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Dietary and Nutritional Selections by Ecologically Diverse Lemurs in Nonnative Forests

Lydia K. Greene[1,2,4] · Marina B. Blanco[1,2] · Casey Farmer[3] · Maire O'Malley[3] · Chloé Gherardi[3] · Mitchell T. Irwin[3]

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One challenge for wild primates is finding foods to satisfy their nutritional demands (Lambert & Rothman, 2015). For populations facing habitat change, this challenge can be exacerbated if preferred foods become rare and if exotic or invasive species replace endemic ones. Whether a population persists under changing conditions can depend, in part, on the availability of alternative foods, the animals' ability to identify and use them, and the physiological limits of nutritional flexibility (Lambert & Rothman, 2015). Field observations showcase examples of primates adjusting their dietary regimens to local conditions (Lambert & Rothman, 2015); however, experimental systems to probe feeding flexibility may further reveal physiological underpinnings of primate responses to changing landscapes.

In Madagascar, ring-tailed lemurs (*Lemur catta*) are omnivores that inhabit diverse habitats in the south, while Coquerel's sifakas (*Propithecus coquereli*) are frugo-folivores that inhabit dry forests in the northwest. These two genera show dietary flexibility within the constraints of their feeding strategies: ring-tailed lemurs consume high-sugar, low-protein items, whereas sifakas eat protein-rich but low-sugar items, including leaves with abundant plant secondary compounds (Yamashita, 2008).

By considering captivity a type of anthropogenic habitat, we document foraging behavior, and determine macronutrient content in selected foods, in ring-tailed lemurs and sifakas housed sympatrically in forest enclosures at the Duke Lemur Center, USA (Figs. 1a,b). Under the hypothesis that lemurs are flexible foragers within physiologically defined limits, we predict that ring-tailed lemurs and sifakas

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✉ Lydia K. Greene
lydiakgreene@gmail.com

[1] Department of Biology, Duke University, Durham, NC, USA

[2] The Duke Lemur Center, Duke University, Durham, NC, USA

[3] Department of Anthropology, Northern Illinois University, DeKalb, IL, USA

[4] Academic Advising Center, Duke University, 4 East Campus Union Drive, Durham, NC 27708, USA

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will successfully find and consume diverse local plants in nonnative forests following intrinsic selection rules, leading to dietary niche differentiation. In other words, they will select for plant parts and macronutrients consistent with patterns of wild kin in Madagascar (Yamashita, 2008).

The subjects were six ring-tailed lemurs (3F, 3M) and six sifakas (3F, 3M) in three groups per species in multi-acre enclosures. LKG conducted all-day observations in spring (May 4–June 20) and summer (August 10–September 15), 2020. We observed both adults per group simultaneously for three consecutive days per season, recording the duration of foraging on nonprovisioned items, plant part, and taxon. In total, we observed lemurs for 505 hours on 36 days. (See supplementary material for details.).

Because sifakas foraged more than ring-tailed lemurs (23% vs. 8% of observation time), we compared behavior using proportional data, i.e., the proportion of total foraging time dedicated to specific plant parts. We calculated mean values per lemur across observation days per season. We entered means as the dependent variables in analyses of variance (ANOVAs) using R software (version 4.2.1). We included species and season as independent variables and used log(x+1) transformations when they improved model fit.

Contemporaneous with observations, we collected 60 samples of consumed items from 30 plant species for nutritional profiling, prioritizing those that accounted for

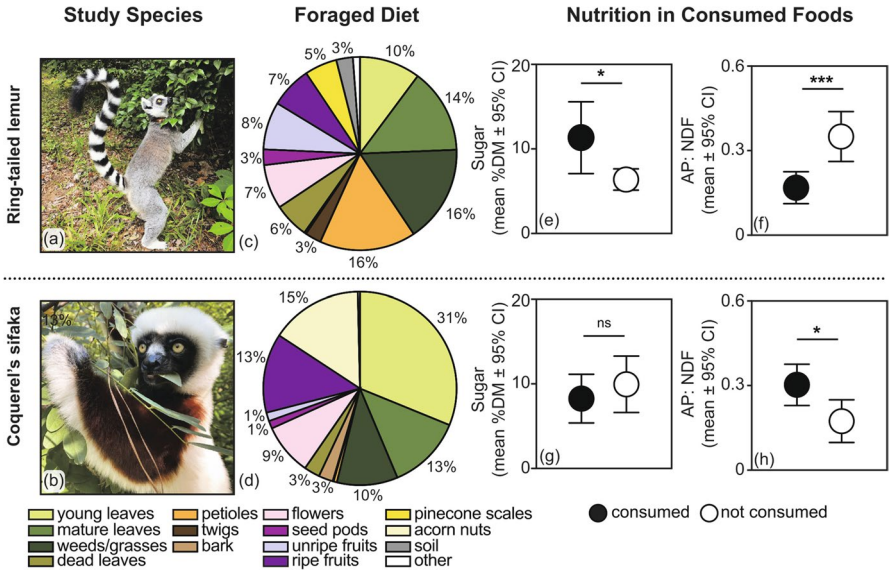

Fig. 1 (**a**) Ring-tailed lemur and (**b**) Coquerel's sifaka. Pie charts depict the mean time the focal (**c**) ring-tailed lemurs and (**d**) sifakas spent foraging for different plant parts as a proportion of total foraging time (excluding provisioned items), with color key listed below. The nutritional composition of foods that were (black) consumed and (white) not consumed by focal (**e, f**) ring-tailed lemurs and (**g, h**) sifakas, including (**e, g**) sugar and (**f, h**) the ratio of available protein to neutral detergent fiber (AP:NDF). ns $p > 0.1$; *$p < 0.05$; ***$p < 0.001$.

>1% of foraging time across conspecifics. Of these, 31 were consumed by sifakas, 19 were consumed by ring-tailed lemurs, and ten were consumed by both. We present analyses of sugar (% dry matter), the ratio of available protein to neutral detergent fiber (AP:NDF), and condensed tannin (CT) presence. (See supplementary material for methodological details and additional macronutrients.) To compare items consumed or not consumed by ring-tailed lemurs (n = 29 vs. 31) and sifakas (n = 41 vs. 19), we analyzed sugar and AP:NDF using Student's *t*-tests and CT presence using chi-square tests.

Ring-tailed lemurs versus sifakas foraged at greater proportions for petioles ($F_{1,21} = 33.06$, $p < 0.001$), twigs ($F_{1,21} = 9.13$, $p = 0.006$), dead leaves ($F_{1,21} = 4.80$, $p = 0.040$), and unripe fruits ($F_{1,21} = 13.64$, $p = 0.001$), but at lesser proportions for young leaves ($F_{1,21} = 10.30$, $p = 0.004$) and bark ($F_{1,21} = 4.34$, $p = 0.050$) (Figs. 1c,d). We found no significant differences in the proportion of foraging time on mature leaves ($F_{1,21} = 0.30$, $p = 0.592$), weeds and grasses ($F_{1,21} = 0.01$, $p = 0.922$), flowers ($F_{1,21} = 0.43$, $p = 0.517$), seed pods ($F_{1,21} = 0.13$, $p = 0.720$), or ripe fruits ($F_{1,21} = 0.10$, $p = 0.762$). Only ring-tailed lemurs consumed pinecone scales and soil; only sifakas consumed acorn nuts.

The items consumed versus not consumed by ring-tailed lemurs had more sugar ($t_{31.23} = 2.28$, $p = 0.029$) and a lower ratio of AP:NDF ($t_{52.96} = -3.53$, $p < 0.001$) (Figs. 1e,f). The items consumed versus not consumed by sifakas did not differ in sugar ($t_{45.27} = 0.79$, $p = 0.433$) but had a greater ratio of AP:NDF ($t_{49.91} = 2.51$, $p = 0.015$) (Figs. 1g,h). CTs were present in 78% of samples and did not vary between consumed or non-consumed items by either species ($\chi^2_1 < 0.001$, $p = 1.000$).

We show that forest-dwelling lemurs living outside their endemic ranges, and offered a choice of wild plants, find diverse foods with specific macronutrients from local species in a manner consistent with congeners in native habitats (Yamashita, 2008). In our study, ring-tailed lemurs consumed flowers, fruits, leaves, petioles, twigs, and pinecone scales; their selections were rich in sugar and/or fiber but limited in protein. In contrast, sifakas consumed young and mature leaves, flowers, fruits, and acorn nuts; their selections were rich in protein relative to fiber. Our results underscore that captive primates express wild-like behavior under relevant conditions. They also emphasize the importance of protein to folivore ecology (Ganzhorn *et al*., 2017).

Captive primates offer potential for experimental research on feeding flexibility and ecological adaptation. Follow-up studies could ask "how" primates know which foods are suitable. Those working in sensory ecology could examine the systems, such as taste and smell, that enable macronutrient detection (Toda *et al*., 2021). Furthermore, research on captive primates could augment studies on wild populations that showcase feeding flexibility by elucidating species-specific limits of dietary tolerance and breadth, and how foraging knowledge is acquired and shared. Understanding the mechanisms that support primate flexibility across conditions could help to define the habitat features, irrespective of endemism, that can simultaneously support at-risk populations and sustainable land practices for local communities (Hending *et al*., 2018).

Ethical Note

The study was approved by Duke University's Institutional Animal Care & Use Committee (Protocol A106- 19- 05).

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Author Contributions LKG and MTI conceived of and designed the study. LKG collected behavioral data, and with CF collected plant samples. CF, MO, CG, and MTI analyzed plant samples. LKG performed statistical analysis with assistance from MBB and MTI. LKG, MBB, and MTI wrote the manuscript. All authors contributed to the final version.

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Data Availability Foraging and nutritional data are available in the supplementary material.

Inclusion and Diversity Statement One or more of the authors on this paper self-identifies as an underrepresented ethnic minority. One or more of the authors on this paper self-identifies as a member of the LGBTQ+ community.

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