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## AUTECOLOGY AND THE CONSERVATION OF INSECTIVOROUS BATS ON MT. MAKILING, PHILIPPINES

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### ABSTRACT

*The diversity and community ecology of an insectivorous bat community on Mount Makiling, Philippines was studied over the course of 17 months between June 1997 and August 1999. Bats were inventoried acoustically using a library of call signatures, through roost searches, and captured using mist nets, a harp trap, and a tunnel trap. Foraging behavior with respect to habitat type and resource abundance was determined through both systematic sampling of acoustic bat activity and insect abundance along transects, and at resource patches (stream pools) during explicit time intervals in the night. This paper provides a summary of the salient information on habitat use, diet, foraging mode, reproductive timing, and roosting preferences gleaned from these data with respect to 22 species of insectivorous bats encountered on Mount Makiling. Additionally, I consider how coexistence mechanisms which maintain local bat diversity, such as habitat selection and the partitioning of resource abundance, may break down in the face of habitat disturbance and loss.*

### Introduction

Insectivorous bats represent the most poorly known, and possibly most threatened, group of mammals in the Philippines (Heaney et al. 1998, Heaney and Regalado 1998). A combination of agility, slow and maneuverable flight, and use of echolocation have allowed insectivorous bats to evade the mist nets of field researchers for decades. Nevertheless, 43 species have been documented, 10 of which are endemic to the archipelago (Ingle

and Heaney 1992, Heaney et al. 1998). However, new endemic species of murids and pteropodids—two groups for which sampling has been relatively intensive—continue to be described today (Heaney et al. 1998, Gonzales and Kennedy 1996), suggesting that this may be only the tip of the iceberg. Use of novel capture devices such as harp traps, and the acoustic monitoring of species-specific echolocation calls have been successful in documenting the diversity and ecology of similar species in Malaysia (Francis 1989; Kingston et al. 1997, 1999, 2000), Papua New Guinea (Bonaccorso 1998) and Australia (Law et al. 1999). New inventory protocols incorporating these and other methods will help fill this gap in the Philippines.

With respect to ecological information, however, Microchiropterans are not far behind other mammal groups. Fruit bats are by far the most studied mammals in the Philippines. Intensive research has been conducted on their foraging ecology (Utzurum 1995), microhabitat use (Ingle 1993), population biology (Heideman and Heaney 1989), reproductive ecology (Heideman 1989, Heideman et al. 1993), and most recently their role in forest regeneration on the forest edge (Ingle unpub. dissertation). The population ecology of murid rodents, in contrast to our relatively extensive knowledge of their distribution and taxonomy (e.g. Musser 1981, Musser and Heaney 1992, Heaney and Rickart 1990), is known from only one intensive study on Mt. Isarog (Balet and Heaney 1997). Until now, no intensive study had been conducted on insectivorous bat ecology in the Philippines. Knowledge of the basic ecological requirements of species is becoming increasingly important as the focus of conservation strategies in the Philippines expands from delineating protected areas to monitoring the animals within them (Danielson et al. 2000). Research which yields complete site inventories of insectivorous bats and ecological data useful in monitoring and conservation planning is needed.

This study represents a step towards this goal. The objectives of this paper are to i) augment the preliminary data of Ingle

(1992) on the diversity and natural history of insectivorous bats on Mount Makiling, ii) summarize some of the first detailed information available on their foraging and roosting behavior, and iii) discuss the implications of these data for the conservation, management, and monitoring of Philippine insectivorous bat communities.

## Methods

Between June and August 1997, and again between June 1998 and August 1999, I studied the diversity and ecology of insectivorous bats on Mount Makiling, Laguna Province, Philippines (Sedlock in press). Mt. Makiling is volcanic in origin and reaches approximately 1115 m at its highest peak. The forest reserve covers approximately 42.44 km<sup>2</sup>, but only about 25 km<sup>2</sup> is covered in either natural forest or plantation forest (Cruz et al. 1991). Mount Makiling is typical among Protected Areas in the Philippines in that it is comprised partly of secondary rather than primary lowland rain forest; also, the forest lies at high elevations on a volcanic mountain surrounded by a mixture of agricultural forest, grasslands, and other crop lands. Mt. Makiling is mildly seasonal, with a dry period between January and April (Pancho 1983). The average daily temperature and humidity during the 14 months of this study (measured at the base of the mountain) was 27.7 °C and 83.7%, respectively. The average annual rainfall, also measured at the base of the mountain, is 1990 mm. During my field season, the majority of rain fell between the months of June and November, with several typhoons hitting the study site in September/October 1998 and July 1999.

I collected data using a variety of methods, including i) random captures using mist nets, a harp trap, and tunnel trap (Sedlock in press); ii) systematic sampling with a bat detector of acoustic activity along transects in forest, agro-forest, and along a creek (Sedlock 2001); iii) systematic sampling of

acoustic activity at insect patches such as stream pools and streetlights (Sedlock 2001); iv) random acoustic sampling; and, v) roost searches by random inspection of rock crevices, tree hollows and caves; tracking bat flight patterns and interviews with local residents, hunters, and gatherers. Voucher specimens were deposited at The Field Museum of Natural History, Chicago.

## Results and Discussion

### *Species accounts*

We captured and/or acoustically encountered 22 species of insectivorous bats on Mount Makiling. Table 1 includes all captured species, and provides the range and sample sizes for standard measurements useful in species identification. Each species account contains two sections. In the first, I address species' habitat preference and foraging behavior gleaned either from netting and trapping data, acoustic monitoring along habitat transects, and fecal analysis. In the second, I characterize any day-roosts we encountered, and compare these to previous roosting data reported in the Philippines as well as other portions of its range. Reproductive data are provided throughout each account with respect to individuals captured within their foraging habitat or at day roosts.

### *Emballonura alecto* (Eydoux & Gervais)

*Emballonura alecto* occurs throughout the Philippine archipelago (Heaney et al. 1998), and in Borneo and Sulawesi (Corbet and Hill 1992). As this species is rarely captured in mist nets, little is known of its foraging behavior and habitat use. On Mount Makiling, the virtual absence of acoustic encounters along forest and creek transects, although this species possesses a detectable and distinct call (Sedlock 2001), suggests that it forages above the forest canopy. However, it

should be capable of foraging within the forest vegetation, as its wing morphology indicates relatively slow, maneuverable flight (Sedlock 2001). Similarly sized species of the genus *Emballonura* in Papua New Guinea forage by hawking and gleaning insects within the understory or tree fall gaps (Bonaccorso 1998).

I encountered two rockfall roosts along forested creeks occupied by *Emballonura alecto* on Mount Makiling. The smaller roost housed only 10-15 bats. The larger of the two (approximately 5 m long, 3.5 m high, and 3 m wide) contained more than 100 bats. In response to disturbance, all of the bats burst out of the roost and circled high in the forest subcanopy at mid-day. After about 15 minutes, most of the bats entered another rock-fall cave less than 50 m away from the original roost. These roosts are similar to those previously reported on Makiling (Ingle 1992), and at other sites in the Philippines (Rickart et al. 1993; Heaney et al. 1991, 1999). Generally, they seem to prefer dimly-lit caverns which afford them a wider range of roosting opportunities than many cave-roosting species. In the Philippines they have been found primarily in rock crevices, rock falls, and at the entrance of larger caves. In Borneo small groups have also been found under the buttresses of fallen tree trunks (Payne et al. 1985).

On Mount Makiling, we captured one lactating female in early August. Ingle (1992) captured six pregnant females in the same roost in April of 1989, and a lactating female in June of the same year. Similar reproductive timing was documented on Leyte and Maripipi Islands, with pregnant females caught during March and April and lactating and juveniles encountered during July (Rickart et al. 1993).

### *Megaderma spasma* (Linnaeus)

*Megaderma spasma* is the only representative of the family Megadermatidae in the Philippines, but it is widespread throughout the archipelago with the exception of the Batanes/

Babuyan region (Heaney et al. 1998). On Mount Makiling, we netted two adult males in secondary lowland forest on 16 June 1997. The bats seemed to be foraging together as they hit the mist net simultaneously. *Megaderma spasma* uses prey-generated cues, rather than echolocation, while foraging (Tyrell 1988). As such, I could not monitor its foraging activity acoustically. However, previous capture records of *Megaderma spasma* are mostly from lightly disturbed and primary lowland forests, and montane forests (Heaney et al. 1991, Ingle 1992, Lepiten 1997, Rickart et al. 1993, Heaney et al. 1999). It possesses short, broad wings affording it slow, maneuverable flight in spite of its large size (Table 1) allowing it to forage effectively in the relatively dense forest understory. On Mount Makiling, *Megaderma spasma* primarily consumes noise-producing prey, such as gryllid, tettigonid orthopterans, and cicadid homopterans (Balete 1988).

We located one *Megaderma spasma* roost in a large tree hollow beside a road in secondary forest (350 m). On 12 June 1998, six bats occupied the roost, and on 15 August 1998 the tree housed eight bats. The entrance opened at the base of the tree, and was approximately 0.7 m high and 0.6 m wide. The ceiling of the hollow rose 4 m off the ground. Balete (1998) monitored two groups of *Megaderma spasma* on Mount Makiling; one in a tree hollow ( $n = 4 - 7$ ), and another in a small cave ( $n = 5$ ). Ingle (1992) located six additional tree hollow roosts containing one to seven bats on Makiling, all with openings at ground-level or 1.5 m high.

### *Hipposideros ater* (Templeton)

Though wide-spread throughout the Philippines and Southeast Asia (Heaney et al., 1998; Koopman, 1989), little is known of *Hipposideros ater*'s habitat preferences since it has only been collected from cave roosts (Rickart et al. 1993, Heaney et al. 1991). On Makiling, a harp trap captured five individuals foraging low along a forest trail at the forest edge,

and a tunnel trap captured two *H. ater* foraging over a small forest stream (Sedlock 2001). *Hipposideros ater* possesses low intensity, high frequency calls (132 kHz), which are difficult to detect with a bat detector at a distance (Sedlock 2001). Nevertheless, I acoustically detected and visually observed several individuals circling low over grasses in the agro-forest at the forest edge together with *H. obscurus* and *R. virgo*. From these modest data, it is not possible to assess the effect of habitat disturbance on individual foraging behavior or subsequently, the population's status. I suspect that given its slow, maneuverable, continuous flight and preference for moths (Sedlock 2001, Bonaccorso 1998, Pavey and Burwell 2000), *H. ater* would be reliant on the forest to some degree. Individuals identified as *H. ater* in Australia have been classified as forest specialists, as they seem to avoid forest gaps (Crome and Richards 1988).

Two identical man-made tunnels perched high on a limestone wall served as roosts for more than 500 *Hipposideros ater* individuals on Mount Makiling. Each tunnel extended approximately 20 m straight into the mountain. Two-thirds of the way in, two chambers (6 m long) opened on either side, such that the floor plan resembled a cross. The ceiling was only 0.7 meters high and just as wide, forcing one to crawl when entering the cave. We made two visits, once on 19 March 1999 and again on 21 June 1999. In March, we captured four adult males, five pregnant and three non-pregnant, adult females from the cave. In June, we encountered only juveniles ( $n = 10$ ) and lactating females ( $n = 10$ ). When we entered the cave, we found solitary juveniles and groups of nursing mothers down each of the "arms" of the tunnel. *Hipposideros ater* shared the cave with a much smaller number of *Rhinolophus macrotis* individuals (approx. 30) which occupied the deepest part of the tunnel. Heaney et al. (1991) found a smaller *H. ater* colony (30-40) in a slightly larger cave on Catanduanes Island, and Rickart et al. (1993)

found a small group in a smaller rockfall shelter on Maripipi Island, Philippines (Rickart et al. 1993). Moderately sized colonies utilizing dark caves have been reported across its range (Bonaccorso 1998, Flannery 1995, Kitchener et al. 1990, Payne et al. 1985). Additionally, Bonaccorso (1998) reported on solitary individuals and small groups roosting in hollow trees and the undersides of large boulders.

***Hipposideros diadema*** (É. Geoffroy)

*Hipposideros diadema* is the largest insectivorous bat in the Philippines, and appears to be flexible in its habitat use and foraging mode. It ranges from Burma to the Solomon Islands, and throughout the Philippines (Heaney et al. 1998). On Makiling, *H. diadema* biased its activity towards riparian and agro-forest habitats, although it utilized the forest as well. Most authors have identified *H. diadema* exclusively as a perch-hunter, sallying off a perch to capture passing insect prey (Brown and Berry 1983, Bonaccorso 1998, Flannery 1995, Pavey and Burwell 2000). On Mount Makiling, *H. diadema* utilizes this energy-efficient foraging mode later in the night when insect abundance declines, but also hawks for insects in the open air (Sedlock 2001). At dusk, when insect abundance is highest, we observed aggregations of individuals (2-10 individuals) foraging just over the agro-forest canopy and high above the canopy in the open air. Switching foraging modes in response to resource availability and structural contexts (aerial hawking may not be fruitful among vegetation due to high wing loading) affords *H. diadema* a broad range of habitats and resource abundances on which it can forage profitably. Its diet of large Hemiptera and Coleoptera (Sedlock 2001) accords with diets of individuals in Australia (Pavey and Burwell 1997) and Papua New Guinea (Bonaccorso 1998). Additionally, the diet of Makiling bats includes swarming insects such as termites and winged ants, resulting from the exploitation of rich insect patches early in the night

(Sedlock 2001).

We did not locate any roosts used by *H. diadema* on Makiling, although we did capture several individuals commuting along a wide trail just below a large rock outcrop where we discovered a cave housing three species of *Rhinolophus* (see *Rhinolophus arcuatus* account). It is possible that another cave is in the vicinity, or that it occupies the same cave but utilizes a different (larger) exit. Nevertheless, large maternity colonies of *Hipposideros diadema* in caves are well documented in the Philippines and across its range (Rabor 1986, Bonaccorso 1998). We captured two pregnant and one lactating female, and one juvenile on 15 and 20 July 1999. On Leyte, Rickart et al. (1993) caught a pregnant female on 28 March, and on Siquijor Island, Lepiten (1995) caught a pregnant female in April.

*Hipposideros diadema* uses a short (15-20 milliseconds), constant frequency (68 kHz) call with a prominent FM terminal sweep. The only species with a call of similar frequency is *Rhinolophus arcuatus*; however, it can be distinguished from *H. diadema* based on its comparatively long duration (80 ms) and short FM sweep at both the start and end of the pulse (Sedlock 2001).

***Hipposideros obscurus*** (Peters)

*Hipposideros obscurus* is a Philippine endemic, but wide-spread and common throughout the archipelago (Heaney et al. 1998). We acoustically detected this species foraging in the forest understory, over forest streams, as well as on the forest edge in an agro-forest. Ingle (1992) caught two individuals on Makiling in secondary forest. At other sites, it has also been captured in both disturbed and primary lowland forest, from 250 to 740 m (Heaney et al. 1991, 1999; Rickart et al. 1993; Lepiten 1995). It seems to forage exclusively in continuous flight, in contrast to similarly sized rhinolophids (e.g. *Rhinolophus arcuatus*) which switch between "fly-

catching" and aerial hawking (Sedlock 2001). *Hipposideros obscurus*' diet consists of a broad range of insects (n = 4 four individual samples), including scarab beetles, click beetles, moths, termites, ants, lygaeid bugs, and flies (Sedlock 2001).

Unlike *Hipposideros ater* and *H. diadema*, *H. obscurus* does not appear to form large colonies, or at least none has been found. On 20 June 1998 and again in August, we found groups of two and five individuals roosting in two separate culverts under an old logging road in second-growth lowland forest. We observed their emergence on one night. The bats emerged just after dark (around 1820 h), and then over the next two hours, flew in and out of the roost, and by 2100 h all bats had returned. In February, we found two individuals roosting in a small (.4 x .5 m), dark compartment in the back of a larger, shallow cave (approximately 6 m deep, 10 m wide and 1.4 m high). One was an adult male, and the other evaded capture. We captured two lactating females over Pili Creek on 15 August 1998, and another on 15 July 1999. An adult female captured in February 1999 was neither pregnant nor lactating. Ingle (1992) captured juveniles on Makiling in July 1989.

*Hipposideros obscurus* uses a short duration (9 milliseconds), high frequency (116 kHz) call. It is easily distinguished from other bat calls on Mount Makiling, but difficult to detect from a distance due to high attenuation rates (Sedlock 2001).

#### *Rhinolophus arcuatus* (Peters)

*Rhinolophus arcuatus* has been captured throughout the archipelago (Heaney et al. 1998), and seems more common in the Philippines than in other parts of its range (Bonaccorso 1998, Payne 1985). On Mount Makiling, *R. arcuatus* biases its foraging activity towards the forest, but also exploits adjacent agricultural habitats (Sedlock 2001). We rarely encountered it foraging in riparian habitats. At other sites in

the Philippines it has also been captured in disturbed forest, but more frequently in primary lowland and montane forest up to 1350 m (Heaney et al. 1991, Rickart et al. 1993). It forages throughout the night among moderately cluttered understory vegetation. *Rhinolophus arcuatus* uses both aerial hawking and "fly-catching" foraging modes, but is less likely to be encountered perch-hunting than the larger *R. inops*. It is also less likely to use the same foraging perch on subsequent nights than *R. inops* (Sedlock 2001). Its diet consists primarily of small scarab beetles and moths, but also termites, ants, leafhoppers, lygaeid bugs, and flies (Sedlock 2001).

In June 1998, we found a large maternity colony of *Rhinolophus arcuatus*, *R. inops* and *R. virgo* at 675 m in natural second-growth lowland forest on Mount Makiling. We found the cave after capturing > 100 bats in mist nets set across a ravine approximately 300 m below the roost in July 1997. Unfortunately, we could not inspect the inside cavern as the openings stood 4 m off the ground and the rocks proved unstable. The main exit was < 1 m high and wide, and the secondary opening, approximately half the size of the first, served mainly as an entrance. Bamboo and vines created a dense, concealing matrix in front of the roost, which all three species expertly negotiated in fast flight. The first bat (*R. virgo*) emerged at 1805 h, and the emergence continued until 2004 h. We did not attempt to formally estimate the population size, but it seemed that more than 5,000 bats occupied the cave. We recorded the emergence using an Anabat II bat detector on two nights. *Rhinolophus arcuatus* emerged first, accompanied by occasional bursts of *R. virgo*. By 1823 h, a continuous stream of *R. arcuatus* and *R. inops* emerged from the largest exit. Between 1843 h - 1900 h, both species continued to emerge, but only intermittently. At 1906 h, *R. inops* began to increase in number, until it was the most common bat emerging at 1945 h. At 2011 h the first bat returned to the roost.

We captured bats exiting the roost on 5 August 1997, 29 June 1998 and again on 28 June 1999. During June we caught 22 *R. arcuatus*. Of the 16 adult females, 10 were pregnant, four were lactating and two were neither pregnant nor lactating. The remaining six of 22 were juveniles caught emerging from the roost much later than the females (0145 h).

*Rhinolophus arcuatus* uses a long (80 ms) constant frequency call at 71 kHz that is intense and easily detected with a bat detector at a distance (> 10 m). Juveniles may use a slightly lower frequency than adults (68 kHz), which overlaps with the CF of *Hipposideros diadema*. However, *H. diadema*'s call has a shorter in duration (15 ms) and has only a terminal FM sweep (Sedlock 2001).

#### *Rhinolophus inops* (K. Andersen)

*Rhinolophus inops* is an endemic, wide-spread species in the Philippines (Heaney et al. 1998). On Mount Makiling, we frequently encountered *Rhinolophus inops* acoustically in the lowland forest and adjacent agro-forest, but rarely in riparian habitats. These data contrast with netting records in which *R. inops* was not common in secondary, disturbed forest (Heaney et al. 1998, Rickart et al. 1993). However, it is unclear how far from the edge of intact forests it will forage. *Rhinolophus inops* possesses high wing loading, making it a fast flier. This, along with the high transport costs associated with large body size and short, broad wings, makes "fly-catching" an effective foraging strategy. *Rhinolophus inops* prefers perch hunting, and does not switch foraging strategies in response to changing resource abundances as *H. diadema* does (Sedlock 2001). The same hunting perches may be used repeatedly over 2-5 nights; however, we could not verify that it was the same bat on the perch each night. Moreover, *R. inops* prefers perching sites above the understory in less cluttered sites than the smaller *R. arcuatus* (Sedlock 2001).

Its diet consists primarily of beetles, but also moths, termites, ants, lygaeid bugs, and flies (n=12 individuals). *Rhinolophus inops* consumes significantly more beetles than the smaller *R. arcuatus* (Sedlock 2001).

*Rhinolophus inops* shared the large roost previously described (see *Rhinolophus arcuatus* account) with *Rhinolophus arcuatus* and *Rhinolophus virgo*. On 29 June 1998, it began emerging from the roost after *R. arcuatus* (1824 h), and continued to exit until 1945 h. During two separate visits in June, we caught nine pregnant females, two lactating, and one juvenile. The juvenile emerged from the roost much later (2314 h) than the majority of adults. In August 1997, we caught three adult males, two females neither pregnant nor lactating, one lactating female, and four juveniles. Rickart et al. (1993) caught pregnant females in March and April on Leyte, and Ingle (1992) captured 13 lactating females on Mount Makiling near their maternity roost in July 1989.

*Rhinolophus inops* uses a long duration (80 ms) CF call between 54-56 kHz. *Rhinolophus macrotis* possesses a CF call of similar frequency (51-53 kHz), but does not overlap with that of *R. inops* (Sedlock 2001).

#### *Rhinolophus macrotis* (Blyth)

*Rhinolophus macrotis* is not currently recognized as an endemic species. Philippine individuals, however, are distinct from those on mainland China and Malaysia (Ingle and Heaney 1992, Heaney et al. 1998). Extremely elusive and difficult to capture, *R. macrotis* remains poorly known. Mist nets, a harp trap, and the tunnel trap all failed to capture it. Nevertheless, the paucity of acoustic encounters with *R. macrotis* (n = 64) relative to *R. arcuatus* (n = 318) and *R. inops* (n = 132) on Mount Makiling—despite its intense, easily distinguished call—suggests that it may be less abundant (Sedlock 2001). Alternatively, this inequity in encounter frequencies could indicate a difference in foraging mode. Its large ears may

permit passive listening to locate prey; the less frequently *R. macrotis* uses echolocation, the less probable it is to be detected. We did observe it flying slowly in circles close to the forest floor on two occasions, but never witnessed it in the act of gleaning insects. *Rhinolophus macrotis* allocated its foraging effort among habitats in a similar manner to other *Rhinolophus* species. It allocated its activity equally between the lowland forest (total passes = 31) and agro-forest (total passes = 27), but rarely foraged over the creek (total passes = 6). Only four of 64 total encounters represented perched bats.

We found *Rhinolophus macrotis* roosting together with *Hipposideros ater* in two man-made tunnels (see *H. ater* account for description). *Rhinolophus macrotis* represented a small proportion of the bats in each roost (< 10%). They segregated themselves from *H. ater*, and occupied the deepest part of the tunnel. On 21 June 1999, we caught nine individuals exiting the roost, eight adult males and one pregnant female.

### *Rhinolophus rufus* (Eyedoux and Gervais)

*Rhinolophus rufus* is endemic to the Philippines, and remains poorly known (Heaney et al. 1998). We did not capture *R. rufus*; however, Ingle (1992) captured one individual on Mount Makiling in 1989. *Rhinolophus rufus* possibly uses a lower call frequency than the other *Rhinolophus* species, since it is much larger (Bogdanowicz et al. 1999). I recorded two unidentified rhinolophid-like calls (i.e. constant frequency, long duration), one at 31 kHz and another at 45 kHz, either of which could belong to *Rhinolophus rufus*. Only five 31 kHz call passes were recorded, two in second-growth lowland forest (450 m), one in an agro-forest (50 m), and one along a forested stream (375 m). I recorded the two 45 kHz passes in an agro-forest (50 m) near the forest edge. Therefore, if either of these calls do indeed belong to *R. rufus*, it is rare. These are high intensity, low frequency calls which travel with minimal attenuation. Therefore, encounter biases resulting

from call detection cannot account for these low pass frequencies. *Rhinolophus rufus* is thought to roost in caves, although Heaney et al. (1991) observed several individuals perched in a shallow rock overhang on Catanduanes Island. Also, there have been accounts of colonies in a large cave in southeastern Luzon (P. Alviola, personal comm.). Further studies on its foraging behavior and population biology are needed.

### *Rhinolophus virgo* (K. Andersen)

*Rhinolophus virgo* is endemic to the Philippines and thought to be widespread throughout the archipelago (Heaney et al. 1998). On Mount Makiling, it actively foraged in lightly disturbed lowland rain forest and the adjacent agro-forest (Sedlock 2001). The majority of foraging activity in the agro-forest occurred at the forest edge early in the evening, so it may be more sensitive to forest disturbance than the activity data indicate. The absence of *R. virgo* at the more disturbed sampling site (50-200 m) further suggests a strong affinity for intact forest. We observed it foraging in small groups of 2 - 3 individuals in the forest understory, circling for several minutes in one area before moving on. Also, we frequently observed it foraging in groups with *Hipposideros ater* and *H. obscurus* in the agro-forest at the forest edge (400 m) before dark. Only one of 86 *R. virgo* passes represented a perched bat. Therefore, it appears that *R. virgo* hunts primarily by continuous aerial hawking. The low frequency of encounters (total passes = 86) relative to *R. arcuatus* (total passes = 318) and *R. inops* (total passes = 132) may be a result of detection biases rather than lower abundances. *Rhinolophus virgo* uses a high frequency call (85 kHz), which attenuates much more quickly than those emitted by other *Rhinolophus* species.

On Mount Makiling we found *Rhinolophus virgo* roosting in a variety of locations. The largest group of individuals occupied the roost described earlier (see



*Rhinolophus arcuatus* account) along with *R. arcuatus* and *R. inops*. *Rhinolophus virgo* represented a small proportion of the roost inhabitants (< 5%). Nevertheless, it appeared that at least 100 individuals emerged from the roost intermittently between 1804 h and 1940 h on 28 June 1998. On the same night, we captured six pregnant females, three lactating, and one neither pregnant nor lactating. We captured no males. On 5 August 1997, we caught three individuals about 250 m from the roost, one pregnant female, one female neither pregnant nor lactating, and an adult male. Culverts under an old logging road through second-growth forest served as day roosts for many *R. virgo*. *Hipposideros obscurus* also used these culverts as roosts, but never shared culverts with *R. virgo*. Generally, we encountered one to six individuals occupying a single culvert. On 21 January 1999, three of the seven available culverts were occupied by single males. Five days later, we captured all six bats occupying one culvert roost. It appeared to be a harem, consisting of one adult male and five adult females. The male was slightly smaller and used a lower call frequency (83 kHz) than the females (86-87 kHz), although generally males and females did not differ in size (forearm lengths;  $F_{1,31} = 0.047$ ,  $P = 0.83$ ). Nevertheless, sexually dimorphic calls may serve a social function in mating and foraging. Individuals seem to move between culverts. An adult male I marked on 12 June 1998 was re-captured in a different culvert on 16 June 1998. We found a single bat perched in a rockfall cavern near Dampalit Creek (460 m), an individual perched on the underside of a large boulder near the large rhinolophid roost, and a bat perched in the hollowed buttressed root system of two balete (*Ficus* sp.) trees—one along Pili Creek and the other in second growth forest about 250 m from Pili Creek

#### *Kerivoula whiteheadii* (Thomas)

*Kerivoula whiteheadii* ranges from southern Thailand,

through Borneo and the Philippines (Heaney et al. 1998). All of the species in the Family Kerivoulinae are poorly known in the Philippines. The individual we captured on Mount Makiling represents only the second specimen from Luzon Island; the first was collected in Isabela Province (Heaney et al. 1998). In Peninsular Malaysia and Australia, harp traps have recently added new records (Kingston et al. 1997) and ecological information (Schulz and Wainer 1997, Kingston et al. 1999) on *Kerivoula* species. Species in the family Kerivoulinae use low intensity, high frequency, short duration, broad-band calls (Kingston et al. 1999) rendering them very difficult to detect with a bat detector at even short distances, and highly capable of detecting the fine threads of a mist net. On Mount Makiling, we caught one juvenile male *Kerivoula whiteheadii* with the tunnel trap over a pool of a small stream. Upon entering the tunnel trap, the bat flew very slowly close to the water surface circling around my legs. Despite its slow flight, it managed to evade my sweep net for several minutes before I captured it. In a large enclosure, I observed it hover around the bases of trees and fly slowly close to the ground. When it perched on the enclosure wall made from netting, it did not hang as most other bats did, but curled into a ball with its head upright. *Kerivoula whiteheadii* possesses the lowest aspect ratio and wing loading of all Mount Makiling species, affording it slow and highly maneuverable flight adaptive for foraging among dense clutter. In Australia, *Kerivoula papuensis* forages on sessile prey, primarily spiders (Schulz and Wainer 1997). Therefore, while previous accounts of this species in the Philippines come from disturbed forest and agricultural areas (Sanborn 1952, Heaney et al. 1998), I suspect that *Kerivoula whiteheadii* frequents intact forest. Use of harp traps in the Philippines may greatly and rapidly increase our understanding of this and other *Kerivoula* species.

***Miniopterus australis*** (Tomes)

*Miniopterus australis* is wide-spread, ranging from India to Australia and throughout the Philippines (Heaney et al. 1998, Koopman 1989). We did not capture *M. australis* on Mount Makiling. However, we suspect that it is quite common there, based on frequently recorded echolocation calls (FM,  $F_{\min} = 61$  kHz) matching the calls used by *M. australis* in Australia. Moreover, we caught *M. schreibersi* and *M. tristis* on Mount Makiling, species commonly found inhabiting large cave roosts with *M. australis* (Heaney et al. 1991, Rickart et al. 1993). Assuming that these calls belong to *M. australis*, on Mount Makiling, it biased its activity toward riparian habitats and the open air (Sedlock 2001). The highest activity along sampling transects occurred between 2200 h and 0000 h on Molawin Creek (50 m). We also recorded it foraging above the canopy in an agro-forest (375 m), and around streetlights on the University of the Philippines campus and along forested roads (350 m). It was never recorded along forest transects.

We did not locate *Miniopterus australis* day roosts on Mount Makiling; however, virtually all previous Philippine records come from cave roosts (Heaney et al. 1991, Rickart et al. 1993). The size of colonies reported from the Philippines (< 100) pale in comparison to those in Australia, where over 100,000 bats occupy a single cave. Dwyer 1968 and Strahan 1983 reviewed the roosting ecology of *M. australis* in Australia. Systematic cave surveys would contribute to our understanding of the distribution and ecology of this species in the Philippines.

***Miniopterus schreibersi*** (Kuhl)

*Miniopterus schreibersi* has a broad distribution from Europe to the Solomon Islands (Heaney et al. 1998). We caught nine individuals with the tunnel trap, representing the first records of *M. schreibersi* on Mt. Makiling. In March 1999, we caught four adult females and two adult males foraging

around a streetlight along a forested road between 2100 h and 2300 h (300 m). In June, we captured one lactating female and an adult male flying along Pili Creek at 2300 h and 2100 h, respectively. Also in June, we caught an adult male flying along a forested road at 2210 h. *Miniopterus schreibersi* is an extremely flexible forager, which may contribute to its success in temperate and tropical habitats. It has a high wing loading and aspect ratio relative to smaller forest understory vespertilionids (e.g. *Myotis muricola*, *Pipistrellus* spp.) rendering it a less maneuverable flier, but providing it fast, energy-efficient travel (Sedlock 2001). On Mount Makiling, it is one of the most common species exploiting the rich streetlight-generated insect patches along a forested road (350 m), and consumes primarily moths and termites (Sedlock in prep. d). On Mount Isarog, Heaney et al. (1999) caught two adult males foraging around a fluorescent light at 1450 m, and Rickart et al. (1993) caught *M. schreibersi* along a road in montane forest at 700 m on Leyte. Therefore, despite its association with forest habitats, it may require fly-ways within the forest to forage. Perhaps the opening of many forests with trails and roads has contributed to its success in tropical regions. Similar patterns of microhabitat use have been reported in Australia (McKenzie and Rolfe 1986) and Indonesia (McKenzie et al. 1995).

We did not locate the day roosts of *Miniopterus schreibersi* on Mount Makiling. However, it is known to occupy caves throughout the Philippines (Heaney et al. 1998, 1991; Rickart et al. 1993), and forms very large colonies in other portions of its range (Dwyer 1966, Strahan 1983).

***Miniopterus tristis*** (Waterhouse)

*Miniopterus tristis* has been recorded in Sulawesi and the Philippines (Corbet and Hill 1992, Heaney et al. 1998). In March on Mount Makiling, we caught one adult female, neither pregnant nor lactating, in the tunnel trap while it

foraged around a streetlight, and we caught one adult male foraging along Molawin Creek in June. These represent the first records of *M. tristis* in Laguna Province. Like *Miniopterus schreibersi*, I frequently recorded it foraging around streetlights and occasionally encountered it foraging along forested streams and roads. *Miniopterus tristis* possesses the highest wing loading among the species captured on Mount Makiling, and as such makes it the fastest, least maneuverable flier. The two individuals I captured had consumed beetles and moths (Sedlock 2001). We did not locate their day roost on Makiling, but the species has been recorded in caves (Rickart et al. 1993, Flannery 1995).

#### *Murina cyclotis* (Dobson)

*Murina cyclotis* occurs from Sri Lanka to Hainan and Borneo (Heaney et al. 1998). It has been recorded throughout the Philippines, and is thought to be moderately common. As with many insectivorous bats, I suspect that *M. cyclotis* is more common in Philippine forests than indicated by prior faunal inventories. We caught a pregnant female in March and an adult male with scrotal testes in July. A mist net set at ground level along a forest trail caught the female, and similarly, a net set along a stream bank caught the male. In the last case, the bat actually escaped from the mist net and fortunately flew into the tunnel trap. Unlike many insectivorous bats, *Murina cyclotis* does not seem to follow fly-ways (e.g. trails, streams, roads) and as such, is more likely to be caught in nets set parallel rather than perpendicular to trails and streams. However, Kingston et al. (1999) caught 22 individuals in Peninsular Malaysia using four-bank harp traps set across forest trails. The most distinctive aspect of its foraging behavior is its use of the dense understory just above the forest floor. *Murina cyclotis* has been recorded in disturbed and primary forest from 50 to 850 m on Leyte (Rickart et al. 1993), in montane forest up to 1500 m in Luzon (Ruedas et

al. 1994), and heavily disturbed forest on Siquijor Island (Lepiten 1995). Its diet has not been studied, although a similar species, *Murina florium*, feeds on beetles and spiders (Schulz and Hannah 1998). In Malaysia, *Murina cyclotis* uses a low intensity, short duration (2.4 millisecond) call starting at 165 kHz and ending at 51 kHz (Kingston et al. 1999). The combination of high frequency and low intensity prohibited me from detecting *M. cyclotis* along transects (and even in hand!) with the Anabat II system. As such, the use of harp traps may be the best strategy for improving our understanding of *Murina cyclotis*' relative abundance across elevational and disturbance gradients. The roosting habitats of *M. cyclotis* are unknown in the Philippines, but there are accounts of *Murina* species roosting among clusters of dead leaves, caves, and in scrubwren and fernwren nests (Schulz and Hannah 1998, Nowak 1994).

#### *Myotis horsfieldii* (Temminck)

*Myotis horsfieldii* ranges from southeastern China through the Malay Peninsula, Sulawesi and is thought to be moderately common in the Philippines (Heaney et al. 1998). *Myotis horsfieldii* represented the most frequently caught species during my field season on Mount Makiling. We caught 63 bats along forested creeks — 34 adult males, and 27 females. We caught pregnant females in May (n = 4) and April (n = 1), lactating females in June (n = 2) and July (n = 1), and two juveniles also in July. Females are slightly, but significantly larger than males based on forearm length (mean  $FA_{\text{male}} = 35.4$  mm, n = 34;  $FA_{\text{female}} = 36.2$  mm, n = 27;  $F_{1,59} = 13.12$ ,  $P=0.001$ ). The majority of captures occurred early in the evening during the first hour after dark; however we captured many individuals in the tunnel trap between 2000 h and 0000 h as well (n = 15). The acoustic activity data confirmed a strong bias towards riparian habitats (855/863 passes) and yielded a similar temporal activity pattern as the

trapping data. *Myotis horsfieldii*'s activity peaked early, declined rather abruptly, and then rose again slightly around midnight. Its diet consists of (in decreasing order) caddisflies, termites, winged ants, moths, beetles, and flies ( $n = 17$  individuals). Over the course of the night, diet breadth of individuals widens as they exploit only rich patches of caddisflies and termites early in the night, expanding later as insect abundance declines. Short duration, broad-band calls and relatively long wingspans allow *Myotis horsfieldii* to forage close to the water and detect emergent insects against the water surface. On Mount Makiling, *Murina cyclotis* and *Kerivoula whiteheadii* are also capable of this foraging strategy, but their smaller size and slower flight may render them less competitive at such rich insect patches. Payne et al. (1985) also observed *Myotis horsfieldii*'s affinity for waterways in Borneo, and observed it roosting in crevices and caves near water. In the Philippines, *M. horsfieldii* had been reported to roost in caves, tunnels and on the underside of large rocks (Heaney et al. 1998, Taylor 1934).

#### *Myotis muricola* (Gray)

*Myotis muricola* ranges from Afghanistan to New Guinea, and is common throughout the Philippines (Heaney et al. 1998, Corbet and Hill 1992). We captured only five individuals, but recorded acoustic activity frequently and over a wide range of habitats. In July, four bats were caught along Pili Creek (375 m), and among these was a lactating female. In September at 2200 h, we hand-caught a juvenile female perched on a low vine (0.4 m) hanging over a forest trail at 400 m. It appeared to be resting after a foraging bout. Its fecal pellets contained winged ants, beetles, and moths (Sedlock 2001). Activity data along habitat transects showed that *Myotis muricola* was most active on higher elevation creeks ( $> 200$  m) early in the evening, and then moved into the forest and agro-forest later in the night (Sedlock 2001). It responded to

rich insect patches, but not as strongly as other small vespertilionids (i.e. *Myotis horsfieldii* and *Pipistrellus* spp.). For example, we infrequently encountered it foraging around streetlights where *Miniopterus* spp. were abundant. Along forest trails, we frequently observed solitary foragers circling in forest gaps or in the open subcanopy. Previous accounts of *M. muricola* on Makiling and other regions of the Philippines have also noted its apparent abundance in the forest understory from 50 m to 1500 m in lowland and montane forest (Ingle 1992, Rickart et al. 1993, Ruedas et al. 1994, Heaney et al. 1999). Ingle (1992) caught individuals in mist nets between 0.5 m and 9.5 m above the ground in the forest. Its roosting habitats are unknown in the Philippines, although it is known to roost in furled leaves of banana plants in Borneo (Payne et al., 1985). On Mount Makiling, *Myotis muricola*'s echolocation call is easily distinguished from that of other species (FM,  $F_{min} = 52$  kHz), and is similar to recordings made of conspecifics in Peninsular Malaysia (T. Kingston, pers. comm.).

#### *Philetor brachypterus* (Temminck)

*Philetor brachypterus* ranges from Nepal to New Guinea, and occurs throughout the Philippines (Heaney et al. 1998). On Mount Makiling, we caught one pregnant and two lactating females in the tunnel trap in July 1999. They flew fast and straight down the creek before they collided with and clung to the netting at the back of the tunnel. They made no attempt to escape in flight. Rather, they tried to crawl out of reach, but generally were easily taken by hand. This behavior, in conjunction with a very high wing loading and aspect ratio, suggests that *Philetor brachypterus* is not a capable flier among obstacles. However, in August 1998 at around 2230 h, we did capture an adult male within second-growth forest in front of the rhinolophid roost described previously (see *Rhinolophus arcuatus* account). It is not clear

if the individual emerged from the rock wall, or was only foraging there. Also on Mount Makiling, Ingle (1992) captured two *Philetor brachypterus* in nets 7 m off the ground above the understory vegetation. Also, on Leyte (Rickart et al. 1993), Mount Isarog (Heaney et al. 1999), and even in Papua New Guinea (Bonaccorso 1998) it occurs in rain forests, occasionally venturing out into agricultural areas (Bonaccorso 1998). Therefore, it seems that *Philetor brachypterus* is most active in the sub-canopy, where the vegetation is not dense, and along riparian habitats. Among understory species on Mount Makiling, it may be superior at finding and exploiting ephemeral, rich insect patches. Fecal pellets of two individuals contained either 100% termites or winged ants, suggesting that they had foraged on insect swarms (Sedlock 2001). There are no data on the roosting habits of *Philetor brachypterus* in the Philippines. In other parts of its range up to 55 individuals have been reported to roost in tree holes 1.5 to 4.5 m above the ground (Bonaccorso 1998, Payne et al. 1985).

#### *Pipistrellus javanicus* (*Pipistrellus* sp. A and B)

The taxonomy of species belonging to the *Pipistrellus javanicus* group are still poorly understood in the Philippines. Differences in skull morphology among specimens collected throughout the Philippines originally identified as *Pipistrellus javanicus* suggest that two species are represented, but their identities are currently uncertain (LR Heaney, pers. comm.). I captured two species *P. javanicus* on Mt. Makiling, and for the sake of discussion, I will refer to them here as *Pipistrellus* sp. A and sp. B. *Pipistrellus* sp. A is lightly smaller than B (Table 1), and its pelage is a dark rufus-brown on the dorsum and venter. *Pipistrellus* sp. B is bicolored, with dark rufus-brown pelage on its dorsum and lighter rufus pelage on its venter. The call used by *Pipistrellus* sp. B is slightly lower than that of *Pipistrellus* sp. A; nevertheless, broad inraspecific variation exhibited by both species prevented me from

distinguishing among them in the field (Sedlock 2001).

Based on acoustic activity, they biased their activity towards Molawin Creek early in the night, and then appeared to spread out into the agro-forest and forest, especially at the higher elevation site (450 m) later in the night (Sedlock 2001). In addition to the creek, they exhibited high activity along the forest edge and around the crowns of emergent trees. During random acoustic sampling at higher elevations (600 - 1000 m), we frequently encountered small groups of *Pipistrellus* spp. foraging low in small forest gaps, and high in the open subcanopy of riparian forests. Moreover, while activity does peak early over the creek, these acoustic data clearly showed that *Pipistrellus* spp. remain active throughout the night. For example, on one night, individuals foraged over our camp at 650 m from 1815 h to 2230 h, and in the morning I recorded them from 0440 to 0530 h.

We caught a total of 19 *Pipistrellus* sp. A. In June and July 1999, we caught four adult males and four adult females along Pili or Molawin Creeks. In April, we caught two lactating females foraging along Molawin Creek at 2300 h. We caught nine juvenile *Pipistrellus* sp. A in May and June, six along a forested road (between 2230 and 0030 h), and two along Molawin Creek (between 2100 and 2000 h). The apparent communication between juveniles was impressive. After placing one bat in a cloth bag, we observed that other bats responded almost immediately to its social calls. In fact, one bat hovered so close to the bag that we caught it by hand. We caught seven *Pipistrellus* sp. B, all on Molawin Creek, between April and June 1999. In April, we trapped two pregnant females, and in May and June, four lactating females and an adult male. The fact that we captured *Pipistrellus* sp. B exclusively on Molawin Creek, and *Pipistrellus* sp. A on both Pili and Molawin, suggests a difference in elevational preferences. Perhaps the smaller *Pipistrellus* sp. A, being more maneuverable and possessing a higher call frequency, can

forage more efficiently on low insect abundances which characterize high elevations than the larger *Pipistrellus* sp. B. Generally, *Pipistrellus javanicus* is thought to prefer montane forest, and be less common in lowland and mossy forests (Heaney et al. 1998, 1999; Payne et al. 1985). My analysis of fecal samples revealed virtually identical diets between species. Both consumed a wide range of insects, including moths, winged ants, leaf hoppers, lygaeid bugs, termites and beetles (Sedlock 2001). The roosting habits of *Pipistrellus javanicus* are poorly known in the Philippines. On Mount Banahao, southeast of Mount Makiling, a solitary bat identified as *P. javanicus* was found roosting in the dead trunk of a coconut tree (AC Diesmos, pers. comm.). In Borneo it has been reported to roost in the thatched roofs of houses (Payne et al. 1985).

#### *Scotophilus kuhlii* (Leach)

*Scotophilus kuhlii* is a common and wide-spread bat, ranging from Pakistan to Taiwan and Bali (Heaney et al. 1998). In the Philippines, this might be the most familiar insectivorous bat to people in towns and cities. It forages over ricefields and around street and house lights at dusk. Moreover, they commonly roost in buildings in huge colonies, although they also roost in tents made from modified palm fronds (Rickart 1989, Rickart et al. 1993). On Mount Makiling, we caught one lactating female foraging around a streetlight on the University of the Philippines, Los Banos campus. In July, we netted one adult male, six lactating females, and eight juveniles exiting an attic roost in Los Banos. *Scotophilus kuhlii* is not a rain forest species, and as such, benefits most from forest degradation and urbanization. Its diet consists of termites, beetles, winged, ants and large lygaeid bugs (Sedlock 2001). Generally, individual diet samples consisted of one insect type, indicative of the exclusive exploitation of rich insect swarms. As a fast and agile flier, *Scotophilus kuhlii* may be a superior competitor at such patchily distributed and ephemeral resources.

#### Foraging behavior, mechanisms of coexistence, and the conservation of insectivorous bat diversity in the Philippines

A thorough site inventory of insectivorous bats has never been conducted in the Philippines, not even on Mount Makiling. Therefore, assessing the impact of habitat loss and disturbance on species diversity through comparative studies of species richness across sites is not possible (e.g. Zubaid 1993, Law et al. 1999, Brosset et al. 1996, Estrada et al. 1993, Schulze et al. 2000). Differences in an animal's behavior across a disturbance gradient may offer a tangible alternative. Moreover, understanding how species coexist within intact forest may help us predict the impact of particular types of disturbance (e.g. habitat reduction, loss of structural complexity on species at the community level. Equipped with this knowledge, one can make an argument for the preservation of the environmental context which supports the greatest bat diversity, independent of one's knowledge of the particular species there. In the following discussion, I will use the behavioral data summarized above to assess the relative tolerance of individual species to local habitat disturbance on Mount Makiling. Then, I will use Mount Makiling's lowland insectivorous bat community as a model to apply what I have learned about mechanisms of coexistence (Sedlock 2001), to assess the potential impact of habitat reduction and disturbance on local bat diversity in a more abstract sense.

My field sites on Mount Makiling and the lowland forest habitats sampled within them, encompass different levels of disturbance and provide an opportunity to assess the effect of habitat alteration on species' foraging behavior. Particularly, the extent to which species utilized the agricultural forests may be indicative of their tolerance for habitat disturbance. All eight species I was able to monitor acoustically along

habitat transects foraged in the agro-forest, including *Rhinolophus arcuatus*, *R. inops*, *R. virgo*, *Hipposideros diadema*, *Myotis horsfieldii*, *M. muricola*, *Miniopterus australis* and *Pipistrellus* spp. Relative to their activity in the forest and creek, *Myotis muricola*, *Pipistrellus* spp., *H. diadema*, and *R. inops* displayed the highest activity in the agro-forest. These species capitalized on the high insect abundance outside the forest, particularly early in the night. For example, *H. diadema* used aerial hawking to exploit rich insect swarms within the agro-forest, but switched to perch-hunting when foraging within the forest. Furthermore, these data indicate that *R. arcuatus* and *R. virgo* (because most agro-forest activity was concentrated on the forest edge) are most intolerant of altered forest habitats. Nevertheless, it seems that replacing grasslands with agro-forests near the forest edge may create opportunities for both people and bats. However, despite the benefits of citrus trees and coconuts over grasslands, these data in no way suggest that agro-forests alone could support current bat diversity. I would argue that the natural mechanisms promoting diversity lie within the forest.

Within the forest on Mt. Makiling, microhabitat selection, resource partitioning and spatial and temporal partitioning of insect abundances provided mechanisms of coexistence for insectivorous bat species (Sedlock 2001). Therefore, habitat disturbance affecting vegetation structural complexity, insect diversity or insect abundance in space and time could—over time—reduce species diversity in predictable ways. For example, reduction of habitat complexity through understory clearing (e.g. collection of firewood, rattan, palms) and selective logging may increase competition between small, forest-living aerial insectivores of the families Rhinolophidae and Vespertilionidae. *Rhinolophus virgo* has a competitive edge over *Pipistrellus* spp. when foraging in cluttered forest micro-habitats due to its echolocation design. Conversely, in the absence of

vegetational complexity, *Pipistrellus* spp. would be the superior competitor and may exclude *R. virgo* over time. Among the vespertilionids, *Kerivoula* and *Murina* seem to coexist with *Myotis* spp., *Pipistrellus* sp. and *Philetor* through microhabitat partitioning, although simplification of the forest understory may not intensify competition between these groups as intensely as in the latter case. *Kerivoula* and *Murina* would still be superior competitors near the ground (e.g. gleaning). However, reduction in ground vegetation may increase predation risk for these slow, hovering bats.

Processes which alter insect diversity and abundance, such as fragmentation as well as disturbance of the forest interior, may greatly affect species whose coexistence depends on resource partitioning and partitioning of insect abundances. For example, Lepidopteran diversity and abundance is associated with host plant diversity (Brown and Hutchings 1997). As such, *Hipposideros ater*, a moth specialist, may suffer from a decline in moth abundance associated with vegetation loss. Generally, though, bats are not specialists on particular insect taxa, therefore changes in species composition, (not richness, e.g. Didham et al. 1998b) associated with disturbance is not the problem *per se*. Rather, bat species specialize on certain insect attributes such as size, hardness, evasiveness, and behavior (i.e. swarming versus dispersed), the reduction in heterogeneity of insects with respect to these attributes could increase competition among bat species. And, indeed, insect diversity does decline with increasing magnitude and time since disturbance (Bolger et al. 2000, Didham 1997, Didham et al. 1998a, Brown and Hutchings 1997). For example, *Rhinolophus arcuatus*, *R. inops* and *Hipposideros diadema* all consumed scarab beetles, but seemed to partition them by size (Sedlock 2001). Alternatively, species whose coexistence depends more on resource patchiness than diversity (e.g. *Philetor brachypterus*, *Pipistrellus* spp. and *Myotis muricola*) may benefit from

disturbance as many insects respond with increased abundance in forest gaps or on the forest edge (e.g. Scarabaeidae, ants; Didham et al. 1997).

Forest disturbance through clearing and selective logging practices can limit roosting opportunities for bats by reducing suitable tree holes (Tidemann and Flavel 1987) and by removing foraging habitat adjacent to cave roosts. Most bat species on Mount Makiling appear to have flexible roosting requirements, although a number of species appear to require relatively large caves as maternity roosts during part of the year (April - August; i.e. *Hipposideros ater*, *H. diadema*, *Rhinolophus arcuatus*, *R. inops*, and perhaps also *R. virgo* and *R. macrotis* and *R. rufus*). Other species may require caves throughout the year, including *Miniopterus schreibersi*, *M. australis*, and *M. tristis*. In temperate (Humphery 1975) and tropical (Arita 1995) regions, cave availability can strongly influence local bat diversity. I suspect that the majority of small to moderate-sized cave roosts utilized by species in continuous forest are cryptic and undisturbed. However, the majority of large, low-elevation caves in the Philippines are heavily disturbed by tourism, guano mining, and hunting. Large cave roosts, particularly if they are in, or adjacent to, forest can house multiple species of bats and should represent a conservation priority in the Philippines. Arita (1995) found that in Mexico, species diversity within caves varied in a nested fashion. The largest caves contained the most, and the most rare species, while smaller caves housed only a few common species (Arita 1995). A nation-wide faunal cave survey is badly needed in the Philippines in order to identify where (and if) these conservation opportunities still exist. As for species reliant on tree holes (i.e. *Megaderma spasma*, *Philetor brachypterus*, *Kerivoula whiteheadii* and perhaps *Rhinolophus rufus*), the conservation of primary forest and the natural succession of trees within those forests is imperative.

Therefore, with respect to the known insectivorous bat species on Mount Makiling, I believe that *Rhinolophus macrotis* and *Rhinolophus rufus* are of special conservation concern. *Rhinolophus macrotis* exhibited low activity based on acoustic encounters despite its easily detected call, and intensive acoustic sampling effort. Similarly, the calls potentially belonging to *Rhinolophus rufus* were fewer than I would expect based on detection biases. Moreover, both species may be reliant on caves as maternity roosts within forest. Interviews with local residents and hunters lead us to a number of unoccupied caves, where they claimed guano collection had once occurred. The accessibility of the forest on Mount Makiling and the resources available at the adjacent University of the Philippines in Los Baños provide an ideal opportunity for radio-tracking studies which may assist in locating roost sites, determining habitat requirements, and making population estimates of *Rhinolophus rufus*. Populations of other species rarely encountered on Mount Makiling, such as *Kerivoula* spp. and *Murina cyclotis*, are quite likely healthy—but difficult to monitor. An intensive harp-trapping study on Makiling could yield reliable abundance estimates, and valuable ecological data for further assessing their conservation status.

The work I conducted on Mount Makiling represents the most thorough effort to understand the local diversity and ecology of microchiropterans undertaken thus far in the Philippines. However, the forest on Mount Makiling is atypical for the Philippines, and such, may not provide the best model for bat communities in the country generally. Makiling is partially covered by secondary tropical lowland forest (between 50 to 1000 m), whereas montane to mossy primary forest (approx. 1000 m to 2000+ m) characterize the majority of remaining—officially protected—forests in the Philippines (Heaney and Regalado 1998). Since secondary tropical forests are less structurally complex (Brown and Lugo 1990), and



may support a less diverse insect fauna than primary forests, the 22 species I recorded on Mount Makiling may only represent a subset of those species coexisting in primary forests. Unfortunately, there are no data available to make such comparisons. Ideally, since local mammal diversity varies with elevation (Heaney and Rickart 1990), and biogeographic region (Heaney 1987, 1993; Heaney and Rickart 1990), what is needed are comprehensive inventory/ ecological studies along elevation and disturbance gradients in each of the biogeographic regions in the Philippines. However in the short term, a more tangible goal would be a comparable study to that conducted on Makiling in primary lowland forest also on Luzon Island. Comparisons of species diversity and foraging behavior may offer insights into the disassembly of insectivorous bat communities, and the association between particular coexistence mechanisms, alteration of the environment, and species loss.

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Table 1. Range (sample size) of external measurements of adult microchiropterans from Mount Makiling, Luzon, Philippines. Measurements in millimeters.

Species	Sex	Weight (g)	Forearm	Total length	Tail	Hind foot	Ear
<i>Emballonura</i>	M	4.8-5.3 (3)	46-48 (3)	62-68 (3)	11-15 (3)	6-9 (3)	10-16 (3)
<i>alecto</i>	F	6.8-7 (2)	46-49 (2)	68-71 (2)	15-22 (2)	8-9 (2)	14-15 (2)
<i>Megaderma</i>	M	15.5-16 (2)	57-60 (2)	72-74 (2)	-	17-18 (2)	36-38 (2)
<i>spasma</i>							
<i>Hipposideros</i>	M	4.1-6.5 (14)	38.6-40.5 (14)	70-75 (5)	26-28 (5)	6-7 (5)	16-18 (5)
<i>ater</i>	F	4.4-6.5 (16)	38.1-41.7 (16)	73-78 (2)	28-30 (2)	6-8 (2)	17-15 (2)
<i>Hipposideros</i>	M	35.5-48.5 (10)	79.6-83.7 (13)	140-145 (3)	41-48 (3)	16-20 (3)	25-31 (3)
<i>diadema</i>	F	33-40.5 (4)	77.9-81.7 (6)	129 (1)	43 (1)	15 (1)	30 (1)
<i>Hipposideros</i>	M	7.1-12 (4)	43.2-46(4)	72 (1)	19 (1)	11 (1)	20 (1)
<i>obscurus</i>	F	9-11.5 (3)	46.2-47.9 (3)	79-80 (2)	21-22 (2)	11-12 (2)	19-20 (2)
<i>Hipposideros</i>	M	5.2 (1)	43 (1)	76 (1)	28 (1)	8 (1)	17 (1)
<i>sp.</i>							
<i>Rhinolophus</i>	M	6.6-9 (3)	43.1-45 (3)	72 (1)	21 (1)	10 (1)	24 (1)
<i>arcuatus</i>	F	6.8-10 (7)	43.2-47.5 (20)	-	-	-	-
<i>Rhinolophus</i>	M	12.5-17 (5)	52.7-56.5 (5)	85-91 (4)	21-23 (4)	13-15 (4)	24-28 (4)
<i>inops</i>	F	11-18 (9)	52.6-56 (19)	84-93 (4)	20-24 (4)	12-14 (4)	26-27 (4)
<i>Rhinolophus</i>	M	5.4-7.5 (8)	43.1-46.1 (8)	75-82 (3)	25-29 (3)	8 (3)	25-26 (3)
<i>macrotis</i>	F	-	45.2 (1)	81 (1)	29 (1)	8 (1)	27 (1)
<i>Rhinolophus</i>	M	4.7-7.0 (9)	37.2-40.0 (9)	68-71 (5)	20-22 (5)	8-9 (5)	19-20 (5)
<i>virgo</i>	F	4.3-6.5 (18)	37.3-41 (24)	58-70 (6)	17-25 (6)	6-8 (6)	16-20 (6)

Table 1. (Continued)

Species	Sex	Weight (g)	Forearm	Total length	Tail	Hind foot	Ear
<i>Kerivoula</i>	M	3.5 (1)	30.7 (1)	79 (1)	37 (1)	5 (1)	16 (1)
<i>whiteheadii</i> *							
<i>Miniopterus</i>	M	8.9-9.5 (3)	42.0-43.7 (3)	98 (1)	47 (1)	9 (1)	12 (1)
<i>schreibersi</i>	F	8.0-11.5 (5)	42.4-44.1 (5)	101-103 (3)	48-51 (3)	8-9 (3)	12-13 (3)
<i>Miniopterus</i>	M	17 (1)	51.7 (1)	132 (1)	60 (1)	8 (1)	16 (1)
<i>tristis</i>	F	16 (1)	53.3 (1)	122 (1)	60 (1)	11 (1)	14 (1)
<i>Murina</i>	M	7.6 (1)	34.6 (1)	90 (1)	32 (1)	9 (1)	15 (1)
<i>cyclotis</i>							
<i>Myotis</i>	M	5.5-8.0 (33)	33.2-37.3 (34)	82.87 (3)	27-36 (3)	10-11 (3)	15-16 (3)
<i>horsfieldii</i>	F	6.0-10.5 (19)	34.3-38.2 (27)	83 (1)	34 (1)	10 (1)	15 (15)
<i>Myotis</i>	M		32.2 (1)				
<i>muricola</i>	F	3.2-4.4 (2)	30.7-31.3 (2)	72-75 (2)	30-32 (2)	5-6 (2)	13-14 (2)
<i>Philetor</i>	M	13.5 (1)	38 (1)	110 (1)	35 (1)	10 (1)	16 (1)
<i>brachypterus</i>	F	13.5-14.0 (2)	33.4-35.9 (2)	91-99 (2)	32-34 (2)	9-10 (2)	14-15 (2)
<i>Pipistrellus</i>	M	4.5-7.0 (4)	30.9-32.6 (4)	77 (1)	31 (1)	6 (1)	10 (1)
<i>sp. A</i>	F	4.5-7.5 (5)	31.5-33.2 (6)	76-80 (3)	31-22 (3)	5-6 (3)	11-12 (3)
<i>Pipistrellus</i>	F	6.3-9.1 (5)	32.1-33.5 (7)	81-85 (6)	31-35 (6)	6 (6)	12-17 (6)
<i>sp. B</i>							
<i>Scotophilus</i>	M	24 (1)	50.3 (1)				
<i>kuhlii</i>	F	15-21 (7)	47.7-51.5 (7)	117-124 (4)	43-48 (4)	11-13 (4)	15 (4)

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