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Ecogeographic Size Variations in Sifakas: A Test of the Resource Seasonality and Resource Quality Hypotheses

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ABSTRACT Ecogeographic size variations have been documented in some but not all sifakas. Few morphometric or body weight data have been available for two critically endangered subspecies of diademed sifakas: Perrier's sifakas (*Propithecus diadema perrieri*) and silky sifakas (*Propithecus diadema candidus*). The objectives of our study were to determine size variations in sifakas and if these variations are related to resource quality and/or resource seasonality. *P. d. perrieri* and *P. d. candidus* were captured, weighed, and measured in northern Madagascar. Body weights and morphometrics were compared with other subspecies of diademed sifakas and indris (*Indri indri*). Differences in body weights and morphometrics between taxa are particularly pronounced for *P. d. perrieri* compared to *P. d. diadema*, *P. d. edwardsi*, and *I. indri*. Most morphometrics varied in comparisons between *P. d. candidus* and the other Indriidae (*P. d. diadema*, *P. d. edwardsi*, and *I. indri*). Average body size in sifakas is positively correlated with annual rainfall and negatively correlated with length of dry season. Sifaka body size is not correlated with protein-to-fiber ratios. Thus, size variations in sifakas are related to resource seasonality rather than resource quality. The relationships between the temporal availability of food resources and sifaka body size reflect complex and regionally varying causalities. Detailed, longitudinal information on the ecological factors underlying food selection and nutrient requirements in sifakas are needed to determine the relationship between ecogeographic variables and body size in sifakas. Am J Phys Anthropol 126:318–328, 2005. © 2004 Wiley-Liss, Inc.

Geographic variations in body size, morphometrics, and genetics have been documented in many species and subspecies of Malagasy strepsirhines (Albrecht et al., 1990; Albrecht and Miller, 1993; Bachmann et al., 2000; Ganzhorn and Eisenbeiss, 2001; Godfrey et al., 1997, 1999; Ravosa et al., 1993, 1995; Razafindraibe et al., 2000; Yoder et al., 2000a,b). For example, Albrecht et al. (1990) found consistent patterns of skull and body size variations in extant and subfossil lemurs. The largest taxa are found in the central highlands, with progressively smaller forms being found in the east, west, northwest, and south. Taxa from the extreme north are variable in size. This pattern of size variation is thought to result from ecogeographic variations in resource productivity, and these variations are at their most extreme in northern Madagascar. However, Albrecht et al. (1990) did not conduct correlation analyses between body size and ecological variables associated with resource productivity.

Ultimately, primate body size is influenced by variations in diet. Because a primate's weight is a function of its volume, larger-sized animals tend to have relatively lower energy requirements than smaller animals (e.g., Ross, 1992; Schmidt-Nielsen, 1997). Large animals also have more energetically efficient positional behavior and larger digestive tracts than smaller animals (e.g., Chivers and Hladik, 1980; Taylor et al., 1982; Warren and Crompton, 1998). A primate must also balance its energy and nutritional needs against the influence of plant secondary compounds that can, for example, impede digestion and nutrient absorption (Glander, 1982). Thus, large-bodied folivorous primates tend

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TABLE 1. Ecogeographic data on annual rainfall, length of dry season, protein-to-fiber ratios, and main habitat type for sifakas and indris

Species	Mean body weight (kg)[1]	Annual rainfall (cm)[2]	Dry season (months)[3]	Protein-to-fiber ratios in leaves[4]	Habitat[5]
P. d. perrieri	4.34	1,250	7	0.34	Dry forests
P. d. candidus	5.27	2,500	6		Wet forests
P. d. edwardsi	5.87	2,650	0	0.20	Wet forests
P. d. diadema	6.45	3,721	5	0.22	Wet forests
I. indri	6.43	3,721	5	0.08	Wet forests
P. tattersalli	3.49	1,639	7	0.20	Dry forests
P. v. verreauxi	3.09	750	8	0.45	Dry forests
P. v. coquereli	3.99	1,500	6	0.53	Dry forests

[1] Present study, Glander et al. (1992), Ravosa et al., (1993), Powzyk (1998), and W. Jungers, personal communication.
[2] Tattersall (1982), Overdorff (1991), Ganzhorn (1992), Meyers (1993), Hemingway (1998), Tan (1999), Wright (1999), and ZICOMA (1999).
[3] Overdorff (1991), Ganzhorn (1992), Meyers (1993), Hemingway (1998), Wright (1999), and ZICOMA (1999).
[4] Ganzhorn (1992), Meyers (1993), and Powzyk (1998).
[5] Present study and Rowe (1996).

to be associated with habitats with lower-quality forage.

Sifakas (*Propithecus*) are an excellent group for testing hypotheses on ecogeographic size variations. There are data on body size, morphometrics, distribution, and ecology for most species and subspecies of sifakas (Table 1). Although previous work was conducted on ecogeographic size variations in sifakas (e.g., Albrecht et al., 1990; Albrecht and Miller, 1993; Bachmann et al., 2000; Ganzhorn and Eisenbeiss, 2001; Godfrey et al., 1997, 1999; Ravosa et al., 1993, 1995; Razafindraibe et al., 2000; Yoder et al., 2000a,b), researchers were forced by available information to analyze only a few subspecies of diademed sifakas (*Propithecus diadema*) and Verreaux's sifakas (*Propithecus verreauxi*). For example, Ravosa et al. (1993, 1995) studied ecogeographic size variations in cranial and postcranial morphometrics as well as body weights of Milne-Edward's diademed sifakas (*Propithecus diadema edwardsi*), golden-crowned sifakas (*Propithecus tattersalli*), Coquerel's sifakas (*Propithecus verreauxi coquereli*), and Verreaux's sifakas (*Propithecus verreauxi verreauxi*). They hypothesized that the observed size variation may be related to a combination of resource seasonality for sifakas ranging into dry forests (moderately sized *P. tattersalli* and *P. v. coquereli*) and semiarid habitats (small-sized *P. v. verreauxi*) and resource quality for sifakas inhabiting eastern rain forests (large-sized *P. d. edwardsi*). However, Ravosa et al. (1993, 1995) were unable to compare body size to ecological variables associated with either resource seasonality or resource productivity due to a lack of data for sifakas.

RESOURCE SEASONALITY HYPOTHESIS

Ravosa et al. (1993, 1995) noted that ecogeographic variations in adult body sizes for some sifakas may result from resource seasonality. They based their supposition on studies by Terborgh (1987) and Terborgh and van Schaik (1987) in which patch size and patch quality were lower in the dry season compared to the wet season in South American rain forests. Thus, highly seasonal habitats may produce strong selective pressures for smaller adult body size. Ravosa et al. (1993, 1995) applied this model to sifakas, noting that the dry season in most forests in Madagascar is characterized by a low availability of high-protein immature leaves, whereas the wet season has a high availability of immature leaves (e.g., Ganzhorn, 1992; Meyers and Wright, 1993; Overdorff et al., 1997). Seasonal fluctuations in rainfall are more pronounced in the dry forests in the west, north, and south compared to those in the wet forests of eastern Madagascar. Presumably, there are concomitant seasonal fluctuations in food resource availability in these forests. The resource seasonality model appears to apply to some species and subspecies of sifakas: the largest taxa are found in the east, with progressively smaller forms found in the west, northwest (NW), and south (Albrecht et al., 1990; Ravosa et al., 1993, 1995). Therefore, this model predicts that there is a significant relationship between seasonality (rainfall [positive correlation] and length of dry season [negative correlation]) and adult body size in sifakas.

RESOURCE QUALITY HYPOTHESIS

Ganzhorn (1992) documented a positive correlation between forage quality (protein-to-fiber ratio) and the biomass of folivorous lemurs in a given forest. Specifically, he found that biomass estimates for folivorous lemurs are highest in western and NW Madagascar, containing forests with the highest protein-to-fiber ratios. Conversely, eastern wet forests have relatively low biomass estimates for folivorous lemurs, and also have the lowest protein-to-fiber ratios. Ravosa et al. (1993, 1995) used the protein-to-fiber ratio developed by Ganzhorn (1992) as a general measure of folivore habitat quality in Madagascar. Ravosa et al. (1993, 1995) noted that large-bodied *P. d. diadema* and slightly smaller *P. d. edwardsi* are found in poorer-quality eastern wet forests, and that the relatively smaller-sized *P. tattersalli* (mean = 3.49 kg) and *P. verreauxi* (mean =

3.09 kg) range into higher-quality dry forests in northern and western Madagascar, respectively. Thus, the resource quality hypothesis predicts that food quality (protein-to-fiber ratios) will correlate with adult body size in sifakas.

Lack of data on body size and morphometrics in Perrier's sifaka (*Propithecus diadema perrieri*) and the silky sifaka (*Propithecus diadema candidus*) has limited our ability to test hypotheses on resource seasonality and quality in sifakas. *P. d. perrieri* and *P. d. candidus* are the rarest and least-studied subspecies of diademed sifakas (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 (Mayor and Lehman, 1999). *P. d. candidus* range into rain forests from Maroansatra to the Andapa Basin and Marojejy Massif in northern Madagascar (Tattersall, 1982).

In this paper, we present quantitative morphometric and body weight data for all subspecies of diademed sifakas. We report morphometric and body weight variations across the complete geographic and taxonomic range of diademed sifakas. The resource seasonality hypothesis was tested by comparing annual rainfall and dry season length to average body size in diademed sifakas, Verreaux's sifakas, and indris (*Indri indri*). To test the resource quality hypotheses, we conducted correlation analyses between body sizes of sifakas and protein-to-fiber ratios of leaves eaten by these lemurs. Based on work by Albrecht et al. (1990) and Ravosa et al. (1993, 1995), we predicted that *P. d. perrieri* (northern dry forest) would have the smallest body weight and morphometrics. We also predicted that *P. d. candidus* (northeast (NE) wet forest) would be intermediate in size between its nearest conspecifics, *P. d. diadema* (eastern and NE wet forest) and *P. d. perrieri*.

METHODS

Study areas

P. d. perrieri are located predominantly in Analamera Special Reserve, Madagascar. This 34,700-ha reserve is located at 12° 44′ S and 49° 44′ E, 52 km southeast of Antsiranana (Diego Suarez) on the Indian Ocean coast (Fig. 1). Analamera is composed of highly fragmented patches of dry and riparian forests. The terrain is hilly and varies in altitude from 10–600 m (Nicoll and Langrand, 1989). Annual precipitation is approximately 1,250 mm, and falls mainly during November–April (ZICOMA, 1999). *P. d. perrieri* were captured in July 1999 at Camp Antobiratsy. This camp 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.

P. d. candidus were captured in June 2000 at the Marojejy Nature Reserve in northeast Madagascar (Fig. 1). This 60,150-ha reserve is located 40 km west of the Indian Ocean, at 14° 26′ S and 49° 15′ E (Nicoll and Langrand, 1989). Marojejy contains a variety of forest types due to its location near the juncture of three biogeographic domains (eastern lowland, central highland, and mountains). Thus, forest types in the reserve vary in relation to altitude, with lowland rain forest occupying areas between 75–800 m. These forests are characterized by high plant species diversity, abundance, and endemicity (Nicoll and Langrand, 1989). The canopy is tall (25–35 m), closed, and continuous. Central highland forests are found at altitudes between 800–1,450 m. The canopy is lower (<20 m) and not as continuous as in eastern lowland rain forest. Annual precipitation is approximately 2,500 mm, and falls mainly during November–May (ZICOMA, 1999). High mountain habitats are found at altitudes greater than 1,800 m, and are characterized by mountain rain forest and lichen forest (Lowry et al., 1997).

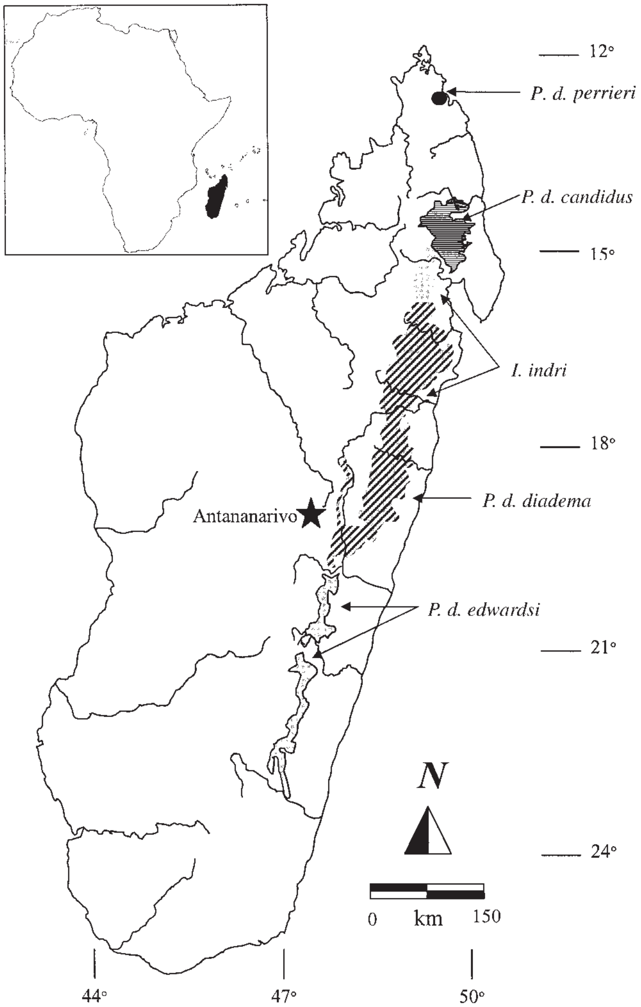

Fig. 1. Distribution of diademed sifakas and *I. Indri* in Madagascar.

Animal capture

Following Glander et al. (1991, 1992), animals were captured using the Pneu-dart™ system. This

TABLE 2. Description of morphometric measurements made during capture (based on Glander et al., 1992)

Measurement	Description
Body length	From crown to tip of tail along ventral side
Tail length	From tip of tail along ventral side to junction of base of tail with perineal area
Hindlimb length	From groin to end of longest digit, excluding nail
Hindfoot length	From heel to end of longest digit, excluding nail
Big toe length	From junction of skin and big toe to tip of big toe, with toe extended perpendicular to digits; nail is excluded
Forelimb length	From axillary region to tip of longest digit, excluding nail
Forefoot length	From heel of hand to end of longest digit, excluding nail
Thumb length	From junction between first and second digits to tip of thumb, excluding nail

system uses disposable nonbarbed darts with a 9-mm needle. The dart is delivered by a carbon dioxide-powered gun. Darts were loaded with Telazol® (A.H. Robbins Co., Richmond, VA), at a dosage of 20 mg/kg of estimated body mass. Darted animals were caught in a hammock when they fell from the trees. Some animals recovered quickly from the capture dosage, and supplementary injections of Telazol® were necessary to complete morphometric measurements. Animals were kept in burlap bags in shaded areas after completion of procedures. The sifakas were released at the capture sites once they recovered enough to walk or climb unaided. None of the animals were injured during the capture procedure. The sifakas did not demonstrate avoidance or flight behavior to our presence following capture.

Captured sifakas were weighed and measured, and their age was estimated (Glander et al., 1991, 1992). Body weights were taken using a 10-kg Pesola® scale. Measurements were taken to the nearest millimeter with a 3-m tape measure and Vernier caliper. Measurements were based on those used by Glander et al. (1992) in their study of the morphometrics of lemurs in SE Madagascar (Table 2). Due to time constraints during capture, measurements could not be completed for *P. d. candidus*. Age was estimated based on tooth wear.

Data analysis

Data on morphometrics and body weights of adult animals were collected from the literature for *P. d. edwardsi* (Glander et al., 1992); *P. d. diadema* and *I. indri* (Powzyk, 1998); and *P. tattersalli*, *P. v. verreauxi*, and *P. v. coquereli* (Smith and Jungers, 1997). Avahi were not included due to a lack of information on morphometrics and ecological data. Body weights were converted to kilograms (Smith and Jungers, 1997). Within each taxa, intersexual differences in morphometric measurements and body weights were compared using *t*-tests. If there were no significant differences between males and females, the total sample was used to determine each mean value. If there were significant intersexual differences, then a mean value for that variable was computed by averaging the mean value for males with the mean value for females. We then tested subspecific differences in morphometric measurements and body weights, using analysis of variance (ANOVA). We ran Tukey post hoc pairwise multiple comparisons to determine interspecific differences in body weights. This pairwise multiple comparison tests for differences between each pair of means using a Studentized range statistic, and can then be used to produce a matrix indicating significantly different group means at an alpha level of 0.05. Levene's test of homogeneity-of-variance was used to determine whether or not equal variances could be assumed in post hoc comparisons. This test computes the absolute difference between the value of a case and its cell mean, and performs a one-way analysis of variance on those differences.

We included data on *P. tattersalli*, *P. v. verreauxi*, *P. v. coquereli*, and *I. indri* for tests of the resource seasonality and resource quality hypotheses. Data on annual rainfall and dry season length for each species and subspecies of sifaka and indri were collected from the literature (Ganzhorn, 1992; Hemingway, 1998; Meyers, 1993; Overdorff, 1991; Tan, 1999; Tattersall, 1982; Wright, 1999; ZICOMA, 1999). We used data from Ganzhorn (1992), Meyers (1993), and Powzyk (1998) on protein-to-fiber ratios of leaves eaten by sifakas in various Malagasy forests (Table 1). For *P. d. perrieri*, we used data from Ankarana, which lies within the historic range of this subspecies. Spearman rank correlations (r_s) were used to determine if average body weight for each taxa of sifaka (dependent variable) covaried with annual rainfall, dry season length, or protein-to-fiber ratios (independent variables). Correlations were conducted for the following groups of indriidae: diademed sifakas, nondiademed taxa, dry forest taxa, wet forest taxa, and all taxa. These groups were selected to determine biogeographic correlates to body size within and between taxa, as well as within and between wet and dry forests. A path diagram was constructed, using correlation values for all taxa group. Path analysis provides a visual means of organizing an interpretation of correlational relationships (Petraitis et al., 1996). There are at least four ways that two variables might be correlated: 1) there is a direct causal relationship; 2) there is an indirect causal relationship via causal chains; 3) there is a noncausal correlation because both variables are caused by a third measured variable, in which case the correlation is spurious; and 4) there is a noncausal correlation due to (unspecified) correlated causes, which is unanalyzable. A path diagram sorts through these relationships to specify explicitly a model that poses a hypothetical relationship among variables. It is important to re-

TABLE 3. Body weights and lengths for four subspecies of P. diadema *and* I. indri

Species	Sex	Body weight (kg)	Body (mm)	Tail (mm)	Hindlimb (mm)	Hindfoot (mm)	Big toe (mm)	Forelimb (mm)	Forefoot (mm)	Thumb (mm)	Source[1]
P. d. perrieri	M	5.00	483	494	460	126	87	262	113	68	1
P. d. perrieri	M	4.20	474	423	519	116	91	316	108	67	1
P. d. perrieri	M	3.70	457	385	455	103	72	329	106	54	1
P. d. perrieri	M	4.00	482	491	476	126	77	314	116	50	1
P. d. perrieri	F	4.60	506	424	404	123	78	338	92	47	1
P. d. perrieri	F	4.30	503	429	484	115	91	340	95	52	1
P. d. perrieri	F	4.40	484	396	503	118	77	340	112	50	1
P. d. perrieri	F	4.60	526	424	539	128	85	310	122	54	1
P. d. perrieri	F	4.30	502	441	474	125	88	335	110	58	1
P. d. candidus	F	6.00	535	490	520		114	333		61	1
P. d. candidus	M	4.70	531	493	495		90	367		60	1
P. d. candidus	M	5.90	500	434	471		75	342		55	1
P. d. candidus	M	4.50	494	459	485		88	355		62	1
P. d. edwardsi	M	5.70	467	463	583	184	106	397	135	65	2
P. d. edwardsi	M	6.00	486	434	530	163	108	365	130	56	2
P. d. edwardsi	M	6.10	485	410	546	173	95	386	133	70	2
P. d. edwardsi	M	5.60	465	435	542	165	104	372	130	65	2
P. d. edwardsi	F	6.50	488	462	593	182	101	415	142	70	2
P. d. edwardsi	F	6.30	457	478	575	187	107	415	140	60	2
P. d. edwardsi	F	6.20	488	452	540	172	97	371	130	58	2
P. d. diadema	M	6.00	490	290	535	177	110	376	130	60	3
P. d. diadema	M	7.10	540	580	560	195	113	348	136	60	3
P. d. diadema	M	7.38	481	484	583	185	94	415	126	56	3
P. d. diadema	M	6.00	490	420	533	180	100	386	130	54	3
P. d. diadema	M	6.00	505	450	542	175	93	365	131	61	3
P. d. diadema	F	6.25	478	492	526	164	110	365	132	47	3
P. d. diadema	F	6.25	528	462	548	175	110	405	130	54	3
P. d. diadema	F	7.25	510	450	530	172	101	392	140	50	3
P. d. diadema	F	7.25	520	490	553	169	110	410	160	62	3
I. indri	M	5.75	540	50	588	171	105	435	142	78	3
I. indri	M	5.90	600	65	660	200	105	468	157	85	3
I. indri	F	6.75	572	60	570	180	109	437	148	63	3
I. indri	F	7.52	680	70	660	195	105	475	160	90	3
I. indri	F	6.25									4

[1] 1, present study; 2, Glander et al. (1992); 3, Powzyk (1998); 4, W. Jungers, person communication.

alize that path diagrams are interpretative rather than causal.

Body weights and measurements in the text are listed as mean ± 1 standard deviation (SD). Statistical analyses were conducted using SPSS 10.1. All statistical tests were two-tailed, and the alpha level was set at 0.05.

RESULTS

Variations in body weights

Table 3 shows the individual weights and measurements for five Indriidae used in our study. A total of 9 adult *P. d. perrieri* (4 males and 5 females) and 4 adult *P. d. candidus* (3 males and 1 female) were captured, weighed, and measured. Table 4 and Figure 2 show average body weights (kg) for each of the five Indriidae. Significant intersexual differences in body weights were found only in *P. d. edwardsi* ($t = 2.70$, df = 4, $P = 0.04$). There is significant variation in body weights among the five Indriidae in our study (F = 26.5, d.f. = 4, $P = 0.0001$). Levene's tests indicated unequal variances ($P > 0.05$) for comparisons between all taxa except for *P. d. diadema* and *I. indri*. Thus, standard *t*-test degrees of freedom were assumed in comparisons of body weight only between *P. d. diadema* and *I. indri*.

P. d. perrieri (4.34 ± 0.37 kg) and *P. d. candidus* (5.27 ± 0.78 kg) do not differ significantly in mean body weights (Tables 4 and 5). *P. d. perrieri* weigh significantly less than *P. d. diadema*, *P. d. edwardsi*, and *I. indri*. *P. d. candidus* weigh significantly less than *P. d. diadema* but not *I. indri* or *P. d. edwardsi*.

Variations in morphometrics

Significant intersexual differences were found only in *P. d. edwardsi* for body length ($t = 3.30$, df = 6, $P = 0.01$) and in *P. d. diadema* for hindfoot length ($t = 2.90$, df = 6, $P = 0.03$). *P. d. perrieri* are smaller than *P. d. candidus* for all morphometric measures, although none of the differences are statistically significant (Table 6). *P. d. perrieri* have significantly shorter hindlimbs, hindfeet, big toes, forelimbs, and forefeet than *P. d. diadema* and *P. d. edwardsi*. *P. d. perrieri* are significantly smaller than *I. indri* for all measures except tail length.

Table 7 shows the results of intertaxa comparisons for morphometric measures, with a focus on *P. d. candidus*. Although morphometric measures vary between taxa, *P. d. candidus* have significantly smaller hindlimb and forelimb lengths compared to *P. d. diadema* and *P. d. edwardsi*. However, body length is significantly longer in *P. d. candidus* than in *P. d. edwardsi*. Compared to *P. d. candidus*, *I. indri* have significantly longer body, hindlimb, forelimb, and thumb lengths

TABLE 4. Average and one standard deviation (in parentheses) for body weights (kg) and morphometric measures (mm) in I. indri *and four subspecies of* P. diadema[1]

Species	Sex	N	Body weight	Body length	Tail length	Hindlimb length	Hindfoot length	Big toe length	Forelimb length	Forefoot length	Thumb length
P. d. perrieri	M	4	4.22 (0.55)	474 (12)*	448 (53)	477 (29)	118 (11)	82 (9)	305 (30)	111 (5)	60 (9)
	F	5	4.44 (0.15)	504 (15)*	423 (16)	481 (49)	122 (5)	84 (6)	333 (13)	106 (12)	52 (4)
	Total	9	4.34 (0.37)	489 (13)	434 (37)	479 (39)	120 (8)	83 (7)	320 (25)	108 (10)	56 (7)
P. d. candidus	M	3	5.03 (0.75)	508 (20)	462 (29)	483 (12)	− (−)	84 (8)	354 (12)	− (−)	59 (4)
	F	1	6.00 (0.00)	535 (0)	490 (0)	520 (0)	− (−)	114 (0)	333 (0)	− (−)	61 (0)
	Total	4	5.27 (0.78)	515 (21)	469 (28)	492 (21)	−	92 (16)	349 (15)	−	60 (3)
P. d. edwardsi	M	4	5.90 (0.24)*	476 (11)	435 (21)	550 (23)	171 (9)	103 (6)	380 (14)	132 (2)	64 (6)
	F	3	6.30 (0.15)*	477 (18)	464 (13)	569 (27)	180 (7)	101 (5)	400 (25)	137 (6)	62 (6)
	Total	7	6.09 (0.34)	476 (13)	447 (23)	558 (24)	175 (9)	102 (5)	388 (20)	134 (5)	63 (5)
P. d. diadema	M	5	6.50 (0.69)	501 (23)	444 (105)	550 (21)	182 (8)*	102 (9)	378 (25)	130 (3)	58 (3)
	F	4	6.70 (0.58)	509 (22)	473 (21)	539 (13)	177 (9)*	107 (4)	393 (20)	140 (13)	53 (6)
	Total	9	6.60 (1.80)	504 (21)	457 (77)	545 (18)	176 (4)	104 (7)	384 (23)	135 (10)	56 (5)
Indri indri	M	3	5.83 (0.11)	570 (42)	57 (10)	624 (51)	186 (21)	105 (0)	452 (23)	150 (11)	82 (5)
	F	2	6.84 (0.64)	626 (76)	65 (7)	615 (63)	188 (11)	107 (3)	456 (27)	154 (8)	77 (19)
	Total	5	6.43 (0.72)	598 (60)	61 (9)	620 (47)	187 (13)	106 (2)	454 (20)	152 (8)	79 (12)

[1] −, no data available.

*$P < 0.05$.

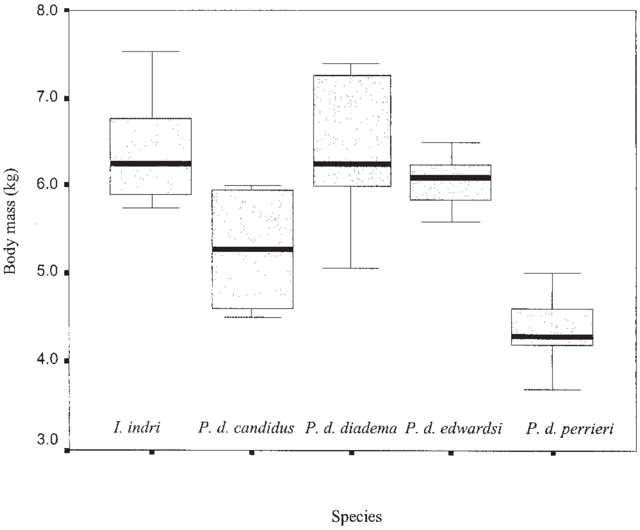

Fig. 2. Body weights for four subspecies of *P. diadema* and *I. Indri*. Thick horizontal line is median, gray area is one standard deviation, and bars are range.

Ecogeographic correlations

Table 8 shows the relationship between the ecogeographic variables and mean body size in diademed vs. nondiademed sifakas. We documented a significant positive correlation between mean annual rainfall and average body size in diademed sifakas ($r_s = 1.00$, $n = 4$, $P = 0.0001$). Average body size in diademed sifakas is not significantly correlated with protein-to-fiber ratios ($r_s = -0.50$, $n = 3$, $P = 0.917$). Mean body size is negatively correlated with the length of the dry season ($r_s = -1.00$, $n = 3$, $P = 0.0001$) in nondiademed sifakas (i.e., *P. tattersalli*, *P. v. verreauxi*, and *P. v. coquereli*). Again, there is no correlation between protein-to-fiber ratios and mean body size in nondiademed sifakas ($r_s = 0.50$, $n = 3$, $P = 0.66$).

Table 9 shows the relationship between the ecogeographic variables and mean body size in sifakas that range into wet vs. dry forests. There were no significant ecological correlates to body size for sifakas in wet or dry forests, although the correlation between mean body size and mean annual rainfall for wet forest taxa approaches significance ($r_s = 0.94$, $n = 4$, $P = 0.051$)

Table 10 shows the relationship between mean body size in all sifakas and the ecogeographic variables associated with the resource seasonality hypothesis (annual rainfall and length of dry season) and the resource quality hypothesis (protein-to-fiber ratios). Average body size in sifakas is positively correlated with mean annual rainfall ($r_s = 0.89$, $n = 8$, $P = 0.002$) and negatively correlated with length of dry season ($r_s = -0.86$, $n = 8$, $P = 0.006$). The correlation between mean annual rainfall and protein-to-fiber ratios approaches significance ($r_s = -0.72$, $n = 7$, $P = 0.064$). Average sifaka body size is not significantly correlated with protein-to-fiber ratios ($r_s = -0.48$, $n = 7$, $P = 0.268$). Thus, large-bodied taxa are found in areas with higher levels of annual rainfall and shorter dry seasons (Figs. 3, 4).

DISCUSSION

Subspecific body weight and size variations

We found that *P. d. perrieri* weigh less than and are smaller in all but two morphometric measures (body length vs. *P. d. edwardsi* tail length vs. *I. indri*) than *P. d. diadema*, *P. d. edwardsi*, and *I. Indri*. Body size and most morphometric variables varied in comparisons between *P. d. candidus* and the other Indriidae (*P. d. diadema*, *P. d. edwardsi*, and *I. Indri*). We were surprised that *P. d. candidus* are not significantly smaller in body weight than *P. d. edwardsi*. However, this similarity in body weight may be an artifact of small sample sizes for *P. d. candidus*. Most statistically significant morphometric differences were documented where *P. d. candidus* was smaller than *P. d. diadema* (hindlimb and forelimb lengths), *P. d. edwardsi* (hindlimb and forelimb lengths), and *I. indri* (body, hindlimb, forelimb,

TABLE 5. Tukey post hoc tests of subspecific differences in body weights[1]

Taxa	*P. d. perrieri*	*P. d. candidus*	*P. d. edwardsi*	*P. d. diadema*	*I. indri*
P. d. perrieri		−0.930	−1.712	−2.108	−2.089
P. d. candidus	0.101		−0.782	−1.178	−1.159
P. d. edwardsi	0.001	0.258		−0.395	−0.377
P. d. diadema	0.001	0.019	0.672		−0.019
I. indri	0.001	0.053	0.821	1.000	

[1] Numbers above diagonal refer to mean difference in body weights. Numbers below line are corresponding *p*-values.

TABLE 6. Differences in postcranial morphometrics for P. d. perrieri *vs.* P. d. candidus, P. d. diadema, P. d. edwardsi, *and* I. indri[1]

Variables	*P. d. perrieri* vs. *P. d. candidus*	*P. d. perrieri* vs. *P. d. diadema*	*P. d. perrieri* vs. *P. d. edwardsi*	*P. d. perrieri* vs. *I. indri*
Body length	P < C	P < D	P > E	P < I***
Tail length	P < C	P < D	P < E	P > I***
Hindlimb length	P < C	P < D***	P < E***	P < I***
Hindfoot length	NA	P < D***	P < E***	P < I***
Big toe length	P < C	P < D***	P < E***	P < I***
Forelimb length	P < C	P < D***	P < E***	P < I***
Forefoot length	NA	P < D***	P < E***	P < I***
Thumb length	P < C	P < D	P < E	P < I***

[1] NA means not applicable because there are no data for *P. d. candidus.* P < C indicates *P. d. perrieri* is smaller than *P. d. candidus.* P < D indicates *P. d. perrieri* is smaller than *P. d. diadema,* and P > D indicates *P. d. perrieri* is larger than *P. d. diadema.* P < E indicates *P. d. perrieri* is smaller than *P. d. edwardsi.* P < I indicates *P. d. perrieri* is smaller than *I. indri*, and P > I indicates *P. d. perrieri* is larger than *I. indri.*

* $P < 0.05$ (*t*-test).

** $P < 0.01$ (*t*-test).

*** $P < 0.001$ (*t*-test).

TABLE 7. Differences in postcranial morphometrics for P. d. candidus *vs.* P. d. diadema, P. d. edwardsi, *and* I. indri[1]

Variables	*P. d. candidus* vs. *P. d. diadema*	*P. d. candidus* vs. *P. d. edwardsi*	*P. d. candidus* vs. *I. indri*
Body length	C < D	C > E*	C < I*
Tail length	C > D	C > E	C > I***
Hindlimb length	C < D**	C < E**	C < I**
Hindfoot length	NA	NA	NA
Big toe length	C < D	C < E	C < I
Forelimb length	C < D*	C < E**	C < I***
Forefoot length	NA	NA	NA
Thumb length	C > D	C < E	C < I**

[1] NA means not applicable because there are no data for *P. d. candidus.* C < D indicates *P. d. candidus* is smaller than *P. d. diadema.* C > D indicates *P. d. candidus* is larger than *P. d. diadema.* C < E indicates *P. d. candidus* is smaller than *P. d. edwardsi.* C > E indicates *P. d. candidus* is larger than *P. d. edwardsi.* C < I indicates *P. d. candidus* is smaller than *I. indri.* C > I indicates *P. d. candidus* is larger than *I. indri.*

* $P < 0.05$ (*t*-test).

** $P < 0.01$ (*t*-test).

*** $P < 0.001$ (*t*-test).

TABLE 8. Spearman rank correlations between ecogeographic variables and body mass in diademed sifakas (numbers above diagonal) and nondiademed sifakas (numbers below diagonal)[1]

Variable	Protein to fiber ratio	Mean annual rainfall	Dry season length	Mean body mass
Protein to fiber ratio		−0.50 (0.91)	1.00 (0.00)	−0.50 (0.91)
Mean annual rainfall	−0.50 (0.66)		−0.80 (0.20)	1.00 (0.00)
Dry season length	−0.50 (0.66)	−0.50 (0.66)		−0.80 (0.20)
Mean body mass	0.50 (0.66)	0.50 (0.66)	−1.00 (0.00)	

[1] Values refer to Spearman rank correlation value, and numbers in parentheses are corresponding *p*-values.

and thumb lengths). Moreover, we found that small-sized *P. d. perrieri* and slightly larger *P. d. candidus* are from the north and northeast, respectively. Larger-sized *P. d. edwardsi* are from southeast Madagascar, and the largest taxa are found in eastern Madagascar (*P. d. diadema* and *I. indri*). This pattern matches the ecogeographic trends described by Albrecht et al. (1990). They found that among sister forms, progressively smaller forms were found in the east, west, northwest, and south. Therefore, we confirm our predictions that *P. d. perrieri* has the smallest relative body weight and body dimensions

TABLE 9. Spearman rank correlations between ecogeographic variables and body mass in sifakas/indri found in wet forests (numbers above diagonal) and sifakas found in dry forests (numbers below diagonal)[1]

Variable	Protein to fiber ratio	Mean annual rainfall	Dry season length	Mean body mass
Protein to fiber ratio		0.00 (1.00)	0.00 (1.00)	0.50 (0.91)
Mean annual rainfall	−0.40 (0.60)		−0.33 (0.67)	0.94 (0.051)
Dry season length	−0.31 (0.68)	−0.63 (0.36)		−0.31 (0.68)
Mean body mass	0.00 (1.00)	0.20 (0.80)	−0.63 (0.36)	

[1] Values refer to Spearman rank correlation value, and numbers in parentheses are corresponding *p*-values.

TABLE 10. Spearman rank correlations between ecogeographic variables and body mass in Indriidae[1]

Variable	Protein to fiber ratio	Mean annual rainfall	Dry season length	Mean body mass
Protein to fiber ratio		−0.727	0.523	−0.487
Mean annual rainfall	0.06		−0.866	0.898
Dry season length	0.22	0.00		−0.861
Mean body mass	0.26	0.00	0.00	

[1] Values above diagonal refer to Spearman rank correlation value, and numbers below diagonal are corresponding *p*-values.

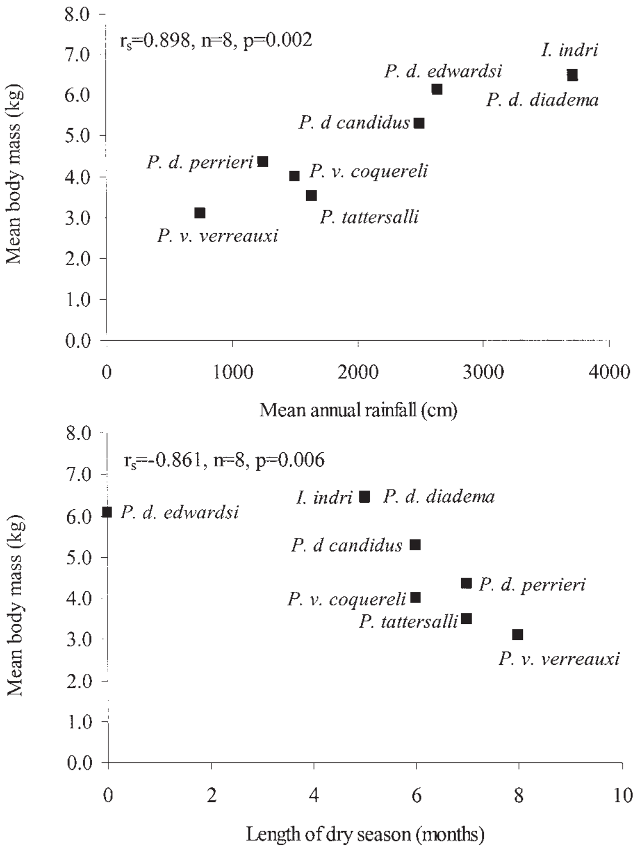

Fig. 3. Relationship between mean body size of sifakas and average annual rainfall levels (above) and length of dry season (below).

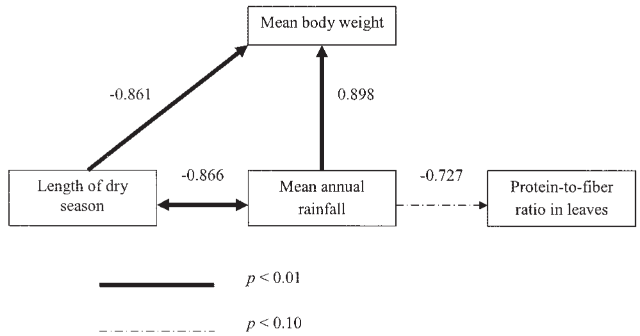

Fig. 4. Path diagram of correlational relationships between mean body weight in sifakas/indris and ecological variables. Numeric values represent associated Spearman rank correlations.

among the diademed sifakas, and that *P. d. candidus* is intermediate in size between its nearest conspecifics. We now address the causative factors of this subspecific variation in body weights.

Ecogeographic size variations

Our data support the resource seasonality model for total annual rainfall and dry season length in *Propithecus* and *Indri* (Table 10). However, we hypothesize that geographic variations in annual rainfall are the key ecological factor affecting body size in Indriidae (Fig. 4). Although we have very small sample sizes for the *P. diadema/Indri* wet forest vs. *P. verreauxi/P. tattersalli* dry forest comparison, there are differential ecological factors influencing Indriidae body weights between these habitats. Specifically, there seems to be a pattern where body weights of taxa in eastern wet forests are positively affected by mean annual rainfall (Table 10). Conversely, ecological correlates to body weights in taxa in the dry forests of western and northern Madagascar are very weak, irrespective of sample size (Table 10). The high correlation (−1.00) between body weight and length of the dry season in nondiademed sifakas may also be an artifact of sample size (Table 9). Furthermore, annual rainfall is strongly correlated to the length of the dry season for the all-taxa group (Table 10). Thus, the length of the dry season may be a spurious correlate to variations in body weights in sifakas. Other research indicates that rainfall rather than length of dry season is the key factor influencing the evolutionary ecology of lemurs. Specifically, it was suggested that lemurs have adapted to survive extended periods of scarcity by mechanisms to conserve energy (Wright, 1999). Lemurs may be distributed to maximize their intake of high-quality food during the rich wet season prior to the lean dry season, in order to optimize infant survival and to increase the potential of females for future reproduction (Ganzhorn, 2002). For example, Ganzhorn (2002) documented that the distribution of *L. ruficaudatus* was most significantly related to the spatial distribution of leaves during the wet season rather than the availability of leaves eaten during the dry season in dry deciduous forests in northern Madagascar. Therefore, geographic variations in annual rainfall may be the ecological factor affecting body weights in Indriidae.

Variations in annual rainfall ultimately affect resource productivity in Madagascar's rain forests, as they do in other tropical regions of the world (e.g., Eisenberg, 1979; Gentry, 1989; Reed and Fleagle, 1995). Generally, there is a positive relationship between total annual rainfall and forest productivity, which ultimately leads to increases in primates' biomass (Kay et al., 1997). Moreover, the dry season in most forests in Madagascar is characterized by a low availability of immature leaves, whereas the wet season has a high availability of immature leaves (e.g., Ganzhorn, 1992; Meyers and Wright, 1993; Overdorff et al., 1997). These seasonal variations in productivity may then affect body size in primates. Furthermore, Ravosa et al. (1993, 1995) noted the primary importance of resource seasonality in explaining size variations in sifakas. Northern dry forests show food resource seasonality for sifakas (Ganzhorn, 1992; Hawkins et al., 1990; Meyers and Wright, 1993; Wilson et al., 1989), although there are few data specific to the current range of *P. d. perrieri*. Eastern wet forests receive considerably more annual rainfall (ca. 2,300–3,000 mm/year) than northern dry forests (Nicoll and Langrand, 1989). Thus, regions with the lowest annual rainfall are characterized by low plant productivity (Kay et al., 1997), which results in small body size in sifakas. Meyers and Wright (1993) found that on an annual basis, eastern wet forests have a more evenly distributed pattern of food resources for sifakas than do northern dry forests. Moreover, polygynous Malagasy lemurs experience very rapid rates of growth (Leigh and Terranova, 1998; Ravosa et al., 1995). For example, Ravosa et al. (1995) documented that *P. d. edwardsi* grow at a faster annual rate than *P. tattersalli*. Ravosa et al. (1995) also noted that dry forests tend to occur in small patches and are characterized by low productivity. They argued that their data support the resource seasonality model because the smallest sifakas are found in dry forests. Body size is not constrained to the same extent in *P. d. edwardsi*, due to dampened resource oscillations in eastern wet forests. Therefore, lack of rainfall in western and northern Madagascar may select for small body size in sifakas. Conversely, wet forests in eastern Madagascar do not constrain body size in sifakas because of reduced seasonal fluctuations in the abundance and availability of food resources.

We should not assume that eastern wet forests provide sifakas with a predictable supply of all food resources, particularly fruit. Ganzhorn et al. (1999) documented that fruit availability is highly unpredictable in the forests of eastern Madagascar. Fruit trees in eastern wet forests bear fruit approximately once every 3 years. Fruit crops are more predictable in western dry forests (Ganzhorn et al., 1999). Although most diademed sifakas are predominantly folivores, they often exploit fruits as a major food resource. For example, Hemingway (1998) observed that the diet of *P. d. edwardsi* is comprised predominantly of leaves (50% of annual diet) and fruit (41% of annual diet). Despite the greater availability of fruit for sifakas in western dry forests, the lemurs in these forests are obligate folivores, and fruits rarely make up more than 20% of the feeding time in any month (Yamashita, 2002). The question arises then as to why sifakas that range into eastern wet forests, where fruiting resources have a stochastic pattern of availability, eat a higher proportion of fruit than sifakas living in western dry forests, where fruiting is a more predictable event? There is also the possibility that seasonal variations in body weight confound our data. Sifakas inhabiting deciduous dry forests tend to lose weight over the dry season (Ganzhorn, 2002). However, such seasonal variations in body weight are unlikely to be a major confounding factor in our study, because our data on body weights were collected during the same time period (May–August). Therefore, relationships between forest productivity, fruit temporal availability, and sifaka body size reflect complex and regionally varying causalities that we cannot fully analyze with the data available at this time.

Our data on body size and protein-to-fiber ratios do not support the resource quality hypothesis. Moreover, any relationships between protein-to-fiber ratios and body weight in sifakas may simply be due to an underlying correlation between mean annual rainfall and protein-to-fiber ratios (Fig. 4). Ultimately, the explanative power of protein-fiber models lies in the importance of protein in the primate diet. Although protein requirements per unit of body weight tend to diminish with increasing total body weight, protein requirements for most species have not been determined in the wild. Oftedal (1991) suggested that most primates require little protein in their diet because they have slow growth rates compared to other mammals. Oftedal (1991) estimated that folivorous primates inhabiting low-quality (i.e., high-fiber, high-tannin) habitats would require at least 7–11% of their daily food intake to be protein for growth and maintenance, and 14% for reproduction. Prosimians differ from other primates in having depressed metabolic rates (Ross, 1992; Snodgrass et al., 2000), which may account for their low protein needs. Moreover, protein absorption can be negatively effected by the presence of tannins in leaves (Foley and McArthur, 1994; Robbins et al., 1987). Leaves eaten by sifakas contain on average only 2–10% available protein by mass of dry weight (Ganzhorn, 1992; Powzyk, 1998). For example, Powzyk (1998) estimated that the annual diet of *P. d. diadema* contained on average 6.8% protein by mass of dry weight. *I. indri* survive on even lower levels of protein intake (4.1% protein by mass of dry weight). Thus, either the estimates by Oftedal (1991) for protein requirements may not be applied to sifakas, or sifakas have lower protein requirements than was previously suggested.

The wide range of protein intake in human and nonhuman primates further complicates ecogeographic models that employ protein-to-fiber ratios. Powzyk (1998) noted that the proportion of protein in the daily diet of Malagasy strepsirhines ranges from 2.0% for bamboo lemurs (*Hapalemur griseus*) to 13.0% for ruffed lemurs (*Varecia variegata*). New World and Old World monkeys seem to require much higher levels of protein, i.e., at least 16.3% protein by dry weight (NRC, 2002). Although the recommended dietary requirement of protein for humans has changed repeatedly over the last 80 years, adult humans are thought to require 0.75 g protein/kg/day (RDA, 1989). However, protein intake varies considerably among human populations. For example, protein intake varies from 0.51 g protein/kg body weight/day in India to approximately 2.0 g protein/kg body weight/day in the USA (Rand et al., 1984). Therefore, detailed data on protein requirements in free-ranging sifakas are needed to rigorously test ecogeographic hypotheses.

CONCLUSIONS

We confirmed our predictions that *P. d. perrieri* (northern dry forest) has the smallest body weight and morphometrics, and that *P. d. candidus* (northeast wet forest) is intermediate in size between its nearest conspecifics, *P. d. diadema* (eastern and NE wet forest) and *P. d. perrieri*. The size variations we documented in sifakas support the resource seasonality hypothesis rather than the resource quality hypothesis. Specifically, we suggest that geographic variation in rainfall is the ecological factor influencing body size variations in sifakas. The premise underlying the resource quality hypothesis (geographic variations in protein-to-fiber ratios) may not reflect critical nutritional components of the diet in primates. Data are needed on the ecological factors underlying food selection and nutrient requirements in sifakas. With these data, we can then determine the causal rather than correlative relationships between ecology and geographic variations in body size.

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