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Fruit Characteristics of Species Dispersed by the Black Lemur (*Eulemur macaco*) in the Lokobe Forest, Madagascar[1]

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ABSTRACT

I describe the fruit characteristics of species closely associated with black lemur seed dispersal (*i.e.*, species that are often dispersed by the black lemur and only dispersed by the black lemur in the Lokobe Forest). A black lemur group was habituated and observed during the day and night for all months of the year (total 1272 h). When fruits were eaten, the plant species was identified, the maturity of the fruit and treatment of the seeds noted, and the fruit described in terms of ripe fruit color, husk thickness, fruit length, and seed length and width. Black lemur feces were searched for seeds; these were identified and signs of damage noted. Other potential dispersers feeding on the fruits of species eaten by the black lemur were also noted. The black lemurs were seen eating the fruits of 70 species. Of these, 51 species were defined as closely associated with black lemur dispersal and 16 species had seeds that were either often preyed upon or wasted by the black lemur, or were seen being eaten by other potential seed dispersers. Fruits of species in the former group were often dull colored (94% of species); rarely less than 1 cm long (6%); rarely had seeds less than 0.1 cm long or less than 0.1 cm wide (2 and 4%, respectively); never had seeds more than 4 cm long or greater than 2 cm wide; and quite often had either thick husks (49%) or thin husks (51%). In contrast, the fruits of the latter group were often brightly colored (75% of species) and nearly always had a thin husk (94%). Also, this latter group included more small and very large fruits and seeds than the former group. Fruit characteristics significantly associated with the former group were: dull color, thick husk, fruit length greater than 2 cm, seed length 1–4 cm, and seed width 1–2 cm. The extent to which these traits are the result of coevolution between plants and the guild of lemur dispersers that includes the black lemur is not clear, but a coevolved lemur–fruit syndrome remains a possibility.

RESUME

Cette étude porte sur la description des caractéristiques des fruits appartenant aux espèces dont la dissémination des graines est étroitement liée au *Eulemur macaco.* Ces espèces sont définies comme étant souvent disséminées par *E. macaco* et uniquement disséminées par *E. macaco* dans la forêt de Lokobe. Dans le but d'identifier ces espèces, un groupe de *E. macaco* a été habitué à la présence humaine et observé jour et nuit pendant tous les mois de l'année (en total 1272 h). Une fois le fruit consommé, l'espèce était identifiée, la maturité du fruit ainsi que le traitement de la graine notés et le fruit était décrit en terme de couleur à maturité, d'épaisseur de l'enveloppe, de longueur de fruit et de longueur et de largeur de graine. Par la suite, les féces sont recherchés afin d'identifier les graines qu'ils contiennent et toutes signes d'endommagement de celles-ci sont notés. Les autres agents de dissémination potentiels, consommateurs des fruits appartenant aux espèces consommées par *E. macaco,* ont été également notés. Les *E. macaco* ont été vu consommer les fruits de 70 espèces. De ces dernières, 51 espèces étaient définies comme étant étroitement liées à la dissémination par *E. macaco* et les graines de 16 espèces sont soit consommées, soit gaspillées par *E. macaco,* soit ont été vu consommées par d'autres agents de dissémination potentiels. Les fruits des espèces appartenant au groupe précédent sont souvent d'une couleur sombre (94% des espèces), d'une longueur rarement < 1 cm (6%), avaient rarement des fruits < 0.1 cm de long ou < 0.1 cm de large (2 et 4% respectivement) et n'ont jamais des graines > 4 cm de long ou > 2 cm de large, et presque souvent avaient une enveloppe épaisse (49%) et presque souvent une enveloppe mince (51%). Par contre, les fruits du dernier groupe sont souvent d'une couleur claire (75% des espèces) et presque toujours ont une enveloppe mince (94%). De plus, ce groupe inclut plus de petits et de très larges fruits et graines que le premier groupe. Les classes des caractéristiques des fruits significativement associées au premier groupe sont: couleur sombre, enveloppe épaisse, longueur de fruit >2 cm, longueur de graine 1–4 cm, et largeur de graine 1–2 cm. Cependant, l'importance du rôle joué par la coévolution entre les plantes et le groupe des lémuriens disséminateurs, comprennant Eulemur m., dans le développement des caractéristiques de ces fruits n'est pas connue.

Key words: black lemur; coevolution; Eulemur macaco; *frugivory; fruit characteristics; Madagascar; prosimian; seed dispersal; tropical rain forest.*

In Madagascar, several prosimian species are highly frugivorous (Wilson *et al* 1989; Richard & Dewar 1991; Overdorff 1988, 1993; Rigamonti 1993; Colquhorn 1993; Birkinshaw 1995; Britt 2000) and important seed dispersers (Hladik *et al.* 1980, Dew 1991, Birkinshaw 1995, Ralisoamalala 1996, Scharfe & Schlund 1996, Dew & Wright

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1998, Ganzhorn *et al.* 1999). Yet, with the exception of the study by Dew and Wright (1998), little information is available concerning the characteristics of the fruits eaten by lemurs or the fruit characteristics of species dispersed by them. In this study, a sample of plant species with fruits that were eaten by a group of black lemurs (*Eulemur macaco*) were identified and divided into two groups: species closely associated with black lemur seed dispersal and species not closely associated with black lemur seed dispersal. The fruit characteristics of species in these two groups are described and compared, with the objective of identifying traits associated with black lemur seed dispersal.

METHODS

STUDY SITE.—The study was conducted in primary, low-elevation humid evergreen forest in the Réserve Naturelle Intégrale de Lokobe on the island of Nosy Be, northwest Madagascar (13°23′–25′S, 48°18′–20′E). The forest is dense, attains 30 m in height, and lacks emergents. Among the tree flora, there are only a few nonnative species, including *Mangifera indica* and *Adenanthera pavonina* that are naturalized around the forest edge. The climate is characterized by high equable temperatures with a maximum monthly mean of 28°C in January and February and a minimum of 23°C in July and August; mean total annual rainfall is 2356 mm (White 1983). Precipitation is distinctly seasonal, with most (*ca* 85% of annual total) falling between November and May.

In addition to the black lemur, other primarily frugivorous vertebrates recorded in the Lokobe Forest include: the Madagascar Bulbul (*Hypsipetes madagascariensis*), the Madagascar Blue Pigeon (*Alectroenas madagascariensis*), the Madagascar fruit bat (*Pteropus rufus*), and the straw-colored fruit bat (*Eidolon dupreanum*). Also, the Madagascar Green Pigeon (*Treron australis*) was seen on the island of Nosy Be but was not recorded in the Lokobe Forest. The bulbul and blue pigeon are known to swallow seeds and void them in a viable state (Birkinshaw 1995); the remaining species probably do the same (Rand 1936, van der Pijl 1957, Goodwin 1983, Benson 1984, Langrand 1990, Rainey *et al.* 1995, Richards 1995, Ganzhorn *et al.* 1999). The alien brown rat (*Rattus rattus*) is abundant in the Lokobe Forest, and although a seed predator, may also occasionally act as a disperser when it fails to exploit its caches of stored seeds.

BLACK LEMUR.—The black lemur (*E. macaco,* Lemuridae) is a cat-sized, group-living, arboreal, cathemeral, prosimian primate. It has a mean head and body length of 41 cm and a mean weight of 2.4 kg (Tattersall 1982, Mittermeier *et al.* 1994). The black lemur is a known seed disperser in the Lokobe Forest, and an estimated 78 percent of their annual diet (in terms of time spent feeding) consists of ripe fruit (Birkinshaw 1995). The group examined in this study included between six and eight individuals. For most of the year, the group fed and ranged within their territory (area = 3.4 ha) and within a narrow band (*ca* 50 m wide) surrounding their territory within the territories of neighboring groups (Birkinshaw 1995; however, in November and December 1992, they traveled up to 400 m from their territory to exploit a superabundant fruit source (*Uapaca louveli*). They were habituated to humans after seven days of discontinuous observation.

IDENTIFYING SPECIES WITH FRUIT EATEN BY THE BLACK LEMUR.—A group of black lemurs was habituated and observed for 838 daytime hours and 434 nighttime hours spread over 18 months (November 1991–March 1993). During each study period, a focal animal was selected and its activity recorded every five minutes (following Altmann 1974). Whenever the focal animal was seen feeding on fruit, the parent tree was marked with a flag, which allowed the tree to be relocated when a herbarium specimen was made (following the methods given in Liesner [1991]). These specimens were identified after the fieldwork by using the literature and the collections of herbarium specimens at the Parc Zoologique et Botanique de Tsimbazaza, Antananarivo.

IDENTIFYING SPECIES CLOSELY ASSOCIATED WITH BLACK LEMUR SEED DISPERSAL.—Species closely associated with black lemur dispersal in the Lokobe Forest were defined as species that (a) were often dispersed by the black lemur and (b) had fruit that were not seen being exploited by other potential dispersers. Species often dispersed by the black lemur were defined as species with fruit that were normally (*i.e.,* on >95% of occasions) eaten by the black lemur when mature, with seeds that were normally swallowed whole (*i.e.,* not chewed or spat out) and voided visibly undamaged. This information was obtained during the course of the lemur observations by recording how the lemurs treated the seeds of the fruits that they exploited, and by collecting,

identifying, and examining (for signs of damage) seeds from black lemur feces.

Birkinshaw (1995) tested the viability of visibly undamaged seed samples defecated by the black lemur for 29 plant species. This was done by counting, over a six-month period, the number of germinations from seed samples of given species that had been collected from black lemur feces and sown (when fresh) in pots containing moist loam/sand mixtures. Some seeds from all species germinated and the mean percent germination was 73.1. In addition, Birkinshaw (1995) estimated (for 16 plant species) the percentage of seeds swallowed by the black lemur during the day that were deposited below the parent plant and fruiting conspecifics. This ranged between 0 and 28.5 percent, according to species. Given these results it seems reasonable to conclude that species with fruits normally eaten when ripe and having seeds normally swallowed whole and voided visibly undamaged, are often dispersed by the black lemur.

Species with fruits eaten by other potential seed dispersers in addition to the black lemur, were identified by means of opportunistic observations of focal fruiting trees made during the course of lemur observations (*i.e.,* the trees observed were fruiting trees in the vicinity of the focal lemur). The list of species so identified is probably incomplete because further observations at different times and places would probably identify additional species to be included on this list. Nevertheless, this information allows the dataset to be improved if not perfected.

FRUIT CHARACTERISTICS.—Fruits seen being eaten by the black lemur were described in terms of: fruit color when ripe, husk thickness (<1.0 mm = thin; ≥ 1.0 mm or husk with dense long hairs = thick), fruit length, and seed length and width. These attributes were chosen because previous studies have shown that they are important in determining the class of frugivore that exploits a fruit (*e.g.,* van der Pijl 1957, 1969; Snow 1971; McKey 1975; Janzen & Martin 1982; Marshall 1983; Gautier-Hion *et al.* 1985; Pratt & Stiles 1985). For this study, "fruits" were defined ecologically as "the smallest independent seed-containing structure at the time when exploited by the frugivore." As such, "fruits" also included arillate seeds and aggregate fruits developing from several separate carpels within a single flower, and multiple fruits formed by maturation of many individual flowers in one inflorescence. Dimensions were measured using a caliper. When possible, the determination was based on a sample of several (typically 10) mature fruits and seeds. Usually these were collected randomly from the plant using a tree pruner, and rarely, as fallen fruit from the ground.

RESULTS AND DISCUSSION

Black lemurs were observed eating the fruit of 70 species. Table 1 lists these plant species and describes the characteristics of their fruit. There was considerable interspecific variation in these traits: fruits were green, brown, yellow, orange, red, blue, or white; they may have had a thick husk or none at all; they ranged in length from 0.8 cm (*Bakerella* sp.) to 25 cm (*Colea purpurescens*); and their seeds ranged in length from less than 0.1 cm (*e.g., Ficus* spp.) to more than 10 cm (*M. indica*) and in width from under 0.1 cm (*Ficus* spp.) to 6 cm (*M. indica*). Table 1 also includes the results of the germination tests for seed samples defecated by the black lemur.

The variability in fruit characteristics is a reflection of the black lemur's ability to exploit different fruit types using different feeding methods. For example: (1) small, thin-husked fruits are brought toward the mouth by bending the fruit-bearing twig with the hand, the fruit is plucked with the mouth, chewed, and the husk, pulp, and seed swallowed; (2) small, thick-husked fruits are processed in a way similar to (1) except that the husk is either spat out or plucked out of the mouth with the fingers prior to swallowing the pulp and seeds; (3) large, thick-husked fruits are plucked with the mouth, carried to a secure location where the fruit, being supported and manipulated by the hands, is opened using the side of the mouth, the husk pried apart using the hands, and the pulp and seeds extracted with the mouth and swallowed; and (4) large, thin-husked fruits are processed in a way similar to (3) except that the pulp and husk are nibbled away from the seed(s) until the seed with whatever pulp remains is small enough to swallow.

Among the 70 species eaten by the black lemur, 57 were identified as being closely associated with black lemur dispersal (= group 1) and 16 as being not closely associated with black lemur dispersal (= group 2); the status of 3 species was undetermined. Figure 1 shows the proportion of species in these two groups in various classes of ripe fruit color, husk thickness, fruit length, seed length, and seed width. Fruits of group 1 species were often green (72.5% of species) and nearly always dull colored (*i.e.,* green, brown, orange, or yellow; 94%), rarely less than 1 cm long (6%), rarely had

TABLE 1. *Fruit characteristics of species closely associated with black lemur seed dispersal (group 1 species) and not closely associated with black lemur seed dispersal (group 2 species).*

Family	Species	Fruit color	Husk	Fruit length[a]	Seed length[b]	Seed width[b]	Other potential dispersers[c]	Percent germination of voided seeds (*N*)
Group 1. Species closely associated with black lemur seed dispersal.								
Agavaceae	*Dracaena* sp. 1	green	thick	medium	medium	medium		
Anacardiaceae	*Sorindeia madagascariensis*	red	thin	very large	quite large	medium		75 (4)
Annonaceae	*Monanthotaxis* sp. 1	red	thin	small	small	small		
Annonaceae	*Polyalthia richardiana*	green	thin	small	medium	medium		
Annonaceae	*Uvaria* sp. 1	brown	hairy	medium	medium	small		
Annonaceae	*Xylopia* sp. 1	brown	thick	medium	medium	small		
Apocynaceae	*Landolphia oblonginerva*	brown	thick	very large	medium	medium		100 (4)
Areaceae	*Dypsis pinnatifrons*	green	thin	very small	small	small		
Areaceae	*D. ampasindavae*	green	thin	small	medium	small		44 (16)
Bignoniaceae	*Colea purpurascens*	green	thick	very large	medium	small		100 (5)
Burseraceae	*Canarium madagascariense*	brown	thin	large	large	medium		86 (14)
Celastraceae	*Salacia madagascariensis*	orange	thin	large	medium	medium		
Clusiaceae	*Calophyllum* sp. 1	green	thick	large	quite large	medium		
Clusiaceae	*Garcinia verrucosa*	green	thick	very large	large	medium		
Combretaceae	*Terminalis calophylla*	green	thin	small	medium	small		7 (29)
Combretaceae	*T. ombrophila*	brown	thin	large	quite large	medium		
Dichapetalaceae	*Dichapetalum leucosia*	green	thin	small	small	small		
Ebenaceae	*Diospyros clusiifolia*	green	thick	very large	quite large	medium		83 (12)
Ebenaceae	*Diospyros* sp. 1	green	thick	small	medium	small		100 (10)
Ebenaceae	*Diospyros* sp. 2	green	thick	medium	quite large	small		80 (5)
Euphorbiaceae	*Uapaca louveli*	green	thick	medium	medium	medium		67 (15)
Fabaceae	*Crodyla madagascariensis*	green	thick	very large	large	medium		
Fabaceae	*Parkia madagascariensis*	green	thick	very large	large	medium		70 (10)
Lauraceae	*Cryptocarya* sp. 1	green	thin	small	medium	medium		
Lauraceae	*Potameia* sp. 1	green	thin	large	quite large	medium		
Loganiaceae	*Strychnos* sp. 1	orange	thick	very large	quite large	medium		75 (4)
Loganiaceae	*Strychnos* sp. 2	green	thick	small	medium	medium		
Mendonciaceae	*Mendonica flagellaris*	green	thick	medium	medium	medium		40 (5)
Menispermiaceae	*Burasaia* sp. 1	green	thick	large	quite large	medium		94 (16)
Menispermiaceae	*Strychnos thouarsii*	green	thick	medium	medium	medium		100 (4)
Monimiaceae	*Tambourissa* sp. 1	brown	thin	very large	medium	medium		
Moraceae	*Ficus cocculifolia*	green	thin	small	small	very small		
Moraceae	*F. lutea*	red	thin	small	very small	very small		
Moraceae	*Streblus mauritianus*	green	thin	large	small	small		85 (26)
Moraceae	*Treculia africana*	green	thick	very large	medium	small		92 (13)

TABLE 1. *Continued.*

Family	Species	Fruit color	Husk	Fruit length[a]	Seed length[b]	Seed width[b]	Other potential dispersers[c]	Percent germination of voided seeds (*N*)
Myrtaceae	*Eugenia* sp. 1	green	thin	medium	medium	medium		71 (7)
Oleaceae	*Noronhia* sp. 1	green	thin	small	medium	small		83 (6)
Oleaceae	*Noronhia* sp. 2	green	thin	small	medium	medium		
Pandanaceae	*Pandanus androcephalanthus*	yellow	thin	large	quite large	medium		
Rubiaceae	*Breonia nossibensis*	green	thin	medium	small	small		29 (7)
Rubiaceae	*Genipa* sp. 1	green	thin	very large	medium	small		30 (10)
Rubiaceae	*Pepeonidium horridum*	green	hairy	small	medium	small		
Rubiaceae	sp. 2 (AP228)[d]	green	thick	medium	medium	medium		
Sapindaceae	*Plagioscyphus* sp. 1	brown	thin	large	quite large	medium		
Sapindaceae	*Macphersonia madagascariensis*	green	thick	large	quite large	medium		66 (6)
Sapindaceae	*Chrysophyllum perrieri*	green	thick	large	quite large	medium		
Tiliaceae	*Grewia* sp. 1	green	thin	very small	small	small		35 (20)
Vitaceae	*Cissus* sp. 1	green	thin	very small	small	small		80 (5)
Vitaceae	*Cissus* sp. 2	green	thin	small	small	small		
Vitaceae	*Cissus* sp. 3	green	thick	medium	small	small		
Family unknown	sp. 1 (CB185)[d]	yellow	thick	large	medium	small		
Group 2. Species not closely associated with black lemur seed dispersal.								
Seed swallowed by the black lemur and defecated visibly undamaged, but fruit also eaten by other potential zoochores.								
Arecaceae	*Dypsis madagascariensis*	green	thin	small	medium	small	BP	53 (15)
Burseraceae	*Protium madagascariense*	red	thin	small	medium	small	B	75 (4)
Moraceae	*Ficus assimilis*	red	thin	small	very small	very small	B, BP, FB	100 (10)
Moraceae	*Streblus dimepate*	red	thin	small	small	small	B	100 (4)
Moraceae	*Trilepisium madagascariensis*	red	thin	small	medium	small	B	
Moraceae	*Trophis montana*	red	thin	small	small	small	B	100 (6)
Seed often preyed upon or wasted.								
Anacardiaceae	*Mangifera indica*	red	thin	very large	very large	large		
Celastraceae	*Cassine aethiopicum*	red	thin	small	small	small	B	
Chrysobalanaceae	*Grangeria porosa*	purple	thin	small	small	small	B	
Clusiaceae	*Garcinia* sp. 2	yellow	thin	small	medium	small		
Combretaceae	*Terminalia catappa*	green	thin	very large	very large	large		
Fabaceae	*Andenanthera pavonina*	red	thin	very large	medium	small		
Flacourtiaceae	*Aphloia theiformis*	white	thin	very small	small	small		
Moraceae	*Ficus soroceoides*	red	thin	small	very small	very small	B	

TABLE 1. *Continued.*

Family	Species	Fruit color	Husk	Fruit length[a]	Seed length[b]	Seed width[b]	Other potential dispersers[c]	Percent germination of voided seeds (*N*)
Rubiaceae	*Gaertnera* sp. 1	blue	thin	small	small	small	B	
Sterculiaceae	*Heritiera littoralis*	green	thick	very large	large	quite large		
Group undetermined								
Loranthaceae	*Bakerella* sp. 1	green	thin	very small	small	small		
Rubiaceae	sp. 3 (CB20)[d]	green	thin	very small	small	small		
Rubiaceae	*Mussaenda* sp. 1	green	thin	small	very small	very small		

[a] Fruit length: <1 cm = very small; 1–2 cm = small; 2–3 cm = medium; 3–4 cm = large; and >4 cm = very large.
[b] Seed length and width: <0.1 cm = very small; 0.1–1 cm = small; 1–2 cm = medium; 2–3 cm = quite large; 3–4 cm = large; and >4 cm = very large.
[c] Potential seed dispersers: B = bulbul; BP = blue pigeon; and FB = fruit bat.
[d] Number of voucher herbarium specimen.

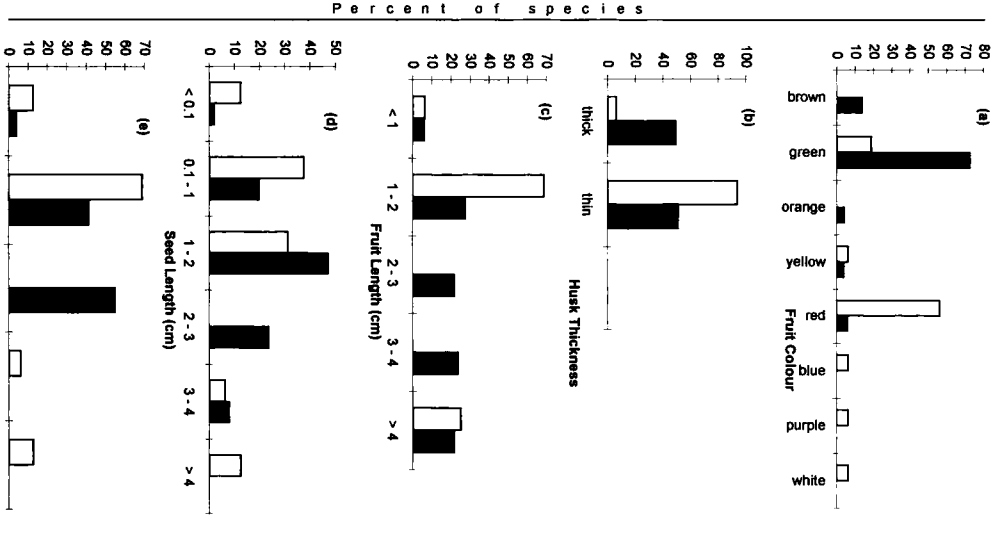

FIGURE 1. Distribution of species closely associated with black lemur seed dispersal (black bars) and species not closely associated with black lemur seed dispersal (white bars); between classes defined by (a) ripe fruit color, (b) husk thickness, (c) fruit length, (d) seed length, and (e) seed width.

seeds less than 0.1 cm long or less than 0.1 cm wide (2 and 4%, respectively) and never had seeds greater than 4 cm long or greater than 2 cm wide, and quite often had either thick husks (49%) or thin husks (51%). The graph of seed length versus percentage of species shows a normal distribution with the largest percentage of species (47%) having seed length 1–2 cm; however, the graph of seed width versus percentage of species is truncated so that there are no species in the width classes greater than the class 1–2 cm, which is also the class with

TABLE 2. *Association of various fruit character classes with species closely associated with black lemur seed dispersal (group 1) and not closely associated with black lemur seed dispersal (group 2).*

Fruit character	Character class	Group 1	Group 2	χ^2 (* = with Yates' correction)	Level of significance (P)
Color	Bright	48	4	29.6*	<0.001
	Dull	3	12		
Husk thickness	Thick	25	1	9.4	<0.01
	Thin	26	15		
Fruit length (cm)	<2	17	12	8.6	<0.01
	>2	34	4		
Seed length (cm)	<1 or >4	15	11	7.9	<0.01
	1–4	36	5		
Seed width (cm)	<1 or >2	23	16	15.1	<0.001
	1–2	28	0		

the largest percentage of species (55%). In contrast, the fruits of group 2 species were often brightly colored (75% of species) and nearly always had a thin husk (94%). In addition, compared to group 1 species, this group included more small and very large fruits and seeds.

Table 2 gives the χ^2 value for the association of various fruit characteristics with the two groups of species. This shows a significant association between the fruit characteristics of dull color, thick husk, fruit length greater than 2 cm, seed length 1–4 cm, and seed width 1–2 cm, and species closely associated with black lemur seed dispersal. These results agree with those of Dew and Wright (1998), who reported that in mid-elevation humid evergreen forest at Ranomafana, lemur fruits were dull-colored (*i.e.,* green or brown), longer than 1 cm, and had seeds longer than 1 cm.

The fruit characteristics of the plant species closely associated with black lemur seed dispersal appear to correspond to the feeding and foraging characteristics of this animal. First, as a prosimian, the black lemur lacks acute color vision (Blakeslee & Jacobs 1985, Bowmaker 1991, Jacobs & Deegan 1993); therefore, brightly colored fruits would not be expected to be more attractive than dull colored fruits. Second, for a relatively large frugivore like the black lemur to feed on small fruits would represent sub-optimal foraging, unless these fruits occurred at high densities, had a highly nutritious pulp, or were available at a time of fruit scarcity. Some of the small fruits exploited by the black lemur were indeed produced at high densities; *e.g.,* the 0.9 cm long and 0.8 cm wide fruits of *Dypsis pinnatifrons* were found on a large, many-branched infructescence such that there were several thousand fruits within a volume of *ca* 1 m^3. Third, the black lemur ingests seeds and thus there is a physical limit to the maximum size of seeds that can be swallowed and thereby dispersed. The longest seeds recorded as dispersed by the black lemur were those of *Cordyla madagascariensis* ($\bar{x}$ = 3.6 cm, SD = 0.2, N = 10) and the widest are those of *Diospyros clusiifolia* ($\bar{x}$ = 1.8 cm, SD = 0.1, N = 10). This was somewhat larger than the largest intact seeds recovered from the feces of *Eulemur fulvus* in the dry forest of west Madagascar (2.0 × 1.5 cm; Ganzhorn *et al.* 1999). Finally, the large proportion of thick-husked fruits among this group of plant species was consistent with the ability of the black lemur to process such fruits efficiently due to its excellent manipulative abilities.

The black lemur belongs to a guild of medium- to large-sized lemurs that share similar feeding and foraging charactersitics. This guild includes extant species (*i.e., Eulemur coronatus, E. fulvus, E. rubriventer,* and *Varecia varieagata*) and probably also extinct species (*e.g., Archeolemur* and *Pachylemur* spp.; Richard & Dewar 1991). The extent to which these lemurs have evolved to exploit fruits with the characteristics described above and/or the extent to which these fruit characteristics have evolved to promote seed dispersal by lemurs is unclear. Fischer and Chapman (1993) and Jordano (1995) have provided evidence that suggests, in general, fruit characterisitics are not closely coevolved with (*i.e.,* they are exapted to) their recent disperser guilds; rather, many fruit characteristics can be explained largely by ancestry and are relatively persistent over time (*i.e.,* similar fruits encounter a succession of different frugivore guilds). Jordano (1995) has suggested that the evolutionary inertia of fruit characteristics is due to constraints imposed by development and integration with predispersal repro-

ductive structures. Nevertheless, given the long period that the Malagasy flora has been isolated and the importance of lemurs in Madagascar's frugivore fauna during this time (Richard & Dewar 1991), the coevolution of at least some fruit characterisitcs (*e.g.,* fruit size; Jordano 1995) with lemurs remains a possiblity. Whatever the coevolutionary relationship between frugivorous lemurs and the plant species they disperse, this study adds support to the proposition of Dew and Wright (1998) that there is a suite of fruit traits associated with lemur dispersal.

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