

## The mammals of Palawan Island, Philippines

Jacob A. Esselstyn, Peter Widmann, and Lawrence R. Heaney

(JAE) Palawan Council for Sustainable Development, P.O. Box 45, Puerto Princesa City, Palawan, Philippines (present address: Natural History Museum, 1345 Jayhawk Blvd., Lawrence, KS 66045, U.S.A.)

(PW) Katala Foundation, P.O. Box 390, Puerto Princesa City, Palawan, Philippines;

(LRH) Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, IL 60605 U.S.A.

**Abstract.**—The mammal fauna of Palawan Island, Philippines is here documented to include 58 native species plus four non-native species, with native species in the families Soricidae (2 species), Tupaiidae (1), Pteropodidae (6), Emballonuridae (2), Megadermatidae (1), Rhinolophidae (8), Vespertilionidae (15), Molossidae (2), Cercopithecidae (1), Manidae (1), Sciuridae (4), Muridae (6), Hystricidae (1), Felidae (1), Mustelidae (2), Herpestidae (1), Viverridae (3), and Suidae (1). Eight of these species, all microchiropteran bats, are here reported from Palawan Island for the first time (*Rhinolophus arcuatus*, *R. macrotis*, *Miniopterus australis*, *M. schreibersi*, and *M. tristis*), and three (*Rhinolophus* cf. *borneensis*, *R. creaghi*, and *Murina* cf. *tubinaris*) are also the first reports from the Philippine Islands. One species previously reported from Palawan (*Hipposideros bicolor*) is removed from the list of species based on re-identification as *H. ater*, and one subspecies (*Rhinolophus anderseni aequalis* Allen 1922) is placed as a junior synonym of *R. acuminatus*. Thirteen species (22% of the total, and 54% of the 24 native non-flying species) are endemic to the Palawan faunal region; 12 of these are non-flying species most closely related to species on the Sunda Shelf of Southeast Asia, and only one, the only bat among them (*Acerodon leucotis*), is most closely related to a species endemic to the oceanic portion of the Philippines. Of the 28 insectivorous bats, 18 species are somewhat to highly widespread in Indo-Australia, 2 are shared only with the Sunda Shelf and Indochina, 1 with the Sunda Shelf alone, 3 occur on the Sunda Shelf and the oceanic Philippines, 1 occurs in Palawan, Sulawesi, and the oceanic Philippines, 2 occur only on Palawan and in the oceanic Philippines, and 1 occurs on Borneo, Sulawesi, and throughout the Philippines. Though the insectivorous bats tend to be widely distributed, these data, particularly the distributions of the non-volant species, strongly reinforce the perception of Palawan Island (and associated smaller islands) as a biogeographic unit of the Sunda Shelf, with only limited similarity to other portions of the Philippine Islands.

---

The Philippine archipelago is remarkable for the large number of indigenous land mammal species (ca. 175), and especially for the number of endemic species (ca. 112). Given its relatively small land area, the Philippines has perhaps the greatest concentration of endemic mammals in the

world (Heaney et al. 1998, Heaney & Regalado 1998, Mittermeier et al. 1997). These species, especially the endemics, are not distributed homogeneously over the country; rather, there is a large number of discrete biogeographic units, and these correspond to the limits of the islands that ex-



isted during periods of low sea level during the late Pleistocene (Heaney 1986, 1991a, 1991b, 2000). With a single exception, current geological evidence indicates that none of these "Pleistocene islands" has had dry-land connections to the Asian mainland or to other areas. Rather, each arose as a *de novo* oceanic island, some from a combination of oceanic crust and volcanic materials, and some as uplifted areas of continental rock that had been submerged for long periods, and all of these have remained isolated by sea channels (Hall 1998, 2002; Heaney 1985, 1986, 1991a). The sole exception is the Palawan faunal region, which generally has been considered to be a portion of the Sunda Shelf, both geologically and biogeographically, with many species shared with Borneo (Dickerson 1928, Everett 1889, Heaney 1986). Although Palawan was initially also a *de novo* oceanic island, its biogeographic affinity to the Sunda Shelf has been thought to be due to the presence of a shallow shelf between Borneo and Palawan with an intervening depth of ca. 145 m (Heaney 1986, 1991a). Previously, evidence indicated that sea levels dropped to about 165 m below present levels during the penultimate glacial episode (Gascoyne et al. 1979), which would have resulted in a dry-land connection of Palawan to Borneo at about 165,000 BP (Heaney 1985, 1986, 1991a). However, recent evidence suggests that sea level dropped only to about 135 m (Rohling et al. 1998) or perhaps as little as 115 m below present levels (Siddall et al. 2003, Voris 2000) during that glacial episode, leaving open the question of when Palawan was connected to Borneo, or if the gap simply became very narrow.

The mammals of Palawan Island, the largest part of the faunal region at 11,785 km<sup>2</sup>, and the associated smaller islands have been documented over the course of more than a century (Allen 1910, Allen 1922, Everett 1889, Heaney et al. 1998, Hoogstraal 1951, Kuntz 1969, Reis & Garong 2001, Sanborn 1952, Taylor 1934, Timm & Bir-

ney 1980), but the fauna is still poorly known in many respects. Little information has been available for most species on ecology and distribution, including habitat requirements, and only a few studies have considered phylogenetic relationships (e.g., shrews: Heaney & Ruedi 1994; bats: Musser et al. 1982; squirrels: Heaney 1979; murid rodents: Musser 1979, Musser & Newcomb 1983, Musser & Heaney 1992; pangolin: Feiler 1998; leopard cats: Groves 1997). In particular, microchiropteran bats have been only superficially documented. The limitations of available data have thus limited understanding of the Southeast Asian fauna, and the Philippine fauna in particular, from both biogeographic and ecological perspectives, and hence limited conservation planning in a nation that is often cited as one of the most in need of effective conservation action (Mittermeier et al. 1999, Ong et al. 2002, Wildlife Conservation Society of the Philippines 1997).

Two of us (Esselstyn and Widmann) recently conducted extensive surveys of the mammals of Palawan Island, focusing on the 15 sites described below. Esselstyn worked from December 1999 to November 2000 at Sites 1–11, emphasizing (though not exclusively) insectivorous bats, which are the mammals most poorly known in the Philippines (Heaney et al. 1998, Heaney & Mallari 2002), and Widmann conducted studies of bats, rodents, and larger mammals from 1997 to 2002 at Sites 12–15; Heaney visited briefly in April 2000. In this paper, we report information collected during these studies, emphasizing new data on bats, and we include additional unpublished records of mammals. We summarize information on all additional species that were not taken during this study but have been documented on the island, and re-examined some key specimens from prior studies. We include descriptions of the habitats where we conducted our surveys because of a general paucity of such information, and use all available information to evaluate conservation status of the mammals. We include



measurements of the skulls of selected species of insectivorous bats that have been especially poorly known.

### Methods

At Sites 1–11, small non-volant mammals were captured using locally made live (cage) traps and Victor (snap) rat traps. Approximately 90% of live traps used measured  $11 \times 11 \times 24$  cm, and 10% measured  $13 \times 16 \times 13$  cm. Trap lines consisting of approximately 70 traps (50 live traps and 20 snap traps) were placed in areas of traversable terrain. Individual traps were placed in locations of likely capture (e.g., near holes, along fallen logs, near root buttresses, etc.) along the line spaced at 5–15 m intervals. Most traps were set at ground level, but in forest habitats we placed 5–15% of the traps in elevated locations up to 2 m above ground level on fallen logs, horizontal vines, etc. All but two trap lines were set for three nights; the exceptions at Sites 3 and 7 were set for five and two nights, respectively. At Sites 12–14, a mixture of live traps were used (see Site descriptions). Most trap lines were baited with fresh grilled coconut coated with peanut butter. Other trap lines were baited with live earthworms or bananas. All traps were checked in the early morning and late afternoon. Baits were changed at least once daily, usually in the afternoon, and as necessary in the early morning. Most live animals were released at the site of capture.

We captured bats using a harp trap (ca.  $2 \times 2$  m, 4 bank), mist nets ( $2 \times 6$  m, 16 mm mesh), butterfly nets, and hand capture at Sites 1–11; only nets were used at Sites 12–15. Harp trap and net locations were selected to be locations of likely capture (e.g., natural canopy breaks, over streams and trails, around fruiting trees, and near potential roosting locations). The harp trap and mist nets were usually set in a location for three nights, and occasionally for only one or two nights. During surveys of caves, we primarily used the harp trap, and its loca-

tion was frequently changed. Mist nets were continuously monitored during peak activity periods from 1800 to 2000 h (at Sites 12 and 13, until 2400 h) and then checked again in the early morning. The harp trap was checked periodically between 1800 and 2100 h and again in the early morning. In forested areas, we searched for bats in potential roosting locations (e.g., hollow trees, rock formations, new banana leaves, etc.). Most bats were released at the site of capture. For many of the bats, we report the proportion of adult females that were pregnant on certain dates. These were palpated externally to determine the presence or absence of an embryo before being released.

Forearm and cranial measurements were taken by L. R. Heaney and D. S. Balete at the Field Museum of Natural History (FMNH). All voucher specimens from Esselstyn, which are cited below as specimens examined, were preserved in fluid (with skulls later removed and cleaned) and cataloged at the FMNH; half of the vouchers have been deposited at the National Museum of the Philippines (NMP). Additionally, data on several previously unreported specimens housed in the University of Michigan Museum of Zoology (UMMZ) and United States National Museum of Natural History (USNM) are included here.

### Site Descriptions

See Fig. 1 for approximate locations of study sites. The province of Palawan includes the main island called Palawan and many smaller, nearby islands. The island is politically divided into 13 municipalities, one of which is Puerto Princesa City; the municipalities and the city are subdivided into barangays, and barangays into sitios.

*Site 1* ( $10^{\circ}03'00''\text{N}$ ,  $119^{\circ}00'44''\text{E}$ ) was in lowland primary forest located along the Taraban River in northern Puerto Princesa Municipality, at elevations ranging between ca. 100 and 200 m. Slope in the area was generally moderate, rising from the river to the ridge-tops. Forest in the area was



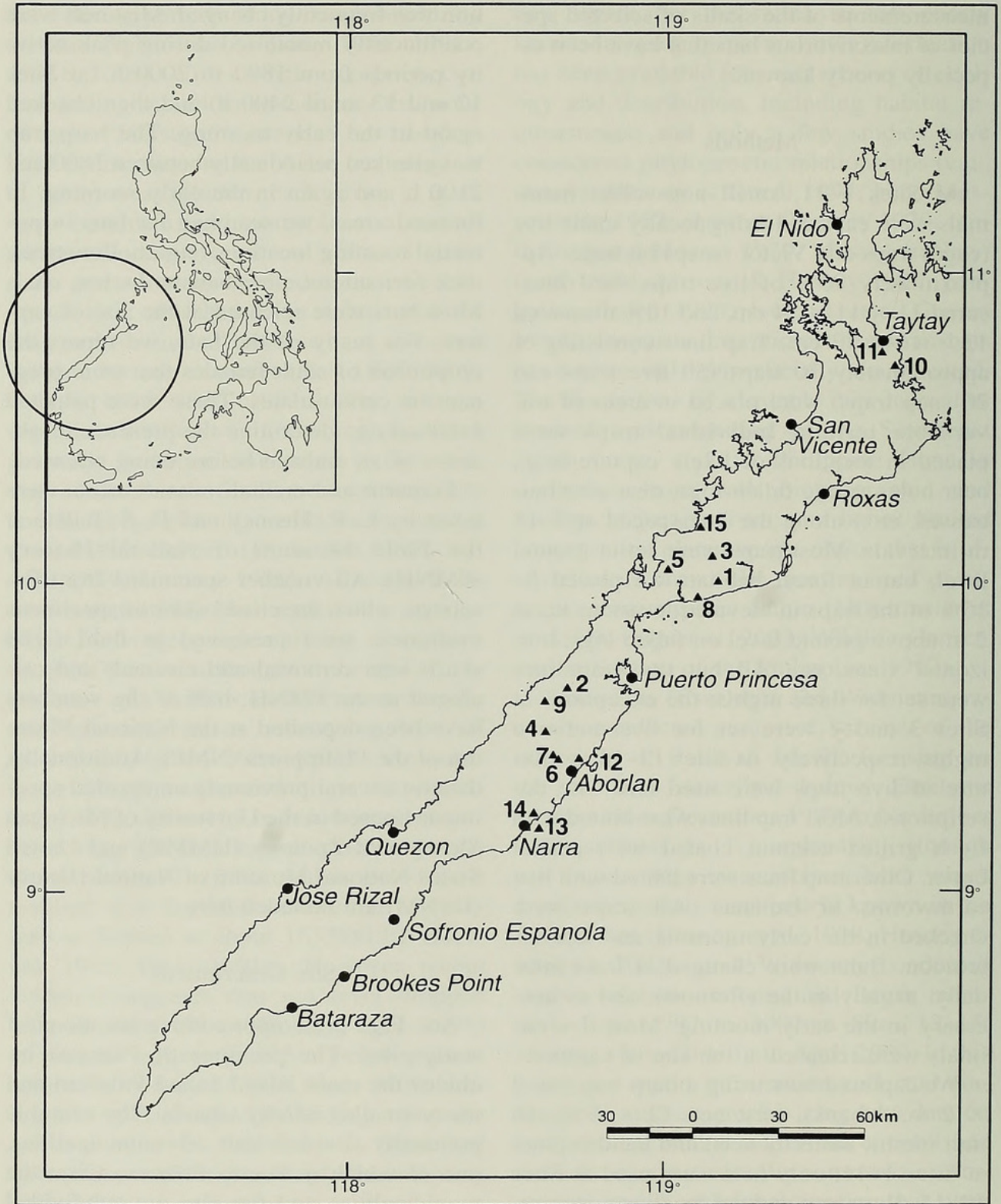


Fig. 1. Map of Palawan Island, showing the locations of the primary towns (solid circles) and research sites (solid triangles), and the position of Palawan in the Philippines (inset).

nearly undisturbed, which is uncommon at this low elevation. We were aware of only one small human-made clearing (ca. 0.5 ha) in the area; other disturbances included col-

lection of minor forest products and hunting of *Sus barbatus* and *Macaca fascicularis*. Canopy ranged from 20 to 30 m in height and was multi-layered. Canopy trees ranged



in diameter from 40–80 cm and had light buttress development. Leaf litter was thin. We surveyed small volant and non-volant mammals for 13 days in January 2000. Four trap lines were run for three nights, yielding 3 *Tupaia palawanensis*, 21 *Maxomys panglima*, and 1 juvenile *Viverra zibetha* in 792 trap-nights. Three of the lines were baited with coconut and peanut butter, while one line was baited with live earthworms. Forty-eight net-nights produced 1 *Cynopterus brachyotis* and 12 harp-nights produced 3 *Rhinolophus acuminatus*, 3 *R. arcuatus*, and 1 *R. creaghi*, plus other means produced 11 *Megaderma spasma* and 1 *R. acuminatus*.

*Site 2* (9°42'14"N, 118°32'01"E) was in lowland primary forest located mid-way up Mt. Salakot, between 300 and 700 m elevation. Slope was rolling to moderately steep. Several small streams dissected the area. The only major human-caused disturbance in the area was an unused helicopter landing pad and an abandoned road; the road had a dense regrowth of ferns and small trees. *Sus barbatus* was hunted, and some almaciga trees (*Agathis* sp.) near the upper reaches of the site had fallen due to over-collection of resin. Agoho trees (*Casuarina* sp.) gradually became more common as elevation increased. Canopy ranged from 15 to 30 m in height and was multi-layered. Canopy trees ranged in diameter from 35–60 cm with the largest emergents reaching 80–90 cm. Buttress systems were only slightly developed and stilt root systems were present above 600 m, but rare. Leaf litter was slightly deeper than at lower elevations. We surveyed small volant and non-volant mammals at this site for 20 days during March and July 2000. Six trap lines (three coconut and peanut butter-baited lines, one banana-baited line, and two earthworm-baited lines) yielded 16 *Tupaia palawanensis*, 55 *Maxomys panglima*, and 1 *Sundamys muelleri* from 1272 trap nights. Fifty-six net-nights yielded 1 *Cynopterus brachyotis*, 1 *Hipposideros diadema*, 8 *Rhinolophus arcuatus*, and 1 *R. creaghi*.

Ten harp-nights yielded 1 *Hipposideros diadema*, 16 *Rhinolophus arcuatus*, 10 *R. creaghi*, 2 *R. virgo*, and 2 *Kerivoula hardwickii*.

*Site 3* (10°07'28"N, 118°59'36"E) was in primary montane and mossy forest located near the peak of Cleopatra's Needle (maximum elevation 1603 m), at elevations ranging from 1300 to 1600 m. Slope was moderate to extreme. Other than a trail to the peak occasionally traveled by tourists, there was little human-caused disturbance in the area. No above-ground sources of water were found near the site, but mist was frequently present: during our stay of two weeks during dry season, the area was almost continuously shrouded by a dense fog. Vegetation type was montane forest up to ca. 1500 m. At this elevation, the vegetation began a transition to mossy forest. In montane forest, the canopy reached a height of approximately 10 m. Trees, rocks, fallen logs, and other stable surfaces were covered with a thin layer of moss; epiphytic ferns and orchids were abundant. Many trees had an adventitious root system, but maintained straight boles. The canopy was more open here than at lower elevations. Above 1500 m, trees were shorter (2–4 m in height) and took on a shrub form above 1550 m. Moss growth was heavier at this elevation, and vegetation became extremely dense at the upper reaches. Pitcher plants (*Nepenthes*) began to appear at about 1500 m and were abundant by 1550 m. We surveyed small volant and non-volant mammals at this site for 12 days during February and March 2000. Three trap lines yielded 1 *Tupaia palawanensis*, 33 *Maxomys panglima*, and 3 *Rattus tiomanicus* in 740 trap-nights. Two lines were run for three nights each and one line was run for five nights; all three lines were baited with coconut and peanut butter. Forty-eight net-nights produced 2 *Rhinolophus arcuatus*, and 12 harp-nights produced no captures; 2 *Pipistrellus javanicus* were captured by hand.

*Site 4* (9°33'45"N, 118°27'54"E) is a cave known locally as "Ma-ngit". It is located



along the Iraan River near Sitio Pamolkoan, Barake, Aborlan, at ca. 430 m elevation. The cave is in a small valley, restricted by mountains to the east and west. A small, seasonal stream flows through the cave. At least six entrances to the cave were evident, and many small tunnels connected medium to small caverns, which ranged from well-lit to completely dark. Very little disturbance was evident in or around the cave due to its isolated location (ca. 10 hour hike from the nearest road). The cave was surrounded by a large expanse of primary lowland forest, but some agricultural areas were present within ca. 5 km. Disturbances to local vegetation included collection of rattan (*Calamus* spp.). We surveyed bats in Ma-ngit Cave for six days during December 1999. We captured 819 bats belonging to seven species (9 *Eonycteris spelaea*, 43 *Hipposideros diadema*, 367 *Rhinolophus creaghi*, 4 *R. virgo*, 9 *Miniopterus australis*, 386 *M. schreibersi*, and 1 *M. tristis*) inside the cave.

*Site 5* (10°05'00"N, 118°51'06"E) is a complex area of limestone karst containing probably greater than 100 caves in Barangays Tagabinet and Cabayugan, Puerto Princesa; elevation is ca. 50 m. Caves in the area ranged from tiny cracks too small to enter, to large complexes of multiple caverns with multiple entrances. Local terrain was generally flat except for the sometimes-massive limestone outcrops, which form high-rising cliffs throughout the area. Caves probably are present all over these complex formations, but only the very few found near ground level were accessible. We captured bats in and around five different caves/cave complexes. These represented some of the most accessible caves in the area. Disturbance at the caves was moderate, with vandalism and guano excavation evident at most caves. Most of the caves were surrounded immediately by agricultural development. Both primary and secondary lowland forests were present in the surrounding hills. We surveyed bats at these caves for 14 days between March and May

2000. A total of 575 bats belonging to 10 species (18 *Cynopterus brachyotis*, 1 *Megaderma spasma*, 100 *Hipposideros ater*, 239 *H. diadema*, 14 *Rhinolophus arcuatus*, 33 *R. creaghi*, 10 *R. macrotis*, 86 *R. virgo*, 15 *Miniopterus australis*, and 59 *M. schreibersi*) were captured.

*Site 6* (9°28'25"N, 118°30'21"E) was a mostly abandoned agricultural area located in Barake, Aborlan Municipality, at elevation ranging from 40–80 m. A small stream flowed through the area and topography was flat to rolling. Vegetation was a mosaic of grassland (primarily *Imperata cylindrica*) with sparse trees (mostly *Vitex* sp.), cashew plantations, dense brush, and very small (<1 ha) areas of secondary growth. Frequent fires appeared to maintain this area as a grassland. We surveyed small volant and non-volant mammals for four days during June 2000. A single trap-line baited with live earthworms yielded 17 *Rattus exulans* in 186 trap-nights. We captured 7 *Cynopterus brachyotis* in 6 net nights, and 1 *Kerivoula whiteheadi* in 3 harp-nights.

*Site 7* (9°29'15"N, 118°29'24"E) was in a narrow band of secondary forest in Barake, Aborlan Municipality, located between disturbed habitat at lower elevation (*Site 6*) and primary and good secondary forest at higher elevation. Elevation ranged from 80–140 m; slope was rolling to moderately steep, and two small streams dissected the area. Canopy height varied from 5–20 m. Woody vines and lianas were common and vegetation was quite dense in areas. Wild bananas (*Musa* spp.) were abundant, but patchy in distribution; leaf litter depth was highly variable. We surveyed this site for small volant and non-volant mammals for four days during June 2000. A single trap line baited with live earthworms yielding 120 trap-nights produced 1 *Rattus exulans*. Six net-nights produced 27 *Cynopterus brachyotis* and 1 *Macroglossus minimus*, and 3 harp-nights yielded 1 *Hipposideros diadema* and 1 *Kerivoula pellucida*.

*Site 8* (9°59'47"N, 118°56'43"E) is a large cave complex located in a limestone



karst formation on top of the first ridge up from San Rafael, Puerto Princess, at an elevation of ca. 250 m. The cave complex is known locally as "Taraw". The cave system appeared to be quite large; we were unable to explore much of it due to a lack of climbing equipment and expertise. Some caverns exceeded 20 m in height, while others were quite small. We found no permanent water in or around the cave, but evidence of storm flow was present. Evidence of vandalism and guano collection was present. A mixture of habitats surrounded the cave complex: between the cave and the community of San Rafael, the vegetation was dominated by brushland and agricultural developments, while on the other side of the cave secondary and primary forest dominated, with mixed areas of slash-and-burn fields. We surveyed bats at this cave for five days during July 2000. We captured 2775 bats representing 10 species (7 *Hipposideros ater*, 43 *H. diadema*, 90 *Rhinolophus acuminatus*, 240 *R. arcuatus*, 239 *R. creaghi*, 25 *R. macrotis*, 151 *R. virgo*, 1257 *Miniopterus australis*, 711 *M. schreibersi*, 4 immature *M. sp.*, and 8 *Myotis macrotarsus*).

*Site 9* (9°39'40"N, 118°27'48"E) is a small cave located in Sitio Labtay, Napsan, Puerto Princess City. The cave, which consisted of a single chamber 1–2 m wide, 3–6 m high, and ca. 30 m long, was in a narrow canyon along the Panagurian River at ca. 280 m. Vegetation in the area consisted of good-quality secondary forest, second-growth forest, and agricultural developments. We trapped bats with a harp trap, mist nets, and a butterfly net in the cave and surrounding forest for five days during August 2000. We captured 73 bats (4 *Cynopterus brachyotis*, 68 *Hipposideros diadema*, and 1 *Rhinolophus arcuatus*).

*Site 10* (10°44'00", 119°34'23") is a cave located near sea level in Sitio Sader, Bantulan, Taytay Municipality. The cave consisted of a single chamber (ca. 3–8 m wide, 3–7 m high, and 40 m long) with a large (>2.5 m diameter) entrance at each end.

Minor damage had been done by both treasure hunters and guano collectors. The surrounding vegetation was dominated by agricultural areas with some strips and patches of residual forest. Large expanses of secondary and logged-over forest were found nearby in the vicinity of Lake Manguao. We captured 115 bats belonging to 4 species (48 *Eonycteris spelaea*, 1 *Rousettus amplexicaudatus*, 64 *Hipposideros diadema*, and 2 *Miniopterus tristis*) using a harp trap and butterfly net at one of the entrances to the cave during three days in October 2000.

*Site 11* (10°46'34"N, 119°31'52"E) was located around the perimeter of Lake Manguao, in Barangays Poblacion and Bantulan, Taytay Municipality. The area was dominated by secondary and logged-over forest, with disturbance from slash and burn agriculture being found throughout the area. The area retained ca. 60% forest cover. Slope was generally moderate to steep, and elevation ranged from ca. 40–250 m. We trapped for small volant and non-volant mammals in forest, agricultural habitats, and two small caves near the lake for 14 days during October and November 2000. We totalled 471 trap-nights in three lines baited with coconut and peanut butter, and captured 3 *Tupaia palawanensis*, 23 *Maxomys panglima*, and 1 *Rattus exulans*. Forty-two net-nights yielded 53 *Cynopterus brachyotis*, 2 *Macroglossus minimus*, and 1 *Rousettus amplexicaudatus*, and 13 harp-nights produced 1 *Megaderma spasma*, 1 *Rhinolophus acuminatus*, 2 *Kerivoula hardwickii*, and 5 *Tylonycteris pachypus*. Additionally, we captured 4 *Megaderma spasma* and 4 *R. acuminatus* by hand.

*Site 12* (9°27'48"N, 118°32'16"E) was located at the "rainforestation" site in Sitio Kandis, Aborlan Municipality, in forest/grassland mosaic at ca. 40 m above sea level, about seven km away from the next good secondary forest in the foothills of the Victoria Range. Charcoal making, logging, rattan collection, grazing and burning were common until 1994 when such activities were made illegal. The terrain was flat to



rolling, dissected by two creeks. The site consisted of 5.5 ha *Imperata cylindrica* grassland interspersed with single shrubs and trees, predominantly *Antidesma ghaesembilla*, which forms the fire climax in more open situations, with *Vitex pubescens*, *Guioa pleuropteris*, *Tarenna stenantha*, *Fagraea fragrans*, *Lantana camara*, and *Mussaenda philippica* in protected areas not affected by fire in the last ten to fifteen years. About 4.5 ha consisted of regenerating forest, close to two seasonal creeks, dominated by *Garcinia benthami*, *G. parviflora*, *Canarium asperum*, *Polyscias nodosa*, and *Baringtonia curranii*. Undergrowth was moderate to very dense. Canopy height was on average eight meters, with some taller emergents such as *Nephelium* sp. and *Dipterocarpus gracilis*. The most conspicuous vine was *Gnetum latifolium*. Macrophytic epiphytes were virtually absent. Leaf litter layer was usually not closed, except in very dry years. Surveys were conducted regularly from 1997–2000 with 10 medium-sized Sherman live traps, 10 commercial live rat traps, and 55 wire mesh traps (measurements equal to medium Shermans). Baits were roasted coconut with peanut butter, but mostly fruits available in the area. A total of 3514 trap-nights yielded 169 small mammals (28 *Tupaia palawanensis*, 8 *Sundasciurus juvencus*, 11 *Rattus exulans*, 16 *Rattus tiomanicus*, 104 *Maxomys panglima*, and 2 *Sundamys muelleri*). Mist nets (2 × 6 m) were set along trails in forest, in grassland, gaps in the shrub cover, and rarely in the canopy (ca. 8 m high). Capture sites were often near or in fruiting shrubs or trees, since the main focus of the study was on frugivores. From 1997 to 2000, a total of 482 net-nights yielded 1257 bats (1 *Acerodon leucotis*, 829 *Cynopterus brachyotis*, 394 *Macroglossus minimus*, 5 *Eonycteris spelaea*, 4 *Rousettus amplexicaudatus*, 18 *Megaderma spasma*, 1 *Hipposideros diadema*, 4 *Scotophilus kuhlii*, and 1 *Murina* cf. *tubinaris*); all but the *M.* cf. *tubinaris* were released.

Site 13 (09°13'N, 118°26'E) was on Rasa

Island, Narra Municipality, a small (8.3 km<sup>2</sup>) shallow coral island, 1.8 km offshore in the Sulu Sea. Approximately two-thirds of the island was covered with mangrove and one-third with coastal forest over limestone. About five percent of the latter had been converted into coconut plantation. Selective logging was done until the early 1990s, resulting in the complete loss of mature *Intsia bijuga*. The mangrove consisted of nine species of the genera *Rhizophora*, *Sonneratia*, *Avicennia*, *Bruguiera*, *Aegicerias*, and *Ceriops*. Canopy height was variable, usually between 8 and 15 m. Emergent trees (e.g., *Garuga floribunda* and *Pterocymbium taluto*) ranged up to 42 m. Leaf litter layer was not closed, except under very dry conditions. Barren coral rocks and crevices were ubiquitous. Buttresses were a common feature of all emergent forest trees. Under open conditions, an herbal layer consisting of *Impatiens* sp. was present. Vines were abundant, including climbing bamboo *Dinochloa* sp., often forming dense tangles. Macrophytic orchids were present, but relatively scarce. Traps and nets were set along a trail within the coastal forest. Traps were baited with roasted coconut with peanut butter, and a few with crickets. Most traps caught hermit crabs. Nets were set in the understory, which was very open from January to April 2002 and only provided very few fruits due to an extended dry spell. Trapping totaled 104 trap-nights, and produced 3 *Rattus tanezumi* and 2 *R. tiomanicus*. Netting totaled 28 net nights, and yielded 2 *Cynopterus brachyotis*, 5 *Macroglossus minimus*, and 5 *Megaderma spasma*; all bats were released, and the rats preserved as vouchers.

Site 14 (9°17'N, 118°27'E) was in freshwater swamp forest in Narra Municipality, in about 5 ha of remnant forest along Taritien River. The habitat was dominated by two woody species, *Nauclea orientalis* and *Pandanus* sp., at lower elevations, which are flooded for at least six months. The herb layer was not extensive and was dominated by *Acrostichum* sp. The higher portions



were dominated by pioneering species of early to medium successional stages, such as *Trema orientalis*, *Vitex pubescens*, and *Commersonia bartramia*. Even during extreme dry spells like that in the first half of 2002, there were isolated open water bodies left, which connected to several creeks during the rainy season. The swamp forest is bordered by ricefields and grassland. Twenty trap-nights yielded 1 *Rattus exulans* and 1 *R. tiomanicus*. Twelve net-nights yielded 27 *Cynopterus brachyotis*, 5 *Macroglossus minimus*, and 1 *Megaderma spasma*; all bats were released and the rats preserved as vouchers.

*Site 15* (10°12'N, 118°55'E) was along the "jungle trail" near the Central Park Station in Puerto Princesa (formerly St. Paul) Subterranean River National Park (PPSRNP). Primary lowland forest on steep slopes ascended from sea level to about 40 m. Five net-nights on 15 September 1996 yielded 1 *Cynopterus brachyotis*, 2 *Rhinolophus arcuatus*, 3 *Rhinolophus virgo*, and 2 *Rhinolophus* sp.; all were released. Additionally, all three authors made visual observations at various times.

#### Accounts of Species

##### Order Insectivora

##### Family Soricidae—Shrews

*Crocidura palawanensis*.—We never encountered this poorly known species. It is endemic to the Palawan faunal region and has been taken in old-growth rain forest and shrubby second growth (Heaney & Ruedi 1994); the holotype came from "deep forest near the sea at . . . Brooke's Point" (Taylor 1934), a second from near sea level in Babuyan, Puerto Princesa (Hoogstraal 1951, Sanborn 1952), and a third from 3600–4350 ft (ca. 1100–1300 m) on Mt. Mantalingajan (USNM); two additional specimens are from Balabac (Heaney & Ruedi 1994). IUCN (2002) lists this species as Vulnerable, but current definitions suggest that Data Deficient would be more appropriate.

*Crocidura* sp.—Reis & Garong (2001)

reported a single humerus of a shrew, substantially smaller in size than *C. palawanensis*, from undated sediments in a small rock-shelter cave near Tabon Cave on Lipuun Point, near Malunut Bay, in Quezon Municipality (near the location of the town of Quezon as shown in Fig. 1). They described the specimen as being similar in size to *C. monticola* from Borneo. We tentatively include it in our tallies of native species of Palawan, but we recommend that it be sought by trapping with small snap-traps baited with live earthworms and pit-fall traps.

*Suncus murinus*.—This introduced commensal is abundant in urban and agricultural areas (Rabor 1986); in forest, it is rarely present, but occasionally is common (Heaney et al. 1989, Heaney & Tabaranza 1997). It is found throughout Asia and Indo-Australia, including the Philippines (Heaney et al. 1998). We observed this species frequently in houses in Puerto Princesa City and the State Polytechnic College of Palawan in Aborlan Municipality.

#### Order Scandentia

##### Family Tupaiidae—Tree Shrews

*Tupaia palawanensis*.—This common species is endemic to the Palawan faunal region (Wilson 1993); it is related to *T. glis*, which is widespread on the Sunda Shelf (Corbet & Hill 1992). It is widespread on Palawan (Taylor 1934), and is usually common in secondary and primary lowland forest, though local densities may be highly variable between apparently similar habitats (Dans 1993, Hoogstraal 1951, Sanborn 1952). It is rare in montane forest, and common but patchy in agricultural areas. We captured and/or observed this species in coconut and cashew plantations, brushy areas with a few small trees (Sites 6, 11, and 12), secondary and logged-over forest (Sites 7 and 11), and primary forest (Sites 1, 2, 3, and 15) from near sea level to 1400 m. IUCN (2002) lists this species as Vulnerable, but we concur with Heaney et al.



(1998) that the species should be delisted due to the variety of habitats used and its apparent abundance. Specimens examined: 2: Site 1 (1), Site 2 (1).

#### Order Chiroptera

##### Family Pteropodidae—Fruit Bats

We follow Ingle & Heaney (1992) and Heaney et al. (1998) in regarding reports of *Haplonycteris fischeri* (Kock 1969) and *Ptenochirus minor* (Yoshiyuki 1979) from Palawan as erroneous, probably originating in mislabeled specimens. *Pteropus hypomelanus* is known from Cuyo Island, at the northeast edge of the Palawan faunal region (Heaney et al. 1998), as well as in the oceanic Philippines and on islets around Borneo, and should be sought on Palawan.

*Acerodon leucotis*.—This poorly known species is endemic to the Palawan faunal region. Hoogstraal (1951) found the species in an area with patches of “much disturbed remnants of original forest and dense second growth forest” on Busuanga Island, and two specimens were taken at Santiago, Iwahig (in Puerto Princesa) on Palawan (Sanborn 1952). A specimen from Bat Island (Barangay Tagburos, in Honda Bay), taken by P. O. Glass in 1978, is housed in the UMMZ. Heaney sighted large numbers of medium-sized, pale-furred flying foxes at Site 15 in April 2000, in the clearing of the old park headquarters near the center of the park (“Central Park”), that were probably this species. Widmann captured one at Site 12 at a height of 5 m, and saw others feeding in the canopy at ca. 8 m height. The IUCN (2002) lists this species as Vulnerable; we regard it as Data Deficient.

*Cynopterus brachyotis*.—Found throughout Southeast Asia; in the Philippines, it is common to abundant in secondary forest and agricultural areas, and rare in primary forest (Heaney et al. 1998); Sanborn (1952) reported many from Palawan. We netted this species frequently in secondary forest and agricultural areas at Sites 6, 7, 11, and 12, in freshwater swamp forest at Site 14,

and in coastal forest on Rasa Island (Site 13). We also captured this species in primary forest in a tree fall gap (Site 1), over a stream (Site 2), and at a place with no visible disturbance (Site 15). We found them roosting in various-sized groups in three caves at Sites 5 (there appeared be less than 50 in each of two caves) and 9 (ca. 300 individuals); although this species occasionally roosts in caves on Borneo (Payne et al. 1985), there are no previous records of such roosts in the Philippines. On several occasions we captured them carrying whole green figs (*Ficus* sp.) during flight; two of these individuals were returning to a cave at Site 5 between 1900–2000 h.

Out of 20 adult females caught at Site 14 on 20 March 2002, 15 were pregnant and 5 were carrying a single suckling young. On 1 and 2 April 2000, we captured three adult females at Site 5; all were carrying a single suckling infant during flight. On 17 May 2000 we captured eight adult females at Site 5; one was pregnant, one was carrying a suckling infant during flight, and two were emaciated and may have recently weaned their young. On this date, we also captured a male with enlarged mammarys (see Francis et al. 1994). On 30 October 2000, among 25 adult females, none were pregnant but one was lactating. Specimens examined: 4, Site 1 (1), Site 5 (3).

*Eonycteris spelaea*.—This widespread Southeast Asian species is common in agricultural areas in the Philippines, where all known roosts are in caves (Heaney et al. 1998, Rickart et al. 1993). Sanborn (1952) reported a large series from a cave above Tanabog, Palawan. We netted five individuals at Site 12, but most of our records came from caves in lowland forest. We found this species roosting in caves at Sites 4 and 10; at Site 4, the roosting population appeared to exceed 2000. At Site 10, there was an extremely large population (probably >50,000) of small pteropodids roosting inside the cave. We captured 49 pteropodids at the entrance to the cave, 48 of which



were *E. spelaea* and one was a *Rousettus amplexicaudatus*. On 19 December 1999, all three adult females we captured at Site 4 were pregnant. On 21 October 2000 at Site 10, we captured 11 adult female *E. spelaea*, four of which were carrying an infant during flight and five of which were pregnant. This species is heavily hunted in some areas of the Philippines (Rickart et al. 1993, Utzurrum 1992), but we observed no evidence of that being the case on Palawan. Specimens examined: 5, Site 4 (3), Site 10 (2).

*Macroglossus minimus*.—In the Philippines, this widespread Australasian species is common in secondary forest and agricultural areas and uncommon in primary forest up to more than 2000 m (Heaney et al. 1998, 1999). We captured this species in secondary lowland forest (Sites 7 and 12) and agricultural clearings (Site 11), usually near wild or domestic banana plants (*Musa* spp.), and in freshwater swamp forest in Narra Municipality and Rasa Island (Sites 13 and 14). Specimens examined: 3, Site 7 (1), Site 11 (2).

*Pteropus vampyrus*.—In the Philippines, this widespread Southeast Asian species occurs in primary lowland forest and adjacent agricultural areas (Heaney et al. 1998; Rabor 1955, 1986; Rickart et al. 1993; Sanborn 1953; Taylor 1934). Widmann estimated 400 individuals on Malinau Island, Aborlan Municipality in 1998, 570 on Rasa Island on 12 November 1999, and a small colony (ca. 40 individuals) at Lagan on Dumaran Island on 27 October 2001, based on departure counts. Flying foxes commonly sighted in Puerto Princesa City around mango and guyabano (= sour sop) trees are probably this species. In 1998, we found two individuals of this species that appeared to have been electrocuted on power lines, one at the Provincial Agriculture Center in Irawan, Puerto Princesa, and the other at the State Polytechnic College, Aborlan. We believe this species to be common overall, but under moderate pressure due to

hunting and perhaps to electrocution on power lines.

*Rousettus amplexicaudatus*.—Within the Philippines, this widespread Southeast Asian species is commonly found in agricultural habitats up to 500 m and rarely in primary lowland forest (Heaney et al. 1998). All known roosting sites are in caves (Heaney et al. 1989, 1991, 1998, 1999; Heidemman & Heaney 1989; Rickart et al. 1993). According to Payne et al. (1985), *R. amplexicaudatus* often roosts in association with *Eonycteris spelaea*. We netted one individual from a cave at Site 10 containing a large population of *E. spelaea*, one in an agricultural clearing in Site 11, and four in forest-grassland mosaic at Site 12; all of these sites are in heavily disturbed areas below 60 m. Specimens examined: 2, Site 10 (1), Site 11 (1).

#### Family Emballonuridae—Sheath-tailed Bats

There are no known records of *Saccolaimus saccolaimus* from Palawan, but its widespread distribution from India to New Guinea, including the oceanic Philippines (Heaney et al. 1998), suggests that it may be present and should be sought.

*Emballonura alecto*.—The Philippine sheath-tailed bat is known from Borneo, the Philippines, and Sulawesi (Heaney et al. 1998); we never encountered this species on Palawan, but Taylor (1934:200) captured five individuals “under an overhanging rock along Iwahig River, near the base of Thumb Peak”.

*Taphozous melanopogon*.—The bearded tomb bat is widespread in southern Asia (Heaney et al. 1998). In the Philippines, it is common in urban areas and lowland areas with limestone caves and rare in forest (Rickart et al. 1993, Sanborn 1952). There is a previous record from the vicinity of Puerto Princesa (Allen 1922), and A. C. Alcalá collected 6 specimens from Sitio Malabusog, Tinitian, Roxas Municipality in



1984 which are deposited in the UMMZ. We never encountered this species.

Family Megadermatidae—False Vampire  
and Ghost Bats

*Megaderma spasma*.—This widespread southern Asian species is common in primary lowland forest and disturbed forest in the Philippines (Heaney et al. 1991, 1998, 1999; Rickart et al. 1993). We captured this species from sea level to ca. 500 m in secondary forest (Site 7), primary forest (Sites 1 and 2), in a bamboo thicket (Site 11), and in or near caves (Sites 5 and 11). It was the most common insectivorous bat netted in forest-grassland-mosaic (Site 12), in swamp forest (Site 14), and in coastal forest (Site 13). At Site 1, we found this species roosting in small groups (<10) in four hollow trees distributed throughout the area. At Site 11 we found ca. 12 individuals roosting in a small cave (ca. 0.5–3 m wide, 0.3–1.5 m high, and 10 m long) along with *Rhinolophus acuminatus*. We also found two individuals roosting in a small cave (also Site 11) that had been severely disturbed by treasure hunters three years earlier. Cranial measurements of three individuals (Table 1) are slightly smaller than those of specimens from Leyte and Biliran (Rickart et al. 1993) and southern Luzon (Heaney et al. 1999). Specimens examined: 3, Site 1 (3).

Family Rhinolophidae—Horseshoe and  
Roundleaf Bats

Several poorly known but apparently widespread species in this family occur on the Sunda Shelf and in the oceanic Philippines and should be sought on Palawan; these include *Hipposideros cervinus* and *H. lekaguli* (Balete et al. 1995, Heaney et al. 1998, Ingle & Heaney 1992).

*Hipposideros ater*.—Occurs from India to Australia (Heaney et al. 1998). Known from lowland and montane forest and caves (Heaney et al. 1991, 1998; Payne et al. 1985, Rickart et al. 1993). We found this species to be uncommon to abundant in

three caves in disturbed lowland forest at 50 to 250 m elevation at Sites 5 (17% of 575 captures) and 8 (<1% of captures). During March to April 2000, none of the 26 females we captured at Site 5 were pregnant or lactating, but on 19 and 20 May 2000, 25 of 30 adult females were pregnant. We have re-examined a specimen from Palawan in the UMMZ identified by Allen (1922) as *H. bicolor*, and a series from the Tigoplan River, Palawan in FMNH reported by Sanborn (1952), and now consider them to be *H. ater*; thus, we now know of no records of *H. bicolor* from Palawan. Cranial measurements of 5 individuals (Table 1) are smaller than those of *H. bicolor* (Heaney et al. 1999, Ingle & Heaney 1992) but match those of *H. ater* (Ingle & Heaney 1992, Rickart et al. 1993). Specimens examined: 5, Site 5 (4), Site 8 (1).

*Hipposideros diadema*.—The diadem roundleaf bat is widespread from Myanmar to the Solomon Islands, with many previous records from Palawan (Allen 1922, Heaney et al. 1998). In the Philippines, it is common in disturbed forest, agricultural areas (Ingle 1992, Rickart et al. 1993), and primary forest (Heaney et al. 1998, Rickart et al. 1993). Reis & Garong (2001) reported specimens from sediments in a rock-shelter near Tabon Cave, Quezon Municipality dated to 11,130 BP. We captured this species from sea level to 600 m in disturbed grassland-forest mosaic (Sites 6 and 12), secondary forest (Site 7), primary forest (Site 2), and at nearly all caves we visited (Sites 4, 5, 8, 9, and 10), and we observed large numbers (probably thousands) in the underground river cave at PPSRNP. All of the roosts we identified held groups of *H. diadema* numbering greater than 200. Thirteen adult females captured in December 1999 included none that were pregnant or lactating. At Site 5 in March to April 2000, none of the 54 adult females were pregnant or lactating, but between 15 and 20 May 2000 26 of 43 were pregnant and one was carrying a suckling infant during flight. One of 21, one of 12, and none of 13 adult females



Table 1.—Means and ranges of cranial measurements of adults of Megadermatidae and Rhinolophidae from Palawan Island, Philippines.

Species	Sex	n	Condylolincisive length	Zygomatic width	Mastoid width	Orbital length	Canine to last molar	Molariform toothrow	Palatal breadth	Palatal length	Forearm length
<i>Megaderma spasma</i>	m	2	—	14.54 (14.52–14.55)	11.27 (11.26–11.28)	7.37 (7.3–7.43)	8.79 (8.67–8.91)	7.07 (6.95–7.18)	3.77 (3.5–4.04)	—	55.7 (55.4–56.0)
	f	1	—	14.17	11.32	7.57	9.0	7.06	3.79	—	54.3
<i>Hipposideros ater</i>	m	3	14.29 (14.21–14.37)	7.83 (7.74–7.90)	8.28 (8.26–8.30)	4.46 (4.3–4.56)	4.8	3.94 (3.72–4.21)	3.28 (3.22–3.33)	4.87 (4.83–4.94)	39.7 (39.4–39.9)
	f	2	14.54 (14.31–14.77)	7.82 (7.76–7.88)	8.31 (8.23–8.39)	4.78 (4.61–4.94)	4.86 (4.75–4.97)	4.05 (4.0–4.1)	3.43 (3.41–3.45)	5.21 (4.95–5.47)	40.3 (40.1–40.4)
<i>Rhinolophus acuminatus</i>	m	1	20.35	10.89	9.81	6.23	7.65	6.15	4.77	7.14	46.2
	f	4	19.44 (1)	10.70	9.68	6.17	7.59	6.01	4.76	6.56 (1)	47.7
<i>Rhinolophus anderseni aequilis</i> (holotype)	m	1	—	10.46 (10.5–10.92)	9.86 (9.63–9.78)	6.19 (6.05–6.21)	7.58 (7.5–7.75)	6.00 (5.78–6.40)	4.51 (4.66–4.95)	—	46.39 (46.6–48.1)
<i>Rhinolophus arcuatus</i>	m	2	18.78 (18.3–19.26)	9.79 (9.72–9.86)	9.52 (9.51–9.52)	5.21 (5.01–5.41)	7.54 (7.52–7.56)	5.52 (5.46–5.57)	4.12 (4.03–4.21)	6.74 (6.51–6.97)	46.5 (45.2–47.7)
	f	3	18.68 (18.41–18.91)	9.53 (9.41–9.62)	9.06 (8.64–9.36)	5.08 (5.02–5.18)	7.14 (6.95–7.47)	5.48 (5.29–5.63)	4.15 (4.08–4.27)	6.31 (6.05–6.48)	46.0 (45.6–46.5)
<i>Rhinolophus borneensis</i>	f	1	16.86	8.64	8.57	4.88	6.65	5.07	4.13	5.84	42.8
<i>Rhinolophus creaghi</i>	m	1	22.26	11.77	11.12	6.7	8.96	6.62	5.34	6.85	54.4
	f	4	20.87 (2)	11.03	10.62	6.25	8.45	6.45	4.83	6.87 (2)	52.4
<i>Rhinolophus macrotis</i>	m	3	17.3 (2) (20.7–21.03)	8.63 (10.83–11.27)	9.37 (10.51–10.78)	4.37 (5.87–6.59)	6.51 (8.39–8.51)	4.87 (6.37–6.52)	3.39 (4.55–5.06)	5.7 (2) (6.76–6.98)	45.5 (51.5–54.6)
	f	2	17.68 (17.21–17.38)	8.66 (8.62–8.64)	9.48 (9.32–9.44)	4.20 (4.33–4.42)	6.63 (6.49–6.53)	4.93 (4.84–4.91)	3.58 (3.36–3.43)	6.37 (1) (5.64–5.76)	47.7 (45.1–45.8)
<i>Rhinolophus virgo</i>	m	3	16.13 (2) (17.28–18.08)	8.87 (8.61–8.70)	8.55 (9.39–9.56)	4.84 (4.17–4.22)	6.16 (6.48–6.78)	4.71 (4.9–4.95)	3.57 (3.41–3.75)	5.08 (2) (46.9–48.5)	40.5 (40.5)
	f	3	16.16 (15.99–16.26)	8.72 (8.78–8.95)	8.48 (8.41–8.72)	4.87 (4.7–4.94)	6.27 (6.04–6.23)	4.72 (4.59–4.85)	3.46 (3.5–3.66)	5.12 (4.85–5.31)	41.5 (39.2–41.3)
			16.16 (15.72–16.48)	8.72 (8.68–8.78)	8.48 (8.45–8.51)	4.87 (4.84–4.89)	6.27 (6.15–6.36)	4.72 (4.67–4.76)	3.46 (3.3–3.56)	5.12 (4.43–5.63)	41.5 (40.8–41.9)



from July, August, and October were pregnant (Sites 8, 9, and 10, respectively). Specimens examined: 5, Site 4 (2), Site 5 (2), Site 9 (1).

*Rhinolophus acuminatus*.—This poorly known species occurs from Thailand to Lombok and Palawan, but not elsewhere in the Philippines (Heaney et al. 1998; specimens from Negros reported by Csorba et al. (2003) as this species were mislabelled). It is found in lowland forest on Borneo (Payne et al. 1985) and in secondary lowland dipterocarp forest on Banggi (Md. Nor 1995). We captured this species in caves from ca. 60 to 250 m in caves (Sites 8 and 11), a bamboo thicket (Site 11), and primary forest (Site 1). At Site 8, we captured 90 individuals out of 2775 captures. At Site 11 we found ca. 20 individuals roosting in a small cave (ca. 0.5–3 m wide, 0.3–1.5 m high and 10 m long) with ca. 12 *Megaderma spasma*. At Site 1, we took two individuals over a small stream just below a rock outcrop containing many fissures suitable for roosting bats. We also captured a single individual in our temporary living quarters at Site 1 after we observed for several days a bat feeding inside our semi-enclosed tent for several minutes daily between 0430 and 0600 h. Of 15 adult females taken in July 2000 at Site 8, one was pregnant and one was lactating. Cranial measurements (Table 1) match those previously available (Ingle & Heaney 1992) that are based on series from Balabac and Busuanga reported by Kuntz (1969) and housed in the USNM. We also refer two specimens collected by A. C. Alcalá on 13 July 1984, at Malabusog, Roxas Municipality housed at UMMZ (162885 and 162886) to this species, and include them in Table 1.

Sanborn (1952) reported a single specimen from Palawan (housed in FMNH) that he regarded as the first record from Palawan. However, we have determined that a single specimen (UMMZ 53112) collected in the late 1800s by the Beal/Steere Expedition and subsequently named *R. anderseni*

*seni aequalis* (Allen 1922) was this species. Heaney compared this specimen, which is the holotype and only known specimen, to series of all species currently known from Palawan. It was unambiguously identified as *R. acuminatus*; as noted by Medway (1977:32), a dorsal connecting process with a prominent triangular point (as shown by Medway 1977 fig. 6a and by Ingle and Heaney 1992 fig. 13a) is present, the base of the sella is not expanded into a cup, the median groove of the horseshoe is not broadened, and papillae are not present. The ears (18 mm) are less than half of the length of head plus body, and the forearm is 46.4 mm. The skull (measurements in Table 1) is virtually identical to those in the series from Sites 1 & 8, including overall size and shape, nasal swellings, braincase breadth and inflation, toothrows, palatal bridge, foramina in the roof of the posterior portion of the nasal passage, and bullae. Because *R. acuminatus* was named by Peters in 1871 (from Gadok, Java), we therefore recognize *R. anderseni aequalis* as its junior synonym. We note that Cabrera (1909) described *Rhinolophus anderseni* “probably from Luzon”. Aside from the holotype of *R. anderseni aequalis*, no specimens have subsequently been referred to this species. Csorba et al. (2003) tentatively assigned *R. anderseni* Cabrera as a junior synonym of *R. arcuatus* on the basis of the original description plus new drawings of the noseleaf and measurements of the skull, but without examining the holotype. We provisionally accept this, but point out the need for direct examination and comparisons. IUCN (2002) lists *R. acuminatus* as Data Deficient. Specimens examined: 8, Site 1 (4), Site 8 (1), Malabusog (2), and the holotype of *R. anderseni aequalis*.

*Rhinolophus arcuatus*.—Widespread from Sumatra to New Guinea (Heaney et al. 1998). Specimens from the Philippines currently identified as *R. arcuatus* may consist of two or more species (Heaney et al. 1991, 1999; Ingle & Heaney 1992; Rickart et al. 1993). Individuals referred to this



“species” have been found in agricultural areas, secondary forest, and primary lowland, montane, and mossy forest (Heaney et al. 1991, 1999; Ingle 1992; Rickart et al. 1993). We regularly captured this species at elevations from sea level to 1400 m in lowland primary forest (Sites 1 and 2), montane forest (Site 3), and caves (Sites 5 and 8). We also captured a single individual in the understory of mature but disturbed forest near a cave at Site 9, and we tentatively identified two individuals from Site 15 (which were released) as belonging to this species. Of 8 adult females taken between 15 and 20 May 2000 at Site 5, 5 were pregnant and one was lactating. Of 22 adult females taken in July 2000 at Site 2, one was lactating, and of 189 captured in July at Site 8, none were pregnant but 14 were lactating. These are the first specimens of this species from the Palawan faunal region. Cranial measurements (Table 1) closely match those of specimens from Leyte (Rickart et al. 1993) and southern Luzon (Heaney et al. 1999). Specimens examined: 5, Site 1 (2), Site 2 (1), Site 3 (2).

*Rhinolophus cf. borneensis*.—A single specimen taken by P. O. Glass on 31 January 1978 at “Sabang, Buenavista” (in Barangay Cabayugan, near Ulugan Bay in Puerto Princesa Municipality, ca. 10°05'N, 118°49'E; UMMZ 161395) appears to be this species. It was previously known from Indochina, the Malay Peninsula, Java, and Borneo, as well as some smaller islands in the southern South China Sea (Corbet & Hill 1992, Csorba et al. 2003); this is the first record from Palawan and from the Philippines. Cranial measurements and features (Table 1) closely match specimens in FMNH from Sarawak, the Natuna Islands, and Sabah, and external features are similar, but because we have only a single specimen, the identification is tentative. On Borneo, “the species roosts in caves, sometimes in colonies of several hundred individuals” (Payne et al. 1985). P. O. Glass (*in litt.*) noted that he captured the specimen in a mist net in a small banana grove in an

area of mixed agricultural/second growth forest within 1 km of mature forest. Specimen examined: 1, from Sabang.

*Rhinolophus creaghi*.—This species was previously known from Borneo and Madura Islands, where it often roosts in caves (Corbet & Hill 1992, Csorba et al. 2003, Koopman 1993, Medway 1977, Payne et al. 1985). This is the first record of this species from Palawan Island and the Philippines. On Palawan, we found it to be common in primary lowland forest from near sea level to at least 700 m. We captured one individual at Site 1 and 11 individuals at Site 2. It roosts in caves, often in large numbers; we captured 368 (45% of captures) at Site 4, 239 (9% of captures) at Site 8, and 33 (6% of captures) at Site 5. Of 135 adult females captured in December 1999 at Site 4, 8 were pregnant. Of 16 captured at Site 5 in March to April, none were reproductively active; of 11 at Site 2 and 151 at Site 8 (July 2000), none were pregnant but one and 12 were lactating, respectively. Cranial measurements (Table 1) show this to be the largest member of the genus on Palawan; our specimens are not distinguishable from a small series from Borneo (FMNH 47071–47075). Two previously unidentified specimens from Mt. Salicod, 2300 ft. (which may be the same mountain as Mt. Salakot, Site 2; P. O. Glass, *in litt.*), taken by P. O. Glass in 1978 and housed in the UMMZ, were taken earlier but were not reported; cranial measurements from these specimens are included in Table 1. This species is listed as Near-Threatened by IUCN (2002). Specimens examined: 7, Site 4 (3), Site 5 (1), Site 8 (1), Mt. Salicod (2).

*Rhinolophus macrotis*.—This poorly known species ranges from India to Sumatra and the Philippines, where it is known from lowland forest with some records from caves (Heaney et al. 1998, Ingle 1992). Our specimens represent the first record from Palawan. We captured this species in or near three caves in disturbed lowland forest at 50–250 m at Sites 5 (10 captures) and 8 (25 captures). The species ap-



pears to be uncommon. At Sites 5 and 8 it represented less than 5% and 1% of our captures, respectively. At Site 5 on 20 May 2000, we captured and examined two adult females; both were pregnant. Of 8 adult females captured in July at Site 8, none were pregnant or lactating. Cranial measurements of 5 individuals (Table 1) fall within or near the range for the species in Ingle and Heaney (1992). Specimens examined: 5, Site 5 (4), Site 8 (1).

*Rhinolophus virgo*.—This Philippine endemic is widely distributed within the Philippines (Heaney et al. 1998). It is known from secondary forest, primary lowland forest, reaching mossy forest on small, low-lying islands, and often roosts in caves (Heaney et al. 1991, Ingle 1992, Rickart et al. 1993); Sanborn (1952) reported a series from Tanabog, Palawan. This species appeared to be rare in the cave at Site 4 (0.5% of captures), common at Site 8 (151 captures, about 6% of total) and abundant in some caves at Site 5 (15% of captures). We also captured this species in primary forest at Sites 2 and 15. Of 29 adult females captured between 27 March and 4 April 2000, none were pregnant or lactating. Of 35 females captured at Site 5 between 15 and 20 May 2000, 16 were pregnant and 5 were lactating. Of 78 females taken at Site 8 in July 2000, 6 were pregnant and 2 were lactating. Cranial measurements (Table 1) fall within the range (Ingle & Heaney 1992) or very near the range (Rickart et al. 1993) of previously available individuals. IUCN (2002) lists this species as Near-Threatened. Specimens examined: 6, Site 4 (2), Site 5 (4).

#### Family Vespertilionidae—Vesper and Evening Bats

This diverse family of bats is generally poorly documented, and more species should be sought on Palawan, including such widespread taxa as *Harpiocephalus harpia*, *Murina cyclotis*, *Myotis ater* (which Hill 1983 and Corbet & Hill 1992 have

shown to be distinct from *Myotis muricola* and to be present on Culion Island in Palawan faunal region), *Philetor brachypterus*, and *Pipistrellus tenuis*.

*Glischropus tylopus*.—This poorly known species is found from Myanmar to the Molucca Islands and Palawan (Heaney et al. 1998). In Peninsular Malaysia it roosts in rock crevices, bamboo, and in new banana leaves (Payne et al. 1985). We never encountered this species, but it is represented by a specimen in the USNM (Hollister 1913).

*Kerivoula hardwickii*.—This species is widespread from India and southern China to the Lesser Sunda Islands and the Philippines (Heaney et al. 1998). It was previously known from lowland, montane, and ridge-top mossy forest from 500 to 1600 m in the Philippines (Heaney et al. 1999, Rickart et al. 1993). Everett (1889) included mention of this species from Palawan. A previous record from UMMZ (Heaney et al. 1998) has been re-identified as *K. whiteheadi*, as noted below. Payne et al. (1985) reported the species to “frequent the understory of tall forest” on Borneo, and Md. Nor (1995) caught one in primary lowland dipterocarp forest on Banggi Island “in the axil of a leaf on a rattan vine 1 m above ground”, and netted them in the understory of primary forest on Balambangan Island. We captured two adult females, one of which was lactating, in a bamboo thicket at Site 11 (ca. 60 m asl), and two individuals in the understory (ca. 2–4 m above the ground) of primary lowland forest at ca. 650 m elevation at Site 2, all in harp-traps. Specimens examined: 3, Site 2 (1), Site 11 (2).

*Kerivoula pellucida*.—This poorly known species is known from the Malay Peninsula, the Sunda Shelf, Jolo, and Palawan (Heaney et al. 1998). Known only from lowland forest (Payne et al. 1985). Taylor (1934) reported two specimens from Palawan (no locality given) that he obtained from a group of seven that he found flying together in daylight: his map (Fig. 13),



shows the locality in the vicinity of Brooke's Point. On 21 June 2000, using a harp-trap we captured an adult female carrying a suckling infant in secondary lowland forest (ca. 80 m) over a small stream at Site 7. Cranial measurements of the adult female (Table 2) are smaller than the one specimen from Davao del Norte, Mindanao available to Ingle and Heaney (1992), but they are otherwise very similar; additional specimens are badly needed to examine patterns of variation. Specimens examined: 2, Site 7 (2).

*Kerivoula whiteheadi*.—This poorly known species is widely distributed from southern Thailand to Borneo and the Philippines (on Luzon, Mindanao, and Palawan; Heaney et al. 1998). In the Philippines, it is known only from near sea level in disturbed forest and agricultural areas (Sanborn 1952). A single specimen in the UMMZ captured by P. O. Glass on 29 Sept. 1978 at Irawan, Puerto Princesa Municipality (noted as 2 km N Irawan, at the base of Mt. Beaufort by P. O. Glass, *in litt.*) was erroneously reported by Heaney et al. (1998) under both *K. hardwickii* and this species. Additionally, two specimens taken "under banana fronds" by C. A. Ross on 8 April 1987 at Barangay Binwang, Quezon Municipality, are housed in the USNM. We captured a single individual of this species in a harp-trap near ground level in a cogon grassland (*Imperata cylindrica*) at Site 6. Cranial measurements of these four individuals (Table 2) are similar to those in Ingle & Heaney (1992) of a specimen from Mindanao, though some variation in size is present; more specimens are needed to assess geographic variation. Specimens examined: 4, Site 6 (1), Irawan, Puerto Princesa Municipality, 60 m (1), and Binwang, Quezon (2).

*Miniopterus australis*.—This common species is found from India to Australia; it is widespread in the Philippines, but this is the first record from Palawan (Heaney et al. 1998). It is known to roost in caves in lowland areas of agriculture or second growth

(Heaney et al. 1991, Rickart et al. 1993, Sanborn 1952). We captured this species in varying numbers at several caves. In primary and disturbed lowland forest at Sites 4 and 5 it was scarce, represented by less than 1% and less than 3% of captures, respectively. At Site 8 it was abundant (45% of 2775 captures). Cranial measurements of 4 individuals (Table 2) are similar to those reported by Ingle and Heaney (1992) and Rickart et al. (1993) from the Philippines, and by Corbet & Hill (1992) from throughout the species range. Specimens examined: 4, Site 4 (2), Site 5 (2).

*Miniopterus schreibersi*.—This common species is found from Europe to the Solomon Islands and is widespread in the Philippines, but this is the first record from Palawan (Heaney et al. 1998). It is common in caves throughout the lowlands in agricultural areas and forest and known from both lowland and montane forest (Heaney et al. 1991, 1999; Rickart et al. 1993; Sanborn 1952). We captured this species in and around caves in disturbed and primary lowland forest at Sites 4, 5, and 8. At Sites 4 and 8 the species was abundant, represented by 47% and 26% of captures respectively. At Site 5 it was common at 10% of 575 captures. Of 214 adult females captured in December 1999 at Site 4, only one was pregnant. Of 36 captured between 15 and 20 May 2000 at Site 5, 15 were pregnant and none were lactating. Of 421 captured at Site 8 in July 2000, none were pregnant but 4 were lactating. Cranial measurements (Table 2) are similar to those reported by Ingle and Heaney (1992) and Rickart et al. (1993) from the Philippines, and by Corbet and Hill (1992) from throughout the species range. IUCN (2002) lists this species as Near-Threatened, but its abundance in heavily disturbed habitat in the Philippines (Heaney et al. 1998, Rickart et al. 1993) makes this inappropriate. Specimens examined: 6, Site 4 (4), Site 5 (1), Site 8 (1).

*Miniopterus tristis*.—This widespread species is found from the Philippines to the Solomon Islands; this is the first record



Table 2.—Means and ranges of cranial measurements of adult Vespertilionidae from Palawan Island, Philippines.

Species	Sex	n	Condylor-incisive length	Zygomatic width	Mastoid width	Orbital length	Canine to last molar	Molariform toothrow	Palatal breadth	Palatal length	Forearm length
<i>Kerivoula hardwickii</i>	m	1	13.39	8.48	7.14	4.05	5.39	3.53	2.72	6.82	33.1
	f	2	13.75 (13.63–13.87)	8.70 (8.64–8.76)	7.29 (7.05–7.53)	4.07 (4.07–4.07)	5.62 (5.50–5.74)	3.74 (3.65–3.82)	2.90 (2.84–2.96)	6.98 (6.91–7.04)	33.6 (33.4–33.7)
<i>Kerivoula pellucida</i>	f	1	13.51	8.26	7.21	3.08	5.57	3.87	2.58	6.94	31.3
<i>Kerivoula whiteheadi</i>	f	4	12.00 (11.85–12.28)	7.56 (7.44–7.64)	6.66 (6.56–6.77)	—	5.17 (5.07–5.22)	3.18 (3.12–3.30)	2.41 (2.34–2.49)	5.82 (5.70–6.08)	29.7 (29.4–30.4)
	m	1	13.25	7.21	7.16	4.46	5.21	3.80	3.06	5.79	36.7
<i>Miniopterus australis</i>	f	3	13.06 (12.90–13.15)	7.39 (7.29–7.58)	7.28 (7.23–7.33)	4.29 (4.16–4.40)	5.19 (5.16–5.21)	3.76 (3.73–3.79)	3.00 (2.91–3.06)	5.66 (5.56–5.79)	37.1 (36.2–37.8)
	m	1	15.33	8.88	8.73	5.31	6.28	4.58	3.65	6.35	47.4
<i>Miniopterus schreibersi</i>	f	5	14.78 (14.67–14.94)	8.42 (8.30–8.57)	8.19 (8.12–8.33)	5.05 (4.90–5.32)	6.14 (6.0–6.25)	4.45 (4.32–4.56)	3.39 (3.26–3.54)	6.43 (6.37–6.48)	42.3 (39.2–43.9)
	m	1	18.50	10.72	9.82	6.51	7.75	5.66	4.62	8.13	54.2
<i>Miniopterus tristis</i>	f	2	18.72 (18.71–18.74)	10.76 (10.74–10.78)	9.76 (9.62–9.93)	6.73 (6.70–6.76)	7.83 (7.75–7.91)	5.73 (5.66–5.81)	4.37 (4.33–4.40)	8.31 (8.31)	53.3 (53.3–53.3)
<i>Murina cf. tubinaris</i>	m	1	14.63	9.11	7.73	5.08	5.23	3.90	3.17	6.64	33.1
<i>Myotis macrotarsus</i>	m	1	17.88	11.8	9.51	6.88	7.30	5.31	4.15	8.58	48.1
<i>Myotis rufopictus</i>	f	1	19.18	12.25	9.68	6.91	8.40	5.88	3.84	9.69	58
<i>Pipistrellus javanicus</i>	m	1	13.30	9.31	7.90	5.15	4.88	3.82	3.33	—	34.0
	f	1	13.03	9.01	7.60	4.89	4.70	3.78	3.23	—	35.5
<i>Tylonycteris pampus</i>	m	1	10.29	7.98	6.71	3.53	3.45	2.69	2.86	3.91	23.4
	f	2	10.24 (10.10–10.34)	7.75 (7.56–7.96)	6.75 (6.59–6.96)	3.74 (3.57–3.80)	3.41 (3.37–3.45)	2.68 (2.59–2.74)	2.75 (2.71–2.81)	3.86 (3.67–4.05)	23.6 (22.8–24.6)



from Palawan (Heaney et al. 1998). The species is known to roost in caves and forage in disturbed forest (Rickart et al. 1993, Sanborn 1952). We captured one specimen in a cave surrounded by old-growth forest at Site 4 and two in a cave surrounded by disturbed areas and secondary forest at Site 10. *Miniopterus tristis* appeared to be consistently less common than the other species of *Miniopterus*. Cranial measurements of 3 individuals (Table 2) are similar to those reported by Ingle and Heaney (1992) and Rickart et al. (1993) from the Philippines, and by Corbet and Hill (1992) from throughout the species range. Specimens examined: 3, Site 4 (1), Site 10 (2).

*Murina* cf. *tubinaris*.—A single specimen of a small tube-nosed bat (genus *Murina*) was taken in a lowland grassland-forest mosaic at Site 12 on 24 March 1997, and is housed in the Staatliches Museum für Naturkunde in Stuttgart, Germany (#49238). The specimen (Table 2) is very similar to a series from Tonkin, Vietnam (FMNH 32203–32204, 46626–46627), though slightly larger. In our specimen, as in the Vietnamese series, the upper tooth-rows converge slightly, the anterior premolars are reduced, and the canines are short but longer than the premolars, as noted by Koopman and Danforth (1989) and Corbet and Hill (1992). The length of forearm (33 mm) falls at the center of the range given by Koopman and Danforth for *M. tubinaris* (28–35 mm), and at the high end given for *M. suilla* (26–33 mm). Koopman and Danforth (1989) considered *M. florum*, *M. suilla*, and *M. tubinaris* to be members of a species group, and perhaps to be conspecific, noting that few specimens are available. Corbet and Hill (1992) re-emphasized the uncertainty in current taxonomy, but took a somewhat different view, referring specimens from Borneo to *M. suilla*, rather than to *M. tubinaris*. While we agree entirely on the need for more specimens and further study, we follow Koopman & Danforth (1989) on referring Bornean specimens to *M. tubinaris*, and provisionally re-

fer the specimen from Palawan to this same species. Specimen examined: 1, Site 12 (1).

*Myotis horsfieldii*.—This common species is distributed from southeastern China to the Malay Peninsula, Sulawesi, and the Philippines (Heaney et al. 1998). On Borneo, the species “roosts in crevices or bell-holes in caves, usually not far from large streams or rivers” (Payne et al. 1985). In the Philippines, it has been recorded in lowland forest and agricultural areas, up to 800 m (Heaney et al. 1998). We never encountered this species; two specimens in the UMMZ taken by A. C. Alcala in Sitio Malabusog, Tinitian, Roxas Municipality in 1984 were reported by Heaney et al. (1998).

*Myotis macrotarsus*.—This species is known from Borneo and the Philippines (Heaney et al. 1998); it roosts in caves near sea level and forages in agricultural areas (Heaney and Uzzurum, unpubl. data). Md. Nor (1995) caught the species over a dry river bed and in the understory of primary lowland forest on Balambangan Island. In a cave in disturbed lowland forest at Site 8, this species was represented by <0.5% of 2775 captures. We also observed small numbers in the cave at PPSRNP. Cranial measurements (Table 2) of one individual show it to be slightly larger than those reported by Ingle & Heaney (1992). IUCN (2002) lists this species as Near-Threatened. Specimens examined: 1, Site 8 (1).

*Myotis rufopictus*.—This poorly known Philippine endemic has been recorded from primary lowland and montane forest (Heaney et al. 1999, Mudar & Allen 1986). We never encountered this species; on Palawan, it is known from a single specimen in UMMZ reported by Allen (1922). We follow Ingle & Heaney (1992) in regarding this as one of several distinct species within the subgenus *Chrysopteron*, rather than recognizing only a single species, *Myotis formosus*, within the subgenus (e.g., Corbet & Hill 1992). This species is not listed by IUCN (2002); we recommend listing as Data Deficient. Measurements in Table 2 of the specimen reported by Allen (1922) were



taken by Heaney. Specimen examined: 1, Puerto Princesa (1).

*Pipistrellus javanicus*.—This species is distributed from Korea to Java and the Philippines (Heaney et al. 1998). Taxonomic status is uncertain; *P. imbricatus* has been reported from Palawan (e.g., Allen 1922, Corbet & Hill 1992, Sanborn 1952), but Ingle and Heaney (1992) were unable to distinguish more than one species of *Pipistrellus* of this size in the Philippines; detailed study is needed. It is common in primary montane forest and uncommon in lowland and mossy forest (Heaney et al. 1999, Ingle 1992, Sanborn 1952). We captured two individuals from a roost in a hollow tree in montane forest (ca. 1300 m) at Site 3. The opening in the tree appeared to have formed where a branch had been broken off the tree and was quite small (ca. 1.5 × 5 cm). Cranial measurements (Table 2) fall within the range of specimens reported by Ingle and Heaney (1992), and are slightly smaller than a series from southern Luzon (Heaney et al. 1999). Specimens examined: 2, Site 3 (2).

*Scotophilus kuhlii*.—This common species is widespread from Pakistan to Taiwan and the Philippines (Heaney et al. 1998); it is abundant in urban and agricultural areas, and roosts in buildings and “tents” made from modified palm leaves (Heaney et al. 1998; Rickart et al. 1989, 1993). Hollister (1913) and Taylor (1934) reported it from Puerto Princesa, Sanborn (1952) reported it from Brooke’s Point, and we found it to be abundant in buildings at the Provincial Agriculture Center, Irawan, Puerto Princesa, and in staff houses of the State Polytechnic College in Puerto Princesa, and in mixed urban/agricultural areas (Site 12).

*Tylonycteris pachypus*.—This tiny bat is widespread from India to the Philippines (Heaney et al. 1998). In the Philippines, it is known from bamboo stands in agricultural areas (Heaney & Alcala 1986); Hollister (1913) reported a specimen from Puerto Princesa. We captured several individuals of this species in a bamboo thicket

at Site 11. Very near the capture site we observed what appeared to be more than a dozen individuals of this species foraging over a few remnant trees in a cleared area with houses that is immediately surrounded by logged-over and secondary forest. Specimens examined: 5, Site 11 (5).

*Tylonycteris robustula*.—This species is also widespread from southern China to the Lesser Sunda Islands and the Philippines (including records from Calauit, Luzon, and Palawan); its habitat is apparently similar to that of *T. pachypus* (Heaney & Alcala 1986, Heaney et al. 1998). We never encountered this species.

#### Family Molossidae—Free-Tailed Bats

This family is generally poorly known in Southeast Asia, partly because they typically fly high above the canopy and are therefore rarely netted. At least one species (*Chaerophon plicata*) is widespread in the region and should be sought on Palawan.

*Cheiromeles torquatus*.—This poorly known species is found from Sumatra to Java, Borneo, and Palawan, but not the rest of the Philippines (Heaney et al. 1998). It roosts in large caves and hollow trees and forages in open areas, over streams, and above forest canopy on Borneo (Payne et al. 1985). We never encountered this species, which was documented on Palawan by Sanborn (1952) based on a single specimen. IUCN (2002) lists this species as Near-Threatened.

*Mops sarasinorum*.—This very poorly known species occurs in Sulawesi and the Philippines; the Palawan record is based on a single specimen in the Senckenberg Museum, Frankfurt (Heaney et al. 1998). It probably occurs in lowland forest (Heaney et al. 1998). We never encountered this species. It is listed by IUCN (2002) as Near-Threatened, but we recommend Data Deficient.

#### Order Primates

##### Family Cercopithecidae—Monkeys

*Macaca fascicularis*.—This common monkey occurs from Myanmar to Timor



and the Philippines (Fooden 1995, Heaney et al. 1998). It is known from agricultural areas near forest, second growth, secondary forest, and primary lowland and montane forest (Heaney et al. 1998, 1999; Rickart et al. 1993); Sanborn (1952) reported specimens from Iwahig, Puerto Princesa, and Brooke's Point. Reis & Garong (2001) reported a specimen from sediments in a rock-shelter near Tabon Cave, Quezon Municipality dated to 11,130 BP. We commonly observed this species at all of our sites (except Site 13), in secondary and primary forest (including mangrove, swamp forest, beach forest, and lowland forest) from sea level to 1000 m; at forest edge near agricultural areas and houses they seem to be less common and more shy. On Palawan, the species is under moderate hunting pressure for meat and the local pet trade, but appeared to have stable populations. In most areas, it was quite wary of humans, but in areas such as the PPSRNP (Site 15), the species did not associate humans with danger, and had become a regular thief of picnic baskets. It is listed by IUCN (2002) as Near-Threatened.

#### Order Pholidota

##### Family Manidae—Pangolins

*Manis culionensis*.—This endemic species of the Palawan faunal region, with records from Palawan and Culion Islands (Heaney et al. 1998), was formerly included within *Manis javanica* (Feiler 1998). It is known from primary and secondary lowland forest, possibly localized in distribution (Allen 1910, Hoogstraal 1951, Sanborn 1952, Taylor 1934). We sighted several in lowland grassland/forest mosaic at Site 12. It is hunted for its skin, which is used to treat asthma. We have seen it for sale in Puerto Princesa and our guide at Site 11 said that it is hunted in logged-over lowland forest in that area. The species was described by local informants as fairly common, but hunting pressure is moderately heavy. *Manis javanica* is listed by IUCN

(2002) as Near-Threatened; *M. culionensis* probably deserves the same status.

#### Order Rodentia

##### Family Sciuridae—Squirrels

*Hylopetes nigripes*.—This large gliding squirrel is endemic to the Palawan faunal region; the number of museum specimens (Allen 1910, Sanborn 1952) suggests that it is common. Reis & Garong (2001) reported two specimens from sediments in a rock-shelter near Tabon Cave, Quezon Municipality dated to 11,130 BP. Taylor (1934) found the species in primary and secondary lowland forest where they nest in cavities in large trees. We observed an individual running up the side of a large hollow tree in primary forest at Site 1, and we frequently heard and twice spotlighted them in mature lowland forest at Site 15. We also heard the distinctive calls several times in selectively logged but largely intact forest near Barake, Aborlan Municipality, in the Victoria Range. According to local residents, the species is common in mature forest and is occasionally hunted as a source of food. IUCN (2002) lists this species as Near-Threatened; by current criteria, it should be listed as Data Deficient.

*Sundasciurus juvencus*.—This tree squirrel is endemic to central and northern Palawan Island (Heaney et al. 1998). Hoogstraal (1951) and Sanborn (1952) reported this species from primary and secondary lowland forest. We commonly observed this species in primary and secondary lowland forest at Sites 1, 2, 7, 11, 12, and in both secondary forest and grassland/degraded forest mosaic at Site 15. We also found it in a very small (<1 ha.) patch of secondary lowland forest surrounded by grassland and agricultural areas at Site 6. We observed the species on Dumarán Island, but not on Malinau or Rasa. The species is reportedly a common pest in coconut plantations. It is occasionally hunted as a source of food and for the local pet trade. It is listed by IUCN (2002) as Endangered, but this is strongly



contradicted by the available data, and we recommend de-listing.

*Sundasciurus rabori*.—This poorly-known species, described from 5 specimens taken at 3600–4350 ft (ca. 1100–1300 m) on Mt. Mantalingajan, is endemic to Palawan Island (Heaney 1979). P. C. Gonzales deposited 2 specimens at the UMMZ that he collected on Mt. Gorangbato in Brooke's Point Municipality in 1984; these are the only reported specimens aside from the original type series from Mt. Mantalingajan (Heaney 1979). Although we worked in some seemingly suitable habitats on Cleopatra's Needle (Site 3), we did not specifically seek this species, and we never encountered it. The IUCN (2002) lists *S. rabori* as Vulnerable, but based on current IUCN criteria, it should be considered Data Deficient.

*Sundasciunis steerii*.—This species is endemic to Balabac and southern Palawan Island (Heaney et al. 1998); Sanborn (1952) reported a large series from Brooke's Point. Heaney et al. (1998) listed it as common in lowland forest and coconut and banana plantations. Because all of our study sites were in central and northern Palawan, we never encountered this species. It is listed by IUCN (2002) as Near-Threatened; since its habitat use is similar to the closely-related *S. juvencus*, it is probably not threatened.

#### Family Muridae—Mice

*Chiropodomys calamianensis*.—This poorly known arboreal mouse is endemic to the Palawan faunal region; it is closely related to species on the Sunda Shelf (Musser 1979). Reis & Garong (2001) reported a specimen from sediments in a rock-shelter near Tabon Cave, Quezon Municipality dated to 11,130 BP. It is known from forest near sea level (Taylor 1934), coconut plantations, bamboo thickets, and buildings (Sanborn 1952); there are 12 specimens from Palawan in FMNH and NMP from the Hoogstraal expedition (Sanborn 1952). The

genus is apparently difficult to capture (Musser 1979); we never encountered this species. We recommend IUCN listing as Data Deficient.

*Haeromys pusillus*.—This species is known only from Borneo, Palawan, and Calauit Islands (Musser & Carleton 1993, Musser & Newcomb 1983). It is cited in Heaney et al. (1998) as "*Haeromys* sp. A" as potentially endemic to Palawan, but we follow Musser (pers. comm.) in treating it as conspecific with *H. pusillus*. We never encountered this species, but Musser & Carleton (1993) cited a specimen from Palawan. A specimen of *H. pusillus* was taken in Sabah, Borneo, in a pit-fall trap near the edge of tall dipterocarp forest (Payne et al. 1985), and A. C. Alcalá stated that he captured the specimen from Calauit (in FMNH) by hand in a bamboo thicket (pers. comm.). IUCN (2002) listed this species as Vulnerable, but based on current criteria, it should be considered Data Deficient.

*Maxomys panglima*.—This common rat is endemic to the Palawan faunal region; the genus is common on the Sunda Shelf, but is absent from oceanic portions of the Philippines (Musser et al. 1979). Sanborn (1952) reported large series from several localities. We found it to be the most commonly captured small mammal in agricultural/forest mosaic at Site 12 (62% of 169 captures), and was common to abundant in secondary forest (Site 11), primary lowland (Sites 1 and 2), and montane forest (Site 3) from near sea level to at least 1550 m. We captured a single juvenile in mossy forest at 1580 m at Site 3. Because we found this species to be common, although sometimes patchy, in all lowland and montane forested sites where we trapped extensively, and in mixed agricultural/second growth areas at Sites 11 and 12, we consider the IUCN (2002) listing as Near-Threatened to be unjustified. Specimens examined: 5, Site 1 (3), Site 3 (2).

*Mus musculus*.—This introduced commensal has a nearly world-wide distribution, although Southeast Asian populations



are sometimes treated as a separate species, *M. castaneus* (Musser & Carleton 1993). It is common in human habitations in urban and rural areas (Heaney et al. 1998). We captured several in a residential area at Site 12, and it is most likely common in such places throughout Palawan.

*Palawanomys furvus*.—This poorly known monotypic genus is endemic to Palawan Island. It has been taken from a single locality on Mt. Mantalingajan and probably occurs in high mountain forest (Musser & Newcomb 1983). Our survey efforts on Cleopatra's Needle (Site 3) failed to find this species; perhaps it is restricted to the more extensive mountain ranges of southern Palawan. The IUCN (2002) lists this species as Endangered; the lack of data and lack of damage to its presumed habitat (montane and mossy forest) suggest that it should be listed as Data Deficient.

*Rattus exulans*.—This introduced commensal species is widespread from Bangladesh to Easter Island (Heaney et al. 1998). The first records from Palawan were named as a distinct species (*luteiventris*) by Allen (1910), but it is currently treated as a junior synonym of *R. exulans* (Musser & Carleton 1993). It is common in agricultural areas (Barbehenn et al. 1973, Rabor 1986) and sometimes present in disturbed forest and rare in primary forest (Barbehenn et al. 1973; Heaney et al. 1991, 1998). We found this species in grassland (Site 6), agricultural areas (Sites 6, 11, 12, and 14), and in secondary lowland forest (Site 7). The species appears to be absent from primary (e.g., Sites 1, 2, and 3) and logged-over forest (e.g., Site 11) on Palawan. Specimens examined: 4, Site 6 (3), Site 11 (1).

*Rattus tanezumi*.—This introduced commensal, formerly included within *Rattus rattus* (Musser & Carleton 1993), is widespread from Afghanistan to New Guinea and Micronesia (Heaney et al. 1998). It is often abundant in urban and agricultural areas and common in disturbed forest up to 1800 m (Danielsen et al. 1994; Heaney et al. 1989, 1999; Rabor 1986; Sanborn 1952).

Hoogstraal (1951) and Sanborn (1952) found them to be common on Palawan in some agricultural and residential areas. We captured three at Site 13, and three in a residential area in Puerto Princesa; vouchers were deposited in the NMP and the collection of the Palawan Council for Sustainable Development.

*Rattus tiomanicus*.—This indigenous rat is found on the Malay Peninsula and the islands of the Sunda Shelf, including Palawan (Heaney et al. 1998). Payne et al. (1985) reported the species from secondary forest, agricultural areas and gardens, scrub, and grassland. We captured this species in grassland/forest mosaic at Site 12 (9% of captures), two in selectively logged forest at Site 13, one in a ricefield at Site 14, and three individuals from mossy forest and the transition zone between mossy and montane forest at Site 3. At Site 3, two individuals were taken at ca. 1580 m during the night and one at ca. 1540 m during the day. Specimens examined: 3, Site 3 (3).

*Sundamys muelleri*.—This moderately large rat is found from southern Myanmar to the Sunda Shelf, including Palawan (Heaney et al. 1998); the genus is absent from the oceanic Philippines. Sanborn (1952) described a subspecies endemic to Palawan, *S. m. balabagensis*, from a single specimen taken at 3000 ft (ca. 900 m) "in thick forest near the top of Mt. Balabag"; two additional specimens in the USNM are from Pinigisan, on the lower slopes of Mt. Mantalingajan at 2100–2500 ft (ca. 640–760 m). Additional specimens from the Palawan region are from Culion Island (Sanborn 1952), Balabac, and Busuanga (USNM; Heaney et al. 1998). On Borneo, the species occurs in forest, often near streams (Payne et al. 1985) at elevations usually below 3500 ft (ca. 1070 m; Medway 1977). Md. Nor (1995) caught the species on Banggi, Balambangan, and Molleangan Islands "mostly in primary forest on low ground and near streams". We captured one individual from a riparian zone in primary forest at ca. 700 m at Site 2, and



two in lowland grassland/forest mosaic at Site 12. Specimen examined: 1, Site 2 (1).

#### Family Hystricidae—Porcupines

*Hystrix pumila*.—The only porcupine found in the Philippines is endemic to the Palawan faunal region; other species occur widely on the Sunda Shelf and continental Asia. Reis & Garong (2001) reported 3 specimens from sediments in a rock-shelter near Tabon Cave, Quezon Municipality dated to 11,130 BP. It is known to occur in secondary and primary lowland forest and to den in abandoned mine shafts (Hoogstraal 1951, Sanborn 1952). We observed this species at dusk along the edge of secondary forest at Site 11, once at night at Site 15 (where it was feeding on fruit of *Terminalia catappa*), and several times at night in grassland/forest mosaic at Site 12. Local guides reported them at Site 14, at the Iwahig Penal Colony in Puerto Princesa, in Rizal Municipality, and in Dumarang Municipality (on the mainland). This was reported as the most important game species for the Tagbanua ethnic community in Barake, Aborlan Municipality (Lacema & Widmann 1999); they are often dug out of their subterranean dens. Not listed by IUCN (2002) but listing as Data Deficient or Near-Threatened seems justified.

#### Order Carnivora

##### Family Felidae—Cats

*Prionailurus bengalensis*.—This small cat is widespread from Siberia to Pakistan and Bali, with reports from the Philippines on Busuanga, Cebu, Negros, Palawan, and Panay Islands only (Heaney et al. 1998, Taylor 1934). The population from the Palawan faunal region was described recently as a distinct subspecies, *P. b. heaneyi*, by Groves (1997); it is well represented by museum specimens (Allen 1910, Sanborn 1952). Rabor (1986) reported the species from agricultural areas and forest from sea level to ca. 1500 m. We spotlighted one

along a river trail in Barake, Aborlan Municipality.

#### Family Mustelidae—Weasels, Otters, and Badgers

*Amblonyx cinereus*.—This otter occurs from India to Taiwan and the Sunda Shelf (Heaney et al. 1998). On Palawan, it is found in coastal rivers and bays (Hoogstraal 1951, Rabor 1986, Sanborn 1952). Payne et al. (1985) and Sanborn (1952) reported the species feeds on crustaceans, mollusks, and fish where there is permanent water and some tree cover. Rangers at PPSRNP reported to Heaney and Widmann that otters frequently visit along the beach and small streams, and local people reported them from the Iwahig River (Puerto Princesa), Aborlan River (Aborlan Municipality), Malatgao and Taritien Rivers (Narra Municipality), and adjacent mangrove and freshwater swamp forest. We received one report of an otter raiding a prawn pond. IUCN (2002) lists this species as Near-Threatened.

*Mydaus marchei*.—This badger is endemic to the Palawan faunal region; it is related to a species that occurs on the Sunda Shelf. It has been documented in mixed grassland and secondary forest (Hoogstraal 1951, Kruuk 2000, Rabor 1986, Taylor 1934), and Sanborn (1952) reported series from several localities. We occasionally smelled its strong odor in areas of mixed agriculture and secondary forest throughout Palawan; we sighted it often in residential and cultivated areas, grassland, and grassland/forest mosaic at Site 12, and rarely in ricefields and freshwater swamp forest at Site 14. One individual living in a den on campus at the State Polytechnic College was easily followed and observed. Because it is widespread and moderately common on Palawan, and is rarely hunted (Grimwood 1976, Kruuk 2000), we agree with Kruuk (2000) that the IUCN listing of this species as Vulnerable is not justified.



## Family Herpestidae—Mongooses

*Herpestes brachyurus*.—The only mongoose found in the Philippines is distributed from the Malaysian Peninsula to Borneo and Palawan (Heaney et al. 1998). The Palawan population was named as a distinct species (*H. palawanus* Allen 1910), but currently is treated as a subspecies (Corbet & Hill 1992). Allen (1910) described them based on one specimen from Iwahig; Sanborn (1952) reported one specimen from Puerto Princesa and one from Brooke's Point, and Rabor (1986) found the species most often near rivers. On Borneo, Payne et al. (1985) found the species to occur in primary and secondary lowland forest, plantations, and gardens. We never encountered this species, but we received reports of them at Site 14.

## Family Viverridae—Civets

*Arctictis binturong*.—The binturong is known from northern Myanmar to the Sunda Shelf (Heaney et al. 1998). On Borneo, the species is arboreal and terrestrial, mostly nocturnal, and occurs in old-growth and secondary forests, sometimes entering agricultural areas near forest (Payne et al. 1985). The Palawan population, which initially was named as a distinct species (*A. whitei* Allen 1910) from four specimens, is still represented by few specimens (Heaney et al. 1998). Rabor (1986) reported observations from primary and secondary lowland forest up to 200 m. Our guide at Site 11 reported that a juvenile repeatedly entered remnant trees that were fruiting in a clearing surrounded by secondary forest. At Site 2, we observed *A. binturong* drinking water from a stream at ca. 400 m during mid-day. We spotlighted one in a fruiting *Ficus* tree at Site 15, and twice saw one in grassland/forest mosaic at Site 12 feeding on fruits of *Guioa pleuropteris*. Local people reported hunting them for food, and also catching them and selling them as pets. The IUCN (2002) listing of *A. binturong whitei* as Vulnerable seems justified.

*Paradoxurus hermaphroditus*.—This common species is found from Sri Lanka to the Lesser Sunda Islands and the Philippines (Heaney et al. 1998). Recorded in agricultural areas and forest over a wide elevational range (Allen 1910; Heaney et al. 1991, 1999; Hoogstraal 1951; Rabor 1986); Sanborn (1952) reported large series from several localities. We often saw them feeding in fruiting trees and shrubs in grassland/forest mosaic at Site 12, and we saw road-kills along the coastal highway. They are hunted, but the large number of museum specimens and sightings indicate that they traditionally have been and probably remain the most common carnivore on Palawan (e.g., Allen 1910, Sanborn 1952).

*Viverra zibetha*.—This civet is found from the Malay Peninsula to Sulawesi and the Philippines (Heaney et al. 1998). Known from primary and secondary lowland, montane, and mossy forest (Allen 1910, Heaney et al. 1999, Rickart et al. 1993). We captured and released a juvenile of this species in a cage trap in lowland primary forest at Site 1, and we observed two in forest-grassland mosaic at Site 12.

## Order Artiodactyla

*Tragulus napu* and *Axis calamianensis* both occur in the Palawan faunal region, but we found no evidence of either species on Palawan Island.

## Family Suidae—Pigs

*Sus barbatus*.—The bearded pig is found from the Malay Peninsula to Borneo and Palawan (Heaney et al. 1998). Rabor (1986) and Payne et al. (1985) reported the species from primary and secondary forest from sea level to the highest peaks; Sanborn (1952) reported a series from Iwahig. Groves (2001) has tentatively suggested that the population of this species from the Palawan faunal region, which has been recognized as a distinct subspecies, may warrant recognition as a distinct species, *Sus ahoenobarbus*. We regularly observed this species



or evidence of its occurrence in forest habitats (including fragmented forest) from sea level to montane forest at ca. 1500 m (Sites 1, 2, 3, 4, 7, and 11). We also observed evidence of the species entering cultivated areas near forest and damaging crops. Wild pigs are heavily hunted on Palawan with snares, low caliber rifles, and small, baited explosive devices known as "pig bombs". The species appears to be locally common, but is in decline due to heavy hunting pressure (Caldecott et al. 1993, Oliver 1992). The IUCN (2002) lists *S. barbatus ahoenobarbus* as Vulnerable.

### Discussion

*Adequacy of sampling.*—Small fruit bats on Palawan (*Cynopterus*, *Eonycteris*, *Macroglossus*, and *Rousettus*) appear to have been fairly completely sampled; no species have been added in over 50 years (excluding the apparently erroneous reports of *Haplonycteris fischeri* and *Ptenochirus minor*), despite extensive netting. It is interesting that our mist netting in primary forest produced very few captures; for example, in primary lowland forest at 150 m elevation (Site 1), we captured 1 fruit bat in 42 net-nights; in primary lowland forest at ca. 500 m (Site 2), we captured 1 fruit bat in 56 net-nights, and in primary montane forest at ca. 1400 m (Site 3), we captured no fruit bats in 48 net-nights. Although our sample size is limited, all of these values fall well below what would be typical on islands in the oceanic portion of the Philippines (Heaney et al. 1989, 1999), suggesting that small fruit bats are not as abundant in primary forest on Palawan (e.g., Heideman & Heaney 1989, Heaney et al. 1989). Indeed, all of the small fruit bats currently known from Palawan predominantly occur in disturbed habitats, in contrast to the oceanic Philippines, where several endemic genera (*Alionycteris*, *Haplonycteris*, *Otopteropus*, and *Ptenochirus*) are most common in old-growth forest.

The ecology of large fruit bats (*Acerodon*

and *Pteropus*) has been very poorly studied on Palawan and elsewhere in the Philippines. This is the direct result of the difficulty in capturing these species by any means other than shooting. Despite the paucity of ecological information on these species, their distribution among major island groups appears to be moderately well understood because their activities and roosts are highly conspicuous, and no additional species have been found on Palawan in over 50 years. It seems unlikely that additional species will be found on Palawan, with the possible exception of *P. hypomelanus*.

Insectivorous bats are clearly the least known of all Palawan mammals. Distributions remain poorly documented, ecological information is scanty for most species, and the taxonomy is often uncertain. Our survey efforts and examination of previously collected insectivorous bats documented eight species (*Rhinolophus arcuatus*, *R.* cf. *borneensis*, *R. creaghi*, *R. macrotis*, *Miniopterus australis*, *M. schreibersi*, *M. tristis*, and *Murina* cf. *tubinaris*) on Palawan for the first time, and several more are noted in the text as very likely to be present.

Our knowledge of small non-volant mammals (including Soricidae, Tupaiidae, Sciuridae, and Muridae) on Palawan is uneven. Some lowland species (e.g., *Tupaia palawanensis*, *Sundasciurus juvencus*, *Maxomys panglima*, *Rattus tiomanicus*, *Sundamys muelleri*, and the non-native murines) are common and well known. Very little is known of several other species (e.g., *Crocidura palawanensis*, *Crocidura* sp., *Sundasciurus rabori*, *Chiropodomys calamianensis*, *Haeromys pusillus*, and *Palawanomys furvus*). Perhaps we failed to locate these poorly known species because we did little trapping in trees or other places above the ground surface (*C. calamianensis* and *H. pusillus*), sampled only one site above 1000 m (*S. rabori* and *P. furvus*), and our trapping techniques were limited, i.e., we did not use pitfall traps (*Crocidura* spp.). The presence of so many poorly known species suggests that other species



may await discovery, especially in high mountain habitats and high in the canopy. Musser & Newcomb (1983) suggested that unknown species are yet to be discovered on Palawan, citing the report of Hoogstraal (1951), which narrated their attempt to capture a "very large rat with a white tail" described to them by native Palaw'an. Other large islands in the Philippines have been shown to support diverse communities of endemic small mammals which are restricted to montane areas (e.g., Heaney 2001, Heaney & Rickart 1990, Rickart 1993), and perhaps the same awaits discovery on Palawan.

Medium to large mammals (Cercopithecidae, Manidae, Hystricidae, the carnivores, and Suidae) are possibly the most thoroughly inventoried subset of Palawan's mammalian fauna. Because of their large size, they are easily observed compared to other mammals. Many of these species are also commonly hunted, so obtaining specimens is often easier than for non-game species. It is unlikely that other medium to large mammals await discovery on Palawan, though the ecology of all requires much additional study.

**Biogeography.**—As noted above, the Palawan faunal region is part of the Sunda Shelf and may have been connected to mainland Asia via Borneo (Everett 1889) during a Pleistocene episode of glacially-induced sea-level lowering (Heaney 1985, 1986, 1991a), though current data leave this uncertain. All other islands in the Philippines are oceanic and have probably never had a dry-land connection to any mainland area (Heaney 1985, 1986, 2001). Of the 58 native species currently known from Palawan Island (tentatively including the small *Crocidura* sp.), 13 species are endemic to Palawan (and usually to some of the smaller islands that were included in Pleistocene Greater Palawan; Heaney 1986); 12 of these are non-volant, all of which have their closest relatives on the Sunda Shelf. Eight of Palawan's 11 native rodents (73%) are endemic; all three non-endemics are mu-

rids. Only one endemic species is a bat (*Acrodon leucotis*), and only it has its closest relatives in the oceanic Philippines. This pattern of endemism is clearly consistent with the geological history of the Philippines and also highlights the importance of the greater vagility of bats over non-flying mammals. Of the 28 insectivorous bats, 18 species are somewhat to highly widespread in Indo-Australia (and some beyond), 2 are shared only with the Sunda Shelf and Indochina (*Rhinolophus acuminatus* and *Rhinolophus* cf. *borneensis*), 1 with the Sunda Shelf only (*Cheiromeles torquatus*), 3 occur on the Sunda Shelf and the oceanic Philippines (*Kerivoula pellucida*, *K. whiteheadi*, *Myotis macrotarsus*), 1 occurs on Palawan, Sulawesi and the oceanic Philippines (*Mops sarasinorum*), 2 occur only on Palawan and in the oceanic Philippines (*Rhinolophus virgo* and *Myotis rufopictus*), and one occurs on Borneo, Sulawesi, and throughout the Philippines (*Emballonura alecto*). These data again demonstrate that the bats are more widely distributed and do not clearly reflect the geological history, as do the non-flying mammal species, which in the Philippines are usually restricted to a single area that was united by dry land during the late Pleistocene. From the highly diverse fruit bat fauna of Borneo (17 species; Payne et al. 1985), only five species extend to the northern continental land-bridge islands of Sabah (Md. Nor 1995). These are the same five non-endemic species that can be found just to the north on Palawan Island.

We note that the combined totals of native non-volant mammal species on Palawan that either are shared with Borneo and other portions of the Sunda Shelf or that are endemic to Palawan and have their closest relatives on Borneo or adjacent areas is 22 out of 24 (92%). The apparent exceptions are *Hylopetes nigripes* (related to *H. alboniger* of Indochina) and *Palawanomys furvus* (an enigmatic genus of unclear phylogenetic position). If this analysis were extended to the entire Palawan faunal region, *Axis*



*calamianensis* (related to *A. porcinus* in Indochina) would also be included here. Four species are widespread in Southeast Asia (including parts of Wallacea), and no species is shared with the oceanic Philippines except for those 4 species (*Macaca fascicularis*, *Prionailurus bengalensis*, *Paradoxurus hermaphroditus*, and *Viverra zibetha*). If *Sus barbatulus*, which occurs on Palawan, the Sunda Shelf, and in the marginal islands of the Sulu Archipelago is counted as a widespread Southeast Asian species, the total rises to five species. These data, in sum, strongly reinforce the conclusion of Everett (1889), based on his analysis of bathymetric features of the ocean floor and the pattern of relationships of the 18 species then known from Palawan and associated smaller islands, that the Palawan faunal region is an extension of the Sunda Shelf, probably due to a fairly recent dry-land connection, with only a small portion of its fauna shared with the oceanic Philippines.

Patterns of species richness relative to island area are also of interest. Insectivorous bats are so poorly known in the Philippines that it is possible only to say that the 28 species documented here compare favorably with most islands in the Philippines; that is, there is no evidence that Palawan is species-poor (Heaney et al. 2002). Fruit bats, on the other hand, are represented on Palawan by only 6 species, and this places their diversity far below that on much smaller islands in the oceanic Philippines; Maripipi, for example, has 10 species, but is only 22 km<sup>2</sup>. It seems certain that Palawan has a depauperate fruit bat fauna, as well as probably having lower fruit bat density, as noted above, compared to the oceanic Philippines (Heaney 1991b). Species richness of non-flying mammals, on the other hand, at 24 is much above the species/area curve documented in the oceanic Philippines, though well below that of islands on the primary portion of the Sunda Shelf (Heaney 1984, 1986; Heaney et al. 2002). It is interesting that carnivores are notably

more diverse on Palawan than in the oceanic Philippines, and murid rodents notably less diverse, for an island the size of Palawan.

*Conservation issues.*—The most pressing issue facing terrestrial wildlife in Palawan is the rapid loss of forest cover, especially in the primary lowland forests that are targeted for logging. Palawan's forests are less commercially valuable than the dipterocarp-dominated forests of the other islands, and, consequently, deforestation occurred later on Palawan. However, once forests were exhausted on Luzon, Mindanao, Negros, etc., commercial logging operations began working in lowland forest on Palawan (Environmental Science for Social Change 1999) during the 1970's and 1980's at unsustainable levels (Quinnell & Balmford 1988, Kummer 1992). Since a logging ban was imposed in the early 1990s throughout the Province of Palawan, logging has declined, but the large commercial operations appear to have been replaced by small-scale, illegal commercial logging. We have seen that forest continues to disappear from the most accessible areas, and forest edges are gradually creeping higher and higher up the contours, in a manner similar to that experienced on Leyte (Rickart et al. 1993) and southern Luzon (Heaney et al. 1999). Lowland primary forest has been eliminated from many parts of Palawan and the destruction shows few signs of easing. Due to almost complete conversion of the coastal plain into ricefields, coconut, or other plantations, distinctive ecosystems such as freshwater swamp forest and beach forest have virtually disappeared (Widmann 1998). Slash and burn agricultural practices have also been very damaging to forests, and Palawan has experienced a population explosion due to high birth and immigration rates.

It should be noted that caves are crucial to maintaining the fauna, since approximately 18 (32%) of Palawan's mammals are bats that roost in caves. Caves have been the focus of much destruction in the Phil-



ippines; common activities in caves on Palawan include guano mining, general vandalism, recreational exploration, and treasure hunting. Unlike many other parts of the Philippines (e.g., Heaney et al. 1991, 1999; Rickart et al. 1993), we never encountered any evidence of cave-roosting bats being hunted on Palawan. We found guano mining to be common, usually near the mouth of caves. Recreational exploration of caves is steadily increasing; many caves are currently being developed or advertised for this purpose, while many more proposals are in the planning stages. At PPSRNP (Site 15), hundreds of visitors may enter a one kilometer stretch of the cave daily. The bats are clearly disturbed by the activity, but the ultimate result of such disturbance is unknown.

Many medium to large sized mammals are under significant hunting pressure on Palawan for their meat, the live animal trade, and medicinal use, as noted above, but few data are available on the impact. The recent and on-going shift from subsistence to market economies among members of the Tagbanua and other ethnic groups may contribute to the decline of some species (Lacerna & Widmann 1999), such as *Sus barbatus*, *Pteropus vampyrus*, and *Hystrix pumila* for meat, *Macaca fascicularis* and *Arctictis binturong* as pets, and *Manis culionensis* for traditional Chinese medicine.

### Acknowledgments

Funding for these studies was provided by the Palawan Council for Sustainable Development, United States Peace Corps, Philippine Cockatoo Conservation Program through the Loro Parque Fundacion, Tenerife, Spain, and the Barbara Brown and Ellen Thorne Smith Funds of the Field Museum. Jun Saldajeno, Apollo Regalo, Benigno Maca, Erlito Porka, and Manual Lardizabal made significant contributions to field work, often under difficult living conditions. Adelwisa Sandalo, Lualhati Tabu-

gon, Ariel Carino, Leilani Berino, Dr. Teresita Salva, Dr. Edgardo Castillo, Dr. Pascencia Milan, Dr. Josef Margraf, Indira Lacerna-Widmann, Siegfried Diaz, Deborah Villafuerte, and the wildlife wardens of Rasa Island provided valuable logistical and administrative support. JAE thanks the Tabugon family for their extraordinary hospitality during his stay on Palawan. We thank A. C. Alcala, P. C. Gonzales, and P. O. Glass for depositing important specimens at UMMZ, and P. Myers for access to those specimens. H. Kafka, J. Mead, and R. Thorington provided access to specimens at the USNM, and F. Dieterlen kindly loaned specimens from SMNH. We are grateful to P. O. Glass for additional details about specimens he collected. Ding Padilla, Clara Simpson, and Lisa Kanellos produced the map in Fig. 1. Eric Rickart gave sound advice during the early stages of the project and Danilo Balete helped with the transport and identification of voucher specimens; Eric Rickart and Robert Timm provided constructive reviews of the manuscript. The Department of Environmental and Natural Resources, through the Protected Areas and Wildlife Bureau and the Provincial Environment and Natural Resources Office, provided permits and encouragement. LRH thanks the Geological Sciences Department, Northwestern University, for use of office space during a sabbatical leave.

### Literature Cited

- Allen, G. M. 1922. Bats from Palawan, Philippine Islands.—Occasional Papers of the Museum of Zoology, University of Michigan 110:1–5.
- Allen, J. A. 1910. Mammals from Palawan Island, Philippine Islands.—Bulletin of the American Museum of Natural History 28:13–17.
- Balete, D. S., L. R. Heaney, & R. I. Crombie. 1985. First records of *Hipposideros lekaguli* Thonglongya and Hill 1974 from the Philippines.—Asia Life Sciences 4:89–94.
- Barbehenn, K., J. P. Sumangil, & J. L. Libay. 1973. Rodents of the Philippine croplands.—Philippine Agriculturist 56:217–242.
- Cabrera, A. 1909. Un nuevo “*Rhinolophus*” filipino.—Boletín de la Real Sociedad Española de Historia Natural Sección Biológica 9:304–306.



- Caldecott, J. O., R. A. Blouch, & A. A. Macdonald. 1993. The bearded pig (*Sus barbatus*). Pp. 136–145 in W. L. R. Oliver, ed., Pigs, peccaries, and hippos: status survey and conservation action plan.—International Union for the Conservation of Nature. Gland, Switzerland, 202 pp.
- Corbet, G. B., & J. E. Hill. 1992. The mammals of the Indomalayan region. Oxford University Press, Oxford, 488 pp.
- Csorba, G., P. Ujhelyi, & N. Thomas. 2003. Horseshoe bats of the world (Chiroptera: Rhinolophidae). Alana Books, Shropshire, 160 pp.
- Danielsen, F., D. S. Balete, T. D. Christensen, M. Heegaard, O. F. Jakobsen, A. Jensen, T. Lund, & M. K. Poulsen. 1994. Conservation of biological diversity in the Sierra Madre Mountains of Isabela and southern Cagayan Province, the Philippines. Birdlife International, Manila and Copenhagen, 146 pp.
- Dans, A. T. L. 1993. Population estimate and behavior of Palawan tree shrew, *Tupaia palawanensis* (Scandentia, Tupaiidae).—Asia Life Sciences 2: 201–214.
- Dickerson, R. E. 1928. Distribution of life in the Philippines.—Monograph, Bureau of Science, Manila 2:1–322 + 42 pls.
- Environmental Science for Social Change. 1999. Decline of Philippine forests. Bookmark, Makati. Map.
- Everett, A. H. 1889. Remarks on the zoogeographical relationships of the island of Palawan and some adjacent islands.—Proceedings of the Zoological Society of London 1889:220–228.
- Fairbanks, R. G. 1989. A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates in the Younger Dryas event and deep-ocean circulation.—Science 342:637–642.
- Feiler, A. 1998. Das Philippinen Schuppentier, *Manis culionensis* (Mammalia: Manidae).—Zoologische Abhandlungen Staat. Museum Tierkunde Dresden 50:161–64.
- Fooden, J. 1995. Systematic review of Southeast Asian long-tail macaques *Macaca fascicularis* (Raffles, [1821]).—Fieldiana Zoology, new series 81:1–206.
- Francis, C. M., E. L. P. Anthony, J. A. Brunton, & T. H. Kunz. 1994. Lactation in male fruit bats.—Nature 367:691–692.
- Gascoyne, M., G. J. Benjamin, & H. P. Schwarz. 1979. Sea-level lowering during the Illinoian glaciation: evidence from a Bahama “blue hole”.—Science 205:806–808.
- Grimwood, I. 1976. The Palawan stink badger.—Oryx 13:297.
- Groves, C. P. 1997. Leopard-cats, *Prionailurus bengalensis* (Carnivora: Felidae) from Indonesia and the Philippines, with the description of two new subspecies.—Zeitschrift für Säugetierkunde 62:330–338.
- . 2001. Taxonomy of wild pigs of Southeast Asia.—Asian Wild Pig News 1:3–4.
- Hall, R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. Pp. 99–132 in R. Hall and J. D. Holloway, eds., Biogeography and geological evolution of SE Asia. Backhuys Publishers, Leiden, 417 pp.
- . 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations.—Journal of Asian Earth Sciences 20: 353–431.
- Heaney, L. R. 1979. A new species of tree squirrel (*Sundasciurus*) from Palawan Island, Philippines (Mammalia: Scuridae).—Proceedings of the Biological Society of Washington 92:280–286.
- . 1984. Mammalian species richness on islands on the Sunda Shelf, Southeast Asia.—Oecologia 61:11–17.
- . 1985. Zoogeographic evidence for middle and late Pleistocene land bridges to the Philippine Islands.—Modern Quaternary Research in SE Asia 9:127–143.
- . 1986. Biogeography of mammals in Southeast Asia: estimates of rates of colonization, extinction, and speciation.—Biological Journal of the Linnean Society 28:127–165.
- . 1991a. A synopsis of climatic and vegetational change in Southeast Asia.—Climatic Change 19:53–61.
- . 1991b. An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae).—Bulletin of the American Museum of Natural History 206:145–167.
- . 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography.—Global Ecology and Biogeography 9:59–74.
- . 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses.—Global Ecology and Biogeography 10:15–39.
- , & A. C. Alcala. 1986. Flat-headed bats (Mammalia, *Tylonycteris*) from the Philippine Islands.—Silliman Journal 33:117–123.
- , & N. A. D. Mallari. 2002. A preliminary analysis of current gaps in the protection of threatened Philippine terrestrial mammals.—Sylvatrop 10(2000):28–39.
- , & J. C. Regalado, Jr. 1998. Vanishing Treasures of the Philippine Rain Forest. The Field Museum, Chicago, 88 pp.
- , & E. A. Rickart. 1990. Correlations of clades and clines: geographic, elevational, and phylogenetic distribution patterns among Philippine mammals. Pp. 321–332 in G. Peters and R. Hutterer, eds., Vertebrates in the tropics. Museum Alexander Koenig, Bonn, 424 pp.
- , & M. Ruedi. 1994. A preliminary analysis of



- biogeography and phylogeny of *Crocidura* from the Philippine Islands. Pp. 357–377 in J. Merriitt, G. Kirkland, and R. K. Rose, eds., *Advances in the biology of shrews*. Special Publications, Carnegie Museum of Natural History.
- , & B. R. Tabaranza, Jr. 1997. A preliminary report on mammalian diversity and conservation status of Camiguin Island, Philippines.—*Sylvatrop* 5(1995):57–64.
- , D. S. Balete, M. L. Dolar, A. C. Alcala, A. T. L. Dans, P. C. Gonzales, N. R. Ingle, M. V. Lepiten, W. L. R. Oliver, P. S. Ong, E. A. Rickart, B. R. Tabaranza, Jr., & R. C. B. Utzurrum. 1998. A synopsis of the mammalian fauna of the Philippine Islands.—*Fieldiana: Zoology*, new series 88:1–61.
- , ———, E. A. Rickart, R. C. B. Utzurrum, & P. C. Gonzales. 1999. Mammalian diversity on Mount Isarog, a threatened center of endemism on southern Luzon Island, Philippines.—*Fieldiana: Zoology*, new series 95:1–62.
- , P. C. Gonzales, R. C. B. Utzurrum, & E. A. Rickart. 1991. The mammals of Catanduanes Island: Implications for the biogeography of small land bridge islands in the Philippines.—*Proceedings of the Biological Society of Washington* 104:399–415.
- , P. D. Heideman, E. A. Rickart, R. C. B. Utzurrum, & J. S. H. Klompen. 1989. Elevational zonation of mammals in the central Philippines.—*Journal of Tropical Ecology* 5:259–280.
- , E. K. Walker, B. R. Tabaranza Jr., & N. R. Ingle. 2002. Mammalian diversity in the Philippines: an assessment of the adequacy of current data.—*Sylvatrop* 10 (2000):6–27.
- Heideman, P. D., & L. R. Heaney. 1989. Population biology of fruit bats (Pteropodidae) in Philippine submontane rainforest.—*Journal of Zoology* (London): 218:565–586.
- Hill, J. E. 1983. Bats (Mammalia: Chiroptera) from Indo-Australia.—*Bulletin of the British Museum (Natural History)*, Zoology 45:103–208.
- , & C. M. Francis. 1984. New bats (Mammalia: Chiroptera) from Borneo and Malaya.—*Bulletin of the British Museum (Natural History)*, Zoology 47:305–329.
- Hollister, N. 1913. A review of the Philippine land mammals in the United States National Museum.—*Proceedings of the United States National Museum* 46:299–341.
- Hoogstraal, H. 1951. Philippine Zoological Expedition, 1946–1947. Narrative and itinerary.—*Fieldiana: Zoology* 33:1–86.
- Ingle, N. R. 1992. The natural history of bats on Mt. Makiling, Luzon Island, Philippines.—*Silliman Journal* 36:1–26.
- , & L. R. Heaney. 1992. A key to the bats of the Philippine Islands.—*Fieldiana: Zoology* new series 69:1–44.
- IUCN. 2002. 2002 IUCN Red List of Threatened Species. [www.redlist.org](http://www.redlist.org). IUCN, Gland, Switzerland.
- Kock, D. 1969. Eine bemerkenswerte neue Gattung und Art Flughunde von Luzon, Philippinen (Mammalia, Chiroptera).—*Senckenbergiana Biologica* 50:329–338.
- Koopman, K. F. 1993. Order Chiroptera. Pp. 137–241 in D. E. Wilson and D. M. Reeder, eds., *Mammal species of the world, a taxonomic and geographic reference*, 2nd edition. Smithsonian Institution Press, Washington, D.C., 1206 pp.
- Koopman, K. F., & T. N. Danforth. 1989. A record of the tube-nosed bat (*Murina florium*) from western New Guinea.—*American Museum Novitates* 2934:1–5.
- Kummer, D. M. 1992. Deforestation in the Post-War Philippines. University of Chicago Press, 177 pp.
- Kuntz, R. E. 1969. Vertebrates taken for parasitological studies by U.S. Naval Medical Research Unit No. 2 on Silliman University—Bishop Museum Expedition to Palawan, Republic of the Philippines.—*Quarterly Journal of the Taiwan Museum*, Taipei 22:207–220.
- Kruuk, H. 2000. Notes on status and foraging of the pantot or Palawan stink-badger, *Mydaus marchei*.—*Small Carnivore Conservation Newsletter and Journal of the IUCN/SSC Mustelid, Viverrid, and Procyonid Specialist Group* 22:11–12.
- Lacerna, I. D. D., & P. Widmann. 1999. Biodiversity utilization in a Tagbanua community, southern Palawan, Philippines. Pp. 52–64 in F. Goltenboth, P. Milan, and V. B. Asio, eds., *Proceedings of the International Conference on Applied Tropical Ecology*, Sept. 8–10 1998, Visayas State College of Agriculture, Baybay Leyte, Philippines.
- Md. Nor, S. 1995. The mammalian fauna on the islands at the northern tip of Sabah, Borneo.—*Fieldiana Zoology*, new series 83:1–51.
- Medway, L. 1977. Mammals of Borneo.—*Monographs of the Malaysian Branch of the Royal Asiatic Society* 7:xii + 1–172.
- Mittermeier, R. A., P. Robles Gil, & C. G. Mittermeier (eds.). 1997. Megadiversity. Earth's biologically wealthiest nations. CEMEX, Monterrey, Mexico, 501 pp.
- , N. Myers, P. Robles G., & C. G. Mittermeier (eds.). 1999. Hotspots. Earth's biologically richest and most endangered terrestrial ecosystems. CEMEX, Mexico City, 431 pp.
- Mudar, K. M., & M. S. Allen. 1986. A list of bats from northeastern Luzon, Philippines.—*Mammalia* 50:219–225.
- Muser, G. G. 1979. Results of the Archbold Expeditions. No. 102. The species of *Chiropodomys*, arboreal mice of Indochina and the Malay Ar-



- chipelago.—Bulletin of the American Museum of Natural History, 162:377–445.
- , & M. D. Carleton. 1993. Family Muridae. Pp. 501–756 in D. E. Wilson and D. M. Reeder, eds., *Mammal species of the world, a taxonomic and geographic reference*, 2nd edition. Smithsonian Institution Press, Washington, D.C., 1206 pp.
- , & L. R. Heaney. 1992. Philippine rodents: definitions of *Tarsomys* and *Limnomys* plus a preliminary assessment of phylogenetic patterns among native Philippine murines (Murinae, Muridae).—Bulletin of the American Museum of Natural History 211:1–138.
- , K. F. Koopman, & D. Calafia. 1982. The Sulawesian *Pteropus arquatus* and *P. argentatus* are *Acerdon celebensis*; the Philippine *P. leucotis* is an *Acerodon*.—Journal of Mammalogy 63:319–328.
- , & C. Newcomb. 1983. Malaysian murids and the giant rat of Sumatra.—Bulletin of the American Museum of Natural History 174(4):329–598.
- , J. T. Marshall, & Boeadi. 1979. Definition of contents of the Sundaic genus *Maxomys* (Rodentia, Muridae).—Journal of Mammalogy 60:592–606.
- Oliver, W. L. R. 1992. The taxonomy, distribution, and status of Philippine wild pigs.—Silliman Journal 36:55–64.
- Ong, P., L. E. Afuang, & R. G. Rosell-Ambal (eds.). 2002. Philippine biodiversity conservation priorities: a second iteration of the national biodiversity strategy and action plan. Philippine Department of the Environmental and Natural Resources, Quezon City, xviii + 113 p.
- Payne, J., C. M. Francis, & K. Phillips. 1985. A field guide to the mammals of Borneo. Sabah Society, Kota Kinabalu. 332 pp.
- Peters, W. 1871. Über die Gattung und Arten der Hufeisennasen, Rhinolophi.—Monatsberichte K. Preussische. Akad. Wissenschaft 301–332.
- Quinnell, R., & A. Balmford. 1988. A future for Palawan's forests?—Oryx 22:30–35.
- Rabor, D. S. 1955. Notes on mammals and birds of the central northern Luzon highlands, Philippines. Part 1. Notes on mammals.—Silliman Journal 2:193–218.
- . 1986. Guide to Philippine Flora and Fauna, vol. 11. Birds and mammals. Ministry of Natural Resources and the University of the Philippines, Quezon City, 213 pp.
- Reis, K. R., & A. M. Garong. 2001. Late Quaternary terrestrial vertebrates from Palawan Island, Philippines.—Palaeogeography, Palaeoclimatology, Palaeoecology 171:409–421.
- Rickart, E. A. 1993. Diversity patterns of mammals along elevational and disturbance gradients in the Philippines: implications for conservation.—Asia Life Sciences 2:251–260.
- , L. R. Heaney, P. D. Heideman, & R. C. B. Utzurrum. 1993. The distribution and ecology of mammals on Leyte, Biliran, and Maripipi islands, Philippines.—Fieldiana: Zoology new series 72:1–62.
- , P. D. Heideman, & R. C. B. Utzurrum. 1989. Tent-roosting by *Scotophilus kuhlii* (Chiroptera: Vespertilionidae) in the Philippines.—Journal of Tropical Ecology 5:433–436.
- Rohling, E. J., M. Fenton, F. J. Jorissen, G. Bertrand, G. Ganssen, & J. P. Caulet. 1998. Magnitude of sea level lowstands of the last 500,000 years. Nature 394:162–165.
- Sanborn, C. C. 1952. Philippine Zoological Expedition 1946–1947: Mammals.—Fieldiana: Zoology 33:89–158.
- . 1953. Mammals from Mindanao, Philippine Islands collected by the Danish Philippine Expedition, 1951–1952.—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 115:238–288.
- Siddall, M., E. J. Rohling, A. Almogi-Labin, C. Hemleben, D. Meischner, I. Schmelzer, & D. A. Smeed. 2003. Sea-level fluctuations during the last glacial cycle.—Nature 423:853–858.
- Taylor, E. H. 1934. Philippine land mammals.—Monographs of the Bureau of Science, Manila 30:1–548.
- Timm, R. M., & E. C. Birney. 1980. Mammals collected by the Menage Expedition to the Philippine Islands and Borneo, 1890–1893.—Journal of Mammalogy 61:566–571.
- Utzurrum, R. C. B. 1992. Conservation status of Philippine fruit bats (Pteropodidae).—Silliman Journal 36:27–45.
- Voris, H. K. 2000. Maps of the Pleistocene sea levels in Southeast Asia: Shorelines, river systems, and time durations.—Journal of Biogeography 27:1153–1167.
- Yoshiyuki, M. 1979. A new species of the genus *Ptenochirus* (Chiroptera, Pteropodidae) from the Philippine Islands.—Bulletin of the Natural Science Museum, Tokyo (Zoology), 5:75–81.
- Wildlife Conservation Society of the Philippines. 1997. Philippine Red Data Book. Bookmark, Manila, Philippines, 240 pp.
- Wilson, D. E. 1993. Order Scandentia. Pp. 131–134 in D. E. Wilson & D. M. Reeder, eds., *Mammal species of the world, a taxonomic and geographic reference*, 2nd edition. Smithsonian Institution Press, Washington, 1206 pp.
- Widmann, P. 1998. A guide to the ecosystems of Palawan, Philippines. Times Editions, Singapore, 120 pp.





Esselstyn, J A, Widmann, Peter, and Heaney, L R. 2004. "The Mammals Of Palawan Island, Philippines." *Proceedings of the Biological Society of Washington* 117, 271–302.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/110035>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/49110>

#### **Holding Institution**

Smithsonian Libraries and Archives

#### **Sponsored by**

Biodiversity Heritage Library

#### **Copyright & Reuse**

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: Biological Society of Washington

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.