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Conservation Threats to Bats in the Tropical Pacific Islands and Insular Southeast Asia

Gary J. Wiles and Anne P. Brooke

Introduction

More than 27,000 islands in 23 countries and territories, spread across millions of square kilometers in the Indo-Pacific, have given rise to a diverse bat fauna characterized by high levels of endemism, particularly in the family Pteropodidae (Flannery 1995; Pierson and Rainey 1992). A total of 354 bat species, including 140 pteropodids and 214 microchiropterans in 9 families (appendix 14.1), reside in the mainly tropical geographic region extending from the Cook Islands in central Polynesia to the subtropical Ryukyu and Ogasawara Islands of Japan, and westward through the Indonesian archipelago (fig. 14.1). This represents about 31% of currently recognized bat species and about 74% of all pteropodids. These inhabit a combined land area of 2,961,600 km², which is smaller than the size of India.

Regional bat diversity is greatest on the large islands off Southeast Asia and in New Guinea, but declines rapidly on the Pacific islands to the east, where only a handful of species occur (table 14.1; Carvajal and Adler 2005; Hall et al. 2004; Hutson et al. 2001; Mickleburgh et al. 1992; Rainey and Pierson 1992). This pattern of occurrence has been strongly influenced by the size and geological history of the islands. Intermittently low sea levels during the Pleistocene reduced interisland distances or connected many of the western islands with the Asian continent on multiple occasions (Voris 2000), promoting the dispersal of bat species and, over time, high levels of endemism and greater species richness. The mountainous nature of many Australasian islands has also contributed to speciation. By contrast, the relative isolation and small sizes of many oceanic islands have greatly hindered their colonization by bats. From a conservation perspective, the region contains 8 of 39 globally recognized hot spots of biodiversity (i.e., Sundaland, Wallacea, the Philippines, eastern Melanesia islands, New Caledonia, Taiwan, Polynesia-Micronesia, and part of Japan), with bats comprising a significant faunal component in most of these (Mittermeier et al. 2005).



Figure 14.1. Map of the 23 countries, territories, and island groups in the Pacific and insular Southeast Asia covered in this chapter, all of which have tropical or subtropical climates. Temperate locations such as New Zealand, Lord Howe Island off Australia, and the main islands of Japan are not discussed, nor are the subtropical Hawaiian Islands.

Within Oceania and insular Southeast Asia, knowledge of the status and natural history of bat populations varies from being fairly good at a few localities in Polynesia and Micronesia to highly incomplete across much of Indonesia, the East Malaysian states of Sarawak and Sabah, the Philippines, and Melanesia. Inadequate information is a serious detriment to preserving bat populations (Hutson et al. 2001; Mickleburgh et al. 2002). Basic data on distribution and habitat preferences are incomplete for many of the region's bats and are entirely lacking for a few taxa. Major taxonomic questions also remain about the status of some species and further interfere with the establishment of conservation priorities.

Latent extinction risk among bats and other mammals is considered high across much of insular Southeast Asia and the tropical Pacific (Cardillo et al. 2006). Regional threats to bats come from a variety of sources, many of which stem from expanding human populations and their ever-increasing pressure on natural ecosystems. Currently, 70 of the region's bat species are recognized as threatened at some level (appendix 14.1), with 11 species classified as critically endangered, 22 as endangered, and 37 as vulnerable (IUCN 2008). Another 30 species are considered near threatened, 177 are of least concern, 71 are data deficient, 2 (*Pteropus pilosus* and *P. tokudae*) are presumed extinct, and 4 have not been evaluated. Of the 6 families with more than 2 species present in the region, the family Pteropodidae has by far the highest percent of threatened members (34.3%, 48 of 140 species), followed by Hipposideridae (12.2%, 5 of

41 species), Vespertilionidae (10.6%, 11 of 104 species), Molossidae (10.0%, 2 of 20 species), Rhinolophidae (7.1%, 2 of 28 species), and Emballonuridae (5.9%, 1 of 17 species).

In this chapter, we summarize available information on five major categories of threats to bat populations in the region: habitat loss and alteration, hunting, cave disturbance, severe storms, and introduced species. We do not discuss several additional concerns, which are described elsewhere. These include global climate change (Rainey 1998), epizootic diseases (Rainey 1998), conflicts with fruit producers (Fujita and Tuttle 1991), and pesticide use (Tarburton 2002). Species are often threatened by multiple factors, some of which work in conjunction to drive populations down. For example, severe tropical cyclones can result in increased hunting of flying foxes (e.g., Pierson et al. 1996) and land clearing can increase human access to nearby caves occupied by bats.

Habitat Loss and Alteration

Forest loss and degradation through logging, development, and fire are the principal threats to biodiversity in many tropical Pacific and insular Southeast Asian countries and territories, with lowland forests and their associated biota being especially vulnerable (Jepson et al. 2001; Sodhi and Brook 2006; Wikramanayake et al. 2002). The vast majority of the region's bats rely on forests completely or to some extent; thus declining forest cover has major impacts on most taxa by reducing foraging and roosting habitats (Hutson et al. 2001; Racey and Entwistle 2003).

Tropical Pacific and insular Southeast Asian countries vary considerably in the amount of forest cover lost over time (table 14.2; FAO 2006). Since 1990, Indonesia has had one of the highest deforestation rates in the world, with more than 280,000 km² of forest permanently lost to human encroachment at a mean rate of decline of about 1.6% annually. More than 90% of the primary forest in the Philippines has already been destroyed, giving it one of the smallest relative amounts of coverage of this habitat for any country in the region. The Solomon Islands, Timor-Leste, the East Malaysian states of Sarawak and Sabah, and Papua New Guinea also show relatively high rates of loss. In Japan there has been extensive clearing for agriculture and other development in the Ryukyu and Ogasawara Islands. Data are imprecise for many of the smaller Pacific nations, but ongoing deforestation rates generally appear to be relatively low (table 14.2). However, it should be noted that forest cover statistics for the region, including those of the FAO (2006), are often misleading because they commonly incorporate habitats of lower ecological value, such as heavily disturbed secondary forests, forest monocultures (e.g., rubber trees) that provide fewer resources for forest bats, and even clear-cut lands left to regenerate naturally. Hence, existing figures can underestimate actual rates of forest degradation and can substantially overestimate coverage by high-quality forests.

Table 14.1. Numbers of bat species per family for 23 countries, territories, and island groups in the tropical Pacific and insular Southeast Asia

Country or island group	Pteropodidae	Rhinolophidae	Hipposideridae	Megadermatidae	Rhinopomatidae
Indonesia	78	20	30	1	1
Sarawak and Sabah (East Malaysia)	16	10	12	1	—
Papua New Guinea	37	4	13	—	—
Philippines	26	10	9	1	—
Brunei	16	6	8	1	—
Solomon Islands	25	—	7	—	—
Taiwan	2	2	2	—	—
Timor-Leste	11	4	4	—	—
Ryukyu Islands (Nansei Shoto) ^c	2	3	1	—	—
Vanuatu	4	—	2	—	—
New Caledonia	4	—	—	—	—
Fiji	4	—	—	—	—
Federated States of Micronesia	4	—	—	—	—
Samoa	2	—	—	—	—
Guam	2	—	—	—	—
Palau	2	—	—	—	—
American Samoa	2	—	—	—	—
Ogasawara and Iwo Islands	1	—	—	—	—
Commonwealth of the Northern Mariana Islands	1	—	—	—	—
Tonga	1	—	—	—	—
Wallis and Futuna	1	—	—	—	—
Niue	1	—	—	—	—
Cook Islands	1	—	—	—	—

Table 14.1. (continued)

Emballonuridae	Nycteridae	Mollossidae	Vespertilionidae	Total species ^a	Endemic species	Threatened species ^b	Sources
12	2	13	65	222	54	33	3, 4, 14, 15, 21, 23, 24, 25
5	1	3	49	97	2	7	21, 23, 24
10	—	6	24	94	17	7	4, 13, 23, 24
3	—	4	25	78	21	6	6, 7, 8, 11, 16, 23
4	1	3	19	58	—	3	17, 23
4	—	1	6	43	14	12	9, 13, 24
—	—	1	29	36	5	—	2, 18, 19, 24
2	—	—	10	31	1	2	10, 22, 23, 24
—	—	1	6	13	5	3	1, 5, 24
1	—	1	4	12	2	5	9, 12, 24
—	—	—	5	9	6	6	9
1	—	1	—	6	1	4	20
1	—	—	—	5	3	3	26
1	—	—	1	4	1	1	9
1	—	—	—	3	1	2	26
1	—	—	—	3	1	2	26
1	—	—	—	3	—	1	9
—	—	—	1	2	2	1	1, 24
1	—	—	—	2	—	2	26
1	—	—	—	2	—	1	9
—	—	—	—	1	—	—	9
—	—	—	—	1	—	—	9
—	—	—	—	1	—	—	9

Sources: 1 = Abe et al. 1994; 2 = BAT 2008; 3 = Bates et al. 2007; 4 = Bonaccorso 1998; 5 = BSCGJ 2005; 6 = Esselstyn 2007; 7 = Esselstyn et al. 2004a; 8 = Esselstyn et al. 2008; 9 = Flannery 1995; 10 = Goodwin 1979; 11 = Heaney et al. 1998; 12 = Helgen 2004; 13 = Helgen 2005; 14 = Helgen 2007; 15 = Helgen and Wilson 2002; 16 = Helgen et al. 2007; 17 = Kofron 2002; 18 = Kuo et al 2006; 19 = Lin et al. 1997; 20 = Palmeirim et al. 2007; 21 = Payne et al. 1985; 22 = Polhemus and Helgen 2004; 23 = SAMD 2006; 24 = Simmons 2005; 25 = Struebig et al. 2006; 26 = Wiles 2005a.

^aIncludes species that have become extirpated or extinct in historic times. Species tallies for the Philippines and Taiwan include some taxa identified only to genus (see BAT 2008; Heaney et al. 1998).

^bIncludes species classified as critically endangered, endangered, or vulnerable by IUCN (2008).

^cIncludes all of Japan's southwestern islands, including the Osumi, Tokara, Amami, Okinawa, Sakishima, Yaeyama, and Daito island groups.

Table 14.2. Forest coverage and amount of change for 23 countries, territories, and island groups in the tropical Pacific and insular Southeast Asia

Country or island group	Total land area (km ²)	Total forest cover in 2005 (km ²) ^a	Total forest cover in 2005 as % of total land area ^a	Primary forest cover in 2005 (km ²)	Mean % annual change in forest cover, 1990–2005	Total forest loss, 1990–2005 (km ²)
Indonesia	1,811,570	884,950	48.8	487,020	-1.61	280,720
Papua New Guinea	452,860	294,370	65.0	252,110	-0.44	20,860
Philippines	298,170	71,620	24.0	8,290	-2.15	34,120
Sarawak and Sabah (East Malaysia)	198,070	125,040 ^b	63.1 ^b	n.a. ^c	-0.67 ^b	19,340 ^b
Solomon Islands	27,990	21,720	77.6	n.a.	-1.44	5,960
Timor-Leste	14,870	7,980	53.7	n.a.	-1.16	1,680
Brunei	5,270	2,780	52.8	2,780	-0.75	350
Locations where forest cover trends are less certain						
	Total land area (km ²)	Total forest cover in 2005 (km ²)	Total forest cover in 2005 as % of total land area	Remarks on continuing forest loss		
Taiwan	35,970	21,000	58.5	Forest cover is stable or slightly increasing. ^d		
New Caledonia	18,280	7,170	39.2	Minor loss continues from logging, mining, and other causes. ^e		
Fiji	18,270	10,000	54.7	Minor overall loss since 1990, but extensive conversion to forests of poorer quality; ^f see Ash 1992 for additional remarks.		
Vanuatu	12,190	4,400	36.1	Extensive logging of lowland forests is ongoing. ^e		
Ryukyu Islands (Nansei Shoto) ^g	4,500	n.a.	n.a.	Some deforestation continues. ^e		
Samoa	2,830	1,710	60.4	Minor overall loss since 1990, but extensive conversion to forests of poorer quality. ^f		
Tonga	720	n.a.	n.a.	Unknown.		
Federated States of Micronesia	700	630	90.6	Minor loss on most islands since 1990, but extensive on Pohnpei (see text). ^{b, j}		
Guam	550	260	47.1	Minor loss since 1990. ^h		
Palau	460	400	87.6	Minor loss since 1990. ^h		

Commonwealth of the Northern Mariana Islands	460	330	72.4	Little or no loss on most islands since 1990, except Anatahan, where loss is nearly complete (see text). ^{b, j}
Wallis and Futuna	274	n.a.	n.a.	Some ongoing loss since the 1980s. ^e
Niue	260	140	53.8	Mean annual loss of forest cover was 1.2% from 1990 to 2005. ^k
Cook Islands	230	160	69.6	Mean annual increase of forest cover was 0.4% from 1990 to 2005. ^k
American Samoa	200	180	89.4	Mean annual loss of forest cover was 0.2% from 1985 to 2001. ^l
Ogasawara and Iwo Islands	100	n.a.	n.a.	Little forest cover remains, thus additional loss is probably minor. ^e

Source: Statistical data originate from FAO 2006 unless otherwise noted and are for the period from 1990 to 2005.

^aIncludes primary and secondary forests, mangroves, and monoculture tree plantations (including nonnative species) used for forest products or protective purpose. Habitats must be greater than 0.5 ha in size and exceed tree heights of 5 m and a canopy cover of 10%, or be capable of reaching these thresholds to qualify as forest. It is unclear whether coconut plantations are consistently included in the data, but other three crops such as oil palm and fruit trees are excluded.

^bl. E. Henson, pers. comm. Data are for the period from 1980 to 2000. Additional background appears in Jomo et al. 2004.

^cN.a. = data are not available or, in a few cases, are considered unreliable as presented in FAO 2006.

^dTsai 1999.

^eSlattersfield et al. 1998.

^fJ. Atherton, pers. comm.

^gIncludes all of Japan's southwestern islands, including the Osumi, Tokara, Amami, Okinawa, Sakishima, Yaeyama, and Daito island groups.

^hG. J. Wiles, pers. obs.

ⁱMerlin and Raynor 2005.

^jC. C. Kessler, pers. obs.

^kFAO 2006.

^lDonnegan et al. 2004.

Techniques for measuring forest cover also frequently differ among studies, further complicating comparisons over time and among countries.

Fragmentation is a significant component of forest disruption and threatens populations of forest-dwelling bats through increased isolation, related stochastic factors, and reductions in microhabitat quality. Size of fragments, degree of isolation, level of matrix contrast, and species vagility are among the factors that affect persistence of bat assemblages in fragmented landscapes (Struebig et al. 2008). Forest fragmentation is considered most severe in the Philippines and the Greater Sunda Islands of Indonesia, whereas comparatively intact tracts of forest persist in New Guinea, Melanesia, and Wallacea (Wikramanayake et al. 2002).

Few analyses of the effects of timber harvest and land conversion on bat communities have been published for insular Southeast Asia and the tropical Pacific; thus it is instructive to look at investigations from neighboring areas to gain a better understanding of impacts. Singapore has lost more than 95% of its original forest cover since the early 1800s and has seen bat species diversity fall by as much as 69–75% for microchiropterans and about 60% for megachiropterans (Lane et al. 2006). Projected declines in species richness are particularly apparent among hipposiderids, rhinolophids, members of the vespertilionid subfamilies Murininae and Kerivoulinae, and other forest-dependent taxa. Surviving species tend to be microchiropterans that prefer open and edge habitats and megachiropterans that are widespread and select agricultural and secondary habitats or that can travel sizable distances (Lane et al. 2006). These dire findings are made worse by the small population sizes for many of Singapore's remaining bats, suggesting that additional extinctions are likely. Research from peninsular Malaysia shows that forest-interior microchiropterans are especially vulnerable to changes in forest structure associated with human disturbance (Kingston et al. 2003; Struebig et al. 2008; Zubaid 1993). Many such species are characterized by wing morphologies and echolocation calls that are adapted for foraging in dense forest understories, and hence are unable to detect prey efficiently in more open environments (Kingston et al. 2003; Meijaard et al. 2005). Additionally, loss of large trees with hollows or exfoliating bark eliminates the preferred roosting sites for some species.

Forest disturbance, clearance, and fires probably represent the most important threats to many bat species in Indonesia and East Malaysia. Preliminary data from Sumatra indicate that logging and conversion of forests to plantations of oil palm and rubber can reduce species richness by 50–88% through the loss of both microchiropterans and pteropodids (Danielsen and Heegaard 1995). In and around the Sangkulirang limestone karst formations in eastern Kalimantan, deforestation has reduced habitat availability for the area's diverse microchiropteran fauna, with forest-roosting species underrepresented in surveys of sites where large mature trees have been lost to fires (Suyanto and Struebig 2007; M. J. Struebig, pers. comm.). In the oligotrophic forests of

southern Kalimantan, populations of species using tree hollows as roosts appear more limited in disturbed locations than in undisturbed ones (Struebig et al. 2006). Elsewhere on Borneo, habitat destruction has probably contributed to the decline of *Cheiromeles torquatus* by reducing opportunities for foraging and roosting in tree cavities (Hutson et al. 2001). Other species reliant on tree hollows (e.g., *Rhinolophus sedulus*, *Megaderma spasma*, *Nycteris tragata*, and *Kerivoula papillosa*) are also considered at risk on this island (Meijaard et al. 2005). Logging, land clearing, and plantation establishment have produced impoverished pteropodid communities in northern Sulawesi, the Sangihe Islands, and islands off Irian Jaya (Meinig 2002; Riley 2002b). Forest loss is also a major threat to *Pteropus vampyrus* on Java (Bergmans 2001).

The greatest threat to Philippine bats is habitat loss (Hutson et al. 2001). At least 18 of 26 pteropodids occur entirely or primarily in forests and have experienced some level of population decline due to land clearing and continuing modification of mature and secondary forests (Esselstyn 2007; Heaney et al. 1998; Mickleburgh et al. 1992; Utzurrum 1992). Deforestation of lowland areas, where pteropodid diversity is greatest (Utzurrum 1998), is one of the chief reasons for the declines of many taxa, especially *Acerodon jubatus*, *Dobsonia chapmani*, *Nyctimene rabori*, and *Pteropus leucopterus* (Heaney and Heide-man 1987; Heaney et al. 1998; Heaney et al. 1999; Stier and Mildenstein 2005). Populations of species inhabiting middle or higher elevation forests, such as *Haplonycteris fischeri*, *Harpyionycteris whiteheadi*, and *Otopteropus cartilagonodus*, are thought to be more stable, but remain vulnerable to changes in extent and quality of habitat (Heaney et al. 1998). Observations by Paalan et al. (2004) suggest that a number of Philippine pteropodids, including some threatened endemics, are somewhat tolerant of moderate forest fragmentation. At least 29 of the country's 52 microchiropteran species also inhabit forest, and many are undoubtedly affected by habitat loss. Heaney et al. (1998) reported that the cutting of large hollow trees during logging has caused substantial harm to some rhinolophids and hipposiderids, particularly those inhabiting lowland dipterocarp forests. Populations of cave-dwelling species (e.g., *Hipposideros bicolor*, *H. pygmaeus*, and *Miniopterus schreibersii*) may be decimated by the elimination of forested foraging habitat near roost caves (Heaney et al. 1999).

Deforestation is a known or potential concern for at least 8 of 37 megachiropterans and 1 microchiropteran in Papua New Guinea (Bonaccorso 1998). Intensive logging on New Britain and New Ireland threatens several species with relatively small geographic distributions, including *Dobsonia praedatrix*, *Pteropus capistratus*, and *Kerivoula myrella* (Bonaccorso 1998). In the Solomon Island chain, habitat disturbance has been implicated in the possible extinction of *Nyctimene sanctacrucis* (Mickleburgh et al. 1992), and timber harvest threatens several rare species of *Pteralopex* that are heavily reliant on primary forests (Bowen-Jones et al. 1997; Fisher and Tasker 1997; Helgen 2005). *Pteralopex taki* roosts in the hollows of large-diameter trees and is therefore vulnerable to

selective timber cutting, as evidenced by its apparent extirpation from the island of Kolombangara following extensive logging operations in the 1970s (Fisher and Tasker 1997; Flannery 1995).

Although total forest coverage has changed little in Fiji and Samoa since 1990, there has been a significant qualitative shift toward increasing amounts of secondary forest and disturbed forest dominated by introduced species (J. Atherton, pers. comm.). Habitat concerns are a conservation issue for all six bat species present in the two island groups (Palmeirim et al. 2005; Palmeirim et al. 2007; Wilson and Engbring 1992). *Pteropus samoensis* is especially dependent on tracts of native forest to meet its foraging and roosting needs, but even *P. tonganus*, which feeds more extensively in disturbed areas, has lost habitat with the conversion of lands to grasslands, sugarcane plantations, and other open sites (Banack 1998; Palmeirim et al. 2005; Palmeirim et al. 2007; Wilson and Engbring 1992). *Mirimiri acrodonta* is restricted to a small area of montane forest on Taveuni, Fiji, most of which is secure within Bouma National Heritage Park. However, further forest clearing on unprotected lower slopes in the future could result in more foraging by *P. tonganus* at higher elevations, thereby increasing competition for *M. acrodonta* (Palmeirim et al. 2005). On a localized scale, Palmeirim et al. (2005, 2007) noted that the removal of large overstory trees outside the mouths of caves used by *Emballonura semicaudata* can promote the growth of shrubby vegetation, thereby blocking entrances and preventing bats from entering.

In Micronesia the largest anthropogenic forest loss on any island during the past several decades has occurred on Pohnpei, where more than 70% of the remaining upland native forest has been destroyed or heavily degraded since 1975 by intensified cultivation of the shrub *Piper methysticum* (Merlin and Raynor 2005), which is used to produce the mildly narcotic drink known as kava or *sakau*. About 120 km² of upland forest was lost by 2002, representing a decline from 42% to 15% of the island's land cover. The impacts of such loss on Pohnpei's two bats, *Pteropus molossinus* and *Emballonura semicaudata*, are unknown but may be moderately severe. On Aguiguan in the Commonwealth of the Northern Mariana Islands, the occurrence of *E. semicaudata* is probably closely linked to the island's remaining forest cover (Esselstyn et al. 2004b). Nonnative ungulates have had an important role in damaging forests and reducing forest cover on a number of the Marianas (Kessler 2002; Wiles et al. 1999; Worthington et al. 2001).

Although large-scale deforestation is certainly harmful to most bat species in insular Southeast Asia and Oceania, many taxa are in fact tolerant of limited anthropogenic habitat modification. This probably results from the long history of human disturbance to native forests in much of the region (e.g., Bayliss-Smith et al. 2003; Mercado 2003) and, for megachiropterans, to the often-shared fruit preferences among bats and people (Marshall 1983; Wiles and Fujita 1992). Near human settlements, sizable areas of forest have long been

converted to agroforest, where tree crops such as breadfruit, coconuts, mangos, avocados, bananas, and numerous other species are interspersed among native trees. Coconut plantations, another food source for pteropodids, have also been widely established for commercial purposes. More than half of the 96 pteropodid species occurring in New Guinea, the Moluccas, and Oceania regularly enter younger secondary forests, gardens, and plantations to feed (Bonaccorso 1998; Flannery 1995; Helgen 2007). This number is lower in the Philippines, where only 7 of 26 megachiropterans visit these types of heavily altered habitats (Heaney et al. 1998). Several widespread taxa (e.g., *Cynopterus brachyotis*, *Eonycteris spelaea*, *Macroglossus minimus*, *Pteropus hypomelanus*, and *Rousettus amplexicaudatus*) are particularly common in agricultural lands, urbanized areas, and disturbed forests, indicating that they have benefited from large-scale habitat change (Abdullah et al. 1997; Hall et al. 2004; Heaney et al. 1998; Helgen 2007; Mickleburgh et al. 1992; Mohd-Azlan et al. 2003). Examples of species known to forage extensively in agroforest include *Melonycteris melanops* (Bonaccorso 1998; Flannery 1995), *Macroglossus minimus* (Bonaccorso 1998; Flannery 1995), *Pteropus tonganus* (Banack 1998; Banack and Grant 2003; Nelson 2003; Palmeirim et al. 2005), and *P. mariannus yapensis* (Falanruw 1988).

By virtue of their many caves and fissured cliffs, limestone karst landscapes are of inherent importance to bat populations across much of the region (e.g., Alcala et al. 2004; Lee et al. 2007; Suyanto and Struebig 2007). However, economic expansion has brought increasing destruction of these ecologically sensitive environments (Clements et al. 2006; Whitten 2002). Karsts are most threatened by quarrying for limestone, which is used in the manufacturing of cement and other products. Wildfires and deforestation are additional concerns.

A number of nations in the region, especially Indonesia, the Philippines, Papua New Guinea, the Solomons, Vanuatu, Japan, and the Northern Mariana Islands, are positioned along the edges of tectonic plates and experience regular volcanic activity. The impacts of volcanism on bat populations in these countries have been rarely described, but major eruptions resulting in the destruction of forested habitats can eliminate or reduce populations on a local scale (also see Pedersen et al., chapter 11, this volume). For example, in the Northern Marianas, recurring volcanic activity since 2003 has eliminated nearly all forest and flying foxes on the island of Anatahan (C. C. Kessler, pers. comm.). This island, which is 32 km² in area, was considered one of the most important remaining sites for *P. mariannus* in the 1980s and 1990s (Wiles et al. 1989; Worthington et al. 2001). Eruptions on other Mariana Islands have reduced the amount of forest available for bats during the past few centuries (Wiles et al. 1989). Tidemann et al. (1990) described the gradual recolonization of the Krakatau Archipelago and nearby parts of Java by at least 11 species of pteropodids and 20 microchiropterans following the cataclysmic eruption in 1883 (also see Shilton and Whittaker, chapter 7, this volume). Long Island off eastern New Guinea lost its biota in a similar destructive eruption in about

1645 and has since been reinhabited by six pteropodids and a single microchiropteran (Thornton et al. 2001).

Hunting

Flying foxes and other bats continue to be a traditional food and delicacy on many islands, although not on all. Historically, flying foxes were taken with a variety of tools and techniques, such as stone projectiles, sticks, long-handled hoop nets, tree platforms, bows and arrows, blowguns, and thorny vines as the bats came to feed at fruiting or flowering trees or flew near the ground at certain locations along flyways (e.g., Chambers and Esrom 1988; Fritz 1904; Kubary 1885; Loeb 1926; MacGillivray 1860). Cave-dwelling pteropodids (e.g., *Dobsonia moluccensis* and *Notopteris macdonaldi*) were sometimes caught by blocking cave entrances with vegetative barricades or fire, and then capturing the animals trapped inside by various means (Dwyer 1968; Palmeirim et al. 2005). Harvesting of bats sometimes involved considerable ritual (Falanrui 1988). As with many birds, aboriginal hunting pressure probably contributed to the extinctions of some megachiropteran species or populations, although habitat loss and ecological changes associated with human settlement were also likely involved (Koopman and Steadman 1995; Steadman 1995, 2006; Weisler et al. 2006).

Within the past 50 years, improved road and boat access to remote areas; the wider availability of firearms, air rifles, and nets; and fewer cultural restrictions have enabled hunters to take increased numbers of flying foxes and other bats relatively easily. In some locations, growing human populations and increased access to markets have also produced greater demand for bats. Overhunting for both subsistence and commercial purposes is considered the greatest threat to larger pteropodids on many islands, including some with few or no people (Brooke and Tschapka 2002; Cousins and Compton 2005; Craig et al. 1994a; Heaney and Heideman 1987; Pierson et al. 1996; Riley 2002b; Stinson et al. 1992; Wiles 1992; Wiles et al. 1989; Wiles et al. 1997). Unfortunately, in many areas where these bats were historically abundant, there are no data on population size to evaluate the impacts of hunting. To our knowledge, the hunting of flying foxes and other pteropodids is not managed sustainably anywhere in the region.

Detailed information on the extent of hunting is rarely available for any population, and no study has monitored long-term harvest levels. Most data have been collected via interviews or questionnaires of hunters and nonhunters. One of the best documented cases is for Niue, where an annual hunting season for *Pteropus tonganus* lasts 2–4 months. In 1998, field surveys estimated the flying fox population at between 2,000–4,000 animals. Interviews after the hunting season estimated that a quarter to half of the bat population was killed (Brooke and Tschapka 2002). Based on the population's size and the reproduc-

tive potential of the species, the number of bats removed was clearly unsustainable. Widespread misperceptions regarding the actual abundance of bats played a significant role in overhunting. Older hunters remembered a much larger bat population in the past and supported limits on hunting, but many others believed an infinite number of bats roosted in areas protected from hunting by a taboo and consequently thought the hunt could continue with no impact on the bat population.

Annual harvests of *Pteropus tonganus* and *P. samoensis* on Tutuila, American Samoa, were estimated to total 500–1,600 animals under normal conditions during the early 1990s (Craig et al. 1994a). However, the increased vulnerability of bats after Cyclone Ofa resulted in an estimated 3,100 bats being killed within six months of the storm.

In Palau, Wiles et al. (1997) estimated roughly that up to 2,000–5,000 *P. mariannus pelewensis* were killed annually and that as many as 40–50% of Palauans occasionally ate bats. Harvest levels of *P. tonganus* are also high in the Cook Islands, although Cousins and Compton (2005) did not estimate total take. Based on questionnaire results, they determined that 8% and 20% of adult respondents on Rarotonga and Mangaia, respectively, hunted flying foxes more than twice per year. The majority of people had little idea of the threat that hunting posed to local bat populations, but most supported restrictions if declining numbers of animals could be demonstrated.

In parts of northern Sulawesi, Indonesia, bats are hunted as a source of meat for family and neighbors and perhaps to limit crop depredation (Lee 2000). Bats, presumably mostly pteropodids, were the second most commonly harvested taxonomic group after rodents, comprising 19–25% of the total wild animals caught in and around two protected areas. Thousands were taken annually and greatly exceeded ungulates, primates, and cuscuses in total biomass. Subsistence hunting of pteropodids also occurs in Java (Fujita and Tuttle 1991), the Sangihe and Talaud Islands (Riley 2002b), Kalimantan (Mohd-Azlan et al. 2003), northern Sumatra (G. Fredriksson, pers. comm.), and probably many other parts of the country.

Pteropodids, including *Eonycteris spelaea* and *Acerodon leucotis*, were among the more commonly caught animals by an impoverished community of shifting cultivators in southern Palawan, Philippines (Shively 1997). Bats and other small game species were exploited on a subsistence basis and were probably targeted because they provided greater hunting success in comparison to larger mammals. Small pteropodids were hunted by 14% of households, with members of those households making an average of 20 trips per year to seek bats and catching a mean of 11.7 bats per trip. Among the 9% of households that hunted *Acerodon leucotis*, a mean of 15 trips per household was made annually to obtain this species, with 3.9 bats caught per trip on average. Blowguns and poles armed with thorns or fish-hooks were the primary capture methods. In a second Philippine study,

bats comprised 11 of the 72 bird and mammal species killed by hunters on Negros (Cariño et al. 2006). Three threatened species (*A. jubatus*, *Dobsonia chapmani*, and *Pteropus pumilus*) were among those captured. Although harvest rates were not calculated, bats collectively were regularly hunted. Most hunters were subsistence farmers who tended to be poorly educated, earned low incomes, and killed bats and other wildlife primarily for home consumption. Remaining hunters were mostly better-educated professional or skilled workers who hunted for recreation. The main capture methods in this study were nylon lines with hooks and air guns.

Megachiropterans are widely hunted in both the Philippines and Papua New Guinea, where at least 14 of 26 species and 12 of 37 species are caught, respectively (Bonaccorso 1998; Esselstyn 2007; Flannery 1990; Heaney et al. 1998; Mickleburgh et al. 1992; Shively 1997; Utzurrum 1992). Even small species such as *Syconycteris australis* are sometimes taken (Craven 1988). Hunting in these countries seriously threatens at least three species, *Acerodon jubatus*, *Aproteles bulmerae*, and *Dobsonia chapmani* (Alcala et al. 2004; Cariño 2004; Flannery and Seri 1993; Heaney and Heideman 1987; Heaney et al. 1998; Paguntalan et al. 2004), and possibly a fourth, *Styloctenium mindorensis* (Esselstyn 2007). Although most species in Papua New Guinea are harvested for their meat, *Dobsonia inermis* and *Melonycteris woodfordi* are collected for their canine teeth, which are used in ornamental necklaces (Bonaccorso 1998).

In Vanuatu, Chambers and Esrom (1988) reported that flying foxes were a common part of the diet and that most people ate them at least occasionally. Recent evidence from Fiji suggests that hunting pressure differs among species. Palmeirim et al. (2005) reported that hunting of *Pteropus tonganus* and *P. samoensis* may be declining because of greater access to alternative forms of protein through modern commerce. However, exploitation remains a concern for *Notopteris macdonaldi* and may be causing some populations in Fiji to decline. In the Mariana Islands, hunting of *P. mariannus* continues on most islands despite legal protection for the species (Lemke 1992; Wiles et al. 1989; Worthington et al. 2001; G. J. Wiles, pers. obs.). Bats are regularly killed on islands with larger numbers (i.e., Rota and islands in the northern half of the island chain) and then smuggled to the main inhabited islands of Saipan, Tinian, and Guam. In 2006 and 2007, bats sold for US\$40 on Rota (P. Wenninger, pers. comm.) to as much as \$100 per animal on Tinian and Saipan. Illegal hunting is also widespread for *P. ornatus* in New Caledonia (Flannery 1995). Hunting has probably caused the near extinction of the subspecies *P. dasymallus formosus*, which survives only on Luta Island (also known as Green or Kashoto Island) off Taiwan (Rainey 1998).

Hunting pressure has not been well-documented in the Solomon Islands, but at least one species, *Pteropus rayneri*, is hunted heavily (Flannery 1995). However, other reports indicate that most people apparently consume pteropodids only on an infrequent basis (Bowen-Jones et al. 1997; Fisher and Tasker

1997; Whewell 1992). In Tonga, harvests of *P. tonganus* appear to be relatively small and of no threat to populations (K. R. McConkey, pers. comm.), and on Ulithi Atoll in the Carolines, only small numbers of people hunt and eat flying foxes (Wiles et al. 1991). On some islands, such as Chuuk, Pohnpei, and Kosrae, bats are not hunted for local use (Rainey 1990).

Cultural factors are sometimes involved in the hunting of pteropodids on islands where people have retained more of their traditional values. For example, on Yap, where flying foxes are considered less desirable than marine foods, only people of certain social strata with limited or no access to the coast hunt flying foxes (Falanruw 1988; M. V. C. Falanruw, pers. comm.). Religious and cultural beliefs prevent some people from eating or catching flying foxes in Vanuatu (Bani 1992; Chambers and Esrom 1988). Localized superstitions also afford some protection to several pteropodids in Papua New Guinea (Flannery and Seri 1990). Traditional hunting methods continue to be employed in some remote locations (Chambers and Esrom 1988; Palmeirim et al. 2005).

Sizable commercial markets for Pacific flying foxes became established on Guam during the 1960s and in the neighboring Northern Mariana Islands probably sometime between the late 1970s and 1985 (Stinson et al. 1992; Wiles 1992; Wiles and Payne 1986; Wiles et al. 1997). This trade resulted in the importation of between 7,600 and 29,500 bats annually (mean = 13,960) to Guam from 1975 to 1994, although estimates exceeding 19,000 animals per year from 1976 to 1980 are very likely inflated. Smaller numbers of flying foxes were shipped to the Northern Marianas, ranging from 750 to 8,600 bats annually (mean = 4,682) from 1986 to 1994. Flying foxes from 11 islands or island groups dominated the trade, with those in Palau, Yap, Pohnpei, Chuuk, Samoa, American Samoa, and perhaps Kosrae seriously depleted for several years or longer (Rainey 1990; Wiles 1992; Wiles et al. 1997). During the 1970s and early 1980s, bats were sent to Guam mainly from nearby islands (i.e., Palau, Yap, Rota, Saipan, and Tinian). However, depletion of many of these sources and changing business factors led to greater exploitation of bat populations on more distant islands (i.e., Samoa, American Samoa, Pohnpei, Tonga, Papua New Guinea, and the Philippines) from about 1982 to 1990 (Wiles 1992). This international trade was greatly restricted in 1989 after seven of the species involved were added to appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and all remaining *Pteropus* and *Acerodon* were placed on appendix II. However, trade continued until 1994 because of a loophole that allowed the importation of Palauan bats (Wiles 1994). Little international smuggling of bats has occurred since then, and it appears that CITES restrictions have been highly successful in terminating this trade (G. J. Wiles, pers. obs.). Several important factors facilitated the existence of this trade, including the expansion of interisland airline traffic, greater availability of refrigeration, and the greater affluence of Chamorro consumers in Guam and the Northern Marianas (Wiles and Payne 1986). Elsewhere in the Pacific,

small-scale shipments of *Pteropus* from Vanuatu to New Caledonia were documented in the 1990s (Rainey 1998).

Intensive hunting to supply market demand is a major threat to flying foxes and other pteropodids in parts of Indonesia, especially northern Sulawesi and Kalimantan (Bergmans and Rozendaal 1988; Clayton and Milner-Gulland 2000; Fujita and Tuttle 1991; Lee et al. 2005; Struebig et al. 2007). Five species, *Pteropus vampyrus*, *P. hypomelanus*, *P. alecto*, *Acerodon celebensis*, and *A. humilis*, have been exploited in alarmingly high numbers, resulting in large population declines (Fujita and Tuttle 1991; Lee et al. 2005; Struebig et al. 2007). Muslim religious beliefs protect many wildlife species from being hunted, but in areas with non-Muslim populations, flying foxes have been intensively hunted as a delicacy and a medicinal. Bat meat and liver are valued as a cure for kidney ailments, general malaise, and respiratory problems, particularly by ethnic Chinese (Fujita and Tuttle 1991). North Sulawesi is a major center of commercial bat harvest, with at least 13 species of 11 pteropodid genera sold (Bergmans and Rozendaal 1988). Hunttable populations of bats reportedly have been eliminated over much of the peninsula (Argeloo 2001 cited in Bergmans 2001; Lee et al. 2005), and hunting to supply demand occurs increasingly farther from Manado and other cities (Bergmans 2001; Lee et al. 2005; Riley 2002a, 2002b). Market surveys indicate that although large numbers of bats are sold, they typically comprise just a small proportion of the total revenue earned by wild meat dealers (Clayton and Milner-Gulland 2000). Riley (2002b) described aspects of the trade in the Sangihe and Talaud Islands. In portions of Kalimantan, demand for flying foxes has expanded greatly since the mid-1990s, especially in the city of Palangkaraya (Struebig et al. 2007). In peat swamp forests near the city, hunters captured over 4,500 *P. vampyrus* during a single month in 2003, when animals became seasonally common (Struebig et al. 2007). Hunters observed noticeable declines in catches between the early to mid-1990s and 2005, and extended their harvest activities to more distant locations. Significant numbers of *Pteropus* are also marketed in Jakarta (Fujita and Tuttle 1991), and commercial harvesting of *Pteropus* and *Rousettus* has been recently observed in northern Sumatra (G. Fredriksson, pers. comm.).

In Sarawak, hunting is thought to be an important cause in the decline of *Pteropus vampyrus* (M. Gual, pers. comm. in Hall et al. 2002), with large numbers being sold in the capitol of Kuching during the late 1980s (Fujita and Tuttle 1991). Heavy market hunting may have eliminated a colony of about 12,000 *Eonycteris spelaea* from Niah Cave during the 1990s (Hall et al. 2002). In this case, trapping occurred inside the cave, a designated national park. This species is caught at other caves in Sarawak as well.

Bats are occasionally sold in local markets throughout the Philippines (T. L. Mildenstein, pers. comm.; L. R. Heaney, pers. comm.), but the extent of this trade is poorly documented. Numbers are probably much smaller than the

number killed for personal consumption. *Acerodon jubatus* and *Pteropus vampyrus* are among the species sold (Cariño 2004; Cayunda et al. 2004).

Smaller commercial markets catering to local demand exist elsewhere. For example, in Palau, a significant portion of the *Pteropus mariannus pelewensis* killed are sold in town rather than being eaten by the hunter's family (G. J. Wiles, pers. obs.), whereas in Vanuatu, only small numbers are available in markets (Chambers and Esrom 1988). In both island groups, a few restaurants serve small numbers of flying foxes to tourists (Chambers and Esrom 1988; Wiles et al. 1997), and one Vanuatu hotel advertises bat hunting on its web site. At least two species of megachiropterans, *P. neohibernicus* and *Dobsonia inermis*, are sold locally in Papua New Guinea (Bonaccorso 1998). There is minor demand for *P. tonganus* in Fiji, with hunters occasionally selling animals directly to customers (Palmeirim et al. 2005; Palmeirim et al. 2007).

The extent that microchiropteran populations in the region are hunted for food or for medicinal purposes is poorly understood, but a number of species are probably caught. *Miniopterus* species and other cave-dwelling insectivorous bats are collected from accessible roost sites by traditional peoples in New Guinea (Craven 1988; Flannery and Seri 1990). Bergmans and Rozendaal (1988) occasionally found microchiropterans, including *Cheiromeles parvidens*, being sold in markets in northern Sulawesi. Hunting is considered a contributing factor in the declines of *Cheiromeles torquatus* in Borneo (Hall et al. 2002; Hutson et al. 2001) and *Chaerephon bregullae* in Fiji (Palmeirim et al. 2005; Palmeirim et al. 2007). Species roosting in bamboo culms (possibly *Tylonycteris*) and furled banana leaves (*Myotis muricola*) are eaten in Kalimantan (Mohd-Azlan et al. 2003). Hutson et al. (2001) remarked on the heavy harvest of insectivorous bats in the Solomon Islands, but did not provide details. *Scotophilus kuhlii* is sometimes harvested in the Philippines, as documented by the presence of 64 animals in a shipment mistakenly sent to Guam in 1987 during the flying fox trade (G. J. Wiles, unpublished data).

Cave Disturbance

Natural and artificial caves provide permanent shelter for numerous bat species in the region. Many locations serve as traditional day roosts and maternity sites, and may be inhabited by more than one species. Sites can support anywhere from one or a few individuals to colonies of thousands. Suitable caves are frequently limited in availability; thus animals often display strong attachment to particular sites. As commonly noted elsewhere in the world (Hutson et al. 2001), sustained disturbance at caves can result in severe long-term impacts on the viability of resident bat populations. In insular Southeast Asia and the tropical Pacific, cave-dwelling bats are vulnerable to many forms of human disturbance, such as guano mining, the collection of edible swiftlet (*Aerodramus* spp.) nests, hunting within caves, rock quarrying, and visitation

by tourists, cavers, and vandals (Hutson et al. 2001). Rates of cave disturbance are considered especially high in the Philippines (Cariño 2004; Hutson et al. 2001), but this is true of other areas as well. Indonesia and Malaysia are by far the largest sources of swiftlet nests for the international nest trade (Lau and Melville 1994), with many caves in both countries experiencing heavy harvest pressure. In the past, nest gathering at some localities (e.g., parts of Sarawak) was traditionally restricted to two or three relatively short periods per year. However, expansion of the trade in recent decades (e.g., nest imports in Hong Kong increased threefold between 1959 and 1988) has led to greater levels of visitation by collectors, many of who now work year-round (Lau and Melville 1994). This has undoubtedly resulted in significantly more disturbance of bats sharing the same caves.

The region's cave-dwelling fruit bats include *Aproteles bulmerae*, *Penthetor lucasi*, and species of *Rousettus*, *Dobsonia*, *Eonycteris*, *Notopteris*, *Ptenochirus*, and *Cynopterus*. Most species roost in the dimly lit portions of caves or beneath overhangs at cave entrances, but *Rousettus* are able to inhabit the deeper reaches of caves because of their ability to echolocate. To date, human activity at caves has been identified as a serious threat to *A. bulmerae*, *D. anderseni*, *D. chapmani*, *E. spelaea*, *N. macdonaldi*, *N. neocaledonica*, *R. amplexicaudatus*, and possibly *D. inermis* (Bonaccorso 1998; Heaney et al. 1998; Heaney et al. 1999; Mickleburgh et al. 1992; Palmeirim et al. 2007). Two of the primary factors for the rarity of *D. chapmani* are cave disturbance from guano mining and the harvesting of animals inside caves (Heaney and Heideman 1987; Paguntalan et al. 2004). These same problems, plus limestone mining at caves, threaten *E. spelaea* in the Lesser Sundas of Indonesia (Mickleburgh et al. 1992). The remaining populations of *N. macdonaldi* in Fiji and *N. neocaledonica* in New Caledonia are both known from small numbers of caves and are therefore particularly vulnerable to disturbance (Flannery 1995; Mickleburgh et al. 1992; Palmeirim et al. 2005; Palmeirim et al. 2007). Dwyer (1968) described the disruptive activities that traditional hunters can have at caves occupied by megachiropterans, in this case *D. moluccensis*.

Only anecdotal accounts seem to exist describing the effects of human cave visitation on the region's microchiropterans. In the Philippines, populations of many rhinolophid species and the molossid *Chaerephon plicatus* have been harmed by cave disturbance, with extirpation of some colonies occurring for *C. plicatus* (Heaney et al. 1998). Heaney et al. (1999) reported that few if any caves in the vicinity of Mount Isarog, Luzon, have escaped frequent disturbance from guano miners and bat hunters. Recreational caving is also considered a growing problem in the country (Hutson et al. 2001). Swiftlet nest collecting is a major disruptive factor for cave bats on the Sangkulirang peninsula of eastern Kalimantan (Suyanto and Struebig 2007) and is partially responsible for the large declines of *Cheiromeles torquatus* in Sarawak (Hutson et al. 2001). Hsu (1997) identified the closure of caves by farmers during the expansion of

croplands as the main threat to bats in Kenting National Park on Taiwan. On Iriomote island in the Ryukyu Islands, publicity on the threatened status of *Hipposideros turpis* produced the undesired outcome of greater public visitation of the caves occupied by the bats (Hutson et al. 2001). During World War II, major cave disturbances and closures must have negatively impacted *Emballonura semicaudata* and other insectivorous species in Micronesia and other parts of the Pacific war theater. However, cave disturbance by people is not currently considered an important threat to *E. semicaudata* (Grant et al. 1994; Palmeirim et al. 2005; G. J. Wiles, unpublished data). Although not directly related to human visitation, forest fires of probable anthropogenic origin have burned into ground-level caves and apparently eliminated resident bat colonies in eastern Kalimantan (Suyanto and Struebig 2007).

Severe Storms

Severe tropical cyclonic storms, known variously as typhoons, cyclones, or hurricanes, are regular occurrences on many Pacific islands, the Philippines, and Taiwan. Most storms produce relatively minor localized damage to natural ecosystems on affected islands and have few if any impacts on bat populations. However, exceptionally strong storms occasionally cause far more damage to forests, which may not recover for several years or longer. The effects of such storms on bat populations can be disastrous, as evidenced by the substantial reductions in flying fox abundance at various locations in both the Pacific and Indian Oceans (Pierson and Rainey 1992). This is especially true in areas of extensive deforestation, where storms may leave no refugia for bats (Pierson et al. 1996). In American Samoa and Samoa, *Pteropus tonganus* and *P. samoensis* decreased by an estimated 80–99% following Cyclone Ofa in 1990 and Val in 1991 (Craig et al. 1994b; Pierson et al. 1996). A similar overall decline of about 80% in *P. tonganus* occurred in the Vava'u archipelago of Tonga following Cyclone Waka in 2001 (McConkey et al. 2004). On the island of Rota in the Northern Marianas, numbers of *P. mariannus* were reduced by an estimated 57% after Typhoon Roy in 1988 (Stinson et al. 1992) and 70% after Typhoon Pongsona in 2002 (Esselstyn et al. 2006). Storm-related losses have been reported, but not quantified, from other locations, including Niue (*P. tonganus*, Cyclone Heta in 2004, Anonymous 2005), the Solomon Islands (*P. rayneri* and *P. tonganus*, Cyclone Namu in 1986, Flannery 1989; *Pteropus* sp., Cyclone Ida in 1972, Bowen-Jones et al. 1997), Vanuatu (*Pteropus* sp., Chambers and Esrom 1988), Fiji (*P. tonganus* and *P. samoensis*, Palmeirim et al. 2005; Palmeirim et al. 2007), and Guam (*P. mariannus*, Wiles 1987b).

Accounts indicate that flying foxes usually suffer much greater mortality during the several months following tropical cyclones than from high winds and flying debris during storm passage. Poststorm mortality typically results from starvation, dehydration, overhunting for food and recreation, and

predation. Extensive defoliation of forests during severe storms not only greatly reduces food availability, but also increases vulnerability to hunting by removing protective cover. Starvation can drive bats to forage diurnally in places they would otherwise avoid, such as on or near the ground and in areas of human activity (e.g., near villages and in plantations). This further exposes animals to human hunting as well as predation. The impacts of cyclone-caused resource scarcity on flying fox populations are probably density-dependent, with smaller (i.e., less dense) populations less likely to be affected. Pierson et al. (1996) observed that *P. tonganus* in Samoa and American Samoa displayed far fewer overt signs of starvation after Cyclone Val than when populations were much larger two years earlier following Cyclone Ofa. Guam's small population of *P. mariannus* showed no evidence of food stress after several major typhoon strikes during the 1990s (G. J. Wiles, pers. obs.) and another in 2002 (Esselstyn et al. 2006). This was also true on Rota, where *P. mariannus* occurs below carrying capacity as well, after two of three large typhoons since 1988 (Esselstyn et al. 2006). However, when combined with restricted ranges or forest availability, even small populations can become vulnerable to extirpation following the worst storms (Palmeirim et al. 2005; Robertson 1992).

Starvation and ground foraging after tropical cyclones have been described by a number of authors (Anonymous 2005; Craig et al. 1994b; Daschbach 1990; Esselstyn et al. 2006; Flannery 1989; McConkey et al. 2004; Palmeirim et al. 2005; Pierson et al. 1996), and flying foxes "blown to the ground" in Vanuatu (Chambers and Esrom 1988) were probably in fact animals searching for food. This type of feeding behavior can result in considerable predation by cats, dogs, and domestic pigs, and even mortality from vehicles on roadways (Anonymous 2005; Palmeirim et al. 2007; Pierson et al. 1996).

Intensive harvest of food-stressed flying foxes has been documented on several islands after major tropical cyclones (Pierson and Rainey 1992). Hunting of *P. tonganus* and *P. samoensis* was severe in Samoa and American Samoa after Cyclone Ofa (Pierson et al. 1996), with data suggesting that it was responsible for about half of all mortality in American Samoa (Craig et al. 1994b). Many bats were apparently killed by boys for recreation rather than for food (Daschbach 1990). Stinson et al. (1992) reported that hunting accounted for roughly two-thirds of the decline in *P. mariannus* on Rota following Typhoon Roy, with hunting-related emigration to neighboring islands responsible for the remaining losses. Intensified poaching also occurred on Rota after Typhoon Pongsona and again caused the majority of the population's decrease (Esselstyn et al. 2006). The capture of large numbers of ground-foraging flying foxes after cyclones has been noted in Vanuatu (Chambers and Esrom 1988) and the Solomons (Flannery 1989). Hunting was also detected in Tonga after Cyclone Waka (McConkey et al. 2004). On Niue, Cyclone Heta struck during the annual hunting season for *P. tonganus* and apparently exacerbated harvest mortality (Brooke 2004).

Direct storm mortality has been documented in only a few instances. S. Campbell (pers. comm.) observed 40–50 dead *P. tonganus* washing ashore in a small bay following Cyclone Waka in Tonga, indicating that animals were blown into the sea and drowned (McConkey et al. [2004] reported this as “large numbers”). Wiles (1987b) presented secondhand evidence of dead *P. mariannus* found under roost trees on Guam.

Flowers and fruits from plants that are sturdy enough to sustain relatively less damage from high winds have been identified as important foods for flying foxes in the first few months following severe tropical cyclones. Examples include coconut flowers (McConkey et al. 2004; Pierson et al. 1996), flowers and fleshy bracts from the woody liana *Freycinetia reineckeii* (Pierson et al. 1996), and *Pandanus* fruits (Stinson et al. 1992). Emerging leaves and petioles can also be important soon after storms (Nelson et al. 2000b; Pierson and Rainey 1992). Although forest recovery usually proceeds fairly rapidly, it can lag substantially after the worst of storms (Elmqvist et al. 1994). In Tonga, McConkey et al. (2004) observed that food resources for flying foxes were still reduced by 85% or more six months after the passage of Cyclone Waka.

Damage from severe tropical cyclones can be highly disruptive to normal foraging and roosting behavior in flying foxes. Food-stressed individuals may respond by becoming more active for longer periods while searching for food and increasing their daytime foraging effort (Esselstyn et al. 2006; Grant et al. 1997; Pierson et al. 1996; Stinson et al. 1992). Dramatic changes in roosting patterns may result from damage to roost trees, the sudden loss of food sources, and hunting and other human activity, or a combination thereof. Brooke et al. (2000) reported that colonies of *P. tonganus* broke into smaller groups and moved frequently among alternate sites after cyclones in American Samoa. This was probably caused initially by heavy damage to primary roost trees, but hunting and greater scarcity of food resources also likely contributed. Colonies coalesced and returned to prestorm roost sites on steep mountain slopes and cliff faces within four years. Stinson et al. (1992) observed a substantial increase in the number of solitary *P. mariannus* after Typhoon Roy on Rota in the Northern Marianas and attributed this to the greater effort needed to find food. However, repeated hunting incidents at the main roosts also kept colonies broken apart. In contrast, the single small colony of *P. mariannus* on Guam temporarily doubled in size the month after Typhoon Pongsona hit the island in 2002, most likely because of immigration from the neighboring island of Rota (Esselstyn et al. 2006).

Impacts of tropical cyclones on microchiropterans are poorly described. In American Samoa, Grant et al. (1994) reported that storm-generated waves from Cyclone Ofa may have destroyed nearly all of the bats in one of the few remaining colonies of *Emballonura semicaudata*, which resided in a sea cave. These authors also speculated that intense stormy weather during the four days of Cyclone Val's passage possibly prohibited foraging and perhaps caused some

animals to starve. Tarburton (2002) attributed the loss of one of the few known remaining colonies of *E. semicaudata* in Samoa to these same cyclones.

Tropical cyclones in the Pacific basin have grown in destructive power, but not frequency, since the mid-1970s in response to global climate change (Emanuel 2005). This trend, if it continues, will undoubtedly have major effects on many of the region's bat populations (Rainey 1998).

Introduced Species

Although the negative impacts of invasive species are commonly observed among island ecosystems (Courchamp et al. 2003; D'Antonio and Dudley 1995; Sherley 2000; Veitch and Clout 2002), relatively few harmful interactions between exotics and tropical Pacific bats have been described thus far. Probably the greatest effect occurs indirectly through perturbations to native habitats, thereby altering food availability for bats. A number of exotic species established in the region have produced large-scale changes in forest composition or reduced the abundance of particular plant species. Ungulates have been introduced to relatively few islands with pteropodids but have caused significant damage to ecosystems on those where they have become well established. On some islands in the Marianas, high densities of feral pigs (*Sus scrofa*), feral goats (*Capra hircus*), and Philippine deer (*Rusa marianna* [formerly *Cervus mariannus*]) have been linked to reduced plant diversity in forests and declines of various food species (e.g., *Artocarpus mariannensis*, *Pandanus tectorius*, *Premna obtusifolia*, *Pipturus argenteus*, *Dendrocnide latifolia*, and probably many others; Kessler 2002; Wiles 2005b; Wiles et al. 1999; Worthington et al. 2001; G. J. Wiles, pers. obs.). Ungulate damage to forests has also been reported in New Caledonia (Bouchet et al. 1995; de Garine-Wichatitsky et al. 2005) and Fiji (Ash 1992). Seed predation by introduced rats (*Rattus* spp.), which are common throughout the tropical Pacific, can substantially reduce the recruitment of some plant species (McConkey et al. 2003), thereby altering habitats. Ecosystem-wide changes such as these likely affect microchiropteran bats as well because of changes in the availability of invertebrate prey. Rats also feed on some fruits (e.g., *Terminalia* spp.) in situ and therefore may directly compete with frugivorous bats for food (Weisler et al. 2006; D. R. Drake, pers. comm.). Introduced insects also have the potential to eliminate some foods regularly eaten by flying foxes. For example, on Guam, a large scarab beetle (*Protaetia orientalis*) introduced in about 1972 commonly swarms on and consumes the freshly ripened fruit of seeded breadfruit (*Artocarpus mariannensis*; G. J. Wiles, pers. obs.), which is eaten by *Pteropus mariannus*. Another insect, the cycad aulacaspis scale (*Aulacaspis yasumatsui*), arrived on the island in 2002. It attacks *Cycas micronesica* and threatens to seriously reduce or entirely eliminate the species from Guam (Terry and Marler 2005). The erythrina gall wasp (*Quadrastichus erythrinae*) is now widespread on Tutuila, American Samoa, where it is destroying

Erythrina variegata, and is newly detected on Guam. These species are food sources for *Pteropus mariannus*, *P. tonganus*, and *P. samoensis*.

Only a few cases of introduced predators killing bats have been reported in the region, but these illustrate the vulnerability of island bats and show that the threat should not be minimized. On Guam, brown tree snakes (*Boiga irregularis*) have been implicated in the decline of *Pteropus mariannus*. Snakes were accidentally brought to the island in the aftermath of World War II, most likely in military cargo shipped from the Admiralty Islands. They are nocturnal and arboreal; individuals may grow as long as 3 m and are able to consume prey up to 70% of their body weight (Rodda et al. 1997; Rodda et al. 1999). Data collected at Guam's main colony of flying foxes from 1982 to 2006 have indicated a largely consistent pattern wherein small pups are routinely recorded with their mothers, but medium-sized young are much rarer, and large young are virtually absent (Wiles 1987b; Wiles et al. 1995; G. J. Wiles, unpublished data; D. S. Janeke, pers. comm.). Most observations were made in areas where native forest bird populations had collapsed, indicating the establishment of high densities of tree snakes. However, for several months in 1983 after the colony moved to a new location where native birds persisted, sizable numbers of larger pups were detected. It is unlikely that the snake played a role in the decline and loss of *Emballonura semicaudata* on the island (Fritts and Rodda 1998; G. J. Wiles, pers. obs.).

Predation on bats by nonnative mammalian predators has apparently been documented only in Samoa and Fiji, where domestic cats, dogs, and pigs have been observed killing *Pteropus* forced to forage on the ground near human habitations after the passage of cyclones (Palmeirim et al. 2007; Pierson et al. 1996). Feral cats have also been suggested as a potentially important predator of *E. semicaudata* in Fiji (Palmeirim et al. 2005; Palmeirim et al. 2007), but supportive data are lacking. Nevertheless, predation by exotic mammals, especially rats and cats, is probably more frequent than indicated by these few records. Support for this contention comes from several islands bordering the geographic area discussed in this chapter. Predation by feral cats, rats, and other mammals has been linked to declines in *Chalinolobus tuberculatus* and *Mystacina tuberculata* in New Zealand (Lloyd 2005; Pryde et al. 2005) and is suspected as a contributing factor in the possible extinction of *Nyctophilus howensis* on Lord Howe Island (Richards and Hall 1998). Feral cats regularly catch *Pteropus melanotus* feeding in shrubs and small trees on Christmas Island in the Indian Ocean (Tidemann et al. 1994), suggesting that other pteropodids may be vulnerable to this predator when circumstances lead to their foraging near the ground.

Other assorted interactions between bats and exotic species have been noted. Biting red ants became established on Choiseul in the Solomons in 1987 and may have altered the roosting patterns of *Pteropus rayneri* by discouraging the use of coconut trees (Bowen-Jones et al. 1997). In the Ryukyus, *P. dasymallus* occasionally die after becoming entangled in the leaf fibers of two nonnative

palms (*Roystonea regia* and *Washingtonia robusta*; K. Kinjo, unpublished data). Spennemann and Wiles (2002) described the deliberate introduction of a disease, avian cholera, to Upolu, Samoa, by European planters in the 1890s to control flying foxes in an effort to limit their damage to fruit crops. Replacement of native forest with introduced trees, especially for the establishment of monocultures for timber, can be detrimental to bats by reducing food availability and roosting opportunities (A. P. Brooke, pers. obs.). Exotic vines and other plants can grow densely at cave entrances (G. J. Wiles, pers. obs.), thereby blocking access for bats.

In contrast to the negative interactions described above, Pacific flying foxes have benefited from the establishment of a number of widely introduced plants that serve as food sources. These include a mix of Paleotropical and Neotropical species, with some of the more commonly recorded being *Annona* spp., *Artocarpus altilis*, *Cananga odorata*, *Carica papaya*, *Ceiba pentandra*, *Eugenia javanica*, *E. malaccensis*, *Mangifera indica*, *Musa* spp. *Passiflora* spp., *Persea americana*, *Psidium guajava*, *Spondias dulcis*, *S. pinnata*, and *Syzygium* spp. (Banack 1998; Nakamoto et al. 2007; Stier and Mildenstein 2005; Wiles and Fujita 1992; Wiles et al. 1997).

Species Accounts

Few populations of bats are regularly monitored in Oceania and insular South-east Asia. Here we briefly review the status and biology of four species from the Pacific whose populations are fairly well known on some islands.

Pteropus mariannus

IUCN endangered; threatened status for the United States; protected in the Commonwealth of the Northern Mariana Islands and on Guam.

Distribution and Genetics

Pteropus mariannus occurs in western and central Micronesia. Koopman (1993) recognized seven subspecies, as follows: *P. m. mariannus* in the southern Marianas, including Guam; *P. m. paganensis* in the northern Marianas; *P. m. ulthiensis* at Ulithi Atoll in the western Carolines; *P. m. pelewensis* at Palau; *P. m. yapensis* at Yap; *P. m. ualanus* at Kosrae; and *P. m. loochoensis* at Okinawa. Flannery (1995) classified *P. m. pelewensis*, *P. m. yapensis*, and *P. m. ualanus* as separate species without explanation, and Yoshiyuki (1989) split *P. m. loochoensis* as also distinct. Flannery's classification (1995) was provisionally followed by Simmons (2005), but we prefer to retain *P. m. pelewensis*, *P. m. yapensis*, and *P. m. ualanus* as part of the species until justification for separation is provided. Furthermore, *P. m. paganensis* is probably an invalid subspecies (Wiles et al. 1989). Preliminary analyses suggest that bats within the Marianas are genetically similar, but distinct from those in Palau (G. McCracken, unpublished data).

Biology

P. mariannus occupies a variety of habitat types, including native forest, coastal strand, mangroves, agroforest, and isolated trees in open areas (Falanruw 1988; Stinson et al. 1992; Wiles and Johnson 2004; Wiles et al. 1997; Worthington et al. 2001). The species is generally colonial, with roosts often containing hundreds of bats and rarely reaching as many as 2,000 animals (Falanruw 1988; Stinson et al. 1992; Wiles et al. 1989; Worthington et al. 2001). In several populations, however, most aggregations hold fewer than 75 bats (Wiles and Johnson 2004; Wiles et al. 1991; Wiles et al. 1997). Solitary animals are present in all populations and sometimes comprise a sizable portion of total numbers. Roosts form at locations seldom visited by people, such as near remote cliffs, at other isolated upland sites, and in mangroves (Falanruw 1988; Stinson et al. 1992; Wiles 1987a; Wiles et al. 1997). *P. mariannus* feeds on the fruits, flowers, and leaves of at least 78 plants (Wiles and Fujita 1992; Wiles et al. 1997). Young are born throughout the year in *P. m. mariannus* and *P. m. yapensis* (Falanruw 1988; Wiles 1987a).

Population Status

Wiles et al. (1989) estimated a total minimum population of 8,700–9,000 *P. m. mariannus* and *P. m. paganensis* for the entire Marianas chain in 1983 and 1984. Abundance has generally declined since then. Numbers on Guam decreased steadily through the 1990s (Utzurum et al. 2003) to fewer than 100 animals in 2006 (D. S. Janeke, pers. comm.). Rota's population has varied from about 2,600 to 1,000 bats since the mid-1980s, with hunting mortality being the major influence on abundance (Esselstyn et al. 2006; Stinson et al. 1992; Utzurum et al. 2003). Numbers stood at about 1,000 in 2003. Populations have remained low, generally fewer than 25 to 200 bats each, on Saipan, Tinian, and Aguihan since the 1970s (Utzurum et al. 2003). The population on Anatahan fell from a minimum of 3,000 bats in 1983 (Wiles et al. 1989) to about 2,000 bats in 1995 (Worthington et al. 2001). Intermittent volcanic eruptions since 2003 have covered much of the island with volcanic ash and further reduced bat numbers to about 110 animals in 2006 (C. C. Kessler, pers. comm.). Sarigan has generally maintained about 125–235 bats since the 1980s, although its population is sometimes supplemented by additional animals from neighboring islands (Wiles and Johnson 2004). The northernmost islands of Guguan, Alamagan, Pagan, Agrihan, Asuncion, and Maug have not been fully surveyed since 1983–1987, when minimum populations were estimated to total about 4,300 bats (Utzurum et al. 2003; Wiles et al. 1989). Brief visits in 2000 and 2001 to some islands were inconclusive.

Population information is much sparser for the other subspecies. Surveys of *P. m. pelewensis* in Palau in 1991 and 2005 did not yield population estimates, but found the subspecies to be fairly common in 1991 and somewhat more abundant in 2005 (Wiles et al. 1997; G. J. Wiles, unpublished data). At Yap,

P. m. yapensis increased from about 1,000 bats in 1981 to about 2,500–5,000 bats in 1986 (Mickleburgh et al. 1992), but no estimates have been made since then. Numbers of *P. m. ulthiensis* at Ulithi Atoll have not been surveyed since 1986, when Wiles et al. (1991) estimated a total of 895–1,060 bats. No valid population estimates exist for *P. m. ualanus*.

Pteropus tonganus

IUCN least concern; protected in Samoa and American Samoa; partially protected in Tonga; five-year ban on hunting in Niue beginning in 2004.

Distribution and Genetics

Pteropus tonganus occurs widely across the southern Pacific (Miller and Wilson 1997). Genetic studies using allozyme electrophoresis and mtDNA found no evident geographic pattern in *P. t. tonganus*, which appears to form a single wide-ranging population from Fiji to the Cooks (Ingelby and Colgan 2003; Utzurrum et al. 2000). Distribution of this subspecies formerly extended eastward to at least Rurutu in the Austral Islands of French Polynesia (Weisler et al. 2006). Two other subspecies include *P. t. geddiei* at New Caledonia, Vanuatu, and the Solomons, and *P. t. basilicus* on Karkar and Koil islands off northern New Guinea (Flannery 1995).

Biology

Colonies range in size from a few individuals to several thousand and prefer tall emergent trees for roosting. Where bats are hunted, colonies seek sites that are difficult for people to reach: cliffs, volcanic craters, steep hills, mangrove swamps, and small uninhabited islands (Brooke et al. 2000; Cousins and Compton 2005; Palmeirim et al. 2005). When not hunted, roosts may occur closer to human habitation, such as throughout the village of Kolovai, Tonga. Colonies are commonly found on small islets in Tonga and Fiji, where animals commute nightly to larger neighboring islands up to 10 km away (McConkey and Drake 2007; Palmeirim et al. 2005). The diet includes numerous fruits and flowers (Banack 1998; Miller and Wilson 1997). Mating and births occur throughout the year (Grant and Banack 1999).

Population Status

Population estimates of *P. t. tonganus* exist for several locations. Regular islandwide roost counts on Tutuila, American Samoa, have been conducted since 1992. Early surveys in 1987–1989 estimated 12,750–28,000 individuals, but unregulated hunting following two severe cyclones in 1990 and 1991 caused the population to decline to about 1,500–2,500 animals (Craig et al. 1994b). After hunting was banned in 1992, colonies regrouped in inaccessible areas and increased to about 6,300 bats by 2000 (Brooke et al. 2000; Utzurrum et al. 2003). Surveys in Tonga during 1995 found a robust population of about 6,000 bats on 14 islands in the Vava'u group (Grant 1998), but abundance fell

by more than 80% after Cyclone Waka hit the area in 2001 (McConkey et al. 2004). Niue's population ranged from an estimated 2,040 to 4,080 bats in 1998 (Brooke and Tschapka 2002), but numbers have declined greatly since then because of uncontrolled hunting and damage from Cyclone Heta in January 2004. Surveys in 2004 failed to detect any colonies, with only 60 bats counted in 27 surveys, a decrease of 95% from those conducted in 1998 at the same locations (Brooke 2004). A five-year ban on hunting enacted in late 2004 may help to restore this population. In the Cook Islands in 2002, abundance was estimated at about 1,730 bats on Rarotonga and about 80 bats on Mangaia, with probably an overall declining trend (Cousins and Compton 2005). Insufficient habitat appears to be the critical factor affecting abundance on Mangaia. In addition, bats are hunted on both islands without restriction. More than half of the global population of *P. t. tonganus* is believed to occur in Fiji (Palmeirim et al. 2005; Palmeirim et al. 2007). Although population estimates do not exist for this island group, animals are plentiful and widespread on large and small islands alike. Some hunting, mostly for personal consumption, occurs here (Palmeirim et al. 2005).

P. t. basilicus was highly visible in 1992 on Karkar Island, Papua New Guinea, although its lowland habitat had been largely converted to plantation forests (Bonaccorso 1998). No recent information is available on population status for Koil Island. Hunting probably threatens populations on both islands (Bonaccorso 1998). Relatively little information is available on *P. t. geddiei*, which is found in New Caledonia, the Solomon Islands, and Vanuatu.

Pteropus samoensis

IUCN near threatened; protected in Samoa and American Samoa.

Distribution and Genetics

Two subspecies exist: *Pteropus samoensis samoensis* in the Samoan archipelago and *P. s. nawaiensis* in Fiji (Banack 2001). Fossil remains predating Polynesian settlement have been found in Tonga (Koopman and Steadman 1995). Ingelby and Colgan (2003) did not observe notable differences in allele frequencies from three Fijian islands (Vanua Levu, Viti Levu, and Taveuni), suggesting few barriers to gene flow. In contrast, Utzurrum et al. (2000) found haplotypes differed greatly within and among island populations, suggesting that *P. samoensis* once had a larger distribution and has undergone a dramatic decline with substantial structuring among islands. *P. samoensis* appears to be most closely related to *P. nitendiensis* from the Solomon Islands (Ingelby and Colgan 2003).

Biology

P. samoensis is most common in or near native forest and forages on a variety of leaves, flowers, and fruits of both native and agricultural plants (Banack 1998; Mickleburgh et al. 1992; Nelson et al. 2000a, 2000b; Palmeirim et al. 2005; Palmeirim et al. 2007). Bats are most active at night but are seen throughout the

day, especially near dawn and dusk, when thermal updrafts are used for soaring (Brooke 2001; Norberg et al. 2000; Thomson et al. 1998, 2004). The species typically roosts singly or in small groups usually comprising either a female and young of the year or a mated pair (Brooke 2001).

Population Status

Surveys of *P. s. samoensis* were initiated in American Samoa in 1986, with an estimated 700 bats present on Tutuila prior to Cyclone Ofa in 1990 and 200–400 bats present after Cyclone Val in 1991 (Utzurum et al. 2003). From 1995 to 2000, the population remained stable at about 900 animals, whereas numbers in the Manu'a Islands remained low at about 100 individuals. The low numbers recorded in Samoa after Cyclone Val had not appreciably increased by 1996 (Brooke 1997; Wilson and Engbring 1992).

P. s. nawaiensis is moderately common in some lowland areas of Viti Levu and Vanua Levu, the two largest islands in Fiji (Palmeirim et al. 2005; Palmeirim et al. 2007). It also occurs on some medium-sized islands, but usually avoids smaller islands.

Emballonura semicaudata

IUCN endangered; candidate status for the United States; protected in American Samoa, Guam, and the Commonwealth of the Northern Mariana Islands (Hutson et al. 2001).

Distribution

Four subspecies occur as follows: *Emballonura semicaudata semicaudata* in Vanuatu, Fiji, Tonga, Samoa, and American Samoa; *E. s. sulcata* in Chuuk and Pohnpei in the central Caroline Islands; *E. s. palauensis* in Palau; and *E. s. rotensis* from Guam to Saipan in the southern Marianas (Koopman 1997; Simmons 2005).

Biology

E. semicaudata is most common on limestone islands with caves and rock overhangs, but also inhabits volcanic islands. Roosts occur in small to large caves, lava tubes, rock depressions, and hollow trees. Illumination at roosts can vary from twilight to dark sections of caves and includes well-lit rock depressions (Palmeirim et al. 2005; Wiles et al. 1997; G. J. Wiles, unpublished data). Zooarchaeological excavations on Guam found skeletal remains common under the overhangs of limestone cliffs (D. W. Steadman, pers. comm.). Most colonies range in size from a few to several hundred bats, but some roosts in Fiji may have once harbored thousands of individuals (Palmeirim et al. 2005; Sawyer and Andrews 1901 cited in Palmeirim et al. 2007; Wiles et al. 1997).

E. semicaudata feeds on aerial insects. The last surviving population in the Marianas, located on the island of Aguiguan, forages preferentially in native forest (Esselstyn et al. 2004b), but elsewhere, animals can forage in a variety of

habitats, including urban areas (Palmeirim et al. 2005; Wiles et al. 1997). Large numbers of individuals have been observed transiting distances of 5 km or more to reach feeding locations in Palau (Wiles et al. 1997).

Population Status

Many populations of *E. semicaudata* have undergone dramatic decline during the past 50 years for reasons that are unclear, but which may involve forest loss, insecticide use, severe tropical cyclones, introduced predators, or human disturbance of caves (Hutson et al. 2001; Palmeirim et al. 2005; Palmeirim et al. 2007). Relatively healthy populations remain only in Palau, Pohnpei, and Chuuk, and on some of Fiji's smaller islands. In Palau, an estimated 5,000–10,000 bats were counted departing several roosting islands, with bats being widespread and regularly detected elsewhere in the island group in 1991 and again in 2005 (Wiles et al. 1997; G. J. Wiles, unpublished data). The species appeared fairly common on Pohnpei in 1999 and Chuuk in 1989 (G. J. Wiles, pers. obs.), but surveys have not been conducted at either location.

Populations elsewhere contain few remaining bats or have been extirpated. In the Marianas, *E. semicaudata* survives only on Aguiñan, where an estimated 450–600 bats occurred in 2008 (G. J. Wiles, unpublished data). The species has experienced tremendous decline in American Samoa and Samoa since the 1970s or earlier (Grant et al. 1994; Hutson et al. 2001; Tarburton 2002) and may now be gone from one or both locations. Populations on Fiji's two largest islands were widespread and common into the 1970s, but surveys made in 2000 and 2001 found only a single colony (Palmeirim et al. 2005; Palmeirim et al. 2007). Fijian populations now persist primarily on smaller limestone islands. Status is poorly known for Tonga (Helgen and Flannery 2002; Koopman and Steadman 1995), and no records exist for Vanuatu since 1929 (Helgen 2004).

Conservation Needs

The threats described in this chapter, combined with the many socioeconomic problems inherent to the region such as large human populations, poverty, ineffective governments, and corruption (e.g., MacKinnon 2006), portray a pessimistic future for bat populations in many parts of insular Southeast Asia and the tropical Pacific. We nevertheless believe that some successes are achievable in conserving bats and concur with the general needs and solutions discussed by Sodhi and Brook (2006), such as improving public awareness, empowering citizens, and increasing resource protection whenever feasible. Two of the greatest challenges in protecting bats throughout the region are preserving adequate amounts of habitat (including roosting sites) and reducing overexploitation of populations. This can only be done by convincing local people that they have a stake in preserving natural resources. There are glimmers of progress, one being the expansion of conservation-oriented nongovernmental

organizations working at the national and local levels. Some groups, such as the Bat Association of Taiwan, work specifically for the benefit of bats, while others like the Foundation for the Philippine Environment and the Palau Conservation Society have sponsored valuable bat-related projects. We are also heartened by the increasing participation of resident biologists working with bats in Taiwan, the Philippines, East Malaysia, and Indonesia.

Greater implementation of improved logging practices and timber concession management, as summarized in Meijaard and Sheil 2008 and Dennis et al. 2008, has begun in the region and offers promise for the conservation of forest-dwelling bats and other biota in production forests. However, for sustainable forest management to succeed on a large scale, greater enforcement and accountability are required as well as increased demand for certified timber in international markets (Meijaard et al. 2005).

Many of the conservation activities recommended in two action plans for bats (Hutson et al. 2001; Mickleburgh et al. 1992) remain pertinent. These include (1) improving public and government support for bats so that meaningful protection of populations and habitats is achieved and (2) conducting inventories, population monitoring, and ecological studies of species. One particular challenge in the region is preventing the overharvesting of bats as food, especially pteropodids. Banning commercial sales of bats may be one useful measure in some locations for reducing harvest pressure (Bennett et al. 2000). Other widely needed efforts are greater enforcement of existing laws and amending conservation laws so that they include bats (Corlett 2007). Several studies have reported that flying foxes have a poor capacity for increase (McIlwee and Martin 2002; Pierson and Rainey 1992), but our experiences suggest that at least some populations of *Pteropus* (e.g., *P. mariannus pelewensis* in Palau [Wiles et al. 1997], *P. m. yapensis* in Yap [Mickleburgh et al. 1992], and *P. tonganus* in American Samoa [Brooke et al. 2000; Utzurrum et al. 2003]) readily respond to reduced hunting pressure and can grow fairly rapidly. This may bode well for the recovery of other pteropodids if harvest levels can be controlled.

Conclusions

Islands in the tropical Pacific and insular Southeast Asia hold more than 350 bat species, or about 31% of the world's total, making the region a major center of bat diversity, especially for pteropodids. Many of these species are thought to be declining, with 28% (100 species) designated as threatened or near threatened by the IUCN. This chapter discusses five important conservation concerns facing bat populations in the region: habitat destruction and alteration, hunting, cave disturbance, severe tropical cyclones, and exotic species.

Deforestation is a major threat for large numbers of forest-dependent bats, especially in Indonesia, the Philippines, East Malaysia, the Solomon Islands,

and Papua New Guinea, which feature some of the world's highest rates of forest loss and alteration. Studies from mainland Southeast Asia reveal the presence of impoverished bat communities after forest disturbance and destruction, and suggest that similar outcomes can be expected in insular Southeast Asia and the Pacific.

Bats are a traditional food source in most of the region and continue to be harvested extensively for both subsistence and commercial purposes. Flying foxes and other pteropodids are targeted because of their larger sizes, but microchiropterans are also caught in some areas. Commercial markets are apparently most active in Indonesia. A large international trade in *Pteropus* that was formerly centered on Guam and the Northern Mariana Islands ended in 1994 after the enactment of CITES restrictions. Heavy harvest pressure in many parts of the region has led to significant population declines in a number of pteropodids and at least one microchiropteran.

Regular human visitation of caves for guano mining, swiftlet nest collecting, hunting, and other activities is believed to have harmed many populations of cave-dwelling microchiropterans and megachiropterans, although regional data are rare on the extent of this problem. Cave disturbance is perhaps most widespread in the Philippines, Indonesia, and East Malaysia, but is probably underdocumented elsewhere.

Exceptionally strong tropical cyclones occasionally strike a number of islands in the region and can produce tremendous damage to forests, leaving resident bat populations vulnerable to starvation, dehydration, and increased hunting and predation. Several studies have documented declines of 57% to possibly as high as 99% in flying fox numbers after major storms.

Relatively few examples of bat populations being harmed by invasive species have been reported to date, probably because of a lack of study. This threat will likely increase in the future, especially on smaller islands where impacts of exotics are often most severe.

Acknowledgments

Matt Struebig deserves special thanks for useful comments and discussions on the bats of Borneo and Indonesia. The following people kindly provided information on a number of topics: Mohamad Tajuddin Abdullah, James Atherton, Don Drake, Jake Esselstyn, Janet Franklin, Gabriella Fredriksson, Melvin Gumal, Larry Heaney, Kris Helgen, Ian Henson, Nina Ingle, Masako Izawa, Dustin Janeke, Jill Key, Tigga Kingston, Kim McConkey, Tammy Mildenstein, Keiko Osawa, Harold Ota, Jorge Palmeirim, and Ruth Utzurum. We also thank Colin O'Donnell, Ted Fleming, and two anonymous reviewers for their comments on the manuscript, and Jan Sharkey for her support during manuscript preparation.

APPENDIX 14.1

Table A14.1. Distribution of 354 bat species in 23 countries, territories, and island groups in the tropical Pacific and insular Southeast Asia

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
Megachiroptera		
Pteropodidae		
<i>Acerodon celebensis</i>	LC	Indonesia
<i>Acerodon humilis</i>	EN	Indonesia
<i>Acerodon jubatus</i>	EN	Philippines
<i>Acerodon leucotis</i>	VU	Philippines
<i>Acerodon mackloti</i>	VU	Indonesia, Timor-Leste
<i>Aethalops aequalis</i>	LC	Indonesia, E. Malaysia, Brunei
<i>Aethalops alecto</i>	LC	Indonesia*
<i>Alionycteris paucidentata</i>	LC	Philippines
<i>Aproteles bulmerae</i>	CR	PNG
<i>Balionycteris maculata</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Chironax melanocephalus</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Cynopterus brachyotis</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Cynopterus horsfieldii</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Cynopterus luzoniensis</i>	LC	Indonesia, Philippines
<i>Cynopterus minutus</i>	LC	Indonesia, E. Malaysia, Brunei
<i>Cynopterus nusatenggara</i>	LC	Indonesia
<i>Cynopterus sphinx</i>	LC	Indonesia, Taiwan*
<i>Cynopterus titthaecheilus</i>	LC	Indonesia, Timor-Leste
<i>Desmalopex leucopterus</i>	LC	Philippines
<i>Desmalopex microleucopterus</i>	NE	Philippines
<i>Dobsonia anderseni</i>	LC	PNG
<i>Dobsonia beauforti</i>	LC	Indonesia
<i>Dobsonia chapmani</i>	CR	Philippines
<i>Dobsonia crenulata</i>	LC	Indonesia
<i>Dobsonia emersa</i>	VU	Indonesia
<i>Dobsonia exoleta</i>	LC	Indonesia
<i>Dobsonia inermis</i>	LC	PNG, Solomons
<i>Dobsonia magna</i>	NE	Indonesia, PNG*
<i>Dobsonia minor</i>	LC	Indonesia, PNG

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Dobsonia moluccensis</i>	LC	Indonesia, Timor-Leste
<i>Dobsonia pannietensis</i>	NT	PNG
<i>Dobsonia peronii</i>	LC	Indonesia, Timor-Leste
<i>Dobsonia praedatrix</i>	LC	PNG
<i>Dobsonia viridis</i>	LC	Indonesia
<i>Dyacopterus brooksi</i>	VU	Indonesia
<i>Dyacopterus rickarti</i>	NE	Philippines
<i>Dyacopterus spadiceus</i>	NT	Indonesia, E. Malaysia, Brunei*
<i>Eonycteris major</i>	DD	Indonesia, E. Malaysia, Brunei
<i>Eonycteris robusta</i>	NT	Philippines
<i>Eonycteris spelaea</i>	LC	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines*
<i>Haplonycteris fischeri</i>	LC	Philippines
<i>Harpyionycteris celebensis</i>	VU	Indonesia
<i>Harpyionycteris whiteheadi</i>	LC	Philippines
<i>MacroGLOSSUS minimus</i>	LC	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines, PNG, Solomons*
<i>MacroGLOSSUS sobrinus</i>	LC	Indonesia*
<i>Megaerops ecaudatus</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Megaerops kusnotoi</i>	VU	Indonesia
<i>Megaerops wetmorei</i>	VU	Indonesia, Brunei, Philippines*
<i>Melonycteris fardoulisi</i>	LC	Solomons
<i>Melonycteris melanops</i>	LC	PNG
<i>Melonycteris woodfordi</i>	LC	PNG, Solomons
<i>Mirimiri acrodonta</i>	CR	Fiji
<i>Neopteryx frosti</i>	EN	Indonesia
<i>Notopteris macdonaldi</i>	VU	Vanuatu, Fiji
<i>Notopteris neocaledonica</i>	VU	New Caledonia
<i>Nyctimene aello</i>	LC	Indonesia, PNG
<i>Nyctimene albiventer</i>	LC	Indonesia, PNG
<i>Nyctimene cephalotes</i>	LC	Indonesia, Timor-Leste, PNG*
<i>Nyctimene certans</i>	LC	Indonesia, PNG

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Nyctimene cyclotis</i>	DD	Indonesia
<i>Nyctimene draconilla</i>	DD	Indonesia, PNG
<i>Nyctimene keasti</i>	VU	Indonesia
<i>Nyctimene major</i>	LC	PNG, Solomons
<i>Nyctimene malaitensis</i>	DD	Solomons
<i>Nyctimene masalai</i>	DD	PNG
<i>Nyctimene minutus</i>	VU	Indonesia
<i>Nyctimene rabori</i>	EN	Indonesia, Philippines
<i>Nyctimene sanctacrucis</i>	DD	Solomon
<i>Nyctimene vizcaccia</i>	LC	PNG, Solomons
<i>Otopteropus cartilagonodus</i>	LC	Philippines
<i>Paranyctimene raptor</i>	LC	Indonesia, PNG
<i>Paranyctimene tenax</i>	LC	Indonesia, PNG
<i>Penthetor lucasi</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Ptenochirus jagori</i>	LC	Philippines
<i>Ptenochirus minor</i>	LC	Philippines
<i>Pteralopex anceps</i>	EN	PNG, Solomons
<i>Pteralopex atrata</i>	EN	Solomon
<i>Pteralopex flanneryi</i>	CR	PNG, Solomons
<i>Pteralopex pulchra</i>	CR	Solomons
<i>Pteralopex taki</i>	EN	Solomons
<i>Pteropus admiralitatus</i>	LC	PNG, Solomons
<i>Pteropus alecto</i>	LC	Indonesia, PNG*
<i>Pteropus anetianus</i>	VU	Vanuatu
<i>Pteropus argentatus</i>	DD	Indonesia
<i>Pteropus aruensis</i>	CR	Indonesia
<i>Pteropus caniceps</i>	NT	Indonesia
<i>Pteropus capistratus</i>	EN	PNG
<i>Pteropus chrysoproctus</i>	NT	Indonesia
<i>Pteropus cognatus</i>	EN	Solomons
<i>Pteropus conspicillatus</i>	LC	Indonesia, PNG*
<i>Pteropus dasymallus</i>	NT	Philippines, Taiwan, Ryukyus

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Pteropus fundatus</i>	EN	Vanuatu
<i>Pteropus gilliardorum</i>	DD	PNG
<i>Pteropus griseus</i>	DD	Indonesia, Timor-Leste
<i>Pteropus howensis</i>	DD	Solomons
<i>Pteropus hypomelanus</i>	LC	Indonesia, E. Malaysia, Philippines, PNG, Solomons*
<i>Pteropus insularis</i>	DD	FSM
<i>Pteropus keyensis</i>	DD	Indonesia
<i>Pteropus lombocensis</i>	DD	Indonesia, Timor-Leste
<i>Pteropus loochoensis</i>	DD	Ryukyus
<i>Pteropus macrotis</i>	LC	Indonesia, PNG*
<i>Pteropus mahaganus</i>	VU	PNG, Solomons
<i>Pteropus mariannus</i>	EN	Palau, FSM, Guam, N. Marianas
<i>Pteropus melanopogon</i>	EN	Indonesia
<i>Pteropus melanotus</i>	VU	Indonesia*
<i>Pteropus molossinus</i>	VU	FSM
<i>Pteropus neohibernicus</i>	LC	Indonesia, PNG
<i>Pteropus nitendiensis</i>	EN	Solomons
<i>Pteropus ocularis</i>	VU	Indonesia
<i>Pteropus ornatus</i>	VU	New Caledonia
<i>Pteropus personatus</i>	LC	Indonesia
<i>Pteropus phaeocephalus</i>	DD	FSM
<i>Pteropus pilosus</i>	EX	Palau
<i>Pteropus pohlei</i>	EN	Indonesia
<i>Pteropus pselaphon</i>	CR	Ogasawara and Iwo Islands
<i>Pteropus pumilus</i>	NT	Indonesia, Philippines
<i>Pteropus rayneri</i>	NT	PNG, Solomons
<i>Pteropus rennelli</i>	VU	Solomons
<i>Pteropus samoensis</i>	NT	Fiji, Samoa, American Samoa
<i>Pteropus scapulatus</i>	LC	PNG*
<i>Pteropus speciosus</i>	DD	Indonesia, Philippines
<i>Pteropus temminckii</i>	VU	Indonesia

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Pteropus tokudae</i>	EX	Guam
<i>Pteropus tonganus</i>	LC	PNG, Solomons, Vanuatu, New Caledonia, Fiji, Wallis and Futuna, Tonga, Samoa, American Samoa, Niue, Cooks
<i>Pteropus tuberculatus</i>	CR	Solomons
<i>Pteropus vampyrus</i>	NT	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines*
<i>Pteropus vetulus</i>	VU	New Caledonia
<i>Pteropus woodfordi</i>	VU	Solomons
<i>Rousettus amplexicaudatus</i>	LC	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines, PNG, Solomons*
<i>Rousettus bidens</i>	VU	Indonesia
<i>Rousettus celebensis</i>	LC	Indonesia
<i>Rousettus leschenaultii</i>	LC	Indonesia*
<i>Rousettus linduensis</i>	DD	Indonesia
<i>Rousettus spinalatus</i>	VU	Indonesia, E. Malaysia, Brunei
<i>Styloctenium mindorensis</i>	DD	Philippines
<i>Styloctenium wallacei</i>	VU	Indonesia
<i>Syconycteris australis</i>	LC	Indonesia, PNG*
<i>Syconycteris carolinae</i>	VU	Indonesia
<i>Syconycteris hobbit</i>	VU	Indonesia, PNG
<i>Thoopterus nigrescens</i>	LC	Indonesia
Microchiroptera		
Rhinolophidae		
<i>Rhinolophus acuminatus</i>	LC	Indonesia, E. Malaysia, Philippines*
<i>Rhinolophus affinis</i>	LC	Indonesia, E. Malaysia*
<i>Rhinolophus arcuatus</i>	LC	Indonesia, E. Malaysia, Philippines, PNG
<i>Rhinolophus borneensis</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines*
<i>Rhinolophus canuti</i>	VU	Indonesia, Timor-Leste
<i>Rhinolophus celebensis</i>	LC	Indonesia, Timor-Leste

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Rhinolophus creaghi</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines
<i>Rhinolophus euryotis</i>	LC	Indonesia, PNG
<i>Rhinolophus ferrumequinum</i>	LC	Ryukyus*
<i>Rhinolophus formosae</i>	NT	Taiwan
<i>Rhinolophus imaizumii</i>	NE	Ryukyus
<i>Rhinolophus inops</i>	LC	Philippines
<i>Rhinolophus keyensis</i>	DD	Indonesia, Timor-Leste
<i>Rhinolophus lepidus</i>	LC	Indonesia*
<i>Rhinolophus luctus</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Rhinolophus macrotis</i>	LC	Indonesia, Philippines*
<i>Rhinolophus madurensis</i>	EN	Indonesia
<i>Rhinolophus megaphyllus</i>	LC	Indonesia, PNG*
<i>Rhinolophus montanus</i>	DD	Timor-Leste
<i>Rhinolophus nereis</i>	DD	Indonesia
<i>Rhinolophus philippinensis</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines, PNG*
<i>Rhinolophus pusillus</i>	LC	Indonesia, E. Malaysia, Taiwan, Ryukyus*
<i>Rhinolophus rufus</i>	NT	Philippines
<i>Rhinolophus sedulus</i>	NT	Indonesia, E. Malaysia, Brunei*
<i>Rhinolophus stheno</i>	LC	Indonesia*
<i>Rhinolophus subrufus</i>	DD	Philippines
<i>Rhinolophus trifoliatus</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Rhinolophus virgo</i>	LC	Philippines
Hipposideridae		
<i>Anthops ornatus</i>	DD	PNG, Solomons
<i>Aselliscus tricuspidatus</i>	LC	Indonesia, PNG, Solomons, Vanuatu
<i>Coelops frithii</i>	LC	Indonesia, Taiwan*
<i>Coelops robinsoni</i>	VU	Indonesia, E. Malaysia, Philippines*
<i>Hipposideros armiger</i>	LC	Taiwan*
<i>Hipposideros ater</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines, PNG*

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Hipposideros bicolor</i>	LC	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines*
<i>Hipposideros boeadii</i>	DD	Indonesia
<i>Hipposideros breviceps</i>	DD	Indonesia
<i>Hipposideros calcaratus</i>	LC	Indonesia, PNG, Solomons
<i>Hipposideros cervinus</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines, PNG, Solomons, Vanuatu*
<i>Hipposideros cineraceus</i>	LC	Indonesia, E. Malaysia*
<i>Hipposideros coronatus</i>	DD	Philippines
<i>Hipposideros corynophyllus</i>	DD	Indonesia, PNG
<i>Hipposideros coxi</i>	DD	Indonesia, E. Malaysia
<i>Hipposideros crumeniferus</i>	DD	Indonesia, Timor-Leste
<i>Hipposideros demissus</i>	VU	Solomons
<i>Hipposideros diadema</i>	LC	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines, PNG, Solomons*
<i>Hipposideros dinops</i>	DD	PNG, Solomons
<i>Hipposideros doriae</i>	NT	Indonesia, E. Malaysia, Brunei*
<i>Hipposideros dyacorum</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Hipposideros edwardshilli</i>	DD	PNG
<i>Hipposideros galeritus</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Hipposideros inexpectatus</i>	DD	Indonesia
<i>Hipposideros larvatus</i>	LC	Indonesia, E. Malaysia*
<i>Hipposideros lekaguli</i>	NT	Philippines*
<i>Hipposideros macrobullatus</i>	DD	Indonesia
<i>Hipposideros madurae</i>	LC	Indonesia
<i>Hipposideros maggietaylorae</i>	LC	Indonesia, PNG
<i>Hipposideros muscinus</i>	DD	Indonesia, PNG
<i>Hipposideros obscurus</i>	LC	Philippines
<i>Hipposideros orbiculus</i>	EN	Indonesia*
<i>Hipposideros papua</i>	LC	Indonesia
<i>Hipposideros pelingensis</i>	NT	Indonesia
<i>Hipposideros pygmaeus</i>	LC	Philippines

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Hipposideros ridleyi</i>	VU	Indonesia, E. Malaysia, Brunei*
<i>Hipposideros semoni</i>	DD	PNG*
<i>Hipposideros sorenseni</i>	VU	Indonesia
<i>Hipposideros sumbae</i>	LC	Indonesia, Timor-Leste
<i>Hipposideros turpis</i>	NT	Ryukyus*
<i>Hipposideros wollastoni</i>	LC	Indonesia, PNG
Megadermatidae		
<i>Megaderma spasma</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines*
Rhinopomatidae		
<i>Rhinopoma microphyllum</i>	LC	Indonesia*
Emballonuridae		
<i>Saccolaimus flaviventris</i>	LC	PNG*
<i>Saccolaimus mixtus</i>	DD	PNG*
<i>Saccolaimus saccolaimus</i>	LC	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines, PNG, Solomons*
<i>Taphozous achates</i>	DD	Indonesia
<i>Taphozous australis</i>	NT	PNG*
<i>Taphozous longimanus</i>	LC	Indonesia, E. Malaysia*
<i>Taphozous melanopogon</i>	LC	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines*
<i>Taphozous theobaldi</i>	LC	Indonesia*
<i>Emballonura alecto</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines
<i>Emballonura beccarii</i>	LC	Indonesia, PNG
<i>Emballonura diana</i>	LC	PNG, Solomons
<i>Emballonura furax</i>	DD	Indonesia, PNG
<i>Emballonura monticola</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Emballonura raffrayana</i>	LC	Indonesia, PNG, Solomons
<i>Emballonura semicaudata</i>	EN	Vanuatu, Fiji, Tonga, Samoa, American Samoa, Palau, FSM, Guam, N. Marianas
<i>Emballonura serii</i>	LC	Indonesia, PNG
<i>Mosia nigrescens</i>	LC	Indonesia, PNG, Solomons

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
Nycteridae		
<i>Nycteris javanica</i>	VU	Indonesia
<i>Nycteris tragata</i>	NT	Indonesia, E. Malaysia, Brunei*
Molossidae		
<i>Chaerephon bregullae</i>	EN	Vanuatu, Fiji
<i>Chaerephon jobensis</i>	LC	Indonesia, PNG*
<i>Chaerephon johorensis</i>	VU	Indonesia*
<i>Chaerephon plicatus</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines*
<i>Chaerephon solomonis</i>	LC	Solomons
<i>Cheiromeles parvidens</i>	LC	Indonesia, Philippines
<i>Cheiromeles torquatus</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines*
<i>Mops mops</i>	NT	Indonesia, E. Malaysia, Brunei*
<i>Mops sarsinorum</i>	DD	Indonesia, Philippines
<i>Mormopterus beccarii</i>	LC	Indonesia, PNG*
<i>Mormopterus doriae</i>	DD	Indonesia
<i>Mormopterus loriae</i>	LC	PNG*
<i>Otomops formosus</i>	DD	Indonesia
<i>Otomops johnstonei</i>	DD	Indonesia
<i>Otomops papuensis</i>	DD	PNG
<i>Otomops secundus</i>	DD	PNG
<i>Tadarida insignis</i>	DD	Taiwan*
<i>Tadarida kuboriensis</i>	LC	Indonesia, PNG
<i>Tadarida latouchei</i>	DD	Ryukyus*
<i>Tadarida teniotis</i>	LC	Indonesia*
Vespertilionidae		
<i>Arielulus circumdatus</i>	LC	Indonesia*
<i>Arielulus cuprosus</i>	DD	E. Malaysia
<i>Arielulus torquatus</i>	LC	Taiwan
<i>Eptesicus serotinus</i>	LC	Taiwan*
<i>Hesperoptenus blanfordi</i>	LC	E. Malaysia*
<i>Hesperoptenus doriae</i>	DD	E. Malaysia*

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Hesperoptenus gaskelli</i>	DD	Indonesia
<i>Hesperoptenus tomesii</i>	VU	E. Malaysia*
<i>Scotophilus celebensis</i>	DD	Indonesia
<i>Scotophilus collinus</i>	LC	Indonesia, E. Malaysia, Timor-Leste
<i>Scotophilus kuhlii</i>	LC	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines, Taiwan*
<i>Scotorepens sanborni</i>	LC	Indonesia, PNG*
<i>Nyctophilus bifax</i>	LC	Indonesia, PNG*
<i>Nyctophilus heran</i>	DD	Indonesia, Timor-Leste
<i>Nyctophilus microdon</i>	DD	PNG
<i>Nyctophilus microtis</i>	LC	Indonesia, PNG
<i>Nyctophilus nebulosus</i>	CR	New Caledonia
<i>Nyctophilus timoriensis</i>	DD	Indonesia, Timor-Leste, PNG*
<i>Pharotis imogene</i>	CR	PNG
<i>Glischropus javanus</i>	DD	Indonesia
<i>Glischropus tylopus</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines*
<i>Nyctalus aviator</i>	NT	Ryukyu*
<i>Nyctalus noctula</i>	LC	Taiwan*
<i>Nyctalus plancyi</i>	LC	Taiwan*
<i>Pipistrellus abramus</i>	LC	Taiwan, Ryukyu*
<i>Pipistrellus angulatus</i>	LC	Indonesia, PNG, Solomons
<i>Pipistrellus ceylonicus</i>	LC	E. Malaysia*
<i>Pipistrellus collinus</i>	LC	Indonesia, PNG
<i>Pipistrellus javanicus</i>	LC	Indonesia, E. Malaysia, Philippines*
<i>Pipistrellus minahassae</i>	DD	Indonesia
<i>Pipistrellus papuanus</i>	LC	Indonesia, PNG
<i>Pipistrellus pipistrellus</i>	LC	Taiwan*
<i>Pipistrellus stenopterus</i>	LC	Indonesia, E. Malaysia, Philippines*
<i>Pipistrellus studeei</i>	DD	Ogasawara and Iwo Islands
<i>Pipistrellus tenuis</i>	LC	Indonesia, E. Malaysia, Timor-Leste, Philippines*

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Pipistrellus wattsi</i>	LC	PNG
<i>Barbastella leucomelas</i>	LC	Taiwan*
<i>Plecotus taivanus</i>	NT	Taiwan
<i>Chalinolobus neocaledonicus</i>	EN	New Caledonia
<i>Chalinolobus nigrogriseus</i>	LC	PNG*
<i>Falsistrellus mordax</i>	DD	Indonesia
<i>Falsistrellus petersi</i>	DD	Indonesia, E. Malaysia, Philippines
<i>Hypsugo imbricatus</i>	LC	Indonesia, E. Malaysia
<i>Hypsugo kitcheneri</i>	DD	Indonesia, E. Malaysia
<i>Hypsugo macrotis</i>	DD	Indonesia*
<i>Hypsugo vordermanni</i>	DD	Indonesia, E. Malaysia, Brunei
<i>Philetor brachypterus</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines, PNG*
<i>Tylonycteris pachypus</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines*
<i>Tylonycteris robustula</i>	LC	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines*
<i>Vespertilio sinensis</i>	LC	Taiwan*
<i>Myotis adversus</i>	LC	Indonesia, E. Malaysia, Timor-Leste, Taiwan*
<i>Myotis ater</i>	LC	Indonesia, E. Malaysia, Philippines*
<i>Myotis formosus</i>	LC	Indonesia, Philippines, Taiwan*
<i>Myotis gomantongensis</i>	LC	E. Malaysia
<i>Myotis hasseltii</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Myotis hermani</i>	DD	Indonesia*
<i>Myotis horsfieldii</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines*
<i>Myotis insularum</i>	DD	Samoa
<i>Myotis macrodactylus</i>	LC	Ryukyu*
<i>Myotis macrotarsus</i>	NT	E. Malaysia, Philippines
<i>Myotis moluccarum</i>	LC	Indonesia, PNG, Solomons, Vanuatu*
<i>Myotis montivagus</i>	LC	Indonesia, E. Malaysia*
<i>Myotis muricola</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines, Taiwan*

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Myotis ridleyi</i>	NT	Indonesia, E. Malaysia, Brunei*
<i>Myotis siligorensis</i>	LC	E. Malaysia*
<i>Myotis stalkerii</i>	DD	Indonesia
<i>Myotis yanbarensis</i>	CR	Ryukyus
<i>Miniopterus australis</i>	LC	Indonesia, E. Malaysia, Brunei, Timor-Leste, Philippines, PNG, Solomons, Vanuatu, New Caledonia*
<i>Miniopterus fuscus</i>	EN	Ryukyus
<i>Miniopterus macrocneme</i>	DD	Indonesia, PNG, Solomons, Vanuatu, New Caledonia
<i>Miniopterus magnater</i>	LC	Indonesia, E. Malaysia, Timor-Leste, PNG*
<i>Miniopterus medius</i>	LC	Indonesia, E. Malaysia, PNG*
<i>Miniopterus paululus</i>	DD	Indonesia, E. Malaysia, Philippines
<i>Miniopterus pusillus</i>	LC	Indonesia, Timor-Leste*
<i>Miniopterus robustior</i>	EN	New Caledonia
<i>Miniopterus schreibersii</i>	NT	Indonesia, E. Malaysia, Brunei, Philippines, PNG, Solomons, Taiwan*
<i>Miniopterus shortridgei</i>	DD	Indonesia
<i>Miniopterus tristis</i>	LC	Indonesia, Philippines, PNG, Solomons, Vanuatu
<i>Harpiocephalus harpia</i>	LC	Indonesia, E. Malaysia, Philippines, Taiwan*
<i>Harpiocephalus mordax</i>	DD	E. Malaysia*
<i>Harpiola isodon</i>	DD	Taiwan
<i>Murina aenea</i>	VU	Indonesia, E. Malaysia*
<i>Murina cyclotis</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines*
<i>Murina florum</i>	LC	Indonesia, PNG*
<i>Murina puta</i>	NT	Taiwan
<i>Murina rozendaali</i>	VU	Indonesia, E. Malaysia*
<i>Murina ryukyuana</i>	EN	Ryukyus
<i>Murina suilla</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Murina tubinaris</i>	LC	Philippines*

Table A14.1. (continued)

Species	IUCN status ^a	Countries, territories, or island groups of occurrence ^{b, c}
<i>Kerivoula agnella</i>	DD	PNG
<i>Kerivoula flora</i>	VU	Indonesia, E. Malaysia
<i>Kerivoula hardwickii</i>	LC	Indonesia, E. Malaysia, Brunei, Philippines*
<i>Kerivoula intermedia</i>	NT	Indonesia, E. Malaysia, Brunei*
<i>Kerivoula lenis</i>	LC	Indonesia, E. Malaysia*
<i>Kerivoula minuta</i>	NT	Indonesia, E. Malaysia, Brunei*
<i>Kerivoula muscina</i>	LC	PNG
<i>Kerivoula myrella</i>	DD	PNG
<i>Kerivoula papillosa</i>	LC	Indonesia, E. Malaysia, Brunei*
<i>Kerivoula pellucida</i>	NT	Indonesia, E. Malaysia, Brunei, Philippines*
<i>Kerivoula picta</i>	LC	Indonesia*
<i>Kerivoula whiteheadi</i>	LC	E. Malaysia, Philippines*
<i>Phoniscus atrox</i>	NT	Indonesia, E. Malaysia*
<i>Phoniscus jagorii</i>	LC	Indonesia, E. Malaysia, Philippines*
<i>Phoniscus papuensis</i>	LC	Indonesia, PNG*

Note: Taxonomy largely follows Simmons 2005, with information on distribution taken from the sources listed in table 14.1. Threatened categories are from IUCN 2008.

^aStatus abbreviations: CR = critically endangered; DD = data deficient; EN = endangered; EX = extinct; LC = least concern; NE = not evaluated; NT = near threatened; VU = vulnerable.

^bAsterisks denote species with geographic ranges extending outside the region. Geographic abbreviations: E. Malaysia = Sarawak and Sabah (East Malaysia); FSM = Federated States of Micronesia; N. Marianas = Commonwealth of the Northern Mariana Islands; PNG = Papua New Guinea.

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