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# From Fruits to Leaves : Seasonal Foraging Dynamics and Nutritional Ecology of Ring-Tailed Lemurs (Lemur catta) at Berenty Private Reserve, Madagascar

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**Résumé**

Les fluctuations saisonnières de la disponibilité alimentaire mettent à rude épreuve les adaptations comportementales et métaboliques des primates dans les forêts sèches et imprévisibles de Madagascar. Cette étude examine les déterminants nutritionnels de la recherche de nourriture chez le lémurien à queue annelée (*Lemur catta*), une espèce menacée, en analysant les relations quantitatives entre la phénologie végétale, la composition en macronutriments et les préférences alimentaires explicites. Des données empiriques ont été collectées dans la forêt galerie « Malaza » de la réserve privée de Berenty durant deux périodes contrastées : novembre 2023 (début de la saison des pluies) et juillet 2024 (saison sèche). Le suivi comportemental de cinq femelles adultes a été réalisé par échantillonnage focal continu (80 heures), tandis que des inventaires de la végétation et des relevés phénologiques semi-quantitatifs ont permis de surveiller les ressources disponibles. Les profils phytochimiques ont été déterminés par spectroscopie proche infrarouge (NIRS). Les résultats révèlent une forte dichotomie saisonnière du régime alimentaire. En novembre 2023, malgré la prédominance du feuillage mature dans la biomasse disponible (85,58 %), la cohorte a adopté une stratégie d'optimisation énergétique, consacrant 68 % de son temps de recherche de nourriture aux rares tissus reproducteurs, principalement les fruits riches en glucides de *Rinorea greveana* et *Cordia sinensis*. La modélisation chimiométrique a confirmé cette préférence, révélant une corrélation positive modérée avec les concentrations en glucides (r = 0,58, p = 0,0878). À l'inverse, la saison sèche de juillet 2024 a entraîné un effondrement quasi total de la disponibilité des fruits (0,60 %), contraignant les individus à se tourner vers des matrices végétales de substitution de faible qualité, dominées par les feuilles d'*Azadirachta indica* et les tiges d'*Opuntia vulgaris*. Durant cette période de pénurie, les corrélations entre les préférences et les caractéristiques nutritionnelles sont restées faibles, reflétant un recentrage crucial sur le maintien des macronutriments, avec de légères tendances positives pour les lipides (r = 0,374) et les protéines (r = 0,232). Ces résultats apportent une preuve irréfutable de la plasticité nutritionnelle évolutive chez *Lemur catta*. Il est crucial de maintenir la diversité des communautés végétales afin d'assurer la viabilité à long terme des populations et leur sécurité micronutritionnelle dans des habitats fragmentés par l'activité humaine et spatialement restreints.

**Keywords:**
*Lémurien catta ;* préférence alimentaire ; composition nutritionnelle ; saisonnalité ; Réserve de Berenty

**Abstract**

Seasonal fluctuations in food availability severely challenge the behavioral and metabolic adaptations of primates in Madagascar's unpredictable dry forests. This study examines the nutritional determinants of foraging in the endangered ring-tailed lemur (*Lemur catta*) by analyzing the quantitative relationships between plant phenology, macronutrient composition, and explicit food preferences. Empirical data were collected in the "Malaza" gallery forest of the Berenty Private Reserve during two contrasting periods: November 2023 (early wet season) and July 2024 (dry season). Behavioral tracking of five adult females relied on continuous focal sampling (80 hours), while vegetation inventories and semi-quantitative phenological surveys monitored resource landscapes. Phytochemical profiles were determined via near-infrared spectroscopy (NIRS). Results reveal a profound seasonal dietary dichotomy. In November 2023, despite mature foliage dominating the available biomass (85.58%), the cohort exhibited an energy-maximizing posture, dedicating 68.00% of foraging time to scarce reproductive tissues, primarily the carbohydrate-dense fruits of *Rinorea greveana* and *Cordia sinensis*. Chemometric modeling supported this preference, displaying a moderate positive correlation with carbohydrate concentrations ($r$ = 0.58, $p$ = 0.0878). Conversely, the dry season in July 2024 triggered a near-total collapse of fruit availability (0.60%), forcing a structural pivot toward low-quality fallback vegetative matrices, dominated by *Azadirachta indica* leaves and *Opuntia vulgaris* stems. During this bottleneck, correlations between preferences and nutritional traits remained weak, reflecting a critical shift toward macronutrient maintenance, with slight positive trends for lipids ($r$ = 0.374) and proteins ($r$ = 0.232). These findings provide unequivocal evidence of evolutionary nutritional plasticity in *Lemur catta*. Crucially, maintaining diverse plant communities remains essential to ensure long-term population viability and micro-nutritional security within anthropogenically fragmented, spatially constrained habitats.

**Keywords:**
*Lemur catta* ; food preference; nutritional composition ; seasonality ; Berenty Reserve

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# 1. Introduction

The ring-tailed lemur (*Lemur catta*) constitutes an emblematic primate lineage endemic to the southern regions of Madagascar, an environment characterized by pronounced climatic seasonality and severe fluctuations in trophic resource availability. Currently classified as Endangered on the IUCN Red List, this species is increasingly subjected to anthropogenically driven habitat fragmentation and loss, which drastically restricts its geographic range (Sussman, 2013). Consequently, these spatial constraints induce a phenomenon of localized demographic compression within protected enclaves, such as the Berenty Private Reserve (Ichino *et al.*, 2009). Such dense aggregations inevitably exacerbate competitive pressure on finite food resources, a vulnerability that becomes particularly acute during the dry season when primary productivity and fruit availability decline sharply.

Extensive literature underscores that food selection in non-human primates is concurrently governed by environmental resource abundance and intrinsic nutritional quality (Yamashita, 2008 ; Chapman & Chapman, 1990). Within *Lemur catta* populations, distinct seasonal shifts in vegetative phenology compel significant adjustments in dietary composition, modulating both the specific flora consumed and the distinct plant parts selected (Sato *et al.*, 2015 ; Norscia *et al.*, 2006; Hladik *et al.*, 2003 ; Simmen *et al.*, 2003). While soluble carbohydrate-rich fruits are preferentially exploited whenever accessible, structural components such as mature leaves, stems, or flowers serve as critical fallback resources during periods of acute environmental scarcity.

Despite the wealth of descriptive literature detailing the dietary repertoire of *Lemur catta*, the precise quantitative interplay between seasonal variations in plant nutritional chemistry and explicit foraging preferences remains insufficiently documented within Malagasy dry deciduous forests. Elucidating this biochemical relationship is paramount to deciphering the nutritional optimization strategies deployed by primates under conditions of structural spatial limitation and heightened intra-group competition.

Accordingly, the present study objective is to quantify the relationship between the macro-nutritional composition of available plant resources and the dietary preferences exhibited by *Lemur catta* within the Berenty Private Reserve. We tested three core hypotheses :

- **(i)** foraging preferences correlate positively with non-structural carbohydrate content during the peak fruiting season;
- **(ii)** under dry-season constraints, food preferences shift significantly toward items yielding higher protein or lipid concentrations ; and
- **(iii)** local plant part availability is insufficient to predict dietary choices, thereby revealing an active, nutrient-driven selection process rather than passive opportunistic consumption.

# 2. Materials and Methods

## 2.1. Materials

### 2.1.1. Study site and environmental baseline

The empirical investigation was conducted within the "Malaza" gallery forest sector of the Berenty Private Reserve, a protected wildlife enclave located in southernmost Madagascar (24°59′S, 46°18′E). This geographic region is ecologically characterized by a semi-arid bioclimatic regime featuring severe intra-annual rainfall fluctuations that directly regulate local vegetative phenology.

Data collection spanned two sharply contrasting bioclimatic periods meticulously selected to capture seasonal environmental extremes: November 2023, representing the onset of the austral wet season, and July 2024, positioning the study at the core of the severe austral dry season. Local microclimatic records during these intervals documented a mean monthly precipitation of 23.4 mm during the wet phase, whereas the dry phase exhibited total hydrological drought with 0.0 mm of recorded rainfall.

### 2.1.2. Animal subjects and cohort description

The study cohort comprised five fully mature adult female ring-tailed lemurs (*Lemur catta*) belonging to a single, historically habituated social group designated as troop C2B. Restricting behavioral monitoring to adult females minimized confounding variables associated with sex-specific energetic demands or transient male dispersal patterns, thereby ensuring a homogenous sampling matrix.

## 2.2. Methods

### 2.2.1. Behavioral sampling and dietary quantifications

Behavioral tracking of the focal subjects relied on continuous focal sampling protocols (Altmann, 1974). Observation

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windows were synchronized with primary daily activity peaks, spanning from 08:00 to 11:30 and from 14:00 to 17:30. This systematic framework yielded a balanced cumulative observation effort of 80 hours distributed equally across both seasonal matrices (40 hours per season).

For each feeding event, the exact ingestion duration, plant taxonomic identity, and specific item consumed (e.g., young leaves, mature leaves, ripe fruits, stems, or flowers) were recorded. Dietary preference was operationally defined and quantified as the proportion of total feeding time allocated to each distinct plant resource.

#### 2.2.2. Vegetation inventory and phenological monitoring

To evaluate the spatial baseline of available resources, a floristic inventory was deployed using randomly distributed 10 × 10 m (100 m²) quadrats within the home range of troop C2B (Tarnaud *et al.*, 2010). All woody phanerophytes exhibiting a diameter at breast height (DBH) ≥ 5 cm were recorded, while succulent and non-woody species were quantified by individual counts. Relative abundance was calculated using standardized community analysis methods (Kent, 2012 ; Magurran, 2004).

Concurrently, temporal plant part availability was assessed through weekly direct phenological surveys of the consumed taxons. Abundance scores for each vegetative organ were determined via a semi-quantitative scale ranging from 0 to 4 (Fournier, 1974), from which phenological expressivity percentages were derived.

#### 2.2.3. Phytochemical analyses and nutritional profiling

Nutritional characterization focused on the most frequently exploited plant parts, which were air-dried via warm ventilated air, shielded from solar radiation, and stored in hermetic containers. Crude protein, crude fat, and ash fractions were determined via near-infrared spectroscopy (NIRS) (Rothman *et al.*, 2011 ; William *et al.*, 1998).

Residual moisture was determined by oven-drying at 105 °C for 8 hours, and mineral content was isolated via furnace incineration at 550 °C for 5 hours (AOAC, 1990). Total carbohydrate content was subsequently calculated by mass difference (Rérat, 1956).

#### 2.2.4. Statistical modeling

The quantitative relationships between dietary preference metrics and macro-nutritional traits were analyzed using non-parametric Spearman's rank correlation coefficients (Zar, 1999). All computational procedures and matrix evaluations were performed within the R statistical environment, with the critical significance threshold established a priori at $p < 0.05$.

**Table 1**. Baseline environmental parameters and behavioral sampling structure across the two study periods.

| Bioclimatic Season | Calendar Interval | Cumulative Observation (Hours) | Monthly Rainfall (mm) | Focal Subjects (Troop C2B) |
|---|---|---|---|---|
| Early Wet Season | November 2023 | 40 | 23.4 | 5 Adult Females |
| Mid-Dry Season | July 2024 | 40 | 0.0 | 5 Adult Females |

The environmental matrix highlights severe macroclimatic divergence, showing a 100% reduction in precipitation from 23.4 mm in November to 0.0 mm in July. Despite this extreme seasonal shift, sampling effort remained perfectly symmetrical across both periods with 40 observation hours each, ensuring statistical consistency for tracking the five focal females.

## 3. Results

### 3.1. Botanical composition of the diet

A cumulative baseline of 80 hours of systematic behavioral observations demonstrated that plant material constitutes the overwhelming majority of the dietary repertoire of *Lemur catta*, accounting for over 90% of total foraging time. Across the dual seasonal matrices, the study group exploited 18 distinct plant species distributed across 14 botanical families. Among these, four taxa exhibited marked ecological dominance within the home range: *Opuntia vulgaris*, *Azadirachta indica*, *Rinorea greveana*, and *Tamarindus indica*. The primary vegetative and reproductive organs selected by the primates comprised mature leaves, young leaves, ripe fruits, stems, and flowers or flower buds.

Pronounced temporal shifts governed dietary diversity between the two climatic seasons. In November 2023, the dietary matrix encompassed 14 plant species, characterized by a highly pronounced preference for fruit-bearing taxa, most notably *Rinorea greveana* and *Cordia sinensis*. Conversely, by July 2024, the structural breadth of the diet contracted to 10 species, transitioning into a regime heavily dominated by the mature foliage of *Azadirachta indica*, supplemented by the succulent structural stems of *Opuntia*

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*vulgaris* and the inflorescences of *Eucalyptus* sp. This seasonal contraction and reliance on alternative resources align with documented primate responses to severe environmental constraints (Sato *et al.*, 2015 ; Irwin *et al.*, 2014 ; Simmen *et al.*, 2003). Taxa that were persistently consumed across both seasons yielded minimal contributions to overall feeding time, confirming their secondary role as critical fallback resources during resource-lean periods (Norscia *et al.*, 2006 ; Chapman & Chapman, 1990).

recorded plant parts, whereas ripe fruits were highly scarce. Remarkably, despite this environmental scarcity, ripe fruits represented the primary dietary component ingested by the focal subjects, comprising 68.00% of total feeding time. This severe discrepancy underscores a robust, positive selection mechanism where lemurs actively bypass abundant structural biomass to exploit high-energy resources, mirroring optimization patterns observed in broader Malagasy frugivores (Sato *et al.*, 2015 ; Hladik *et al.*, 2003).

**Table 2. Taxonomic composition and seasonal distribution of plants parts consumed by *Lemur catta* during the wet season (November 2023) and the dry season (July 2024) at Berenty Reserve, Madagascar**

| Plant Family | Species | Vernacular name | Relative abundance (%) | Plant part eaten | |
|---|---|---|---|---|---|
| | | | | November | July |
| Cactaceae | *Opuntia vulgaris* | Raketa | 12,39 | St | St |
| Myrtaceae | *Eucalyptus sp* | Kininina | 1,71 | - | BFl/Fl |
| Aloeaceae | *Aloe vahombe* | Vahombe | 2,56 | - | St |
| Asparagaceae | *Dracaena trifasciata* | - | - | RFr | - |
| Boraginaceae | *Cordia caffra* | Varogasy | 0,43 | YL | - |
| Boraginaceae | *Cordia sinensis* | Varombazaha | 0,85 | RFr | - |
| Capparaceae | *Capparis virgata* | - | 0,43 | ML | - |
| Capparaceae | *Maerua filiformis* | Sorety | 0,43 | ML | ML |
| Crassulaceae | *Kalanchoe laetivirens* | - | 5,13 | ML, YL | Fl |
| Didiereaceae | *Allaudia humbertii* | Songombarika | 2,14 | - | FA |
| Fabaceae | *Tamarindus indica* | Kily | 5,13 | FJ | ML, FrV |
| Meliaceae | *Azardirachta indica* | Nimy | 8,97 | ML | ML |
| Moraceae | *Ficus sycomorus* | Adabo | - | - | FrM |
| Salvadoraceae | *Azima tetracantha* | Filofilo | 0,85 | ML | ML |
| Violaceae | *Rinorea greveana* | Tsatsake | 8,97 | RFr | - |
| Cactaceae | *Cereus sp* | Tsilo | 0,43 | BFl | - |
| Acanthaceae | *Juticia dejecta* | - | - | ML | - |
| Liliaceae | *Dipcadi heterocuspe* | - | - | Fl | - |

Note : Mature leaf (ML), Young leaf (YL), Ripe fruit (RFr), Stem (St), Flower Bud (FlB), Flower (Fl)

The dietary catalog reveals a contraction from 14 species consumed in November to 10 in July, tracking a sharp decline in resource richness. Despite a high relative environmental abundance of 12.39% for *Opuntia vulgaris*, lemurs actively diversified their intake across 14 botanical families to secure critical macro-nutritional balances.

## 3.2. Availability of plant parts and consumption

Phenological monitoring during the early wet season in November established that mature leaves formed the baseline structural biomass of the habitat, constituting 85.58% of all

By the mid-dry season in July, the phenological landscape underwent a profound transition, exhibiting a near-total collapse of fruit availability, which dropped to a mere 0.60% of environmental assets. In response to this acute landscape depletion, the behavioral feeding activity of *Lemur catta* shifted decisively toward mature foliage and alternative succulent parts. This synchronized shift confirms that while the species possesses an innate preference for high-energy fruits, its feeding framework is structurally flexible, allowing a rapid transition to lower-quality fallback vegetative structures to navigate seasonal climatic bottlenecks (Yamashita, 2008b ; Norscia *et al.*, 2006).

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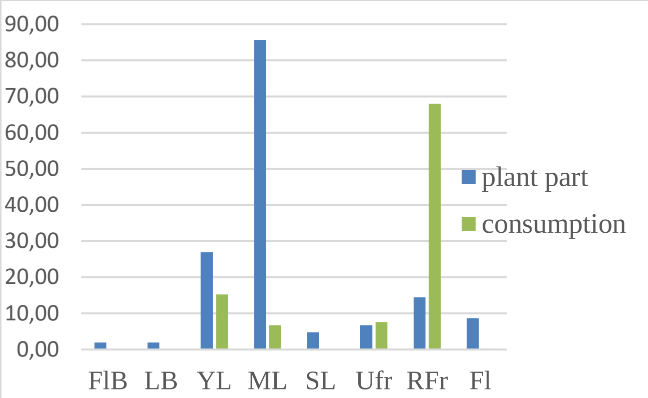


Note : Flower bud (FlB), Leaf bud (LB), Young leaf (YL), Mature leaf (ML), Senescent leaf (SL), Unripe fruits (UFr), Ripe fruits (RFr), Flowers (Fl)

Figure 1: Phenological availability versus relative consumption of plant parts by *Lemur catta* during the early wet season (November 2023) at Berenty Private Reserve

The wet-season data demonstrate highly active foraging selection, where ripe fruits were heavily targeted to comprise 68.00% of total dietary ingestion. This stands in stark quantitative contrast to their limited phenological presence in the forest, which was strongly outmatched by an abundant but bypassed mature leaf biomass of 85.58%.

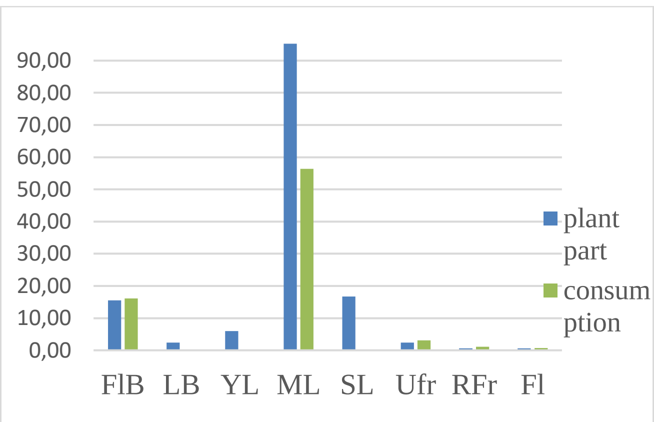


Figure 2: Phenological availability versus relative consumption of plant parts by *Lemur catta* during the mid-dry season (July 2024) at Berenty Private Reserve

The dry-season matrix reveals total landscape depletion, marked by a near-complete collapse of environmental fruit availability down to 0.60%. Consequently, the lemurs exhibited extreme behavioral flexibility, shifting their primary dietary consumption almost entirely toward structural fallback resources, notably mature foliage, to survive the severe macroclimatic resource bottleneck.

## 3.3. Nutritional composition and food preference

Biochemical modeling of the exploited food items unveiled significant variations across species, specific plant parts, and seasonal intervals. Crude protein content fluctuated between a baseline of 2.36% in *Rinorea greveana* fruits and a maximum concentration of 30.41% in *Capparis virgata* foliage. Total non-structural carbohydrates peaked sharply within frugivorous items, reaching an absolute value of 97.64% in *Rinorea greveana*. Conversely, crude fat levels remained consistently depressed across most vegetative items, dipping as low as 0.94%, while ash content varied from 7.78% to 18.14%, highlighting a vital mineral intake from taxa like *Cordia caffra* during stressful dry intervals (Yamashita, 2008a).

Chemometric correlations between explicit feeding preferences and macro-nutritional properties varied fundamentally across the seasonal baseline. During the early wet season, foraging choices exhibited a moderate positive trend with total carbohydrate concentrations ($r$ = 0.58, $p$ = 0.0878), signaling a metabolic focus on rapidly assimilable energy sources to fuel increased locomotion (Yamashita, 2008b). In contrast, preference correlated negatively with protein and showed no link to lipids ($r$ = –0.467, $p$ = 0.173). By July, these patterns reversed into non-significant positive trends for crude proteins ($r$ = 0.232, $p$ = 0.519) and crude lipids ($r$ = 0.374, $p$ = 0.287), alongside a negative correlation with carbohydrates ($r$ = –0.326, $p$ = 0.359). This mathematical shift indicates that during periods of fruit scarcity, *Lemur catta* modifies its selection criteria, favoring protein- and lipid-dense fallback items like *Azadirachta indica* leaves and *Opuntia vulgaris* stems to satisfy basic maintenance requirements (Righini *et al.*, 2015 ; Hladik *et al.*, 2003).

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**Table 3. Phytochemical profiles and relative dietary consumption of plant items exploited by *Lemur catta* across contrasting seasons**

| Period | Species | Plant parts | Consumption | Ash (%) | CP (%) | Fat (%) | TC (%) |
|---|---|---|---|---|---|---|---|
| Nov | *Azadirachta indica* | ML | 3,84 | 11,09 | 23,96 | 3,14 | 61,81 |
| Nov | *Azima tetracantha* | ML | 0,57 | 13,05 | 23,77 | 1,00 | 62,18 |
| Nov | *Capparis virgata* | ML | 1,24 | 15,22 | 30,41 | 2,48 | 51,89 |
| Nov | *Cordia caffra* | YL | 4,22 | 18,14 | 23,48 | 0,00 | 58,37 |
| Nov | *Cordia sinensis* | Rfr | 19,88 | 7,78 | 11,09 | 0,99 | 80,14 |
| Nov | *Kalanchoe laetivirens* | L | 1,05 | 10,61 | 15,65 | 5,15 | 68,60 |
| Nov | *Maerua filiformis* | ML | 0,48 | 11,75 | 24,68 | 2,36 | 61,22 |
| Nov | *Opuntia vulgaris* | St | 0,80 | 23,43 | 21,67 | 0,94 | 53,96 |
| Nov | *Rinorea greveana* | Rfr | 45,84 | 0,00 | 2,36 | 0,00 | 97,64 |
| Nov | *Tamarindus indica* | YL | 9,91 | 0,00 | 14,66 | 0,00 | 85,34 |
| July | *Azadirachta indica* | ML | 48,82 | 12,16 | 18,43 | 9,81 | 59,60 |
| July | *Opuntia vulgaris* | St | 18,35 | 10,14 | 14,27 | 7,41 | 68,19 |
| July | *Eucalyptus sp* | Fl/FlB | 16,13 | 8,14 | 11,21 | 5,75 | 74,90 |
| July | *Tamarindus indica* | ML | 3,93 | 10,00 | 16,65 | 10,00 | 63,35 |
| July | *Tamarindus indica* | UFr | 3,07 | 4,89 | 3,87 | 1,55 | 89,69 |
| July | *Aloe vera* | ML | 2,82 | 9,25 | 13,79 | 3,97 | 72,99 |
| July | *Allaudia humbertii* | ML | 2,15 | 13,19 | 17,93 | 11,57 | 57,31 |
| July | *Maerua filiformis* | ML | 1,44 | 8,89 | 19,78 | 5,21 | 66,12 |
| July | *Ficus sp* | RFr | 1,07 | 11,22 | 11,01 | 6,11 | 71,67 |
| July | *Rinorea greveana* | ML | 0,00 | 8,71 | 15,2 | 4,36 | 71,73 |

Note : Crude protein (CP), crude fat (CF), Total carbohydrate (TC)

Biochemical modeling demonstrates an active seasonal pivot, with consumption of *Rinorea greveana* fruits maximizing carbohydrate intake at 97.64% in November. In July, feeding shifted decisively to *Azadirachta indica* foliage, which optimized structural intake by supplying a substantial crude protein fraction of 18.43% and 9.81% fat.

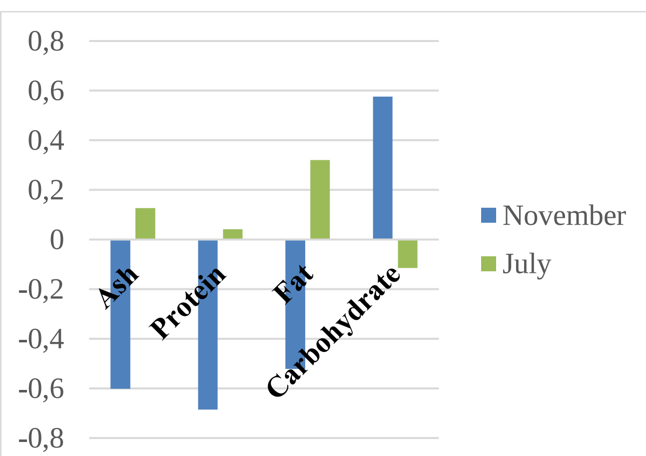


Figure 3: Statistical correlation matrix modeling the relationship between *Lemur catta* feeding preference percentages and the macro-nutritional traits of exploited plant items

The chemometric model reveals a seasonal divergence in selection drivers, transitioning from a carbohydrate focus in November ($r = 0.58$; $p = 0.0878$) to protein-lipid maintenance in July. While wet-season intake actively avoided protein biomass ($r = -0.467$), dry-season stress stimulated positive trends for structural proteins ($r = 0.232$) and crude fats ($r = 0.374$).

## 4. Discussion

### 4.1. Seasonal dietary switching

The empirical findings elucidate a pronounced, structurally demarcated seasonal dichotomy in the foraging patterns of *Lemur catta*, directly reflecting the severe microclimatic shifts and vegetative phenological fluctuations characteristic of southern Malagasy gallery forests. During the early wet season, the targeted consumption of lipid- and carbohydrate-dense fruits underscores an opportunistic, energy-maximizing foraging posture whenever high-quality resources achieve

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landscape abundance (Sato *et al.*, 2015 ; Hladik *et al.*, 2003 ; Anne *et al.*, 2003). This seasonal propensity toward preferential frugivory mirrors behavioral adjustments documented across a spectrum of sympatric and allopatric Malagasy primates navigating ephemeral resource flushes (Sato *et al.*, 2015).

Conversely, the severe contraction of available fruit biomass during the mid-dry season prompts a dramatic behavioral pivot toward structural folivory. This temporal transition from high-quality reproductive tissue to lower-grade vegetative matter represents a classic dietary fallback strategy widely documented among wild anthropoids and strepsirrhines subject to acute environmental scarcity (Irwin *et al.*, 2014 ; Norscia *et al.*, 2006 ; Chapman & Chapman, 1990). Rather than maintaining a rigid taxonomic dietary niche, *Lemur catta* demonstrates substantial demographic and behavioral resilience by expanding its ecological envelope to include abundant, albeit fibrous, structural components that alleviate immediate starvation risks during resource bottlenecks.

### 4.2. Nutritional optimization

On a phytochemical level, the clear preference displayed for carbohydrate-rich fruits (e.g., *Rinorea greveana*) and tender young foliage (e.g., *Tamarindus indica*) during November aligns precisely with optimal foraging paradigms optimizing net energy assimilation rates (Yamashita, 2008b). Non-structural carbohydrates serve as the primary, rapidly metabolizable metabolic substrate required to sustain the intensive energetic costs of territory defense, reproductive mating cycles, and heightened locomotion that typically define the onset of the austral wet season (Yamashita, 2008b).

During the mid-dry season constraint, the absolute scarcity of fruit matrices forces an immediate reliance on mature leaves and alternative succulent structures, which introduce severe mechanical and chemical processing challenges due to elevated structural fiber and secondary metabolite concentrations (Yamashita, 2008a ; Hladik *et al.*, 2003). The non-significant positive correlation trends observed in July with crude proteins and lipids mathematically support a calculated nutritional mitigation mechanism. This posture prioritizes macronutrient maintenance over pure caloric maximization, allowing the focal subjects to satisfy basal metabolic requirements under severe energy deficits (Righini *et al.*, 2015). Key dominant taxa, specifically *Azadirachta indica* and *Opuntia vulgaris*, emerge as critical lifeline resources, sustaining the cohort either via exceptional local biomass density or by offering reliable micro-nutritional configurations that prevent severe physical degradation during seasonal dry-forest crunches.

### 4.3. Adaptive significance

The profound seasonal dietary variation observed within the Berenty cohort provides compelling evidence of evolutionary nutritional plasticity, widely recognized as a pivotal adaptive mechanism for survival within the arid, highly unpredictable bioclimatic zones of Madagascar (Yamashita, 2008b ; Norscia *et al.*, 2006). This ecological flexibility is multi-dimensional, combining highly opportunistic behavioural dynamics with specialized physiological and gastrointestinal adaptations that facilitate the structural degradation and assimilation of complex, fibrous structural components during acute food stress (Yamashita, 2008a).

Such macro-nutritional resilience is highly critical for *Leumur catta* populations trapped within isolated forest fragments like the Berenty Private Reserve, where anthropogenically driven spatial barriers restrict wide-ranging migratory tracking of seasonal resources (Sussman, 2013 ; Ichino *et al.*, 2009). Consequently, this evolutionary flexibility underscores that the long-term demographic viability of this endangered primate is entirely dependent on its capacity to navigate intense seasonal bottlenecks by dynamically pivoting across diverse botanical properties to secure physiological equilibrium.

## 5. Conclusion

This investigation elucidates the intricate mechanisms governing the nutritional ecology of *Lemur catta* within the highly seasonal, spatially constrained bioclimatic framework of the Berenty Private Reserve. By bridging behavioral tracking with precise phytochemical quantifications, the study demonstrates that seasonal microclimatic fluctuations dictate a profound behavioral and metabolic pivot. During the early wet season, foraging dynamics are characterized by an energy-maximizing posture that actively selects carbohydrate-dense reproductive tissues despite their landscape scarcity. Conversely, the acute environmental depletion of the mid-dry season triggers a transition toward low-quality, fibrous fallback vegetative and succulent biomass, where selection criteria shift toward satisfying baseline macronutrient requirements for crude protein and lipids.

The structural innovation of this research lies in its quantitative integration of high-resolution near-infrared spectroscopy (NIRS) profiling with explicit behavioral preference metrics, a framework that addresses a critical empirical gap in the nutritional ecology of Malagasy dry-forest primates. While historical literature has frequently classified *Lemur catta* as a fundamentally opportunistic

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generalist, this chemometric modeling provides unequivocal evidence of active, non-random metabolic optimization strategies operating beneath landscape constraints. Such pronounced nutritional plasticity represents an evolutionary lifeline, ensuring physiological resilience against severe climate bottlenecks.

Crucially, however, the empirical findings reveal that this adaptive flexibility is entirely contingent upon the structural maintenance of highly diverse botanical communities. In isolated, anthropogenically fragmented habitats where migratory resource-tracking is prohibited, the preservation of key dominant and secondary fallback taxa is paramount. Consequently, micro-nutritional security must be recognized as a core pillar of strategic conservation frameworks designed to guarantee the long-term population viability and demographic persistence of this endangered strepsirrhine.

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## Reference

1. Altmann, J. (1974). Observational study of behavior: Sampling methods. Behaviour, 49(3-4), 227–267. https://doi.org/10.1163/156853974X00034

2. AOAC. (1990). Official methods of analysis (15th ed.). Association of Official Analytical Chemists.

3. Chapman, C. A., & Chapman, L. J. (1990). Dietary variability in primate populations. Primates, 31(1), 121–128. https://doi.org/10.1007/BF02381142

4. Fournier, L. A. (1974). Un método cuantitativo para la medición de características fenológicas en árboles [A quantitative method for measuring phenological characteristics in trees]. Turrialba, 24(4), 422–423.

5. Hladik, A., Ramasiarisoa, P., & Simmen, B. (2003). Food intake and dietary overlap in native Lemur catta and Propithecus verreauxi and introduced Eulemur fulvus at Berenty, southern Madagascar. International Journal of Primatology, 24(5), 949–970. https://doi.org/10.1023/A:1026214313264

6. Ichino, S., Soma, T., Miyamoto, N., Sato, H., & Koyama, N. (2009). Population dynamics of ring-tailed lemurs (*Lemur catta*) at Berenty Reserve, Madagascar: A 20-year study. Primates, 50(1), 1–10. https://doi.org/10.1007/s10329-008-0111-z

7. Irwin, M. T., Raharison, J.-L., Raubenheimer, D., Chapman, C. A., & Rothman, J. M. (2014). Nutritional correlates of the lean season: Effects of seasonality and frugivory on the nutritional ecology of diademed sifakas. American Journal of Physical Anthropology, 153(1), 78–91. https://doi.org/10.1002/ajpa.22410

8. Kent, M. (2012). Vegetation description and data analysis (2nd ed.). Wiley-Blackwell.

9. Magurran, A. E. (2004). Measuring biological diversity. Blackwell Publishing.

10. Norscia, I., Carrai, V., & Borgognini-Tarli, S. (2006). Influence of dry season food quality and quantity on behavior and feeding strategy of *Propithecus verreauxi* in Kirindy, Madagascar. International Journal of Primatology, 27(4), 1001–1022. https://doi.org/10.1007/s10764-006-9053-x

11. Rérat, A. (1956). Méthodes de détermination des glucides en vue de l'estimation de leur valeur énergétique. Annales de Zootechnie, 5(3), 213–236. https://doi.org/10.1051/animres:19560302

12. Righini, N., Garber, P. A., & Rothman, J. M. (2015). The effects of plant nutritional chemistry on food selection by Mexican black howler monkeys

2026, Vol. 4, Issue 1
DOI : https://www.doi.org/10.65857/raee.026.v4.i1.45

(Alouatta pigra): The role of lipids. American Journal of Primatology, 77(1), 1–12. https://doi.org/10.1002/ajp.22306

13. Rothman, J. M., Chapman, C. A., & Van Soest, P. J. (2011). Methods in primate nutritional ecology: A user's guide. International Journal of Primatology, 32(3), 542–566. https://doi.org/10.1007/s10764-011-9513-3

14. Sato, H., Santini, L., Patel, E. R., Yamashita, N., Colquhoun, I. C., & Donati, G. (2015). Dietary flexibility and feeding strategies of Eulemur: A comparison with Propithecus. International Journal of Primatology, 36(5), 879–900. https://doi.org/10.1007/s10764-015-9860-5

15. Simmen, B., Mignot, E., Fichtel, C., & Randrianjafy, H. (2003). Ring-tailed lemur home ranges correlate with food abundance and nutritional content at a time of environmental stress. International Journal of Primatology, 24(5), 973–999. https://doi.org/10.1023/A:1026266330194

16. Sussman, R. W. (2013). A preliminary assessment of the status of primate conservation in Madagascar. Primate Conservation, 2013(28), 1–9. https://doi.org/10.1896/052.028.0116

17. Tarnaud, L., Garcia, C., Krief, S., & Simmen, B. (2010). Apports nutritionnels, d'énergie et équilibre énergétique chez les primates humains et non humains : Aspects méthodologiques. Bulletins et Mémoires de la Société d'Anthropologie de Paris, 22(1-2), 1–16. https://doi.org/10.1007/s13219-010-0003-y

18. William, J. F., Norris, K. H., Barnes, R. F., & Shenk, J. S. (1998). Ecological applications of near-infrared reflectance spectroscopy: A tool for rapid, cost-effective prediction of plant and animal tissue composition. Oecologia, 116(3), 293–302. https://doi.org/10.1007/s004420050657

19. Yamashita, N. (2008a). Chemical properties of the diets of two lemur species in southwestern Madagascar. International Journal of Primatology, 29(2), 339–364. https://doi.org/10.1007/s10764-008-9242-7

20. Yamashita, N. (2008b). Food selection in Lemur catta in relation to food chemistry and mechanical properties. American Journal of Physical Anthropology, 135(3), 182–194. https://doi.org/10.1002/ajpa.20727

21. Zar, J. H. (1999). Biostatistical analysis (4th ed.). Prentice Hall.