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The Bats of Madagascar: A Conservation Challenge

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ABSTRACT

Madagascar has more than 40 recognized species of bats, distributed among seven families, over half of which are endemic to the island, including the family Myzopodidae. While some are recognized as threatened by the IUCN Red List, most of Madagascar's bat species are actually too poorly studied to estimate their conservation status. Further research is needed on the important aspects of bat ecology: roosting patterns and preferences, foraging and habitat use, and diet. Bats perform several important ecosystem services, including pollination and seed dispersal. However, they nevertheless face several common threats such as hunting, persecution, deforestation and disturbances due to tourism and mining. This case study concludes by looking at the conservation outlook for the island's bats.

1. INTRODUCTION

Bats are the only mammals capable of true flight, having membranes that stretch between elongated arm and hand bones, and usually between their legs. In most cases, bats have the ability to echolocate, or produce sound that they can use to perceive their surroundings even in total darkness (Wilson et al. 1996; Fenton 1999). They share this ability with mammals as varied as dolphins, tenrecs, and shrews (Thomas et al. 2004).

Chiroptera, the order of bats, is the mammal order with the second highest number of species after rodents – 1,116 recognized as of 2005, with more described since (Simmons 2005; Goodman 2011). Bats occur on all major land masses except Antarctica (Simmons 2005). Simmons (2005) recognizes 18 families of bats distinguished by notable morphological variations. Feeding habits of bats vary greatly as well. Although most bats feed on insects, other arthropods, or fruit and flower parts, some bats also consume leaves, fish, frogs, blood (a few species in the Americas), birds, and other mammals (Patterson et al. 2003). Foraging behavior and morphological adaptations often vary in accordance with food habits. Various aspects of the fascinating biology of bats have even been the subjects of research for human medical purposes. For instance, bats are extremely long–lived for mammals of their size and research has focused on why this is so, with the aim of understanding aging in humans (e.g., Lambert et al. 2007; Wilhelm et al. 2007). Also, vampire bat anticoagulants may have applications for treating strokes (e.g., Diaz–Ricart 2006).

Evolutionary biologists have traditionally recognized two main groups, or suborders, of bats: Megachiroptera and Microchiroptera (Koopman 1993). The Megachiroptera consisted only of the family *Pteropodidae* (Mickleburgh et al. 1992), or Old World fruit bats, and the Microchiroptera included all other bats (Hutson et al. 2001). Pteropodids differ from other bats in having simple, elongated faces, a claw on their second digit as well as their first, large eyes that reflect light, and not using *laryngeal* echolocation (although species belonging to the genus *Rousettus* use tongue–clicks to echolocate and other Old World fruit bats also use a form of echolocation; Schoeman and Goodman 2012; Boonman et al. 2014). Recent phylogenetic analyses using molecular data suggest that the Pteropodidae are actually members of the revised Yinpterochiroptera suborder, along with several other bat families previously considered Microchiroptera (Teeling et al. 2005; Tsagkogeorga et al. 2013). However, other analyses conducted using both molecular and morphology data indicate that certain previously recognized groups remain valid (Giannini and Simmons 2005; Teeling et al. 2005).

Madagascar possesses a rich community of bats with a high proportion of endemics relative to other islands. The conservation needs of these bats may differ, as well as differ from those of other endemic Malagasy vertebrates. Although we still have much to learn about the ecology and conservation needs of bats, we can identify threats to their survival and strategies that will promote bat conservation on Madagascar. In the following sections, the general aspects of bat diversity, ecology, and survival threats will be discussed with an emphasis on the ecology and conservation needs of bats in Madagascar.

1. BIODIVERSITY

1.1 Richness and Endemism

Bat biologists currently recognize approximately 44 species of bats on Madagascar (Peterson et al. 1995; Goodman and Cardiff 2004; Simmons 2005; Goodman et al. 2005a,b, 2006a,b,c, 2010a, 2015; Goodman and Ranivo 2004; Goodman 2011; Christidis et al. 2014). Studies continue to identify species not previously recorded as present on the island and cryptic species not previously recognized as distinct species (e.g. Christidis et al. 2014, Goodman et al. 2015). The current assemblage is distributed amongst seven families (Table 1).

Several different principles may have influenced the number of bat species observed in Madagascar. For a variety of reasons (e.g., climate, historical stability, greater land mass globally, mid–domain effect), tropical areas generally have more species than temperate areas. Indeed, more bat species tend to occur in the tropics than in temperate zones, and Madagascar's bat species richness is comparable to the larger area of Europe (Stebbings and Griffith 1986).

The principles of species–area relationships and island biogeography may also be operating. Larger areas generally have more species, given their potential for greater habitat diversity. In addition, MacArthur and Wilson (1967) indicated that far fewer species tend to occur on islands because of the reduced likelihood of new species reaching distant islands, and the increased probability of species going extinct in smaller areas. For example, only 18 species of bats occur in the UK, but more than 31 species are found in Europe (Stebbings and Griffith 1986; Altringham 2003). Madagascar, similarly, has fewer species than some continental tropical areas of comparable or smaller size. The smaller neotropical territory of French Guyana, for instance, has over 102 species of bats (Charles–Dominique and Brosset 2001). Although the extent of sampling and recognition of genetically–distinguished cryptic species undoubtedly differs between areas in southern Africa and Madagascar, Mozambique (at a similar latitude, larger, and not far from Madagascar) has approximately 45 bat species; Zimbabwe (smaller than Madagascar) has approximately 61 species; and Namibia (larger than Mozambique), has approximately 26 species of bats (Taylor 2000). Also in accordance with species–area relationships, Madagascar has many more species than the much smaller Comoros archipelago, which only has nine (Peterson et al. 1995; Louette et al. 2004; Goodman et al. 2010b).

Amongst large tropical islands, Madagascar appears to have a predictable level of species richness. A comparable 27 extant bat species, for instance, occur on the neotropical island of Cuba (Silva Taboada 1979; Dávalos 2004) and the whole continent of Australia has only around 75 species (Koopman 1984; Mickleburgh et al. 2002). Perhaps because of historical patterns of diversification, or because of Madagascar's greater distance from other landmasses, higher latitude, or status as an oceanic rather than a continental shelf island, Madagascar has lower bat species richness than many large islands in Southeast Asia. These include Papua New Guinea (92 species; Bonaccorso 1998), Sulawesi (60 species), Borneo (98 species), Java (66 species), and Sumatra (63 species; Koopman 1989). On the other hand, the number of families of bats occurring on Madagascar is comparable to those on New Guinea and Borneo (Eger and Mitchell 2003).

Most of the bats of Madagascar are either endemic to the island or the island plus its immediate neighbors (Table 1). Of the approximately 44 species, 32 (73%) occur only on Madagascar and an additional five species (a total of 89%) occur on Madagascar and other islands in the western Indian Ocean. This level of endemism is slightly lower than that of other mammal groups on the island (Goodman et al. 2003), but it is higher than the 38% endemism exhibited by bird species (Hawkins and Goodman 2003) and is relatively high for a bat species assemblage. Indeed, of countries with more than ten endemic bat species, Madagascar has the highest proportion of endemics (Mickleburgh et al. 2002), and both the number of known endemics and the

Table 1. Distribution and conservation status of bats occurring on Madagascar. Species names and distributions are based on references cited in text and as species description authors. IUCN= International Union for the Conservation of Nature; GMA = draft Global Mammal Assessment (IUCN, unpublished); LC = Least Concern; NT = Near Threatened; DD = Data Deficient; EN = Endangered; VU = Vulnerable.

FAMILY	SPECIES AND AUTHORS	GLOBAL DISTRIBUTION OF SPECIES	DISTRIBUTION IN MADAGASCAR	IUCN STATUS
Pteropodidae	*Eidolon dupreanum* (Schlegel 1867)	Madagascar	Widespread	LR/LC ver 2.3 (1994)
	Pteropus rufus (Tiedemann 1808)	Madagascar	Widespread	VU A2acd ver 3.1 (2008)
	Rousettus madagascariensis (Grandidier 1928)	Madagascar	Widespread	NT ver 3.1 (2008)
Hipposideridae	*Hipposideros commersoni* (Geoffroy 1813)	Madagascar	Widespread	NT ver 3.1 (2008)
	Triaenops auritus (Grandidier 1912)	Madagascar	N	VU B1ab(iii) ver 3.1 (2008)
	Triaenops furculus (Trouessart 1906)	Madagascar + Aldabra + Cosmoledo	W	LC ver 3.1 (2008)
	Triaenops menamena (Goodman and Ranivo 2009; ex. *T. rufus* Milne–Edwards 1881)	Madagascar	N,W,S	LC ver 3.1 (2008)
Emballonuridae	*Coleura kibomalandy* (Goodman et al. 2012) [/ *C. afra* (Peters 1852)]	Madagascar [+ Africa + Arabian Peninsula]	N,W	Not evaluated
	Emballonura atrata (Peters 1874)	Madagascar	E	LC ver 3.1 (2008)
	Emballonura tiavato (Goodman et al. 2006c)	Madagascar	N,W	LC ver 3.1 (2008)
Emballonuridae	*Taphozous mauritianus* (É. Geoffroy 1818)	Madagascar + Africa + Comoros + Mascarenes + Aldabra	Widespread	LC ver 3.1 (2008)
Nycteridae	*Nycteris madagascariensis* (Grandidier 1937)	Madagascar	N	DD ver 3.1 (2008)
Myzopodidae	*Myzopoda aurita* Milne–Edwards and A. (Grandidier 1878)	Madagascar	E	LC ver 3.1 (2008)
	Myzopoda schliemanni (Goodman et al. 2006b)	Madagascar	W	LC ver 3.1 (2008)

Table 1. continued

FAMILY	SPECIES AND AUTHORS	GLOBAL DISTRIBUTION OF SPECIES	DISTRIBUTION IN MADAGASCAR	IUCN STATUS
Molossidae	*Chaerephon atsinanana* (Goodman et al. 2010)	Madagascar	E	Not evaluated
	Chaerephon jobimena (Goodman and Cardiff 2004)	Madagascar	N,W,S	LC ver 3.1 (2014)
	Chaerephon leucogaster (Grandidier 1869)	Madagascar + Africa	Widespread/W	LC ver 3.1 (2014)
	Mops leucostigma (Allen 1918)	Madagascar	Widespread	LC ver 3.1 (2014)
	Mops midas (Sundevall 1843)	Madagascar + Africa + Arabian Peninsula	SW,E (St. Maire)?	LC ver 3.1 (2014)
	Mormopterus jugularis (Peters 1865)	Madagascar	Widespread	LC ver 3.1 (2008)
	Otomops madagascariensis (Dorst 1953)	Madagascar	N,W,S	LC ver 3.1 (2008)
	Tadarida fulminans (Thomas 1903)	Madagascar + Africa	S	LC ver 3.1 (2008)
Vespertilionidae	*Myotis goudoti* (Smith 1834)	Madagascar + Comoros	Widespread	LC ver 3.1 (2008)
	Miniopterus aelleni (Goodman et al. 2009)	Madagascar + Comoros	N,C,W	Not evaluated
	Miniopterus brachytragos (Goodman et al. 2009)	Madagascar	N,E,W	Not evaluated
	Miniopterus egeri (Goodman et al. 2011)	Madagascar	N,E	Not evaluated
	Miniopterus gleni (Peterson et al. 1995)	Madagascar + Comoros	Widespread	LR/NT ver 2.3 (1994)
	Miniopterus griffithsi (Goodman et al. 2010)	Madagascar	S	Not evaluated
	Miniopterus griveaudi (Harrison 1959)	Madagascar + Comoros	N,W	DD ver. 3.1 (2008)
	Miniopterus mahafaliensis (Goodman et al. 2009)	Madagascar	C,S,W	Not evaluated
	Miniopterus majori (Thomas 1906)	Madagascar + Comoros	E	DD ver 2.3 (1994)
	Miniopterus manavi (Thomas 1906)	Madagascar + Comoros	Widespread	DD ver 2.3 (1994)

Table 1. continued

FAMILY	SPECIES AND AUTHORS	GLOBAL DISTRIBUTION OF SPECIES	DISTRIBUTION IN MADAGASCAR	IUCN STATUS
Vespertilionidae (continued)	*Miniopterus petersoni* (Goodman et al. 2008)	Madagascar	S,E	DD ver. 3.1 (2008)
	Miniopterus sororculus (Goodman et al. 2007)	Madagascar	C,S	LC ver 3.1 (2008)
	Hypsugo bemainty (Goodman et al. 2015) [/ *H. anchietae*]	Madagascar	W	Not evaluated
	Neoromicia malagasyensis (Peterson et al. 1995)	Madagascar	SC	Endangered B1ab(iii) ver 3.1 (2008)
	Neoromicia matroka (Thomas and Schwann 1905) [/ *N. capensis*]	Madagascar	C,E	LC ver 3.1 (2008)
	Neoromicia robertsi (Goodman et al. 2012) [/ *N. malagasyensis*]	Madagascar	E,C	Not evaluated
	Pipistrellus hesperidus [kuhlii] (Temminck 1840)	Madagascar + Africa	W,SW	LC ver 3.1 (2008)
	Pipistrellus raceyi (Bates et al. 2006)	Madagascar	E,W	DD ver. 3.1 (2008)
	Scotophilus borbonicus (Geoffroy 1803)	Madagascar? + Réunion	SW?	CR A1 c ver 2.3 (1994)
	Scotophilus robustus (Milne–Edwards 1881)	Madagascar	Widespread	LC ver 3.1 (2008)
	Scotophilus marovaza (Goodman et al. 2006a)	Madagascar	W	LC ver 3.1 (2008)
	Scotophilus tandrefana (Goodman et al. 2005b)	Madagascar	W	DD ver. 3.1 (2008)

proportion of endemicity have grown in recent years. Bat species–level endemism is approximately 30% for Cuba (Dávalos 2004), approximately 11–27% for Papua New Guinea (Bonaccorso 1998; Mickleburgh et al. 2002), 18% for Sulawesi, 5% for Borneo, 8% for Java, and 2% for Sumatra (Koopman 1989). Madagascar is also unique, along with New Zealand and the Mystacinidae family, in possessing its own endemic family, namely the Myzopodidae. This family was also, until recently, one of only two families of bats with only one species. The remarkable myzopodids possess adhesive disks at the position of their thumbs and feet that allow them to attach to leaves of plants such as the *Ravenala* palm (Schliemann and Goodman 2003; Goodman et al. 2006b). The myzopodids are considered of conservation importance because of their taxonomic distinctiveness (Mickleburgh et al. 2002).

1.2 Biogeography and Community Composition

1.2.1 Origins of the Taxa on Madagascar

Madagascar's unique position as a large island off Africa and part of an important group of Indian Ocean islands appears to explain the island's bat community composition. Nonetheless, several questions remain.

Based on genetic analysis, the majority of Malagasy bat taxa have origins in Africa (Christidis et al. 2014). Madagascar is only 400 km from the continent and several islands occur between the two landmasses. One would, therefore, expect a close affinity with African groups even though the island broke away from Africa and India before the appearance of bats (Wells 2003; Teeling et al. 2005). Several species on Madagascar are also found in Africa (Table 1). Other species are relatively closely related to African and African/Western Asia taxa. These species are *Eidolon dupreanum* and *Triaenops* spp. (Eger and Mitchell 2003) and *Neoromicia* spp. (Simmons 2005). *Rousettus madagascariensis*, *Nycteris madagascariensis*, and the *Scotophilus* spp. are also most likely of African origin (Eger and Mitchell 2003), although these genera occur in Asia as well (Simmons 2005). *Emballonura* is another genus that does not occur in Africa and is essentially limited to southeast Asia and Madagascar (Eger and Mitchell 1996), but recent genetic work suggests that the Indo–Pacific *Emballonura* derived from a single dispersal event probably from Africa (Ruedi et al. 2012). The presence and taxonomic affinity of *Pteropus* on Madagascar is more difficult to explain and likely of Asian origin (Christidis et al. 2014). *Pteropus* is a genus widespread in the Pacific and Indian Oceans and it reaches Tanzania's Pemba Island, but is absent from mainland Africa. Its occurrence in Madagascar and surrounding islands but not in Africa is puzzling. It was assumed to have reached Madagascar via oceanic ridges that linked the western Indian Ocean to India during the Pleistocene (Eger and Mitchell 1996) and the distance between the mainland and Pemba Island is only ca. 50 km.

Several genera of bats on Madagascar have a broader global distribution. *Mormopterus*, for instance, occurs on Madagascar, in the Australian region, and in the Neotropics (Eger and Mitchell 1996). Two genera (*Mops* and *Otomops*) have African and Asian distributions (Eger and Mitchell 1996; Simmons 2005). Other genera have African, Asian, and Australian/Pacific distributions: *Hipposideros*, *Taphozous*, *Chaerephon*, *Hypsugo*, and *Miniopterus* (Eger and Mitchell 1996; Simmons 2005). The remaining genera *Tadarida*, *Myotis*, *Eptesicus*, and *Pipistrellus*, have worldwide distributions (Eger and Mitchell 1996).

As an endemic and, until recently (Goodman et al. 2006b), monospecific family, the Myzopodidae has uncertain taxonomic affinities. Teeling et al. (2005) place it amongst the Noctilionoidea superfamily, which includes several Neotropical groups and the Mystacinidae of New Zealand.

1.2.2 Missing Groups/Guilds

Although Madagascar possesses a bat assemblage with high levels of endemism and family richness, several taxonomic groups that are present in Africa are missing from the island. In addition, certain bat feeding guilds are not represented.

Three families of bats that occur in Africa do not occur on Madagascar. These are the Rhinopomatidae (also in Asia), Megadermatidae (also in Asia and Australia), and the Rhinolophidae (also in Europe and Asia). It is uncertain why the other families of bats occurring in Africa would have colonized Madagascar but not these three widespread families.

No bats on Madagascar are known to feed on vertebrates, but some of these feeding gaps could be due to a lack of research on bat diet on the island. Also, there appear to be relatively few foliage–roosting bats, with the *Myzopoda* spp. as notable exceptions, and no leaf tent–roosting bats. Much remains for researchers to learn about the foraging and roosting habits of bats on the island.

1.3 Species Distribution and Conservation Status

Several biologists collected bat specimens on Madagascar in the 1800s and early 1900s and those specimens remain an important resource for taxonomists today. These collectors described several Malagasy bat species including *Mops miarensis* (Grandidier 1870; now *Mops midas miarensis*), *Myzopoda aurita*

(Milne–Edwards 1878), *Triaenops auritus* (Grandidier 1912), *Rousettus madagascariensis* (Grandidier 1929) and *Nycteris madagascariensis* (Grandidier 1937). Jean Dorst aggregated known information on bats of the island into a review (Dorst 1947b), a key (Dorst 1947a), and a description of their biogeography (Dorst 1948a). Dorst also revised the genus *Triaenops* (Dorst 1948b) and described *Otomops madagascariensis* (Dorst 1953). R.L. Peterson collected bats on the island in 1967 and assembled a thorough analysis of the Malagasy fauna based on his collection and his study of previously collected specimens. It was not until after his death that J. L. Eger and L. Mitchell published this work (Peterson et al. 1995).

As part of a series of extensive vertebrate surveys that have covered most of the important conservation areas in Madagascar, biologists in recent years have added substantially to the knowledge base of Malagasy bats. Collections made during these surveys have revealed new species (e.g., Goodman and Cardiff 2004; Goodman et al. 2005b, 2006a,b,c, 2015) and helped to piece together distributions and broad habitat preferences (e.g., Goodman 1999; Goodman et al. 2005a). In spite of this work, taxonomic uncertainty has endured for some bat species (Christidis et al. 2014; Goodman et al. 2015). Work on Microchiropterans in addition to taxonomic and phylogenetic work included studies of the biology of *Myz. aurita* (Schliemann and Goodman 2003), and echolocation descriptions and analyses (Russ et al. 2003). Significant progress has also been made in the field of pteropodid ecology (Racey et al. 2009). Biologists now have access to more extensive information on roost distribution (MacKinnon et al. 2003), diet and seed dispersal (Bollen and Elsacker 2002; Long 2002; Ratrimomanarivo 2003), frugivory (Hutcheon 2003), pollination (Baum 1995; Andriafidison et al. 2006a,b), foraging habitat and niches (Dammhahn and Goodman 2014), and the impact of hunting (Ranivo 2001; Razakarivony 2003).

Several Malagasy bat species appear to occur throughout the island or even on other land masses and these are most likely of minor conservation concern (Table 1). Others, of potentially greater conservation concern, occur only on portions of the island. Several species appear to have Malagasy distributions more or less restricted to the eastern humid forest areas, including *Em. atrata*, *Myz. aurita*, and *Ne. matroka* (Table 1). Records of other bats appear limited to western or western and drier parts of the country: *Triaenops menamena*, *Emballonura tiavato*, *Myzopoda schliemanni*, *Chaerephon jobimena*, *O. madagascariensis*, *Scotophilus tandrefana*, and *S. marovaza* are the Malagasy endemics in this category (Table 1). The distribution of *Scotophilus cf. borbonicus* is insufficiently known (Goodman et al. 2005b). *Neoromicia malagasyensis* has one of the most restricted distributions of all Malagasy bats and researchers have only observed it in and around Parc National d'Isalo (Goodman and Ranivo 2004); two other endemic species, *Tr. auritus* and *Ny. madagascariensis*, appear to occur only in the northern part of the country (Table 1).

The most recent IUCN–based assessment of the conservation status of the bats of Madagascar in the IUCN Red List, indicated that one species is endangered, three species are vulnerable, and two species are near threatened (Table 1). The pteropodids are all listed as vulnerable or near threatened. Several bat species on the island are too poorly known to estimate their conservation status (Table 1). For instance, no one has recorded an occurrence of *Ny. madagascariensis* since 1910 (Peterson et al. 1995).

2. ECOLOGY

2.1 Roosting

2.1.1 Role in Life History

Bats spend most of their time roosting (Altringham 1996). Roosting and roost characteristics may serve several important functions for bats.

Roosts allow bats to rest and reduce energy and water use. In addition to providing sites that protect bats from harsh weather, roosts may also provide appropriate microclimatic conditions—temperature, relative humidity, and airflow—that may allow bats to minimize their thermoregulatory costs (Altringham 1996). Bats may even enter torpor or hibernate to drastically reduce these costs, and may seek microclimates that allow them to enter torpor during periods of low food or water availability. Clustering bats may also reduce thermoregulatory costs because of the presence of other heat–generating bats. The need to reduce thermoregulatory costs in roosts can be critical to bat survival.

Roosts also provide opportunities for social interactions between bats. Roost sites may facilitate mating opportunities and allow for maternal care of young bats (Altringham 1996). Roosts may also allow for information transfer, potentially about foraging and roosting sites (Altringham 1996).

Bats may reduce predation risk and competition with other vertebrates by selecting appropriate roost sites (Altringham 1996). Roosting deep in caves, for instance, effectively protects bats from avian predators during their rest time. Swallows and swifts may be the only non–chiropteran vertebrates to compete with bats for roosting space in certain conditions.

Bats may require more than one roost site at a given time. Not only may they need both day and night roosts, but they may also rely on multiple day roosts to satisfy their requirements. Roost fidelity may vary greatly between species (Lewis 1995).

Roosting patterns may also vary by sex, region, and season (Racey and Entwistle 2003). Different portions of a bat population may roost in different areas, and may even require different roosting conditions. Maternity colonies, for instance, may require different roosting conditions than those of solitary males.

2.1.2 Roosting Preferences

Given the important functions that roosts serve for bats, it is not surprising that bats appear to preferentially choose certain types of roosts. Great variation exists in the selectivity of bats for particular roosting conditions; some may tend to select certain special roost sites, while others may select roost sites more opportunistically (Altringham 1996). Bats in Madagascar roost in caves, rock crevices, human dwellings, bridges, tree cavities, and in tree branches and foliage.

Caves provide relatively safe, dark environments for roosting. Research in other countries has shown that bats may select certain types of caves, and locations within given caves, based on a variety of cave characteristics. Caves that are longer or have more internal surface area seem to have higher species richness. This may simply reflect, however, the high diversity of roosting habitat in bigger caves or the increased detection probability in caves that are larger and thus hold more individuals of each species (Arita 1993, 1996; Brunet and Medellín 2001). Cave microclimate patterns may also influence roost site selection and cave use by bats (Dwyer 1971; Hurst and Lacki 1991; Clark et al. 1996; Brunet and Medellín 2001). Other properties of caves, including their geomorphology, and the landscape surrounding the entrances, may further influence the use of a cave by a given bat species and, ultimately, species richness (Sherwin et al. 2000; Brunet and Medellín 2001; Ball 2002). Presence or abundance of predators or parasites may influence cave selection (Lausen and Barclay 2002) and tendencies of some bat species to associate with others may also influence cave occupancy (Rodríguez–Durán 1998; Rodríguez–Durán and Soto–Centeno 2003).

Most of the bats on Madagascar have been reported to roost in caves. These cave–roosting species include *Ei. dupreanum*, *R. madagascariensis*, the Malagasy *hipposiderids*, the Malagasy *emballonurids*, many of the molossids (*Ch. jobimena*, *Mormopterus jugularis*, *O. madagascariensis*), and many of the vespertilionids (*Myotis goudoti*, *Miniopterus gleni*, *Mi. majori*, *Miniopterus manavi*; Peterson et al. 1995; Bayliss and Hayes 1999; Russ et al. 2003; Goodman and Cardiff 2004). Of these species, *R. madagascariensis*, *Triaenops* spp., *Coleura afra*, *My. goudoti*, *Mi. gleni*, and *Mi. majori* are only known to roost in caves.

Studying characteristics of caves used by different species can reveal the potential basis for selection of cave roosting sites by those species. At Ankarana, for example, several species select caves that have larger entrances and longer total passage lengths (*Ei. dupreanum*, *R. madagascariensis*, *Hipposideros commersoni*, *O. madagascariensis*, and *Mi. gleni*; Cardiff 2006). In addition, a few of the species at Ankarana select caves based on mean temperature and one appears to select caves based on distance to nearby open water areas (Cardiff 2006).

Rocky areas may provide rock crevices as well as caves for bats to roost in and several bat species in Madagascar roost in rock crevices. These include *Ei. dupreanum* (Peterson et al. 1995), *Em. atrata* (Peterson et al. 1995), *Taphozous mauritianus* (Peterson et al. 1995), and a few molossid species: *O. madagascariensis* (S. Cardiff, pers. observ.) and *Mor. jugularis* (Goodman and Cardiff 2004). This is likely an underestimate of the number of species that roost in rock crevices, as bats are often difficult to detect in such roosts.

Many bats also make use of structures built by humans for roosting. Such structures in Madagascar include houses, schools, churches, other public buildings, unused vehicles, bridges, and tunnels. Occupied buildings usually have a double layer of roofing or a roof and ceiling combination that provide a space for bats to roost in, but bats may also roost within palm thatching (Ratrimomanarivo and Goodman 2005). The bats that are known to occupy human constructions in Madagascar include the emballonurids *Em. atrata* and *Tap. mauritianus*, and the molossids *Chaerephon leucogaster*, *Ch. pumilus*, *Mops leucostigma*, *Mop. midas*, and *Mor. jugularis* (Goodman and Cardiff 2004; Peterson et al. 1995). *Scotophilus robustus* and *S. marovaza* also occupy buildings (Goodman et al. 2005b, 2006a).

Trees can also serve as bat day roosts. Bats in Madagascar may roost under the bark of large trees (e.g., Goodman and Cardiff 2004) or in actual hollow cavities deeper in the trunk (Andriafidison et al. 2006a). Bats known to roost in tree cavities include *Mi. manavi* and *Mop. leucostigma* (Andriafidison et al. 2006a). Although relatively few bats in Madagascar appear to roost in tree cavities, further research on roosting habits may alter that perception. A few species of bats also occupy day roosts in the foliage and amongst the branches of trees. *Pteropus rufus* only roosts in camps in large trees and *Ei. dupreanum* sometimes also roosts in trees (MacKinnon et al. 2003, Figure 1). Other bat species known to roost on tree branches or in foliage include *Hi. commersoni* in small numbers (J. Lazar, pers. comm.), *Myz. aurita* (Schliemann and Goodman 2003), *Mop. leucostigma*, and *Mop. midas* (Andriafidison et al. 2006a). Since *S. marovaza* roosts in palm leaf thatching on houses, it may also roost in such palm leaves on actual trees (Ratrimomanarivo and Goodman 2005). The importance of tree roosts for bats in Madagascar is generally not well understood and should be examined further to evaluate the impact of forest clearing and conversion on bats.

Figure 1. A colony of Pteropus rufus at Analalava, a community ecological reserve in eastern Madagascar. Photo: Leighton Reid

2.1.3 Ecological Function of Bats in Cave Roosts

Bats often roost in large numbers in caves and may dramatically alter abiotic and biotic conditions in caves through the introduction of body heat and the production of tremendous quantities of bat feces, or guano.

Body heat and moisture from bats in caves, combined with the decomposition of bat guano, can lead to temperatures and humidity levels that would not otherwise occur in those caves (Harris 1970). Bat guano, as well as dead bats, represents an important source of organic material that serves as a nutrient base for rich and diverse communities of cave arthropods. The presence of guano can influence the structure of the invertebrate community more than the environmental conditions present in the cave (Ferreira and Martins 1999; Ferreira et al. 2007). In some rare cases, other cave vertebrates may feed directly on bat guano (Fenolio et al. 2006).

Researchers have studied the invertebrate and non-mammalian vertebrate fauna of caves on Madagascar, including invertebrates associated with bat guano and remains (e.g., Keiner 1964; Decary and Keiner 1970). In Ankarana, a wide variety of invertebrates are associated with bat guano and dead bats, including several endemic troglobitic springtails (Wilson 1982, 1985; Palacios-Vargos and Wilson 1990). The importance of guano to cave invertebrate communities and their endemic invertebrates in Madagascar remains inadequately investigated.

Because of their role in structuring the cave invertebrate community, bats are considered keystone species in caves. Because they also modify their environment in a way that extends temporally beyond their presence in caves, bats can also be considered ecosystem engineers (Wright and Jones 2006; Hastings et al. 2007).

Guano in caves has benefited humans directly as well. The layering found in large piles of guano has allowed scientists to elucidate the composition of paleo-environments and past environmental change (e.g., Bird et al. 2007). Guano has also proved to be a valuable fertilizer, estimated at one colony of molossids in Thailand to be worth USD 135,000 per year (Leelapaibul et al. 2005). Humans have used bat guano for fertilizer in Madagascar as well (Besairie and Collignon 1971; Goodman et al. 2008b), but guano extraction also has the potential to disturb bats.

2.2 Foraging and Habitat Use

Bats forage for fruit and animal prey, and drink water in a variety of habitats. Globally, such habitats include forests, deserts, agricultural lands, urban areas, wetlands, ponds, and lakes.

Capture locations of most mammals in Madagascar provide an important clue to habitat use and are usually considered representative of the requirements of the species. The capture of a bat either at its roost or while commuting, however, provides only limited information about the specific vegetation features the bat requires for foraging. It is for this reason that, despite thousands of captures at roosts, there are still very few data on foraging habitats of Malagasy bats. Nonetheless, it is possible to generalize based on some field observations, and information available for the same or related species outside Madagascar.

For example, molossid bats are usually associated with open habitats where they hawk over water and agricultural land. Their characteristic long, thin wings and loud, low-frequency echolocation make them ill-suited to foraging near vegetation, although they may frequently fly and feed above the canopy of forests. *Taphozous mauritianus* is likely to exhibit foraging behavior similar to molossids because of their morphological similarities.

In the dry deciduous forests of western Madagascar, Kofoky et al. (2006) and Rakotoarivelo et al. (2007) studied the habitat use of Microchiropterans using bat detectors and mist nets. They determined that high capture levels in the forest were probably associated with mass emergence from day roosts in rock features and caves found mostly inside the forest. Later in the evening, bat foraging activity was highest along the edge of the forest, where the trees adjoined agricultural land and where flying invertebrate abundance was higher. Similarly, *Myz. aurita* appears to select relatively degraded habitats for foraging (Ralisata et al. 2010). The observation that many microchiropteran species on Madagascar are not dependent on intact forest (Goodman et al. 2005a; Randrianandrianina et al. 2006; Rakotoarivelo et al. 2007) may be partly explained by their use of edge habitats for foraging, which are not thought to be important for most other endemic vertebrates. Linear habitat elements appear to be important to many bats (Mickleburgh et al. 2002).

Areas of open freshwater may also be important habitats for bats. Open water often is a source of insects that may serve as food for bats. Bats also need to drink and require stretches of open water large enough to allow them to descend to the water and drink while in flight. While open water areas are most likely important habitats for bats, no one has quantitatively evaluated their importance in Madagascar.

2.3 Diet

Bats eat a wide variety of plants and animals around the world (Patterson et al. 2003). Field observations, experimental trials, and fecal analyses have been widely used in many countries to describe their diets.

There is an impressive body of literature on the diet of two of the Malagasy fruit bats, *P. rufus* and *Ei. dupreanum* (e.g., Bollen and Van Elsacker 2002; Hutcheon 2003; Bollen et al. 2004; Jenkins et al. 2007; Long and Racey 2007; Picot et al. 2007), but relatively little is known about the diet of *R. madagascariensis* (Andrianaivoarivelo et al. 2012).

Madagascar's fruit bats have a varied diet that consists of nectar, pollen, leaves, and fruit. In a survey of the available literature, it was estimated that *P. rufus* feeds on 114 plant species, *Ei. dupreanum* on 39 species, and *R. madagascariensis* on six species, including the planted fruit tree Dimocarpus longan (Andrianaivoarivelo et al. 2007). These data likely all underestimate the actual dietary diversity, which will certainly increase as more research is carried out. Fecal analysis that omits pollen grains, for example, will underestimate the true diversity of the bats' diet and the contribution made by flowers. In fact, the diets of *P. rufus* and *Ei. dupreanum* contained large percentages of plant taxa (64% and 48%, respectively) identified based on the presence of pollen grains (P.A. Racey, unpubl. data). Available information suggests that the diet of *P. rufus* can vary between regions, but that consumption of *Ficus* spp., *Psidium* spp., and *Mangifera indica* occurs across regions (Hutcheon 2003; Jenkins et al. 2007; Long and Racey 2007). In the areas around Réserve Spéciale (RS) d'Ankarana, *P. rufus* appear to commonly feed on *Ceiba pentandra*, and *Grewia sp.* seeds are common in the feces of *Ei. dupreanum* (S. Cardiff, pers. observ.).

The ability of Madagascar's fruit bats to feed on both native plants and introduced species is thought to be a main reason behind their continued existence in degraded landscapes (Brooke 2001). For example, sisal (*Agave sisalan*) pollen is a key resource for *P. rufus* at Berenty Private Reserve, and flower parts of Eucalyptus have been found in the feces of both this species and *Ei. dupreanum* (Jenkins et al. 2007; Long and Racey 2007; Picot et al. 2007). Observations of nectarivory on native plants are scarce, but *P. rufus* feeds on nectar and pollen of planted sisal (Long and Racey 2007) and fruit bats have been known to visit baobabs (Adansonia spp.) and *Ceiba pentandra* (Baum 1995; Andriafidison et al. 2006b).

Because most studies in Madagascar have analyzed fecal contents to determine diet, there is a lack of data available on the specific foraging ecology of fruit bats. Many fruits have seeds that are too large to be swallowed, and plant species that bear large fruits will also be underestimated in the diet of fruit bats if surveyed by fecal collection only.

The diet of Microchiropterans on Madagascar is much less well understood than that of Microchiropterans in some other countries and that of pteropodids on Madagascar, with relatively few published accounts (Razakarivony et al. 2005; Andrianaivoarivelo et al. 2006; Andriafidison et al. 2007; Rajemison and Goodman 2007; Rakotoarivelo et al. 2007, Ralisata et al. 2010). Most of these studies analyzed the composition of bat feces. *Myz. schleimanni* in western Madagascar fed primarily on Lepidoptera and Blattaria (Rajemison and Goodman 2007). A study of *Mop. leucostigma*, *Mor. jugularis*, and *Ch. pumilus* in eastern Madagascar by Andrianaivoarivelo et al. (2006) revealed that major differences in diet occurred between seasons rather than between species, at least at the ordinal level of prey. The three species fed primarily on Coleoptera, but Lepidoptera and Hemiptera contributed significantly to feces volume and Diptera were also important for *Mop. leucostigma* (Andrianaivoarivelo et al. 2006). *O. madagascariensis* at Parc National Tsingy de Bemaraha fed primarily on Lepidoptera and Coleoptera (Andriafidison et al. 2007). An analysis of the stomach contents of *Em. tiavato*, *Hi. commersoni*, *Tr. rufus*, *Mi. manavi*, and *Myo. goudoti* from western and northern Madagascar indicated that the Isoptera and Coleoptera orders were commonly consumed by these bats, and that *Hi. commersoni* tended to consume primarily Coleoptera (Razakarivony et al. 2005). *Hi. commersoni* also consumed primarily Coleoptera according to fecal analysis (Rakotoarivelo et al. 2007). *Triaenops* spp. may consume primarily Coleoptera (Rakotoarivelo et al. 2007), while debris in the stomachs of *Hi. commersoni* and *Myo. goudoti* suggested that they glean prey from foliage or from the forest floor (Razakarivony et al. 2005). Still, much remains for bat biologists to learn about differences in the diets of Microchiropterans on Madagascar with respect to species, seasons, and regions.

2.4 Ecosystem Services

2.4.1 Pest Control

In other parts of the world, molossid bats play an important role in reducing populations of insect pests. Studies in North America (Lee and McCracken 2005) and Thailand (Leelapaibul et al. 2005), for example, suggest that large *Tadarida spp.* colonies can consume vast quantities of insects including large quantities of crop pests. This biological pest control serves an important ecosystem service. Molossids and other bats may provide pest control services to farmers of Madagascar, but this has yet to be properly studied.

2.4.2 Pollination

Pteropodids in Africa and Asia and other bats in the neotropics can play important roles in the pollination of various plants. By moving pollen on their fur between flowers and plants of the same species, the bats guarantee or increase fruit production for those plants. By spreading pollen from one plant to another, these bats provide an essential ecological function.

There are few detailed studies on pollination by fruit bats available from Madagascar. However, observations of fruit bats feeding on flowers, backed up by descriptions of floral morphology, have been used in Madagascar to strongly imply that fruit bats are pollinators. Perhaps the most significant example comes from the baobab trees of western and northern Madagascar. While four of the six endemic *Adansonia* species are pollinated by insects, two, *A. suarezensis* and *A. grandidieri*, are probably pollinated by fruit bats (*Ei. dupreanum*) and lemurs (Baum 1995). The flowers of these plants are large, white, and heavily scented. They also open at dusk and therefore possess all of the characteristics of flowers adapted for nocturnal mammalian pollinators. In addition, *P. rufus* and *Ei. dupreanum* appear to feed on the nectar and probably pollinate *Ceiba pentandra*, a tree of economic importance on the island (Andriafidison et al. 2006b). In some cases, fruit bats may be more important than lemurs as pollinators of baobabs, trees of conservation importance that can be considered flagship species for conservation (Andriafidison et al. 2006b).

2.4.3 Seed Dispersal

Vertebrate frugivores that ingest whole seeds and defecate them at locations some distance from the parent plant contribute to seed dispersal. Old World fruit bats are prolific consumers of fruit and are important agents of seed dispersal (Marshall 1983; Shilton et al. 1999; Hodgkinson et al. 2003). In some oceanic islands, the role of flying foxes in seed dispersal is thought to be especially important because of the absence of other large frugivores (Cox et al. 1991). Neotropical frugivorous bats also disperse fruit seeds. Bats are sometimes considered keystone species because of their role in pollination and seed dispersal (Mickleburgh et al. 2002).

Madagascar's native frugivore community is depauperate (Goodman and Ganzhorn 1997) and apart from fruit bats, only primates (e.g., Birkinshaw 2001; Dew and Wright 1998), a small number of bird species (Bollen et al. 2004), and possibly bush pigs (Andrianjaka 2003) act to disperse seeds. There have been a number of investigations on the diet of Madagascar's two largest fruit bats (Table 2).

Both *P. rufus* and *Ei. dupreanum* have varied diets

Table 2. A summary of the dietary richness of P. rufus and E. dupreanum from different parts of Madagascar.

SPECIES	SPECIES RICHNESS OF FOOD PLANTS	HABITAT/REGION	SOURCE
P. rufus	15	Gallery forest, south	Raheriaisena 2005
	15	Gallery forest, south	Long and Racey 2007
	40	Littoral forest, south-east	Bollen and Elsacker 2002
	8	Degraded humid forest and plantations, east	Jenkins et al. 2007
E. dupreanum	16	Agricultural landscape, central highlands	Ratrimomanarivo 2003
	31	Agricultural landscape, central highlands	Picot 2005

consisting of endemic forest tree species and cultivated/introduced fruit crops. Common seeds in the feces of these fruit bats include guava, *Psidium cattleianum*, and *P. guajava*. The fruits of a number of forest tree species (e.g., *Ficus* spp., *Polyscias* spp.) are also eaten by flying foxes, but the relative importance of fruit bats compared to other frugivores for dispersing forest tree seeds is known only from a single site (Bollen et al. 2004). In general, lemurs have a relatively small home range and are reluctant to cross open areas, such as the patches of degraded land between Madagascar's increasingly fragmented forests and therefore have a limited capacity to disperse seeds between forests. On the other hand, lemurs are the only frugivores that can disperse large seeds and they are also active in all layers of the forest. By contrast, flying foxes can travel great distances every night to their feeding sites (Long 2002) and can easily cross unfavorable habitats, thereby providing a unique ecological service to the island's remaining forests. Unlike lemurs, flying foxes can only ingest small seeds, and they are also restricted to feeding in canopy trees or on the forest edge.

An assessment of the relative efficiency of a seed disperser must take into account more than just whether the bat ingests the seed or not; other important factors include the deposition site and germination rate. There is increasing evidence from Madagascar that passage through a bat's alimentary tract increases the germination success in seeds from many plant species (Ratrimomanarivo 2003; Andriafidison 2004; Picot 2005; Picot et al. 2007). Considerably more research is needed in this area, but it is already clear that bats consume vast quantities of seeds and that many of these seeds, when defecated, are viable. No Malagasy frugivores, other than the pteropodids, have the capacity to transport seeds regularly between fragmented forest blocks. Species transported include those that serve as important food sources for other frugivores (*Ficus* spp.), and plant species of value to humans (e.g., *Psidium* spp.).

2.5 Predation

Globally, raptors and snakes are perhaps the most common predators of bats (Altringham 1996). A variety of other animals, however, including monkeys, cats, other bats, frogs, fish, and large arthropods also feed on bats in various parts of the world (Altringham 1996). In Madagascar, researchers have documented only limited information on bat predation by animals other than humans. This information indicates that birds and snakes feed on bats on the island. Carnivores and arthropods could also potentially feed on bats in caves or tree roosts. Even Scolopendra centipedes occasionally feed on live bats in caves in other countries (Molinari et al. 2005) and this could possibly occur on Madagascar as well. Carnivores, such as *Fossa fossana*, might also be able to attack bats in roosts that are easily accessible from the ground.

A number of reports have documented the presence of bats in owl pellets. Goodman et al. (1993) reported the presence of *Tap. mauritianus*, *Mor. jugularis*, and *Mop. midas* in the pellets of barn owls (*Tyto alba*) from Andasibe and the Beza Mahafaly areas in Madagascar. A skull of *Co. afra* in fragments of a raptor pellet probably belonging to *Tyto alba* was recently found at

Ankarana (Goodman et al. 2008a). Barn owls are often seen around the entrances to caves in the evening in the Ankarana area. The owls also appear to have fed on large numbers of *R. madagascariensis* at a site in western Madagascar (Goodman and Griffiths 2006). Bat hawks (*Macheiramphus alcinus*) are also known from several areas on the island (Morris and Hawkins 1996) and have been observed waiting near a cavity roost of *Mi. manavi* and *Mop. leucostigma* during emergence time (Andriafidison et al. 2006b). Falcons have been observed pursuing large molossid emergences at Ankarana (S. Cardiff, pers. observ.). Diurnal raptors might also be able to attack pteropodids in their tree roosts.

Some anecdotal evidence indicates that snakes feed on bats at cave roosts in Madagascar. A boid was observed at the entrance to a cave with many microchiropterans emerging at Ankarana, and persistently moved close to bats handled by researchers (S. Cardiff, pers. observ.). In Anjohikinakina Cave, Tsingy de Bemaraha National Park, a survey team observed a snake predating a *Tr. rufus* from the colony (P. A. Racey, pers. comm.). Boas could also potentially feed on pteropodids in tree roosts.

3. THREATS

3.1 Hunting

Hunting of large bats is a serious threat in some parts of the world. On several Pacific islands, for instance, hunting appears to be an important cause of decline in *Pteropus* spp. (e.g., Brooke and Tschapka 2002) and is an important cause of conservation concern for many pteropodids (Mickleburgh et al. 1992, 2002). The threat posed by human consumption of pteropodids also justified listing *Pteropus* spp. under the Convention on the International Trade in Endangered Species (CITES; Mickleburgh et al. 2002).

At least as of 2008, all bat species in Madagascar can be legally hunted (in season, outside of protected areas) because they are classified as 'game' ('animaux gibbiers') and are not listed as protected species under national wildlife legislation. While in theory hunters need to apply for a permit from the Ministry of the Environment, Water, Forests and Tourism before catching bats, this procedure is rarely enforced. Hunting was the primary reason that *P. rufus* and *Ei. dupreanum* were given draft listings of "vulnerable" by the Global Mammal Assessment (IUCN, unpubl.). Under CITES, *Pteropus* spp. are controlled and cannot be exported, or can only be exported with special permits. *P. rufus*, for example, is listed under Appendix II and can only be exported with special permits, and no stated export allowance occurred in recent years.

The main reason that bats are hunted in Madagascar is to provide food for local people. There is major regional variation in the extent to which bats form an important part of the diet of local communities, being highest in the west and lowest in the southwest (MacKinnon et al. 2003). This variation has traditionally followed ethnic preferences and beliefs, but as increased mixing and movement of individuals occurs in Madagascar, the boundaries between areas where bats are eaten and where they are not eaten are becoming less clear. In some areas of the west, there is considerable commercial demand for fruit bat meat, which, together with heavy and sustained hunting at certain roosts, gives cause for major conservation concern (MacKinnon et al. 2003).

Fruit bats are the bats most commonly eaten by people in Madagascar. Although *R. madagascariensis* is eaten by people in the north and east (Golden 2005; Rakotonandrasana and Goodman 2007; Cardiff et al. 2009), there are few reports of this bat from restaurants or markets. In central Madagascar, *Ei. dupreanum* is the only relatively common fruit bat and its roosts are regularly visited by hunters who trap bats using smoke and nets or sticks there and in other parts of the island (MacKinnon et al. 2003; Cardiff et al. 2009). With the apparent exception of the southwest, *P. rufus* is eaten throughout Madagascar. Hunting methods for *P. rufus* include the use of nets hung between or by trees to catch foraging bats, and even felling of roost trees and beating of bats on the ground (MacKinnon et al. 2003; Jenkins et al. 2007).

Microchiropterans are also eaten in some regions and are an important source of food for people in times of hardship. *Hi. commersoni*, a large microchiropteran, is eaten between January and March in southwestern Madagascar (Golden 2005). This species is killed during emergence from cave roosts and is particularly sought after by local people because of its seasonal fatty deposits. It is also hunted within at least one cave at Ankarana by hunters using sticks (Cardiff and Befourouack 2008; Cardiff et al. 2009). Other species occasionally harvested by people include *Tr. rufus*, *Ch. leucogaster*, *Mop. leucostigma*, *Mop. midas*, *Mor. jugularis*, *Miniopterus* spp., and *S. robustus* (Goodman et al. 2008b).

The impact of hunting on Megachiropterans has yet to be assessed. There is some evidence that excessive hunting has led to roost desertions (MacKinnon et al. 2003), but unless roost sites are monitored over the long–term it is difficult to determine whether the bats return. Evidence suggests that a small *Ei. dupreanum* colony south of Ankarana was historically larger in size and piles of ash and the presence of over fifty batting sticks around the colony site suggest that harvesting played a role in the colony's decline (Cardiff et al. 2009). The high local demand for large bats as a food source in western Madagascar may exceed the replacement capacity of populations, in part because flying foxes give birth to a single pup each year. The least damaging form of hunting is at the foraging site, where bats are trapped while feeding on fruits or flowers using nets or hooks. Any form of disturbance to roosting bats, especially shooting or people regularly approaching the bats, may have serious impacts on those populations. Hunting could, however, be managed sustainably if the location, timing, methods, and frequency of hunting were closely controlled.

Other reasons for hunting fruit bats are direct persecution (see below), sport, and medicine. Fruit bat fat is highly valued as a remedy for colds and flu, and can be bought at some pharmacies. Sport hunting is not common, but is particularly destructive because it involves the use of shotguns, which appear to be a significant cause of roost site abandonment (MacKinnon et al. 2003).

3.2 Persecution

Bats have been maligned in many cultures around the world and are often persecuted by people (Mickleburgh et al. 2002). In some cases, fruit bats are persecuted because of their perceived consumption of large quantities of valuable fruit. Synanthropic bats are also persecuted because some people do not want them living in their houses. In some cases, people destroy bats or roost sites because people perceive them, usually mistakenly, as carriers of dangerous diseases that people can readily contract. Although vampire bats in South America do cause the death of cattle from rabies, cave roosts with many species of bats are sometimes poisoned or destroyed (Mickleburgh et al. 2002).

The hunting of game species in Madagascar requires permits; however, any unprotected animal (e.g., fruit bats) that is perceived to be damaging the livelihoods of people can be legally killed at any time. As fruit bats are, at times, prodigious consumers of cultivated fruits, there is considerable potential for conflict with people. Fruit bats like to eat mangoes and are often considered to be pests during the fruiting season. Preliminary research, however, suggests that the bats may feed on ripe fruit whereas commercial harvesters harvest unripe fruit for transport to market. As there is considerable loss due to windfall, there is no evidence that the bats are having a detrimental impact on the commercial value of the crop. In fact, by removing ripe fruit the bats may be denying potential pathogens or fungi with a vital resource and may, therefore, be providing an ecological service to the owners of mango trees. Litchi fruits are a very important economic crop in Madagascar, which exports over 20,000 tonnes every year, supplying 70% of the European demand. Few data are available on the impact of predation on litchis, but they appear to form an important part of the diet of all three Malagasy fruit bats in some areas (Hutcheon 2003).

Molossid bats roost in large colonies in buildings (e.g., offices, hospitals, schools) and are often unpopular because of the acrid, pungent smell associated with the colonies. There are many reported cases of molossids being deliberately trapped and killed because of these offensive odors.

3.3 Tourism and Roost Disturbance

Tourism is an important component of strategies to promote conservation and sustainable development in Madagascar and other less industrially developed countries and nature tourism can benefit conservation. If not managed carefully, however, some forms of tourism may have negative impacts on particular ecosystems and populations of plants and animals, including bats.

Tourists in some countries, including Madagascar, may disturb bats at tree roosts. *P. rufus* are easily disturbed at their roosts, but their roosts do not often occur in tourist zones of the few protected areas in which the bats roost (MacKinnon et al. 2003). New tourist zones should be selected and developed carefully in relation to bat colonies and should avoid any form of disturbance. One option, as seen at Berenty Private Reserve, is to escort tourists quietly to within a few hundred meters of roosting *P. rufus*. With binoculars, it is possible to enjoy exceptional views of the bats without disturbing the colony (Rahaingodrahety et al. 2008). A balance needs to be struck between conserving roosting bats, and giving visitors the opportunity to see the animals and learn about their ecology from well–informed guides.

Globally, caves can face special conservation threats because their biotic communities can be sensitive to human visits and because they are at times used by humans for depositing waste. Caves can also connect directly with the aquifer, and often hold unique communities and endemic troglobitic species in addition to bats. Human visits to caves and cave tourism may disturb bats and may even cause bats to abandon roosts. Research in temperate climates indicates that cave visits by humans to maternity or hibernating colonies can negatively affect bat populations (Thomas 1995; Johnson et al. 1998; Mann et al. 2002). These effects may lead to changes in relative abundance of bats roosting in particular caves (Tuttle 1979), with some bats more likely to occur or breed in less–disturbed roosts (e.g., Ho and Lee 2003).

In Madagascar, several caves in protected areas are open to tourists. In the Parc National (PN) Ankarana, two bat caves receive visits by tourists throughout the year and an additional six receive tourist visits almost exclusively during the dry season. Bats may be more vulnerable to disturbance during the dry season when they are in torpor. In PN Tsingy de Bemaraha, tourists frequently enter a number of caves on the park's trail circuit, but these appear to have a low diversity of bats and visits occur only during the dry season (Kofoky et al. 2006). In PN Ankarana, the cave that receives the most visits holds large populations of *R. madagascariensis* and *Ei. dupreanum*, and potential conflicts exist between bat conservation and ecotourism development.

Disturbance from tour groups to bats in RS Ankarana consists of human voices, artificial illumination, and flash photography. Some people have indicated that tour guides once used sticks to intentionally disturb the bats for tourists, but this behavior may now occur only rarely in RS Ankarana (S. Cardiff, pers. observ.); it does happen, however, at a *R. madagascariensis* roost on Ile Sainte Marie (R. Jenkins, pers. observ.). Given that some pteropodids in other parts of the world appear to habituate to the presence of humans (e.g., Parris and Hazell 2005), *Ei. dupreanum* and *R. madagascariensis* may also eventually ignore some forms of tourist behavior. Extreme disturbance, such as bright illumination, flash photography, and approach to minimal distances would, however, most likely disturb even habituated bats. In addition, habituated bats might be more vulnerable to hunting in the low tourist season. Results of behavioral observations at Ankarana suggest that maintaining tourists at a distance of at least 12m from bats and minimizing direct illumination of bats can reduce apparent behavior change caused by low–intensity tourist visits (Cardiff et al. 2012).

Another potential argument for restricting cave tour visits to bat roosts lies with the tentative results of disease studies of bats. Although the risks are not well understood and bats are often mistakenly maligned and persecuted as carriers of disease, increased exposure of humans to bat roosts could possibly lead to increased risk of disease transmission from bats to humans, including the risk of histoplasmosis from bat guano (Gugnani and Muotoe–Okafor 1997). Much remains unknown about the role of bats as vectors of newly emergent viral and other diseases and their relevance to Madagascar (Breed et al. 2006; Iehlé et al. 2007; Lagadec et al. 2012; Wilkinson et al. 2014).

3.4 Pesticides

Organochlorine pesticides, such as DDT, may be particularly detrimental to bats (Clark 2001; Mispagel et al. 2004; Racey and Entwistle 2003; Allinson et al. 2006). Scientists have implicated chemically–treated timber present in attics and agricultural pesticides as causes of declines in bat populations in several parts of the world (Racey and Entwistle 2003). Use of DDT is on the rise again in some countries and this use could represent a renewed threat to non–target species such as bats (Mickleburgh et al. 2002).

Many toxic agricultural chemicals have been and continue to be used in Madagascar, but their effects on bat populations are unknown. Around Ankarana, for instance, cotton and sugar cane are grown and sprayed with pesticides in fields immediately adjacent to limestone caves with bat colonies (SGC, unpubl. data). For cotton production, chemicals allowed for use in 2003 (according to the HASYMA, the cotton company) included thodicarb (probable carcinogen, cholinesterase inhibitor), endosulfan (acutely toxic, endocrine disruptor), cypermethrine (possible carcinogen), profenofos (cholinesterase inhibitor), carbosulfan (cholinesterase inhibitor), enfuracarb (cholinesterase inhibitor), monocrotophos (acutely toxic, cholinesterase inhibitor), and chlorpyriphos (cholinesterase inhibitor). Although DDT is officially not allowed for agricultural use, it may be informally applied as well (S. Cardiff, pers. observ.).

3.5 Mining

Mining can have devastating impacts on habitats that are important to bats. Mining may lead to deforestation and contamination of water bodies. Industrial mining tends to occur near areas of importance to biological diversity (Miranda et al. 2003). Mining of limestone areas, the caves and crevices of which often represent important bat roosting habitat, occurs in many parts of the world and has even been planned within protected areas (Mickleburgh et al. 2002).

Mines may also have benefited bats in some parts of the world where abandoned mine tunnels have apparently served as suitable roosting habitat. Mine tunnel closure or collapse, or resumption of mining activities, however, may lead to sudden loss of habitat for those bats (Mickleburgh et al. 2002). Also, use of radioactive mines by bats has generated concern over the bats' exposure to radiation and ensuing DNA damage (Meehan et al. 2004).

Mining occurs and is planned in many areas of Madagascar. Industrial mining permitting has affected conservation planning in Madagascar, with mining concessions overlapping with 33% of new conservation areas planned for 2005 and 21% of those for 2006 (Cardiff and Andriamanalina 2007). Mining interests are exploring and beginning the extraction of a wide variety of precious stones and metals on the island. Mining activities may impact bat roosting and foraging habitat in several ways.

In some cases, artisanal miners may use caves to search for precious stones or metals, and their activities may disturb cave–roosting bats (Cardiff et al. 2009). The lights (e.g., electric torches or palm–leaf torches) and noise of the miners may disturb the bats, affecting bat energy expenditures, reproduction, and, subsequently, abundance. In addition, miners in some areas of Madagascar, such as Ankarana, set fires in caves, as they do in their tunnels, to soften rocks for digging (Cabinet ADAPT 1999). Such burning would disturb bats with increased light and also threaten them with rising smoke that could potentially asphyxiate them. The prevalence and overall impact of cave burning, however, remain unreported.

Industrial surface mining activities may cause deforestation that impacts bat roosts or their feeding sites. In some cases, such as that of the QIT Madagascar Minerals (QIT/QMM) mine near Fort–Dauphin (Vincelette et al. 2003), large industrial operations may intentionally clear forest in order to access mineral deposits. Such large scale clearing may include sites of forest–roosting bats and the QIT mine could, in fact, clear a forest in which a colony of 75–100 Pteropus rufus roosts (Jenkins, unpubl. data). *P. rufus*, however, often moves roost sites (although the reasons are poorly understood) and the loss of a single roost may be less of a threat than the destruction of suitable feeding sites.

Limestone is used to make cement in Madagascar and increasing demands for this commodity may encourage mining of new limestone areas that include bat roosts; several limestone mining exploration permits covering hundreds of hectares had been granted as of 2006 (Cardiff, unpubl. data). Other mining activities, such as the proposed Ambatovy nickel mine near Moramanga, may also require limestone as part of their treatment process (Lavalin 2005).

3.6 Fire

Fire is one of the main methods used to expel *Ei. dupreanum* from their rocky roost sites (MacKinnon et al. 2003) and bush fires are a threat to *P. rufus*

(Jenkins et al. 2007). Fire is a traditional management tool for farmers across much of Madagascar and a large proportion of the island's grasslands are set ablaze each year (Kull 2003). Fire is used to clear old growth from fields to prepare agricultural land before planting and to stimulate fresh grass growth in pasture. 'Tavy' (swidden, or slash and burn) farmers also use fire to clear new areas of forest. *P. rufus* roosts are particularly vulnerable to fire because they are located in large trees, often in small forest fragments surrounded by savanna or scrub habitats (Jenkins et al. 2007).

3.7 Forest Clearance

Loss of forest cover is a major threat to many bat species around the world (Mickleburgh et al. 2002). Bats may depend on forest as foraging habitat or may actually roost in trees. Other elements of mixed agricultural landscapes, such as riparian buffer forests and hedgerows, can also represent valuable foraging habitat for bats (Mickleburgh et al. 2002).

Given that deforestation in Madagascar is a threat to the survival of the island's endemic vertebrates, it may appear strange to question whether bats are negatively impacted by the loss of forest vegetation. However, the survival of some species in relatively degraded areas and the use of artificial roosts by others has led to the conclusion that many Malagasy bats are not wholly dependent on large expanses of intact forest (Goodman et al. 2005a). Nonetheless, forests may represent important habitat to species even though those species can occur in areas without forests; also, more bats may use trees for roosting in Madagascar than we are currently aware of since little research has occurred in that area. Some species (such as *Em. tiavato*, *Tr. auritus*, and *Myo. Goudoti*) may have a strong association with forest habitat (Goodman et al. 2005a; Randrianandrianina et al. 2006). Species that are able to forage in degraded and mixed agricultural habitat may, nonetheless, have specific roosting requirements and roost site protection ought to be a priority for those species. More research is needed to determine the impact of deforestation on bats, both in terms of changes or loss of foraging habitats, and the destruction of roost sites. In particular, close attention should be paid to understanding the relationship between roosting and foraging sites, and its importance to bats in Madagascar.

To conserve bats, the gamut of habitat types and features required during their life cycle must be protected. As many bat species have particular needs for roosting or feeding, the habitats required at night (feeding) may be different and distant from the essential day habitats (roosts). This is in stark contrast to most of Madagascar's other endemic mammals, which tend to live their entire lives inside intact forests.

3.8 Climate Change

Climate change may affect bats globally in a variety of way. Changes in vegetation caused by climate change may lead to increases in range for some species, but decreases for others (Scheele et al. 1996). In Australia, increased temperature may have contributed to the movement of a Pteropus camp to an urban roost site (Parris and Hazell 2005). In New Zealand, increased temperatures in winter may cause an increase in bat energy expenditure during a time of low food availability or increased abundance of mammalian bat predators (Pryde et al. 2005). Alternatively, increased temperatures may allow for northward range expansions of hibernating northern temperate bats or for montane expansion for low temperature–limited tropical bats (Humphries et al. 2002; LaVal 2004). Climate change also has the potential to alter distribution of infections that harm bat populations. Introduction of the white nose syndrome fungus to bat populations in North America has had a devastating impact on bat populations (Blehert et al. 2009) and it is possible climate change could influence the spread of such infections.

The current and future impacts of climate change on Madagascar remain poorly resolved. El Niño Southern Oscillation events do appear to correlate with vegetation growth in Madagascar (Ingram and Dawson 2005) and anthropogenic climate change may alter the frequency of El Niño events. This could lead to changes in fire frequency and vegetation cover on the island (Ingram and Dawson 2005). These changes in climate and vegetation may alter roosting and foraging habitat availability for some bats. Climate change could alter temperature and humidity patterns in currently suitable roosts. In addition, cyclone frequency and strength are also predicted to increase in the southwestern Indian

Ocean (McDonald et al. 2005). Cyclones and hurricanes can have severe effects on bat communities in other parts of the world (Jones et al. 2001; Mickleburgh et al. 2002), and any increase in frequency or strength of cyclones hitting Madagascar could particularly affect populations of bats. Some *Pteropus rufus* roost site desertions are already attributable to cyclones knocking down roost trees on the island (MacKinnon et al. 2003).

3.9 Being Ignored

Bats are a fundamental component of the endemic Malagasy mammal fauna, yet scientists have historically neglected them. As a result, bat conservation and research on the island is in its infancy. Many vertebrate surveys during the 1980s and 1990s were completed in Madagascar without any reference to bat species in the parks and forests visited. The situation is quickly improving: a good example is the 1998 survey of Tampolo forest that omitted bats and the 2004 survey that included bats. Government hunting policy, however, remains inadequate for protecting bats.

4. CONSERVATION

4.1 Priorities

Given limited resources, especially in less industrially developed countries such as Madagascar, conservation efforts ought to be targeted carefully to maximize the conservation benefit.

Conservation of bats could base priorities for action on high bat species richness or diversity, or on the presence of bats species or groups of bat species that provide desired ecosystem services, that are rare, that are endemic, that represent a high level of taxonomic uniqueness (such as members of the endemic Myzopodidae), or that have vulnerable or threatened populations. Conservation work could then focus on geographic areas of known occurrence of high species richness or of the selected species. For instance, an unprotected cave roost with high species richness could be protected, or hunting patrolling and education could be increased in an intact forest with a hunted *P. rufus* roosting colony. Alternatively, conservation work could focus on ecosystems or habitat characteristics where the desired bat conservation criteria (high species richness, etc.) may occur. An area of intact forest and karst could be protected if modeled species occurrence patterns indicated the likelihood of high species richness in such areas.

In Madagascar, species conservation assessments are incomplete, but threat levels indicate the pteropodids as well as *Hi. commersoni*, *Tr. auritus*, and *Ne. malagasyensis* are possible priorities for conservation. The pteropodids' role in pollination and seed dispersal, or their importance as a food resource, would grant them priority status if selection was based on those ecosystem services. Prioritization based on species' roles in possible pest control and guano production would select large colonies of molossids as priorities for conservation. The myzopodids, as members of an endemic family, could be considered priorities based on their taxonomic uniqueness. Patterns of distribution and species richness on the island are not yet sufficiently understood to allow for large–scale prioritization based on that criterion, although analyses in some regions may approach the level of information needed (Goodman et al. 2005a).

To create conservation priorities at a large spatial scale based on the modeled distribution of bat habitat use would require firm knowledge of habitat and ecosystem use by bats. Although researchers have made great strides in understanding in recent years, their knowledge of bat habitat use on the island is likely not yet sufficient to allow for such modeling.

4.2 Education and Awareness

Given that bats are viewed primarily as food, pests, or nuisances, and are often associated with horror films, it is fair to say that the general public in Madagascar would benefit from more information about the lives of bats.

A conservation and education awareness program concerning bats should engage all levels of society. Conservation professionals could be targeted by the provision of factual reference material and training workshops. Integrating programs about bats into primary school education has the potential to provide generations of children with information about bats that leads to understanding, much as they already receive for some of Madagascar's other important wildlife species. Community initiatives that strive to raise the awareness of adults regarding the importance of bats would likely have their greatest impact in areas with threatened roosting colonies; such efforts are already underway in some communities (Jenkins et al. 2007). Educational efforts could lead to the creation of government policies that better protect bats from hunting and habitat loss.

4.3 Protected Areas and Bats

Around the world, efforts to conserve the most threatened terrestrial species include the establishment of protected areas that exclude or regulate the amount and type of human disturbance. This approach is particularly successful for species that occur and remain wholly within reserve boundaries, and is most challenging for species that migrate over large distances. Because bats were not included in many vertebrate surveys in Madagascar, it is difficult to assess the contribution that the island's park network makes to bat conservation. Malagasy Microchiropterans that roost in houses and other buildings receive no benefit from protected areas; however, synanthropic species are thought to be relatively common and not in need of protection. The status of the rare *S. tandrefana* has yet to be evaluated.

Most other Microchiropterans on the island roost in caves and these are more or less well represented in parks and reserves. Several protected karst areas in the north and west are good examples of areas with important bat caves that are official protected areas, but other sites known to contain high bat diversity (e.g., Anjohibe) are still unprotected. Even some important bat caves around the protected area of Ankarana in the North remain unprotected (Cardiff et al. 2009).

Madagascar's fruit bats are also a conservation priority because they are endemic and, therefore, of conservation concern, and many of their roosts occur outside of protected areas. There are only three known roosts of *R. madagascariensis* inside protected areas in Madagascar and, as noted by others (MacKinnon et al. 2003), *P. rufus* colonies are poorly represented in the parks. Some large *P. rufus* colonies receiving protection from ancestral taboos occur in forests very close to villages, indicating that these bats can benefit from conservation measures. Conservation efforts should favor increasing protection at roosts that already occur within parks, and establishing new protected sites specifically for bats.

4.4 Roost Site Conservation

Because bats often roost in large colonies, the sheer numbers of bats may attract predators and humans with traps and guns. And since the bats are concentrated in one spot when roosting, they are also more vulnerable to other pressures, such as forest clearance, persecution, or fire. Given these pressures and the paucity of data on bat feeding sites, it is not surprising that roost conservation is considered a priority in Madagascar (MacKinnon et al. 2003; Goodman et al. 2005a; Jenkins et al. 2007).

Roost conservation, however, can be difficult to implement. Bats may regularly move between different roosts in response to disturbance, temperature shifts and seasonal changes, food availability, and predation and parasite loads. A thorough understanding of the roosting ecology of the targeted species would be needed to ensure that limited conservation resources be efficiently deployed.

Conservation of roost sites may be of greatest importance for species that use only one type of roost. As described above, *P. rufus* only roosts in trees and several species of bats only roost in caves. Depending on other criteria used for prioritizing, conserving roost sites for those more selective species may be a greater priority than conserving roost sites for species that roost in buildings, caves, and tree cavities.

Consideration of the importance of general roost type to bat species, as well as an understanding of the specific roosting habitat requirements of species in a particular area could allow managers to develop conservation priorities for that area. For cave roost sites, managers could seek to prioritize caves with high species richness, caves with species of potential conservation concern, or caves with species with either very particular or rare roost requirements. Such cave roost requirements could include caves that have larger entrances and longer total passage lengths (Cardiff 2006). In some cases, such as at Ankarana, multiple priority criteria can lead to the selection of the same caves as priorities for conservation (Cardiff 2006).

Roosts, in theory, provide a good opportunity for biologists to assess the population size of certain bat species on a regular basis. The conservation status of many Malagasy vertebrates is often extrapolated using changes in the forest cover. This approach is not appropriate for all bats, but without some form of method to assess population change, it will become increasingly difficult to revise the current IUCN Red List for bats.

Occasional visits to roosts as part of a population survey are not ideal because the absence of bats could be the result of actual population decline, roost site abandonment due to human activities, or regular roost site switching and seasonal movement. Given these difficulties, it is probably best to monitor permanent roost features (e.g., caves) at a selected number of sites on a regular basis. For roosts associated with trees, and especially those of *P. rufus*, it will be necessary to monitor a number of roosts within a given area on a regular basis and to conduct wider–scale, even national surveys at least once a decade to determine the rate at which roosts are destroyed.

4.5 Monitoring

Natural resource managers will be better able to conserve bat populations if they are able to identify threatened populations and the factors responsible for the threatened status, and reduce or eliminate those causes. In order to identify threatened populations, however, managers need baseline information about populations. Monitoring of bat populations can provide that baseline.

Many techniques are available to researchers and managers for monitoring bat populations (Bat Conservation Trust 2007). The most appropriate technique may depend on the species and setting, and different situations may require the use of multiple methods to obtain an accurate assessment. Large, tree–roosting bats may be reliably monitored by visual or disturbance counts if foliage is not too dense and the colony not too dispersed (Kunz et al. 1996). Cave–roosting bats may be monitored using a variety of techniques. These include interior survey counts for easily identifiable bats that do not roost in deep crevices and that are not so disturbed by human observers that an accurate count is impossible. Cave passages must also be accessible to observers. Video recording with infrared light provides a means of limiting disturbance and obtaining accurate counts (e.g., O'Donnell 2002). One may also monitor cave populations by recording echolocation calls during bat emergence from caves, observing emergences with night vision equipment, video–recording emergences with infrared video, using laser beam counters (motion detectors), thermal imaging and, potentially, pit–tag counters for smaller cave openings (Kunz et al. 1996; Bat Conservation Trust 2007; Betke et al. 2008). Capture–mark–recapture studies may also provide reliable estimates at roost–sites or in foraging habitats. Researchers must take care, however, to use appropriate marking methods that minimize bat injuries (Kunz et al. 1996).

Any monitoring strategy must account for possible routine switching of roosts (Lewis 1995), seasonal changes in roost use, and seasonal changes in emergence patterns. Emergence activity, for example, may change dramatically between the wet and dry season for some species in Madagascar (S. Cardiff, pers. observ.).

The simplest and cheapest bats to monitor are large species that roost in colonies. Managers may, in some situations, obtain daytime counts, evening dispersal or morning return of *P. rufus* with relatively little equipment or expertise (Jenkins et al. 2007; Long and Racey 2007).

The appropriate method to estimate the number of bat individuals roosting in caves depends on the bat species, because species have different roosting habits and different sensitivities to various types of disturbance. Bats may also vary in their sensitivity to disturbance according to season, as some bats enter torpor in the dry season. Interior surveys of caves using regular artificial, white lighting may provide reliable counts of *Ei. dupreanum*, *Myo. goudoti*, and *Miniopterus* spp. in the dry season in Ankarana (S. Cardiff, pers. observ.). *Ei. dupreanum* individuals in cracks in cliff faces, however, may be indistinguishable and, therefore, uncountable until emergence (S. Cardiff, pers. observ.). Reliability of *Myo. goudoti* and *Miniopterus* spp. interior counts may also depend on time of day and season, as these bats may fly more readily at times and cause double counting as one proceeds through a cave. These species can also roost in areas that are difficult to access. Although white lighting may allow counts of *Hi. commersoni* and *Ch. jobimena* in caves, counts of large colonies of these species may require video recording for accuracy. These bats, as well as *Mor. jugularis*, can also roost at sites that are too high in the cave to observe properly. White light may also allow repeatable counts of *O. madagascariensis*, but such counts may disturb the bats and observation with infrared lighting seems advisable. Infrared video recording also provides repeatable counts of *R. madagascariensis* in caves, but such equipment is expensive. If *R. madagascariensis* emerge from only one, accessible cave entrance, monitoring staff may use cheaper night–vision equipment to count emerging individuals, the eyes of which reflect the infrared light well. Interior infrared video recording may also allow for reliable counts of *Triaenops* spp. in large colonies that might fly too readily for observation when exposed to regular light. In some cases, such as with dispersed or small colonies of bats that fly readily upon observer approach in caves with multiple entrances, it may only be possible to monitor their continued presence at a given roost rather than actual population numbers (S. Cardiff, pers. observ.).

Acoustic monitoring can also be used to determine the presence of species at a roost or foraging site, and provide an abundance estimate. A reference library of recordings of bats identified to species, with tissue voucher samples such as wing punches, where possible, is a prerequisite to acoustic monitoring. Determination of distinguishing characteristics between calls of different species must also precede acoustic monitoring and, in some cases, calls will be too similar to successfully identify some species. Reference recordings should be made with high quality time expansion devices (Parsons and Obrist 2004). These recordings can be made successfully without causing the bat to greatly alter its calls by tying a thin fishing line to the bat and allowing it to fly along a fixed fishing line (Szewczak 2000). Frequency division devices, such as Anabat, may provide some advantages by allowing for automatic recording of calls and instantaneous recording, but reference calls must also then be made with frequency division recording and frequency division fails to properly capture some call characteristics, such as the frequency at which the call has the greatest energy. Reference call recordings and acoustic monitoring must also give proper consideration to surrounding vegetation and other clutter that may cause the bat to alter its call. In Madagascar, bat biologists have already collected hundreds of reference calls for use in monitoring (e.g., Russ et al. 2003, Kofoky et al. 2009).

Monitoring proceeds with the identification of species based on comparison with reference calls (Bat Conservation Trust 2007). Where the number of bat species present is known to be low and bats calls are easily distinguishable by frequency of greatest energy, monitoring teams can use cheaper heterodyne detectors to identify the frequency of greatest energy. These can also serve to alert observers counting bats to their approach (O'Donnell 2002). The number of bat passes or feeding buzzes, as indicated by the number of calls heard or recorded, can serve as an index of bat activity, but can differ greatly from the number of individual bats flying through an area. These can potentially be used in studies of habitat use by bats, and several studies on Madagascar have applied acoustic monitoring for that purpose (Kofoky et al. 2006; Randrianandrianina et al. 2006; Rakotoarivelo et al. 2007). Acoustic monitoring, therefore, is generally more appropriately used to identify the presence of species rather than their relative abundance.

None of the observational methods allow verification of individual bat identities. If a species has low roost fidelity, then counts of populations in selected roost sites may not provide an accurate impression of population trends for an area. Evaluating roost site fidelity using marked bats would allow one to estimate the reliability of observational counts.

5. BRIGHTENING THE FUTURE OF BAT CONSERVATION

Bats in Madagascar and elsewhere constitute an important part of global biodiversity. The bats of Madagascar represent a unique assemblage of bat species with high endemicity and many rare species. Bats on Madagascar, and globally, often perform important functions in the ecosystem and for humans by controlling pests, pollinating plants, and dispersing seeds. They are even considered keystone species for their role in those processes and their role in structuring invertebrate communities in caves. Bats face numerous threats from hunting, from habitat loss, from deforestation, pollution, and roost disturbance, and from climate change. Efforts to limit hunting where unsustainable, to protect bat roosts inside and outside protected areas, to expand protected areas, and to strategically monitor roosts, will be essential to conserving bats on Madagascar and around the world. Conservation organizations in Madagascar can look internationally to projects by Bat Conservation International, Lubee Bat Conservancy, and the Bat Conservation Trust for ideas and resources. The Madagasikara Voakajy and WWF Ecology Training Program and Vahatra bat projects have also done much to build the capacity necessary to advance bat research and conservation that we hope will allow the bats of Madagascar to overcome the many threats to their survival.

GLOSSARY

Assemblage: a set of species or other taxonomic group occurring in a defined area that may or may not exhibit certain ecological relationships among them

Carcinogen: a substance or agent that promotes or causes cancer

Chiroptera: the order of bats, from the Greek "hand wing"

Cholinesterase inhibitor: a chemical that inhibits a cholinesterase enzyme from breaking down acetylcholine, and that thus affects neuromuscular transmission

Continental shelf island: an island that lies on a continental shelf and is separated from the larger continental mass by relatively shallow water; Madagascar is sometimes called a microcontinental island because it is separated from Africa by a rift

Echolocate: to emit sound waves and listen to the echo in order to locate objects or navigate

El Niño Southern Oscillation (ENSO): a global coupled ocean–atmosphere phenomenon; it represents a set of interacting parts of a single global system of coupled ocean–atmosphere climate fluctuations that come about as a consequence of oceanic and atmospheric circulation. ENSO is the most prominent known source of inter–annual variability in weather and climate around the world (~3 to 8 years) and affects areas in and around the Pacific, Atlantic, and Indian Oceans. In an El Niño event, Pacific trade winds die down, causing warmer surface water to accumulate off western North and South America. This leads to increased rainfall, storm activity, and flooding in the Americas (especially the southwestern United States and Peru) and drought conditions in Australia and other areas in the western Pacific and the Indian Ocean

Endemic: occurring in the absence of human intervention only in a defined geographic or ecological area [in epidemiology, endemic means instead that a pathogen is maintained in a host population without the need for external inputs]

Endocrine disruptor: substance that causes adverse biological effects by interfering with the endocrine system and disrupting the physiologic function of hormones

Feeding guild: a group of species in a community that is functionally similar based on food habits or foraging behavior; examples include aerial insectivorous bats and gleaning bats

Histoplasmosis: a disease caused by the fungus *Histoplasma capsulatum* with symptoms including lung infection and, in African histoplasmosis (*Histoplasma capsulatum var. duboisii*), granulomatous lesions in the skin, subcutaneous tissues, and bones

Laryngeal: concerning the larynx, or voicebox, the mammalian organ in the neck that protects the trachea, houses the vocal cords, and produces sound

Microclimate: a local, external atmospheric zone where the climate differs from the surrounding area

Monospecific: a property of a genus or family that contains only a single known species

Oceanic islands: islands in the ocean that do not lie on a continental shelf

Old World: the terrestrial part of the Earth consisting of Africa, Eurasia, surrounding islands, and usually Australia

Organochlorine pesticide: a chemical including carbon, hydrogen, and chlorine elements that is used to kill insects or other organisms; examples include dioxin, DDT, dicofol, heptachlor, endosulfan, chlordane, mirex, and pentachlorophenol

Pleistocene: a geological epoch preceded by the Pliocene, followed by the Holocene, and lasting approximately from 1.8 million to 12,000 years before the present

Pteropodidae: a family of bats traditionally representing the sub–order Megachiroptera and consisting of bats with elongated faces, relatively large eyes, and claws on the second digit, as well as the first

Seed dispersal: the movement of plant seeds possibly leading to successful germination and growth of the plant seeds

Taxonomic affinity: the relative closeness of the phylogenetic relationship of one taxonomic group to another

Thermoregulatory costs: the energetic costs that an animal experiences in order to establish or maintain a certain internal temperature range

Torpor: a state of regulated hypothermia in an endotherm that conserves energy during cold periods, or periods of limited food or water availability

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