PLANT ANIMAL INTERACTIONS

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Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics

Abstract The goal of this study was to assess the relative importance of food availability and its quality for the spatial distribution of a folivorous lemur species, *Lepilemur ruficaudatus*, from the highly seasonal dry deciduous forest of Madagascar. Males and females of this species showed opposite changes of body mass and body condition during the dry and the wet season. Male body mass declined during the dry season that coincides with mating, while female body mass remained constant. During the wet season that coincides with lactation, female body mass declined but male body mass increased. This indicates that changes in body mass are not linked as much to environmental seasonality as to mating and reproduction. The distribution of *L. ruficaudatus* was most significantly related to the spatial distribution of leaf protein during the wet season. Neither the availability nor the chemical composition of leaves eaten during the dry season affected the spatial distribution of *L. ruficaudatus*. These findings are consistent with hypotheses that constraints are most severe during the times of lactation and weaning and that distributions of primates reflect their food requirements in order to optimize their reproductive success. They are inconsistent with the idea that the lean dry season is the most stressful time of year for lemurs in energetic or nutritive terms.

Keywords Madagascar · Primates · *Lepilemur ruficaudatus* · Seasonality · Bottom-up processes

Introduction

An important goal of ecological research is to understand the importance of bottom-up and top-down processes for the distribution and abundance of animals. Both com-

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ponents are considered important for herbivores (e.g. Sinclair and Arcese 1995; contr. to Croft and Ganslosser 1996; Krebs et al. 1999; Ostfeld and Keesing 2000). However, apart from socioecological models (e.g. Crook and Gartlan 1966; Wrangham 1980; Sterk et al. 1997) studies of primate population and community ecology have concentrated on bottom-up effects. According to these studies, primate species adapt their ranging pattern to food distribution measured as the number of food species per unit area (e.g. Oates 1987; Barton and Whiten 1994). If food availability drops dramatically below the level of average years, primates and other animals starve to death (reviewed by van Schaik et al. 1993; Gould et al. 1999). Other studies provide evidence that primate biomass declines with increasing phenological seasonality (Ripley 1979; Tutin and White 1999), with interannual predictability of food production (Ganzhorn et al. 1999), or with the productivity of keystone resources (mainly fruiting trees) during lean seasons (Terborgh 1983; Gautier-Hion and Michaloud 1989; reviewed by Janson and Chapman 1999).

The results emphasizing seasonal food scarcity are in partial disagreement with findings that primate densities in general (Janson and Chapman 1999) and densities of leaf eating primates in particular increase with increasing food quality in all major primate radiations (Oates et al. 1990; Ganzhorn 1992; Peres 1997). Leaf quality (measured in terms of protein and fibre concentrations) declines with the lifespan of leaves (Coley 1983) and consequently, increases in more seasonal deciduous forests (Ganzhorn 1992; Cunningham et al. 1999). This is possibly due to a fundamental allometry between longevity and metabolism (Reich 2001). Therefore we are left with the discrepancy that more seasonal forests provide food of higher quality than evergreen forests [thus favouring high primate densities in seasonal forests (Ganzhorn et al., in press)] but that seasonal forests are thought not to provide sufficient food year-round (thus limiting primate densities).

Few attempts have been made to integrate quantitative and qualitative traits of food for diet selection in pri-

mates and their distribution in space and time (Barton and Whiten 1994; reviewed by Janson and Chapman 1999). However, understanding the relative impacts of food quality and food quantity on the distribution of primates is not only important for understanding limiting constraints for the distribution of primates and their community structure (Fleagle et al. 1999), but also different forms of competition over limited food resources as some of the main components shaping the distribution of females which provide the basis for the evolution of various forms of social systems in primates (Wrangham 1980; Sterk et al. 1997) and other mammals (Clutton-Brook 1991; Wolff 1993; Ostfeld and Keesing 2000). For this, it is important to understand which components are actually limiting and when they are limiting.

Therefore, the goals of this study were to assess the relative importance of qualitative and quantitative food characteristics for the distribution of primates. For this, *Lepilemur ruficaudatus*, a small folivorous lemur from the dry deciduous forest of Madagascar was used as a model. *L. ruficaudatus* are mainly folivorous and have stable home ranges of about 1 ha that are occupied year-round. The composition of their food species changes between the wet and the dry season, and males and females do not seem to differ in food selection criteria (Ganzhorn and Kappeler 1996; Pietsch 1998; reviewed by Thalmann and Ganzhorn, 2002). This species provides a suitable model because, due to their mainly folivorous diet and small home ranges, it is possible to measure food characteristics much more precisely than for other species with more catholic diets and larger home ranges.

In order to discriminate between effects of food quality and seasonal bottlenecks the following questions were addressed:

1. Are there indications that food is actually limiting?
2. Does *L. ruficaudatus* show selectivity for leaf chemicals during the wet and the dry season and do the criteria of selectivity in relation to leaf chemistry change between seasons?
3. Is the distribution of *L. ruficaudatus* correlated with the distribution of wet or of dry season food (or both)?
4. What are the relative contributions of qualitative and quantitative components of food characteristics for the distribution of *L. ruficaudatus* and what does this allow us to conclude about limiting factors?

Materials and methods

Study site

The study was carried out at two sites (N5 and CS7) in the forestry concession of the Centre de Formation Professionnelle Forestière de Morondava (CFPF) between 1988 and 1998. The plots are part of a large (>12,000 ha) deciduous dry forest in western Madagascar (Forêt de Kirindy/CFPF) 60 km north of Morondava (44°39′E, 20°03′S). N5 and CS7 are about 3 km apart. The dimensions of the study areas were: for N5, 500×500 m=25 ha; and for CS7,
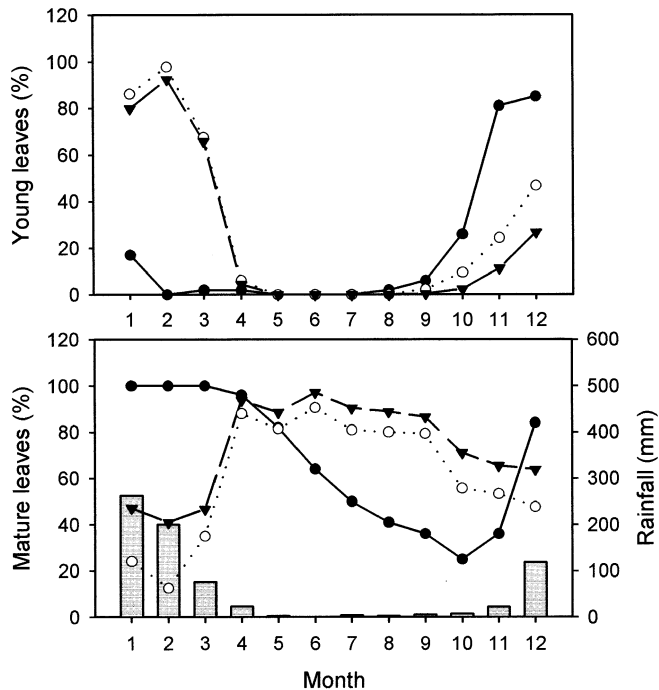
Fig. 1 Percentage of different sized trees with young and mature leaves; ● overstorey trees; ○ trees ≥10 cm diameter at breast height (DBH), representing the canopy layer below the overstorey trees; ▼ understorey trees (5–9.9 cm DBH). The sum of percentages can exceed 100% because trees could bear mature and young leaves simultaneously. *Bars* represent mean monthly rainfall averaged over 10 years. Data for overstorey trees are from Sorg and Rohner (1996)

22 ha, irregularly shaped, one side of the study area is 500 m long. Each area is dissected by a rectangular grid of trails spaced 25 m apart. Intersections are marked and numbered permanently. The climate is highly seasonal with little or no rain from April to November (Sorg and Rohner 1996; Fig. 1).

Tree density in the Forêt de Kirindy/CFPF is around 700–800 trees with diameter at breast height (DBH) ≥10 cm/ha. Due to edaphic variation, tree density and the number of morphospecies per hectare vary substantially. In the edaphically wetter study site CS7, the number of tree morphospecies and ∝ diversity is higher than in the drier part of the forest, as represented by N5. Three hundred trees ≥10 cm DBH identified along a 240-m transect in CS7 were assigned to 63+ morphospecies with Fisher's α≥24.3. Only 30+ morphospecies were identified along an identical transect in N5 with Fisher's α≥8.3 (Abraham et al. 1996). A general introduction to the forest is given by Ganzhorn and Sorg (1996).

Animals

L. ruficaudatus is a 750–800 g nocturnal lemur species. They are solitary or pair-living and mainly folivorous. Home ranges of single individuals or pairs sharing a home range (with almost identical ranges of both partners) are about 1 ha with nightly travel distances of <100 m to about 1,000 m (Pietsch 1998; Drack et al. 1999). Home ranges remain stable within and between several years (J. U. Ganzhorn, Hilgartner and Zinner, unpublished data). In Kirindy/CFPF and in other forests within a radius of 30 km around Kirindy/CFPF, 134 *L. ruficaudatus* were captured from their day shelter at different times of the year between 1993 and 1998. Animals were marked individually with passive transponders (Trovan) or by ear marks.

Estimating body condition of animals

Body mass and tibia length of animals were measured using a spring balance and callipers, respectively. Body condition was estimated as the residuals resulting from the allometric regression between tibia length and body mass. Each individual entered the morphometric analyses only once. The allometric relation between tibia length (x in mm) and body mass (y in g) is: $y=-761.4+14.9x$ ($r=0.74$, $P<0.001$, $n=107$; tibia length was not available for all 134 animals).

Distribution of *L. ruficaudatus*

The distribution of *L. ruficaudatus* in the Kirindy Forest/CFPF was determined by systematic surveys within the two study areas during the dry season between 29 August and 9 September 1994 by the author and P. M. Kappeler. This time of year is past the mating season and represents early pregnancy. Thus, the distribution of males and females should not be influenced by activities associated with mating or infant care. Surveys were carried out between 1800 hours and 2400 hours by walking slowly (about 1 km/h) along marked and measured trails. Animals can be spotted with headlamps by their eyeshine. All sightings of *L. ruficaudatus* during one survey carried out along the trails running north-south in both study areas (N5 and CS7; representing about 10 km of trails per study site) were mapped. Only one survey was carried out to avoid repeated records of the same individual. Since trails are spaced only 25 m apart and few trees have leaves in August and September, it is unlikely that we missed many animals.

Since average home range areas of *L. ruficaudatus* in the Kirindy Forest/CFPF measure about 1 ha, the study sites were subdivided into 1-ha subplots (twenty-five 1-ha subplots in N5 and 22 subplots in CS7; five of the subplots of CS7 were smaller than 1 ha because the area is dissected by a creek). These subplots were used as units for all subsequent analyses. Subplots were defined on a map and lemur sightings were assigned to the subplot where they were encountered.

Qualitative aspects of food selection

The composition of food consumed by *L. ruficaudatus* was determined in N5 and CS7 from 1988 to 1996 for the wet and the dry season (Ganzhorn 1992; Ganzhorn and Kappeler 1996; J. U. Ganzhorn et al., unpublished data). Only leaves are considered here. Since behavioural observations were concentrated in N5 only these data were used here to assess selection criteria. "Food items" were collected and dried in the sun for chemical analyses. Since actual food items could not be collected (because they were eaten), care was taken to sample leaves with the same characteristics as those that had been eaten by the animals (such as sampling from the exact food tree, position in the crown, exposure to the sun, age of leaves). Leaves were analysed for their concentrations of acid detergent fibre (ADF) and soluble protein (SP) as described previously (Ganzhorn 1992). These chemicals were chosen because they are assumed to represent key constituents determining the quality of food in terms of primary components (Oates et al. 1990). The ratio of protein to fibre was used as a measure of food quality. Each feeding event and the associated plant sample was considered as an independent datapoint. Each food tree was sampled only once.

To assess selection criteria during the wet season, samples of mature leaves were collected from one to five trees of the most abundant species along three transects spaced at 125 m distance in N5. Not all tree species occurred on all transects. Data of the chemical analyses were averaged per tree species. This sample was considered as a "representative sample" of what was potentially available in the forest and corresponds to the methods used previously to characterize the chemical profile of leaves available in other tropical forests (Oates et al. 1990; Ganzhorn 1992). During the dry season, leaves were collected from all tree species that

still had some leaves during that time of year. This sample served as a representative sample of leaves available during the dry season. The chemical composition of actual food plants collected during the wet and dry season was then compared with the composition of these representative samples. This approach was favoured over the option of contrasting the chemical composition of "food items" versus "non-food items" because "non-food items" cannot be defined unambiguously (Janson and Chapman 1999).

N5 and CS7 differ by tree species composition due to edaphic reasons (contr. to Ganzhorn and Sorg 1996). Therefore food species composition differs between the two sites. Based on a limited number of food samples, selection criteria of lemurs based on chemical properties do not differ between sites (J. U. Ganzhorn, unpublished data).

Quantitative aspects of food

Phenology

Phenological data have been collected for overstorey trees of economic importance over 7 years (Sorg and Rohner 1996). These overstorey trees were spread over a large area, thus providing a representative sample for the whole forestry concession. Since, on a qualitative basis, overstorey trees are known to have different phenological characteristics than smaller trees (Rakotonirina 1996), the abundance of young and mature leaves was recorded for 250 trees of 5–9.9 cm DBH (understorey trees) and 224 trees ≥10 cm DBH of the vegetation descriptions listed below in N5 and in CS7 between September 1994 and August 1995. From September 1995 to May 1996 only half of the number of trees were measured. The trees were taken from the vegetation descriptions at trail intersections of three transect lines running in parallel and spaced 125 m apart. Phenological states were recorded bimonthly. For the present purpose young and mature leaves were classified as absent or present. All species and individuals were pooled per survey. The percentages of trees with leaves were averaged per month and years separately for the two age classes of leaves. Details of phenological characteristics differ between N5 and CS7. But the overall seasonal changes relevant for the present paper are similar. Due to space limitations only data for N5 are presented.

Measuring quantitative food availability

At each intersection of the trails, four trees ≥10 cm DBH (large and medium-sized trees) and four trees of 5–9.9 cm DBH (small trees) were measured in 1994 using the nearest-individual method (Kent and Coker 1992). For this, the distance and DBH of the nearest tree to the centre of the trail intersection was measured in each 90° sector around each trail intersection. This was done for one tree ≥10 cm DBH and one tree of 5–9.9 cm DBH per 90° sector. Thus, eight trees were recorded per trail intersection. Trees were identified to morphospecies. Most of the 1-ha subplots described above contained 16 intersections of trails with the associated vegetation descriptions (8×16=128 trees per 1-ha subplot).

These data were used to estimate the potential food abundance for *L. ruficaudatus* within the 1-ha subplot. First, the number of trees belonging to food tree species of *L. ruficaudatus* were counted. This number represents an estimate of the representation of food trees within any potential home range (i.e. the variable "number of food trees"). Each of these trees was measured according to its basal area at breast height ($\pi \times r^2$; r=DBH/2) divided by the squared distance of the tree to the trail intersection. Since DBH of trees is correlated with crown diameter, DBH could be used as substitute for the amount of leaves available per tree (Ganzhorn 1995). The distance of any given tree to the central sampling point can be used as an estimate of tree density. These measures of food availability were averaged for each 1-ha subplot and multiplied by the number of food trees to give an estimate of the total amount of food available per 1-ha subplot (i.e. the variable "total amount"). Separate estimates were calculated for the wet and for the dry sea-

son. Five of the 22 plots in CS7 had <16 intersections. For these plots the amount of food available was lower than for full-sized 1-ha subplots. If *L. ruficaudatus* would respond to the amount of food available the chances of encountering animals would change accordingly. Removing these incomplete plots does not change the results of the analyses.

Measuring the quality and availability of potential food resources

Leaves of *Lepilemur* food tree species as of 1994 were collected in N5 and in CS7 in 1994 and 1995 from trees of the vegetation samples used to quantify food availability (see previous paragraph). One to four replicates of leaves of each tree species were sampled for N5 and CS7 separately. The mean of the concentrations of leaf chemicals per species and per study site was assigned to all individuals of the given food tree species recorded in the vegetation samples of N5 and CS7, respectively. The concentrations of chemicals were averaged over all food trees per 1-ha subplot to estimate the quality of leaves available within any given 1-ha subplot.

The variables measured to estimate food quantity (number of food trees, total amount) and food quality (ADF, SP, ratio of SP to ADF) within the 1-ha subplot entered the analysis in their original form. In order to estimate combined effects of food quality and quantity within the 1-ha subplot, each variable of the two categories was multiplied by each of the variables of the other category, resulting in another six variables. All variables were calculated separately for the wet and for the dry season. This resulted in 11 variables×2 seasons=22 variables for the analyses. In addition the variables used to quantify food availability were summed over both seasons.

Linking qualitative and quantitative aspects of food to the distribution of *L. ruficaudatus*

The number of *L. ruficaudatus* per 1-ha subplot was related to the variables measured or calculated to describe quantitative and qualitative aspects of food per 1-ha subplots. The numbers of *L. ruficaudatus* per 1-ha subplot deviated from a normal distribution but the residuals after regression analyses did not differ from normality. Statistical tests are listed in the Results section and were calculated using SPSS (1999).

Results

## Indications of seasonal food limitations: the phenological basis

Different sized trees show different phenological characteristics in relation to the highly seasonal rains (Fig. 1). Large overstorey trees that extend above the closed canopy layer start producing new leaves in September with a peak in November and December. The occurrence of young leaves is delayed by about 1 month in trees ≥10 cm DBH, that create a closed canopy below the overstorey trees. Understorey trees (5–9.9 cm DBH) produce new leaves even later. The peak of new leaf flush of these trees is in January and February. The temporal difference in the occurrence of new leaves is significant between all three tree size classes (Kolmogorov-Smirnov test: $D_{max}>0.256$, $P<0.001$).

Mature leaves are available year round. However, overstorey trees start shedding their leaves in May while a high percentage of the smaller trees retain the mature leaves throughout the dry season and start shedding them

when overstorey trees start producing new leaves. The shedding process of mature leaves does not differ significantly between medium sized and small trees, but both groups retain their mature leaves significantly longer than the overstorey trees (Kolmogorov-Smirnov-test: $D_{max}>0.49$, $P<0.001$). Thus, on a community level the flush of new leaves and shedding of mature leaves follows a tree size-related sequence.

Indications of seasonal food limitations: body mass and condition of *L. ruficaudatus*

The mean body mass of all animals was 704.1±125.9 g (range 275–948 g; $n=134$). This sample also included juveniles. For the analyses of seasonal changes in body mass and body condition only animals with body mass ≥600 g were included. These animals were assumed to be sexually mature. Based on behavioural observations, the year was subdivided into four periods: pre-mating/mating season (June–August), post-mating season (September and October), birth season (December and January), and lactation and weaning (January–April, including one male captured in May). The pre- and post-mating season coincide with the dry season. Birth, lactation and weaning coincide with the wet season for the most part. The coincidence of mating, birth, and lactation with environmental seasonality prohibits statistical separation of the effects of organismal from environmental factors on body mass and body condition. Therefore
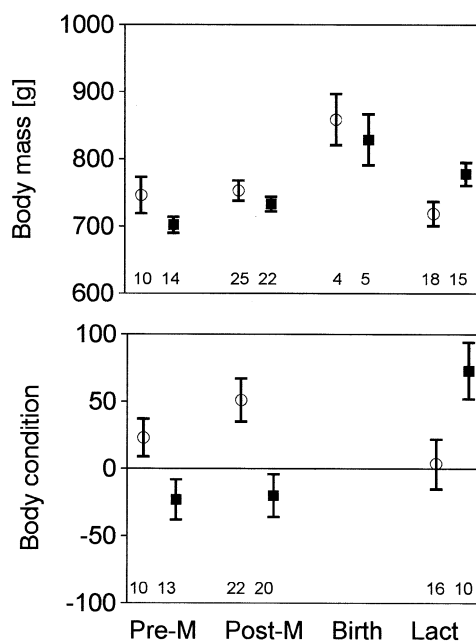
Fig. 2 Seasonal variation in body mass and body condition of adult female (○) and male (■) *Lepilemur ruficaudatus* (≥600 g); body condition defined as the residuals of the allometric regression between tibia length and body mass. Values are means and SEs. *Numbers* represent sample size. *Pre-M* Pre-mating, *Post-M* post-mating, *Lact* lactation

the two sets of factors (organismal, i.e. variation based on animal reproductive physiology; and environmental, i.e. based on seasonal changes in ambient conditions) were analysed by using two different approaches.

On average, males had lower body mass than females throughout the year except late in the wet season during times when females were lactating (Fig. 2). The differences are more pronounced when body condition is considered. Females were in much better condition than males during the mating season which corresponds to the dry season. The situation is reversed during the wet season which corresponds to the time of lactation. According to two-way ANOVAs, there are very strong interactions between seasonal changes and gender (Table 1) confirming that the two sexes reacted very differently to seasonal variation.

Qualitative aspects of food selection

During the wet season, leaves as eaten by *L. ruficaudatus* had lower fibre and higher protein concentrations resulting in higher quality (as measured by the ratio of protein to fibre) than found in the representative samples of leaves available at that time of the year (Mann-Whitney

U-tests: $z=4.12$, 2.50 and 4.10, respectively, $P\leq0.01$; Table 2). During the dry season, food items contained lower fibre but also lower protein concentrations than the representative sample of leaves ($z=4.55$ and 3.53, respectively, $P<0.001$). As a consequence of the low protein concentrations, food quality did not differ from the representative sample during the dry season ($z=0.99$, $P>0.3$). The lower protein concentrations in food items than in the representative sample may be a consequence of sampling the representative sample during the dry season. During that time of year all items available had been sampled. This included some high quality young leaves sampled in August and September. These young leaves were available only in small quantities. The bulk of leaves eaten by *L. ruficaudatus* at that time of the year consisted of mature leaves with low protein contents. Thus, the representative sample of the dry season may not reflect food availability adequately.

Between seasons the concentrations of protein and the ratio of protein to fibre in food items eaten by *L. ruficaudatus* changed significantly (Mann-Whitney U-test: protein: $z=4.32$, $P<0.001$; protein/fibre: $z=4.04$, $P<0.001$; Table 2). Both variables were lower in the dry than in the wet season. Fibre concentrations in food items did not change significantly between seasons.

Table 1 Effects of seasonality and gender on body mass and body condition of *Lepilemur ruficaudatus*. Seasonality is considered either from the animals' perspective as pre-mating, post-mating, birth, and time of lactation and weaning (organismal seasonality), or as environmental variation, dividing the year into a dry and a wet season. Body condition was calculated as the residuals from the allometric regression between tibia length and body mass. No data are available for body condition for the birth season

	Organismal variation			Environmental variation		
	F	*df*	*P*	*F*	*df*	*P*
Body mass						
Season	6.93	3	<0.001	5.03	1	0.027
Sex	0.29	1	0.589	0.36	1	0.549
Season×sex	3.35	3	0.022	7.44	1	0.007
Model, error	4.50	7, 105	<0.001	4.07	3, 109	0.009
Body condition						
Season	1.88	2	0.159	2.96	1	0.089
Sex	1.08	1	0.302	0.04	1	0.840
Season×sex	8.47	2	<0.001	16.96	1	<0.001
Model, error	4.59	5, 85	0.001	7.34	3, 87	<0.001

Table 2 Chemical composition of leaves eaten by *L. ruficaudatus* and comparative representative samples of leaves from the Kirindy Forest/Centre de Formation Professionnelle Forestière de Morondava. All data are from site N5. Values are medians (*in italics*), quartiles (*to the left and the right of the median*) and sample size (*n*) for the wet and the dry season. *ADF* Acid detergent fibre, *SP* soluble protein

Component	Wet season		Dry season	
	Food items of *L. ruficaudatus*	Representative sample	Food items of *L. ruficaudatus*	Representative sample
ADF	17.5-*24.4*-30.8***	28.8-*34.1*-40.7	21.2-*26.5*-33.5***	29.5-*37.4*-41.8
n	43	34	74	30
SP	5.8-*7.3*-11.0**	5.2-*6.1*-7.4	3.0-*4.7*-7.8***	6.1-*7.3*-10.8
n	47	36	72	32
Protein/ADF	0.20-*0.32*-0.51***	0.13-*0.19*-0.23	0.12-*0.17*-0.29	0.14-*0.21*-0.30
n	43	34	72	30

*$P\leq0.05$; **$P\leq0.01$; ***$P\leq0.001$ (differences between the concentrations in food items and the representative leaves according to Mann-Whitney U-tests)

Table 3 Percentage of occurrence of trees ≥5 cm diameter at breast height in the random vegetation descriptions describing N5 and CS7. Only tree species with abundances ≥1% are listed. Tree species belonging to a species fed upon by *L. ruficaudatus* and for which chemical analyses are available among the vegetation sample of either N5 or CS7 are marked in *italics*

Species	N5	CS7
Astrocassine pleurostyloides	*2.1*	
Astrotrichilia asterotricha		1.7
Berchemia discolor		1.1
Baudouinia fluggeiformis	*2.1*	2.6
Bivinia jalberti	1.6	2.3
Buxus madagascariensis	9.1	5.9
Commiphora arofy		3.4
Cedrelopsis grevei	*1.1*	1.6
Cedrelopsis mampandry		2.3
Cedrelopsis mantaora		1.1
Colubrina decipiens	1.1	1.3
Dalbergia sp.		*7.4*
Diospyros intricantha		*1.1*
Diospyros microphylla	*1.4*	
Diporidium ciliatum	1.2	
Enterospermum resinosum	1.7	
Fernadoa grevei	*3.4*	*1.1*
Grewia cyclaea		2.9
Grewia sp.	*1.6*	*5.4*
Noronhia sp.	1.2	
Operculicaria gumifera		1.6
Pittosporum sp.	1.3	
Rothmannia tropophylla	2.8	
Securinega seyrigii	35.0	8.3
Strychnos decussata	2.7	6.4
Strychnos vacacoua	9.8	6.7
Terminalia sp.		*3.1*
Xyloolaena sp.		1.4
Chemical analyses available for food species <1% abundance in the vegetation sample		
Canthium sp.	*0.3*	*0.6*
Dalbergia sp.	*0.3*	
Foetidia asymmetrica	*0.1*	
Macphersonia gracilis	*0.3*	
Terminalia sp.	*0.6*	
No of trees in vegetation sample	3,504	2,368
No of tree species in vegetation sample	84	124
% Trees represented by species ≥1% abundance	79.2	68.7

Distribution of *L. ruficaudatus* in relation to food distribution and food quality

The quantitative vegetation description was based on 3,504 and 2,369 trees in N5 and CS7, respectively. In N5 and CS7, respectively, 29.9% and 34.4% of the trees belonged to potential food tree species for which chemical analyses were available (Table 3).

In total, 48 and 27 *L. ruficaudatus* individuals were located during the systematic transect walks in N5 and CS7, respectively. The number of animals per 1-ha subplot varied between zero and five. According to the stepwise regression, the number of *L. ruficaudatus* individuals (y) in the forty-seven 1-ha subplots was related significantly only to the number of food trees per 1-ha subplot×the average concentration of soluble protein in their leaves during the wet season (x) ($y=0.012\ x+0.007$, $F=9.24$, $P=0.004$, $n=47$; $R^2=0.170$). Once this variable was included no other variable entered the model with a significance level of $P≤0.05$.

Discussion

Animal populations are influenced by top-down and bottom-up processes. Among these temporal and spatial characteristics of food abundance, food distribution and food quality are considered prime factors acting from the bottom up. As a consequence, they are involved in many hypotheses concerning the evolution of life history traits, social systems, the distribution of individuals in space and time, and community composition (Krebs et al. 1999; Ostfeld and Keesing 2000).

However, up to now there is no unifying concept on how food may be limiting and which characteristics of the nutritional bases are relevant in evolutionary terms. Limiting constraints might range from micro- and macronutrients (Robbins 1983), adaptations to detoxify secondary plant chemicals (Rosenthal and Berenbaum 1992a, 1992b; Lawler et al. 2000), morphological features (dentition, gut, body mass) and associated metabolic limitations (Hughes 1993) to food availability. The latter seems to be the most obvious factor but it turned out that it is probably the most difficult to measure in a way that reflects reality at the level of simple food abundance (e.g. Chapman et al. 1994) and with respect to energy (nutrient) intake in relation to energy (nutrient) expenditure (Cuthill and Houston 1997). In particular, food availability per se does not always need to coincide directly with reproductive success. In rodents, some species respond to pulsed mast fruiting with increased reproduction (Ostfeld and Keesing 2000) while other sympatric species of similar size cease to reproduce after mast fruiting (Bieber 1998; Schlund et al., in press). Thus, the same phenomenon can impose different constraints on seemingly similar organisms.

The goal of the present study was to assess the relationships between the seasonally changing distribution, abundance and chemical quality of food and the distribution of folivorous lemurs, using *L. ruficaudatus* as an example. The data on bottom-up factors allow conclusions to be drawn about limiting resources for the spatio-temporal distribution of animals in a highly seasonal tropical dry forest. Top-down factors were not considered as they are assumed to act uniformly over the whole study area.

High quality young leaves were not available during the dry season except at its very end. Mature leaves were present year-round with a decline from large to small trees and lowest availability towards the end of the dry season. Thus, food availability is higher during the wet than during the dry season. However, contrary to expectations, the dry season does not seem to represent an energetic bottleneck for the animals. Rather, males and females showed opposite changes in body mass at different times of the year. Females were able to maintain their

body mass throughout the lean dry season while male body mass declined significantly at that time of year, possibly due to mating activities. In contrast, male body mass increased during the wet season (and prior to the mating season), while female body mass declined, probably due to the energetic demands of lactation.

Further support for the hypothesis that the dry season is not the limiting season under normal conditions comes from the observation that the distribution of *L. ruficaudatus* is closely correlated with protein availability during the wet season. These results suggest that *L. ruficaudatus* adjust their year-round home ranges more to the presence of high quality leaves that are used as food during the wet season, i.e. at times when leaves seem superabundant, rather than to the presence of trees that can be used for feeding during the dry season. Again this does not support the idea that the dry season represents the harshest time for *L. ruficaudatus* due to restricted food supply. Rather, the ranges are distributed to optimize access to high quality food during lactation and in preparation for the next dry season.

The interpretations are consistent with observations on *Propithecus verreauxi*, another folivorous/frugivorous lemur of the seasonal dry forests of Madagascar. This species weighs about 3 kg. Mating occurs in the wet season and births in the dry season with weaning in the following wet season. Even though both sexes lose weight over the dry season, changes in body mass show significant interactions between sex and season, indicating different responses of the sexes to (unspecified) seasonal constraints. The survival of offspring and the chance of reproduction in the next year depended strongly on the body condition of the female (Richard et al. 2000). Similarly, the survival of *Lemur catta* females and infants during an unusually severe drought (*L. catta* is another lemur species of the seasonal dry forest), was linked to their body condition achieved prior to the upcoming dry season (Gould et al. 1999).

The results of the two latter studies seem inconsistent with the suggestion that lemurs optimize food intake during the wet season because both studies showed that severe dry seasons have negative effects on the survival and reproduction of the animals. However, there may be tradeoffs between adaptations to cope with unusually severe dry seasons and the need for the rapid acquisition of nutrients and energy during a relatively short richer season and their subsequent metabolization during the lean time of the year. In the case of *L. ruficaudatus*, locomotion is relatively expensive due to their low resting metabolic rate (Schmid and Ganzhorn 1996; Drack et al. 1999). Under dry season conditions, the payoff of the sparse, high quality items may simply not be high enough to warrant the costs of searching. This is reflected by a reduction in activity of the vicarious *L. leucops* in the south of Madagascar during the dry season (Nash 1998).

The pattern observed for *L. ruficaudatus* is similar to that of sex-specific seasonal changes in body mass of the omnivorous *Microcebus murinus* in the same forest (Schmid and Kappeler 1998) and recorded under constant conditions in the laboratory (Perret and Aujard 2001). This indicates a similar adaptation of lemurs so that an "average" dry season per se does not pose energetic constraints on these lemurs. Rather, changes in body mass seem closely linked to reproduction. This interpretation is supported by recent findings that torpor in *M. murinus* during the cool dry season does not result in energy savings, but rather seems to reduce water requirements during the dry season (Schmid and Speakman 2000).

Therefore, in evolutionary terms, the phenomenon exemplified by *L. ruficaudatus* might have to be understood as two processes with different time frames. From a long-term perspective, lemurs have adapted to survive extended periods of food shortage. Lemurs seem to do this through seasonal changes in behaviour (reviewed by Wright 1999) and on a physiological level through a seasonal reduction of their metabolic rate. Apart from their low metabolic rates in general (Müller 1985), all lemur species studied so far reduce their metabolic rate during months that correspond to the lean season in Madagascar, possibly entering a state that has been coined "walking torpor" (Pereira 1993). In *Microcebus* spp., *Lemur catta* and *Eulemur fulvus* this change in metabolic rate is triggered by changes in the photoperiod (Petter-Rousseaux 1980; Pereira 1993; Pereira et al. 1999; Schmid 2000; Perret and Aujard 2001; Wrogemann et al. 2001).

These physiological adaptations might have evolved for the conservation of energy. They seem to be characteristic for lemur radiation as a whole and provide the constraining background for the evolution of other adaptations (Jolly 1966; reviewed by Wright 1999). Primates without the option to reduce their metabolic rates have to adopt other solutions to make it through lean times (Terborgh and van Schaik 1987). While lemur adaptations for energy conservation seem real, meteorological and comparative phenological data are too scarce to investigate whether lemur adaptations might have evolved as a consequence of particularly harsh environments or whether they simply represent a different solution to a problem that has been solved otherwise in other primate radiations (Wright 1997).

Constrained by the adaptations for energy conservation described above, lemurs optimize their chance for future reproduction and the chance for their offspring to survive the next lean season by optimizing food intake during the wet season, prior to the upcoming lean season. This time of year coincides with lactation and weaning in lemurs. While different lemur species mate and give birth at different times of the year, lactation and weaning is highly synchronized and concentrated towards the end of the wet season (Wright 1999). Therefore, within the norm of the possible reaction of any given species and modified by additional factors, the present data are consistent with the idea that female distribution reflects the distribution of resources which are limiting in the short-term with immediate consequences for the survival of the present offspring and the potential for future offspring (e.g. Wrangham 1980; Sterck et al. 1997; Wright 1999; Richard et al. 2000).

In conclusion, the present life history traits of lemurs can be interpreted as the result of evolution acting on two different time scales. From a long-term perspective lemurs have adapted to survive extended periods of scarcity by mechanisms to conserve energy (Jolly 1966; Wright 1999). Within these phylogenetic constraints extant lemurs adapt their distribution to optimize the intake of high quality food during the rich wet season prior to the lean dry season in order to optimize infant survival and to increase the potential of females for future reproduction. The discrepancy between studies emphasizing quantitative over qualitative food characteristics and vice versa might be a consequence of considering different evolutionary time scales and of studying the radiations of different primates that have found different solutions to similar environmental constraints.

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