas, Mexico

	RC3			RH		
	SR[a]	No. of stems	DOM[b] (m²)	SR	No. of stems	DOM (m²)
CFS[c]	21	140	11	26	186	24.4
Fig trees	2	3	0.1	6	11	11.8
Big trees	2	5	2.9	8	18	16.8

[a] Species richness

[b] Dominance (sum of basal area)
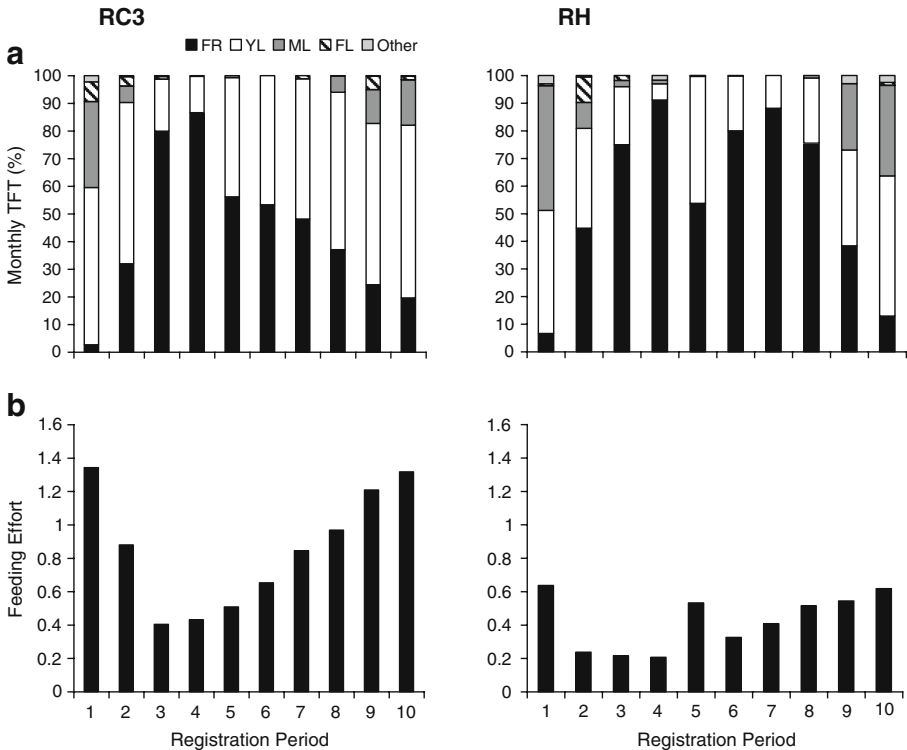
[c] Consumable fruit species

Fig. 3 Seasonal variation in diet and feeding effort (the ratio of time spent feeding and traveling divided by time spent at rest) of 2 groups of Mexican mantled howlers inhabiting different forest fragments in Los Tuxtlas, Mexico. FR = fruit; YL = young leaves; ML = mature leaves; FL = flowers.

(period 5). The RH group then returned to high levels of fruit consumption from August to October (periods 6, 7, and 8), by feeding heavily from nonfig fruits during period 6 and from figs during periods 7 and 8, while the RC3 group showed intermediate levels of fruit consumption and fed little from figs (Table II). Both groups consumed little fruit from November to March (periods 9, 10, 1 and 2). However, during periods 2 and 9 the RH group was able to consume some figs, and the RC3 group did the same in period 2, although less than the RH group (Fig. 2a; Table II).

Leaf consumption showed the opposite seasonal tendency, as fruit and leaf consumption correlate highly in both groups (RH, $r_s=-0.85$, $p<0.01$; RC3, $r_s=-0.99$, $p<0.01$). The consumption of flowers by the RC3 group correlates positively with leaf consumption (RC3, $r_s=0.84$, $p<0.01$) and negatively with fruit consumption (RC3, $r_s=0.84$, $p<0.01$), although we found no relationship in the RH group owing to the very little time they spent consuming flowers (leaf consumption, $r_s=0.45$, $p=0.20$; fruit consumption, $r_s=-0.580$, $p=0.08$). The consumption of other food items correlates positively with leaf consumption (RH, $r_s=0.68$, $p<0.01$; RC3, $r_s=0.61$, $p<0.01$) and negatively with fruit consumption (RH, $r_s=-0.69$, $p<0.01$; RC3, $r_s=-0.63$, $p<0.01$) in both groups (Fig. 3a).

The number of species consumed per period also changed with time (Table II) and correlates positively with the consumption of leaves (RH, $r_s=0.82$, $p<0.01$; RC3, $r_s=0.70$, $p<0.05$) and negatively with the consumption of fruit in both groups (RH,

Table II Seasonal variation in the feeding ecology of 2 groups of Mexican mantled howlers inhabiting forest fragments in Los Tuxtlas, Mexico

	Group	Period										Mean (± SD)
		1	2	3	4	5	6	7	8	9	10	
No. of species	RH	22	10	10	5	8	9	7	6	11	12	10.0 (4.8)
	RC3	30	26	13	18	22	12	15	21	20	22	19.9 (5.6)
Ficus (%)	RH	55.2	62.6	63.6	37.5	78.3	22.0	68.8	81.0	59.6	65.8	59.4 (17.9)
	RC3	12.5	32.0	34.5	20.5	15.7	1.7	33.5	19.0	25.4	22.0	21.7 (10.3)
% of fruit *Ficus*[a]	RH	29.5	99.0	80.4	35.1	89.0	27.0	69.2	74.0	92.0	71.6	66.7 (26.7)
	RC3	0.0	79.0	33.0	20.0	20.4	3.0	54.0	0.0	66.0	17.3	29.3 (28.2)
% of leaves *Ficus*[b]	RH	57.2	39.5	13.5	67.8	60.3	0.8	65.6	95.6	45	58.8	50.4 (27.4)
	RC3	13.0	7.4	86.0	23.0	9.7	0.0	14.0	31.4	18.0	23.0	22.6 (24.0)
Mean DBH (m)	RH	1.2	1.2	1.7	1.5	1.4	2.1	2.1	2.5	1.4	1.2	1.6 (0.5)
	RC3	0.5	0.6	0.6	0.6	0.6	0.7	0.6	0.5	0.6	0.6	0.6 (0.1)
Mean feeding time (min)	RH	20.5	12.6	20.6	18.6	35.2	16.8	27.3	39.9	27.5	23.4	24.2 (8.4)
	RC3	15.6	11.7	14.5	15.9	13.9	23.1	27.2	22.4	17.0	17.9	17.9 (4.8)

Values reported represent totals for the period

[a] Percentage of overall fruit consumption that corresponds to *Ficus*

[b] Percentage of overall leaf consumption that corresponds to *Ficus*

$r_s=-0.82$, $p<0.01$; RC3, $r_s=-0.70$, $p<0.05$). However, we found no relationship between the number of species consumed and the consumption of either flowers or other items in either group (flowers: RH, $r_s=0.57$, $p=0.08$; RC3, $r_s=0.54$, $p=0.10$; other items: RH, $r_s=0.61$, $p=0.06$; RC3, $r_s=0.33$, $p=0.36$). The number of species consumed by the RH group was higher in every period and significantly higher overall than in the RC3 group ($U=7.5$, $p<0.01$) Table II.

The use of fig trees by the RH group was also higher in every period and significantly higher overall than that by the RC3 group ($U=5$, $p<0.01$; Table II). The mean DBH of the food sources consumed by the RH group was higher than that found in the RC3 group in every period and significantly higher overall ($U=6$, $p<0.01$; Table II). The mean DBH of the food sources consumed correlates positively with fruit consumption and negatively with leaf consumption in the RH group ($r_s=0.73$, $p<0.01$, and $r_s=0.72$, $p<0.01$, respectively), although there is no significant relationship in the RC3 group (fruit: $r_s=0.33$, $p=0.35$; leaf: $r_s=-0.33$, $p=0.35$). Finally, the mean time spent feeding from each food source per period was higher in the RH group than the RC3 group overall ($U=24$, $p<0.05$) and in nearly all of the periods Table II.

Feeding Effort

Overall, feeding effort was higher in the RC3 group than in the RH group (mean±SD RH=0.42±0.17, RC3=0.86±0.35: $U=16$, $p<0.05$). In both groups feeding effort correlates negatively with fruit consumption (RH, $r_s=-0.76$, $p<0.01$; RC3, $r_s=-0.98$, $p<0.01$) and positively with leaf consumption (RH, $r_s=0.85$, $p<0.01$; RC3, $r_s=0.98$, $p<0.01$; Fig. 3b). However, there is no relationship between feeding effort and either the consumption of flowers of other food items in either group (flowers: RH, $r_s=0.02$,

p=0.96; RC3, r_s=0.65, p=0.11; other food items: RH, r_s=0.55, p=0.10; RC3, r_s= 0.41, p=0.24).

Discussion

The 2 groups we observed exhibited notable differences in their diet and feeding effort throughout the year, consistent with the fact that the availability of important food resources differed between their home ranges. Both groups showed a very similar and marked peak in fruit consumption between April and June, coinciding with the annual major peak in fruit production reported for the Los Tuxtlas region (Fig. 1). However, between August and October, when a secondary, less intense period of fruit production is reported, the RC3 group reduced fruit consumption considerably, while the RH group, with a higher availability of both consumable fruit species (CFS) and *Ficus* in their home range, maintained high levels of fruit consumption. We observed the lowest levels of fruit consumption in both groups between November and April, coinciding with the annual period of fruit scarcity reported for the region. However, principally by feeding from figs, the RH group maintained intermediate levels of fruit consumption during periods 2 and 9, and the RC3 group did the same during period 2, although to a lesser extent.

Despite the marked differences in the availability of both CFS and figs between home ranges, both groups consumed practically no fruit from late January to early March, coinciding with the lowest reported point in fruit availability in Los Tuxtlas, and switched to diets consisting almost entirely of leaves. This suggests that fruit was equally unavailable in both habitats during this period and indicates that seasonal patterns of fruit production can sometimes be more important than habitat characteristics in determining the diet of howlers. Nevertheless, in general, living in a larger and more preserved home range allowed the RH group to maintain a higher and more constant level of fruit consumption. These results highlight the importance of long-term data in studies of the diet of primates in fragments and suggest that any short-term studies would be more likely to find differences between groups living under different conditions during periods of resource scarcity than during periods of abundance.

Phenological data was unavailable during the study period, an important limitation in our analyses. However, evidence suggests that changes in fruit consumption by the 2 focal groups do reflect the variation in fruit production in their habitat. First, howlers are known to consume fruit when it is available (Estrada 1984; Glander 1981; Milton 1980). Second, variation in fruit consumption in our focal groups was consistent with the reports of fruit production for the Los Tuxtlas region (Estrada and Coates-Estrada 1991, 2001; Estrada *et al*. 1999; Ibarra-Manríquez and Oyama 1992). Finally, we found very few significant differences in precipitation and temperature either between the study period and the period from 1989 to 2005 or between the study period and the years for which quantitative data on plant phenology were available. This suggests that there are unlikely to have been significant changes to the general patterns of plant phenology in the region during the study period. However, long-term studies of plant phenology in the Los Tuxtlas region are needed to understand fully the way in which the availability of different food resources may affect howlers in forest fragments. This may be particularly

important given that in the future climate change is predicted to have significant effects on plant phenology and vegetation structure (Chapman *et al*. 2005).

In a previous study we observed that howlers visited more food sources when feeding from more leaves, which, in turn, resulted in more traveling, more feeding, and less resting (Dunn *et al*. 2009). Accordingly, and in agreement with our prediction, we found that feeding effort was negatively related to fruit consumption and positively related to leaf consumption in both study groups. This could be explained by the lower amount of energy howlers probably gain per food patch (Glander 1981; Milton 1979), as well as the need to diversify food sources when consuming leaves. In general, animals are thought to diversify food sources when consuming leaves to: 1) obtain the best complement of nutrients (the nutrient constraint hypothesis; Westoby 1978), and 2) avoid an overload of particular toxins or digestibility reducing compounds (the detoxification limitation hypothesis; Freeland and Janzen 1974). Our results support the fact that howlers diversify food sources when consuming leaves, as we found that fruit consumption was negatively related to the number of species consumed. These results are also consistent with the predictions of optimal foraging theory (MacArthur and Pianka 1966), as when fruit was reported to be more limited, howlers made adjustments to their diet, consuming more leaves and a greater number of species.

Despite the relationship we found between fruit consumption and feeding effort, the differences in feeding effort we observed between groups cannot be explained solely by differences in fruit consumption. This is because fruit consumption was very similar in both groups during the primary peak in fruit consumption and during the lowest point in fruit consumption, yet the feeding effort of the RH group was only about half of that of the RC3 group during these periods. Although this agrees with our prediction that the RH group, with a higher availability of fruit in its home range, would exhibit a lower overall feeding effort than the RC3 group, it is interesting to note that there were differences in feeding effort between groups, despite there being no difference in diet between groups at these times. This may be related to the fact that the RH group was able to feed from bigger food sources (Table II), which generally contain more plentiful resources (Chapman *et al*. 1992) and are depleted more slowly (Chapman 1988). By feeding from larger food sources, the RH group was able to spend more time feeding from each food source than the RC3 group, which allowed them to reduce their feeding effort. In our previous study (Dunn *et al*. 2009), we established that when feeding from larger food sources the 2 focal groups traveled shorter distances, spent less time traveling and feeding, and rested more. Here we observed that the availability of big trees was particularly important to the RH group during the period of lowest fruit consumption (presumably also the period of lowest fruit production), as, unlike the RC3 group, the RH group was able to maintain a low and constant feeding effort by feeding from big trees.

The results from this study suggest that CFS, big trees and figs may all be key elements promoting the persistence of howlers in forest fragments because fruit consumption and food source size were related to feeding effort, while fig trees can provide an important source of fruit both during periods of general fruit scarcity and abundance. Although figs have frequently been cited as an important fallback food during periods of resource scarcity (Shanahan *et al*. 2001; Terborgh 1983, 1986),

they have also been shown to provide a nutritionally balanced staple food resource for some primate species throughout the year (Felton *et al.* 2008). The availability of these 3 key elements probably allow howlers to maintain a higher and more constant level of fruit consumption, which results in a lower and more constant feeding effort and, therefore, more resilience to the seasonal changes in the availability of resources. However, it is important to stress the fact that a year-long study of only 2 groups is not enough to make general conclusions about the general responses of howlers to forest fragmentation. Therefore, our results should be interpreted as preliminary.

At present we are unable to determine the importance that the differences in feeding effort we observed between groups may have for the conservation prospects of the howler groups we observed. However, studies with other primate species suggest that increases in feeding effort may negatively affect fitness, as researchers have related increases in feeding effort to higher levels of stress (*Papio anubis*: Sapolsky 1986; *Lemur catta*: Cavigelly 1999). Further, relatively small increases in stress have been shown to predict individual survival in primates (Pride 2005). Howlers may be particularly sensitive to changes in feeding effort, as data on their foraging strategy show that they travel almost solely to reach food sources, and that they minimize the costs of procuring foods and generally conserve energy by maximizing their time spent resting (Milton 1980). Therefore, the future of howlers in small forest fragments, or forested areas where the availability of these key resources are reduced, may be seriously threatened. Such processes may be particularly threatening to howler survival during years of very low fruit production (Foster 1982). To confirm whether increases in feeding effort negatively affect howlers in forest fragments, future research should relate feeding effort with glucocorticoid levels, which have been widely applied as a means of measuring the impact of environmental disturbance on stress in wildlife (Busch and Hayward 2009).

Appendix I

The 69 species reported as sources of fruit (defined as Consumable Fruit Species [CFS]) for Mexican mantled howlers. Plant nomenclature was used according to the Missouri Botanical Garden database (http://mobot.org/W3T/search/vast.html). We also included the changes proposed by the Angiosperm Phylogenetic Group (APG 2003) to the family level

Anacardiaceae
    Spondias mombin L.
    S. radlkoferi Donn.Sm.
    Tapirira mexicana Marchand

Annonaceae
  Cymbopetalum baillonii R.E.Fr.
  Rollinia mucosa Jacq.
Aquifoliaceae
  Ilex valeri Standl.
Araceae
  Monstera tuberculata Lundell
Araliaceae
  Dendropanax arboreus (L.) Decne. & Planch.
Areacaceae
  Shceelea liebmannii Becc.
Bombacaceae
  Pachira aquatica Aubl.
Boraginaceae
  Cordia alliodora (Ruiz & Pav.) Oken
  C. dodecandra DC.
  C. stellifera I.M.Johnst.
  Tournefortia hirsutissima L.
Burseraceae
  Protium copal (Schltdl. & Cham.) Engl.
Caesalpinaceae
  Dialium guianense (Aubl.) Sandwith
Chrysobalanaceae
  Couepia polyandra (Kunth) Rose
  Hirtella triandra Sw.
Clusiaceae
  Rheedia edulis
Ebenaceae
  Diospyros digyna Jacq.
Euphorbiaceae
  Croton schiedeanus Schltdl.
  Omphalea oleifera Hemsl.
  Sapium nitidum (Monach.) Lundell
Fabaceae
  Albizia purpusii Britton & Rose
  Andira galeottiana Standl.
  Diphysa macrophylla Lundell
  Pterocarpus rohrii Vahl
Lauraceae
  Nectandra ambigens (S.F. Blake) C.K. Allen
Malvaceae
  Robinsonella mirandae Gómez Pompa
Menispermaceae
  Abuta panamensis (Standl.) Krukoff & Barneby
Mimosaceae
  Inga acrocephala Steud.
  I. paterno Harms

Moraceae
  Brosimum alicastrum Sw.
  Castilla elastica Sessé ex Cerv.
  Chlorophora tinctoria (L.) Gaudich. ex Benth
  Ficus colubrinae Standl.
  F. cotinifolia Kunth
  F. eugeniaefolia (Liebm.) Hemsl.
  F. insipida Willd.
  F. jimenezii Standl.
  F. lundellii Standl.
  F. maxima Mill.
  F. obtusifolia Kunth
  F. perforata L.
  F. pertusa L. f.
  F. petenensis Lundell
  F. sp.
  F. tecolutensis (Liebm.) Miq.
  F. trigonata L.
  F. tuerckheimii Standl.
  F. yoponensis Desv.
  Poulsenia armata (Miq.) Standl.
  Pseudolmedia oxyphyllaria Donn. Sm.
  Trophis mexicana (Liebm.) Bureau
Myrtaceae
  Eugenia acapulcensis Steud.
Rhamnaceae
  Gouania lupuloides (L.) Urb.
Rubiaceae
  Psychotria simiarum Standl.
Sapindaceae
  Cupania dentate DC.
Sapotaceae
  Dipholis minutiflora Pittier
  Mastichodendron capiri (A. DC.) Cronquist
  Sideroxylon capiri (A. DC.) Pittier
  S. portoricense Urb. subsp. *minutiflorum* (Pittier) T.D. Penn
Solanaceae
  Lycianthes heteroclita (Sendtn.) Bitter
Sterculiaceae
  Guazuma ulmifolia Lam.
Ulmaceae
  Ampelocera hottlei (Standl.) Standl.
Urticaceae
  Cecropia obtusifolia Bertol.
  Coussapoa purpusii Standl.
Verbenaceae
  Citharexylum affine D. Don

Vitaceae
  Cissus gossypiifolia Sta

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