

Forest access restores foraging and ranging behavior in captive sifakas

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Abstract

Captive wildlife benefit from ecologically informed management strategies that promote natural behaviors. The Duke Lemur Center has pioneered husbandry programs rooted in species' ecology for a diversity of lemurs, including housing social groups in multiacre forest enclosures. We systematically document the foraging and ranging patterns of Coquerel's sifakas (*Propithecus coquereli*) living in these forest enclosures. Coquerel's sifakas are seasonal frugo-folivores that exhibit striking feeding flexibility in the wild. They are also one of the few members of the Indriidae family to persist in captivity. During all-day follows in the spring and summer of 2 consecutive years, we tracked the behavior of 14 sifakas in six forest enclosures. The sifakas' ranging and foraging patterns reflected those of wild sifakas in western Madagascar: On average, DLC sifakas occupied 3-day home ranges of 1.2 ha, traveled 473 m/day, and spent 26% of their time foraging for wild foodstuffs. The sifakas foraged most for young and mature leaves, fruits, nuts, and flowers from 39 plant species, especially red maple (*Acer rubrum*), tulip poplar (*Liriodendron tulipifera*), black locust (*Robinia pseudoacacia*), grapevine (*Vitis rotundifolia*), hickory (*Carya* spp.), and white oak (*Quercus alba*). Foraging patterns varied across seasons, enclosure areas, and groups, potentially reflecting differences in phenology, microhabitats, and individual preferences. While demonstrating that captive-bred primates express wild-like behaviors under ecologically relevant conditions, our results underscore the feeding flexibility of the Coquerel's sifaka. Captive wildlife exhibiting the range of species-specific behaviors are key resources for ecological research and might be best suited for future reintroductions.

KEYWORDS

Duke Lemur Center, feeding ecology, home range, lemur, nutrition

1 | INTRODUCTION

Diverse wildlife species are maintained under human care for various reasons, including conservation breeding, visitor education, and noninvasive research. Captive populations thus serve as safety nets, ambassadors, and proxies for their wild kin. Nevertheless, the success of captive wildlife colonies is often challenged by artificial conditions

far removed from those experienced in nature that can underlie behavioral, health, and reproductive concerns (Coe, 1989; Penfold et al., 2014). Ecological research can play a valuable role in optimizing husbandry practices for diverse wildlife species in captivity. Ecological data from wild populations can inform species-specific diets (Chatpongcharoen et al., 2021; Crissey & Pribyl, 1997; Williams et al., 2015) and social and housing conditions (Fàbregas et al., 2012;

Frederick & Fernandes, 1996; Swaisgood & Schulte, 2010), while also contributing to the design of enrichment and experiences that encourage natural behaviors and minimize stereotypic ones (Kistler et al., 2009; Rabin, 2003; Wagman et al., 2018). Furthermore, ecologically informed management can improve the relevance of research data collected on managed populations and can help develop strategies to best prepare captive-bred individuals for eventual reintroduction or translocation to natural or restored habitats (Reading et al., 2013; Tetzlaff et al., 2019).

The Duke Lemur Center (DLC), in Durham NC, has pioneered husbandry strategies for lemurs rooted in species' ecologies. The DLC is an AZA-accredited, noninvasive research center that houses the largest and most diverse collection of lemurs outside of Madagascar. On-site programs focus on promoting lemur welfare and managed breeding to maintain genetic diversity, which are advanced by ecological research. Recent examples include replacing or supplementing provisioned fruits for frugivores with greens and vegetables (Greene, Clarke, et al., 2020) based on accruing data demonstrating key nutritional differences between wild and orchard produce (Schwitzer et al., 2009); optimizing seasonal diets and housing conditions for dwarf lemurs to enable seasonal fat deposition and hibernation (Blanco et al., 2021; Blanco, Greene, Ellsaesser, et al., 2022; Blanco, Greene, Klopfer, et al., 2022) based on new understanding of hibernation physiology in wild dwarf lemurs (Blanco et al., 2018; Fietz & Ganzhorn, 1999); and using fecal transplants to help individuals recover from enteric infection and antibiotic administration (Bornbusch et al., 2021; McKenney et al., 2017) based on sightings of coprophagy in lemurs (McKenney et al., 2018; Weir, 2014) and developing frameworks about gut microbial ecology (McKenney et al., 2018; Trevelline et al., 2019).

The DLC is also well known for allowing diurnal lemurs to range in forested enclosures called Natural Habitat Enclosures (NHEs). The DLC currently maintains nine forest enclosures that vary in size from 0.5 to 6.6 ha of Duke Forest. Enclosures are ringed by a fence straddled by a grassy area on both sides. Forest enclosures contain a rich assemblage of trees and plants: They are typically dominated by hardwoods and conifers, including pine, oak, and hickory, as well as poplar, maple, and sweetgum, and in various states of succession (Oosting, 1942). DLC lemurs occupy forest enclosures typically from April–October when overnight temperatures reliably remain above 3–5°C. Allowing lemurs consistent access to forest enclosures has contributed to the research data generated at the center, spanning advances in diverse fields of study from behavior, reproduction, and endocrinology (Grebe et al., 2019; Pereira et al., 1987, 1990; Starling et al., 2010), development and life history (Pereira, 1993), microbiome science (Bornbusch et al., 2020; Greene et al., 2018), and biomechanics (Wunderlich et al., 2014). Moreover, granting forest access to lemurs promotes multiple axes of health and has been shown to reduce stereotypic behavior (Garrison, 1993) and stress (Seeley et al., 2021), modify the gut microbiome (Greene et al., 2018), improve reproductive success (Haring, 1988; although see Weigler et al., 1994) and increase opportunity for foraging and exploration (Ganzhorn, 1986, 1987).

Here, we document the foraging and ranging behavior of DLC Coquerel's sifakas (*Propithecus coquereli*) when housed in forest enclosures. Coquerel's sifakas are large-bodied (3–5 kg), diurnal lemurs from the Indriidae family that live in Madagascar's northwest dry forests. Like other sifakas (Irwin, 2007; Lehman & Mayor, 2004; Pichon et al., 2010; Sato et al., 2016), they are seasonal frugivores in the wild and forage for a rich array of leaves, fruits, flowers, and bark (McGoogan, 2011; Richard, 1974). Fruits, flowers, and young leaves tend to dominate sifaka diets in the rainy season, while mature leaves and bark are more readily consumed in the dry season (Richard, 1974). Coquerel's sifakas in Madagascar are listed as Critically Endangered (Louis et al., 2020); however, they are among the more resilient members of their family. Although large forest blocks are preferable (Eppley et al., 2020), Coquerel's sifaka groups can inhabit forest patches as small as 2.5 ha (Ramilison et al., 2021) and home ranges (estimated from 2 to 3 observation days) can be as small as 1–6 ha (E. Rambeloson, pers. communication). Coquerel's sifakas can also flexibly adapt to some degree to changing landscapes by feeding on mangrove leaves (Chell et al., 2020) and human-cultivated plants, such as mango, kapok, and tamarind (Ramilison et al., 2021; Salmona et al., 2014).

This feeding flexibility is perhaps partly why Coquerel's sifakas persist under human management outside of Madagascar, when few other members of the Indriidae family have (Roulet, 2014 & DLC in-house records). The DLC's colony of Coquerel's sifakas was largely established in the 1980s (then listed as *P. verreauxi coquereli*) (Haring, 1988) and current members are 2–6 generations removed from the wild. The colony is genetically robust (Guevara, Webster, et al., 2021), but is also strongly susceptible to diarrheal illness, enteric pathogens, and infection (Cassady et al., 2018; Charles-Smith et al., 2010; L. Ellsaesser, DVM, pers. communication). Decades of housing and dietary optimization, based on accruing data from Madagascar, aimed specifically to boost outdoor access and foliage intake (Campbell et al., 2001; Haring, 1988; Macedonia, 1987) and led to significant reductions in health problems while improving the colony's reproductive success (Haring, 1988). Preliminary research documented sifakas foraging on 16 plant species in forest enclosures (Abhau, 2007), though these observations were limited to a handful of animals across few hours and days. We currently lack understanding of how the DLC sifaka colony uses space and food resources in forest enclosures, and how, in turn, such use benefits sifaka nutrition and health.

Here, we add to our understanding of sifaka behavioral flexibility linked to ecologically informed management through systematic observations during all-day follows in the springs and summers across two calendar years. Under the hypothesis that ecologically relevant husbandry conditions promote wild-like behavioral repertoires, we expect sifaka groups with forest access to display seasonal ranging and foraging behavior consistent with that of their wild peers in western Madagascar. In particular, we expect sifakas to occupy multiacre home ranges and travel each day in search of wild foodstuffs. We expect sifakas to spend considerable time and effort foraging for a seasonal and diverse diet that comprises fruits, flowers,

leaves, petioles, soils, and bark. We further expect both the time spent foraging, and the composition of foraged diets, to vary within and across days, seasons, enclosures, and social groups relative to food availability and/or selective preference.

2 | MATERIALS AND METHODS

2.1 | Study subjects and housing

The subjects were 14 adult, Coquerel's sifakas maintained at the DLC (Table 1). The subjects ranged in age from 3 to 17 years at the time of study and resided in one of seven social groups that comprised an adult breeding pair and variably included the pair's offspring. All DLC sifakas are individually recognizable via distinctive features. Per DLC protocols, minimally one sifaka per group bore a radio collar that emits a unique frequency and could be tracked using standard telemetry.

At the DLC, staff periodically check on animals from 8:30 to 16:00 each day. Once per morning (9:30 a.m. to 11:30 a.m.), sifakas are offered a standard, provisioned diet, consisting of a high-fiber chow, assorted vegetables, leafy greens, and beans or nuts. In the early afternoon (2:00 p.m. to 3:30 p.m.), sifakas are offered one type of foliage from a selection of local plants (Table 2). This afternoon foliage is offered no matter if sifakas are housed in forest enclosures or not. Water is always freely available.

Our study took place during spring (May–mid June) and summer (mid-August–September). We collected observational data on social groups with access to forest enclosures between 1.1 and 6.6 ha

(2.8–16.2 acres) (Table 1). These enclosures are situated in three different areas of the facility, including the “Triplex” area (NHE2 & NHE4), the “Miaro” area (NHE3 & NHE5), and the “Aty-ala” area (NHE6 & NHE9). At all times, sifakas with forest access also have access to covered shelters.

2.2 | Data collection

One of us (L. K. G.) collected foraging and ranging data during the spring and summer of 2020 and 2021. In Year 1, we focused on three sifaka pairs per season; in 2021, we focused on five pairs per season. In both study years, pairs were observed for 3 consecutive days, once per season, during all-day follows. At sunrise, we used radio telemetry to track collared individuals to their sleeping sites. We began data collection once the group was located and paused once the sifakas had finished the bulk of their provisioned diet, typically by 11:30 a.m. We resumed data collection in the early afternoon and continued until it became too dark to reliably record foraging behavior or until the sifakas stopped foraging for >20 min. We paused observations for thunderstorms or heavy rainfall. Most of our data were collected between 6:30 a.m. and 11:30 a.m. and from 2:00 p.m. to 7:00 p.m., seasonally dependent.

During observation days, we collected ranging behavior using a handheld GPS unit (Garmin GPSMAP 64st). Because members of sifaka groups typically forage in proximity, we recorded a GPS point each time the focal female moved >10 m in any horizontal direction. We recorded foraging behavior of the focal female and male per group concurrently. We recorded the start and stop time of each

TABLE 1 Study subjects, natural habitat enclosures (NHEs), and seasons

| Study year | Season | Enclosure (ha) | Area | Subjects | Group size |
|------------|--------|----------------|---------|----------------------------------|------------|
| 2020 | Spring | NHE2 (2.91) | Triplex | Gisela and Rupert (Gi and Ru) | 4 |
| | | NHE5 (2.35) | Miaro | Gertrude and Remus (Ge and Re) | 2 |
| | | NHE6 (1.58) | Aty-ala | Beatrice and Elliot (Be and El) | 2 |
| | Summer | NHE2 | Triplex | Gisela and Rupert | 4 |
| | | NHE5 | Miaro | Gertrude and Remus | 2 |
| | | NHE6 | Aty-ala | Beatrice and Elliot | 2 |
| 2021 | Spring | NHE4 (6.56) | Triplex | Rodelinda and Marcus (Ro and Ma) | 3 |
| | | NHE3 (1.51) | Miaro | Lupicina and Gabe (Lu and Ga) | 3 |
| | | NHE5 | Miaro | Gertrude and Remus | 2 |
| | | NHE6 | Aty-ala | Beatrice and Elliot | 2 |
| | | NHE9 (1.13) | Aty-ala | Furia and Thrax (Fu and Th) | 2 |
| | Summer | NHE2 | Triplex | Gisela and Rupert | 4 |
| | | NHE3 | Miaro | Lupicina and Gabe | 3 |
| | | NHE5 | Miaro | Gertrude and Remus | 2 |
| | | NHE6 | Aty-ala | Bertha and Ferdinand (Br & Fe) | 2 |
| | | NHE9 | Aty-ala | Furia and Thrax | 2 |

| Common name | Scientific name | Family | Parts foraged | Importance |
|----------------------------|----------------------------------|----------------|--|------------|
| Red maple | <i>Acer rubrum</i> | Sapindaceae | YL, ML, PT, BK, BD ^a | +++ |
| Tulip poplar ^b | <i>Liriodendron tulipifera</i> | Magnoliaceae | YL, ML, FL, FR, PT, BK | +++ |
| Hornbeam | <i>Carpinus caroliniana</i> | Betulaceae | ML | ++ |
| Black locust | <i>Robinia pseudoacacia</i> | Fabaceae | YL ^a ML, SP, BK | +++ |
| American beech | <i>Fagus grandifolia</i> | Fagaceae | ML | ++ |
| Redbud ^b | <i>Cercis canadensis</i> | Fabaceae | YL, ML, FL ^a BD ^a SP | ++ |
| Black cherry | <i>Prunus serotina</i> | Rosaceae | YL, FR | + |
| Flowering dogwood | <i>Cornus florida</i> | Cornaceae | FR, BK | + |
| Sweetgum ^b | <i>Liquidambar styraciflua</i> | Altingiaceae | YL, ML, FR, PT, BK | ++ |
| Black tupelo | <i>Nyssa sylvatica</i> | Nyssaceae | YL, ML, FR, BK | + |
| American persimmon | <i>Diospyros virginiana</i> | Ebenaceae | YL, ML | - |
| Sourwood | <i>Oxydendrum arboreum</i> | Ericaceae | YL | + |
| White ash | <i>Fraxinus americana</i> | Oleaceae | ML | + |
| Hickory | <i>Carya glabra and ovata</i> | Juglandaceae | YL, NT, GL, BK | +++ |
| Red juniper | <i>Juniperus virginiana</i> | Cupressaceae | BK | - |
| Red mulberry | <i>Morus rubra</i> | Moraceae | YL, FR | ++ |
| Mimosa ^b | <i>Albizia julibrissin</i> | Fabaceae | YL, ML, FL, SP, BK | ++ |
| Loblolly pine ^b | <i>Pinus taeda</i> | Pinaceae | YL, ML, BK | ++ |
| White oak | <i>Quercus alba</i> | Fagaceae | YL, NT, PT, GL, BK | +++ |
| Red oak | <i>Quercus rubra and falcata</i> | Fagaceae | YL, NT, PT, GL, BK | ++ |
| Willow oak | <i>Quercus phellos</i> | Fagaceae | NT | ++ |
| Muscadine ^b | <i>Vitis rotundifolia</i> | Vitaceae | YL, BD, FR, VN | +++ |
| Honeysuckle | <i>Lonicera caprifolium</i> | Caprifoliaceae | YL, ML | - |
| Common greenbrier | <i>Smilax rotundifolia</i> | Smilacaceae | ML, SP, VN | + |
| Poison ivy | <i>Toxicodendron radicans</i> | Anacardiaceae | YL, ML | + |
| Autumn olive | <i>Elaeagnus umbellata</i> | Elaeagnaceae | ML, FR ^a | + |
| Viburnum | <i>Viburnum spp.</i> | Adoxaceae | ML, FR | - |
| Blackberry | <i>Rubus occidentalis</i> | Rosaceae | YL | + |
| Hillside blueberry | <i>Vaccinium pallidum</i> | Ericaceae | YL, ML | - |
| Multiflora rose | <i>Rosa multiflora</i> | Rosaceae | YL | - |
| Winged sumac ^c | <i>Rhus copallinum</i> | Anacardiaceae | YL, ML, FL, PT, BK | NA |
| Bush clover ^b | <i>Lespedeza cuneata</i> | Fabaceae | YL, FL | + |
| Rhomboid mercury | <i>Acalypha rhomboidei</i> | Euphorbiaceae | YL | + |
| White clover | <i>Trifolium repens</i> | Fabaceae | FL | + |
| Common vetch | <i>Vicia sativa</i> | Fabaceae | SP | - |

TABLE 2 List of identified plants and parts foraged by sifakas, and their relative importance in the diet

| Common name | Scientific name | Family | Parts foraged | Importance |
|----------------|---------------------------------|----------------|---------------|------------|
| Dogfennel | <i>Eupatorium capillifolium</i> | Asteraceae | YL | + |
| Ragweed | <i>Ambrosia sp.</i> | Asteraceae | YL, SP | - |
| Partridge pea | <i>Chamaecrista fasciculata</i> | Fabaceae | YL, SP | + |
| Tick trefoil | <i>Desmodium sp.</i> | Fabaceae | YL | + |
| Chamber bitter | <i>Phyllanthus urinaria</i> | Phyllanthaceae | YL | + |
| Goldenrod | <i>Solidago sp.</i> | Asteraceae | FL | - |

Note: Plant importance: -, plants that account for <1% of foraging time across all individuals. +, plants that account for >1% foraging time in minimally two individuals in minimally one season. ++, plants that account for >1% of foraging time across all individuals in minimally one season. +++, plants that account for >5% of foraging time across all individuals in one season.

Abbreviations: plant parts: BD, Buds; BK, Bark; FL, flowers; FR, fruits; GL, galls; ML, mature leaves; NT, nuts; PT, petioles; SP, seed pods; VN, vines; YL, young leaves.

^aAnecdotal sightings outside of study observations.

^bForaged by sifakas and provisioned to sifakas by DLC staff.

^cNever foraged by sifakas during the study, but routinely provisioned by DLC staff.

foraging bout, as well as the plant part (e.g., young leaves, fruits, flowers) and plant identification, if known. Plant identities were assigned based on visual assessments of leaf, flower, fruit, and bark appearance. In cases of uncertainty, we checked identifications against the DLC's in-house database and used Google Photos to compare photographs to online databases.

Foraging bouts ended after 10 s of inactivity. Individuals were recorded as "out-of-view" when their behavior could not be reliably recorded. Occasions were rare when it was impossible to record behavior from both individuals concurrently; however, when they did occur, we documented the female's behavior only. On a handful of observation days, we lost sight of the sifakas high in the canopy but were able to reliably record behavior based on the consistent dropping of foraged items to the forest floor, including leaves, flower petals, nut casings, and fruit skins. Using this regimen, we collected 626.08 h of animal observation on 48 days, split evenly between the spring and summer.

2.3 | Analyses of ranging behavior

We used GPS points to determine seasonal home range sizes and daily travel distances. GPS points were imported and analyzed in the QGIS program (version 3.4.5 Madeira) (QGIS, 2022). We manually adjusted any points that fell outside the fence lines, so as not to overestimate ranging patterns. We determined home range size in hectares (ha) using minimum convex polygons for each group per season. We determined travel distances, in meters, by joining adjacent GPS points and determining linear distances between points. We first calculated daily path lengths, that is, the total distance traveled per observation day. Because the hours of animal observation differed between days, we also calculated travel rates, in

meters/hour, by dividing the daily path length by the hours of animal observation per day.

Home range sizes and daily path lengths were normally distributed, and travel rates were normally distributed following log transformation. We computed three linear mixed models (LMM) implemented with the glmmADMB package (version 0.8.3.3) (Skaug et al., 2016) in the RStudio program (version 1.3.959) (RStudio Team, 2020) and with R software (version 4.0.2) (R Core Team, 2020). In each model, we included one metric as the dependent variable, season (two categories: spring or summer) and enclosure size (two categories: large or small, based on a cutoff of 2 ha) as explanatory variables, and group identity as a random variable. We additionally included study year (two categories: one or two) as an explanatory variable, but it always failed to reach statistical significance and we report results from the simpler models.

2.4 | Analyses of foraging behavior

We used behavioral data to first determine the percentage of time sifakas spent foraging on nonprovisioned items. For each sifaka on each observation day, we summed the time spent foraging on individual plant parts (e.g., fruits, young leaves) and plant species (e.g., red maple, sweetgum) and divided it by total foraging time. We averaged values across observation days per individual, such that each sifaka was represented only once per season. We used these proportional data for descriptive analyses and data visualizations.

We next determined foraging rates on nonprovisioned items. For each sifaka on each day, we subtracted the total out-of-view time from the total focal hours. We divided foraging time (in minutes) by the duration of animal observation (in hours). We used the same method to determine foraging rates on plant parts. Given the

challenge of identifying items when sifakas were foraging in the grassy areas of their enclosure, we define young and mature leaves as those that come from trees, tree vines, and shrubs specifically; we exclude weeds and grasses in this category. We analyzed foraging rates in a series of mixed models (MM). In all models, each observation day per animal was entered as a unique data point. We entered foraging rates as the dependent variable, season (two categories: spring or summer), enclosure area (three categories: Triplex, Miaro, or Aty-ala), and animal sex (two categories: female or male) as the independent variables, and individual nested within social group and study year (two categories: Year 1 or Year 2) as random terms. The data best fit a negative-binomial distribution, and we applied the zero-inflation correction factor when appropriate. The exception to this analytical pipeline was flower foraging, which was restricted almost wholly to spring. We report only descriptive patterns for flower foraging.

We next asked if foraging rates vary throughout the day. We focused on eight time-bins, split between mornings and afternoons, that captured the bulk of our behavioral data. In the morning, we grouped data from 6:00 to 8:00, 8:00 to 9:00, 9:00 to 10:00, and 10:00 to 11:00; in the afternoon, we grouped data from 14:00 to 15:00, 15:00 to 16:00, 16:00 to 17:00, and 17:00 to 19:00. For each time bin on each observation day per sifaka, we calculated foraging rates, adjusted for out-of-view times. We used these data in an additional mixed model in which we entered foraging rate as the dependent variable, provisioning expectation (two categories: yes or no) and time of day (two categories: morning or afternoon) as the explanatory variables, and individual sifaka nested within its social group as a random term. We consider the hours from 9:00 to 11:00 and from 14:00 to 16:00 as the hours when sifakas expect provisioned food items from DLC staff, and the hours before 9:00 and after 16:00 as the hours when sifakas do not expect food items from DLC staff.

3 | RESULTS

3.1 | Ranging behavior

DLC sifakas traveled in their forest enclosures each day to occupy 3-day home ranges of 0.61–1.98 ha, with an average of 1.15 ha (Figure 1a–d). Three-day home range size did not vary seasonally (LMM: $z = 0.83$, $p = .41$; Figure 1e), but it did vary by the total size of the forest enclosure (LMM: $z = 2.58$, $p = .001$). Specifically, sifakas in big forest enclosures (i.e., larger than 2 ha) had average 3-day home ranges of 1.35 ha, whereas those in small forest enclosures (i.e., smaller than 2 ha) had average home ranges of 0.95 ha. Within seasons, sifakas in larger and smaller enclosures thus used respectively, 50% and 65% of the available space across 3 consecutive days.

In contrast to home ranges, daily travel distances and hourly travel rates varied seasonally and were consistently greater in summer compared to spring. Average daily path length for sifaka groups was 382.2 m in spring and 539.9 m in summer. Travel rates

averaged 58.3 m/h in spring and 85.1 m/h in summer. These seasonal differences attained statistical significance for daily path lengths (LMM: $z = 4.89$, $p < .001$, Figure 1f) and hourly travel rates (LMM: $z = 4.93$, $p < .001$, Figure 1g). Sifakas traveled equivalent distances per day when residing in small versus large forest enclosures (LMMs: $z < 1.09$, $p > .28$ for both metrics).

3.2 | Foraging results by plant part

DLC sifakas spent considerable time in their forest enclosures foraging for a seasonal frugo-folivorous diet. They routinely foraged in the upper canopy, mid-canopy, and on the forest floor for various leaves, vines, and weeds, as well as reproductive and woody plant parts (Figure 2). In spring, foraged diets were dominated by leaves and other foliage (62%), flowers (14%), fruits (8%), and nuts (5%); In summer, sifakas reduced foraging time on leaves (51%) and flowers (0.1%), but increased time spent foraging on nuts (22%) and fruits (12%) (Figure 2). Bark and dead foliage each comprised ~3%–4% of foraging time each across seasons. Sifakas did eat some soil, but geophagy was a rare occurrence in our study.

On average, sifakas foraged for 15.6 min/h (26% of time). These rates varied across days and individuals, ranging from 3.5 to 30.9 min/h/day (6%–52% of time). Total foraging rates did not vary by season (MM: $z = 0.46$, $p = .65$) such that sifakas spent equivalent time foraging in spring and summer. Nevertheless, rates did vary significantly throughout the day. Sifakas foraged significantly more in the afternoon hours compared to the morning hours (MM: $z = 3.54$, $p < .0001$), and in the early-morning and late-afternoon hours compared to midday (MM: $z = 6.11$, $p < .0001$, Figure 3), that is, they foraged more outside of staff hours.

Although total foraging rates did not vary seasonally, the time spent foraging on specific plant parts did (Figure 4). Sifakas spent significantly more time foraging for young leaves in spring (MM: $z = 8.18$, $p < .0001$) and mature leaves in summer (MM: $z = 8.54$, $p < .0001$) (Figure 4a). Flower foraging (i.e., flowers entirely eaten or foraged for pollen) was nearly exclusively restricted to spring: We noted only one occurrence of flower foraging in summer, but spring rates averaged 2.91 min/h/day. Rates of fruit foraging did not vary seasonally (MM: $z = 1.08$, $p = .28$); however, rates of nut foraging were significantly greater in summer than spring (MM: $z = 5.35$, $p < .0001$; Figure 4b) and rates of bark foraging were greater in spring compared to summer (MM: $z = 1.93$, $p = .05$; Figure 4c). We found no seasonal variation in rates of foraging for either petioles (MM: $z = 1.02$, $p = .31$) or dead foliage (MM: $z = 1.17$, $p = .24$).

In addition to the seasonal variation in foraging rates, we found geographical differences across the DLC (Figure 5). Whereas sifakas foraged equivalently for young leaves across all areas (MM: $z < 0.34$, $p > .74$ for all comparisons), rates of mature leaf foraging were reduced in Triplex versus Miaro sifakas (MM: $z = -2.45$, $p = .01$; Figure 5a) and trended toward being reduced in Triplex versus Aty-ala sifakas (MM: $z = -1.82$, $p = .07$). Aty-ala sifakas spent more time foraging for fruits than either Miaro or Triplex

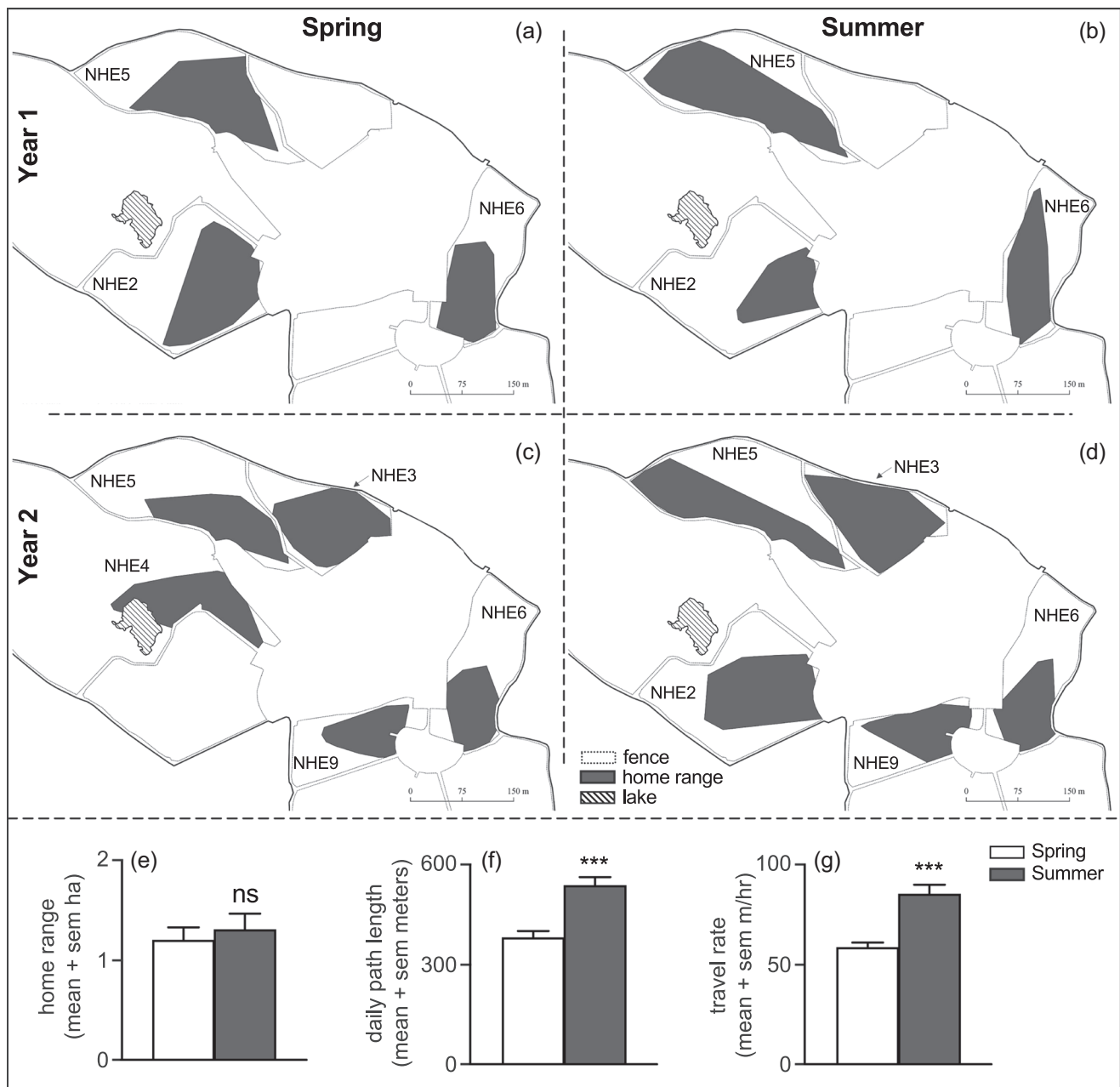


FIGURE 1 Home ranges and traveling patterns. Depicted in 2D space are the home ranges sifakas occupied across 3-day observation periods in the (a, c) spring and (b, d) summer of years (a, b) one and (c, d) two. Home ranges are mapped against topographical features of the Duke Lemur Center, including fences bordering the forest enclosures. (e) Home range size in ha, (f) daily path lengths in meters, and (g) hourly travel rates in meters/hour are graphed relative to season. *** $p < .001$.

sifakas (MM: $z > 3.6$, $p < .004$ for both comparisons), but less time foraging for nuts compared to Triplex sifakas (MM: $z = -2.19$, $p = .03$) (Figure 5b). Rates of flower foraging by *Aty-ala* sifakas (average 3.33 min/h) were respectively, 8x and 13x greater than were foraging rates for flowers by *Miaro* and *Triplex* sifakas. We found no geographical differences in rates of foraging on petioles, barks, or dead foliage.

In contrast to these geographic and temporal patterns, we found no differences in foraging rates between male and female sifakas, with one minor exception. Sifaka pairs tended to forage in close

proximity and on the same items, but we noted that males trended toward spending less time foraging for mature leaves (MM: $z = -1.79$, $p = .07$).

3.3 | Foraging results by plant identification

DLC sifakas foraged for minimally 39 unique species from 36 genera and 25 plant families (Table 2). At the family level, plants from Fabaceae accounted for the greatest number of foraged species

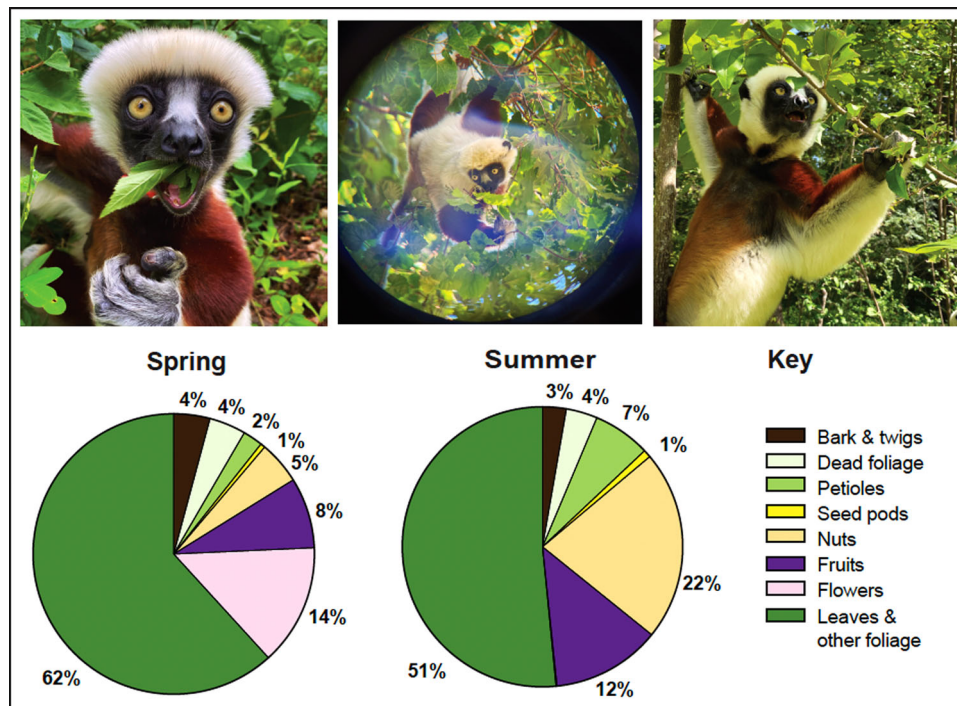


FIGURE 2 Top row: Photographs of sifakas “Ro” foraging for blackberry leaves on the forest floor; “Ge” foraging for grapevine leaves in the upper canopy; and “El” foraging for silverberry leaves in the mid-canopy. Bottom row: Pie charts depicting the proportion of plant parts in the sifakas’ foraged diets, averaged across individuals in spring (May–June) and summer (August–September). Each plant part is represented by a unique color. Photographs by L. K. G.

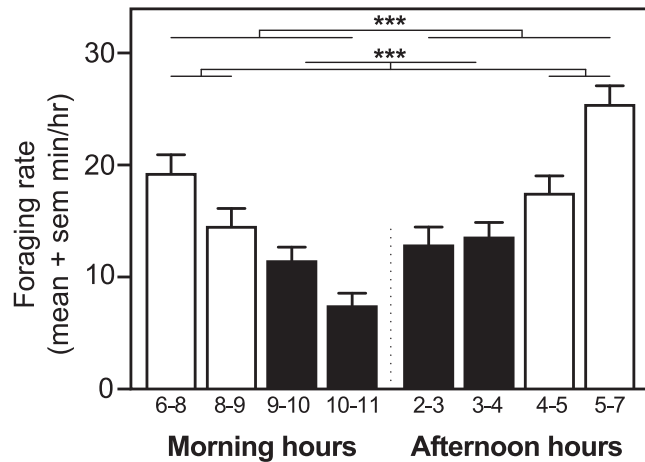


FIGURE 3 Sifaka foraging rates across the day. Depicted here are the mean minutes per hour sifakas spent foraging, on average, on nonprovisioned items in the morning (left) and afternoon (right) hours, including time bins when expectation of provisioned foods is low (white bars) and time-bins when expectation of provisioned foods is high (black bars). *** $p < .001$.

(20.5%), followed by Fagaceae (10.2%), Rosaceae and Asteraceae (7.6% each). At the species level, red maple (*Acer rubrum*) was the most foraged taxon. Maple was foraged by every individual sifaka in both seasons, accounting for 21.7% and 23.0% of average foraging time, respectively in spring and summer. Only three other plants were

foraged by every sifaka in every season, including tulip poplar (*Liriodendron tulipifera*), grapevine (*Vitis rotundifolia*), and bush clover (*Lespedeza cuneata*) which respectively, accounted for 17.9%, 10.4%, and 3.23% of average foraging time in spring and 3.6%, 13.4%, and 4.9% of average foraging time in summer. Three additional plants accounted for >5% of average foraging time in one season, including hickory (*Carya* spp.) in spring, black locust (*Robina pseudoacacia*) and white oak (*Quercus alba*) in summer. Fifteen plants accounted for >1% of average foraging time within one season: hornbeam (*Carpinus caroliniana*), American beech (*Fagus grandifolia*), redbud (*Cercis canadensis*), sweetgum (*Liquidambar styraciflua*), black tupelo (*Nyssa sylvatica*), red mulberry (*Morus rubra*), mimosa (*Albizia julibrissin*), loblolly pine (*Pinus taeda*), red oak (*Q. rubra* and/or *falcata*), willow oak (*Q. phellos*), greenbrier (*Smilax rotundifolia*), poison ivy (*Toxicodendron radicans*), autumn olive (*Elaeagnus umbellata*), blackberry (*Rubus occidentalis*), and rhomboid mercury (*Acalypha rhomboidei*). For most of the top plants, sifakas foraged for more than one plant part (Table 2).

The sifakas showed selection for most plants across seasons (Figure 6). In spring, the top five plants were red maple, tulip poplar, grapevine, hickory, and red mulberry that together accounted for 60.6% of average foraging time; in summer, the top five plants were red maple, white oak, grapevine, black locust, and bush clover that together accounted for 63.0% of average foraging time. Black cherry (*Prunus serotina*), sourwood (*Oxydendrum arboreum*), and red mulberry were only foraged in spring, whereas white ash (*Fraxinus americana*), partridge pea

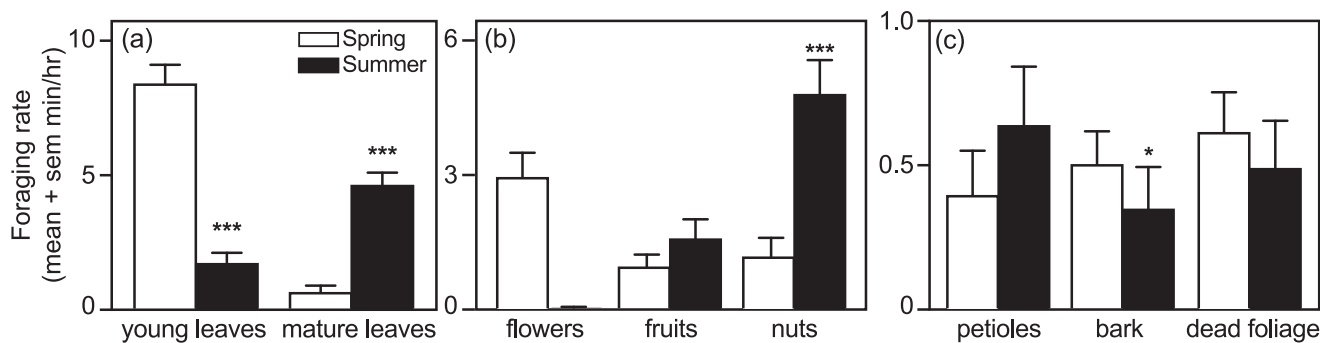


FIGURE 4 Sifaka foraging rates across seasons. Depicted here are the mean minutes per hour sifakas spent foraging each day, on average, on (a) leaves, (b) reproductive plant parts, and (c) on woody items and dead foliage, in the spring (white bars) and summer (black bars) months. * $p < .05$; *** $p < .001$.

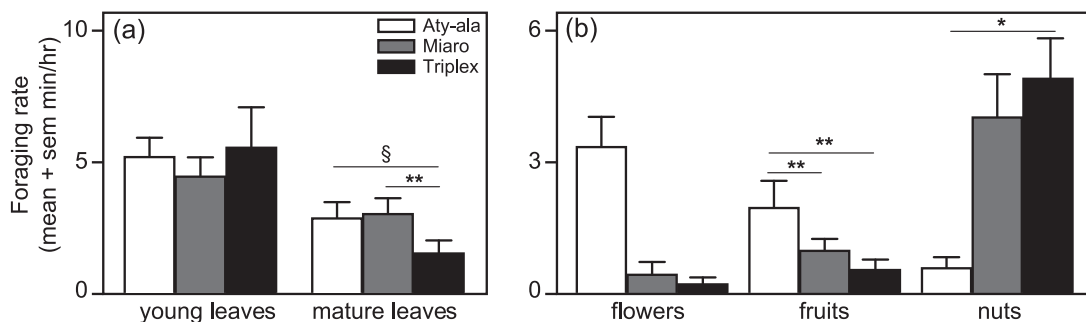


FIGURE 5 Sifaka foraging rates by enclosure area. Depicted here are the mean minutes per hour sifakas spent foraging each day, on average, on (a) leaves and (b) reproductive plant parts across all seasons in enclosures in the Aty-ala area (white bars), Miaro area (gray bars), and Triplex area (black bars). § $p < .1$; * $p < .05$; ** $p < .01$.

(*Chamaecrista fasciculata*), chamber bitter (*Phyllanthus urinaria*), and rhomboid mercury were only foraged in summer.

We noted differences in plant selection across social groups, which sometimes contributed to the seasonal patterns described above. For example, in spring, red mulberry accounted for 26.5% of foraging time for individuals Gi and Ru but was negligibly foraged by the other groups. Likewise in spring, white clover (*Trifolium repens*) accounted for 3.3% of foraging time for sifakas Be and El, while in summer, willow oak, rhomboid mercury, and white ash respectively, accounted for 9.5%, 11.7%, and 2.1% of foraging time by sifakas Fu and Th, Gi and Ru, and Lu and Ga. All these plants seasonally accounted for <0.1% of foraging time for the other groups. Interestingly in summer, the sifakas that foraged most for white oak (Ge, Re, Gi, Ru) also foraged most for poison ivy, which accounted for 3.2% of foraging time by these individuals.

4 | DISCUSSION

We show that captive sifakas, when maintained in large forest enclosures, display foraging and ranging behaviors that reflect those of their wild peers across western Madagascar. The sifaka groups in our study occupied 3-day home ranges that, although constrained by enclosure size, fell within the lower limits of estimated home ranges

reported for wild sifakas in the dry forests, of ~1–30 ha (Harshbarger, 2021; Lehman & Mayor, 2004; McGoogan, 2011; Norscia et al., 2006; Ramilison et al., 2021; Richard, 1985; E. Rambelison, pers. communication). The sifakas traveled distances each day within known daily path lengths for wild sifakas in the dry forests, of ~200–2000 m (McGoogan, 2011; Norscia et al., 2006; Pichon & Simmen, 2015). The proportion of time the sifakas foraged each day was largely consistent with activity budgets for wild sifakas, of ~20%–60% (Dinter et al., 2021; Hemingway, 1999; Pichon et al., 2010). Like wild sifakas (Lehman & Mayor, 2004; McGoogan, 2011; Pichon et al., 2010; Richard, 1974; Sato et al., 2016), captive sifakas selected a flexible frugo-folivorous diet dominated by leaves, fruits, nuts, flowers, petioles, and bark from dozens of plant species. Chosen plants and plant parts differed across seasons, enclosure areas, and groups, potentially reflecting variation in phenological or geographical availability, or in individual preferences. Our results highlight that primates bred in captivity for multiple generations can and do express wild-like behaviors under ecologically relevant conditions (Blanco et al., 2021). Moreover, our results underscore the feeding flexibility of the Coquerel's sifaka, which may ultimately contribute to this species' resilience to heterogeneous, challenging, and changing landscapes.

That Coquerel's sifakas intuitively “know” which plants are safe to eat in foreign forests seemingly depends on a suite of

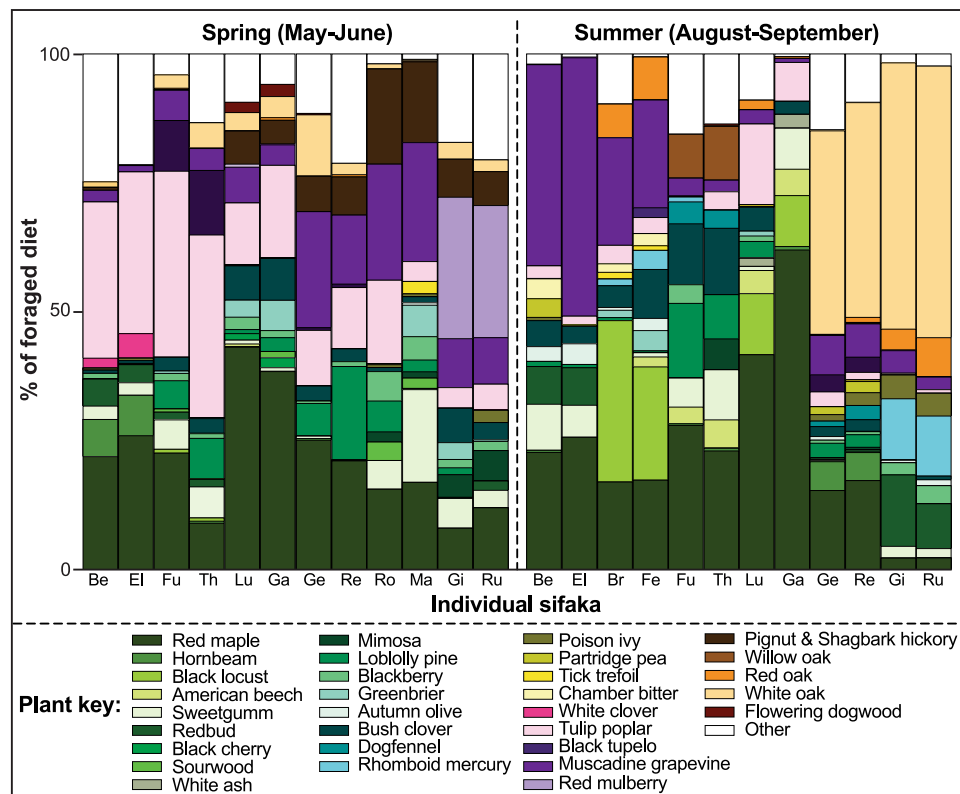


FIGURE 6 The top plants foraged by sifakas. Shown here are stacked bar charts of plant taxa that comprised >1% of foraging time by minimally two sifakas within one season. Each column represents the total foraging time per individual sifaka when averaged across all observation days within a season, including spring (left) and summer (right). Plants are represented by unique colors and common names are provided in the plant key; taxonomic information is provided in Table 2. Other (white) refers to the summation of all plants that failed to reach the 1% cutoff. Sifaka names are abbreviated along the x-axis and correspond to the abbreviations in Table 1.

interconnected genetic, sensory, digestive, and microbial mechanisms. At the genetic level, sifaka genomes show deep-rooted selection for numerous genes related to diet and folivory, including those involved in xenobiotic metabolism, nutrient absorption, and microbial nitrogen salvage (Guevara, Greene, et al., 2021; Guevara, Webster, et al., 2021). At the sensory level, sifakas use olfactory and visual cues to locate food items and to discriminate foods at different stages of maturity (Irwin, Jean-Luc raharison, et al., 2007; Rushmore et al., 2012). Changes to bitter taste receptors (Guevara, Webster, et al., 2021) likely lead to the sifakas' tolerance for leaf tannins (Yamashita, 2008) and may enable them to consume a broader range of items. At the digestive level, the sifaka gastrointestinal system is of intermediate complexity between that of a true frugivore and that of a true folivore and facilitates the metabolism of diverse foodstuffs (Campbell et al., 2000; Greene, Williams, et al., 2020). Whereas elongated small intestines ensure that sugars, proteins, and lipids are readily absorbed, an enlarged cecum and long colon ensure the space and time for gut microbes to ferment recalcitrant leaves into bioavailable fuel. At the microbial level, sifakas host dense and diverse assemblages of microbes in the lower gut that contribute to fiber and tannin digestion: Sifaka gut microbiomes track dietary intakes and/or resource availability across days (Greene et al., 2018),

seasons (Springer et al., 2017), and habitats (Greene et al., 2019, 2021) and in so doing, may enable their hosts to digest diverse and available resources in real time.

With an evolutionary and ecological toolkit to exploit various resources, the Coquerel's sifakas granted access to North Carolinian forests spent fully a quarter of their time foraging for wild foodstuffs. In spring, the sifakas prioritized an array of young leaves, tulip poplar flowers, mulberries, and hickory nuts, whereas in summer, they focused mostly on mature leaves, muscadine grapes, and white oak acorns. Although these results broadly match the phenology of endemic plants in the Piedmont region (Beck, 1977; Funderburk & Skeen, 1976), documenting seasonal plant-transect data per enclosure and establishing botanical plots to track local phenology could help tease apart if foraging patterns are driven solely by availability or if individual preferences are also at play. Future studies could beneficially compare the nutritional composition of commonly foraged items by Coquerel's sifakas at the DLC and in Madagascar to ask if they select for foods with similar macro or micronutrient profiles across habitats. Integrating data on the lemurs' gut microbiomes and epigenomes could help clarify how sifakas adapt to diverse foods over ecological and evolutionary timescales (Ideraabdullah & Zeisel, 2018; Kolodny & Schulenburg, 2020), and

integrating data on body mass, circulating metabolites, hormones, electrolytes, nutrients, and other blood markers could clarify the health and nutritional implications of such dietary breadth (Irwin et al., 2010). Applying such approaches to sifakas (and other species) under naturalistic conditions in captivity could illuminate the proximate mechanisms that enable feeding flexibility and local adaptation, including to habitats in Madagascar comprising a greater proportion of exotic species (Konersmann et al., 2021).

While recognizing the potential for captive lemurs to exhibit wild-like behavior, we also note that hourly foraging rates tracked the rhythm of human caretakers. Most notably, the sifakas' foraging effort was greatest before, and especially after staff hours. These daily patterns could reflect biological motivation to forage across the day, especially in the heat of summer, but they also match the timing of diet and leaf offerings. Anecdotally, we noted that sifaka groups often "waited" by gates or feed sites in anticipation of provisioned fare and were strongly sensitive to staff presence. While provisioning and staff oversight ensure that each sifaka consumes adequate nutrition each day, reducing chow and leaf volumes might spur more consistent foraging and ranging behavior. Likewise, offering fare once per day in randomized locations and at randomized times might boost exploration and increase home range usage. There is growing recognition across zoo, lab, and domesticated colonies that animals benefit from a "work-for-food" model that promotes cognitive stimulation, foraging and exploration, and decreases inactivity (Kemppinen et al., 2008; Rosenberger et al., 2020; Wagman et al., 2018). For forest-dwelling lemurs, further decreasing the animals' reliance on human interaction, while encouraging greater use of wild resources, may contribute to the animals' mental and physical health. It may also blur the boundaries between captive and wild conditions, providing relevance to socioecological data stemming from captive populations and better preparing individuals for potential reintroduction to Madagascar (Britt et al., 2004).

Beyond highlighting the role of nonharmful research in understanding captive animal welfare, we argue that captive wildlife, living under ecologically relevant conditions and expressing the full range of species-specific behaviors, provide opportunity to address fundamental questions in conservation biology, ecophysiology, and ecology. Animals maintained at facilities like the DLC are individually known from birth, have meticulously kept medical, social, and life-history records (Zehr et al., 2014), can be closely monitored and routinely sampled, and are available for safe experimentation. Innovative experiments could test hypotheses within optimal foraging theory, nutritional and sensory ecology, and reintroduction biology that are often limited by correlative field data and small sample sizes. Ultimately, we encourage facilities housing captive wildlife species, particularly those that serve as genetic safety nets for endangered kin, to incorporate ecological research and "renaturalization" strategies into management programs.

AUTHOR CONTRIBUTIONS

Lydia K. Greene conceived of and designed the study with Marina B. Blanco and Erin E. Ehmke. Lydia K. Greene collected the data. Lydia

K. Greene and Jean-Basile Andriambelason analyzed the data. Lydia K. Greene drafted the manuscript with Marina B. Blanco. All authors contributed to the final version.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

This study was approved by the Duke Lemur Center's Research Committee and Duke University's IACUC (protocols A106-19-05 and A039-21-02). The study was performed in compliance with all regulations regarding the care and use of captive primates, including the US National Research Council's Guide for the Care and Use of Laboratory Animals and the US Public Health Service's Policy on Human Care and Use of Laboratory Animals.

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