

CHAPTER FOURTEEN

Ecologically Enigmatic Lemurs: The Sifakas of the Eastern Forests (*Propithecus candidus*, *P. diadema*, *P. edwardsi*, *P. perrieri*, and *P. tattersalli*) *Mitchell T. Irwin*

INTRODUCTION

The sifakas of Madagascar's eastern forests are some of the most visually distinctive members of eastern lemur communities, by virtue of their unique and often brightly colored pelage combined with their large body size, upright posture, and long, powerful legs. Many serious authors have interrupted their scientific writing to comment on their striking physical beauty; for example: "They are certainly the most beautiful lemurs of Madagascar" (Petter et al., 1977: 344). However, these sifakas' ecology is equally distinctive and enigmatic relative to other lemur groups, a fact that escaped notice until the last few decades. As noted by many authors

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(e.g., Petter et al., 1977), eastern sifakas (particularly rainforest taxa) are much harder to observe than western sifakas, due to lower population density and denser habitat. As might be expected, the earliest in-depth studies of western sifakas (e.g., Jolly, 1966; Richard, 1978) significantly predated similar studies of eastern sifakas (e.g., Wright, 1987).

While eastern sifakas were last chronologically, they certainly are not least in terms of uniqueness among Malagasy lemurs. In terms of diet, eastern sifakas are relatively catholic: not as dedicated to reproductive parts (flowers/fruits/seeds) as *Eulemur*, nor as dedicated to folivory as *Avahi*, *Lepilemur*, or *Indri*. Their social groups are neither as large as the gregarious *Eulemur* and *Hapalemur*, nor as small as the mostly solitary *Avahi*, *Lepilemur*, and other nocturnals. In fact, several aspects of their ecology and life history do not fit neatly into established categories. They have gradually become much better studied, yet the functional significance of, and interrelationships between, these basic elements of their ecology remain poorly understood.

TAXA AND DISTRIBUTION

Originally, two species of sifaka were recognized in Madagascar: *P. verreauxi* occupying the dry southern and western forests, and *P. diadema* occupying the eastern rainforests (Tattersall, 1982). Simons (1988) described a third species, *P. tattersalli* from Daraina in the far north, which appears to be most closely related to *P. verreauxi* (possibly the sister taxon of the subspecies *P. v. coquereli*; Pastorini et al., 2001; Rumppler et al., 2004).

Within *P. diadema*, four subspecies have been traditionally recognized: *perrieri*, *candidus*, *diadema*, and *edwardsi*. These four “types” of diademed sifaka are allopatric, distributed along a north–south gradient, and easily distinguished by virtue of their distinct and colorful pelages. *P. d. perrieri*, the northernmost taxon, has the smallest distribution, being restricted to the Analamera Special Reserve and small forest fragments to the west. *P. d. candidus* has a slightly larger range, from the Marojejy massif in the north to the Antainambalana river in the south. *P. d. diadema* extends from the Antainambalana river in the north to the Onive river in the south; populations in the southwestern part of this range (between the Mangoro and Onive rivers) are morphologically different, and may be taxonomically distinct from *P. d. diadema* (CBSG, 2002; Glander and Irwin, unpublished data). Finally, *P. d. edwardsi* is found from the Onive river in the north to the Manampatrana river in the south.

A fifth “type,” *P. d. holomelas*, had been recognized historically based on collection information, but has been subsumed (Tattersall, 1986) into *P. d. edwardsi*, as these two forms appear to have been sympatric. However, the extirpation of populations from areas thought to be inhabited by this variant means that we might well have lost a fifth taxon in historic times.

The taxonomic level at which these “types” of *Propithecus diadema* should be recognized has been subject to debate; all are allopatric in the wild, and therefore reproductive isolation cannot be demonstrated. Karyotypic differences exist (Rumper et al., 2004; Mayor et al., 2004) with *P. d. edwardsi* having a karyotype of $2n=44$ and all other types having $2n=42$. Mayor et al. (2004) propose that sequence differences in mitochondrial DNA warrant the elevation of these types to species, following the phylogenetic species concept. Following these authors, I will treat these four taxa as full species, within the “diadema group,” which is still considered to be monophyletic on both morphological and molecular grounds.

All told, the distribution of eastern sifakas is extremely broad (Figure 1, Table 1), spanning from 12.75 to 22.75 degrees south, with an altitudinal range between sea level and 1650 m. Most remaining eastern forest is occupied by sifakas, except the extreme southeast (south of the Manampatrana river), the Masoala peninsula in the northeast, and the transitional “Sambirano” forest in the northwest (Mittermeier et al., 1994; Irwin et al., 2005). This broad range harbors marked climatic variation. Average temperature decreases from north to south, while seasonal variation increases; superimposed upon this is a decrease in temperature with increasing elevation (Donque, 1972). Rainfall is high throughout most of the east, owing to the steep ascent of the trade winds striking the eastern escarpment, and annual rainfall is typically 1500–4000 mm/year. However, the northern tip of the island, near Antsiranana and Vohémar (including the range of *P. perrieri* and *P. tattersalli*), has no escarpment; rainfall is much lower (1000–1500 mm/year) and this region’s forests are consequently much drier.

Sifaka species have presumably evolved ecological and behavioral adaptations to these varying environments, but these have thus far been underexplored and are a promising direction of future research. For now, it is interesting to note this group’s wide range in body mass, which correlates with climatic variables (Lehman et al., 2005); this is suggestive of ecological differences.

FEEDING ECOLOGY

Plant Parts

Although sifakas have morphological specializations for folivory (e.g., long gastrointestinal tract, enlarged cecum) and long gastrointestinal transit time (Campbell et al., 2000, 2004), both western and eastern sifakas actually have a quite varied diet (only in the dry season does foliage truly dominate the diet). The diet of eastern sifakas includes high proportions of foliage, fruits, seeds, and buds/flowers (Table 2). *P. edwardsi* has the most equitable diet, with relatively equal amounts of foliage, fruits, and seeds. *P. diadema* at Mantadia and Tsinjoarivo are more folivorous, with 45–55% of feeding time devoted to leaves.

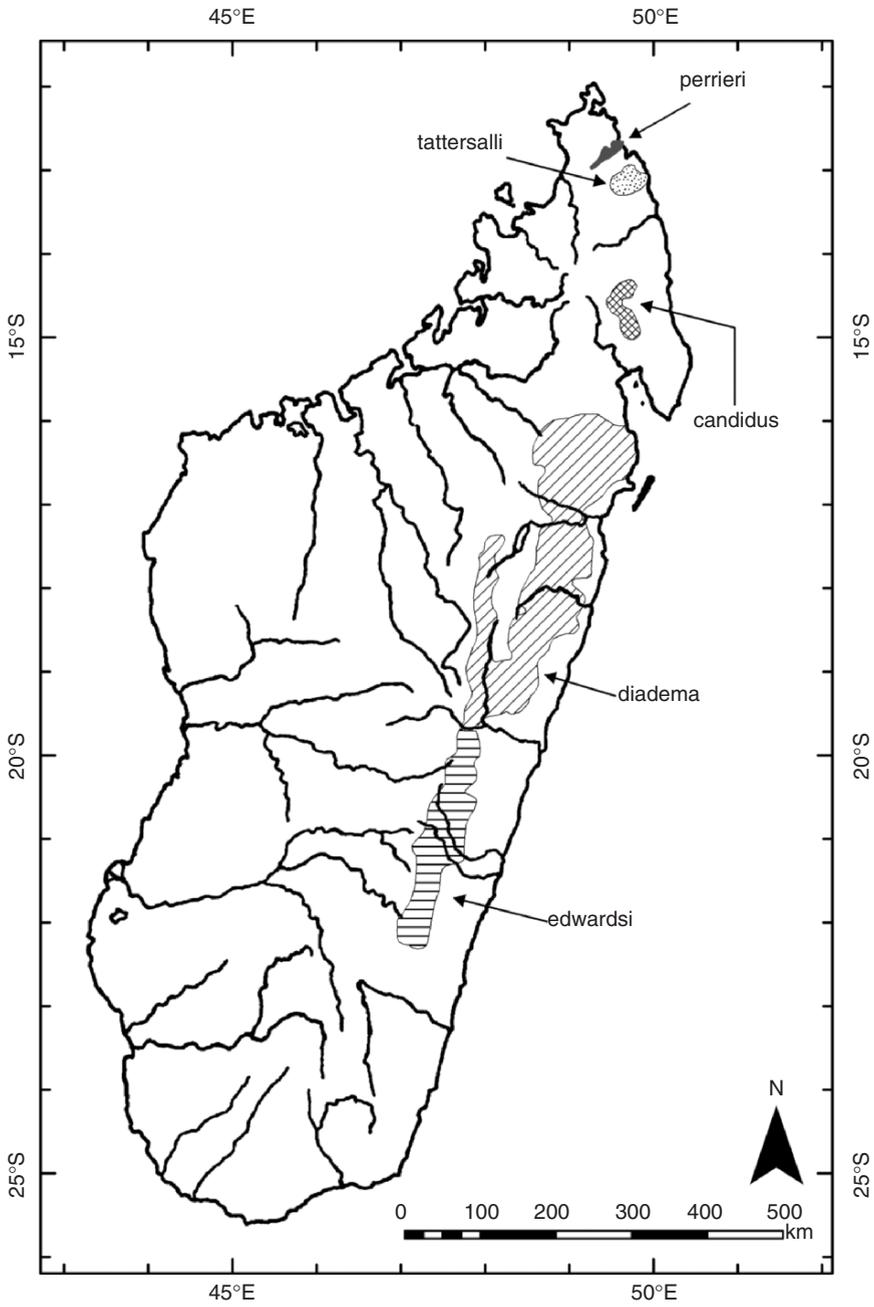


Figure 1. Distribution of eastern sifakas within Madagascar.

Table 1. Sifaka taxa found in Madagascar's eastern forests (from north to south)

Taxon	Geographic range	Altitudinal range (m)	Estimated population size ^a	Protected areas ^b	IUCN Red List status ^c	References ^d
<i>P. perrieri</i>	Analamera Special Reserve and isolated fragments to the west ^e	~56–249 ^f	~915	Analamera SR (<i>P. diadema</i>)	CR	1,2
<i>P. tattersalli</i>	Daraina, from Loky R. (N) to Manambato R. (S)	0–700	6100–10,000	None	CR	1,3
<i>P. candidus</i>	From Marojejy massif (N) to Antainambalana R. (S)	700–1875	100–1000	Marojejy NP, Anjanaharibe Sud SR	CR	1,4
<i>P. diadema</i>	From Antainambalana R. (N) to Onive R. (S)	300–1650	1000–10,000	Mantadia NP, Mananara Nord NP, Zahamena NP/ RNI, Betampona RNI, Ambatovaky SR	CR	1,4,5
<i>P. edwardsi</i>	From Onive R. (N) to Manampatrana R. (S)	625–1600	20,000	Ranomafana NP, Andringitra NP	EN	1,4,6

^a These figures are from disparate sources and may not be internally consistent. For example, Irwin et al., (2005) found a higher population size for *P. edwardsi* than the earlier estimate of Mittermeier et al., (1994); hopefully further studies will increase the estimated population size of *P. candidus* and *P. diadema*.

^b Abbreviations: NP, National Park; RNI, Integral Nature Reserve; SR, Special Reserve.

^c Following IUCN Red List of Threatened Species. www.redlist.org, accessed 9 September 2005.

^d References: 1, Mittermeier et al., (1994); 2, Banks et al., (in press); 3, Vargas et al., (2002); 4, Goodman and Ganzhorn (2004); 5, Irwin (unpublished); data); 6, Irwin et al., (2005).

^e *P. perrieri* was previously found at Ankarana Special Reserve, west of Analamera (Hawkins et al., 1990); more recent surveys (Banks et al., in press) failed to locate sifakas at Ankarana, suggesting they have been extirpated.

^f No study has expressly measured this taxon's altitudinal range; Banks (personal communication) recorded *P. perrieri* census sightings between 56 and 249 m, but as Analamera Special Reserve has an altitudinal range of ~0–750 m, the true range for this taxon could be higher.

Table 2. Relative contributions of different plant parts (measured as percentage of overall feeding time) to the diet of eastern sifakas. Because of strong seasonal variation in diet, only long-term (≥ 1 year) studies are included

Taxon / population	Food type					
	Fruits	Seeds	Flower buds + flowers	Foliage	Other / Unknown	(Soil) ^a
<i>P. diadema</i> , Tsinjoarivo (Irwin, 2006), 4 groups	23.9	7.3	15.1	53.1	0.6	(0.35)
<i>P. diadema</i> , Mantadia (Powzyk, 1997), 2 groups	6.2	30.9	15.0	44.4	3.5	(0.33)
<i>P. edwardsi</i> , Ranomafana (Hemingway, 1995), 2 groups	30.4	35.4	5.3	28.2	0.6	(0.38) ^b
<i>P. tattersalli</i> , Daraina (Meyers, 1993), 3 groups	46.2	0	13.3	38.7	1.7	?

^a A subset of time devoted to "Other / Unknown."

^b Value for one group only; second group consumed soil "only rarely."

Among primate groups on other continents, eastern forest sifakas' diet is most similar to the asian colobines (e.g., Davies, 1991; Meyers, 1993; Koenig and Borries, 2001). These colobines also have morphological adaptations for folivory (in this case, foregut fermentation), a diverse diet, and seasonal variation quite similar to that of eastern sifakas.

While all *Propithecus* consume large amounts of foliage, it has been suggested that *P. verreauxi* in western and southern forests tends to be a *frugivore*-folivore, while eastern *Propithecus* tends to be a *granivore*-folivore (Richard, 2003). However, recent evidence does not completely bear out this generalization. While eastern sifakas at some sites (Ranomafana: Hemingway, 1995; Mantadia: Powzyk, 1997) fit this pattern, *P. diadema* at Tsinjoarivo more closely fit the frugivore-folivore model; they often consume fruit pulp and discard seeds (Irwin, 2006). The reason for this discrepancy is unclear, but it is possible that floristic changes related to Tsinjoarivo's high altitude create a fruit guild more like that of drier forests.

The sifakas' relatively catholic diet is in stark contrast to most other lemur groups, which tend to specialize on specific plant parts. Most *Eulemur* taxa in eastern rainforests concentrate heavily on reproductive parts (flowers and fruits), and consume very little foliage (Overdorff, 1993). Most other groups (*Avahi laniger*, *Indri indri*, and *Lepilemur* spp.) are more dedicated to folivory (Ganzhorn et al., 1985; Ganzhorn, 1988; Harcourt, 1991; Powzyk, 1997). In the southern part of their range, rainforest sifakas are the most folivorous of their diurnal lemur communities; in the north they are sympatric with *Indri*, a similar-sized indriid more fully devoted to folivory (Powzyk and Mowry, 2003). In all regions, they are considerably less folivorous than the sympatric nocturnal genera *Avahi* and *Lepilemur*.

There are conflicting reports concerning which plant parts are preferred. *P. tattersalli* at Daraina, *P. edwardsi* at Ranomafana, and *P. diadema* at Mantadia track

immature leaf availability (consumption of this resource is positively correlated with its availability; Meyers and Wright, 1993; Powzyk, 1997). In contrast, Irwin (2006) found highly significant positive correlations between fruit availability and consumption in *P. diadema* at Tsinjoarivo, suggesting that fruit is the preferred resource. Finally, newer data from Ranomafana (Wright et al., 2005) also suggest that *P. edwardsi* at Ranomafana track fruit availability. Further research is necessary, particularly to control for such confounding factors as chemical variation among plant species and the preferred maturity level (i.e., ripeness) of selected foods.

Finally, eastern sifakas differ from other sympatric lemurs in their treatment of fruits and seeds (Overdorff and Strait, 1998). *Eulemur* species mainly derive nutrients from pulp, either dropping whole seeds at the feeding tree or ingesting and defecating them whole. Sifakas, in contrast, either consume pulp and drop seeds (Irwin, 2006) or, more commonly, masticate the seeds they consume (some smaller seeds [e.g., *Ficus* sp.] may be consumed whole). *Eulemur* feces often contain multiple whole seeds, while sifaka feces are usually homogeneous with no discernible plant parts. As a result, unlike *Eulemur* species (Overdorff, 1993; Dew and Wright, 1998), sifakas provide limited or no seed dispersal.

Seasonality

All populations for which long-term data are available show extreme seasonal variation in diet composition (Meyers, 1993; Hemingway, 1995; Powzyk, 1997; Irwin, 2006). Generally, sifakas consume high levels of fruit and/or seeds in the rainy season (December–April) when these are most abundant; during this time fruits and seeds can account for 70–90% of feeding time. Diet in the remaining months is more variable but fruit and seeds generally constitute less than 10% of feeding time. *P. edwardsi* at Ranomafana consume more leaves at this time, but still maintain a modest intake of fruit and seeds (including seeds from fallen, rotting fruit; Hemingway, 1995). *P. diadema* at Mantadia consume high levels of leaves, as well as flowers and fern fronds, during this time (Powzyk, 1997).

P. diadema at Tsinjoarivo follow a different strategy (Irwin, 2006). They consume high levels of young leaves at the beginning (May–June) and end (October–November) of the dry season, but rely on flowers during the height of the dry season (July–September), spending up to 50% of feeding time on this resource. Their diet at this time is heavily monotonous, with the buds, flowers, and leaves of a hemiparasitic mistletoe (*Bakerella clavata*) accounting for 45–70% of feeding time. This is an extreme and unusual level of devotion to a single species.

Taxonomic Composition of Diet

The taxonomic composition of diet appears to be relatively flexible, varying widely between study sites (Table 3). Myrtaceae is the dominant plant family for *P. edwardsi* at Ranomafana and *P. diadema* at Mantadia but Loranthaceae

Table 3. Preferred food resources for eastern sifakas, ranked by feeding time

Study site	Ranomafana	Mantadia	Tsinjoarivo	Tsinjoarivo fragments
Taxon	<i>P. diadema</i>	<i>P. diadema</i>	<i>P. diadema</i>	<i>P. diadema</i>
Top plant families	Myrtaceae Sapindaceae Sapotaceae Erythroxylaceae Moraceae <i>Chrysophyllum boivinianum</i> (Sapotaceae) <i>Plagioscyphus tonvelli</i> (Sapindaceae) <i>Erythroxylum sphaeranthum</i> (Erythroxylaceae) <i>Treculia africana</i> (Moraceae) <i>Eugenia</i> (<i>Syzygium</i>) sp. 23 (Myrtaceae)	Myrtaceae Euphorbiaceae Clusiaceae Loranthaceae Sapotaceae <i>Tinnodia perrieri</i> (Euphorbiaceae) <i>Protobius ditrimena</i> (Anacardiaceae) <i>Chrysophyllum boivinianum</i> (Sapotaceae) <i>Syzygium</i> sp. 1 (Myrtaceae) <i>Syzygium</i> sp. 2 (Myrtaceae)	Loranthaceae Lauraceae Clusiaceae Pitrosporaceae Apocynaceae <i>Bakerella clavata</i> (Loranthaceae) <i>Ocotea</i> sp. 1 (Lauraceae) <i>Garcinia</i> sp. (Clusiaceae) <i>Pittosporum verticillatum</i> (Pitrosporaceae) <i>Salacia madagascariensis</i> (Celastraceae)	Loranthaceae Rutaceae Araliaceae Euphorbiaceae Myrsinaceae <i>Bakerella clavata</i> (Loranthaceae) <i>Melicope</i> sp. (Rutaceae) <i>Schefflera</i> sp. (Araliaceae) <i>Macaranga</i> cf. <i>ankafinensis</i> (Euphorbiaceae) <i>Embelia concinna</i> (Myrsinaceae)

Sources: Hemingway (1995), Powzyk (1997), Irwin (2006).

Table 3. Preferred food resources for eastern sifakas, ranked by feeding time—Cont'd.

Study site	Darina Z (wettest)	Darina A (intermediate)	Darina M (driest)
Taxon	<i>P. tattersalli</i>	<i>P. tattersalli</i>	<i>P. tattersalli</i>
Top plant families	Fabaceae Sapindaceae Anacardiaceae Myrtaceae Annonaceae	Fabaceae Anacardiaceae Olacaceae Araliaceae Malvaceae	Fabaceae Ebenaceae Combretaceae Sapindaceae Anacardiaceae
Top plant species	<i>Filicium longifolium</i> (Sapindaceae) <i>Cynometra</i> sp. (Fabaceae) <i>Eugenia</i> sp. (Myrtaceae) <i>Cordyla madagascariensis</i> (Fabaceae) <i>Xylopia flexuosa</i> (Annonaceae)	<i>Baudouinia fluggeiformis</i> (Fabaceae) <i>Albizia boivini</i> (Fabaceae) <i>Pongamiopsis</i> sp. (Fabaceae) <i>Olea lanceolata</i> (Olacaceae) <i>Cynometra</i> sp. (Fabaceae)	<i>Pongamiopsis cloiselli</i> (Fabaceae) <i>Diospyros lokohensis</i> (Ebenaceae) <i>Terminalia</i> sp. 1 (Combretaceae) <i>Erythrophysa belini</i> (Sapindaceae) <i>Tamarindus indica</i> (Fabaceae)

Source: Meyers, 1993

dominates for *P. diadema* at Tsinjoarivo. In the drier forests at Daraina, leguminous trees (Fabaceae) dominate the diet of *P. tattersalli*. Even over small spatial scales, diet composition can vary widely, such as between pristine forest and fragments at Tsinjoarivo (Table 3a) and among drier and wetter sites at Daraina (Table 3b).

SPATIAL ECOLOGY

Home Range

Rainforest sifakas occupy home ranges of 30 to 80 ha. At Mantadia, two *P. diadema* groups used home ranges of 33 and 42 ha (Powzyk, 1997), while *P. edwardsi* at Talatakely have similar-sized home ranges (~ 38 ha; Wright, 1995; Powzyk, 1997), as do *P. candidus* at Marojejy (44 ha; E. Patel, personal communication). *P. diadema* groups in continuous forest at Tsinjoarivo occupy between 70 and 80 ha but groups in fragments occupy 20–37 ha (Irwin, 2006).

In contrast, sifakas in the drier forests of the north have smaller home ranges, similar to those of western sifakas (Jolly, 1966; Richard et al., 1991). Meyers (1993) reports home ranges for *P. tattersalli* at Daraina between 4.4 and 12.3 ha, and *P. perrieri* home ranges at Analamera during the short study of Lehman and Mayor (2004) were even smaller: 1 to 1.1 ha. It thus appears that local ecology determines home range size more than phylogeny: three “diadema group” sifakas in humid forests have large ranges, while two taxa in drier forests (one “diadema group,” one *P. tattersalli*) have small ranges. Why drier forests sustain higher sifaka densities is not entirely clear, but it has been suggested that food quality is a key issue (e.g., Powzyk, 1997). Drier forests in western and northern Madagascar have higher leaf “quality” (measured as the ratio of extractable protein to acid detergent fiber; Ganzhorn, 1992). This difference (surprisingly) may outweigh the cost of food shortages during the protracted dry season.

Day Range

P. diadema at Mantadia have long daily path lengths (1629 m/day; Powzyk, 1997) while those of *P. edwardsi* at Ranomafana are shorter (670 m/day; Wright, 1987). *P. diadema* in continuous forest at Tsinjoarivo (Irwin, 2006) show intermediate values (987 m/day), as do *P. tattersalli* (461.7–1077 m/day; Meyers, 1993) and *P. candidus* (710 m/day; E. Patel, personal communication). These values are similar to those reported for western sifakas (Jolly, 1966; Richard, 1978) which is surprising given the marked difference in home range.

Daily path length is longest during the rainy season (approximately December to March) and shortest during the dry season (July–October) (Meyers, 1993;

Powzyk, 1997; Irwin, 2006). This suggests that it requires more ranging effort to procure an adequate supply of the fruits which are preferred in the rainy season. In contrast, the leaves and flowers used as a fallback in the dry season may be more uniformly available, or sifakas may be less selective about which plant species are used. Further research is necessary to adequately explain this pattern.

SOCIAL ORGANIZATION AND BEHAVIOR

Group Composition

Early field studies noted the variability in sifaka group composition (e.g., Petter et al., 1977). However, they suggested that “. . . the ancestral group structure of *Propithecus* is monogamous, and that a normal group was composed of a pair of adults and two to three offspring of different ages” (p. 379), proposing that the larger observed group sizes may be due to habitat disturbance (possibly representing aggregations of multiple family groups). However, field studies have confirmed for eastern sifakas (as did Jolly, 1966, and Richard, 1978, for western sifakas) that monogamous groups are not the rule.

P. edwardsi at Talatakely (Ranomafana) live in groups of three to nine individuals, with a mean of 4.6¹ (Wright, 1995; Pochron et al., 2004), while those at the Vatoharanana trail system live in groups of 2–8, with a mean of 4.3 (Hemingway, 1995). Groups of 3–6 individuals (mean = 4.8) were observed for *P. diadema* at Mantadia (Powzyk, 1997), while *P. diadema* at Tsinjoarivo have been observed in groups of 4–7 (mean = 4.9; Irwin, 2006, unpublished data). *P. tattersalli* have slightly larger group sizes (3–10; Meyers, 1993), similar to those of western sifakas (Richard, 1978). Such intermediate group sizes open the door for several group types. Assuming that stable groups have at least one breeding male and female, four distinct types are possible: polygynous, polyandrous, polygynandrous, and monogamous pairs. Such variability is less likely in larger groups (usually polygynandrous) or smaller groups (usually monogamous).

Indeed, Pochron and Wright (2003), using data from 46 group-years for *P. edwardsi* at Talatakely (Ranomafana), found an average of 3.2 adults per group and a surprisingly even distribution of the four possible group types. Since the competitive regime would be expected to vary greatly in different group types, these differences may have profound effects on other aspects of social life. However, Pochron and Wright (2003) found no effect of group type on infant birth rate and survival. They argue that feeding competition limits group size, causing small, nonuniform social groups, but mating may occur more freely across group boundaries (as in *P. verreauxi*: Richard, 1985). However, mating season influxes have not yet been observed in eastern sifakas to the same degree known

¹Totals include infants and only data from December or January were used whenever possible.

in *P. verreauxi*, and preliminary genetic data provide no evidence for extragroup paternity (Morelli and Wright, in preparation).

The dataset of Pochron and Wright is by far the largest for eastern sifakas, but as it derives from a disturbed (selectively logged) site, one must consider the possibility it does not represent the “natural” state. However, data from *all* other behavioral studies conducted in pristine forests (Meyers, 1993; Hemingway, 1995; Powzyk, 1997; Irwin, 2006) show similar group sizes and variable composition. It therefore appears that the variable social structure described by Pochron and Wright is typical of eastern sifakas, though further study is necessary to better understand the causes and consequences of this variability.

Dispersal

As with social organization, patterns of natal dispersal do not follow any hard-and-fast rules. In most primates, one of the sexes tends to be philopatric (Pusey and Packer, 1987); only in a few species do both sexes commonly disperse. Based on available evidence, eastern sifakas seem to rank among those rare species having no sex bias in dispersal. In *P. edwardsi*, roughly half of males *and* females disperse, usually at 4–5 years of age (though females may travel greater distances); this dispersal is usually “motivated” by targeted aggression from adults (Wright, 1995; Pochron et al., 2004). Other individuals of both sexes remain, and reproduce, in their natal group.

Pochron et al. (2004) suggest that this opportunism may be due to slow reproduction and high infant mortality. The combination of small groups and slow reproduction means that a given sifaka generally cannot have enough same-sex kin to form the social networks seen in other male- or female-bonded primates. Therefore, animals may be equally willing to stay in their natal group should breeding opportunities become available, or disperse to find breeding opportunities elsewhere. This opportunism may also apply throughout adult life for males; secondary dispersal has been observed among males, but not females (Pochron et al., 2004).

Behavioral studies at other sites have not lasted long enough to provide definitive confirmation of this pattern; the natural rarity of dispersals means that only longer-term studies (i.e., >5 years) can provide a balanced view of dispersal. However, it is worth noting that among *P. diadema* at Tsinjoarivo, the three observed dispersal events have involved two females and one male (Irwin, 2006; Irwin and Raharison, unpublished data).

Intragroup Relations

Sifaka groups tend to have relatively stable dominance relations among individuals (e.g., Meyers, 1993; Hemingway, 1995), but the patterns of dominance vary from group to group. Intersexual relations are difficult to quantify for two reasons: first, aggression rates are extremely low (with a high percentage of undecided

encounters), and second, the variable social structure may lead to different social environments and therefore different dominance relationships (Overdorff and Erhart, 2005). Available evidence from various sites is, however, consistent with the definitions of female feeding priority and true female dominance (Pochron et al., 2003), but only under certain circumstances; the situation is still less clear-cut than for some lemurs (e.g., *Lemur catta*). For example, in groups with multiple adult females, the dominant female appears to be consistently dominant over males, but the same is not always true for subordinate females (e.g., Hemingway, 1995).

Patterns of association (as measured by proximity) among males and females are also variable from group to group, and therefore difficult to categorize (Meyers, 1993; Hemingway, 1995). This aspect of group life may also be strongly influenced by the variation in group composition and relatedness of same-sex animals.

Infanticide has been observed in *P. edwardsi* (Wright, 1995; Erhart and Overdorff, 1998), always perpetrated by newly immigrant males. Although infanticide would seem less likely to be adaptive among seasonal breeders, the life history of sifakas (see below) is such that early loss of an infant could increase the chances of conception in the following breeding season.

Intergroup Relations

Despite the maintenance of stable territories (e.g., Wright, 1995), eastern sifakas interact directly with neighboring groups only rarely (e.g., three encounters observed among two groups over more than 1 year at Mantadia: Powzyk, 1997; two encounters among two continuous forest groups over 1 year at Tsinjoarivo: Irwin, 2006). *P. tattersalli* has a higher encounter rate (a few encounters per month; Meyers, 1993), consistent with their smaller home ranges. In general, these low encounter rates may be at least partly due to their low population density. When groups do encounter one another, the interactions are generally agonistic, particularly between same-sexed animals, but they usually involve chasing and vocalizing, without much serious fighting. The primary means of territorial “defense” appears to be scent-marking (Pochron et al., 2005), females using an anogenital gland and males using anogenital and chest glands. Scent-marking is a complex social activity and more research is required to fully understand its causes and consequences, as it likely serves a number of functions (which may differ between males and females; Lewis, 2005). However, indirect evidence for sifakas (e.g., Powzyk, 1997:225; Pochron et al., 2005) indicates that scent marks can serve as “signposts” to conspecifics, marking territorial boundaries.

LIFE HISTORY AND REPRODUCTION

After consistently proving to be unique and enigmatic in all aspects of their ecology discussed thus far, it would seem unfitting if sifakas had an ordinary life history; indeed recent studies have proved that this is not the case. Like all extant lemurs,

the reproductive schedule of sifakas is tightly constrained seasonally (most primate species reproduce year-round or show more moderate seasonality; e.g., Koenig et al., 1997). In *P. edwardsi* and *P. diadema* mating occurs in December and January, while birth occurs between May and July, with the majority in June (Wright, 1995; Pochron et al., 2004; Irwin, 2006). *P. tattersalli* breeds slightly later (Meyers, 1993), like western sifakas: mating in January–February, and births in late July.

Average interbirth interval (IBI) at Talatakely, Ranomafana, is 1.56 years (Pochron et al., 2004); in other words, 1 year for roughly half of births and 2 years for most other cases. This is in contrast to many smaller lemurs, which give birth every year. The roughly even split between 1- and 2-year IBIs suggests a possible pressure to speed up infant development (i.e., reduce time to weaning). Sifakas who are metabolically ready to conceive 12 months after a previous conception can do so, but those who become ready at 13 or 14 months must wait until the 24th month postbirth, due to the strict estrous seasonality. This delay might have led to selective pressures to reduce mothers' postbirth metabolic costs, thereby reducing "recovery time."

In terms of infant development, Godfrey et al. (2004) showed that indriids have a slow somatic growth rate relative to other lemurs. This is contrary to the expected pressures of seasonal reproduction, as well as the predictions of the risk aversion hypothesis of Janson and van Schaik (1993). This hypothesis suggests that more folivorous taxa should have rapid development, because the relative lack of food competition lessens the starvation risks associated with rapid growth. However, the slow body growth seen in *Propithecus* and other indriids is paired with an unusually fast rate of dental development (this family is unusual in the extent to which somatic and dental development rates are decoupled). Godfrey et al. (2004) suggest that accelerating the development of adult dentition at the expense of other body tissues may get infants to independence as soon as possible (the high-fiber diet of *Propithecus* requires more dental competence than the softer diet of frugivores). By achieving dental competence earlier than other similar-sized primates, sifakas shorten the dependency period and the mother's overall postbirth metabolic cost, thereby promoting her own survival. It has further been proposed (Wright, 1999) that reproduction is timed to place weaning at the season of peak food availability (March), further reducing the mother's costs at this time. This explanation for sifakas' unusual combination of life history traits fits nicely with what is known about Madagascar's impoverished environments, and with the "Energy Conservation Hypothesis" of Wright (1999).

However, while mothers may succeed at shortening their infants' march to independence, the infants themselves do not fare that well. Roughly half of infants die before 1 year of age at Talatakely, and only about one quarter of females reach reproductive age (Pochron et al., 2004). The only reason this population sustains itself seems to be a long reproductive life span (>20 years; Wright, 1995; Pochron et al., 2004). Adult females seem to follow the "bet-hedger" strategy of Richard et al. (2002), slowing down their reproductive output and reducing investment in

individual offspring to aid their own long-term survival. This fits well with what is known about both the paucity *and* the unpredictability of Madagascar's environment; reducing investment makes reproduction possible in average years, and a long life span makes it possible to wait out bad years (Godfrey et al., 2004). However, the unfortunate combination of fast acquisition of adult dentition and a long life span bodes poorly for the state of teeth in elderly individuals. Indeed, observations at Ranomafana indicate that some older animals may suffer from extreme tooth wear, and an impaired ability to feed (King et al., 2005).

PREDATION

Being among the largest of living lemurs, eastern sifakas suffer lower overall predation pressure relative to most lemurs. However, predation by the fossa (*Cryptoprocta ferox*) is ubiquitous, having been recorded for *P. edwardsi* (Wright et al., 1997), *P. diadema* at Mantadia (Powzyk, 1997) and Tsinjoarivo (Irwin and Raharison, in preparation), *P. candidus* (Patel, 2005), *P. perrieri* (Mayor and Lehman, 1999), and *P. tattersalli* (Goodman, 2003). The fossa is the largest Malagasy carnivore, at 6.75 kg (Hawkins, 2003); despite being only slightly larger than adult eastern sifakas, it seems adept at taking both young and adults. No successful predation by birds on eastern sifakas has been recorded (Goodman, 2003), but the presence of antipredator responses indicates that several raptors are considered a threat (Karpanty and Grella, 2001).

RESILIENCE TO HABITAT CHANGE AND FRAGMENTATION

As mentioned earlier, eastern sifakas were studied much later than western sifakas; later still was the development of research programs (in either region) investigating sifakas' responses to habitat fragmentation and alteration. Early studies followed the general trends of primatology, studying groups within habitat which was as pristine as possible. The (valid) reasons for doing so were academic (understand a species' *true* behavior) as well as practical (increase the chances your study groups would last at least as long as your study period). However, the rate of habitat conversion in Madagascar (and elsewhere) has reached crisis proportions: Green and Sussman (1990) estimated that the eastern rainforest cover in 1985 had already diminished to 34% of its original extent, and an extrapolation of the observed disappearance rate predicts a complete loss of this ecosystem ca. 2020. What forest remains is increasingly fragmented and impacted by human activities. The impact of these changes on lemur populations can no longer be ignored.

So what are the prospects for eastern sifakas? Understanding the nature of the threat is the first step. One can conceptualize the threats fragmentation poses to sifaka populations as three sequential challenges. First, direct anthropogenic

effects (e.g., hunting) threaten most proximately. Second, fragmentation-related habitat changes may affect the ecological compatibility between sifakas and their habitat—and even if compatibility is maintained, it may be through compromises which affect other aspects of behavior. Finally, on the longest time scale, there is the demographic threat of population subdivision and constrained dispersal.

The immediate anthropogenic effects are hard to estimate and notoriously variable among regions. In many areas, sifakas are protected from hunting by *fady* (taboo); these often apply preferentially to sifakas and indri because of their large size and orthograde posture (resembling humans or human ancestors). However, this protection is by no means universal. *P. edwardsi* is hunted throughout much of its range, especially the northern part (Irwin et al., 2005). Other eastern sifakas seem to be protected in some, but not all, regions. This threat is controllable through human activities (unlike the purely ecological pressures); it is important that education and enforcement of applicable laws (which deem hunting of lemurs illegal) continue to be applied and extended in rural areas where sifakas live.

The second threat, loss of ecological compatibility, is only beginning to be investigated. My dissertation research (Irwin, 2005a,b, 2006) compared the ecology and behavior of two *P. diadema* groups resident in forest fragments and two in continuous forest at Tsinjoarivo. I found that continuous forest groups relied on various tree species to provide fruit during the rainy season, but relied heavily on a small hemiparasitic mistletoe (*Bakerella* cf. *clavata*) during the middle of the dry season (devoting 45–70% of monthly feeding time to this one species). For these groups, mistletoe is a fallback resource. Fragment groups ate fewer fruits, and the loss of preferred fruit trees forced them to consume mistletoe at high levels throughout the year; for them, mistletoe is best described as a *staple*. Arrigo-Nelson (2005) similarly found reduced frugivory and loss of preferred fruit resources in disturbed areas for *P. edwardsi* at Ranomafana, suggesting that this pattern may be consistent across sites.

The fact that groups in fragmented or disturbed habitats can sustain themselves, however, is not in itself reason to discount the threat of habitat change; one must consider the effects of behavioral shifts. One direct line of research involves the nutritional composition of foods; this is currently being studied at Tsinjoarivo. If the altered diet is less nutritious, long-term effects on body condition and reproduction would be apparent. Indeed, reduced body mass of adult sifakas in fragments has already been documented, for *P. edwardsi* at Ranomafana (Dehgan, 2003), and *P. diadema* at Tsinjoarivo (Glander and Irwin, unpublished data). Other effects are also apparent: for example, fragment groups have greatly reduced group cohesion and an increased rate of feeding alone (Irwin, 2005b). The mistletoe on which they rely has an extremely small crown diameter (<2m); animals are forced to spread out because sharing food patches is impractical (and subordinates are unlikely to be tolerated by dominant individuals). These altered resource distributions and decreased group cohesion could lead to altered food competition regimes and changes in social behavior which could affect group structure and reproduction.

The third major threat is the demographic consequence of population subdivision. Even when populations can emerge unscathed from the first two threats, they may be threatened by the longer-term effects of inbreeding and reduced dispersal opportunity. The severity of this threat depends on how reluctant individuals are to cross the nonforested areas between fragments. Most eastern sifakas, in contrast with western congeners, seem extremely reluctant to do so. Dehgan (2003) found that a *P. edwardsi* group in a forest fragment did not leave the forest fragment in which they lived, except to cross distances less than 30 m to smaller satellite patches. Among two *P. diadema* groups in forest fragments at Tsinjoarivo, no crossing between patches was observed during a 1-year study (Irwin, 2006). One adult male did later disperse secondarily across open areas, but only after the rest of his group was decimated by predation. In contrast, Mayor and Lehman (1999) noted that *P. perrieri* regularly crosses open areas, in one instance traversing 600 m. These results suggest that sifakas in drier forest may be predisposed to crossing between fragments, possibly because they have historically lived in more open (possibly mosaic) habitats. Rainforest sifakas, in contrast, may be more suspicious of open areas due to their long evolutionary history in dense forest with little need to come to the ground.

The long time scale of demographic threat means that long-term study is necessary before assessing whether fragmented populations are population sinks, or whether they can be a viable part of the larger population. Given the increasing rarity of pristine forests in Madagascar, the ability to include fragmented populations in effective population sizes would definitely paint a better picture for conservation; only time will tell us for which species this approach is justified.

CONSERVATION SITUATION

Currently, *P. candidus*, *P. diadema*, *P. perrieri*, and *P. tattersalli* are classified as “Critically Endangered” by the IUCN (Table 1), and *P. edwardsi* is classified as “Endangered.” Extinction of one or more of these taxa is an imminent possibility, due to their relatively small population sizes, fragmented and discontinuous habitats, and the continuing human threats. The geographic range and population size of *P. edwardsi* and *P. diadema* are still relatively large (though further research is necessary to determine the status of the Tsinjoarivo *P. diadema*); however, *P. candidus*, *P. perrieri*, and *P. tattersalli* all occupy relatively small ranges.

Before comparing the conservation situation of eastern and western sifakas, it is useful to contrast some key aspects of their ecology. On a typical distribution map, the two groups look relatively balanced: four taxa more-or-less evenly spaced along the west and southwest, five more-or-less evenly spaced along the east. However, important differences in ecology may make the eastern sifakas (and particularly the rainforest taxa) much more seriously threatened.

First, eastern rainforest sifakas (*P. edwardsi*, *P. diadema*, and *P. candidus*) as well as *P. perrieri* live at low population densities (2–10 individuals/km²; Wright,

1995; Irwin et al., 2005; Banks et al., in press). *P. verreauxi* is on the order of 6 to 100 times more densely packed (Richard, 2003) and *P. tattersalli* is intermediate at 17–28 individuals/ km² (Vargas et al., 2002). Second, rainforest sifakas appear much less able to live in human-dominated landscapes. It is common, where they are not hunted, to find *P. verreauxi* in small forest patches near villages and water sources. This is likely due to small home range requirements, and tolerance of human-favored tree species (e.g., mango, *Mangifera indica*). The same is not true of rainforest sifakas; *P. diadema* at Tsinjoarivo do not range in human-dominated forest patches (usually dominated by *Eucalyptus* and *Pinus*) but require endemic forest trees and a minimum patch size of around 25 ha (Irwin, unpublished data). Third, the dry forest sifakas' predisposition to cross open areas gives them a demographic resiliency in fragmented habitat which rainforest taxa may not share.

Thus, it is not possible to directly compare eastern and western sifakas based on geographic range, or perhaps even population size. These ecological "disadvantages" of eastern sifakas should be considered when developing conservation priorities and action plans.

SUMMARY

The five eastern sifakas have until recently been poorly studied relative to their western congeners. However, several surveys and long-term studies, starting with Wright's study of *P. edwardsi* in the mid-1980s, have taken great strides to even the playing field. Eastern sifakas share many similarities with western *P. verreauxi*, but differ in their larger body mass, lower population density, and larger home ranges (in rainforest taxa). Many aspects of *Propithecus* ecology, social organization, and behavior remain enigmatic, not fitting well into theory developed for anthropoid primates and even set apart from other lemur taxa. Continuing research is necessary to understand the causes and consequences of these aspects of sifaka life and, perhaps more importantly, to adequately protect their dwindling populations in the face of drastic habitat loss and fragmentation.

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