BRIEF REPORT

Dietary Patterns in Perrier's Sifakas (*Propithecus diadema perrieri*): A Preliminary Study

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Some lemur species range into only one habitat type, whereas others range into a variety of habitats. Because plant community structure can differ between habitats, dietary patterns may vary for conspecific groups of primates that range into more than one type of habitat. The goal of our study was to determine how habitat variation influences dietary patterns in Perrier's sifakas (*Propithecus diadema perrieri*) that range into both dry and riparian forests in northern Madagascar. We collected 542 hr of data on the behavior and diet of two groups of *P.d. perrieri* from 7 June to 4 August 1998 at Camp Antobiratsy in Analamera Special Reserve, Madagascar. We computed indices of dietary diversity for each group and dietary/plant species similarity between groups. *P.d. perrieri* in group 1 fed predominantly in dry forest (72.7% of feeding records, n = 660), whereas those in group 2 fed most often in riparian forest (73.7% of feeding records, n = 666). The index of dietary similarity (0.986) was significantly higher than the index of plant species similarity (0.767). Although the *P.d. perrieri* in the two study groups fed predominantly in different forest habitats, they ate similar food items in very comparable proportions (but not from the same plant species). However, based on habitat availability measures, neither group fed where they were expected to feed. Am. J. Primatol. 62:115–122, 2004.   © 2004 Wiley-Liss, Inc.

INTRODUCTION

Malagasy strepsirhines are found in a wide variety of habitats, from dry deciduous forests to evergreen humid forests. Although some lemur species prefer

only one habitat type, others range into a variety of habitat types [Fleagle, 1999]. There can be considerable abiotic and biotic differences between adjacent habitat types. For example, plant community structure varies considerably between riparian and dry forests in northern Madagascar [Lowry et al., 1997]. The question arises, then, as to how dietary patterns may vary for conspecific groups of primates that range into both dry and riparian forests.

Although dietary patterns have been documented in some lemur species living in different habitats [Sussman, 1987; Meyers, 1993; Powzyk, 1998; Yamashita, 2002], they have not been investigated in Perrier's sifakas (*Propithecus diadema perrieri*). *P.d. perrieri* is the rarest and least-studied *Propithecus diadema* subspecies, and it has one of the smallest distributions of any lemur [Mittermeier et al., 1994]. *P.d. perrieri* are found only in the fragmented dry and riparian forests just south and east of Anivorano Nord in northern Madagascar. In this work we examined certain aspects of dietary variation in the habitats of adult *P.d. perrieri* using data from a study in Analamera Special Reserve.

MATERIALS AND METHODS

We collected data on the behavior and diet of *P.d. perrieri* from 7 June to 4 August 1998 at Camp Antobiratsy in Analamera Special Reserve, Madagascar. This 34,700-ha reserve is located 42 km east of Anivorano Nord on the Indian Ocean coast of Madagascar, at 12° 44′ S and 49° 44′ E. Camp Antobiratsy is located at 12° 48′ 26″ S, 49° 32′ 04″ E along the banks of the Andampy River in the southern section of the Reserve [Mayor & Lehman, 1999].

Camp Antobiratsy is near three distinct habitats: grassland, dry forest, and riparian forest. The grasslands are dominated by various species of Poaceae [Bosser, 1969], and contain some intermittent woody vegetation, such as *Uapaca bojeri* (Euphorbiaceae). The forest habitats differ considerably in floral composition, diversity, and abundance [Lowry et al., 1997]. The dry forests are dominated by trees in the plant families Leguminoceae and Bignoniaceae. The riparian forest is dominated by plants from the Sapotaceae and Burseraceae families. At our study site, dry forest is found on the slopes above the riverbanks of the Andampy River. The canopy is discontinuous and low (ca. 10 m high), and the tallest trees are 21 m high. The understory is thick with vines. Riparian forest is found along the riverbanks of the Andampy River. The understory is open, and the canopy is continuous and closed (ca. 25 m in height). The maximum observed tree height in the riparian forest is 34 m.

The conservation status of the park precluded the collection of plants or clearing of trails to conduct botanical censuses. Local guides provided the local names of all plants eaten by *P.d. perrieri*. Scientific names were noted whenever possible with the assistance of guides who studied the feeding ecology of *P.d. edwardsi* at Ranomafana National Park. The intergroup comparisons of plants used by sifakas include observations in which at least the local names were collected.

Three groups of *P.d. perrieri* ranged into forests near Camp Antobiratsy. Two groups that showed the least response to our presence were selected for study. We habituated animals in the two groups over a 2-week period. Habituation was considered to be completed when the study animals no longer responded with either vocalizations or flight behavior to the presence of our research team. Group 1 consisted of three animals (two adult males and one adult female). One of the adult males disappeared sometime during the night of 9 July 1998. Group 2

consisted of four animals (one adult male and three adult females). We darted all adult sifakas in groups 1 and 2 after the habituation period, and then fitted them with color-coded collars and tags following Glander et al. [1991]. No animals were harmed during darting, and none showed any adverse reactions to us after they were released.

We did not use transect lines to determine home-range sizes because the forest fragments used by the *P.d. perrieri* were small, we observed that the sifakas made use of all areas within each fragment, and the conservation status of the reserve precluded trail-cutting. We measured forest fragments with a compass, GPS, and a 25-m tape measure. Group 1 had a total home range of 1.07 ha (dry forest = 0.83 ha, riparian forest = 0.24 ha) and group 2 had a home range of 1.01 ha (dry forest = 0.31 ha, riparian forest = 0.70 ha). We did not observe any intergroup contact or aggression. None of the animals ranged into an area used by another group.

We used focal-animal instantaneous sampling to collect 542 hr of data (6,507 individual activity records (IARs)) each day for one randomly selected individual in each group. Every 5 min we recorded the following data: 1) activity (feeding, resting, traveling, etc.); 2) food category and local name; 3) height of animal above ground (in meters); and 4) habitat type.

Following Stacey [1986], we computed indices of dietary diversity (I_D) for each group and dietary/plant species similarity between groups (I_C). I_D is given by:

$$I_D = \frac{1}{\sum P_i^2},$$

where P_i is the relative percentage contribution to the diet of the ith food category. The resulting values range from 1.0 (consumption of single food category) to infinity (consumption of multiple food categories). The I_C measures similarities of diets and plant species between different groups:

$$I_C = \frac{\sum X_i Y_i}{\sqrt{\sum X_i^2 Y_i^2}},$$

where X_i is the relative contribution of the food category or plant species i to the diet of one group, and Y_i is the relative contribution of the same food category or plant species to the diet of the second group. This index ranges from 0 (no similarities in proportion(s) of food categories or plant species) to 1 (same food categories or plant species exploited in same proportions).

We used randomization tests to compare diversity indices between the two groups. These comparisons were conducted to determine whether one index was statistically different from another index. Randomization tests were used because they are robust to small sample sizes, and they require no assumptions regarding the underlying distribution of the data [Manly, 1997]. These tests involved the use of data and observed indices for each group, and comparisons between groups (i.e., I_D and I_C). An equivalent number of random values equal to the number and range of categories and/or plant species used to determine the observed indices were generated using the ''dRandReal'' macro in Microsoft Excel. These random values were then used to create random indices. This procedure was repeated 1,000 times to create a statistical distribution in which to compare the observed values. The number of times a random index value was equal to or greater than an observed index value indicates how probable that distribution of values was according to randomly distributed detections [Manly, 1997].

Chi-square (χ^2) tests were used to determine whether the frequency distribution of feeding locations, as measured by their proportion of available habitat, differed significantly from their representation in the group range as a whole. In this study, the IARs are given as percentages of total counts (e.g., % of total feeding IARS) and with associated sample sizes (n). The alpha level was set at 0.05. We conducted the chi-square tests using SPSS 10.0 (SPSS Inc., Chicago, IL).

RESULTS

Group 1 was sighted most frequently in dry forest (79.0% of total habitat IARs, n = 2574), and group 2 was sighted mostly in riparian forest (83.1% of total habitat IARs, n = 2702). Animals in both groups rarely ranged into grassland (Table I). Feeding behaviors accounted for 27.8% of total activity records for sifakas in group 1 (n = 908), and 27.8% of total activity records for sifakas in group 2 (n = 904). Feeding behaviors occurred only in the riparian or dry forests. The diet of the sifakas in both study groups consisted predominantly of leaves, flowers, and fruits (Table I). Group 1 fed more in dry forest (73.2% of total feeding IARs, n = 665) than in riparian forest (26.8% of total feeding IARs, n = 243). These observed values differ significantly from expected values based on available habitat types ($\chi^2 = 4.20$, d.f. = 1, $P = 0.004$). Group 2 fed more in riparian forest (73.1% of total feeding IARs, n = 661) than in dry forest (26.9% of total feeding IARs, n = 243). The observed feeding pattern in group 2 differed significantly from expected values ($\chi^2 = 4.52$, d.f. = 1, $P = 0.001$).

Group 1 fed on 35 plant species, and group 2 fed on 28 species of plants (Table II). The index of dietary diversity (I_D) was 6.12 and 6.35 for groups 1 and 2, respectively (Table I). These values do not differ significantly (d.f. = 5, $P = 0.7$). The index of dietary similarity ($I_C = 0.986$) was significantly higher than the index of plant species similarity ($I_C = 0.767$) between our two study groups (d.f. = 5, 62; $P = 0.001$).

DISCUSSION

The dietary patterns of *P.d. perrieri* in our study groups are broadly similar to those reported for sifakas at other dry-forest sites in Madagascar [Meyers, 1993; Yamashita, 2002]. For example, Meyers [1993] reported that Tattersall's sifakas (*Propithecus tattersalli*), which are found approximately 100 km south of Camp Antobiratsy, feed predominantly on leaves and fruit in June and July. The significant difference we documented between the index of dietary diversity and index of plant species similarity indicates that our two study groups ate similar food categories in comparable proportions, but not from the same plant species. These dietary patterns are similar to those described by Sussman [1987] in his theory of species-specific dietary patterns. Sussman's [1987] theory states that two populations of the same primate species ranging in different habitats will feed on the same proportion of food items (fruit, leaves, flowers, buds, petioles, and seeds), as well as on a similar number and proportion of plant species. This species-specific dietary patterns results from morphological and physiological adaptations that limit dietary variability. For example, Sussman [1987] documented similar indices of dietary diversity for conspecific groups of *Lemur catta* at Antserananomby ($I_D = 6.37$) and Berenty ($I_D = 6.51$). These indices are similar to those we computed for *P.d. perrieri* in Analamera ($I_D = 6.12–6.35$). However, the index of dietary similarity (I_C) for Sussman's [1987] study groups was 0.854, which is lower than the I_C of 0.986 for *P.d. perrieri* observed in the

TABLE I. Habitat Use and Diet for Two Groups of *P. d. perrieri* in Analamera Special Reserve

| | Individual activity records | | | |
| | Group 1 | | Group 2 | |
Category	n	%	n	%
Habitat use				
Dry forest	2,574	79.0	539	16.6
Riparian forest	682	21.0	2702	83.1
Grassland	1	0.0	9	0.3
Total	3,257	100.0	3250	100.0
Location of feeding				
Dry forest	665	73.2	243	26.9
Riparian forest	243	26.8	661	73.1
Grassland	0	0.0	0	0.0
Total	908	100.0	904	100.0
Diet				
Leaves	501	55.2	406	44.9
Flowers	259	28.5	234	25.9
Fruit	139	15.3	177	19.6
Buds	5	0.6	49	5.4
Petioles	4	0.4	24	2.7
Seeds	0	0.0	14	1.5
Total	908	100.0	904	100.0
Index of dietary diversity (I_D)	6.12		6.35	
Index of dietary similarity (I_c)	0.986			
Index of plant species similarity (I_c)	0.767			

present study. Although this difference appears negligible, fairly large differences in feeding patterns can result in small differences in the index. Similar results have been documented in sifakas at other dry-forest sites in Madagascar. Based on data in Meyers [1993], we estimated high indices of dietary similarity ($I_C = 0.942$–0.960) for *P. tattersalli* despite intersite differences in plant community structure, species composition, and phenological patterns. Meyers [1993] concluded that dietary diversity is a stable trait in *P. tattersalli*, and in other sifakas that live in dry-forest habitats. Yamashita [2002] documented species-specific dietary patterns in her study of six groups of Verreaux's sifakas (*Propithecus verreauxi verreauxi*) in southern Madagascar. Although the *P. v. verreauxi* foraged in different microhabitats, Yamashita [2002] concluded that the sifakas exhibited a uniform pattern of dietary composition (mean $I_C = 0.593$, range $= 0.448$–0.786). Thus, our data lend some support to Sussman's [1987] theory of species-specific dietary patterns.

Our analysis enabled us to differentiate between feeding behaviors linked to habitat availability vs. those related to species-specific patterns. Based on habitat-availability measures, the sifakas in both of our study groups exhibited dietary patterns unrelated to habitat availability. This comparative approach does not support Sussman's [1987] theory of species-specific dietary patterns. The differences between Sussman's [1987] results and ours may stem from the use of overly-generalized dietary classifications (fruit, leaves, etc.) and subtle but important interannual and intergroup differences in diet. Although Powzyk [1998] documented species-specific dietary patterns for indris (*Indri indri*) and diademed sifakas (*Propithecus diadema diadema*) in the humid forests of eastern

TABLE II. Top 10 Plants Exploited by *P. d. perrieri* in Groups 1 and 2

Plant species	Family	Local name	Parts eaten	Group 1			Group 2			Total		
				n	%	Rank	n	%	Rank	n	%	Rank
Mangifera indica	Anacardiaceae	Manga	Flowers	199	40.6	1	231	31.8	1	430	35.3	1
Tamarindus indica	Caesalpiniaceae	Madiro	Fruit	128	26.1	2	101	13.9	3	229	18.7	2
Unknown		Somotrorama	Leaves	0	0.0	NA	131	18.0	2	131	10.7	3
Ficus pachyclada	Moraceae	Vaora	Fruit	0	0.0	NA	71	9.8	4	71	5.8	4
Sclerocaryan sp.	Anacardiaceae	Sakoa	Buds, petioles	0	0.0	NA	70	9.6	5	70	5.8	5
Pittosporum ochrosiifolium	Pittosporaceae	Mainbovitsika	Leaves	0	0.0	NA	56	7.7	6	56	4.6	6
Sideroxylon sp.	Sapotaceae	Nato	Leaves, flowers	47	9.6	3	0	0.0	NA	47	3.9	7
Diospyros sp.	Ebenaceae	Jobiampototra	Leaves	19	3.9	6	26	3.6	7	45	3.7	8
Olax sp.	Olacaceae	Kimbimba	Leaves	13	2.7	8	17	2.3	8	30	2.5	9
Unknown		Vonga-vonga	Flowers	25	5.1	4	0	0.0	NA	25	2.1	10
Unknown		Tsotsoro	Leaves	23	4.7	5	0	0.0	NA	23	1.9	11
Dalbergia sp.	Leguminoceae	Manary	Flowers, leaves	15	3.1	7	0	0.0	NA	15	1.2	12
Unknown		Bijojofo	Leaves	0	0.0	NA	14	1.9	9	14	1.2	13
Unknown		Vahi	Leaves	11	2.2	9	0	0.0	NA	11	0.9	14
Unknown		Famoha	Flowers	10	2.0	10	0	0.0	NA	10	0.8	15
Landolphia sp.	Apocynaceae	Vopingotra	Seeds	0	0.0	NA	10	1.4	10	10	0.8	15
Total				490	100.0		727	100.0		1,217	100.0	

Madagascar, the relationship only held true when she used the broad food categories of leaves, flowers, fruit, and ''other.'' A more detailed dietary analysis using specific categories, such as immature and mature leaves, revealed significant intergroup differences in dietary patterns for both lemur species. The time frame of our study may not have been long enough for us to determine dietary patterns. Chapman et al. [2002] documented considerable interannual variability in diet for red colobus monkeys. They found significant, consistent, within-group changes in diet over a 4-year period. For example, the time spent feeding on leaves increased from 56% in 1994 to 76% in 1998. The plant parts and species eaten by the eight colobus groups inhabiting different types of forest (e.g., pristine, logged, and riverine) varied among groups. Therefore, our comparative data do not support species-specific dietary patterns in *P.d. perrieri*.

It is important to note that our lack of data on home range, resource availability, and resource abundance may not be confounding variables, based on the results of other studies of sifakas in dry forests [Meyers, 1993; Yamashita, 2002]. Meyers [1993] found that for *P. tattersalli*, significant intergroup variations in daily path length or monthly home range area did not correlate with daily time spent feeding or average feeding-bout duration. Meyers [1993] also documented that the only significant correlation between feeding time by *P. tattersalli* on a food item (mature leaves, immature leaves, flowers, and fruit) and its availability was for immature leaves. Yamashita [2002] determined that conspecific groups of *P. v. verreauxi* shared many key food species that appeared to be independent of local abundance.

Our data provide only partial support for species-specific dietary patterns in *P.d. perrieri*. We plan to conduct longitudinal studies of *P.d. perrieri* to determine the precise ecological correlates to dietary patterns in this critically endangered lemur. Moreover, these long-term studies will enable us to determine whether there are consistent interannual changes in dietary patterns.

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