CHAPTER 13

The Ecology and Conservation of Malagasy Bats

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Introduction

Despite the important contribution that bats make to tropical biodiversity and ecosystem function, as well as the threatened status of many species, conservation initiatives for Madagascar's endemic mammals have rarely included bats. Until recently, most mammalogical research in Madagascar concerned lemurs, rodents, and tenrecs. This focus resulted in a dearth of information on bat biology. However, since the mid-1990s considerable advancement has been made following the establishment of capacity-building programs for Malagasy bat biologists, and bats are now included in biodiversity surveys and a growing number of field studies are in progress.

In this chapter we summarize the advances made in recent years in understanding the diversity of Malagasy bats and briefly describe their biogeographic affinities and levels of endemism. We draw attention to the importance of understanding the ecology of these animals and why this is a prerequisite to their conservation. In discussing monitoring and hunting, we highlight some of the reasons that make bat conservation notably different from other vertebrate conservation challenges on the island.

The Diversity of Malagasy Bats

The recent surge of interest in Malagasy bats has resulted in the discovery and description of nine new taxa on the island. The rate of new discoveries quickly makes statements on endemism and species richness out of date. For example, of the 37 bat taxa listed for Madagascar in table 13.1, only 29 were treated in the 2005 Global Mammal Assessment in Antananarivo. Further, at least six additional taxa are currently being described (by S. M. Goodman and colleagues). These advances are partly because taxonomists working on Malagasy mammals only relatively recently turned their attention to bats. Further, molecular systematic techniques have provided important insights into the evolutionary relationships of the island's bats (e.g., Russell et al. 2007; Russell et al. 2008a;

Table 13.1. The diversity of Malagasy bats

Family	Species	Distribution
Pteropodidae	*Pteropus rufus*	Madagascar VU
	Eidolon dupreanum	Madagascar VU
	Rousettus madagascariensis	Madagascar NT
Emballonuridae	*Emballonura atrata*	Madagascar
	Emballonura tiavato[a]	Madagascar
	Coleura afra[b]	Madagascar, Africa, Middle East
	Taphozous mauritianus	Madagascar, Africa, Mauritius, Réunion, Aldabra
Hipposideridae	*Triaenops rufus*	Madagascar
	Triaenops furculus[c]	Madagascar
	Triaenops auritus	Madagascar NT
	Hipposideros commersoni	Madagascar NT
Vespertilionidae	*Miniopterus manavi*	Madagascar, Comoros
	Miniopterus majori	Madagascar
	Miniopterus gleni	Madagascar
	Miniopterus sororculus[d]	Madagascar
	Myotis goudoti	Madagascar
	Scotophilus robustus	Madagascar
	Scotophilus tandrefana[e]	Madagascar
	Scotophilus marovaza[f]	Madagascar
	Scotophilus cf. borbonicus	Madagascar, Réunion
	Pipistrellus raceyi[g]	Madagascar
	Pipistrellus hesperidus[g]	Madagascar, Africa
	Eptesicus matroka	Madagascar
	Neoromicia malagasyensis[h]	Madagascar VU
	Neoromicia melckorum[g]	Madagascar, Africa
	Hypsugo anchietae[g]	Madagascar, Africa
Nycteridae	*Nycteris madagascariensis*	Madagascar
Molossidae	*Chaerephon leucogaster*	Madagascar, Africa
	Chaerephon pumilus[i]	Madagascar, Africa, Comoros
	Chaerephon jobimena[j]	Madagascar
	Mops leucostigma	Madagascar
	Mops midas	Madagascar, Africa
	Mormopterus jugularis	Madagascar
	Otomops madagascariensis	Madagascar
	Tadarida fulminans	Madagascar, Africa
Myzopodidae	*Myzopoda aurita*	Madagascar
	Myzopoda schliemanni[k]	Madagascar

Source: Information on the distribution is taken from Simmons 2005.

Note: Taxa new to Madagascar since the last summary of the chiropteran fauna (Eger and Mitchell 2003) are annotated. Conservation status from the Global Mammal Assessment meeting held in 2005. VU: vulnerable; NT: near threatened. New taxa have yet to be evaluated, and the remainder are LC: least concern.

[a]Goodman et al. 2006a.

[b]First recorded in Madagascar in 2004 (Goodman et al. 2005a; Goodman et al. in press b).

[c]The *Triaenops* on Aldabra and Cosmoledo (Seychelles) is described Goodman and Ranivo 2008.

[d]Goodman et al. 2007b.

[e]Goodman et al. 2005b.

[f]Goodman et al. 2006b.

[g]Bates et al. 2006.

[h]Goodman and Ranivo 2004.

[i]The populations occurring in the western Seychelles (Aldabra and Amirantes) appear to be a separate species (Goodman and Ratrimomanarivo 2007).

[j]Goodman and Cardiff 2004.

[k]Goodman et al. 2007a.

Russell et al. 2008b; Lamb et al. 2008). Another reason is that survey teams are spending an increasing amount of time in the western deciduous forests, away from the eastern humid forests that have traditionally received most attention from biologists, and voucher specimens with associated tissue samples are being collected.

Surveys in western Madagascar have resulted in the discovery of six endemic bat species new to science: *Scotophilus marovaza* (Goodman et al. 2006b), *Scotophilus tandrefana* (Goodman et al. 2005b), *Chaerephon jobimena* (Goodman and Cardiff 2004), *Myzopoda schliemanni* (Goodman et al. 2007a), *Pipistrellus raceyi* (Bates et al. 2006), and *Emballonura tiavato* (Goodman et al. 2006b). All of these taxa, with the exception of *P. raceyi*, are restricted to the drier habitats of the island.

Scotophilus marovaza occurs in synanthropic settings and probably has a wide distribution across the anthropogenic savanna of central western Madagascar (Ratrimomanarivo and Goodman 2005; Goodman et al. 2006b). *Scotophilus tandrefana* is known from only a few specimens (Goodman et al. 2005b) and appears to be a rare member of the bat community (Kofoky et al. 2007).

The taxonomy of Malagasy pipistrelles has been unclear for sometime, with authors referring to undescribed taxa (Eger and Mitchell 2003; Russ et al. 2003; Goodman et al. 2005a). The situation has now been clarified and includes the description of a new *Pipistrellus* that shows affinities to three southeast and east Asian taxa (Bates et al. 2006).

Other new bat taxa recently described for Madagascar are either African species found on the island for the first time or taxonomic revisions and resurrections. Three mainland African species have recently been found in Madagascar: *Coleura afra* (Goodman et al. 2005a; Goodman et al. 2008a), *Hypsugo anchietae*, and *Neoromicia melckorum* (Bates et al. 2006). *Neoromicia malagasyensis* was also given full species status by Goodman and Ranivo (2004) and this conclusion has been supported by further anatomical characters described by Bates et al. (2006).

On the basis of recent morphological and molecular studies, the genus *Triaenops* in the western Indian Ocean comprises four taxa: *T. auritus*, *T. furculus*, and *T. rufus* restricted to Madagascar and a new species occurring on the Aldabra atoll in the western Seychelles (Ranivo and Goodman 2006; Russell et al. 2007; Russell et al. 2008a; Goodman and Ranivo 2008). Recent morphological studies on another genus in the family Hipposideridae, *Hipposideros*, indicate that there might be a cryptic species on Madagascar (Ranivo and Goodman 2007b).

A number of projects have been completed or are currently under way to examine patterns of phylogeographic and geographic variation in Afro-Malagasy Molossidae bats. Classically two subspecies of the molossid *Mops midas* have been recognized: an African mainland form (*M. m. midas*) and a endemic Malagasy form (*M. m. miarensis*). Recent morphological and molecular studies indicate that these two populations cannot be differentiated

(Ratrimomanarivo et al. 2007). This is best explained by a recent colonization of Madagascar by this taxon or regular genetic exchange, through dispersal, between the two populations. *Mops leucostigma* shows considerable morphological variation between eastern and western populations on Madagascar, but these differences cannot be explained by genetic variation (Ratrimomanarivo et al. in press). The closest sister taxa to *Mops leucostigma* is *M. condylurus*, and these two species are separated by considerable genetic distances (Ratrimomanarivo et al. in press).

Two Malagasy species, *Emballonura atrata* and *Myzopoda aurita*, have recently been split into two, each with an eastern and western species (Goodman et al. 2006a; Goodman et al. 2007a). Taxonomic advances of this nature have profound impacts on species conservation status, and previous assessments quickly become obsolete. The challenge now is to describe the natural history and ecology of newly described Malagasy bat species so that conservation assessments and recommendations can be made using robust field data.

The Biogeography of Malagasy Bats

The affinities of the island's bat fauna are primarily Afrotropical, as Madagascar shares six of the eight families of bats found in Africa. Three genera (*Eidolon*, *Coleura*, and *Triaenops*) are Afrotropical in origin, and three (*Pteropus*, *Emballonura*, and *Mormopterus*) are Oriental and occur in Madagascar as well as India (*Pteropus*), Asia (all three), and Australia (*Pteropus* and *Mormopterus*), but not on the African mainland, with the exception of odd records of *Mormopterus*.

Although Madagascar's bat fauna is depauperate compared to other large islands (Hutson et al. 2001; Jones et al., chapter 6, this volume), its isolation since before the evolution of contemporary living bat groups and their subsequent dispersal over water has resulted in high levels of endemism. Based on published new species descriptions as of early 2008, 26 of the 37 (70%) taxa are endemic to Madagascar and 28 endemic to Madagascar and nearby islands. The remarkable family Myzopodidae is of particular interest to zoologists and conservationists because it is endemic and, like the Thyropteridae in South America, its members have adhesive pads on the thumb and sole (Schliemann and Maas 1978).

Compared to other large islands such as Papua New Guinea and the Philippines (Heaney 1991), Madagascar's megachiropteran fauna, with three species, is particularly depauperate and forms part of a generally species-poor frugivore community (Goodman and Ganzhorn 1997). Fleming et al. (1987) pointed out that Madagascar is "strikingly depauperate in frugivorous birds," and Hawkins and Goodman (2003) noted that although 15 of the 96 forest bird species are frugivorous to some extent, only seven are obligate frugivores. Although the majority of the island's lemur species eat fruits, leaves, and nectar, none appears to rely solely on fruit.

Surveys, Progress, and Capacity Building

Until the late 1980s, knowledge of bat distribution in Madagascar had resulted principally from museum collecting trips, the most significant being that of Randolph L. Peterson in 1967, summarized (posthumously) in Peterson et al. 1995. In 1989 the first contemporary expedition devoted solely to surveying bats using mist nets and observations at roost sites visited Réserve Naturelle Intégrale de Marojejy (Pont and Armstrong 1990), which has subsequently been reclassified as a national park. Despite this lead, many subsequent vertebrate surveys did not incorporate bat inventories (e.g., Rakotondravony and Goodman 1998; Goodman and Rasolonandrasana 1999; Goodman and Wilmé 2003). Bayliss and Hayes (1999) found 11 species of bat in the Makira Forest area of the northeast, underlining relatively high levels of species richness and the need for further exploration of the island's chiropteran fauna. The chiropteran, and therefore mammalian, species richness at many sites in Madagascar was incompletely sampled despite the efforts of field teams charged with documenting the island's vertebrate diversity. An example is the rapid biodiversity assessment of Parc National d'Ankarafantsika, which was completed without a bat specialist (Alonso et al. 2002). Although the mammal team noted the occurrence of *Hipposideros commersoni* (Rakotondravony et al. 2002), subsequent surveys of bats at this site revealed the presence of nine species (Goodman et al. 2005a), including individuals of two endemic taxa new to science, *Myzopoda schliemanni* and *Scotophilus marovaza* (Goodman et al. 2005a; Goodman et al. 2006b; Goodman et al. 2007a).

Russ et al. (2003) heralded a new era of bat survey work on Madagascar through their use of a variety of trapping techniques (harp traps, mist nets, and flap nets) and electronic bat-detecting equipment. An important addition was the use of time-expansion detectors, an apparatus widely used in Europe (e.g., Russ 1999; Russ and Montgomery 2002; Russo and Jones 2003), in conjunction with a library of echolocation calls, which continues to expand (Russ et al. 2003; Kofoky et al. 2009). The echolocation calls of some Malagasy bats, such as *Myzopoda aurita* and *Triaenops rufus*, are distinctive enough that additional information about distribution can be obtained from bat detectors alone.

Since 2000, surveys for bats have become better integrated into forest biodiversity assessments in Madagascar. For example, although no bat survey was published in a monograph devoted to a vertebrate inventory of Station Forestière de Tampolo in 1997 (Ratsirarson and Goodman 1998), four species were recorded at this site in 2003, when a bat team was included in a follow-up inventory project (Ifticene et al. 2005).

The relative dearth of local bat biologists was one reason for the comparative lack of interest in Malagasy bats before 1990. Although a program organized by WWF-Madagascar, known as the Ecology Training Program, trained close to 240 Malagasy students in survey methods for reptiles, amphibians, birds, and land mammals, bats were not regularly included until the early 2000s. Further, nearly 80 higher university degrees in evolutionary and conservation biology were the direct results of this program, but only in recent years did they include theses and scientific publications on bats (e.g., Goodman and Ranivo 2004, 2008; Ratrimomanarivo and Goodman 2005; Razakarivony et al. 2005; Ranivo and Goodman 2006, 2007a, 2007b; Rakotonandrasana and Goodman 2007; Rakotonandrasana 2008; Ranivo 2007; Ratrimomanarivo et al. 2007). In October 2007 the Ecology Training Program was turned over to a Malagasy international association known as Vahatra to continue under the direction of Malagasy biologists.

Beginning with a student expedition from the United Kingdom and two projects funded by the U.K. government's Darwin Initiative between 1999 and 2004, a program was launched to raise the capacity of Malagasy students to conduct research on bats and to engage in associated conservation activities. The first phase of this project, known as Tetikasa Fikajiana Fanihy, focused exclusively on fruit bats and the second phase, called Lamin'asa Fiarovana Ramanavy, on the island's insectivorous bats. These two projects led to the creation in 2005 of the Malagasy biodiversity organization, Madagasikara Voakajy, dedicated to the conservation of threatened vertebrates, and a permanent bat conservation team. A growing number of Malagasy students (18 by 2008) are benefiting from these training and graduate programs with experience in bat ecology (e.g., Ranivo 2001; Ratrimomanarivo 2003; Andriafidison 2004; Ralisata 2005; Razafindrakoto 2006; Rakotoarivelo 2007), and Malagasy researchers associated with these projects have a prominent role in scientific research on bats (Andriafidison et al. 2006a; Andriafidison et al. 2006b; Andrianaivoarivelo et al. 2006; Randrianandrianina et al. 2006; Rakotoarivelo et al. 2007; Kofoky et al. 2007). The results of these two different capacity-building programs are now evident, and Malagasy bat scientists are active in conservation research, taxonomy, and field surveys.

Malagasy Megachiroptera

Pteropus rufus

The Madagascar flying fox *Pteropus rufus* (500–750 g) is most commonly found in the lowlands, within 100 km of the coast, or on offshore islands, although some roosts have been found in the Central Highlands (MacKinnon et al. 2003). Roosting bats are noisy and conspicuous and are found in large trees, often near freshwater, but also in mangroves. During a national survey in 1999 and 2000 that covered about a third of Madagascar, 100,000 individuals were counted in roosts. Roosting aggregations varied from 10 to 5,000 animals, although large colonies were rarely encountered, and the median size was 400 individuals (MacKinnon et al. 2003). Roost sites are also known from plantations of introduced trees, mostly *Eucalyptus*. Few roost sites were found inside Madagascar's protected-area network, but were most often located in small areas of forest, either as thin strips along estuaries or small fragments surrounded by water, savanna grassland, or agricultural land. At dusk *P. rufus* can be seen setting out from the eastern coast of Île Sainte-Marie toward the main island (Goodman 1993), which from shore to shore is a minimum distance of around 50 km. A limited radio-tracking study at Berenty revealed that *P. rufus* traveled 5–17 km to its foraging sites each night (Long 2002).

Eidolon dupreanum

Eidolon dupreanum (250–340 g) roosts in crags and cliffs, in caves, and occasionally in the dense foliage of trees such as *Raphia* and coconut palms. Colonies typically consist of 10–500 individuals with a median of 200, although three roosts with more than a thousand individuals occurred in the Réserve Spéciale d'Ankarana in 1999 (P. A. Racey, unpublished). This species is found throughout Madagascar, including the Central Highlands, where the human population is relatively high and there is little remaining intact native forest (MacKinnon et al. 2003).

Rousettus madagascariensis

Rousettus madagascariensis is the smallest Malagasy fruit bat species (50–75 g) and the only one that can hover. It roosts in caves and cliff crevices and can occur in colonies of several hundred individuals, usually beyond the twilight zone. Although known from most forested parts of the island (MacKinnon et al. 2003; Goodman et al. 2005a), there are many reported captures and observations from near human settlements and agricultural land. Despite its apparent wide distribution, few roost sites have been located by biologists, and few details are available about its ecology.

The Ecology of Malagasy Megachiroptera

Diet

The diet of Malagasy fruit bats is of interest because of their dual role as pollinators and seed dispersers (Hutcheon 2003). Most research has focused on describing the diet of *Pteropus rufus* (Bollen and Van Elsacker 2002; Long 2002; Andriafidison 2004; Bollen et al. 2004; Raheriarsena 2005), with two studies on *Eidolon dupreanum* (Ratrimomanarivo 2007; Picot et al. 2007), and only one that included *Rousettus madagascariensis* (Razafindrakoto 2006). Overall, pollen and fruit remains from 110 plant species of 70 genera and 46 families have been identified from the feces and ejecta of Malagasy fruit bats (table 13.2). This is an impressive number for a single island when compared with 289 plant species in 59 families recorded by Fujita and Tuttle (1991) for megachiropterans as a whole.

Table 13.2. Plant species found in feces of *Pteropus rufus* (P) and *Eidolon dupreanum* (E) in the form of pollen, seeds, and fruit

Plant family	Plant species[a]	Vernacular name	Pollen		Fruit	
			P	E	P	E
Pinaceae	*Pinus* sp.			y		
Agavaceae	*Agava sisalana*	laloasy, taretra	y	y		
Anacardiaceae	*Mangifera indica*	manga			y	y
Anacardiaceae	*Poupartia caffra*	sakoambanditsy		y		
Anacardiaceae	*Poupartia minor**	sakoa	y	y		
Anacardiaceae	*Protorhus grandidieri*	sohihy	y			
Anacardiaceae	*Rhus perrieri**	tsilaitse				y
Anacardiaceae	Sp. 1			y		
Apocynaceae	*Pachypodium geayi**	vontaka		y		
Araliaceae	*Cussonia bojeri*					y
Verbenaceae	*Avicennia marina*	afiafy	y			
Bombacaceae	*Adansonia grandidieri**	renala	y	y*		
Bombacaceae	*Adansonia suarezensis**			y*		
Bombacaceae	*Adansonia za**	za	y			
Bombacaceae	*Bombax* sp.			y		
Bombacaceae	*Ceiba pentandra*	kapoaky	y	y*		
Burseraceae	*Commiphora* sp.	daro			y	
Cactaceae	*Cereus* sp.	raketam-bazaha			y	
Cactaceae	*Opuntia monocantha*	raketa		y		
Cactaceae	*Opuntia vulgaris*	raketa		y		
Capparaceae	*Crateva excelsa*				y	
Capparaceae	*Maerua filiformis*	somangy			y	y
Caricaceae	*Carica papaya*	papaier, papay			y	y
Celastraceae	*Gymnosporia polyacantha**	tsingilofilo, filofilo			y	y
Fabaceae	*Bauhinia hildebrandtii**		y	y		
Fabaceae	*Cassia siamea*		y			
Fabaceae	*Colvillea racemosa*	sarongaza	y	y		
Fabaceae	*Delonix adansonioides**	malamasafoy	y	y		
Fabaceae	*Tamarindus indica*	kily			y	y
Combretaceae	*Terminalia catappa*	atafa, badamier	y*			
Asteraceae	*Helichrysum* sp.			y		
Asteraceae	*Vernonia* sp.			y		
Boraginaceae	*Celtis philippensis*	varo			y	y
Boraginaceae	*Cordia caffra*	varo			y	y
Cupressaceae	*Cupressus* sp.			y		
Cyperaceae	*Cyperus* sp.			y		
Ericaceae	*Erica* sp.			y		
Euphorbiaceae	Sp.1			y		
Aphloiaceae	*Aphloia theiformis*	voafotsy		y		y
Flacourtiaceae	*Flacourtia indica*	lamoty			y	y
Flacourtiaceae	*Flacourtia* sp.	lamoty			y	
Gentianaceae	Sp.1				y	
Liliaceae	*Lilium* sp.			y		
Liliaceae	*Dianella ensifolia*					y
Meliaceae	*Azadirachta indica*	nimo			y	
Meliaceae	*Melia azedarach*	voandelaka		y	y	y
Fabaceae	*Acacia dealbata*	dalbata		y		
Fabaceae	*Acacia* sp. 2			y		
Fabaceae	*Albizia lebbeck*	bonara	y	y		
Fabaceae	*Albizia tulearensis**	maindoravy	y	y		
Fabaceae	*Parkia madagascariensis**		y*			
Moraceae	*Ficus antandronarum**	nahodahy			y	
Moraceae	*Ficus baroni*	aviavy, aviavindrano			y	y
Moraceae	*Ficus botryoides**	lazo				y

Table 13.2. *(continued)*

Plant family	Plant species[a]	Vernacular name	Pollen P	Pollen E	Fruit P	Fruit E
Moraceae	*Ficus brachyclada*	fonofonjanahary			y	
Moraceae	*Ficus cocculifolia**	adabo				y
Moraceae	*Ficus grevei**	amota, fihamy-be				y
Moraceae	*Ficus humbertii*	maharesy			y	
Moraceae	*Ficus madagascariensis**	aviavy			y	
Moraceae	*Ficus megapoda**	fihamy				y
Moraceae	*Ficus menabeensis**	fihamy			y	
Moraceae	*Ficus pachyclada**				y	
Moraceae	*Ficus pyrifolia**	nonoke			y	y
Moraceae	*Ficus soroceoides*					y
Moraceae	*Ficus trichopoda**	aviavy				y
Moraceae	*Morus alba*					y
Moraceae	Sp. 1			y		
Musaceae	*Musa* spp.	ankondro				
Myrtaceae	*Eucalyptus camaldulensis*		y			
Myrtaceae	*Eucalyptus* sp.	kininim-boasary	y			
Myrtaceae	*Eugenia jambos*	jambarao, rotra		y		
Myrtaceae	*Eugenia sakalavarum**	rotran'ala		y		
Myrtaceae	*Psidium cattleianum*				y	y
Myrtaceae	*Psidium guajava*	goavy, gavo			y	y
Oleaceae	*Noronhia seyrigii*	tsilatse			y	
Arecaceae	Sp.			y		
Passifloraceae	*Adenia olaboensis**	holaboay			y	y
Passifloraceae	*Adenia* sp. 2				y	
Passifloraceae	*Passiflora caerulea*					y
Piperaceae	Sp.				y	
Poaceae	Sp.			y		
Portulacaceae	*Talinella grevei**	dango			y	y
Rosaceae	*Prunus* sp.					y
Rosaceae	*Rubus moluccanus*					y
Rosaceae	Sp.			y		
Rubiaceae	*Adina microcephala*	soaravy		y		
Rutaceae	Sp.			y		
Salvadoraceae	*Salvadora angustifolia**	sasavy, tanisy				y
Sapindaceae	*Litchi chinensis*				y	
Sapotaceae	Sp.				y	
Sarcolaenaceae	Sp.				y	
Smilacaceae	*Smilax* sp.					y
Solanaceae	*Solanum* cf. *orianthum*				y	
Solanaceae	*Solanum* sp.	hazonosy			y	y
Solanaceae	*Solanum mauritianum*					y
Sterculiaceae	*Dombeya* sp. 1			y		
Sterculiaceae	*Dombeya* sp. 2		y			
Tiliaceae	*Grewia cyclea**	selimpasy			y	y
Tiliaceae	*Grewia grevei**	seliboka			y	y
Tiliaceae	*Grewia saligna*					y
Tiliaceae	*Grewia tulearensis**					y
Tiliaceae	*Grewia* sp. 5				y	
Tiliaceae	*Grewia* sp. 6	sely			y	
Tiliaceae	*Grewia* sp. 7				y	
Ulmaceae	*Celtis bifida**	tsiambanilaza				y
Ulmaceae	*Celtis philippensis*		y		y	
Ulmaceae	*Trema* cf. *orientalis*	andrarezo-rezina	y	y		

[a]Endemic to Madagascar.

* = observations suggest bat-pollinated.

Dietary studies conducted at different locations in Madagascar have produced strikingly dissimilar results. In a fragmented humid littoral forest in southeast Madagascar, Bollen and Van Elsacker (2002) found that *P. rufus* fed on 40 plant species in 27 genera, belonging to 21 families, mainly Rubiaceae (*n* = 8), Euphorbiaceae (*n* = 5), and Moraceae (*n* = 3). Less than 100 km away, in a 200-ha fragment of dry gallery forest constituting the Réserve Privée de Berenty, surrounded by 30,000 ha of sisal (*Agave sisalana*) and some remnant spiny bush, the dietary breadth was much narrower, with 17 species, and none of those eaten in the littoral forest (Long and Racey 2007). At Berenty, sisal pollen was the most important item in the diet, which consisted of a mixture of native and endemic forest species (*Tamarindus indica*, *Celtis philippensis*, *Ficus megapoda*, *F. grevei*, *F. pachyclada*, and *Grewia* spp.), as well as locally cultivated and introduced fruits (*Mangifera indica*, *Psidium* cf. *cattleianum*, *Poupartia caffra*, *Cordia sinensis*, and *Cereus* spp.). In terms of percentage occurrence, pollen represented 40% of the diet of *P. rufus*, leaf material 22%, fruit 16%, and the remainder classed as unknown. Sisal pollen consisted of 36% of protein by dry mass, and the bats extracted 73% of it (Long 2002), an efficiency that matches that of blossom bats and pygmy possums in Australia, which have evolved as flower specialists (Law 1992).

The question arises in all diet studies across the geographic range of *Pteropus*, where dietary breadth varies from 17 species recorded in the Berenty study to 52 species recorded for *P. mariannus* in the Mariana Islands (Wiles et al. 1997), as to whether *Pteropus* eat all available foods or display some preference. Comparisons of availability and use at Berenty revealed that some foods were eaten whenever they occurred, like sisal pollen and presumably also nectar; tamarind (*T. indica*) leaves and fruit; mango (*M. indica*) fruit; *F. polita*, *F. grevei*, and *F. pachyclada* fruit; and *Eucalyptus* flowers. Plants such as *Celtis* (leaves and fruit) were eaten in most months that they were available, but were not consumed in other months, suggesting some level of preference. The bats also made transient use of species such as *Cordia sinensis* (Long 2002). Together the data suggest that *P. rufus* is a generalist that feeds on flowers, fruits, and leaves of native and introduced plants, and this apparent plasticity facilitates its survival in deforested landscapes occupied by human settlements and plantations (Jenkins et al. 2007a).

Effect of Frugivory on Germination Rate of Seeds

The fruits of many trees are adapted to attract frugivores to facilitate seed dispersal. Flying bats sometimes carry large drupes, but dispersal is mainly through the defecation of ingested seeds or ejecta from seeds spat out at the feeding site or nearby consumption sites in boluses of fibrous plant material. In addition to the act of dispersal, the bats may assist the fitness of the plants by increasing the germination rates of seeds passed through their alimentary tracts. Passage of seeds through bats or lemurs (or spat out by feeding bats) had a positive effect on germination compared to seeds taken from intact fruit

Table 13.3. Differences in proportion of germinated seeds from different origins, 4–6 weeks after sowing

	Seed origins			
Plant species	**Bat feces**/ ripe fruit	**Bat ejecta**/ ripe fruit	**Lemur feces**/ ripe fruit	**Bird feces**/ ripe fruit
Ficus baroni	+E			
Ficus pyrifolia	+E			
Ficus grevei	+P	+P		
Ficus megapoda	+P	n.s.		
Ficus pyrifolia	+P*	+P		
Ficus menabeensis	+P	+P	+Lc	—
Ficus madagascariensis	+P*	n.s. ?		
Ficus antandronarum	+P*	n.s. ?	+Lc	
Ficus humbertii	n.s. ?	n.s. ?		
Ficus sp. 10		+E	+Pv, +Lc	—
Psidium guajava	+P			
Maerua filiformis	+E			
Talinella grevei	+E, +P			
Grewia grevei	+E			
Grewia cyclea	+E			
Grewia saligna	n.s. (E)			
Grewia tulearensis	+E			
Gymnosporia polyacantha	+E		+Lc	
Aphloia theiformis	n.s. (E)			
Solanum mauritianum	n.s. (E)			

Note: + indicates that the proportion of seeds that had germinated after 4–6 weeks was significantly higher for those from the source in **bold** than that of seeds from ripe fruit. — indicates that a significantly lower proportion of the source in bold had germinated. N.s. indicates that there was no significant difference. A blank cell indicates that no test was carried out. Where seeds of more than two sources were tested, * indicates that a significantly higher proportion of seeds germinated from the first source stated in the column, compared to seeds from any other source tested. Bat feces were collected from *Pteropus rufus* (P) and *Eidolon dupreanum* (E). Lemur feces were from *Lemur catta* (Lc) and *Propithecus verreauxi* (Pv.) Bird feces were from *Treron australis*. $n = 10$ samples each of 10 seeds for all but *Ficus megapoda*, where $n = 6$ samples, each with 10 seeds.

(table 13.3; P. A. Racey and J. L. MacKinnon, unpublished data); the proportion of seeds that germinated 4–6 weeks after planting was significantly higher than seeds taken from ripe fruit for 16 of 20 (80%) plant species. For all four plant species for which seeds were also obtained from feces of lemur species (*Lemur catta* and *Propithecus verreauxi*; table 13.3), there was also a higher germination rate than seeds planted from ripe fruits. For one of these four species, *Ficus antandronarum*, the positive effect was significantly higher in the case of seeds from bat feces than for seeds from any other source.

Evidence that seeds voided through feces or handled and spat out by Megachiroptera germinate in field conditions is sparse, although there are numerous observations that the plants growing beneath *E. dupreanum* cliff roosts and *P. rufus* tree roosts differ from those comprising the surrounding vegetation (e.g., Picot 2005). We know that the bats eat the fruit and swallow the seeds, and that the defecated seeds are viable and germinate, but there is virtually no information from Madagascar on patterns of seed dispersal from the moment the bat removes the fruit from the plant to when it alights in its day roost. Unknown features of seed dispersal represent priorities for research on the island and include aspects such as gut retention times, the contribution of seeds dispersed in the mouth, defecation patterns in flight, and the dispersal of invasive plant species.

Malagasy Megachiroptera as Pollinators

The role of *Eidolon helvum* in pollinating the silk cotton tree or kapok *Ceiba pentandra* has been suggested in Africa (Baker and Harris 1959) and in India (Singaravelan and Marimuthu 2004). Andriafidison et al. (2006b) have extended these observations to *E. dupreanum* and *Pteropus rufus* on Madagascar, where the introduced kapok tree is still used as a commodity in the west, although it no longer has an export value.

Madagascar has six endemic baobab species (*Adansonia*), three of which are endangered (IUCN 2006), and Baum (1995) suggested that megachiropteran bats play an important role in pollinating two species. Andriafidison et al. (2006b) report that *E. dupreanum* was the only mammal visiting the endangered *A. suarezensis*. *E. dupreanum* and two species of lemur, *Phaner furcifer* and *Mirza coquereli*, made nondestructive visits to flowering *A. grandidieri*, which is also endangered, making them potential pollinators. Lemurs cannot climb baobab trunks because of the smoothness of their bark, and must enter the trees from adjacent trees. Therefore, in circumstances where *A. grandidieri* is isolated from other trees, *E. dupreanum* may be the sole animal pollinator, and maintains the reproductive cycle of this species as *E. helvum* does for *A. digitata* in mainland Africa (Baum 1995).

The role of Malagasy fruit bats in pollination and the contribution of nectar and pollen to their diet have yet to be fully documented. For example, Bollen and Van Elsacker (2002) did not include an assessment of pollen consumption in their detailed study of the diet of *P. rufus*. By comparison, Ratrimomanarivo (2003, 2007) identified 23 different plants from pollen grains in her study of the diet of *E. dupreanum*. Further field research is likely to reveal the role of Megachiroptera in the pollination of many more Malagasy plants. The strongest candidate for such pollination is *Rousettus madagascariensis*, because of its ability to hover when feeding on nectar, which causes less damage to the reproductive parts of flowers than alighting on them. Start (1972) observed *R. aegyptiacus* visiting *A. digitata* on mainland Africa, and *R. madagascariensis* feeds on the nectar of kapok and cultivated bananas (*Musa* spp.) (R. Andrianaivoarivelo, pers. comm.). Thus, as a relatively small fruit bat capable of flying inside closed canopy forest, *R. madagascariensis* is potentially an important pollinator in Malagasy forests.

Landscape Species

Madagascar's fruit bats move between roosts presumably in response to changing food supply and, particularly for the two larger species, because of human disturbance (Long 2002; Jenkins et al. 2007a). These dispersal aspects, perhaps across considerable distances, make it difficult to delineate the habitat types and structures necessary for their survival within protected areas, which on Madagascar tend to be relatively small. Other endemic land mammals are restricted to relatively intact forests, which provide either a natural (largely untouched habitat, geological formations, or rivers) or anthropogenic (reserve boundary) limit to where conservation is focused.

Conservation actions associated with Madagascar's fruit bats should take into account their interaction with the landscape, in terms of both roosting and feeding requirements. Additional field research is needed on all three Malagasy fruit bats to better understand their landscape ecology (sensu Sanderson et al. 2002). In particular, more information is required on roost dynamics and on the location of foraging sites. While many studies have described the diet of *Pteropus rufus* from feces collected at roosts, very few have identified the sites where the bats actually feed. A successful landscape approach would involve conservation of roosts used by a local population of fruit bats in combination with long-term protection of feeding sites.

Natural Disasters and Disease

Cyclones have adverse and long-lasting effects on tree-roosting bats such as *Pteropus* (Racey and Entwistle 2003). Three hundred and sixty two cyclones occurred in Madagascar between 1920 and 1972 (Ganzhorn 1995), and some of these are likely to have had severe impacts on *P. rufus*. The numbers of these bats in Berenty was apparently reduced by storms at the end of November 1999 and by the first cyclone of 2000 (E. Long, pers. comm.).

Recent virological research on Malagasy fruit bats has revealed that individuals of all three taxa test positive for antibodies against Nipah, Hendra, and Tioman viruses (Iehlé et al. 2007). These viruses are responsible for emerging diseases in Southeast Asia that have important detrimental effects on local humans (Reynes et al. 2005), although the epidemiological implications on Madagascar are unknown. In parts of Africa and Asia, large fruit bat colonies are not uncommon within villages and cities, and day roosts are often close to temples, houses, parks, and agricultural areas. This is in notable contrast to Madagascar, where fruit bat day roosts are virtually unknown close to human settlements, presumably because there is considerable hunting pressure on these animals. However, the zoonotic transfer of these different viruses to humans through residual bat saliva, urine, or feces remaining on unwashed fruits may be important. Little is known about the negative aspects of these viruses on the bats themselves. Clearly, this area of research needs to be examined.

The Conservation of Malagasy Megachiroptera

Malagasy fruit bats are under severe pressure from human predation and habitat loss in many parts of the island, and *Pteropus rufus* is listed as vulnerable by the IUCN. MacKinnon et al. (2003) reported that 27 of 154 *P. rufus* sites

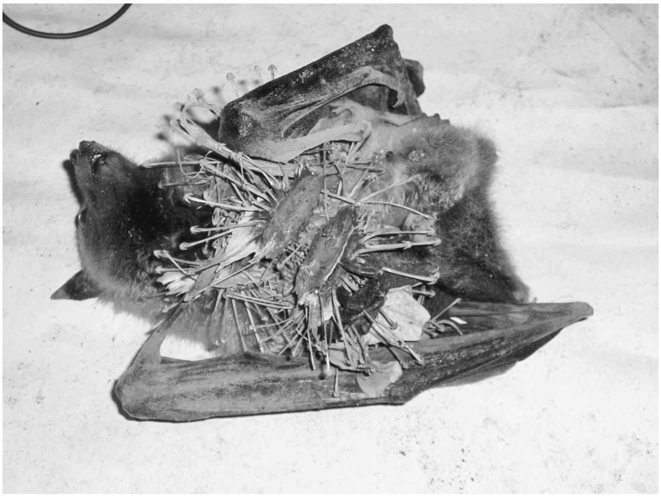

Figure 13.1. *Pteropus rufus* snared in the burrs of *Uncarina grandidieri* placed in flowering kapok *Ceiba pentandra*. Photo by D. Andriafidison.

surveyed (17.5%) had been abandoned in the previous ten years, mainly as a result of hunting with guns, although in some areas, abandonment coincided with felling of roost trees to hunt bats. Although few *P. rufus* roosts are recorded in reserves and parks, traditional beliefs have protected bats in some areas, because it is generally forbidden for Muslims to eat bats and taboo for some cultural groups (e.g., the Mahafaly and the Antandroy). However, increased mobility and the extent of human migration on the island means that some hunting of bats occurs in most areas surveyed.

Fruit bats are hunted at roosting and feeding sites using different methods. Setting nets around trees that are flowering or fruiting is a principal method of subsistence and commercial hunting for *P. rufus* in the west during the dry season, and the nectar-rich kapok is a preferred netting site. Nets have also been observed set high in the forest canopy, near roosting bats (Jenkins et al. 2007a). People also catch bats by placing bundles of *farehitra* (*Uncarina grandidieri*) fruits in feeding trees (fig. 13.1), the fishhooklike barbed spines of which snag their wings. All three fruit bat genera are also targeted by slingshot-wielding children when they feed on kapok flowers in the west. A particularly distinctive method of hunting *P. rufus* involves almost completely felling a roost tree. The hunter returns the following day when the bats are perched in their roost and quickly cuts through what remains of the bole, and as the tree falls bats are killed or stunned. *Eidolon dupreanum* are smoked out of cave or crevice roosts by fires lit directly underneath, and emerging bats are either hit with sticks or netted. *Rousettus madagascariensis* is potentially highly vulnerable to hunting at its roosts because locally produced traps can achieve high capture rates as the bats emerge from cave roosts or visit en masse trees with ripening fruits.

Madagascar's native land mammals are mostly dependent on the remaining areas of intact forests. High rates of deforestation combined with nearly unparallel levels of endemism have been used to categorize the country as an international biodiversity hot spot (Brooks et al. 2002). As noted above, Malagasy fruit bats do not conform to this conservation paradigm because, although the bats are endemic, they often survive in small areas of native or planted forest and sometimes in close proximity to humans.

Conservation of Malagasy fruit bats is therefore a major challenge because it poses a series of unique situations and obstacles to conservationists. The main conservation issues facing fruit bats in Madagascar include low levels of awareness by people about their local bat fauna, damage to roosts, Malagasy wildlife law, and the absence of a monitoring protocol, which could detect population fluctuations. These are discussed in more detail below.

Awareness

Because bats have been absent from the education, training, and conservation agendas in Madagascar, many professionals in the environment sector do not have access to adequate information about their diversity, ecology, and conservation. Bats are rarely treated in the same way as other endemic mammals, and only a few organizations explicitly consider bats in conservation plans. The important ecological role provided by fruit bats, in addition to the ongoing harvest for the bushmeat trade, should lead to fruit bats being specifically included in management plans and conservation projects.

A series of awareness-raising activities in operation since 1999 have successfully conveyed the importance of bat conservation to a variety of organizations in Madagascar. This approach needs to be developed and expanded to include both regional workshops and the provision of literature, in French and Malagasy, to the environment and conservation sectors in Madagascar, in addition to site-specific conservation workshops that engage statutory authorities, local communities, and conservationists.

Making environmental education available to the public is another important way of raising the awareness about Malagasy bats. Other islands in the western Indian Ocean have tested a number of different techniques for transferring relevant bat conservation messages to local communities (Trewhella et al. 2005). In Madagascar, education projects are being introduced to children attending rural primary schools in areas with roosting fruit bats (O'Connor et al. 2006).

Damage to Roosting Sites

Although *Eidolon dupreanum* and *Rousettus madagascariensis* face relatively few threats at their roost sites other than hunting, *Pteropus rufus* is vulnerable to other forms of disturbance. The latter species' reliance on large trees makes its roosts susceptible to wildfire, timber extraction, and loss of sites to expanding agriculture. Once *P. rufus* roosts are destroyed, the bats must find alternative sites. Given that *P. rufus* shows strong roost-site selection, the loss of any extant roosts may cause major disruption to local populations.

Malagasy Wildlife Law

Madagascar's animal species are listed under three categories in legislation that was updated in 2006 (Décret No. 2006-400; Durban 2007). Category 1 provides the highest protection, and the species on this list either receive full protection from hunting and collecting (class 1) or can be exploited with authorization from the relevant authority (class 2). Category 2 represents crop pests, which can be legally killed throughout the year and consists of introduced species (with the possible exception of bush pigs, *Potamochoerus*). Madagascar's fruit bats are listed as game species in category 3 and their hunting, while legal, is subject to restriction based on season (1 May to 1 September) and a valid authorization. Thus, despite being considered threatened species by the IUCN, *P. rufus* is legally hunted in Madagascar and restrictions on hunting category 3 species are difficult to enforce. However, the updated 2006 Malagasy wildlife law should be viewed as a positive development, especially the newly defined hunting season for fruit bats, and it offers considerable potential for further refinements.

Human-Bat Interface

Fruit Depredation

As prodigious consumers of fruit, Malagasy Megachiroptera can come into conflict with subsistence farmers and commercial fruit producers. Malagasy law allows the killing of fruit bats and other animals during any season (i.e., outside of the hunting period) if they are believed to threaten or damage economic livelihoods, people, or livestock. Local communities should request authorization for killing the animals from the Ministre de l'Environnement, des Eaux et Forêts, which should also supervise the operation, which cannot be undertaken at night, with the use of fire, or within protected areas. The consumption of the killed animals as bush meat is decided by the local community. This law permits culling operations during the day, which for fruit bats inevitably means roost disturbance, but outlaws killing at night while they feed on fruit crops. Field research to quantify the loss of commercial fruits to Megachiroptera is urgently required. Predation of fruits, such as litchi (*Litchi chinensis*) and mango (*Mangifera indica*) by Megachiroptera need not necessarily impinge on livelihoods. For example, a pilot study in western Madagascar found that *P. rufus* preferred ripe mangoes while villagers collected only unripe mangoes (P. A. Racey unpublished data). Natural losses of fruit to wind and rain, and the impact of birds and certain lemur species must also be considered before blaming bats for reduced harvests. A scientific appraisal could be used to better inform local communities and government about the actual impact of fruit bats. If fruit bats are major pests, then mitigation measures could be developed by fruit producers and bat conservationists working together. In reality, aggregations of foraging Megachiroptera on fruiting trees are a relatively accessible source of additional protein for local people, so that, under current socioeconomic conditions, mitigation measures may be realistic at only a few sites.

Sport Hunting

All of Madagascar's game species, including the three fruit bats, can be legally hunted for sport. A permit from the Ministre de l'Environnement, des Eaux et Forêts is required for all hunting regardless of the method used, and those who apply to hunt with a firearm must already be in possession of a valid shotgun license from the provincial authorities (rifles are only issued to high-ranking officials, military, or police). Although the Malagasy authorities may want to curtail sport hunting, it will be difficult to do so because of the lack of distinction between hunting bats for sale to commercial outlets or for local consumption. Perhaps the best solution would be to outlaw the use of guns for hunting roosting bats.

Bats as Bush Meat

Fruit bats are a popular source of meat in many parts of Madagascar. They are hunted for both local subsistence and for commercial purposes. In some parts of Madagascar, such as the southeastern towns of Vangaindrano and Farafangana, fruit bats are regularly the "plat du jour" in small restaurants (*hotely*) (fig. 13.2). In most cases, these animals come from local hunters and sometimes from commercial hunters. According to Malagasy law, authorization for large-scale hunting is required from the Ministre de l'Environnement, des Eaux et Forêts, and a report of the actual numbers of animals obtained under each permit must be submitted to the ministry within one month after the closure of the hunting season.

Bushmeat hunting is a threat to bats because exploitation rates may exceed rates of reproduction and the practice disrupts roost sites. Typically, the larger fruit bat species produce one young per female per year (Racey and Entwistle 2000), and puberty in *Pteropus* is typically achieved at one to two years of age and in *Rousettus* at between seven months and a year (Hayssen et al. 1993). It is likely that puberty in *Eidolon* occurs at an age similar to *Pteropus.*

It is difficult to obtain accurate data on the numbers of bats taken by hunters. In one questionnaire survey of 13 villages on the central western coast, between Morondava and Belo sur Tsiribihina, there was an average of five groups of hunters per village, each group taking approximately six *P. rufus* per night for 17 days during the 45-day flowering period of the kapok tree. Given these data, each village took an estimated 500 bats per year, and overall the 13 villages annually accounted for 6,500 bats (Razakarivony 2003).

In the Boeny region of western Madagascar, hunters informed a survey team in 2006 that a group of eight men visit the local *P. rufus* roosts two or three times a week. The bats were trapped in nets placed close to the roost, and after approximately 100 were captured, they were taken to nearby markets and sold for the equivalent of US$0.50 each to local restaurants (Rakotoarivelo and Randrianandrianina 2007). The owner of a roadside restaurant near Mahajanga in western Madagascar, with a reputation for serving fruit bats, mentioned that in 2000 about 30 *P. rufus* were served per day (fig. 13.3). At numerous village restaurants in western Madagascar, live fruit bats can be found waiting processing and distribution.

Because of its habit of occupying day roosts in fissures on cliff faces or deep in caves, the slightly smaller *Eidolon dupreanum* is more difficult to hunt than *P. rufus*. However, at numerous sites *E. dupreanum* are often smoked out by hunters and subsequently abandon their roosts. Thirty percent of the 60 roost sites surveyed 1999–2001 had been abandoned because of hunting (MacKinnon et al. 2003).

Information on the hunting of *R. madagascariensis* is sparse although reported harvests from two roosts in the Makira Plateau by local people were considered unsustainable (Golden 2005). Some specific information exists from Île Sainte-Marie on the exploitation of this species (Rakotonandrasana and Goodman 2007). A colony of approximately 200–300 individuals, before the

Figure 13.2. Cocotte of cooked *Pteropus rufus* at the ferry terminal to Belo sur Tsiribihina. Photo by P. A. Racey.

Figure 13.3. Panniers full of live *Pteropus rufus* awaiting preparation for the table at a hotel near Morondava. Photo by J. L. MacKinnon.

breeding season, was observed in a cave on the eastern side of the island, and this species is hunted by local people for their popular meat. Based on interviews with a local guide, who is one of the exploiters of this resource, bat hunters from different parts of Île Sainte-Marie visit this cave during the months of November to December and May when the bats are "notably fat." The principal method for their capture, which involves four to five people, is for two hunters to enter the cave and throw wood sticks about 60 cm long toward the area of the cave ceiling with roosting bats. Wounded individuals fall to the ground and are collected. The other hunters remain at the relatively small mouth of the cave with waving tree branches to inhibit the bats from leaving, and at the same time wounding other individuals that encounter the branches. Each "hunt" lasts for up to 1 hour and may yield between 30 and 40 individuals. During the hunting months, the cave may be visited up to once a week, hence an estimated 360–480 bats may be taken locally each year.

Trade

Small numbers of living Malagasy fruit bats are exported every year, presumably for the zoo trade, and this form of utilization comes under commercial exploitation in the national legal system and is subject to an export permit. As *P. rufus* is on appendix II of CITES, international trade is controlled and requests for export are authorized by the CITES scientific authority in Madagascar.

Conservation Status of Malagasy Fruit Bats

A major challenge facing bat conservation in Madagascar is to establish monitoring programs that can be used to better assess patterns of population fluctuation in fruit bats. Conservationists often use the IUCN Red List as an international standard for assessing the conservation status of species. The categories used to assign levels of threat include an often complex classification system (www.iucnredlists.org) based on aspects of the following parameters: (1) an inferred, observed, or suspected decrease in the population size of a given species; (2) a small geographic range; (3) small population size; and (4) a high probability of extinction as shown by quantitative analyses.

Fruit bats in Madagascar are widespread and are therefore, based on this four-point classification, only likely to be ranked as a threatened species based on information about population decline. In the 2005 Global Mammal Assessment, held in Antananarivo, *P. rufus* was classed as vulnerable A2acd and *E. dupreanum* as A2abcd. The A2 represents a population decline of more than 30% in the last 10 years and the subcategories refer to (a) direct observation, (b) indirect observation or index, (c) occurrence or habitat quality, and (d) levels of exploitation. For land mammal species dependent on relatively intact forests, population trends can be extrapolated from changes in vegetation cover, but this is not the case for fruit bats.

Although methods (evening-dispersal counts or day-roost counts) are available to estimate the population size of foliage-roosting fruit bats such as *Pteropus*, monthly variation in both occupancy and abundance raises concerns about the use of such snapshot surveys for reliable assessment of population size. *Rousettus madagascariensis* are difficult to count accurately in their roosts, but they can be easily caught and marked as they exit cave roosts. *Eidolon dupreanum* are difficult to observe or catch, and population estimates are complicated to obtain, although some roost sites do offer biologists the possibility of capturing emerging bats.

Three types of data should be collected at Malagasy fruit bat roosts on a regular basis, if the IUCN Red List criteria are to be applied with more confidence in the future: presence/absence of the bats, an estimate of population size using a consistent technique and observers, and actual or impending threats. In order to collect the appropriate data for future assessments, specific measures need to be taken by field research teams. We recommend the following:

1. Monitor the abundance of *P. rufus* at day roosts on a regular (e.g., monthly) basis in different regions.
2. At sites where demand for fruit bat meat is highest, work with local hunters and communities to properly assess the levels of exploitation and population size.
3. Monitor the frequency of hunting activities at roosts. Signs of hunting include used shotgun cartridges, fire (in caves or under cliffs), nets, throwing sticks, and long poles used to elevate nets.

The Future of Fruit Bat Conservation

Upgrading Malagasy fruit bats to protected species under Malagasy law (category 1, class 1) may be a desirable option. However, this action alone would be unlikely to achieve the desired impact of species conservation, because the consumption of bat meat has a strong tradition in many regions of Madagascar and significant resources would be required to encourage cultural change. In reality, this option may become tenable only if the species appears to move closer toward extinction in the wild. However, if additional field studies reveal a continuing decline in fruit bat populations, recommendations can be made to place certain species on the protected list (category 1, class 2). This would have the advantage of prohibiting sport hunting and of more closely monitoring and controlling exploitation levels by setting quotas that can be reflected in the number of permits issued. *Pteropus rufus* is currently one of only a few CITES appendix II species on Madagascar that are listed as game (class 3), and most of the other taxa fall under category 1, class 2. Potential revisions to the legal status of Malagasy fruit bats must be based on scientific assessments and a national roost-monitoring project. An investigation of bats as bush meat and a study on fruit depredation are needed.

There is also considerable potential to augment the conservation measures for fruit bats in other ways: (1) ensuring no hunting at day roosts within protected areas; (2) including fruit bat roosts within the boundaries of new protected areas; and (3) creating special protected areas for fruit bats, either through formal reserves or the establishment of local laws (*dina*) in areas where communities wish to conserve their fruit bats. Options 2 and 3 offer the possibility of sustainable management of *P. rufus* colonies sufficiently large to provide local communities with meat through site-specific restrictions on hunting quotas, periods, and methods.

Ecology of Microchiroptera

Microchiroptera contribute about one-third of Madagascar's nonmarine mammal fauna (Goodman et al. 2008b). On the basis of the current understanding of the island's microchiropteran fauna, some species are found across most of the island, others occur in specific biomes, and only a few appear to be geographically localized. Studies on the ecology of these animals have certainly lagged behind taxonomic research, which hinders reliable assessments of their conservation status. Below we summarize available ecological information for Malagasy microchiropterans based on their distribution, roosting requirements, diet, and foraging habitat.

Distribution of Malagasy Microchiroptera

Some species (ca. one-third) are widespread on Madagascar, but most are restricted to certain parts of the island, probably in association with habitat or bioclimatic conditions. The eastern chain of mountains is aligned along a north-south axis, which accounts for major differences in rainfall and vegetation between the eastern and western parts of the island, and numerous bat taxa appear to be restricted to one side or the other. Based on a recent ecomorphological study, microchiropteran species that have broad distributions across the western drier parts of the island, which shows extensive bioclimatic differences, show little clinal variation in size (Ranivo and Goodman 2007a). Further, there is considerable variation in the phylogeography of certain groups. For example, *Triaenops furculus* shows a strong correlation between haplotypic structure and latitude, while the congener *T. rufus* expresses considerable haplotypic variation, which does not seem to be correlated with geographic factors (Russell et al. 2007). Hence, these two aspects give the impression that, for certain taxa, there are still considerable dispersal movements across their geographic distributions, or in recent geological times there was substantial population growth and range expansion.

Species restricted to the western flank of Madagascar include *Emballonura tiavato*, *Scotophilus marovaza*, and *T. furculus*, and three additional taxa, *Chaerephon jobimena*, *Otomops madagascariensis*, and *Mops midas*, also occur in the drier lower southwestern area of the Central Highlands (Eger and Mitchell 2003; Goodman and Cardiff 2004; Goodman et al. 2005a; Goodman et al. 2006a; Goodman et al. 2006b). *Chaerephon leucogaster* shares a broadly similar distribution to the preceding species, but it is also recorded from the humid northeast.

Species with more restricted distributions include *S. tandrefana* (Goodman et al. 2005b) and *Pipistrellus hesperidus* in the southwest (Bates et al. 2006), *T. auritus* (Ranivo and Goodman 2006; Russell et al. 2007) and *Nycteris madagascariensis* in the north (Peterson et al. 1995), *C. afra* to the northwest (Goodman et al. 2005a; Goodman et al. 2008a), *M. schliemanni* to the midwest (Goodman et al. 2007a; Rakotoarivelo and Randrianandrianina 2007), *Tadarida fulminans* to the south central and southeast (Jenkins et al. 2007b), and *Neoromicia malagasyensis* to the area around the Isalo Massif in the southwestern Central Highlands (Goodman and Ranivo 2004; Bates et al. 2006).

Species that have been found only in the eastern humid forest zone are *Myzopoda aurita* and *Emballonura atrata* (Goodman et al. 2006a; Goodman et al. 2007a) and *Neoromicia melckorum* (Bates et al. 2006). Taxa with distributions that extend across the east-west divide and thus potentially occur over a large area, and in some cases are also very common, include *Taphozous mauritianus*, *Hipposideros commersoni*, *Pipistrellus raceyi*, *Miniopterus manavi*, *Mi. majori*, *Mi. gleni*, *Myotis goudoti*, *Scotophilus robustus*, *Chaerephon pumilus*, *Mormopterus jugularis*, and *Mops leucostigma*. There are also cases of eastern species that occur in parts of the Central Highlands (e.g., *Eptesicus matroka*) and western species with their eastern limit in the Central Highlands (*Mops midas*).

On a coarse scale, it appears that there are both north-south and east-west influences in the geographic distribution of the microchiropteran community. Species that are restricted to the north or south tend to have smaller ranges than those associated with eastern and western areas. Further survey work and

Figure 13.4. *Myzopoda aurita* on a banana leaf at Kianjavato, eastern Madagascar. Photo by P. A. Racey.

associated genetic studies are needed to understand aspects of the evolutionary history of speciation and, in particular, to map distributions on a finer scale so that the influence of biotic and abiotic factors on these patterns can be better understood (e.g., Ratrimomanarivo et al. 2008).

Roosting Requirements

Eger and Mitchell (2003) divided the different types of bat roosts into foliage, hollows (trees or caves), and crevices. Apart from the megachiropteran examples of *Pteropus rufus* and *Eidolon dupreanum* (see above), there are few records of foliage roosting in Malagasy bats. *Myzopoda aurita* is a foliage-roosting species using the large leaves of *Ravenala madagascariensis*—this is based on an observation in 1947 (cited in Schliemann and Maas 1978), notes on the behavior of a captive individual (Göpfert and Wasserthal 1995), and recent radio-tracking studies in the east (P. A. Racey, unpublished data). The distinctive suckerlike pads on the wrists and ankles of the bat are used for clinging to the leaves of plants, but in light of recent observations of *M. schliemanni* roosting inside a cave (Kofoky et al. 2006), more information into the roosting ecology of *Myzopoda* is needed (fig. 13.4).

Most information on the roosting preferences of Malagasy microchiropterans comes from caves and buildings, structures that can be readily surveyed by biologists (e.g., Ratrimomanarivo et al. 2007; Ratrimomanarivo et al. 2008). *Hipposideros commersoni* roosts in buildings, tree foliage, and caves. In Madagascar, *Taphozous mauritianus* roosts in buildings, crevices, and rock formations and on tree trunks, whereas in mainland Africa it also uses the outside walls of buildings (Skinner and Chimimba 2005). Bats thought to be obligate cave dwellers (including rock crevices and drainage pipes) include *Miniopterus gleni*, *Triaenops rufus*, *T. furculus*, *T. auritus*, *Otomops madagascariensis*, *Myotis goudoti*, and *Emballonura atrata*. In the Parc National de Kirindy-Mite, two microchiropteran species, *Miniopterus manavi* and *Mops leucostigma*, were found roosting in a large hollow in a baobab tree, *Adansonia grandidieri* (Andriafidison et al. 2006a). In the same park, *Mops midas* and *M. leucostigma* roosted in the canopy of coconut palms (Andriafidison et al. 2006a), and *Chaerephon leucogaster* was found under the bark of a dead tree (Goodman and Cardiff 2004).

Most molossids in Madagascar, however, roost in caves, rock crevices, or buildings (Goodman and Cardiff 2004). A distinct colonial architectural style of single-storied civic or municipal concrete buildings, such as schools, offices, and hospitals, has a suspended ceiling, separating the attic from the main floor, to which bats gain access through aeration holes in the roof soffit. *Mormopterus jugularis* is a common synanthropic bat across much of Madagascar (Goodman and Cardiff 2004; Andrianaivoarivelo et al. 2006). Other species such as *Chaerephon pumilus*, *C. leucogaster*, and *Mops leucostigma* also regularly occur in synanthropic settings and often roost together in the same roof cavity (Goodman and Cardiff 2004). In contrast to these other molossids, *Otomops madagascariensis* is known only from caves, whereas the closely related *O. martiensseni* around Durban, South Africa, is found only in buildings (Fenton et al. 2002).

Madagascar has four known species of *Scotophilus* (Goodman et al. 2005b; Goodman et al. 2006b). Across its African and Asian range, this genus is commonly known as "house bat," but only recently on Madagascar have roosts of two *Scotophilus* species been located in buildings (Ratrimomanarivo and Goodman 2005); the roost sites of *S. tandrefana* and the possibly extinct *S.* cf. *borbonicus* are unknown. *S. marovaza* roosts in dense layers of palm leaves (*Bismarckia nobilis*) used for roofing buildings, and it is likely that the bats naturally use leaves of standing palms. *S. robustus* in eastern Madagascar have been found during the day in cavities within the brick and clay walls of buildings, a type of roost likened to natural cavities in rocks or trees (Ratrimomanarivo and Goodman 2005). Similar diversity of roost types occur in African *Scotophilus* species, where some species, such as *S. viridis*, often roosts in tree cavities and others, such as *S. dinganii*, roost in buildings (Skinner and Chimimba 2005).

Manmade structures thus provide suitable roosting habitats for many Malagasy bats, such as palm-roof huts, brick cavities, and spacious attic spaces of concrete buildings. As modern buildings became common, following colonization by Europeans, bats associated with concrete structures seem to have benefited while those relying on palm roofs have probably declined in more urbanized areas. In many cases, particularly for certain molossid species, the individuals occupying concrete-building roost sites certainly outnumber those in known natural rock shelters. This begs the question whether bats using natural roosts have shifted to these manmade structures or there has been a subsequent increase in population associated with the colonization of these buildings.

Over the next decades, many of the civic and municipal buildings with classical colonial architecture will become dilapidated and be replaced by different architectural styles. Further, there is a tendency in buildings occupied by bats for the false ceilings to be removed, which in turn forces the bats to occupy other day-roost sites. What impact these changes will have on molossid populations remains to be seen, but the use of custom-built bat houses in village and town settings might be considered as a means of maintaining levels of synanthropically dwelling bats and mitigating possible population declines.

The Diet of Malagasy Microchiropterans

In contrast to the island's megachiropterans, there is little information available on the diet of microchiropterans. Surprisingly, despite the abundance of publications using fecal analysis from various parts of the world (e.g., Kunz et al. 1995; Barlow 1997; Rydell and Yalden 1997; Schulz and Wainer 1997; Seamark and Bogdanowicz 2002), little has been published until recently on microchiropteran diet on Madagascar. These studies include a single fecal pellet from *Myzopoda aurita* (Göpfert and Wasserthal 1995) and the stomach contents of 80 voucher specimens of five insectivorous species from western Madagascar (Razakarivony et al. 2005). In the latter study sample sizes were small and sampling periods only a few days at each site, and based on available data the authors concluded that none of the five bat species examined were dietary specialists but rather changed their diet according to insect availability.

Rakotoarivelo et al. (2007) analyzed the diets of five species by fecal analysis based on samples collected over the course of numerous visits across seasons. They found that *Hipposideros commersoni*, *Triaenops rufus*, *T. furculus*, *Myotis goudoti*, and *Miniopterus manavi* often ate Coleoptera, Hemiptera, and Lepidoptera. *H. commersoni* fed mainly on Coleoptera, *T. rufus* and *T. furculus* fed mainly on Lepidoptera, and *My. goudoti* was the only species to have significant representation of Hymenoptera, Neuroptera, and Araneae in its feces. *Mi. manavi* had a more general diet that included more Hemiptera than the other bat species. Although Diptera were the most abundant insects trapped in the immediate study zone of the dietary study, they were less commonly encountered in feces than Coleoptera, Lepidoptera, and Hemiptera. In addition to differences between species, there was also a significant seasonal shift in dietary composition, particularly for Lepidoptera, which were more prevalent in the diet of all species during November (the beginning of the wet season) as compared to July (the dry season).

In a study of three molossids, *Mops leucostigma*, *Mormopterus jugularis*, and *Chaerephon pumilus*, from about 1,000 m elevation in the eastern part of the island, Andrianaivoarivelo et al. (2006) found high dietary overlap between these taxa and major seasonal changes in dietary composition. As with vespertilionids and hipposiderids in western Madagascar, Hemiptera was an important food source during all sampling periods, with considerable numbers of Coleoptera identified in the scats during the austral summer and Diptera during the austral winter. Therefore, there appears to be a similar seasonal pattern of Coleoptera and Diptera consumption across bat families from sites in eastern and western Madagascar.

A study of fecal pellets of *Myzopoda schliemanni* collected in western Madagascar by Rajemison and Goodman (2007) found that Lepidoptera and Blatteria constituted the majority of this species' diet and Coleoptera and Hymenoptera were notably less common. There was also evidence that this bat is able to glean prey from vegetation.

Foraging Habitat

It is important to know which habitats bats require for foraging in order to assess their dependence on different vegetation types or structural features of the landscape. Goodman et al. (2005a) discussed information on the apparent lack of dependence of different bat species on relatively intact forest habitat and highlighted the importance of caves as roosts.

Kofoky et al. (2007) used mist nets and acoustic methods to assess habitat use by bats in the Parc National de Bemaraha, an area of karst in western Madagascar with natural forest cover. Trapping results indicated that that four microchiropteran species, *Triaenops rufus*, *T. furculus*, *Miniopterus manavi*, and *Myotis goudoti*, were associated with the forest interior. The results, however, were heavily influenced by the location of mist nets, and it is likely that catch efficiency was higher in mist nets set across narrow forest trails than in the more open areas at the forest edge. Surveys at this same site using bat detectors revealed highest rates of activity (Kofoky et al. 2007) and foraging (Rakotoarivelo et al. 2007) at the ecotone between the forest and open nonforested area. Invertebrate sampling with light and malaise traps also indicated the highest abundance of potential prey was at the forest edge (Rakotoarivelo et al. 2007). The results appear to indicate that the bats roosted in caves in the forest, and used forest trails and other access routes to commute to foraging sites located at forest edges. These results are particularly important in relation to the study of Goodman et al. (2005a), who concluded that only 5 of the 27 bat species of western Madagascar might depend on relatively intact forest. The other species were classified as non–forest dependent and, by extrapolation, are unlikely to be seriously affected by a reduction in the extent and quality of the island's remaining natural forests. This conclusion was reached for some species based on their presence in caves located in areas without substantial areas of remaining natural forest. The work of Kofoky et al. (2007) and Rakotoarivelo et al. (2007) indicate that bat-foraging habitats are often associated with forest edges and ecotones.

Randrianandrianina et al. (2006) investigated, in eastern Madagascar, habitat use by bats in a landscape with rain forest and anthropogenic habitats. Mist-netting, acoustic surveys, and roost searches revealed that *Myotis goudoti*, *Emballonura atrata*, *Miniopterus manavi*, and *Mi. majori* were documented in relatively intact natural forest, whereas molossids, *Eptesicus matroka*, and *Neoromicia melckorum* mainly used degraded forest and agricultural habitats. Acoustic evidence of molossids was also detected in the relatively intact forest, but less commonly than in other habitats, suggesting that these bats may forage above the canopy. Capture rates of bats in natural forest was low, and only a single roost site was found inside the two protected areas that were included in the survey. Two of the bat species recorded from degraded habitats outside the reserve were new records for Madagascar, indicating that there is much to learn about species composition and habitat use of its microchiropteran communities. Some Malagasy bats, unlike the island's other endemic land mammals, appear well adapted to survive in human-modified habitats. There is growing evidence that some bat species prefer forests for feeding, although the dense vegetation structure provides limited foraging opportunities and most feeding occurs in gaps or edges.

Conservation of Malagasy Microchiroptera

Even though only one endemic Malagasy microchiropteran species (*Neoromicia malagasyensis*) is currently considered threatened using IUCN Red List criteria based on the Global Mammal Assessment (Schipper et al. 2008), this may be in part associated with the lack of details for other species required for a proper evaluation of their conservation status. In order to rectify this situation and provide greater insight into the steps that might be needed to protect the island's bat fauna, the following aspects need to be addressed:

1. There is currently insufficient data on the use of habitats both spatially (i.e., forest dependency) and temporarily (i.e., roosting dynamics) by a range of bat taxa, and further field studies are needed.
2. Some widely distributed species (e.g., *Otomops madagascariensis*) are known only from a few localities, but whether this is associated with sampling artifacts or reflects genuine uncommonness needs to be investigated. Further field surveys, particularly with bat detectors, are needed, as well as updating and completing the available library of Malagasy bat calls based on recent taxonomic revisions.
3. Some species are widespread and locally common. Bats that aggregate in large colonies at a few sites are potentially vulnerable to many types of disturbance. More detailed information is needed on the location of these sites and population movements. Little is known about dispersal of any species, let alone differences between sex and age classes.
4. Some species face severe hunting pressure but details of off-take, seasonality, and cultural aspects required to evaluate such pressure are lacking.

At least in the drier parts of Madagascar, it appears that geology is an important determinant of chiropteran species richness. Goodman et al. (2005a) found differences in the taxonomic composition of bat communities occurring in areas of exposed sedimentary rock (limestone and sandstone), as compared to alluvial soils, with the highest species richness in limestone karst. This distinction was attributed to the myriad of caves, crevices, fissures, and other cavities present in sedimentary rock. Protected areas harbored up to 16 bat species in Madagascar's karst regions, which are nationally important sites for mammal conservation; management plans for the bats occurring at these sites need to be established. In particular, caves with important roosts must be safeguarded, such as Anjohikinakina in Parc National de Bemaraha (Kofoky et al. 2007) and the caves in Réserve Spéciale d'Ankarana (Cardiff 2006).

Data on hunting of Microchiroptera by humans are even sparser than for Megachiroptera. *Hipposideros commersoni*, the largest microchiropteran species on Madagascar, is often hunted from January to March when they accumulate fat. This bat varies in weight from 32 g to close to 100 g (Ranivo and Goodman 2007b). Goodman (2006) reported heavy hunting pressure on *H. commersoni* in southwestern Madagascar when low food availability resulted in human famine. During episodes of near starvation, hunters cut trails in forest surrounding limestone sinkholes, where the bats roosted, and during the evening emergence, the animals were guided along the trails by fencelike barriers up to 2 m high. Flying bats were hit with whiplike batons and the levels of off-take, up to 30 per night per hunter or about 2,700 per hunting season, are presumably not sustainable even in the short term. The same survey reported hunting of *Mormopterus jugularis* in caves and incidental capture of other species such as *Triaenops rufus* and *Miniopterus gleni*. According to Golden (2005), people living in the Makira Forest in the northeast eat *Miniopterus manavi*, a species weighing less than 8 g, but had a low taste preference for this species.

Under Malagasy law, microchiropterans are collectively placed in the same group as fruit bats and receive no formal protection, except for animals occurring within protected areas. Hunting in some areas poses a clear threat to *H. commersoni*, and this aspect was the main reason for its "Near Threatened" IUCN Red List status during the Global Mammal Assessment (Schipper et al. 2008).

Conclusions

Remarkable advances have been made in the past decade in understanding the chiropteran fauna of Madagascar from the perspective of the species present and their distributions. However, important information is still lacking on aspects of their evolutionary history, systematics, ecology, and vocalizations. Further and more intensive field studies are needed to fill in critical details about ecological constraints associated with population dynamics, dispersal, and geographic distributions; these data are paramount for having a broader view of the fauna and steps needed for its conservation. Further, given the frequency with which taxa new to science are being described from the island, current conservation assessments do not respond fast enough to taxonomic progress and need to be more frequent.

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