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Synopsis and Biogeography of the Mammals of Camiguin Island, Philippines

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Abstract

Biodiversity surveys in the 1960s and 1990s on Camiguin Island, a geologically young, volcanically active oceanic island surrounded by deep water, have demonstrated the presence of 24 species of land mammals. Three species (one insectivore and two rodents) are not native to the Philippines, but all others (one insectivore, 12 bats, one monkey, four rodents, two small carnivores, and one ungulate) are indigenous. Among those captured in the 1990s were two previously unknown species of murid rodents in the genera *Apomys* and *Bullimus* that are endemic to Camiguin. The discovery of two new species on such a small island (ca. 265 km^2) is remarkable; Camiguin is currently the smallest island in the Philippines known to have unique species of mammals. Total species richness of nonvolant mammals on Camiguin is low, but relative to islands that were once part of Pleistocene Greater Mindanao, Camiguin is not depauperate. However, its fauna is not ecologically balanced in the same way as the faunas of the islands that were part of Greater Mindanao: ground-living shrews (*Crocidura*) and rodents (*Apomys*, *Bullimus*, *Crunomys*, and *Rattus*) from lowland forest, along with some large mammals (*Macaca*, *Paradoxurus*, and *Sus*) are well represented on Camiguin, but all the arboreal small mammals that characterize lowland forest on Mindanao (*Sundasciurus*, *Exilisciurus*, *Cynocephalus*, and *Tarsius*), ground-living small mammals from montane habitats (*Urogale*, *Podogymnura*, *Batomys*, *Limnomys*, and *Tarsomys*), and one large mammal (*Cervus*) are absent. Additionally, at least two genera of fruit bats (*Haplonycteris* and *Megaerops*) that are fairly common in lowland rain forests on Mindanao are absent on Camiguin. The presence of some nonvolant mammals demonstrates that dispersal across the deep but narrow intervening channel takes place, but the presence of two species endemic to Camiguin and the absence of other species that are present on nearby Mindanao implies that dispersal probably is rare. The Asian house shrew (*Suncus murinus*) was remarkably abundant in primary forest at high elevation; this species has also been found to be abundant in montane primary forest on Negros Island, which also has low total species richness. Species richness of small nonflying mammals was greatest at fairly high elevation.

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Introduction

The Philippine Islands present a remarkable theater for the study of the ecology and evolution of mammalian diversity. Its islands range in size from less than one hectare to over 100,000 km^2, with geological age varying from under 1 million

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years to over 40 million years. These islands represent many sets of historically distinct geological units of remarkably varied origins; some had land-bridge connections to the Asian mainland in the past (those of the Palawan group), but most are purely oceanic in origin (Heaney, 1986, 1991b, 2000; Heaney & Rickart, 1990; Hall, 1998, 2002). The mammals that have evolved in this diverse archipelago include at least 111 species endemic to the archipelago out of 172 native terrestrial species; with endemism at 64%, the Philippine fauna is one of the most distinctive in the world (Mittermeier et al., 1997, 1999; Heaney & Regalado, 1998). While most of the endemic species occur on the large islands of Luzon, Mindanao, Mindoro, Negros, and Palawan (e.g., Heaney, 1986, 1993, 2000; Heaney et al., 1998; Rickart et al., 1998), significant numbers occur on the smaller islands as well, especially those surrounded by deep water (e.g., Heaney, 1986, 2004; Goodman & Ingle, 1993; Heaney & Tabaranza, 1997; Musser et al., 1998).

As noted by Heaney and Tabaranza (2006a), Camiguin, an island of 265 km^2 located about 10 km north of Mindanao in the Bohol Sea, is one such deep-water island, with a minimum depth to Mindanao of 385 m. It is steeply mountainous, with several active volcanic cones that reach to a maximum elevation of about 1600 m. A series of biological surveys on Camiguin in the late 1960s that focused on birds (see Balete et al., 2006) also yielded some mammal specimens, and an earlier report on those surveys (Heaney, 1984) concluded that the island had no endemic mammal species and was depauperate. Subsequent studies on other islands made us suspect that those earlier surveys were incomplete because so few mammal species had been obtained and because the number of nonvolant mammal specimens was small (thus indicating limited sampling effort). Further, on the basis of biogeographic patterns elsewhere in the Philippines, we predicted the presence of several endemic small mammals on Camiguin (Heaney, 2004). To investigate the hypotheses that the previously measured species richness was low because of incomplete surveys and that about two endemic species should be present, we returned to Camiguin briefly in 1992 and more extensively in 1994 and 1995 to conduct additional mammal inventories in all the major habitats along the elevational gradient, especially by trapping small mammals at higher elevations where there were few records from the 1960s. As indicated in a brief preliminary report (Heaney & Tabaranza, 1997), we found eight additional species on the island that are widespread in the Philippines, plus two previously unknown endemic species of rodents. The purpose of this paper is to summarize the results of the 1994 and 1995 mammal surveys and integrate those data with information from the 1960s, including information on habitat associations, relative abundance, and ecology of the species.

Methods

Prior Reports

The first report of mammals from Camiguin Island was that of Gray (1843), who reported *Paradoxurus hermaphroditus*. Three field teams from Silliman University led by Dioscoro S. Rabor collected mammals on Camiguin in 1967, 1968, and 1969; specimens were deposited at the Delaware Museum of Natural History (DMNH) and Royal Ontario Museum (ROM); for details, see Heaney and Tabaranza (2006a). Several specimens were reported by Peterson and Fenton (1970); all known specimens from the 1960s were examined and summarized by Heaney (1984). All data included in this paper from the 1960s specimens are based on data in Heaney (1984), except as noted below.

Recent Data

Field studies were conducted during three periods in 1992, 1994, and 1995; general methods and site descriptions are given in Heaney and Tabaranza (2006a). Sampling during 1995 followed methods used on Leyte, Luzon, Negros, and other islands (Heaney et al., 1989, 1999; Rickart et al., 1991, 1993) to facilitate quantitative comparisons. Nonvolant small mammals were caught in traps; during 1995, all traps were Victor rat snap traps. Most were baited with fresh fried coconut coated with peanut butter, but a few were baited with live earthworms. During 1994, several National live traps were used, in addition to Victor rat traps, and were baited with coconut bait. Bats were captured in 12-m mist nets. Voucher specimens were prepared in fluid or as skeletons and have been deposited at The Field Museum of Natural History (FMNH), National Museum of the Philippines (NMP), and Mindanao State University–Iligan Institute of Technology (MSU-IIT). Most specimens were autopsied for reproductive information. The size of embryos was measured as crown to rump length (CRL). Subadult animals are defined here as those that have not completed cranial growth, especially those having unfused basicranial sutures; these young animals have pelage that is usually softer and grayer than that of adults and are noticeably lower in weight and females are usually nulliparous. Young adults are older; they have nearly completed cranial growth but have not yet reached adult weight and, usually, have not yet reproduced or are pregnant for the first time. Adults have completed cranial growth and adult pelage, and usually the females are multiparous. Comments on distribution and use of scientific names are based on Heaney et al. (1998) unless additional sources are mentioned. Records of specimens examined are summarized at the end of each account; such summaries include site number and the number of specimens (in parentheses).

External measurements and weights reported here were taken in the field by members of the field team on fresh animals. Cranial measurements were taken by Heaney with digital calipers graduated to 0.01 mm. Comparisons of cranial measurements are to published records of specimens measured in the same manner by Heaney.

Accounts of Species

Order Insectivora

Family Soricidae—Shrews

Crocidura beatus Miller, 1910

The Mindanao shrew is widespread on islands in the Mindanao Faunal Region (Heaney & Ruedi, 1994; Heaney et al., 1998); these are the first records from an island that was not part of the late Pleistocene island of Greater Mindanao (Heaney, 1986). This shrew has most often been found in primary forest, especially at higher elevations; is usually uncommon in secondary forest; and is absent outside of forest (Heaney et al., 1989; Rickart et al., 1993).

Crocidura beatus was trapped on Camiguin at three forest sites in May 1994 and March 1995 (Fig. 1, Table 1). It was uncommon in secondary lowland forest at 1000 m elevation (Site 4), in disturbed lower montane forest at 1200 m elevation (Site 5), and in primary montane forest at 1275 m (Site 7). It was most often trapped under tree roots and live vegetation. None were taken in agricultural areas at 150 m (Site 3), or in mossy forest at 1475 m (Site 8, where there was limited sampling; Table 1). This use of habitat is consistent with data from islands on Greater Mindanao (Rickart et al., 1993; Heaney et al., unpubl. data).

In 1994 and 1995, three adult females were trapped; one was pregnant with a single embryo (CRL = 10 mm). A multiparous, nonpregnant female weighed 13 g; an adult male weighed 7 g. Both cranial and external measurements (Table 2) are within stated ranges for Mindanao (Heaney & Ruedi, 1994) but are slightly smaller than those of series taken on Biliran, Leyte, and Maripipi (Rickart et al., 1993).

SPECIMENS EXAMINED—Total 5. Site 4 (2 FMNH, 1 MSU-IIT); Site 5 (1 FMNH); Site 7 (1 FMNH).

Suncus murinus (Linnaeus, 1766)

The Asian house-shrew occurs widely in Asia and Indo-Australia; it now occurs throughout the Philippines, though it is not native to the country. It is abundant in urban and agricultural areas; on islands with low mammal species richness such as Negros, it is sometimes abundant in disturbed forest and occasionally in primary forest (Heideman et al., 1987; Heaney et al., 1989, 1991), but on islands of average species richness, it is usually rare or absent from forest (Heaney et al., 1989, 1998, unpubl. data; Rickart et al., 1993).

A single subadult specimen from Mt. Timpoong Peak was available previously (Heaney 1984). In 1994–1995, we captured this species from 150 to 1475 m, and it was the most common species at the three highest sites, all in primary forest (Table 1, Fig. 1). It was especially abundant in montane forest at 1275 m (Site 7). It was moderately abundant in primary mossy forest (Site 6; elev. 1300 m) and in lower mossy forest at 1475 m elevation (Site 8) but was much less common in heavily disturbed lowland agricultural land at 150 m (Site 3). This pattern of abundance is quite different from that on the species-rich islands of Biliran, Leyte, Luzon, Maripipi, and Mindanao, where specimens were never caught in primary forest (Heaney et al., 1989, 1999, unpubl. data; Rickart et al., 1993) but similar to the species-poor island of Negros, where *S. murinus* was abundant in transitional mossy/montane forest and in mossy forest at

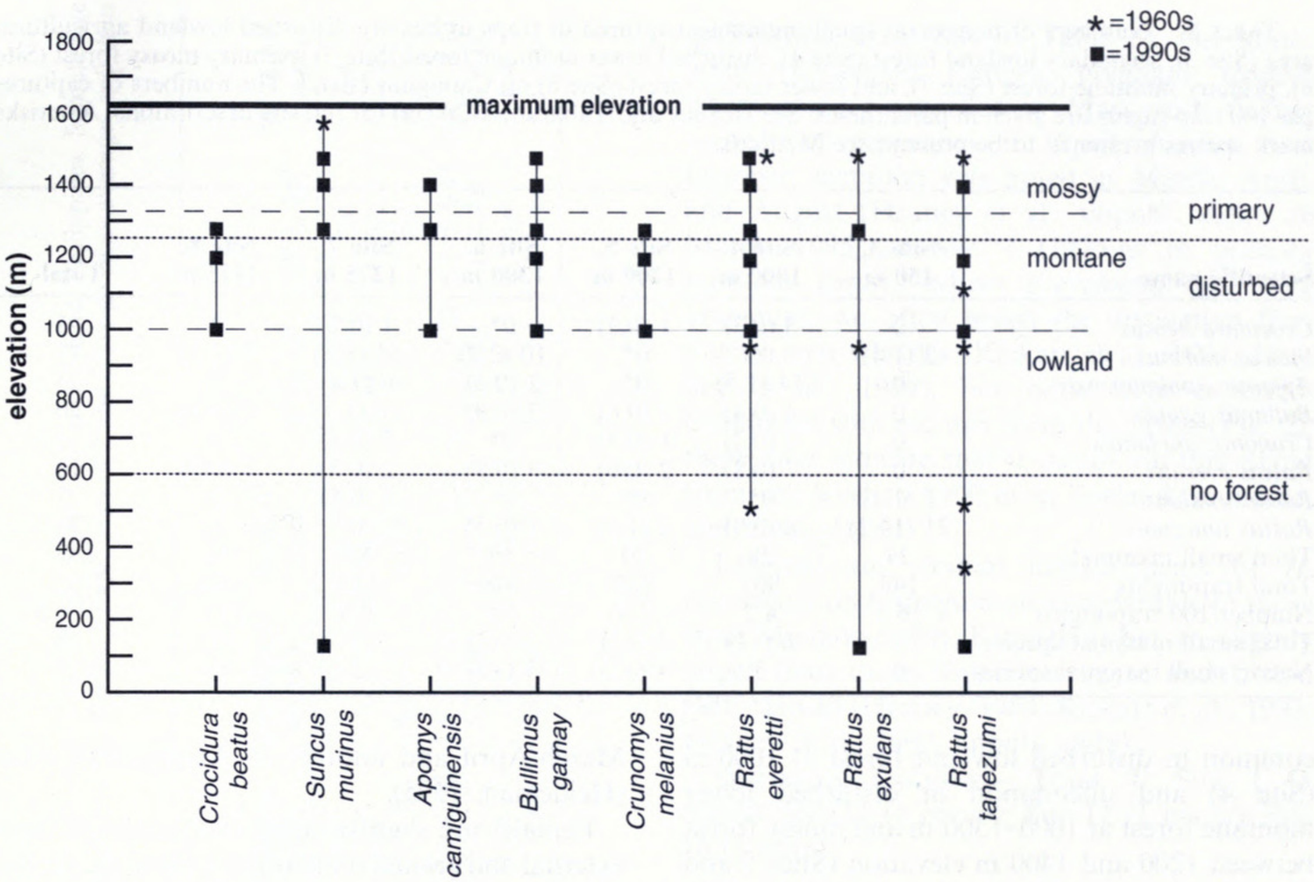

FIG. 1. Elevational range of nonvolant small mammals (Insectivora and Rodentia) on Camiguin Island, Philippines. Records from the 1960s are indicated with stars and from the 1990s by solid squares. The approximate original boundaries of primary lowland, montane, and mossy rain forest along the elevational gradient are indicated. The condition of forest along our transect in the middle 1990s is indicated as nearly absent (below 600 m), disturbed by logging and agriculture but present as second growth (about 600–1250 m), and primary or lightly disturbed by human activities and landslides (above about 1250 m). Elevations from the 1960s were rough estimates (see text).

1280 m (Heaney et al., 1989), which is similar to Sites 6 and 7.

Suncus murinus was most often trapped in runways or clear areas beneath fallen and rotting logs, under roots of trees, or under horizontal trunks of live trees as well as in runways near large boulders. Many were caught during daylight hours.

Five adult females with a mean weight of 32 ± 4.5 g (range = 27–39 g) were pregnant; litter sizes for four of these were one, two, three, and three. Thirteen nonpregnant parous females (those with large mammae) weighed an average of 28.8 ± 4.1 g (range = 22–35 g), and nulliparous females (those with small mammae) weighed 20.6 ± 2.2 g (range = 17.5–23 g, N = 10). Adult males (defined as those with large testes) had a mean weight of 36 ± 5.8 g (range 24–48 g, N = 27). Males are conspicuously larger than females in this species (Table 2).

SPECIMENS EXAMINED—Total 78. Site 3 (2 MSU-IIT); Site 6 (10 MSU-IIT); Site 7 (56 FMNH); Site 8 (9 FMNH); Site 15 (1 DMNH).

Order Chiroptera
Family Pteropodidae—Fruit Bats
Cynopterus brachyotis (Muller, 1838)

The common short-nosed fruit bat is widespread in Southeast Asia and is common throughout the Philippines. It ranges from sea level to at least 1250 m and is typically found in agricultural areas; it is also common in secondary lowland forest but usually rare in primary forest (Heaney et al., 1998).

Our limited netting on Camiguin during 1994–1995 (Table 3) indicated that *C. brachyotis* was abundant in a highly disturbed lowland agricultural area at 10 m elevation (Site 1) and was common in a heavily disturbed lowland agricultural area at 100 m (Site 2; Table 3). It was less

TABLE 1. Numbers of nonvolant small mammals captured in traps in heavily disturbed lowland agricultural area (Site 3), secondary lowland forest (Site 4), disturbed lower montane forest (Site 5), primary mossy forest (Site 6), primary montane forest (Site 7), and lower mossy forest (Site 8) on Camiguin Island. The numbers of captures per 100 trap-nights are given in parentheses. See Heaney and Tabaranza (2005a) for full site descriptions. Asterisks mark species presumed to be present; see Methods.

Scientific name	Site 3, 150 m	Site 4, 1000 m	Site 5, 1200 m	Site 6, 1300 m	Site 7, 1275 m	Site 8, 1475 m	Total
Crocidura beatus	0	3 (0.3)	1 (0.3)	0*	1 (0.2)	0	5
Suncus murinus	2 (1.4)	0*	0*	10 (2.9)	56 (8.5)	9 (2.3)	77
Apomys camiguinensis	0	14 (1.5)	0*	2 (0.6)	9 (1.4)	0	25
Bullimus gamay	0	4 (0.4)	2 (0.6)	3 (0.9)	10 (1.5)	1 (0.3)	20
Crunomys melanius	0	2 (0.2)	1 (0.3)	0*	2 (0.3)	0	5
Rattus everetti	0	7 (0.8)	2 (0.6)	3 (0.9)	2 (0.3)	2 (0.5)	16
Rattus exulans	2 (1.4)	0*	0*	0*	5 (0.8)	0	7
Rattus tanezumi	21 (14.2)	8 (0.9)	4 (1.2)	1 (0.3)	0	0	34
Total small mammals	24	38	10	19	85	12	188
Total trap-nights	148	907	339	348	655	386	2783
Number/100 trap-nights	16.2	4.2	2.9	5.5	9.9	3.1	6.8
Total small mammal species	3	6 (+1)	5 (+3)	5 (+3)	7	3	8
Native small mammal species	0	5	4 (+1)	3 (+2)	5	2	5

common in disturbed lowland forest at 1000 m (Site 4) and uncommon in disturbed lower montane forest at 1000–1300 m and mossy forest between 1200 and 1400 m elevation (Sites 5 and 6). Limited netting did not detect this species in montane primary forest at 1275 m elevation (Site 7). The occurrence of *C. brachyotis* in these habitats is consistent with records from other Philippine islands; for example, on Catanduanes, Leyte, Luzon, and Negros, this species was most abundant in agricultural land and secondary forest (Heaney et al., 1989, 1991, 1999; Heideman & Heaney, 1989; Ingle, 1992; Rickart et al., 1993), similar to Sites 1 and 3 to 5 on Camiguin. Records from the 1960s indicate that the species occurs along the entire elevational gradient, from sea level to near the peaks, although most specimens are from below 1000 m (i.e., below the transition to montane forest; Fig. 2).

Eight adult females (mean = 29.5 ± 4.72 g) taken in May 1992 and 1994 were pregnant with single embryos (CRL = 5–26 mm). Two of the pregnant females (22 and 35 g) and three non-pregnant ones (32.5–39 g) were lactating. Adult females with enlarged mammae but not pregnant or lactating had mean weight of 29.2 ± 2.3 g (range = 26–33.2 g, N = 13). Five nulliparous females had a mean weight of 16.5 g ± 2.0 g (range = 14–19 g). Males with abdominal testes had a mean weight of 27.4 ± 2.6 g (range = 22–32.5 g, N = 15). On Negros Island, this species probably produces two young per year, one in March/April and another in August/September (Heideman, 1995).

Females are slightly larger than males in most external and cranial dimensions (Table 4), a trend quite similar to specimens from Mt. Kitanglad, Mindanao (Heaney et al., unpubl. data). Specimens from Biliran, Leyte and Maripipi, in contrast, showed the opposite trend (Rickart et al., 1993).

SPECIMENS EXAMINED—Total 91. Site 1 (27 FMNH); Site 3 (5 MSU-IIT); Site 4 (4 FMNH, 14 MSU-IIT); Site 6 (1 FMNH, 3 MSU-IIT); Site 11 (12 DMNH); Site 12 (3 DMNH); Site 13 (6 DMNH); Site 16 (2 ROM); Site 17 (14 ROM).

Harpyionycteris whiteheadi Thomas, 1896

The harpy fruit bat has been reported previously from Camiguin (Peterson & Fenton, 1970), as well as from Marinduque, Masbate, Mindoro, Negros, southern Luzon, and throughout Greater Mindanao (Heaney et al., 1998, 1999). It is generally restricted to primary or lightly disturbed forest; it is usually rare in lowland forest but often is moderately common in montane forest from roughly 800 m to at least 1800 m. It apparently feeds heavily on the fruits of viney pandans (*Freycinetia* spp.) and figs (*Ficus* spp.); (Heaney et al., 1989, 1999; Heideman & Heaney, 1989; Rickart et al., 1993).

In May 1992, we netted one pregnant female weighing 123 g with a single embryo (CRL = 28 mm) at 10 m elevation, in a lowland

TABLE 2. Mean (±SD) and range of selected external and cranial measurements of adult shrews (Soricidae) from Camiguin Island, Philippines. Sample size smaller than N is indicated by the number enclosed in parentheses after the range. Measurements taken from sample sizes of 2 and 3 are given as averages and their ranges. All measurements except weight are in millimeters.

Species	Sex	N	Total length	Tail length	Hind foot	Weight (g)	Condylo-basal length	Braincase width	Interorbital breadth	Rostral length	I^1 to M^3	P^4 to M^3	M^2 to M^2 (labial)
Crocidura beatus	M	1	127	58	14	7.0	19.6	9.5	4.7	8.2	8.9	5.0	6.4
	F	2	128	58	14	6.0 (1)	20.3	9.4	4.7	8.7	9.2	5.2	6.2
			127–129	57–58	12–15		20.2–20.5	9.4–9.5	4.5–4.8	8.6–8.8	9.2	5.2	6.1–6.2
Suncus murinus	M	9	184 ± 5.7	63 ± 3.5	20 ± 0.4	38 ± 3.6	28.0 0.62	12.2 ± 0.22	5.4 ± 0.19	11.8 ± 0.22	12.8 ± 0.20	6.9 ± 0.11	8.8 ± 0.14
			177–192 (8)	58–69 (8)	20–21	30–42	26.7–28.6	11.7–12.5	5.2–5.8	11.4–12.1	12.6–13.1	6.7–7.0	8.6–9.0
	F	3	177	58	18	23	26.2	11.4	5.2	11.0	12.0	6.4	8.4
			174–182	54–58	18–19	26–33	24.8–26.6	11.1–11.6	5.1–5.2	10.6–11.2	11.6–12.4	6.2–6.6	8.1–8.6

agricultural area (Site 1; Table 3). On Mindanao (Kitanglad Range), pregnant females were similarly recorded in May, with further records of pregnancy in April, August, and October; lactation was noted in March, April, and August (Heaney et al., unpubl. data). In March 1995, at Site 7 (1275 m in primary montane forest), where *Freycinetia* spp. were abundant, we often heard the distinctive *Harpyionycteris* whistles (Rickart et al., 1993; Heaney et al., 1999), but none were captured. Combined with records from the 1960s (Fig. 2), these data indicate that it occurs on this island from sea level to 1500 m in lowland, montane, and mossy forest.

External and cranial measurements of *H. whiteheadi* on Camiguin are comparable to those from Mindanao (Mt. Kitanglad) but are slightly larger than those found on Leyte and Luzon (Mt. Isarog) (Heaney, 1984; Rickart et al., 1993; Heaney et al., 1999, unpubl. data).

SPECIMENS EXAMINED—Total 4. Site 1 (1 FMNH); Site 11 (1 DMNH); Site 12 (1 DMNH); Site 16 (1 ROM).

Macroglossus minimus (E. Geoffroy, 1810)

The dagger-toothed flower bat occurs from Thailand to Australia and is found throughout the Philippines (Heaney et al., 1998). Within the Philippines, it occurs in virtually every habitat in the country, from sea level to at least 2250 m. It is often abundant in agricultural and heavily disturbed areas, is common in secondary forest, and usually is uncommon in primary forest. It is most often associated with domestic or wild banana (*Musa* spp.; Heaney et al., 1989, 1999; Heideman & Heaney, 1989; Rickart et al., 1993).

On Camiguin, our limited netting showed *M. minimus* to be abundant in a highly disturbed lowland agricultural area at ca. 10 m elevation (Site 1), present in a heavily disturbed lowland agricultural area at 100 m (Site 3), uncommon in disturbed lowland forest at 1000 m (Site 4), common in disturbed lower montane forest at 1000–1300 m (Site 5), and present in mossy forest between 1200 and 1400 m elevation (Site 6; Table 3). Limited netting did not detect this species in primary montane forest at 1275 m elevation (Site 7). Combined with prior records, it is apparent that this species occurs on Camiguin from sea level to at least 1200 m, in lowland and montane forest, in both disturbed and undisturbed forest (Fig. 2).

TABLE 3. Numbers of fruit bats captured in mist nets in a lowland agricultural area (Site 1), heavily disturbed lowland agricultural area (Site 3), secondary lowland forest (Site 4), disturbed lower montane forest and primary mossy forest (Sites 5 and 6 concurrently), and primary montane forest (Site 7) on Camiguin Island during 1992, 1994, and 1995. The number of captures per net-night are given in parentheses. See Heaney and Tabaranza (2006a) for full site descriptions. Asterisks indicated species observed but not netted (see text).

Scientific name	Site 1, 10 m	Site 3, 150 m	Site 4, 1000 m	Sites 5 and 6, 1200–1400 m	Site 7, 1275 m
Cynopterus brachyotis	27 (4.5)	5 (1.67)	18 (0.75)	4 (0.29)	0
Harpyionycteris whiteheadi	1 (0.17)	0	0	0	0*
Macroglossus minimus	15 (2.5)	1 (0.33)	4 (0.17)	9 (0.64)	0
Ptenochirus jagori	8 (1.33)	0	16 (0.67)	1 (0.07)	0
Total fruit bats	51	5	35	14	0
Total net-nights	6	3	24	14	8
Fruit bats per net-night	8.5	1.67	1.46	1.00	0

Six adult females netted in May 1992 and 1994, with a mean weight of 15.2 ± 3.2 g (range = 12.5–20.3 g), were pregnant with single embryos. Four parous females with large mammae but neither pregnant nor lactating had a mean weight of 18.5 ± 1.78 g (range = 16–20 g). Three adult males weighed between 16 and 19 g. A juvenile male and a juvenile female each weighed 5 g. On Mindanao (Kitanglad Range), pregnant females were recorded in April to August and October, while lactating females were recorded in May, September, and October (Heaney et al., unpubl. data). Heideman (1995) documented that this species undergoes aseasonal breeding and postpartum estrus on Negros Island and has several young per year.

Comparison with specimens of *M. minimus* from Biliran, Dinagat, Leyte, Luzon (Mt. Isarog), Maripipi, and Mindanao (Kitanglad Range) shows that while the overall variation

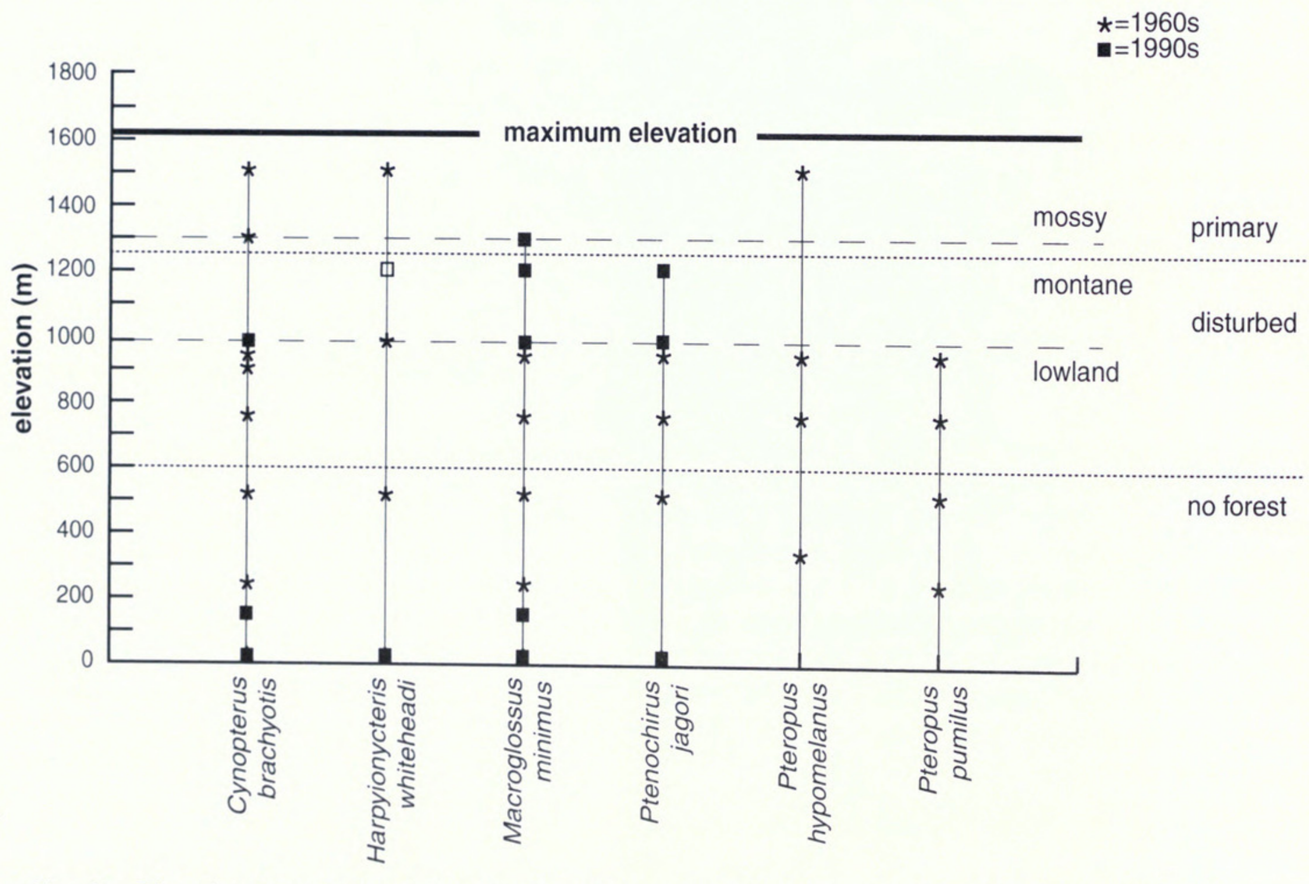

FIG. 2. Elevational range of fruit bats (Pteropodidae); symbols and boundaries as in Figure 1. The open square indicates a documented record without a voucher specimen (see text).

TABLE 4. Mean (±SD) and range of selected external and cranial measurements of adult fruit bats (Pteropodidae) from Camiguin Island, Philippines. Sample size smaller than N is indicated by the number enclosed in parentheses after the range. Measurements taken from sample sizes of 2 and 3 are given as averages and their ranges. All measurements except weight are in millimeters.

Species	Sex	N	Total length	Tail length	Hind foot	Ear	Forearm	Weight (g)	Condylo-basal length	Zygomatic breadth	Inter-orbital width	Mastoid breadth	Rostral length	C^1 to last M	Molariform toothrow
Cynopterus	M	8	90 ± 5.1	9 ± 1.9	13 ± 1.1	16 ± 1.4	62 ± 2.5	27 ± 2.4	27.4 ± 0.52	18.1 ± 0.26	6.0 ± 0.32	11.5 ± 0.25	8.6 ± 0.42	9.3 ± 0.28	6.5 ± 0.19
brachyotis			83–96	6–12	12–15 (6)	13–17	58–65	22–28	26.6–28.2	17.6–18.5	5.4–6.2	11.3–12.0	7.7–9.2	9.0–9.6	6.3–6.8
	F	10	96 ± 1.6	8 ± 2.2	—	17 ± 0.8	65 ± 2.1	29 ± 1.7	27.0 ± 0.76	18.2 ± 0.68	6.0 ± 0.22	11.6 ± 0.36	8.6 ± 0.52	9.1 ± 0.38	6.4 ± 0.27
			94–98	4–12 (9)		16–18	62–69	27–32	26.1–28.1	17.1–19.1	5.6–6.4	10.9–12.1	8.0–9.8 (9)	8.5–9.7	6.0–6.8
Harpyionycteris	M	1	145	0	25	22	84	—	40.5	24.3	6.9	15.3	—	15.7	11.8
*whiteheadi**	F	2	157	0	26	20	86	123	41.9	25.1	6.8	15.8	11.8	16.2	12.4
			155–159		26 (1)	17–23	84–88	123 (1)	41.5–42.4	25.1	6.7–6.9	15.8–15.9	11.7–11.9	16.1–16.4	12.3–12.5
Macrogolossus	M	6	74 ± 1.5	—	12	16 ± 1.0	43 ± 1.2	17 ± 2.9	25.2 ± 0.72	15.4 ± 0.38	5.0 ± 0.42	10.3 ± 0.49	10.0 ± 0.37	8.9 ± 0.34	5.6 ± 0.28
minimus			72–76		10–14 (3)	14–17	42–45	12–20	24.6–26.2	14.9–15.8 (4)	4.5–5.7	9.8–10.8	9.3–10.3	8.5–9.4	5.1–5.9
	F	4	75 ± 2.6	—	12	16 ± 0.5	44 ± 1.3	16 ± 3.8	25.5 ± 0.79	13.9 ± 0.23	4.7 ± 0.23	10.2 ± 0.13	9.7	9.0 ± 0.42	5.5 ± 0.12
			73–78		12 (2)	15–16	42–45	12–20	24.4–26.2	13.6–14.1	4.4–5.0	10.0–10.3	9.6–10.0 (3)	8.5–9.4	5.3–5.6
Ptenochirus	M	10	117 ± 8.6	13 ± 1.4	19 ± 1.7	21 ± 1.7	85 ± 3.1	75 ± 3.0	35.1 ± 0.58	24.6 ± 0.49	7.3 ± 0.28	14.7 ± 0.34	10.9 ± 0.42	12.5 ± 0.26	8.8 ± 0.29
jagori			105–128	11–15	16–21 (7)	18–24	80–89	70–78	34.0–36.2	23.8–25.6	6.8–7.7	14.3–15.4	10.2–11.8	12.1–12.9	8.5–9.3
	F	8	124 ± 7.0	12 ± 1.8	19	20 ± 1.2	82 ± 1.3	71 ± 4.5	34.8 ± 0.65	24.0 ± 0.64	7.1 ± 0.28	14.6 ± 0.33	10.4 ± 0.27	12.0 ± 0.32	8.4 ± 0.28
			113–131	9–14	17–20 (3)	19–22	80–83	63–75	33.8–35.9	23.0–25.1	6.8–7.6	14.2–15.0	10.0–10.8	11.5–12.6	8.0–8.9
Petropus	M	3	228	0	42	28	141	—	61.3	35.2	8.8	20.2	22.7	23.4	16.4
*hypomelanus**			219–239		40–45	26–29	139–142 (2)		61.3 (1)	32.2–37.5	8.3–9.2	20.1–20.4 (2)	22.3–23.3	22.8–24.0	16.2–16.5
	F	2	211	0	38	30	134	—	61.0	34.8	9.1	19.6	22.2	23.6	16.1
			200–222		34–43	30–31	131–138		59.7–62.3	33.9–35.6	8.6–9.5	19.2–20.1	21.7–22.6	23.4–23.7	16.1
Pteropus	M	4	168 ± 12.5	0	35 ± 2.5	22 ± 2.2	106 ± 2.2	—	49.2 ± 1.39	27.9 ± 0.47	7.3 ± 0.61	17.6 ± 0.36	16.8 ± 0.54	18.0 ± 0.39	12.6 ± 0.10
*pumilus**			151–179		32–38	19–24	102–107		48.3–51.3	27.6–28.6	6.8–8.2	17.1–17.9	16.1–17.3	17.6–18.4	12.5–12.7
	F	3	178	0	34	21	105	—	48.6	27.5	6.9	17.2	17.0	17.5	12.2
			168–189		32–34	17–24	103–108		47.5–49.7	27.4–27.6 (2)	6.8–7.5	17.0–17.3 (2)	16.0–17.6	17.1–17.7	11.9–12.5

* Includes measurements from Heaney (1984).

in cranial and external measurements is slight. Camiguin specimens tend to cluster consistently within the upper ranges of most features measured (Table 4; Heaney and Rabor, 1982; Heaney et al., 1991, 1999, unpubl. data; Rickart et al., 1993).

SPECIMENS EXAMINED—Total 56. Site 1 (15 FMNH); Site 3 (1 MSU-IIT); Site 4 (4 MSU-IIT); Site 5 (8 MSU-IIT); Site 6 (1 MSU-IIT); Site 11 (12 DMNH); Site 13 (5 DMNH); Site 14 (2 DMNH); Site 17 (8 DMNH).

Ptenochirus jagori (Peters, 1861)

The musky fruit bat is a common Philippine endemic, occurring throughout the archipelago with the exception of the Batanes/Babuyan and Palawan faunal regions from sea level to at least 1800 m (Heaney et al., 1998). Our limited netting on Camiguin showed *Ptenochirus jagori* to be common in a lowland agricultural area at 10 m elevation (Site 1), less common in disturbed lowland forest at 1000 m (Site 4), and scarce in primary mossy forest at 1300 m (Site 6; Table 3). Combined with records from the 1960s, these data indicate that the species is widespread in lowland and montane rain forest from sea level to at least 1200 m (Fig. 2), though probably its abundance declines with increasing elevation and with increasing levels of disturbance (Table 3), as noted elsewhere (Heaney et al., 1989, 1999, unpubl. data; Heideman & Heaney, 1989; Rickart et al., 1993; Lepiten, 1997).

Three adult females, netted in May 1992 and 1994, weighing an average of 70 g (range = 68–75 g), were pregnant with a single embryo each (CRL = 5–10 mm). Three nonpregnant females with large mammae had an average weight of 73.5 g (range = 72–74 g), and two nulliparous females weighed 67 and 68.5 g. Eleven adult males had a mean weight of 73.2 ± 4.7 g (range = 64–78 g, N = 11). Pregnant females of *P. jagori* have been recorded also in May on Luzon (Mt. Isarog) (Heaney et al., 1999). On Mindanao (Kitanglad Range), pregnant females were recorded in March, May, July, and August and lactating females in May to June and August to December (Heaney et al., unpubl. data). Heideman and Powell (1998) found that on Negros Island, *P. jagori* gives birth to a single young twice each year: the first in late March or early April and the second in August. It was further discovered that this species undergoes delayed implantation and early development that lasts for five months, shorter than in two other endemic species of Philippine pygmy fruit bats, *Haplonycteris fischeri* and *Otopteropus cartilagonodus*, where the phenomenon was first detected (Heideman, 1989; Heideman et al., 1993; Heideman & Powell, 1998). Additionally, this condition was apparently exhibited by primiparous young adult females only, allowing them to give birth only once in their first year, which had the effect of enabling them to synchronize breeding with the adult females the following year (Heideman & Powell, 1998).

Males are somewhat larger than females in most cranial and external dimensions, as on Biliran, Leyte, and Maripipi (Table 4; Rickart et al., 1993). Cranial and external measurements (Table 4) are noticeably larger than those for series from Catanduanes and southern Luzon and were similar to those from Biliran, Leyte, and Maripipi (Heaney, 1984; Heaney et al., 1991, 1999; Rickart et al., 1993).

SPECIMENS EXAMINED—Total 46. Site 1 (8 FMNH); Site 4 (16 MSU-IIT); Site 6 (1 MSU-IIT); Site 11 (6 DMNH); Site 13 (6 DMNH); Site 17 (9 ROM).

Pteropus hypomelanus Mearns, 1905

The common island flying fox occurs from Thailand to Australia and is found throughout the Philippines with the exception of the Palawan faunal region. It is often common in agricultural areas from sea level to ca. 900 m and is absent in primary forest (Heideman & Heaney, 1989; Heaney et al., 1991, 1998; Utzurrum, 1992; Rickart et al., 1993). Records from the 1960s document it from Camiguin at elevations from about 250 to 1500 m (Fig. 2), but we netted none in the 1990s; because this species typically flies above the canopy and our nets were set not more than about 4 m above the ground, our failure to catch any does not necessarily indicate any change in their abundance.

External and cranial measurements show only slight variations with those of specimens from Dinagat, Panay, Leyte, and Maripipi (Heaney & Rabor, 1982; Rickart et al., 1993).

SPECIMENS EXAMINED—Total 8. Site 10 (2 DMNH); Site 12 (1 DMNH); Site 13 (2 DMNH); Site 17 (3 ROM).

Pteropus pumilus Miller, 1910

The little golden-mantled flying fox is endemic to the Philippines (aside from a single population on Miangas Island, Indonesia, adjacent to Mindanao) and occurs throughout the archipelago, with the exception of the Batanes/Babuyan and Palawan regions (Heaney et al., 1998). Previously reported from Camiguin as *P. tablasi*, the species was revised to include *P. tablasi* and *P. balutus* as synonyms under *Pteropus pumilus* (Klingener & Creighton, 1984). It is associated with primary and good secondary lowland forest from sea level to about 1100 m, and it is uncommon outside of forest. Additionally, it is most common on small islands and is uncommon to rare on larger islands. *Pteropus pumilus* often is netted in clearings or on ridgetops (Heideman & Heaney, 1989; Utzurrum, 1992; Rickart et al., 1993).

We did not encounter *P. pumilus* during the 1990s, but the 1967–1969 surveys obtained 42 individuals at four sites from ca. 250 to nearly 1000 m elevation (Fig. 2). As with *Pteropus hypomelanus*, this species usually flies above the canopy, so our failure to catch any in the 1990s does not necessarily indicate a change in their status on the island.

SPECIMENS EXAMINED—Total 42. Site 11 (19 DMNH); Site 13 (2 DMNH); Site 14 (1 DMNH); Site 17 (20 ROM).

Family Emballonuridae—Sheath-tailed Bats

Emballanura alecto (Eydoux and Gervais, 1836)

The Philippine sheath-tailed bat is a common cave-dwelling species that occurs throughout most of the Philippines and is also known from Borneo, the Moluccas, and Sulawesi (Koopman, 1989). It has been recorded only in lowland areas (450 m and below) in disturbed forest and agricultural areas with scattered remnant forest, with most captures recorded from caves, under large boulders, or in man-made tunnels (Heaney et al., 1991, 1999; Rickart et al., 1993). We did not record this species during our fieldwork in 1994 and 1995, but in 1967 specimens were taken from Tag-ibo Cave at 400 ft (ca. 120 m) and at 1400–3300 ft (ca. 400–1000 m) on Mt. Mambajao (see also Heaney, 1984).

Comparison of external and cranial measurements with series from Leyte and Biliran shows little variation (Table 4; Rickart et al., 1993).

SPECIMENS EXAMINED—Total 4. Site 17 (2 ROM); Site 18 (2 ROM).

Family Rhinolophidae—Horseshoe-nosed Bats

Rhinolophus arcuatus Peters, 1871

The arcuate horseshoe bat is widespread from Sumatra to New Guinea and throughout the Philippines (Heaney et al., 1998), including the Palawan faunal region (Esselstyn et al., 2004). It is most often encountered from lowlands to at least 1350 m in agricultural lands to primary lowland and montane forest and occasionally roosts in caves (Heaney et al., 1991, 1999; Rickart et al., 1993). Two groups that differ in size and habitat are recognized within this species: a smaller morphotype, designated *R. arcuatus*—s, that occurs in the lowlands or disturbed habitats, and a larger one, designated *R. arcuatus*—l, found in forest at higher elevations (Ingle & Heaney, 1992).

In May 1994, we netted this species at 1000 m elevation in disturbed lowland forest (Site 4). Of two adult females netted, one (15 g) was pregnant with one large embryo (CRL = 28 mm), and the other was lactating (12.5 g). Pregnancies in this species were recorded also in March on Luzon (Mt. Isarog) and in April on Biliran, Leyte, and Maripipi (Rickart et al., 1993; Heaney et al., 1999).

Cranial and external measurements (Table 5) of the Camiguin specimens are consistently larger than those in series from Biliran, Leyte, Luzon (Mt. Makiling), Maripipi, and Mindanao (Mt. Kitanglad), which all fall within the dimensions of the smaller morphotype, *R. arcuatus*—s (Ingle & Heaney, 1992; Rickart et al., 1993; Heaney et al., 1999, unpubl. data). Instead, their external and cranial dimensions are comparable to the larger morphotype, *R. arcuatus*—l (Ingle & Heaney, 1992). Systematics in this "species" are badly in need of detailed study.

SPECIMENS EXAMINED—Total 10. Site 4 (4 MSU-IIT); Site 13 (6 DMNH).

Rhinolophus inops K. Anderson, 1905

The Philippine forest horseshoe bat is common to abundant in primary lowland and montane forest from sea level to 2250 m and is usually rare in secondary forest and mossy forest (Heaney et al., 1991, 1998, 1999; Rickart et al., 1993). Improvements in our understanding of Philippine *Rhinolophus* lead us to reidentify the single specimen from Site 13, reported as *R. subrufus* by Heaney (1984), as *R. inops*. We netted two additional males in disturbed lowland forest at 1000 m (Site 4). Cranial and external measurements (Table 5) are slightly larger in most dimensions than those of the series from Biliran, Leyte (Rickart et al., 1993), and Mindanao (Mt. Kitanglad; Heaney et al., unpubl. data); we suspect that regional morphs corresponding to the Pleistocene islands (Heaney, 1986) are present.

Specimens Examined—Total 3. Site 4 (2 MSU-IIT); Site 13 (1 DMNH).

Rhinolophus virgo K. Anderson, 1905

The yellow-faced horseshoe bat is an endemic species widespread within the Philippines. It is usually encountered in primary lowland forest from 250 to 1100 m; several records are from caves (Heaney et al., 1991; Rickart et al., 1993). We obtained one adult female from the edge of a small tree-fall gap in primary montane forest at 1275 m on 22 March 1995 (Site 7). It has small mammae and showed no indication of reproductive activity. Cranial dimensions (Table 5) fall within the range of those from Leyte and Maripipi but are slightly smaller than those from Mindanao (Mt. Kitanglad; Rickart et al., 1993; Heaney et al., unpubl. data).

Specimens Examined—Total 1. Site 7 (1 FMNH).

Family Vespertilionidae—Common Bats

Murina cyclotis Dobson, 1872

The round-eared tube-nosed bat is widespread in southern Asia and was previously known in the Philippines from a few specimens from the central and southern portion of Greater Luzon as well as Greater Mindanao, Sibuyan, and Siquijor, with records from disturbed and primary lowland and montane forest from 250 to 1500 m (Heaney et al., 1991, 1998, 1999, unpubl. data; Rickart et al., 1993; Ruedas, 1994; Lepiten, 1997). We netted one adult female in May 1994 in secondary lowland forest at 1000 m (Site 4).

Specimens Examined—Total 1. Site 4 (1 MSU-IIT).

Pipistrellus javanicus (Gray, 1838)

The Javan pipistrelle is found from Korea to Java and throughout the Philippines. It is generally common in primary montane forest and uncommon in primary lowland and mossy forest, though it has been found from sea level to 2250 m (Ingle, 1992; Heaney et al., 1998, 1999, unpubl. data). A single skin without a skull, tentatively identified as this species, was obtained from Camiguin by the 1960s surveys. In March 1995, two were netted in primary montane forest at 1275 m (Site 7). Cranial and external measurements (Table 5) are comparable with those of a series from Mindanao (Mt. Kitanglad) in most dimensions (Heaney et al., unpubl. data).

Table 5. Mean (±SD) and range of selected external and cranial measurements of adult microbats (Emballonuridae, Rhinolophidae, and Vespertilionidae) from Camiguin Island, Philippines. Sample size smaller than N is indicated by the number enclosed in parentheses after the range. Measurements taken from sample sizes of 2 and 3 are given as averages and their ranges. All measurements except weight are in millimeters.

Species	Sex	N	Total length	Tail length	Hind foot	Ear	Forearm	Weight (g)	Condylo-basal length	Zygomatic breadth	Inter-orbital width	Mastoid breadth	Rostral length	C^1 to last M	Molariform toothrow
*Emballonura alecto**	F	2	6.2	11	8	15	44	—	13.8	8.7	2.8	—	—	5.5	4.0
			6.2	11	8	15	44 (1)		13.6–13.9	8.5–8.9	2.7–2.9			5.3–5.6	3.9–4.0
*Rhinolophus arcuatus**	M	6	74 ± 4.5	18 ± 1.7	11 ± 0.4	21 ± 0.4	43 ± 3.2	—	19.8 ± 0.43	10.1 ± 0.24	1.8 ± 0.19	10.0 ± 0.17	8.5 ± 0.27	7.8 ± 0.17	5.6 ± 0.06
			71–83	16–21	11–12	20–21	40–48 (5)		19.3–20.4 (5)	9.8–10.5	1.4–1.9	9.8–10.2	8.2–8.8	7.5–7.9	5.5–5.7
*Rhinolophus inops**	M	1	87	22	12	21	51	—	23.2	12.1	2.1	11.2	10.4	9.3	6.8
Rhinolophus virgo	F	1	69	24	9	18	39	—	15.7	8.2	2.0	8.2	6.6	5.9	4.6
Pipistrellus javanicus	M	1	82	34	9	11	34	—	13.1	8.8	3.6	7.5	—	4.7	3.7
	F	1	—	—	—	—	—	—	13.1	9.1	3.7	8.1	—	4.8	3.8

* Includes measurements from Heaney (1984).

SPECIMENS EXAMINED—Total 3. Site 7 (2 FMNH); Site 13 (1 DMNH).

Order Primates

Family Cercopithecidae—Monkeys

Macaca fascicularis (Raffles, 1821)

The long-tailed macaque occurs from Burma to Timor and is found throughout the Philippines (Fooden, 1995; Heaney et al., 1998). It is found in agricultural areas near forest, in second-growth and secondary forest, as well as primary forest from sea level to at least 1800 m in lowland and montane forest (Goodman & Ingle, 1993; Rickart et al., 1993; Heaney et al., 1999). We did not collect any specimens, but in March 1995 we obtained the skull of an adult individual from a hunter who had killed the macaque in a forested area above Mahinog a few years earlier. Also in March 1995, a local hunter who was a member of our team saw two macaques a short distance from our camp at 1100 m elevation (Site 7) in primary montane forest. He reported that the macaques were fairly common in what remained of lowland primary forest and good secondary forest at that time and were actively hunted.

SPECIMENS EXAMINED—Total 1. Above Mahinog (1 FMNH).

Order Rodentia

Family Muridae—Rats and Mice

Apomys camiguinensis Heaney and Tabaranza, 2006

A previously unknown species of *Apomys* (Musser, 1982) was trapped on Camiguin in May 1994 and March 1995 (Heaney & Tabaranza, 1997) and described in this volume (Heaney & Tabaranza, 2006b). The Camiguin forest mouse is moderately large for the genus, averaging about 40 g. It is marked by a number of subtle morphological characters, and molecular data show it to be most closely related to *Apomys hylocoetes* and *A. insignis* from Mindanao and to an unnamed species from Leyte and Biliran (Steppan et al., 2003; Heaney & Tabaranza, 2005b). This species was common (Table 1, Fig. 1) in disturbed lowland forest at 1000 m (Site 4) and in primary montane forest at 1275 m (Site 7) and relatively uncommon in primary mossy forest at 1200–1400 m (Site 6). It was not found in heavily disturbed lowland agricultural land (Site 3, elev. 150 m), lower montane forest (Site 4, elev. 1000–1300 m), or lower mossy forest (Site 8, elev. 1475 m), but there was limited sampling at all of these (Table 1). Most specimens were taken from traps placed in primary montane forest underneath root tangles and beneath fallen and rotten logs on a moderate slope. All individuals were captured at night.

A pregnant female taken on 29 May 1994 weighed 40.5 g and had a single embryo (CRL = 30 mm). Adult females with large mammae but not pregnant weighed 39 ± 2.1 g (range = 37.5–42 g, N = 5); two of these, taken 23 May 1994 and 17 March 1995, each had two placental scars. Nulliparous females (with small mammae) were lighter and had an average weight of 35 g (range = 34–36). Females have two pair of inguinal mammae. These data indicate a litter size between one and two. Males with scrotal testes had a mean weight of 41.3 ± 4.7 g (range = 36.5–48 g, N = 11); testis size ranged from 15 × 16 mm to 8 × 12 mm. Males with abdominal testes weighed 33.0 ± 5.0 g (range = 28–34 g, N = 5) and had testis size of 5 × 8 mm.

SPECIMENS EXAMINED—Total 25. Site 4 (14 MSU-IIT), Site 6 (2 MSU-IIT); Site 7 (9 FMNH).

Bullimus gamay Rickart, Heaney and Tabaranza, 2002

A previously unknown species of *Bullimus*, recently described as *B. gamay* (Rickart et al., 2002), was captured on Camiguin in May 1994 and March 1995. The Camiguin forest rat was incorrectly assigned to *Tarsomys* by Heaney and Tabaranza (1997) and was designated "*Bullimus* sp. A" by Heaney et al. (1998). It was trapped from 900 to 1475 m (Fig. 1, Table 1) but not in heavily disturbed lowland agricultural land from sea level to 300 m (Site 3). Most specimens were taken from traps placed in runways beneath root tangles and rotten logs or near large rocks. This species was most common in primary montane forest at 1275 m (Site 7). It was less common in disturbed lower montane forest at 1000–1300 m (Site 5) and in primary mossy forest at 1200–1400 m (Site 6). It was rare in secondary lowland forest at 1000 m (Site 4) and in lower mossy forest at 1475 m (Site 8). *Bullimus bagobus* occurs in similar habitat on Mindanao but also occurs at lower elevation where good forest persists (Heaney, 2001; Heaney et al., unpubl. data); this suggest that *B. gamay* should also be sought at lower elevations on Camiguin.

Parous females with large mammae weighed an average of 370 g (range = 360–390 g, N = 3), while nulliparous young adult females with small mammae were lighter, having a mean weight of 276 ± 53.7 g (range = 210–345 g, N = 5). Adult males with scrotal testes had an average weight of 402 g (range = 240–500 g; N = 3) and had testis size ranging from 21 × 30 mm to 27 × 35 mm). Among the nine individuals taken in May 1994, the smallest was a nulliparous young female weighing 210 g, while among the 11 individuals captured in March 1995, two were juveniles, a male weighing 120 g and a female weighing 125 g. No pregnant females were taken in May 1994 and March 1995, but a lactating female (360 g) was taken on 18 March 1995, and a female taken on 29 May 1994 had three placental scars. This suggests that females give birth in February and March. Three females had three pairs of mammae and one had four pairs, indicating that litter size most likely does not exceed three.

SPECIMENS EXAMINED—Total 20. Site 4 (4 MSU-IIT); Site 5 (2 MSU-IIT); Site 6 (3 MSU-IIT); Site 7 (10 FMNH); Site 8 (1 FMNH).

Crunomys melanius Thomas, 1907

The Mindanao shrew-mouse was previously known only from Leyte and Mindanao from near sea level to 1550 m, apparently in primary lowland rain forest; it is rare in collections (Musser & Heaney, 1992; Heaney et al., 1998; unpubl. data; Rickart et al., 1998). On Camiguin, we found it to be uncommon in heavily disturbed lowland agricultural land at 1000 m (Site 4), in disturbed lower montane forest at 1200 m (Site 5), and in primary montane forest at 1275 m (Site 7; Table 1, Fig. 1). It was trapped beneath rotten logs and wood tangles in an area with few dead leaves and little moss. It occurs down to sea level in good forest on Mindanao (Heaney et al., 1998; Heaney, 2001) and should also be sought at lower elevations on Camiguin.

Two of the five specimens we captured were females. An adult female taken on 17 March 1995, with enlarged mammae and weighing 71 g, had recently given birth; it had three placental scars (one left, two right), and the uterus was swollen. The other female (62.5 g), probably nulliparous, had small mammae. Two adult males (60 g and 72 g) had scrotal testes (15 × 8 mm); the third male, taken on 24 May 1994, was a small juvenile (28 g) with abdominal testes. These scanty data imply that March, April, and May are months of reproductive activity. Females have two pairs of mammae, indicating that litter size is small.

Cranial and external measurements (Table 6) are similar to but slightly larger than those from Leyte and Mindanao (Kitanglad Range and Mt. Apo; Rickart et al., 1993, 1998; Heaney et al., unpubl. data).

SPECIMENS EXAMINED—Total 5. Site 4 (2 MSU-IIT); Site 5 (1 MSU-IIT); Site 7 (2 FMNH).

Rattus everetti (Gunther, 1879)

The common Philippine forest rat is a widespread endemic species (excluding the Babuyan/Batanes, Palawan, and Sulu groups) found in primary and disturbed lowland, montane, and mossy forest from sea level to 2400 m (Heaney et al., 1991, 1998, 1999; Musser & Heaney, 1992; Rickart et al., 1993).

During 1994–1995, we found this 250–350 g rodent to be fairly common at all sampling sites from disturbed lowland forest at 1000 m, through montane forest to mossy forest at 1475 m; specimens from the 1960s were taken at 500 m (Table 1, Fig. 1); on Mindanao, it occurs down to sea level (Heaney, 2001; Heaney et al., unpubl. data). It was trapped under root tangles and beneath fallen logs, in hollow spaces beneath live trees, and near mounds of soil and rotting leaves.

Five parous adult females from May 1994 and March 1995 had a mean weight of 271 ± 28.8 (range = 240–300 g, N = 5). During the same months, five nulliparous females (with adult pelage) weighed 188 ± 21.4 g (range = 160–215 g), and four females with juvenile pelage weighed 116 ± 31.0 g (range = 77–150 g). Females have four pairs of mammae, indicating moderate litter size. None were pregnant, and we were unable to count placental scars; previous studies also produced little data on litter size (Heaney et al., 1999, unpubl. data). Males with scrotal testes, recorded in May 1994 and March 1995, had a mean weight of 288 ± 69.8 g (range = 210–375 g, N = 4), and the largest males had testes size of 33 × 52 mm and 30 × 50 mm. Three males with abdominal testes, during the same months, weighed an average of 207 g (range = 160–295 g).

Cranial and external measurements (Table 6) are comparable to those from Biliran, Leyte, and Maripipi but slightly smaller than series from Dinagat, Mindanao (Kitanglad Range), and Siargao (Heaney & Rabor, 1982; Heaney et al., 1991, 1999, unpubl.; Rickart et al., 1993).

SPECIMENS EXAMINED—Total 28. Site 4 (6 MSU-IIT); Site 5 (2 MSU-IIT); Site 6 (3 MSU-IIT); Site 7 (8

TABLE 6. Mean (±SD) and range of selected external and cranial measurements of adult murid rodents (Muridae) from Camiguin Island, Philippines. Sample size smaller than N is indicated by the number enclosed in parentheses after the range. Measurements taken from sample sizes of 2 and 3 are given as averages and their ranges. All measurements except weight are in millimeters.

Species	Sex	N	Total length	Tail length	Hind foot	Ear	Weight (g)	Basi-occipital length	Inter-orbital width	Zygomatic breadth	Mastoid breadth	Nasal length	Maxillary molari-fom toothrow	Diastema
Apomys camiguensis	M	6	260 ± 4.4	148 ± 7.4	33 ± 1.0	19 ± 0.8	41.1 ± 5.39	29.2 ± 0.48	5.2 ± 0.12	14.9 ± 0.29	12.9 ± 0.20	11.1 ± 0.50	6.0 ± 0.20	7.3 ± 0.26
			254–266	140–160	31–34	17–19	39–48.5	28.6–29.8	5.1–5.4	14.6–15.3 (5)	12.6–13.1 (5)	10.5–11.8	5.8–6.3	6.8–7.5
	F	4	254 ± 6.6	146 ± 4.8	32 ± 1.3	18 ± 2.2	38.5 ± 3.54	28.3	5.2 ± 0.22	14.8 ± 0.43	12.6	11.0 ± 0.58	6.0 ± 0.14	7.1 ± 0.27
			246–262	140–150	31–34	15–20	34–42	27.9–28.7 (3)	4.9–5.4	14.3–15.3	12.2–12.8 (3)	10.3–11.7	5.9–6.2	6.8–7.4
Bullimus gamay	M	1	398	175	54	26	305	47.5	8.2	25.7	19.6	20.3	9.1	13.4
	F	5	372 (3)	154 (3)	49 (3)	25 (3)	334 (3)	48.2 ± 0.81	7.9 ± 0.33	25.8 ± 0.46	18.9 ± 0.60	20.4 ± 0.91	9.0 ± 0.20	14.3 ± 0.69
			358–385	124–180	45–51	23–27	295–360	47.4–49.0	7.4–8.2	25.3–26.3	18.4–19.8	19.4–21.5	8.7–9.1	13.7–15.3
Crunomys melanius	M	1	185	81	24	15	28	31.3	6.3	14.8	12.7	13	4	8.8
Rattus everetti	M	2	462	246	46	24	255	47.5	6.5	24.7	18.6	19.3	9.5	13.1
			456–468	245–248	44–47	24–25	255 (1)	46.8–48.3	6.3–6.7	24.7–24.8	18.7–18.8	19.3 (1)	9.2–9.8	12.8–13.4
			443	434	46 ± 1.9	23 ± 0.9	238	47.1 ± 1.95	7.0 ± 0.20	25.4 ± 1.05	18.7 ± 0.39	18.8 ± 1.79	9.3 ± 0.34	13.5 ± 1.05
	F	5	388–456 (3)	224–252 (3)	44–49	22–24	190–285	45.5–49.9	6.8–7.4	24.3–26.7	18.3–19.2	17.3–21.9	9.0–9.8	12.6–14.9
							(3)	(4)		(4)	(4)			
Rattus exulans	M	5	263	130	27 ± 0.4	18 ± 1.3	69	31.3 ± 0.99	5.1 ± 0.12	16.3	13.6 ± 0.49	11.8 ± 0.52	5.5 ± 0.15	8.6 ± 0.61
			250–277	118–144	26–27	17–20	61–76	29.8–31.8	5.0–5.3	15.7–17.0	12.9–14.0	11.2–12.4	5.3–5.6	7.8–9.3
			(3)	(3)			(3)	(4)	(4)	(2)	(4)	(4)	(4)	(4)
	F	1	—	—	25	17	41	28	4.7	14.4	12.7	10.2	5	7.3
Rattus tanezumi	M	15	349 ± 9.8	182 ± 10.9	34 ± 1.7	21 ± 1.0	—	40.7 ± 1.08	6.5 ± 0.31	21.0 ± 1.01	16.6 ± 0.66	15.7 ± 0.58	7.1 ± 0.22	11.4 ± 0.57
			339–373	162–195	31–36	19–23		39.5–42.6	6.0–6.9	19.3–21.9	15.7–17.8	14.8–16.5	6.7–7.5	10.5–12.1
			(12)	(11)	(12)	(12)		(10)	(10)	(5)	(9)	(10)	(11)	(11)
	F	7	358 ± 19.4	188 ± 12.5	35 ± 1.4	21 ± 1.7	—	40.4 ± 1.24	6.4 ± 0.30	20.7 ± 0.62	16.5 ± 0.45	15.5 ± 1.08	6.8 ± 0.33	11.1 ± 0.40
			324–382	173–205	33–36	18–23		38.1–41.7	5.9–6.8	19.9–21.2	15.9–17.2 (6)	14.0–16.9	6.5–7.2	10.7–11.8
										(4)		(5)	(6)	(6)

FMNH); Site 8 (2 FMNH); Site 11 (4 DMNH); Site 12 (1 DMNH); Site 13 (2 DMNH).

Rattus exulans (Peale, 1848)

Known as the Polynesian rat or the spiny rice-field rat, *R. exulans* is not native to the Philippines; through mostly accidental dispersal by humans, it occurs from Bangladesh to Easter Island and throughout the Philippines, especially as a pest in agricultural areas. On Camiguin, we found this small (60–75 g) rat to be moderately common in heavily disturbed lowland agricultural land at ca. 150 m (Site 3) and in primary montane forest at 1275 m (Site 7) but not at other sites. Records from the 1960s also show it to be present in mossy forest at ca. 1500 m. This distribution is similar to that found on Negros, where it occurs in high-density agricultural areas and in mossy forest at an elevation of 1500–1650 m (Heideman et al., 1987; Heaney et al., 1989). Both Camiguin and Negros have very few native rodents, and this may influence the ability of nonnative species to invade the forest since the nonnatives are absent or very rare in mature forest on species-rich islands such as Leyte, Luzon, and Mindanao (Heaney et al., 1989, 1999, unpubl. data; Rickart et al., 1993).

In March 1995, one nulliparous female weighing 41 g was trapped. Two adult males (71–76 g) with scrotal testes and two young adults (49–61 g) with scrotal testes were trapped at the same time. They typically become reproductive at a young age and have many large litters each year (Barbehenn et al., 1973). Cranial and external measurements (Table 6) are comparable to those of Dinagat, Leyte, and Mindanao (Mt. Kitanglad), but slight variations in most dimensions are discernible (Heaney & Rabor, 1982; Rickart et al., 1993; Heaney et al., unpubl. data).

SPECIMENS EXAMINED—Total 15. Site 3 (2 MSU-IIT); Site 7 (5 FMNH); Site 12 (1 DMNH); Site 13 (7 DMNH).

Rattus tanezumi Temminck, 1844

Previously known in the Philippines as *Rattus rattus* and *Rattus mindanensis*, the Oriental house rat is a widespread nonnative rodent in the Philippines; it occurs from Afghanistan to Indomalaya, New Guinea, and Micronesia (Musser & Carleton, 1993). This 140–200-g rat is most often found as a pest in urban and agricultural areas but can be common in disturbed forest up to 1800 m (Heideman et al., 1987; Heaney et al., 1989, 1991, 1998, unpubl. data; Rickart et al., 1993). On Camiguin, we found *R. tanezumi* to be very abundant in heavily disturbed agricultural land at 150 m (Site 3; Table 1). It was less common in secondary lowland forest at 1000 m and in disturbed lower montane forest at 1000 m (Site 4) and 1200 m (Site 5), and a single individual was trapped in primary mossy forest at 1400 m (Site 6). Four nestling juveniles were found in a new slash-and-burn clearing near Site 7, but no *R. tanezumi* were caught in adjacent mature forest. Taken together with records from the 1960s, these data indicate that *R. tanezumi* occurs from sea level to the highest peaks on Camiguin, although it tends to be most common at lower elevations and in disturbed habitats.

Pregnant females had a mean weight of 126 ± 57.6 g (range = 63–200 g, N = 4). Females with large mammae but not pregnant had a mean weight of 151 ± 16.7 g (range = 130–169 g, N = 9); three of these had placental scars (three, four, and eight scars). Nulliparous females had a mean weight of 93 ± 39.8 g (range = 67–160 g). Males with scrotal testes had a mean weight of 169.4 ± 22.7 g (range = 141–199 g, N = 8); a subadult with scrotal testes weighed 105 g. These data indicate large litter size (up to eight) and very early reproduction, as is typical for the species (Barbehenn et al., 1973). External and cranial measurements (Table 6) are comparable to those of Biliran, Leyte, Maripipi, and Mindanao, with only slight variation.

SPECIMENS EXAMINED—Total 69. Site 3 (21 MSU-IIT); Site 5 (4 MSU-IIT); Site 6 (1 MSU-IIT); Site 7 (4 FMNH); Site 9 (2 DMNH); Site 10 (6 DMNH); Site 11 (3 DMNH); Site 12 (6 DMNH); Site 13 (22 DMNH).

Order Carnivora

Family Viverridae—Civets

Paradoxurus hermaphroditus Jourdan, 1837

The common palm civet occurs from Sri Lanka to Hainan and the Lesser Sunda Islands and is widespread in the Philippines (Heaney et al., 1998). It has been recorded in agricultural and forested areas from sea level up to at least 2400 m (Heaney et al., 1991, 1999, unpubl. data). We did not capture any palm civets, but in March 1995 we were given a mandible from a specimen taken by local hunters in the mountains above Mahinog, thus confirming the earlier report by Gray (1843). A local hunter identified *P. hermaphroditus* from pictures as being common on Camiguin.

Specimens Examined—Total 1. (1 fmnh).

Viverra tangalunga Gray, 1832

The Malay civet (or tangalung) is found from peninsular Malaysia to Sulawesi and is widespread in the Philippines (Heaney et al., 1998). It has been found in primary and secondary lowland, montane, and mossy forest from sea level to at least 1700 m (Rickart et al., 1993; Heaney et al., 1999). We did not obtain any on Camiguin, but a local hunter identified *Viverra tangalunga* from photographs as being present on Camiguin; we tentatively accept this as a valid record.

Order Artiodactyla
Family Suidae—Pigs

Sus philippensis Nehring, 1886

The Philippine warty pig is a Philippine endemic that occurs in the Greater Luzon, Greater Mindanao, and Mindoro faunal regions; its numbers are declining (Oliver, 1992, 1999). It formerly was abundant from sea level to at least 2800 m in all habitats; now it is common only in remote forests (Heaney et al., 1991, 1999, unpubl. data; Oliver, 1992, 1999; Garcia & Deocampo, 1997).

On Camiguin in March 1995, we observed hoof marks of wild pigs from disturbed lowland forest at 1000 m up to primary montane forest at 1275 m elevation (Site 7). Near the sampling site at 1475 m (Site 8), we saw an active pig nest, and scattered pig trails were in clear evidence. A local hunter said that they were commonly hunted and often sold in a small local market at Owakan, Mahinog Municipality, but not in coastal cities. We were given two adult mandibles by hunters from pigs captured in forest in the early 1990s in the mountains above Mahinog.

Specimens Examined—Total 2. Above Mahinog (2 fmnh).

Analysis and Discussion

Adequacy of Sampling: What Is Present and What Is Absent?

Before interpreting field data, it is necessary to evaluate the extent to which they are complete and reliable. In doing so here, we follow the procedures used by Heaney et al. (1989, 1991, 1999) and Rickart et al. (1993).

Fruit Bats—Because pteropodid bats lack sonar systems, they are easily captured in mist nets. The 1960s surveys, which focused on birds, yielded many fruit bat specimens (Heaney, 1984), most of them almost certainly from mist nets. Those efforts obtained six species of fruit bats (Fig. 2). Our netting in 1992–1994 yielded no additional species but was not extensive. We consider it quite possible that some additional species may be present, especially *Eonycteris spelaea* and *Rousettus amplexicaudatus*, since both occur very widely in the Philippines (Heaney et al., 1998), and possibly the large *Acerodon jubatus* and *Pteropus vampyrus*, which fly high above the canopy and so are difficult to capture. However, our sampling was sufficient that we consider it quite unlikely that the species that are abundant and easily captured on Mindanao and associated islands (Heaney et al., 1989, unpubl. data; Rickart et al., 1993) are present on Camiguin, especially *Haplonycteris fischeri* and *Ptenochirus minor* and probably *Megaerops ecaudatus*. Suitable habitat for the high-elevation specialist *Alionycteris paucidentata* is very limited in area on Camiguin, if present at all; although we did limited netting in that habitat, we think it very unlikely that this species is present.

Sampling along the elevation gradient probably has produced a partial picture of variation in species richness (Fig. 2) but as noted may be incomplete because our netting in 1992–1995 was not extensive (Table 3).

Insectivorous Bats—Insectivorous bats use sophisticated sonar systems to navigate. They are thus difficult to capture in mist nets, which were our only means of capturing them; further, our mist-netting efforts in 1992–1995 were limited in extent (see Heaney & Tabaranza, 2006a; Table 3). For this reason, we believe that our sample of six species is likely to be quite incomplete and is not usable for estimates of species richness, as is often the case (Heaney et al., 2002). Our data contribute, however, to general knowledge of the natural history of these poorly known animals.

Nonvolant Small Mammals—Shrews, rodents, and other small mammals that can be captured in traps were poorly sampled by the 1960s field teams, which focused their efforts on birds (and secondarily on fruit bats). During 1994 and 1995, we accumulated 2783 trap-nights at six sites that included all major habitat types on the island, yielding 188 captures (Table 1). A species-accumulation curve for these data (Fig. 3) shows that the number of species recorded for

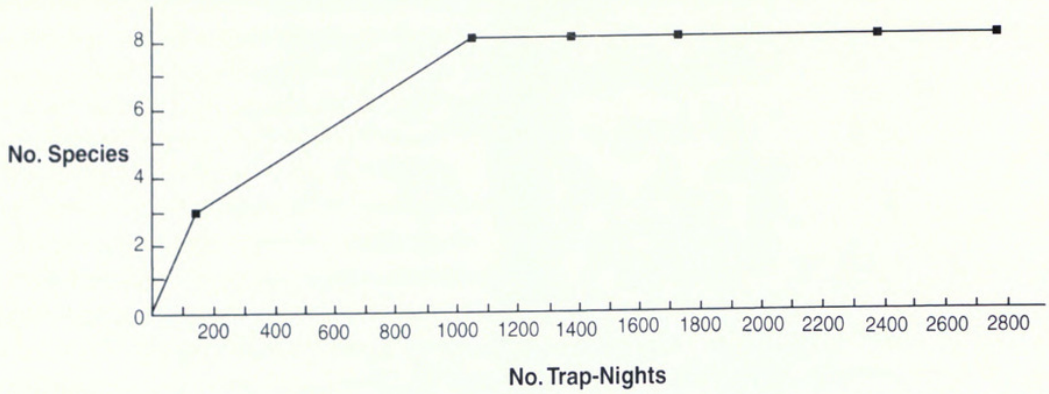

FIG. 3. Species accumulation curve for nonvolant small mammals on Camiguin Island. The points shown are for Sites 1 and 3 to 6, as described in the text.

the island reached a peak of eight species (including five nonnative species) by the end of sampling at the second site (1055 trap-nights) and showed no further gain as we approached the total of nearly 2800 trap-nights. Local hunters either were unfamiliar with squirrels or knew them from Mindanao; given their conspicuousness (Heaney et al., unpubl. data), they are very unlikely to be present. We conclude that the island is unlikely to support other species of small mammals that are present on Mindanao, including gymnures (*Podogymnura*), tree shrews (*Urogale*), squirrels, or murid rodents (e.g., *Batomys*, *Limnomys*, and *Tarsomys*). Further, the sampling along the elevational gradients was sufficiently intense that we are likely to have an accurate assessment of the pattern of species richness above about 800 m, although it must be noted that extensive habitat destruction at lower elevations may have had an extensive impact on the current patterns (discussed below).

MEDIUM AND LARGE MAMMALS—We collected information only on the presence and absence of large mammals and a mixed set of medium-sized species (none of which are readily captured in traps such as the ones we used), not on detailed habitat use. We observed carefully during all our time in the field for any evidence of additional species, and we interviewed many residents of the islands and showed them photos of potential species; some of these residents are active hunters. Neither we nor our informants had any evidence for tarsiers, flying lemurs, or deer on the island, though many people knew of deer and tarsiers on Mindanao, and a few knew of flying squirrels and flying lemurs. We consider it unlikely that species other than those listed here are present given the voucher specimens we obtained and the concordance between our specimens and the information received from local hunters. Thus, we conclude that deer are absent, along with the smaller but conspicuous species such as tarsiers, squirrels, and flying lemurs.

Elevational Patterns

Though our limited netting prevents us from commenting on the patterns of diversity and abundance of bats along the elevational gradient on Camiguin, our trapping data (Table 1) provide a reasonably complete picture of the general patterns among nonvolant species. The highest density we encountered was at Site 3, in agricultural land at ca. 150 m. However, these were all nonnative rats and a shrew, representing only three species, a pattern that we have often seen (e.g., Heaney et al., 1989; Rickart et al., 1991). The five native small mammal species were all present (or suspect to be present) from 1000 to 1300 m and declined in species richness to two species near the peak of Mt. Timpoong at Site 8 (Table 1). Density (measured as the number captured per 100 trap-nights) more than doubled from 1000 to 1275 m, then fell to a much lower level near the peak at 1475 m. However, much of the change in density was driven by the remarkably large numbers of *Suncus murinus* at the upper elevations; they were not taken at 1000 or 1200 m (though they were taken at 150 m), were fairly common at 1300 and 1475 m, and were exceptionally abundant at 1275 m, where we often saw and heard them during the day. These patterns for species richness, though limited in extent, are similar to those from elsewhere in the Philippines, where species richness is generally low at low elevations, increases to about the area of transition from montane to mossy forest, and declines with increasing elevation in mossy forest (Rickart et al., 1991; Heaney, 2001). The pattern of overall abundance is also similar to that documented elsewhere, except that *Suncus murinus* is remarkably abundant in the high-elevation montane and mossy forest, where usually it is absent (Heaney, 2001). We have previously noted the abundance of *S. murinus* in similar habitat only once, on Negros Island (Heaney et al., 1989), which is notably depauperate of small mammals (Heaney, 1986). This raises a question: Is Camiguin depauperate, relative to its area, in comparison to other islands in the Philippines? This question is addressed in the next section.

Biogeographic Implications

BATS—Because our focus in conducting field studies concentrated primarily on nonvolant mammals, we note only that we are confident that the fruit bat community on Camiguin is at least somewhat depauperate relative to similar elevations on Mindanao and associated islands. At least two species usually common at lower and middle elevations, *Haplonycteris fischeri* and *Ptenochirus minor*, are almost certainly absent. Both of these are primarily associated with old-growth rain forest and generally do not travel long distances out from under the canopy of forest (Heaney et al., 1989, 1998; Heideman & Heaney, 1989; Rickart et al., 1993). Some additional species probably also are absent (*Alionycteris paucidentata* and *Megaerops wetmorei*); they also are associated with old-growth rain forest, though *A. paucidentata* in a distinctive high-elevation habitat (*M. wetmorei* is poorly known). This level of reduction in species richness is striking in view of the tight correlation between species richness and island area previously found (Heaney, 1991a). However, the uncertainty regarding the potential absence of *Eonycteris* and *Rousettus* leads us to be cautious in defining the extent to which species richness is low.

NONVOLANT MAMMALS—The data are more certain regarding both small mammals (shrews and murid rodents) and the medium and larger mammals (deer, squirrels, and so on). It seems certain that many genera present in the lowlands and in montane habitats on Mindanao and associated islands are absent: tree shrews (*Urogale*), flying lemurs (*Cynocephalus*), tarsiers (*Tarsius*), tree squirrels (*Sundasciurus*), pygmy squirrels (*Exilisciurus*), flying squirrels (*Petinomys*), a murid (*Tarsomys echinatus*), and deer (*Cervus*). Among the murid rodents, *Batomys* is also absent though often found in montane forest on Mindanao and associated islands (Rickart et al., 1993). *Limnomys bryophilus*, *L. sibuanus*, and *Tarsomys apoensis* also occur on Mindanao but only above about 1900 m elevation (Musser & Heaney, 1992; Heaney et al., 1998; Rickart et al., 2003).

Those species of nonvolant mammals that are present on Camiguin form a group that is quite consistent in one respect. Not all lowland species from Mindanao are present, but all those that are present on Camiguin are among the relatively few species that are common in the lowlands of Mindanao—or were present before human destruction of lowland rain forests. As shown by Musser and Heaney (1992), Heaney (2001), and Heaney et al. (unpubl. data), *Crocidura*, *Apomys*, *Bullimus*, *Crunomys*, *Rattus everetti*, *Paradoxurus*, *Viverra*, and *Sus* are among the few mammals that occur (or occurred until recently) on Mindanao in lowland forest. With only one exception (*Tarsomys echinatus*), all those lowland species of Mindanao noted above as being absent from Camiguin are arboreal species. In other words, the nonvolant mammal fauna of Camiguin is composed only of nonarboreal small mammals from Mindanao (or are their sister taxa) and all the lowland larger mammals (all of which are also not arboreal). We conclude that the mammalian fauna of Camiguin is highly biased; that is, it is composed entirely of species shared with and/or derived from Mindanao, but it is not a random sample of the Mindanao fauna; rather, it is comprised of species that occur (or occurred before deforestation) on the lowland forest floor of Mindanao, not in the forest canopy and not in the montane or mossy forest.

Does the absence of arboreal mammals mean that Camiguin has a species-poor nonvolant mammal fauna relative to other islands in the Philippines? Perhaps surprisingly, the answer is clearly no. With nine native nonvolant mammals, Camiguin falls almost precisely on the same species-area curve as the islands that made up Greater Mindanao (Mindanao, Leyte, Bohol, Biliran, and Maripipi). While the fauna is biased toward lowland, ground-living murid rodents, and small omnivorous carnivores, the species richness is not reduced relative to islands that were recently connected to Mindanao itself (Heaney, 1986; Rickart et al., 1993). However, the nonvolant small mammal community is apparently sufficiently species-poor to allow a nonnative shrew (*Suncus murinus*) to invade primary montane forest. The presence of this shrew in similar habitat has been noted on Negros Island, which is also species poor (Heaney et al., 1989), but not on other islands in the Philippines (e.g., Rickart et al., 1991, 1993). We predict that *S. murinus* will be found in primary montane forest on other islands in the Philippines with five or fewer native shrews and rodents.

Conservation and Management

As noted by Heaney and Tabaranza (1997, 2006a), the native mammal fauna of Camiguin is dependent on the continued survival of good-quality forest at all elevations. The two mammal species unique to Camiguin, in particular, apparently depend on forest with little or no disturbance, most of which currently occurs in steep areas above 800 m elevation. These forested areas are also crucial to the well-being and stability of the human population, for they are the source of water for the island and protect the lowlands from potentially devastating floods and landslides. Additionally, our observations indicate that the medium and large mammals have been depleted by overhunting; these require protection if they are to survive. The people of Camiguin benefit both personally and economically from the beautiful landscape and seashores of the island, both through the tourism they make possible and from the environmental stability they engender. Protecting the forests will benefit the people and wildlife equally.

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