Dietary habits of two threatened co-roosting flying foxes (Megachiroptera) Subic Bay Philippines

Samuel Cord Stier

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DIETARY HABITS OF TWO THREATENED CO-ROOSTING FLYING FOXES
(MEGACHIROPTERA), SUBIC BAY, PHILIPPINES

By
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B.A. Brown University, 1990

Presented in partial fulfillment of the requirements for the degree of
Master of Science
The University of Montana
2003

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Dr. Stephen F. Siebert, Chairperson
Dean, Graduate School

Date
5-13-03
I studied the dietary habits of two threatened flying fox species, *Acerodon jubatus* and *Pteropus vampyrus*, at Subic Bay, Philippines, in an effort to provide managers with information useful for protected area zoning, compatible use planning, hunter education/regulation, and forest restoration design. The results also provide insight into the autecology and interspecific relationships of these co-roosting species.

I used fecal analysis, interviews of bat hunters, and personal observations to describe the dietary habits of both bat species. Dietary items were deemed 'important' if used consistently on a seasonal basis or throughout the year, ubiquitously throughout the population, and if they were of known nutritional importance. Of the 771 droppings examined over a 2.5 year period, seeds from *Ficus* spp. were predominant in the droppings of both species and met these criteria, particularly hemi-epiphytic species (41% of *A. jubatus* droppings) and *Ficus variegata* (34% of *P. vampyrus* droppings, 22% of *A. jubatus* droppings). Information from bat hunter interviews expanded the knowledge of dietary composition of both bat species, and corroborated the fecal analyses and personal observations.

Results from this study suggest that *A. jubatus* is a forest obligate, foraging on fruits and leaves from plant species restricted to lowland, mature natural forests, particularly using a small subset of hemi-epiphytic and other *Ficus* species throughout the year. In contrast, *P. vampyrus* has a broader diet, including fruits, leaves, and flowers; forages in both natural and agroforests; and uses a wider variety of fruit than does *A. jubatus* in natural forest habitats. A small subset of the available *Ficus* spp. are also used heavily by *P. vampyrus* throughout the year. One or both species regularly dips into the ocean surface on the wing, presumably to obtain sodium during later grooming.

The diets of these species suggest that lowland forests are critical for their persistence, and that forests with mature, large diameter trees, upon which hemi-epiphytic *Ficus* spp. establish, are especially important for *A. jubatus*. Forests associated with rivers and coastal areas also appear to be particularly important habitat types for these bat species, as many of their food plants are riparian-associated, and foraging areas in proximity to oceans facilitates the acquisition of sodium.
Preface

The present work is the result of four years spent as a U.S. Peace Corps Volunteer in the Philippines, as part of a cooperative program between the U.S. Peace Corps and the University of Montana School of Forestry. I left for the Philippines in April 1997 and returned in June 2001. During this time period, I conducted an investigation into the dietary habits of two species of bats, or flying foxes (Suborder Megachiroptera, Family Pteropodidae), located at Subic Bay, in the southwest corner of Luzon island.

I chose to study the dietary habits of these species for several reasons. The first and foremost was a personal interest in tropical forest ecology, driven by an interest in ecology and evolution more generally, and heightened specifically by years of fatalistic projections of the future of tropical forests as conveyed by popular culture, media, many scientists, development and non-profit organizations.

Large flying foxes are a group of species worthy of conservation attention for many reasons. Their large size, often colonial roosting habits, and extensive foraging areas make them susceptible to hunting and habitat degradation, which are leading causes of their decline. Large flying foxes also play important roles in forest maintenance and renewal, can function as “umbrella” species due to the relatively large foraging areas required to sustain them, and finally, serve as “flagship” species generating conservation awareness and concern in the public sphere, where conservation decisions are often effectively made.

Very little is known ecologically about these species, including their diet, and this project seemed to be an opportunity to provide information useful for conservation purposes. Dietary information in particular has relevance for plant-eating species limited by a lack of foraging habitat. But despite all of these very good reasons, for anyone who has seen the drama of flying foxes sailing over tropical forests, it might be more appropriate to say that this topic and these species chose me.

This certainly is not a study that attempts to comprehensively characterize the diets of these two species. However, it is intended to provide detailed information on at least some of their food plants, a firm basis for initial conservation actions, and an indication of potential dietary items to be the subject of further investigation. The time I spent working in the Philippines with local governments and communities resulted in several tangible and less tangible benefits for the conservation of these impressive wildlife species and the equally impressive forests they reside in and are a part of. It is hoped that putting this work in the form of this thesis will allow these efforts to reach wider audiences, and prove of value in motivating and guiding further conservation action.

The thesis is organized into three chapters followed by appendices, and is structured somewhat like a journal article might be. However, it is longer, due to the greater depth and breadth the thesis format allows. While articles for publication will be prepared out of the materials provided herein, the thesis is intended to provide a more complete resource for consultation.

Sam C. Stier
November 2002
Acknowledgments

If a string were tied between all the people who made this project possible, it would make a mess! But, to me, it would look something more like a perfect snowflake. Wildlife research and conservation is a group endeavor, and pervading this one was a recognition and thankfulness for all the people without whom this effort could not have succeeded.

First and foremost I would like to acknowledge the bravest woman I know, Tammy Mildenstein, who was with me every step of the way, during the good times and the bad, through typhoid, typhoons and leaches, who pointed with awe at the flying foxes overhead, and watched with me in amazement at the rain-soaked python hunting on the dark forest floor. Her love of people and nature was both fuel and a bearing to go by. Thank you for your steadfast friendship, advice and spirit.

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I would also like to thank the community of people at the University of Montana, a good group of people in a hopeful place, including in particular Drs. Scott Mills, Jon Graham, Paul Alaback, Dick Hutto, Roman Biek, Michael Schwartz, and the amazingly diligent and helpful staff at the Interlibrary Loan Office.
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“Science...is essentially an organized form of wonder...”

- Douglas Chadwick 1983:12, *A Beast the Color of Winter*
Chapter 1: The Importance of Natural Forests to Endemic Terrestrial Fauna in the Philippines

**Biodiversity and forests: a long association**

The land area of the Philippines is equivalent to the state of Arizona (300 million square km). For such a small country, species richness and rates of endemism are remarkably high. For example, of the birds that breed in the Philippines, 172 of 395 species (44%) are found nowhere else in the world, as are 214 of 293 (73%) reptiles and amphibian species (Wildlife Conservation Society of the Philippines 1997). With 172 native mammal species, the Philippines has more diversity than Madagascar (100 species), in only half the area (Heaney et al. 1998). One hundred and eleven of these mammals (64%) are endemic; indeed, the Philippines may have the highest per-area mammal richness of any country on Earth (Heaney et al. 1998).

The exceptionally rich endemic biota is largely a forest-dwelling community. Several researchers have observed a general association between the endemic terrestrial fauna of the Philippines and its natural forests (see Heaney 2001, and citations therein; also Brooks et al. 1997: 387, Brooks et al. 1999a: 1066). Elmer Merrill, the pre-eminent Philippine botanist in the early 20th century, pointed out that, “It is practically certain that before the advent of man in the Philippines most of the country was covered with unbroken forest of one type or another, from sea level to the tops of the highest mountains.” (1926: 58, also Whitford 1911: 12). It is not surprising, therefore, that the country’s endemic terrestrial fauna would be dependent upon its forests, especially when one considers that it is in this vegetation type that the biotic community must have evolved.
Forest cover status

The case today in the Philippines is of a radically transformed landscape from the “advent of man”. However, a precise estimate of remaining forest cover in the Philippines is elusive (Kummer 1992, Kummer 2003, pers. comm.). There are several problems with arriving at a reliable percentage of forest cover, some of which are inherent to the task and not unique to the Philippines alone. Definitions of “forest”, technical difficulties involved in acquiring data, and human errors in interpreting such data have all played a role in complicating the characterization of forest cover in the Philippines (Kummer 1992: 43-68).

The “original” extent of forest in the country is unknown, making ultimate deforestation figures necessarily imprecise. Spaniards estimated forest cover to be 92% in 1575 (IBON Foundation 1997), although it is unclear by what means such an estimation was produced. Kummer (1992) points out that one difficulty with reconstructing the forest cover of the Philippines is that, like its forests, most of the forestry records have been lost, burned up, or are simply unreliable due to inaccuracies and incompleteness. A fire in Manila in 1897 destroyed most of what Spanish forest records existed up to that point, while records from the various forestry schools were destroyed during World War II. Since WWII, several forest inventories conducted in the 1950’s and 60’s have apparently disappeared without a trace, while other data from the official government source, the Forest Management Bureau, suffer from inadvertent and deliberate errors, all of which are detailed in Kummer’s (1992) thorough review of the subject.

Nonetheless, reasonable estimates indicate rapid loss of forest cover in the Philippines since WWII. Forest cover of about 50% of total land area (150 of 300 million

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sq. km) in 1950 plummeted to about half that amount (22-24%) in the late 1980's (Kummer 1992). The FAO (2000) estimates current natural forest cover at about 17%, but this includes secondary forest formations. Perhaps the most reliable forest degradation statistics relate to the loss of lowland dipterocarp forest, for which, due to their commercial value and exploitation, better records exist. Whitford (1911: 17) estimated that 7,770,000 hectares of old-growth dipterocarp forests existed in the Philippines in 1911, while only 800,000 hectares remained in 1997 (Forest Management Bureau 1998), a loss of some 90% of the most species-rich and structurally diverse forests in less than a century.

**Biological importance of secondary forests?**

Secondary forest cover in the Philippines (a wide range of plant communities including savannah and brushland to closed-canopy formations) is roughly 14.4% of the country’s land area (FAO 2000). How endemic species respond to second growth forests is as unknown as it is relevant to the future of biodiversity in the country. The few studies which shed light on this question (e.g., Maranan 1999, Brown and Alcala 1994, Redfern 1993 and citations therein) suggest endemic species are not prevalent in secondary forests.

One reason for this pattern is suggested by the origin of secondary forests in the Philippines. Merrill (1926) observed that the rate of endemism in plant communities differed between primary and secondary forests, with 54% and 31% endemic species among flora, respectively. Merrill argued that based on this evidence, the prevailing assumption that the relative isolation of the country suggests non-endemic species are
introduced), the secondary forest community was likely to have been significantly expanded by the arrival of humans and subsequent forest clearing.

"...[A] high percentage of the species now dominant in the open areas must have been introduced into the Archipelago after the advent of man and after sufficient time had elapsed for man to have provided the habitats to which these species are adapted. The great bulk of the species found in the settled areas and in the open grassland and secondary forests are those which absolutely cannot persist under primary-forest conditions. They are for the most part species of very wide geographic distribution that certainly have not originated in the Archipelago, but which must have developed their characteristics as to habitat in nonforested regions or in thinly forested countries." (1926: 69).

While natural disturbances (e.g., typhoons, volcanic activity, etc.) must have also provided habitats for some secondary forest species, if Merrill’s interpretation of the low rate of endemism of these forests is correct, then secondary forests present late successional associated endemic Philippine fauna with an essentially exotic plant community, with all of the attendant ecological incompatibilities this implies. Therefore, primary forests may be all the more uniquely important to the endemic terrestrial fauna of the Philippines.

*Forest cover and biodiversity patterns at a finer scale*

The majority of primary forest cover in the Philippines today coincides poorly with patterns of species richness. Most of the remaining primary forest in the Philippines exists at high elevations (> 1000 m) and is clumped in relatively small areas of the archipelago, such as in the Sierra Madre and northern Central Cordillera mountains of Luzon, and some of the mountains of the Eastern Visayas, Palawan and Mindanao (Kummer 1992, Myers 1988, and see Brooks et al. 1999a: 1076). Meanwhile, endemic terrestrial biodiversity is scattered and exhibits extreme regional variation in its distributional patterns. Many endemic species have relatively small geographic ranges
within the archipelago (Dickerson et al. 1928, Heaney and Rickart 1990, Heaney 1991) presumably because of the island-nature of the country, the complexity of its biogeographical history (e.g. see Heaney 1986), and large variation in the distributional patterns of endemic terrestrial biodiversity along elevational gradients (Heaney et al. 1989, Heaney and Rickart 1990, Rickart 1993, Dickinson et al. 1991). When diversity is clumped, it is often in the lowlands, where, for instance, 78% of the Philippines’ endemic bird species are found (Dickinson et al. 1991).

With the Philippines’ endemic terrestrial biodiversity closely associated with its primary forests, and the country having no other significant reservoirs of endemic terrestrial biodiversity which would remain following the total removal or disturbance of this biome, the country’s remarkable natural heritage necessarily stands or falls in large measure with the condition of its primary forest resources. However, scattered as it is in diminished fragments across the second largest archipelago in the world, the amount of remaining primary forest is insufficient given patterns of endemic species distribution. This is reflected in the fact that the Philippines already has more critically endangered endemic bird species than any other country in the world, regardless of country size (23% or 40 of 172 endemics; Collar et al. 1994), while its mammalian fauna is the world’s most threatened on a per-area basis (30% or 52 of 172 species; Heaney et al. 1998). Despite the importance of its forests, and the endangerment of its biota, the Philippines has received little ecological study to provide decision-makers with information useful for the conservation of the country’s natural heritage. The research presented in the following chapter is an attempt to address this short-coming for two particularly important vertebrate species.
INTRODUCTION

Large flying foxes (Megachiroptera, Pteropodidae; forearm length > 110 mm) are a group of species particularly worthy of conservation attention. The megachiroptera, or "megabats", perform important ecological functions that contribute to forest maintenance and renewal, through pollination and seed dispersal (e.g. see Rainey et al. 1995, and citations therein). Meanwhile, their large size, often colonial roosting habits, and large foraging areas make them susceptible to hunting and habitat degradation, which are leading causes of their decline (Mildenstein 2002, Mickleburgh et al. 1992). In fact, large flying foxes are one of the most threatened subgroups of bats, particularly in Southeast Asia (see compilations in Mildenstein 2002). Their role in forest development, and typically large foraging areas, means that conservation efforts aimed at flying foxes can benefit both the forests and the creatures inhabiting them.

There are two main reasons why dietary studies of threatened tropical species can provide information helpful for conservation and management purposes. First, what animals eat is important. Foraging habitat is one of the most fundamental limiting resources for wildlife, including bats (Findley 1993); management of foraging habitat thus often creates the largest response or change in wildlife populations (Leopold 1933). Second, often what wildlife managers can best manage are plants. Because of the relative stability of plant communities (and hence, ease of monitoring), it is often more feasible for conservation managers to manage plant communities, rather than the wildlife that ultimately depends upon the vegetation. Thus, because dietary studies result in
vegetatively referenced data, and plants in turn have their own growth and habitat requirements, once a species’ diet is known the particular needs of the plants important to them can be managed for practicably.

I studied the diets of two large, threatened flying fox species at Subic Bay, Philippines, in an effort to provide managers with information useful for protected area zoning, compatible use planning, hunter education/regulation, and forest restoration design. The results also provide insight into the autecology and interspecific relationships of these co-roosting species. My choice of two megachiropterans as study subjects resulted from a confluence of factors. Their level of endangerment (*Acerodon jubatus*) and vulnerability (*Pteropus vampyrus lanensis*) was one factor. The relatively strong interactive role of flying foxes in the forest ecosystem also made them attractive for conservation research; megachiropterans are thought to be a relatively important species group to forest regeneration processes, due to their role in pollination and seed dispersal (see Rainey et al. 1995, and citations therein). Third, because nightly foraging forays send them tens of kilometers out from their roost (Marshall 1983, Liat 1966, Peirson and Rainey 1992, McWilliam 1985-86, Melvin Gumal, WCS wildlife researcher, pers. comm.), flying fox home ranges can cover hundreds of square kilometers of area, and thus large megachiropterans can serve as “umbrella” species, in the sense of species whose home range encompasses the home ranges of many other species sharing the same general habitat (e.g., Suter et al. 2002). Lastly, and perhaps most importantly, given the social nature of the conservation effort, large megachiropterans can fill the role of “charismatic megafauna”, or “flagship” species, due to their size, conspicuousness, and interesting appearance and habits. Both *A. jubatus* and *P. vampyrus* performed this role at
Subic Bay, where tens of thousands of tourists per year visited the area and gathered at the forest’s edge near the roadside roost to stare, wonder, and take photographs (pers. obs.).

*Acerodon jubatus* (Eschscholtz, 1831) Zool. Atlas, part 4:1 was the first endemic species to be described from the Philippines, in 1831 (Utzurrum 1992). In the intervening some 170 years, there have been no published dietary or ecological studies of the species. One study that refers to the species and contains some basic ecological information grouped all large Philippine bats (Utzurrum 1984, and see Utzurrum 1995). The only mention of dietary items of the species at all comes from Utzurrum (1984), who concluded *A. jubatus* used four *Ficus* species, though without quantifying this use. Furthermore, the methods she used (ejecta size, teeth and palatine impressions) were not able to distinguish between the large Philippine flying foxes (*Acerodon jubatus, Pteropus vampyrus,* and *Pteropus hypomelanus*), while mist netting and sightings in the vicinity of fruiting trees allowed use only to be inferred. Most tabular information on dietary components used by *Pteropus vampyrus* (Linnaeus, 1758) *Syst. Nat.,* 10th ed., 1:31 is cursory and comes from other regions (see Liat 1966, Medway 1969, Gould 1977, Utzurrum 1984, Fujita 1991, and Widmann 1996). More detailed and quantified dietary information is needed to provide a clearer scientific foundation for conservation strategies of these species.
STUDY OBJECTIVES

The objectives of this study were to:

1. Derive information on the composition of *A. jubatus*’ and *P. vampyrus*’ diets,
2. Compare both species’ diets,
3. Describe important dietary items for these species, and
4. Provide managers with information for conservation planning, by applying study results to address
   a. the assessment of critical habitats,
   b. compatible-use planning,
   c. hunter education/regulations, and
   d. the design of forest restoration projects.

STUDY AREA

*Biophysical description of study site*

The Subic Bay Forest Reserve (120.09-120.22°E longitude, 14.45-14.51°N latitude) is in the southwestern corner of the large northern island of Luzon, Philippines (Figure 1). The reserve covers portions of the Zambales and Bataan provinces, and is about 130 km by road from the capital city of Manila, or 65 km by air (Magdaraog 1992).

The island of Luzon originated, as did much of the archipelago, through a combination of plate collision and subsequent uplift and vulcanism; it was never connected to the Asia mainland (Heaney 1986, 1991). The local geology of the study area is largely influenced by previous lava flows and pyroclastic deposits from two volcanic centers, Mt. Balikibok and Mt. Natib (Department of the Navy 1991a). Volcanically-generated mudflows transported andesites, basalts, and agglomerates to the coast where
these mixed with shallow marine sands and silts, consolidating ultimately into conglomerates, sandstones and siltstones. Subsequent weathering produced a soil mantle generally classified as antipolo clay loam (Department of the Navy 1981).
The topography of the area is characterized by series of narrow valleys separated by ridges, the lowest elevation at sea level along the coast and the highest at Mt. Santa Rita, a volcanic vent (485 m), and Hill 394, a convergence of valleys (394 m). Sporadic volcanic vents and hills due to uplift and erosion typify the area (Department of the Navy 1981). This low-lying complex is part of a larger geological feature known as the Natib Caldera, a 2.5-km-wide crater resulting from a volcanic eruption, whose rim is composed of several peaks, the main ones being Mt. Santa Rosa (about 900 m), Mt. Natib (1253 m) and Mt. Silanganan (910 m). Much of the caldera above 400 m is forested and part of the adjacent Bataan National Park. The entire Bataan Peninsula is composed essentially of two volcanoes, Natib and to the south Mariveles, and the entire province is fused to the rest of Luzon by pyroclastic material. To the immediate north lie the Zambales Mountains of the province of the same name.

The monsoonal climate of western Luzon is shared with much of mainland southeastern Asia, that from about the Isthmus of Kra northward throughout much of Burma, Thailand, Cambodia, Vietnam and Laos (Whitmore 1984: 55). Due to the Zambales Mountain Range and other mountain ranges lying to the northeast, the Subic Bay area experiences a pronounced dry season during the Northeast Monsoon, with heavy rainfall during the Southwest Monsoon (Department of the Navy 1981, Whitmore 1984: 56). The majority of the mean annual rainfall (83.4%) occurs from June to September, with the rest falling over the remaining 8 months of the year (URS 2001). Mean annual rainfall is 324.65 cm (135.27 inches; Department of the Navy 1981).

The Subic Bay Forest Reserve lies on the northwestern slopes of Mt. Natib, and is approximately 9,856 hectares in size (Magdaraog 1992). The forest contains mangrove,
beach, riparian, and lowland dipterocarp (Dipterocarpaceae) formations; the latter comprises the majority of the area. Classic description of the lowland dipterocarp formation can be found in Whitmore (1984, and see Richards 1952), but a reference more specific to the study site and its peculiarities can be found in Whitford (1906, 1911). Whitford (1911) subdivides the lowland dipterocarp formation in the Philippines into several types, placing the study area into the Lauan-Apitong type, a dipterocarp formation extending from sea-level to 300 or 400 m, distinguished climatically by its relatively long dry season, and subsequently differing both floristically and structurally from other dipterocarp formations. Floristically, apitong (*Dipterocarpus grandiflorus*) co-dominates the dipterocarp component of this forest type with white lauan (*Shorea contorta*), along with many species adapted to seasonally dry conditions and often exhibiting deciduous habits (e.g., kupang, or *Parkia roxburghii*). Structurally, this is the most open of the dipterocarp subtypes, and large trees are often interspersed with groves of bamboos (Graminae), creating a savannah or park-like matrix (Whitford 1906). Estimates of the typical board feet per acre of the Lauan-Apitong forest type are about two-thirds (63%) of the Lauan forest type (28,520 board feet vs. 45,157 board feet; Whitford 1911: 24, 19), which exemplifies the relative openness of the type.

The Lauan-Apitong forest type is divided further by Whitford (1906) into forest formations of differing floristic composition and dominance, shifting primarily along elevational gradients. For example, the lowest forest formation is the Bambusa-Parkia (*Bambusa spp.-Parkia roxburghii*) formation, ranging from sea level to about 175 m (Whitford 1906). Above all of the formations of the Lauan-Apitong forest type lies the Tanguile-Oak (*Shorea polysperma-Quercus spp.*) forest type, ranging from 400 - 500 m.
to 800 - 900 m (Whitford 1911). The Tanguile-Oak forest type found in association to the Subic Bay Forest Reserve actually lies beyond its borders, in the adjacent Bataan National Park, which has substantially higher mountains. A principal distinction of this forest type from the Lauan-Apitong type results from its altitude, which creates conditions for greater amounts of rainfall more evenly distributed throughout the year. This forest type exists above both the wetter Lauan forest type as well as the seasonally dry Lauan-Apitong forest type of the lower elevations.

**Conservation significance of the study site**

Wildlife research of the Subic Bay Forest Reserve appears to be scarce to nonexistent during the U.S. Navy’s occupation of the area (Department of the Navy 1981: D-8, Magdaraog 1992: 40). However, following the establishment of a government environmental department (the Ecology Center), some research projects have been undertaken, primarily to inventory species diversity in the area (e.g. URS 2001, Fernando et al. 1998, Balatibat et al. 1996, Dalmacio and Fernando, no date).

The Subic Bay Forest Reserve is a rarity at several geographic scales. It is the last significant tract of lowland seasonal forest on Luzon, and one of only two sizable lowland forests remaining on the entire island. Within the whole archipelago, it is one of only a handful of lowland forests remaining and one of only two or three forests that reach the coast (URS 2001). In conjunction with Bataan National Park, the Subic Bay Forest Reserve is also one of only two or three forests in the country that encompass a complete elevational gradient, extending from beach through lowland and montane forest types. The Reserve’s seasonal forest is also regionally rare, because Asia contains only 7% of the world’s remaining seasonal tropical forests (Whitmore 1997).
While many threatened species, both plant and animal, are found within the Subic Bay Forest Reserve, less appreciated is that these species have high population densities. One consequence of the area’s unique history (next section) is that many of its wildlife populations have received relatively low hunting pressure, a major difference from virtually all other forests in the country. Sizable populations of threatened animal and plant species found within the Subic Bay Forest Reserve include, for example, the endangered green racquet-tail parrot (*Prioniturus luconensis*; IUCN 2000, see also Kennedy et al. 2000, and see Mallari et al. 2001), and the critically endangered tree, white lauan (*Shorea contorta*; IUCN 2000), which is the most dominant tree within the Subic Bay Forest Reserve (URS 2001).

**The role of the U.S. in establishing the Subic Bay Forest Reserve**

The Subic Bay Forest Reserve was the site of a former U.S. Naval Facility for nearly a century, and the United States has had a pivotal role in the protection of Subic Bay’s forest. Under the Spanish, construction of the naval base began in 1885, and they completed several large construction projects in the harbor (i.e., dredging) and along a portion of the coast (Department of the Navy 1990). The U.S. government acquired the Subic Bay naval station from the Spanish in 1898, following the Spanish-American War (Department of the Navy 1990). On November 9, 1901, U.S. President Theodore Roosevelt reserved the area for use by the U.S. Navy, under Executive Order No. 40 (Magdaroag 1992). In 1908, American Governor General of the Philippines James Smith reserved 6,740 hectares of forest adjoining the naval base to serve as a water supply (Magdaroag 1992). The area of construction on the Base increased markedly under the U.S., moving for the first time south of the Boton River (Department of the Navy 1990)
and extending into the present-day Naval Magazine area by 1955 (Department of the Navy 1981).

During its tenure, the U.S. Navy maintained a sawmill on the Base with a daily capacity of 5,000 board feet, clearing forest for development purposes as well as conducting selective logging. Some of this wood was used for on-base construction, while some was exported for use by bases outside the Philippines (Magdaraog 1992). The Bureau of Forest Development of the Philippines (1976, in Magdaraog 1992) reported that the Navy logged 13,867,174 board feet, or a total gross volume of 65,411.20 cubic m of wood, at 50% utilization efficiency. During the latter 1970’s, logging was stopped at the request of the Philippine government (Magdaraog 1992).

The influence of the Base on forests outside its boundaries is suggested by aerial photos from 1944 (National Air Survey Center, Visual Image Presentations, 4321 Baltimore Ave., Bladensburg, MD, 20710), in which the Olongapo valley area appears as primarily grazing lands surrounded by forest with a very low population density. Today, the area is a dense urban environment containing approximately 300,000 people (Magdaroag 1992) and no natural lowland forest exists beyond the Base. Presumably, the economic benefits of the Base were a strong attractant for immigrants. At the time of its withdrawal, about 12,000 Filipino nationals were directly employed by the Base, which also supported 11,000 permanent U.S. personnel as well as accommodating up to 11,000 additional sailors and marines from visiting U.S. Navy ships (Steckler 1992), many of whom interacted economically with Olongapo City.

The establishment of the U.S. Navy at Subic Bay had both positive and negative consequences for the protection of forests and wildlife in the area. During their tenure,
the U.S. Navy attracted immigrants, cleared and selectively logged forests, but also protected the forest inside the Base from fire, encroachment, and hunters. While the U.S. Navy protected these forests for reasons other than biodiversity conservation, there is no doubt that, without the presence of the Base, the lowland portion of Subic Bay’s forests would have experienced the same fate as lowland forests elsewhere throughout the country and been cleared. As a result of their inclusion in the naval base, these forests were effectively “time capsuled” through a century of deforestation rivaling the world’s most extreme. In April 1992, as the U.S. Navy was in the process of departing from the Base, the U.S. Ambassador to the Philippines and the Philippine Secretary of Environment and Natural Resources expressed concern over the future of the Base’s natural resources by requesting the assistance of World Wildlife Fund – U.S. in mobilizing international support for protection activities. The U.S.D.A. Forest Service provided the first significant funding support for these purposes (WWF 1994).

Recent history

The eruption of Mt. Pinatubo on June 15, 1991 dropped millions of tons of volcanic material on the Base and adjoining forest, creating a “moonscape environment” (Department of the Navy 1991b: II-1). The entire area was covered by some six and one-half inches of ash and sand, weighing approximately 62 pounds per cubic foot (about the same as water) when dry and approximately 95 pounds per cubic foot when wet (Department of the Navy 1991). The effect of the volcanic fallout on the ecological functioning of the area is unknown, however an above-average number of forest trees were reportedly bare from dropping their leaves after the event (Magdaraog 1992, Tim Fisher, pers. com.).
In December 1991, the Philippine senate voted to require the departure of the U.S. military from the Subic Bay Naval Facility. Withdrawal was completed on November 24, 1992 (Steckler 1992). The base had been the largest overseas U.S. naval facility, encompassing at its height some 25,000 hectares (Magdaraog 1992). The former base has subsequently been converted into an Economic Freeport Area, in which a mixture of development and forest protection activities continue (Magdaraog 1992, Mallari et al. 2001).

**STUDY SPECIES**

“In the middle of the Bay, about a Mile from the Shore, there is a small low woody Island, not above a Mile in Circumference... This Island was the Habitation of an incredible number of great Batts, with bodies as big as Ducks, or large Fowl, and with vast wings...”

- William Dampier 1697, *en route* through the Philippine Islands

**Biological background and conservation status**

*Acerodon jubatus* and *Pteropus vampyrus* belong to Order Chiroptera, Suborder Megachiroptera, of which there is one family (Pteropodidae). These species are known as Old World flying foxes, megachiroptera(ns) or “megabats”. *A. jubatus* is endemic to the Philippines, and was formerly found throughout the country except for the Palawan and Batanes/Babuyan island groups. The species is divided into two subspecies: *A. j. jubatus* and *A. j. mindanensis*, distinguished only by size (see Heaney and Rabor 1982: 9). They have apparently disjunct ranges; *A. j. mindanensis* is found in western and southern Mindanao, while *A. j. jubatus* is found elsewhere (Taylor 1934). The common name of *A.*
*jubatus* is the Golden Crowned Flying Fox, or sometimes the Golden-capped Fruit Bat (*Zorro volador filipino*: Spanish), while local names vary widely depending on area (e.g., paniki, bayakan, naval, ugi).

*A. jubatus* is the largest bat in the world in terms of weight and one of the very largest in terms of wingspan (Heaney and Heideman 1987, Kunz and Jones 2000). Adult *A. jubatus* typically weigh approximately one kilogram or more (Mildenstein 2002, Ingle and Heaney 1992) and have wingspans up to 1.5 m or more (Kunz and Jones 2000), and forearm lengths ranging from 165 to 215 mm (Ingle and Heaney 1992). Adult bodies are typically 255-310 mm long (Ingle and Heaney 1992). The species roosts in canopies in large groups, breeds in November, and gives birth in April/May (Mickleburgh et al. 1992 and citations therein; pers. obs.). The Wildlife Conservation Society (1997) reports the species’ habitat as being primary lowland forest up to 1,100 m (and see Mildenstein 2002).

*P. vampyrus lanensis* is an endemic subspecific member of a species that ranges throughout Southeast Asia, and is found throughout the Philippines except the Batanes/Babuyan island group, in the northernmost part of the archipelago (Heaney et al. 1998). Their range overlaps with that of *A. jubatus* except for the Palawan island group. The common name of *P. vampyrus* varies depending on its location within its sizable range throughout Southeast Asia, but in the Philippines its common name is the Philippine Giant Fruit Bat. Local names also vary widely (e.g. paniki, bayakan, francis, negro).

*Pteropus vampyrus lanensis* is very similar in size to *A. jubatus*, but it is generally lighter than *A. jubatus* in the Philippines (at 725-810 g) and has a similar wingspan (Ingle
and Heaney 1992, Kunz and Jones 2000). The species’ roosting and breeding habits are similar to *A. jubatus* (pers. obs., Mickleburgh et al. 1992 and citations therein), and *P. v. lanensis* typically roosts together with *A. jubatus*. The species’ habitat is recorded as forest and agroforest from sea level to 1,300 m (Mickleburgh et al. 1992).

*Acerodon jubatus* is listed as endangered by the IUCN as well as being on Appendix II of CITES; population sizes and numbers of roosts are thought to have declined substantially due to the dual pressures of deforestation and hunting (Heaney et al. 1998; Utzurrum 1992, Mickleburgh et al. 1992). *Pteropus vampyrus lanensis* is considered vulnerable (Mickleburgh et al. 1992). Population sizes and numbers of roosts are also thought to have declined appreciably in the last century (Heaney et al. 1998), and it is, likewise, hunted heavily (Mickleburgh et al. 1992).

**Historical records**

Both *A. jubatus* and *P. vampyrus* roost in the same 1-2 ha stand of trees at the Subic Bay Forest Reserve, sometimes in different trees and sometimes together in the same trees. While I was unable to find historical records of the Subic Bay colony, anecdotal reports suggest the colony has resided in the area for at least 50 years, if not much longer. A security guard posted at the base stated that his grandfather reported the bats being present as early as the sinking of the USS New York in World War II (Officer Bautista, Subic Bay Freeport, pers. comm., February 19, 2000). Further anecdotal reports, from a number of individuals who had worked in the base since the Vietnam War, suggest that the bats’ residence within the base had been continuous for at least the last 30 years.
It is not known how the size of the current bat population at Subic Bay differed in the past. We have little evidence of the historically "natural" population size of either species in the Philippines. The first evidence comes from the 20th century and is scant. Visiting a colony in southern Mindanao, for example, Taylor (1934: 146) stated: "A conservative estimate of the bats in this colony based on the area of the forest inhabited, and on counts of specimens in several trees from various parts of the area, was about 150,000." For such an old and rare record, whose accuracy would be particularly desirable, it seems notable that Taylor appeared first to be making a methodical population estimate (by obtaining an average for the number of bats in a tree and then multiplying this times the number of trees found in the area occupied by the roost), and second to be making a "conservative" estimate. The size of Subic Bay's colony has recently been estimated to be 23,666 (Mildenstein et al. 2002) or about 84% smaller than the colony reported by Taylor (1934).

METHODS

From April 1998 – March 2001, I investigated the dietary habits of A. jubatus and P. vampyrus by studying fecal matter, conducting interviews with bat hunters, and making opportunistic personal observations of feeding activity.

Fecal sample collection

Initially, I made observations of the bats at their roost over several weeks using binoculars, and identified roost trees that were exclusively occupied by one or the other bat species on a consistent basis. While distinguished from other species in the Philippines by their large size, the two species are difficult to distinguish from each other.
at a distance. However, if the pelage of the head and back can be seen, they are easily
differentiated (pers. obs., see Ingle and Heaney 1992: 12, also Kunz and Jones 2000). The
difference in pelage patterning and coloration is the easiest diagnostic field characteristic
available to distinguish the two species. The trees I identified as consistently used by one
or the other bat species (but not both) were potential trees under which to collect
droppings.

During the day, I visited each prospective dropping collection tree to determine if
the sub-canopy space was relatively clear from the canopy to the forest floor. If so, I tied
a guide rope to each selected tree, which I carried back out to the forest edge. Guide
ropes allowed me to locate the trees again in the dark and work at night, and minimize
disturbance to the bats that depart nightly for foraging (see Thomas 1988).

On the night of fecal collections, I followed the guide ropes back to target trees,
cleared away any obstructing vegetation, and staked plastic to the ground beneath the
trees’ canopy areas. The following day at dawn I rescanned the roost to determine if the
selected roost trees were still occupied by the expected bat species. That evening (24
hours after setting the plastic sheets), I again followed the guide ropes through the forest
to the trees, where I collected bat droppings from the plastic sheets randomly, by
throwing a weighted piece of colored tape on the plastic and taking the closest dropping
to the tape. I did not collect residues considered to be scattered from the impact of
droppings, defined as being immediately adjacent (within 5 cm) to a previously collected
dropping and having the same appearance. I placed each collected dropping in a separate
zip-lock plastic bag for transport and later processing.
Fecal analysis

I rinsed each dropping individually through a .3 mm mesh and examined the remaining material through a magnifying glass. I described remaining material by its botanical identity (e.g., anther, insect gall, seed, funicle, leaf fragment) and gross morphological features (e.g., size, shape, color) in a ledger with each entry identified by a unique number. I noted the presence/absence of seed type or other material in each dropping of a collection, and tallied the number of droppings per collection by bat species that contained each type of dietary item. I expressed the use of a dietary item as a percentage of droppings out of the total in which it was present (i.e., frequency of occurrence), to give an index of the population-wide use of a dietary item (Cortes 1997). I stored representative material from each dropping in alcohol for any necessary re-examination.

I compared seeds from each dropping with a reference collection, which I assembled from opportunistic surveys of fruiting trees throughout the study area (particularly Ficus spp.), and seeds from herbarium samples. I identified trees from which the seeds came, and trees determined by bat hunter interviews and personal observation to be used by bats, by using a combination of field guides and lexicons (Jensen 1999, Hensleigh and Holaway 1988, Guzman et al. 1986, and Salvosa 1963), keys (Pancho 1983, Corner 1965, Corner 1952), and original botanical or other descriptions (King 1887, Elmer 1906a, 1906b, 1907, 1908, 1911, 1914, Williams 1921). I further verified tree species identity using the herbaria at the National Museum of the Philippines, Manila, and identified seeds to the lowest possible taxa.
Bat hunter interviews

I interviewed bat hunters after visiting their respective communities several times over a three-year period, during which time I became familiar to community members. Over several visits, I let my interest in learning from bat hunters about the diets of the two bat species be known. With the help of community members, bat hunters were identified, approached, and interviewed.

The interview procedure began with an informal discussion about the bat species in the area, during which I determined whether or not the hunter readily distinguished between the large megachiropterans found in the study area (A. jubatus, Pteropus vampyrus, and P. leucopterus). This was confirmed with the use of photographs of each species. If the hunter appeared to be familiar with distinguishing between the species, I then explained my interest in learning what these species ate, whether their diets were the same or differed, and any other natural history information about the bats based upon the hunter’s personal experience.

I evaluated interviews for their quality based upon the distinction hunters made between each species or morphotypes, the clarity and depth of their information, and corroboration with other methods of observation. From the results of this initial canvas of bat hunters, I identified a key informant based upon this quality criteria. I then conducted follow-up interviews with this key informant.

Personal observations

I observed the bats during foraging, either when bats foraging were accidentally encountered or at trees suspected of being fed upon. I identified bat species whenever possible, using binoculars and light from a headlamp. To examine the use of Parkia
P. roxburghii flowers, I walked a transect approximately 4 km long (following a road) during the flowering period, examining each P. roxburghii tree encountered for foraging bats. For visitation by bats to the surface of the ocean, I stood on a pier or within a mangrove at sunrise or sunset periodically throughout the year, watching for bats descending across the sky towards the ocean in a characteristic descent-glide posture, projected their path towards the water through the belt of dark, intervening land on the horizon, and placed the binocular’s field of view on the appropriate area of the sea to wait and observe if the bats in fact contacted the surface of the water.

**Tree phenology surveys**

Within the same period of time as fecal collections (November 1998 - October 2000), I made a separate investigation of the phenology of Ficus variegata trees in the study area to look for relationships between the use of this tree species’ fruit by the bats and its availability in the bats’ environment. *F. variegata* is a dioecious (i.e., male and female flowers are on separate individuals), self-standing fig tree, with figs borne on woody spurs or tubercules along branches and trunk (i.e., califlorous). Approximately every 6 weeks, at the same time of the bat dropping collections, I surveyed an average of 33 female (seed-bearing) *F. variegata* individuals, estimated the percentage of tubercules on each tree that bore figs, and the size (small, medium, or large) of the figs. Each record was then given a rank (0-5), with trees having a higher percentage of fig-bearing tubercules and large figs receiving a higher rank (e.g., 80-100% tubercules with large figs = 5) than trees having a lower percentage of fig-bearing tubercules and smaller figs. These ranks were added for all trees per sample period to give an index of the population-level patterns of abundance of *F. variegata* figs (see Spencer et al. 1996).
Data analysis

I used a variety of statistical tests to analyze the data, and carried out the analysis using SPSS (version 11.0.1). Two sample t tests were used to compare means of normally distributed data, while Mann-Whitney tests was used to compare means of non-normally distributed data (see results).

RESULTS

Fecal analysis sampling effort

I collected and examined a total of 771 droppings over a 2.5-year period, from April 1998 to October 2000 (482 A. jubatus droppings, 289 P. vampyrus droppings). I made a total of 17 different collections of A. jubatus droppings and 13 collections of P. vampyrus droppings. These collections were made throughout the year at approximately 6-week intervals, averaging 28 droppings/collection for A. jubatus (SD = 11) and 22 droppings/collection for P. vampyrus (SD = 7).

Fecal analysis

Seeds from a single genus, Ficus (Moraceae), dominated the fecal droppings, with two-thirds (66%) of all bat droppings containing Ficus spp. seeds. Seventy-nine percent of all A. jubatus droppings contained Ficus spp. seeds, with no month below 49% (SD = 12%, n = 482; Figure 2). Almost half of P. vampyrus droppings contained Ficus spp. seeds (mean = 48%, SD = 25%, n = 289; Figure 2). To compare the means of Ficus spp. seeds in both bat species’ droppings, I used a Welch’s approximate t test for independent samples (Zar 1984: 131). The mean values of Ficus spp. seeds in the droppings of the two bat species were significantly different (t = 4.194, df = 16, p = .001).
Figure 2. Presence of *Ficus* spp. seeds in *A. jubatus* and *P. vampyrus* droppings over a 30-month period

A large majority of the *Ficus* seeds came from only two kinds of fig trees, *Ficus x* and *F. variegata*. *Ficus x* designates a morphotype of one or more monoecious fig species of the subgenus Urostigma (i.e., hemi-epiphytic *Ficus* spp.), inclusive of *F. subcordata*. Seeds from *Ficus x* appeared in 41% of the droppings of *A. jubatus* (SD = 13.6%, n = 395; Figure 3), and in 13% of those from *P. vampyrus* (SD = 10.9%, n = 254; Figure 3). These averages were significantly different using a two sample t test (t = 5.56, df = 22, p < .001).
Figure 3. Presence of *F. x* seeds in *A. jubatus* and *P. vampyrus* droppings over a 23-month period

*Ficus variegata* seeds appeared in 22% of the droppings of *A. jubatus* (SD = 12.7%, n = 395; Figure 4), and in 34% of those from *P. vampyrus* (SD = 20.5%, n = 254; Figure 4), but these differences were not significant (Two sample t test; t = -1.681, df = 22, p = .107).
Figure 4. Presence of *F. variegata* seeds in *A. jubatus* and *P. vampyrus* droppings over a 23-month period

I found trace amounts of other *Ficus* species’ seeds in the droppings, including: *F. aurantiaca* (21 of *A. jubatus* droppings, 1 of *P. vampyrus*), *F. crassiramea* (15 of *A. jubatus* droppings), *F. religiosa*, and *F. psuedopalma* (1 dropping each from *P. vampyrus*).

Anthers from flowers of *Parkia roxburghii* appeared in 37% of *P. vampyrus* droppings collected during the flowering season of that species (December 1998 and 1999 pooled), but none in the droppings of *A. jubatus*. I found leaf fragments in a small number of droppings of both *A. jubatus* and *P. vampyrus*, with a significantly greater
appearance of this item in the droppings of *A. jubatus* (Mann-Whitney test, $U = 41$, $p = .022$).

**Bat hunter interviews**

I carried out interviews with 13 bat hunters from 4 different villages surrounding the study area, and 2 follow-up interviews with one key informant. Bat hunter interviews provided information about dietary components of both bat species, frequency of use, and dietary comparisons between each bat species. Thirteen dietary items resulting from these interviews met quality criteria (Table 1), while there were an additional 31 “suspected” bat plants (i.e., plants deserving further investigation based on these interviews; Appendix A).

**Personal observations**

I detected several food items through personal observation (Table 1) and details of these observations are discussed in the following section. In addition to plant species, I opportunistically observed that both bat species collected ocean water. About 20-30 either/both *A. jubatus* and *P. vampyrus* individuals dipped their abdomens into ocean water mid-flight regularly throughout the year, with a couple hundred individuals “ocean-dipping” on at least two occasions.
TABLE 1. Tabulation of food items used by three species of megabats based on fecal analysis, bat hunter interviews, and personal observations. Botanical authorities are from Fernando et al. (1998), Salvosa (1963), and Pancho (1983) for Ficus spp.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Aj</th>
<th>Pv</th>
<th>Pl</th>
<th>Resource</th>
<th>Use</th>
<th>Source of information</th>
<th>Degree of certainty</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bombax ceiba</em> L.</td>
<td>x</td>
<td>x</td>
<td></td>
<td>Fr</td>
<td>Inc.</td>
<td>2</td>
<td>C</td>
</tr>
<tr>
<td><em>Broussonetia luzonica</em> (BL) Burr.</td>
<td>x</td>
<td>x</td>
<td>Fr</td>
<td>Inc. (for Pv)</td>
<td>3 (for Pv)</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td><em>Ceiba petandra</em> (L.) Gaertn.</td>
<td></td>
<td></td>
<td>x</td>
<td>Fl</td>
<td>Inc.</td>
<td>3</td>
<td>C</td>
</tr>
<tr>
<td><em>Chrysophyllum cainito</em> L.</td>
<td></td>
<td></td>
<td></td>
<td>Fr</td>
<td>Inc.</td>
<td>3</td>
<td>C</td>
</tr>
<tr>
<td><em>Erythrina fusca</em> Lour.</td>
<td></td>
<td></td>
<td></td>
<td>Fl</td>
<td>F</td>
<td>2,3</td>
<td>C</td>
</tr>
<tr>
<td><em>F. aurantiaca</em> Griff.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Inc.</td>
<td>1</td>
<td>C</td>
</tr>
<tr>
<td><em>F. crassiramea</em> Miq.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Inc.</td>
<td>1</td>
<td>UC</td>
</tr>
<tr>
<td><em>F. pseudopalma</em> Blco.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>IF</td>
<td>1</td>
<td>UC</td>
</tr>
<tr>
<td><em>F. religiosa</em> L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>IF</td>
<td>3</td>
<td>C</td>
</tr>
<tr>
<td><em>Ficus subcordata</em> Bl.</td>
<td></td>
<td></td>
<td></td>
<td>Fr</td>
<td>F</td>
<td>1,2,3</td>
<td>C</td>
</tr>
<tr>
<td><em>F. variegata</em> Bl.</td>
<td></td>
<td></td>
<td></td>
<td>Fr</td>
<td>Inc.</td>
<td>3</td>
<td>C</td>
</tr>
<tr>
<td><em>Mangifera altissima</em> Blanco</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Inc.</td>
<td>3</td>
<td>C</td>
</tr>
<tr>
<td><em>M. indica</em> L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Inc.</td>
<td>3</td>
<td>C</td>
</tr>
<tr>
<td><em>Nauclea orientalis</em> L.</td>
<td></td>
<td></td>
<td></td>
<td>Fr</td>
<td>Inc.</td>
<td>2,3</td>
<td>C</td>
</tr>
<tr>
<td><em>Octomeles sumatrana</em> Miq.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>F (for Pv)</td>
<td>2,3 (for Pv)</td>
<td>C</td>
</tr>
<tr>
<td><em>Parkia roxburghii</em> G. Don</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Inc. (for Pl)</td>
<td>2 (for Pl)</td>
<td>C</td>
</tr>
<tr>
<td><em>Psidium guajava</em> L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>F (for P)</td>
<td>2,3 (for P)</td>
<td>C</td>
</tr>
<tr>
<td><em>Pterocymbium tinctorium</em> (Blanco) Merr.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Inc. (for Pl)</td>
<td>2,3 (for Pl)</td>
<td>UC</td>
</tr>
<tr>
<td><em>Syzygium</em> spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Inc.</td>
<td>3</td>
<td>C</td>
</tr>
</tbody>
</table>

1 = fecal analysis, 2 = personal observation, 3 = hunter interview
Aj = *Acerodon jubatus*, Pv = *Pteropus vampyrus*, Pl = *Pteropus leucopterus*
Fr = fruit, Fl = flower
F = frequent; data suggests resource is used regularly, IF = infrequent; data suggests resource is used infrequently, Inc. = inconclusive data to determine frequency
C = reasonable certainty; quality of data is considered high, UC = reasonable uncertainty; quality of data is considered uncertain. Use of *F. crassiramea*, *religiosa*, and *psuedopalma* is considered uncertain because of their rarity in droppings, lack of corroboration with other lines of evidence, and the possibility in the case of *F. crassiramea* that other Ficus spp. not included in the reference collection could share the same seed morphology.

*Exotic species
Phenological study

Ficus variegata exhibited interspecific asynchronous fruiting patterns, with individuals in fruit during all months of the year except possibly September (when no collections were made). An index (based on fig counts; see Methods) to the population-level fruit abundance of F. variegata showed peaks in abundance followed by fruiting lows (Figure 5), with two of three notable peaks falling at the beginning or middle of the rainy season (May – September). Although some trees had fruit at all times of the year, fruit abundance varied greatly. For example, trees having 60-100% of tubercules carrying mature figs varied between 5-46% of the population (Mean = 19%, SD = 11.4%).

Figure 5. F. variegata abundance over a 24-month period
**DISCUSSION**

*Use of figs*

Hunters suggest that fruit bat diets may be broad. For example, one hunter remarked that both species used “…many different kinds of plants in the forest,” it was “…hard to list them all.” (L. Abraham, pers. comm.). However, he also reported that balete (subgenus Urostigma, genus *Ficus*) is a favored tree; if there were a balete and a non-balete tree to choose from, the balete would be visited preferentially. This description matches Marshall’s (1983) description of megachiropterans having catholic diets, but having favored food plants.

The results of this study suggest that a sizable proportion of particularly *A. jubatus*’ diet is made up of a small number of plants, most notably figs, and in particular, *Ficus subcordata* and other unidentified *Ficus* spp. known under the local name payapa. This group of species (*Ficus x*) comprised an average of 41% of *A. jubatus* droppings, were found in every month in which droppings were collected (i.e., all months except June, September and November), with relatively little variation (SD = 13.6%) between months (further identification of species in this group, Urostigma, is complicated by unclear systematics). *F. variegata* contributed to a lesser but still appreciable extent, averaging 22% of *A. jubatus* droppings, occurring in all months sampled (as above), and varying also slightly (SD = 12.6%) between samples. Together, *F. x* and/or *F. variegata* fig seeds were found in an overall average of almost two-thirds (62%) of *A. jubatus* droppings throughout the study period.

The consistently high use of *Ficus* spp. in each month sampled suggests that use on the intervening nights between samples is probably similarly high. Utzurrum (1984)
found that ripe figs may last on trees for several weeks, and nightly visitation by large Philippine megabats (i.e. *A. jubatus*, *P. vampyrus* and/or *P. hypomelanus*) to individual fruiting fig trees lasted between 17 days to 1.5 months. Other megachiropterans have been found to use the same foraging sites repeatedly over weeks or months (Palmer et al. 2000, and citations therein, see also Urtzurrum 1984).

Figs have figured prominently also in the diets of other megachiropterans (e.g., *Epomops buettikoferi* and *Micropteropus pusillus*, Thomas 1984: 459; *Hypsignathus monstrosus*, Bradbury 1977: 247; *Pteropus alecto*, Palmer et al. 2000: 173; *Eidolon helvum*, Okon 1974: 36; *Pteropus poliocephalus*, Eby 1998: 449, Parry-Jones and Augee 1991: 118; *Cynopterus brachyotis*, Tan et al. 1998: 301, 304, *Cynopterus horsfieldii*, Funakoshi and Akbar 1997: 99-100; *Pteropus rufus*, Bollen and Elsacker 2002: 43; see also Ratcliffe 1932: 45). Some researchers have argued that the generalized reliance on "core plant" taxa hypothesized by Fleming (1986) and implied in the work of others (e.g., Marshall 1983) does not apply to Pacific island megachiroptera (Banack 1998). However, the work upon which this conclusion is based omitted examination of *Ficus* spp. because of sampling difficulties, even though *Ficus* spp. were clearly being used (see Banack 1998: 1960).

Figs in this study appear to be dietary staples; a staple exists when a dietary item makes up a large amount of the overall diet throughout the year (see e.g., Gautier-Hion and Michaloud 1989). This does not preclude them from also acting as a keystone resource. A keystone resource exists when a dietary item sustains a population during times of overall resource scarcity, and figs are commonly discussed as keystone resources.
(Terborgh 1986a, Lambert and Marshall 1991). However, possible periods of resource scarcity were not examined in this study.

Two requirements of staples are that they are available seasonally or throughout most of the year on a consistent basis, and they are of high nutritional and/or energetic value. The *Ficus* genus is characterized by having asynchronous fruiting patterns among conspecifics, with some individuals producing fruit throughout the year. This reflects the tight symbiotic relationship between this genus and its sole pollinators (agaonid wasps), which breed and develop inside figs and cannot live for probably more than a few weeks outside of them (Janzen 1979). However, while figs are available throughout the year, fruit abundance can vary a great deal. Mature *F. variegata* figs were available at all times during the phenological study, but the average percentage of trees having 60-100% of their tubercules carrying mature figs varied from 5-46%. Following peaks in abundance, which tended to occur during the onset or within the middle of the rainy season (and see Spencer et al. 1996), there were notable lows in *F. variegata* fig abundance (Fig. 5). At these times bat hunters reported avoiding *F. variegata* trees because of a lack of figs and bats.

Importantly, both bat species in this study appeared to be selective of the *Ficus* spp. they used, and many fig species in the foraging area showed no evidence of use at all. This was true of even the commonest of fig species (*F. nota*). It is important to note that selection of *Ficus* spp. is species specific (see e.g., Shanahan et al. 2001), and I would agree with Utzurrum (1984: 82) that: “These detailed studies [showing species specific use of specific fig species] are critical since the often-mentioned importance of
figs as a food resource may not hold true for all species of *Ficus*, and might lead to the generalization that fig species may just be as acceptable to other frugivores.”

It is difficult to generalize about the nutritional or energetic value of figs (hereafter I will treat energetic value as though it were a facet of nutrition). Work on fig nutrition has grown in recent years, with some researchers emphasizing that the nutritional value of figs varies by species (Wendeln et al. 2000). Some research has found figs to be lower than other available fruits in various nutrients (Milton 1981, Borges 1993), while others argue that figs have comparatively high nutritional value (Nelson et al. 2000).

While more specific nutritional information on the fig species used by *A. jubatus* and *P. vampyrus* is wanting, two important general points about fig nutrition can be made. First, different fig species may provide comprehensive nutrition in combination with one another, even though nutritional value clearly varies by fig species (Wendeln et al. 2000). Second, figs are generally considered a superior source of calcium (O’Brien et al. 1998, Nelson et al. 2000), which may be a particularly important nutrient for bats (Barclay 1994, 1995). Swartz et al. (1992) demonstrated that the forces on bat wing bones during flight are uniquely substantial among mammals because of torsional (i.e., twisting) stress. Bats may therefore need to be near adult size, with fully calcified bones, before they can fly and feed independently. Indeed, young bats are not typically weaned until reaching 71% of adult body mass, whereas young of other mammals are typically weaned at 40% of adult body mass (Barclay 1994, 1995). Nursing bats thus create nutrient costs for calcium-supplying mothers that are higher than in equivalently sized non-flying mammals, which can be weaned when smaller (Barclay 1994, 1995).
The importance of figs to reproducing bats is suggested by data from Palmer et al. (2000: 175, see Table 4), who recorded higher use of figs at a maternity roost than at a mixed-sex roost of *P. alecto* in Australia. Bat hunters I interviewed also noted that the number of bats visiting payapa, balete, and tangisang bayawak (*Ficus* spp. from the subgenus Urostigma and *F. variegata*) increased during May, June and July (the lactation period), and that these were predominantly pregnant females or females carrying young. Unfortunately, I was not able to test this by comparing frequency of occurrence measures of droppings containing these seeds between months when females were pregnant and lactating and months when they were not, because I collected droppings from trees containing both males and females. There are new techniques available in the analysis of fecal matter using steroid concentrations (e.g., estrogen) that may permit this comparison to be done in future studies (see Litvaitis 2000: 183, and citations therein). Nonetheless, it is interesting that the four collection periods with the highest incidence of *F. variegata* use (April, May, and July 1999, and April 2000), and the three collection periods with the highest incidence of *F. x* use (May and August 1999, and May 2000) by *A. jubatus* were all during late pregnancy/lactation periods.

**Use of riverine forests**

Many of the major food plants used by both *A. jubatus* and *P. vampyrus* are found predominantly along rivers, a pattern suggested in studies of other flying fox species (e.g., McWilliam 1985-86). For example, *Ficus* spp. are generally more common in riparian areas than in drier upland forest (see e.g., Gautier-Hion and Michaloud 1989: 1829), and more specifically, *F. variegata* is most common along watercourses (Weiblen et al. 1995: 391). At least 23% of all bat plants recorded in this study (Appendix B) are
associated with riparian areas, an estimate which may increase with better distributional information. In a companion radio-telemetry tracking study, use of riparian areas by these bats was four times more than expected, given the availability of this habitat type in the study area (Mildenstein 2002). This supports the view that *A. jubatus* and *P. vampyrus* forage heavily on plants found in riverine forests.

**Comparison of diets between *A. jubatus* and *P. vampyrus***

The results of this study demonstrate that *P. vampyrus* feeds from plants in both natural and agroforests, whereas *A. jubatus* appears to feed on plants found only in natural forest (Table 1). While *A. jubatus* likely feeds on more species than recorded in this study, *A. jubatus* appears to be a forest obligate. In addition, bat hunters regard *A. jubatus* as *bantay bahay* (literally: “home guard”), meaning the species does not leave the forest to forage (although it appeared to regularly cross open areas between forests). In contrast, *P. vampyrus* was recorded feeding on at least four agriculturally planted trees: *Mangifera indica* (mango), *Chrysophyllum cainito* (starapple), *Psidium guajava* (guava), and *Erythrina fusca* (*E. fusca* may be native in the Philippines and found in natural forests, but not in the study area, where its use by *P. vampyrus* was associated with high densities planted to provide shade for coffee plantations). Others have noted *P. vampyrus* feeding on different orchard fruits (e.g., rambutan, *Nephelium lappaceum*, and langsat, *Lansium domesticum*; Medway 1969: 11, Liat 1966). Local patterns of foraging movements also suggest this dietary difference, with *P. vampyrus* alone leaving the roost *en masse* in a northward direction from approximately January to May each year, 1998-2001 (pers. obs.; observations based on wing morphology), away from most of the native forests and towards an area of agricultural trees (see also Pierson et al. 1996: 446). This
period of the year and direction of flight coincide with the season of ripe mangos and location of many mango orchards.

Despite the use of some agroforest species by *P. vampyrus*, it also appears to depend upon natural forest plants. The largest number of species used by *P. vampyrus* were natural forest plants (11/16, or 69%; *E. fusca* was excluded because it is an agroforest species in the study area), and the *Ficus* spp. that appeared heavily in *P. vampyrus* droppings throughout the year are all natural forest plants. In a companion radio-tracking study, Mildenstein (2002) found *P. vampyrus* to be in natural forests more than expected given its availability in the study area, and in agroforests less, although the species disappeared entirely for the middle of the night and was inferred to be visiting agroforests during this interim. A countrywide survey of *P. vampyrus/A. jubatus* roosts found *P. vampyrus* only in areas where some natural forests remain (Mildenstein et al. 2002). Valuable nutrients found uniquely or in abundance in figs as compared to agricultural fruits (Nelson et al. 2000) may partly explain the continued reliance of *P. vampyrus* on natural forests despite its use of some agricultural resources.

Within natural forests, *P. vampyrus* used a greater diversity of plant species than did *A. jubatus* (11 vs. 5); its diet in natural forests appears to be broader than *A. jubatus*. *P. vampyrus*’ diet also includes almost all of the same plants fed on by *A. jubatus*. The one exception, *F. crassiramea*, while not found in any *P. vampyrus* droppings, was not heavily used by *A. jubatus*, being in only 15 of 395 droppings (< 4%). *P. vampyrus* thus appears to have a broader diet of natural forest plants than *A. jubatus*, while also subsuming the diet of *A. jubatus*. Some bat hunters described *A. jubatus* as being more “picky” about the types of plants it used than *P. vampyrus*.

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Each bat species also appeared to differ in the class and frequency of the plant resources used, namely flowers and leaves. Whereas there were no records of *A. jubatus* feeding on flowers, *P. vampyrus* fed on flowers of at least five plant species. Bat hunters indicated that if *A. jubatus* fed on flowers at all, it was rare. This is not a consequence of these resources being in agroforests; 4 of 5 of the flowers recorded as used by *P. vampyrus* were in natural forests. For instance, kupang (*Parkia roxburghii*) flowers were used avidly by *P. vampyrus*. This tree is one of the most common in the study area from sea level to about 175 m (Whitford 1966, Fernando et al. 1998, URS 2001), being present in high numbers even within the roost site itself, and produces copious pendulous flowers in late November/early December. In contrast to *P. vampyrus*, *A. jubatus* was never observed feeding on *P. roxburghii* flowers, nor were anthers from kupang flowers evident in its droppings. It is perhaps interesting that blunter muzzles are sometimes inferred to mean a greater reliance on fruit than nectar (e.g. see Marshall and McWilliam 1982: 64) and of the two species, *A. jubatus* has a blunter muzzle (pers. obs).

Widmann (1996) also recorded *P. vampyrus* using the flowers of *Pterocymbium tinctorium* and *Cocos nucifera*, and Gould (1977) observed them feeding on *Durio zibethinus* flowers. It is noteworthy that at least 4 of the 5 flowers *P. vampyrus* was observed to use in this study, and both *P. tinctorium* and *D. zibethinus* flowers, are ‘big bang’ or mast flowering species, plants that produce their flowers over a short period, e.g., a few weeks (see Fleming 1982: 304).

Results from the fecal analysis suggest that *A. jubatus* uses leaves significantly more frequently than *P. vampyrus* does. Because of the manner in which megabats ingest only the liquid contents of leaves (Lowry 1989), evidence of leaf matter is
underrepresented in fecal droppings (Kunz and Diaz 1995). Thus no absolute measure of use can be inferred from this information. However, making the assumption that leaf use is underrepresented to the same degree in both bat species, comparisons between their relative use should be valid.

Protein has sometimes been considered a limiting nutrient for frugivorous bats, since fruits are generally low in nitrogen (Thomas 1984, Courts 1998). Thomas (1984) hypothesized that largely frugivorous bat species over-ingest fruits in order to obtain enough protein in their diets. However, both flowers and leaves can contain substantial amounts of protein (Law 1992, Kunz and Diaz 1995, Ruby et al. 2000), and both are used by many megachiropteran species (Marshall 1985). The relatively greater use of leaves by *A. jubatus* might help explain how this species obtains sufficient protein in an otherwise all-fruit diet.

In summary, it appears that 1) *A. jubatus* is a forest obligate, feeding primarily on fruits and leaves but, apparently, not flowers, 2) *P. vampyrus* has a much wider dietary breadth than *A. jubatus*, feeding on fruits, leaves, but also flowers, using resources from both natural forest and agroforest and, within natural forests, using more plant species than *A. jubatus*, 3) essentially all the plants used by *A. jubatus* are used also by *P. vampyrus*, i.e., the diet of *A. jubatus* is a subset of the diet of *P. vampyrus*, and 4) *P. vampyrus* depends upon natural forests for foraging despite also using agroforests.

*The diet of P. leucopterus*

This study records the first dietary information of the poorly known, endangered and endemic *P. leucopterus* (see Heaney et al. 1991, Mickelburgh et al. 1992, Heaney et al. 1998 for further information on this species). It is interesting that most of the plants *P.
leucopterus fed upon are also fed upon by P. vampyrus (Table 1), and I observed P. leucopterus feeding in the same trees as P. vampyrus at the same time on two occasions. Also of note is the fact that, like P. vampyrus, P. leucopterus fed on flowers and plants in both natural and agroforests.

**Interspecific competition in differing landscapes**

*Acerodon* and *Pteropus* are closely allied genera (Koopman 1989). *Acerodon jubatus* and *P. vampyrus* are similar in size, roost together in the same camps, forage in overlapping ranges, and are both phytophagous. At the same time, foraging habitat is considered generally limiting for megachiropterans (Findley 1993), and probably is for these species as well (see discussion on page 54-55). For example, there is a clear positive correlation between colony sizes of *A. jubatus* and *P. vampyrus* and the forest vegetation available to them (Appendix C; Mildenstein et al. 2002), suggesting that population sizes are at least partly controlled by foraging habitat. A question worth considering is whether there are indications from the dietary information as to how these two species may co-exist or compete.

During the time *P. vampyrus* is feeding in agroforests, *A. jubatus* and *P. vampyrus* are not feeding in the same place, nor on the same plant species. However, when *P. vampyrus* returns to feed in natural forests, it becomes difficult to discern whether or not resource partitioning occurs or whether competitive interactions exist. Within natural forests, the diets of both species overlap, *A. jubatus*’ diet almost completely subsumed by that of *P. vampyrus*. Because these species are likely limited by foraging habitat, these facts alone would suggest competitive dynamics in natural forests.
Whether the use of agroforests by *P. vampyrus* reduces competitive pressure with *A. jubatus* through resource partitioning, or whether it subsidizes *P. vampyrus* populations and results, ultimately, in increased competition between these species in natural forests, is unclear. Whatever the case may be, *P. vampyrus* and *A. jubatus* populations have probably been in flux in response to whichever of these forces are in fact at play for as long as they have co-habited, while the balance of forces themselves have been in flux in response to anthropogenic changes on the landscape.

It is interesting that the number of *P. vampyrus* droppings containing *Ficus* seeds during mango season is significantly lower than the number of droppings containing *Ficus* seeds during non-mango season ($t = -6.04$, $df = 11$, $p < .001$), while no such difference is found in *A. jubatus* droppings ($t = 1.78$, $df = 15$, $p = .095$). This would be what one expects to find if *P. vampyrus* fed on fewer figs during mango season (mango season also roughly corresponds to the flowering and fruiting season of many agricultural crops, e.g. cashew, *Annacardium occidentale*). Although these fruits do not contain equivalent nutrients (e.g., see Nelson et al. 2000), the foraging time required to obtain items in agroforests may reduce the amount of foraging *P. vampyrus* can undertake in natural forests.

Competitive interactions have been observed in megachiropteran species at food sources (e.g. Marshall and McWilliam 1982: 64), and specifically involving *Pteropus vampyrus* (Gould 1978). I observed what appeared to be food defense behavior in juveniles of *A. jubatus* and *P. vampyrus*. Several juveniles of both species were feeding in a fruiting *Nauclea orientalis* tree, when an *A. jubatus* individual approached, swiped at, and dislodged juvenile *P. vampyrus* individuals from the tree (pers. obs.). Richards
(1995: 81) noted that the shift southward of the distribution of *Pteropus poliocephalus* coincided with the expansion from the north of the more aggressive *P. alecto*. He also classified their dietary habits together, suggesting the ultimate cause of the displacement may have been competition for food. This modern-day expansion is particularly provocative because *P. poliocephalus* is endemic to Australia, while *P. alecto* has an extralimital distribution that includes New Guinea, from where it may have recently arrived (Richards 1995: 82).

Aside from direct competition, there is also indirect competition through the removal of shared resources. Population declines due to interspecific competition for food have been indicated in other megachiropterans. Thomas (1985) used mark-recapture estimates to record a 50% decline in *Micropteropus pusillus* populations when the sympatric *Epomops buettikoferi* ate the majority of the two bats' shared dry season food (*Ficus campensis*).

In addition to forest removal adversely effecting *A. jubatus* population numbers, *P. vampyrus* may exert competitive pressure on *A. jubatus* populations through resource removal in natural forests. The use of agroforests by *P. vampyrus* may effectively “subsidize” *P. vampyrus* populations, which in turn would create greater competitive pressure between these species in natural forests (see Pierson et al. 1996 for a possible similar pattern with *Pteropus samoensis* and *P. tonganus* in the south Pacific islands of Samoa). This being the case, conservation management for *A. jubatus* populations may have to include agricultural land use considerations beyond forest areas.
Why do bats dip in the ocean?

On numerous occasions throughout the year, I observed large bats (either/both *A. jubatus* and *P. vampyrus*) flying low over the ocean and dipping their chests and abdomens into the water. I also observed this behavior at a distance of about 20 feet, by unidentified bats on Honda Island, Palawan. At Subic Bay, typically ~ 20-30 bats/night could be seen dipping in the ocean before it became too dark to see, and on two occasions many hundred bats were seen “ocean dipping” over the same small body of water, Triboa Bay. On the basis of wing shape, some of the bats dipping in the ocean were *P. vampyrus* individuals (pers. obs.). *Acerodon jubatus* has been recorded “drinking” ocean water by collector John Whitehead in 1894 (Thomas 1898: 383), though it is not clear from his comments whether this action was definitively *A. jubatus* as distinguished from *P. vampyrus* (the assertion of drinking versus dipping ventral fur is likely to be erroneous). Both Whitehead and Rabor (1977) observed *A. jubatus* (and/or possibly *P. vampyrus*) “drinking” from rivers in Abra province (the Abra and Baay rivers, respectively); it is unclear if these rivers are tidal.

The bats in this study visited the surface of the ocean throughout the year, in groups of varying sizes. The frequency of this behavior and observation of this behavior in other megachiropterans (Bergmans 1978, and sites therein, and see Checke and Dahl 1981: 227, Ripley 1960, Ratcliffe 1961) suggests the behavior may be integral to the lives of these species in some way. I hypothesize along with Ratcliffe (1961) that ocean-dipping provides bats with salt, and further, that this is a critical resource that limits the distribution of some species (see later section).
Physiologically, sodium is an important nutrient involved in multiple daily functions, such as the regulation of body fluid volume and osmolarity, muscle contraction and nerve impulse transmission, acid-base balance and more, with severe sodium deficiency resulting in retarded growth, reduced reproductivity, and death (Robbins 1993: 44, 47-48, Batzli 1986). Deficiencies also lead to softening of bones, impaired protein utilization, and lowered dietary energy (Robbins 1993: 47-48). Thus sodium, in addition to energy, affects the utilization of two nutrients considered potentially limiting to megachiropterans, namely calcium and protein.

While sodium is the sixth most common element in the Earth’s crust, comprising 2.4% of its weight (Botkin and Keller 1982), and is an important nutrient for animals, it is not so for plants. A few plants concentrate salt (i.e., halophytes), but very few terrestrial plants overall require sodium (Robbins 1993; e.g., figs are typically low in sodium, Nelson et al. 2000, and see citations in Studier et al. 1983). Furthermore, an inverse relationship exists between potassium and sodium such that increased ingestion of potassium decreases the body’s sodium retaining capability (Robbins 1993, Crampton and Lloyd 1959). Plants are often high in potassium (Robbins 1993, but see Ruby et al. 2000), especially fruits (Consumer Nutrition Center 1982), including figs (Nelson et al. 2000, and see citations in Studier et al. 1983). Therefore, one might expect that plant-eating bats have difficulty meeting their sodium requirements. Fecal sodium of thirteen plant-eating bats (New World) examined by Studier et al. (1994) showed low levels, an indication that all were indeed sodium deficient.

Every known naturally occurring element on Earth is found in ocean water (Groves 1989: 45), so it is not immediately obvious what bats obtain from such visits.
Nonetheless, salt seems a likely candidate. While most elements exist only in trace amounts in the ocean, sodium and chloride are by far the most abundant elements in seawater by weight, excepting oxygen and hydrogen (Groen 1967: 40, Table 4, Arx 1962: 121, Table 5-1). Captive flying foxes often lick the skin of human visitors incessantly (pers. obs.), a behavior often interpreted as friendliness, but which may reflect a sodium-deficient diet. Flying foxes such as *P. vampyrus* have been observed to urinate on themselves (pers. obs., Brooks, pers. comm.); subsequent grooming would reingest excreted salt. Some 80% of ingested sodium, even in sodium-deficient animals, is excreted in urine (Robbins 1993), and ingesting urine for salt has been recorded in other mammals (Robbins 1993). It is interesting to note that hunger for salt probably evolved concomitant with the evolutionary migration of animals from sea to land (Fitzsimons 1979), a connection which in the case of some megachiropterans may not have been entirely severed.

**Personal observations**

Several food items were detected by opportunistic personal observation (Table 1). In most cases, these observations were singular or few in number, so the frequency of use of these dietary items could not be determined from this information alone, although they often corroborated with other information (particularly from hunter interviews). Two exceptions are *P. vampyrus’* use of *Parkia roxburghii* flowers, and one or both species’ use of ocean water, for which I did obtain some frequency of use data. I observed 18 *P. vampyrus* individuals feeding on *P. roxburghii* flowers (no *A. jubatus*), as well as one *P. leucopterus* individual and an unidentified bat believed to be *Cynopterus brachyotis*. The
apparently heavy use of these flowers by *P. vampyrus* and not *A. jubatus* corroborates well with hunter interviews and the fecal analysis.

**Juvenile feeding**

On two successive evenings in the month of September many individuals (~15) of both species were seen feeding on the fruits of the same bangkal tree (*Nauclea orientalis*); from their size it was clear these individuals were all juveniles. The tree was also relatively close to the roost (within ~ 1 kilometer). Although this was not explored, it may be important to investigate whether the diet of juveniles differs from adults, and whether food resources near the roost are critical for juveniles just learning to fly and forage.

**CONSERVATION IMPLICATIONS**

"Evening as soon as the Sun was set, these Creatures would begin to take their flight from this Island, in swarms like Bees, directing their flight over to the Main Island; and whither afterwards I know not."

- William Dampier 1697: 258, *Dampier in the Philippines*

*A. jubatus’ reliance on forests*

While hunting by humans is clearly a major factor in the decline of megachiropterans, including *A. jubatus* (Mickelburgh et al. 1992), the availability of suitable foraging habitat appears to be even more important for these species. There is a direct correlation between forest area and the size of *A. jubatus/P. vampyrus* populations (Mildenstein et al. 2002; Appendix C), which strongly suggests that both these species are food limited. Food is considered a likely limiting factor in Old World fruit bats for a
number of reasons (see review in Findley 1993), including the high metabolic costs of both endothermy and flight (see discussion and citations in Law 1994), roost movement patterns which track food resources (Eby 1991, Parry-Jones and Augee 1991, Nelson 1985-86), and correlations between bat populations and food abundance (e.g., Law 1994, Thomas 1985).

The marked dependence of \textit{A. jubatus} on lowland natural forests for foraging makes it particularly susceptible to extinction from forest loss. Furthermore, \textit{A. jubatus} is not observed above 1,100 m (Wildlife Conservation Society 1997) and its food plants are found only in the lowland forests (see Appendix B). Most initial forest destruction in the Philippines results from commercial logging (Kummer 1992), an activity conducted predominantly in the lowlands and a process which, over the last century and particularly post-WWII, has likely devastated \textit{A. jubatus} populations. Lowland forests in the Philippines have declined by some 90% in the last century (Chapter 1). Of note is that the hemi-epiphytic \textit{Ficus} spp. used so heavily by \textit{A. jubatus} (e.g., \textit{F. subcordata}) predominantly establish on large-diameter trees (Leighton and Leighton 1983), the size class of trees targeted by commercial logging. Reductions in other animal populations tied to hemi-epiphytic figs have been recorded in selectively logged forests in Asia, and have been speculated to be the result of the removal of large-diameter trees (e.g., Johns 1983, 1987).

**\textit{Pteropus vampyrus’} reliance on forests**

Despite the use of agroforests by \textit{P. vampyrus} for foraging, the species appears to be partially dependent on natural forests for foraging as well. A majority of the plant species used by \textit{P. vampyrus} are found in lowland natural forests (see Appendix B), and
some of these are used heavily. For example, *Parkia roxburghii*, whose use by *P. vampyrus* appeared pronounced in every mode of examination taken in this study (fecal analysis, hunter interview, personal observation), is a native tree found in abundance below 175 m in the study area. Virtually no forest at this low elevation is left in the Philippines except at the study area (Kummer 1992). *Pteropus vampyrus*’ continued use of natural forests despite its use of some agricultural resources may be a result of valuable nutrients found uniquely or in abundance in natural forest plants (e.g., figs) as compared to agricultural resources (see Nelson et al. 2000). In a survey of 12 roost sites throughout the Philippines, colonies in areas without natural forest did not contain *P. vampyrus* (Mildenstein et al. 2002).

*The forest's reliance on the bats*

Old World flying foxes like *A. jubatus* and *P. vampyrus* are important to forest maintenance and renewal by performing pollination and seed dispersal services (see Rainey et al. 1995, and citations therein). For some plants, megabats are important pollinators and seed dispersers (e.g., Cox et al. 1991, Rainey et al 1995), and the geographic distribution of some plant-visitng bats and these plants appear to coincide (Pijl 1956, 1957, Rainey et al. 1995). At the same time, megabats, by being the only mammalian seed dispersers capable of transporting pollen and seeds between distant forest areas, are also uniquely important in maintaining gene flow between plant populations (Richards 1990, Shilton et al. 1999). They also are important for local seed dispersal (Leeuwen 1935, Utzurrum 1995), as well as seed dispersal into cleared areas (Thomas 1982).
In Subic Bay, *Parkia roxburghii* (kupang) provides a good example of the importance of *P. vampyrus*’ pollination services to the forest. *Parkia* in the Old World is a bat-pollinated genus (Baker and Harris 1957), and in the study area is visited heavily by *P. vampyrus*. Though two other megabats, *C. brachyotis* and *P. leucopterus* appear to also visit *P. roxburghii* flowers in the study area, the sheer number of *P. vampyrus* over these other species suggests that they are likely to be the principal pollinators. In forests below 175 m at Subic Bay, *P. roxburghii* is extremely common, comprising as much as 50% of the canopy area (pers. obs., see also URS 2001), and is a major structural component of the now virtually extinct Bambusa-Parkia (cf. Whitmore 1906) forest type.

*Cascading trophic effects*

The forest renewal function of flying foxes serves not only their own needs, but also the needs of many other animal species in the forest. For instance, dozens of hours of observation during the phenological study of *F. variegata* demonstrated that at least six vertebrate species at Subic Bay ingest the figs of *F. variegata* and potentially distribute its seeds: *A. jubatus*, *P. vampyrus*, *C. brachyotis*, *Macaca fascicularis* (the long-tailed macaque), *Bopsittacus lunulatus* (the guiabero parrot), and *Treron pompadora* (the pompadour green-pigeon).

It is unlikely that non-bat visitors to *F. variegata* are effective seed dispersers of this tree. Utzurrum (1984) found macaques to be seed predators of several fig species, ingesting large amounts of figs while still unripe. Pompadour green-pigeons were observed ingesting predominantly immature or male figs of *F. variegata* (pers. obs., but see Lambert 1989b). Guiaberos methodically opened figs and cracked their seeds, the distinctive sound by which the presence of this tiny green parrot in a *F. variegata* tree

50
was often first discovered; droppings of guiaberos showed no sign of intact seeds (pers. obs.). Thus, flying foxes are probably the primary dispersers of *F. variegata* seeds at Subic Bay, and the large flying foxes probably disperse many more seeds than *C. brachyotis* due to their abundance. While *F. variegata* is clearly an important food source of the large flying foxes, it may also be important for these other visitors to *F. variegata* as well. For example, guaiberos were observed using *F. variegata* figs in every month the phenological surveys were taken (unpublished data, and see Lambert 1989a).

**Use of riverine forests**

The marked use of riverine plant species by both species is of interest and concern, because the river-floodplain ecosystem is often the first to be cleared for agriculture, particularly in Asia (Welcomme 1979: 86). Indeed, the “extensively-distributed riparian/inundation forest ecosystems in Southeast Asia [are] now largely removed by humans,” (Dudgeon 1999: 89). This suggests that for the conservation of these species, as well as possibly other megachiropterans, relatively intact riparian forests are a particularly important habitat for protection efforts. In Subic Bay, the riparian zones of many streams have intact forest vegetation. However, riparian zones have also been sites of clearing and development, previously by the U.S. Navy and now by the Subic Bay Metropolitan Authority.

**Habitat implications of ocean water use**

If the ocean provides a critical resource for flying foxes, we might expect their distributions to be essentially coastal. Sodium availability, for example, is considered a major controlling factor in determining the density of some mammal populations (citations in Studier et al. 1983). To my knowledge, no one has suggested that some
megachiropteran distributions are limited by proximity to the ocean to satisfy salt requirements. In fact, some megachiropteran species and populations are found hundreds of miles from coasts. However, I hypothesize that the ocean exerts a profound influence on the distribution of certain megachiropteran species, particularly large megachiropterans.

Although distribution maps are somewhat incomplete, many large flying fox species appear to show a decidedly coastal distribution. Barring a complete review of the distribution of large megachiropterans, certain accounts are suggestive of this pattern. Ratcliffe (1931: 23) conducted a survey of approximately 242 day roosts of *Pteropus* spp. in Australia. Of these he states: “It will be noted that all the areas specially cited are on the coast. Although the flying fox (especially, and possibly solely, *Pt. scapulatus*) extends far inland, it is very markedly a coastal animal. By far the greater proportion of the total population is to be found within 50 miles of the sea.”

Similarly, *P. vampyrus* appears to have a predominantly coastal distribution. *P. v. edulis* has been reported by Goodwin (1979: 88) as “...seen only near the coast at sea level on Timor.” Medway (1969) reports that the species is most common in coastal areas of Malaya. Mohd-Azlan, Zubaid, and Kunz’s (2001: 151, Figure 1) exhaustive survey of *P. vampyrus* roosts in Peninsular Malaysia (115 sites) demonstrates that the vast majority of their colonies are distributed near coasts. Almost all of the sites are only seasonally used, but of note is the fact that the only records of permanent, all-year roosts (3) are located in mangroves, i.e., on the coast. Distributional maps derived from collection locations of *P. vampyrus*, *P. hypomelanus*, and *P. lylei* (Lekagul and McNeely 1977, Kunz and Jones 2000) also suggest a primarily coastal distribution of these large flying
foxes across Southeast Asia (see also Flannery 1995). The genus *Pteropus*, the most species-rich in the family (56/174 species; Rainey et al. 1995), and which contains most of the family’s largest species, is overwhelmingly found on Pacific islands (Rainey and Pierson 1992), i.e., in proximity to oceans.

But what of flying foxes found far inland? For example, Rabor (1955) collected a *P. vampyrus* individual at Massisat, Abra province, about 80 km from the coast of western Luzon, even though a typical foraging distance for *P. vampyrus* is 15-20 km (M. Gumal, pers. comm.); Rabor notes that locals report the bats appear in this area seasonally (Sept.-Dec.). This concurs with Payne et al.’s (1985: 172) characterization of *P. v. natunae*, found “…throughout lowland coastal areas, occasionally invading the interior during the fruiting season.” Australian flying foxes appear far inland, but Ratcliffe (1931: 45-46) points out that when they do so, it is only on a temporary basis (see also Richards 1987). Although Pijl (1957: 309) believed plants motivated the journey, his observation that, “Most colonies of *Pteropus* in Malesia are situated near the sea, and when they are situated inland the animals travel every night to the sea, unless there is a more attractive crop in the interior,” is likewise provocative. While sodium is an essential mineral nutrient for mammals, the detrimental effects of sodium deficiency can take up to a year to manifest themselves (McDonald et al. 1973, Maynard, Loosli et al. 1979), suggesting that daily intake is not required and flying foxes could spend considerable – though not indefinite - periods of time away from coastal areas.

While a more thorough examination of these distributional patterns could investigate whether island size, topography and/or vegetation are possible explanations for this distributional pattern, it seems unlikely that these factors would fully explain the
decidedly coastal distribution observed in many large flying foxes, particularly because many of the species discussed here are found on large land masses (e.g., the Southeast Asian mainland) which contain lowland, interior forests. Though it is clear many megachiropteran populations and species are found inland and far from the ocean, further investigation may find these are predominantly the smaller species (whose sodium requirements are lower), and when not, the foraging or roosting of larger megachiropterans inland may prove temporary (as the above suggests), and/or associated with tidal rivers or other salty water bodies (see e.g., Ratcliffe 1961).

It would follow that any megachiropterans reliant on ocean water to meet salt requirements will decline as their coastal habitats are destroyed. Importantly, the further roosting and foraging habitat become from ocean water, the greater foraging distances to obtain salt increase, consequently increasing the energetic costs of obtaining this resource. A further consequence of the removal of coastal forest habitat is that not only must flying foxes travel greater distances to obtain their salt requirement, but that the trip may not simultaneously be used to gather forest resources. Rather, flying foxes are forced to undertake the roundtrip journey to satisfy a single mineral need, while still having to obtain the rest of their daily dietary intake. The only remaining forest on the Philippine island of Bohol, for example, is many kilometers inland, and the large flying foxes roosting there are typically seen flying to the coast every evening at sunset (pers. obs.), a seemingly contradictory flight pattern explained by the necessity of obtaining salt from the ocean before returning to feed in the inland forests (see Pijl 1957). It follows that roosting and foraging habitat in proximity with salt water may be particularly important for the conservation of large flying foxes.
Reforestation

“The prevention of further destruction of the virgin forest, and the reforestation of the grassy regions on nonagricultural lands, both by the prevention of fires and by planting, are the greatest forestry problems of the Philippine Islands.”

- H.N. Whitford 1911: 15

One corollary to dietary investigations that identify important habitats for protection is the identification of important habitat areas for restoration, and which plant species to use. For example, this study suggests that restoration of riparian areas would be a relatively high priority, and plant species of use and importance to both bat species could grow well here (e.g., *F. variegata*). A majority of the bat plants identified in this study, at least 57% (Appendix B) are sun-loving, forest edge or forest gap species, potentially suitable for direct planting in degraded areas.

Several once-forested areas in the study site have been proposed for reforestation in the Subic Bay Protected Area Plan (URS 2001). Subic Bay Freeport contains many available grassland areas for reforestation and there are important advantages to conducting such activities here. One objective of establishing the Subic Bay Freeport was to maintain this important reservoir of Philippine biodiversity (Magdaraog 1992). The administration of the Freeport includes a capable government department responsible for environmental management (the Ecology Center). In addition, because the area is not under heavy agricultural pressure or other encroachment, there are significantly less competing interests for these grassland areas than in many other areas of the country. The proximity of natural forests would also provide a ready source of nursery stock adapted to local conditions. Successful reforestation projects have been undertaken in nearby areas.
(e.g., Tala, in Bataan Province) by local people's organizations, using wildlings from the forest for nursery stock.

A proposal written by myself resulted in a project funded by Shell-Philippines (the Bat Habitat Restoration Project) which was a 20-ha reforestation effort in the Freeport using plant species of importance to the large flying foxes. To my knowledge, this is the first time a reforestation effort was designed around key food plants of threatened wildlife species in a tropical area. The strategy taken in the Bat Habitat Restoration Project could be broadened to include food plants of other threatened wildlife species in the area, and provide opportunities to conduct innovative reforestation efforts that might serve as flagship projects in a country where strategic reforestation for biodiversity conservation is desperately needed.

**Targeted forest restoration and dietary ‘importance’**

There are advantages to a habitat-based approach to reforestation that targets the needs of threatened species, over and above the usual calls for using native species in reforestation efforts. Because there is a limited amount of time before species go extinct in heavily reduced habitats (e.g., see Brooks et al. 1999b, Cowlishaw 1999, Brooks et al. 1999a, Brooks et al. 1999c, Brooks et al. 1997), and the tropical forest areas which contain most of the world's biodiversity have become dramatically reduced and fragmented (Whitmore and Sayer 1992, Achard et al. 2002), there is a consensus amongst scientists that a large-scale extinction of species is currently underway (Pimm and Brooks 1997, Simberloff 1986). While the use of native plants over exotic plantations is likely, in general, to be better for imperiled biodiversity, it could be yet more effective to address the specific habitat needs of those species known to be at risk. ‘Targeted Forest
Restoration' is a process wherein key habitat components important for threatened species are identified and integrated into the design of reforestation efforts. Such a strategy has the best chance of deflecting extinction processes by boosting wildlife populations through the creation of particularly high-quality habitat, in the shortest possible period of time, for the species that need it most.

Unfortunately, few dietary studies actually identify important dietary components. Many dietary studies of megachiropterans, for example, provide only lists or tabulations of dietary items used, with no quantification of that use (e.g., Marshall 1985, Richards 1990, Entwistle and Corp 1997, Eby 1998, Widmann 1996, Mickleburgh et al. 1992, Dobat and Peikert-Holle 1985, Fujita 1991, Funmilayo 1979, Ratcliffe 1932). While often impressively thorough, these studies are of little use in designing focused forest restoration projects because the relative importance between dietary items is not distinguished; all dietary items are treated as effectively equal.

Nor does quantification ensure that those dietary items identified as 'important' are in fact biologically relevant. There is no consensus amongst researchers how best to quantify dietetically important items, and most studies rely on one or more measures of numerical importance, frequency of occurrence, volumetric or gravimetric values, or preference indices (see reviews in Hyslop 1980, Litvaitis et al. 1994, Cortes 1997). Critical reviews of dietary studies have focused only on the biases inherent in these various methodological approaches (e.g., Litvaitis 2000). There is no a priori reason, however, why the dietary item which in aggregate is the most numerous, largest, heaviest, or most used relative to its availability in the environment, must be a limiting resource or dietetically important to the survival of a species. Garshelis (2000: 130), in
discussing some of the assumptions in habitat analysis studies, describes an analogous situation:

"...one might imagine a situation in which an animal used a habitat substantially more than its availability, but used it only for sleeping. If that habitat became more available, the animal would not be expected to sleep more, so its selection for it would appear to decline. A management agency that produced more of this habitat because results of a habitat selection study showed it to be used disproportionate to its availability would be disappointed to find that these efforts made the animal’s selection for it drop."

This example highlights the disconnection that can exist between various measures of resource 'importance' and resources that are, in fact, limiting a population.

This study was designed to test dietary items for 'importance' using three criteria:

1. **Consistency.** The dietary item is present consistently in the species' diet, either seasonally or throughout the year.

2. **Ubiquity.** When used, the dietary item is used by a sizable proportion of the population (as indicated by frequency of occurrence, a measure of the population-wide use of a dietary item), and

3. **Nutrition.** There is some reason to believe the dietary item provides important nutritional (or energetic) value.

If a dietary item meets all three of these criteria, it would be difficult to explain why the dietary item is used except that it is biologically relevant, or an important dietary component. Conversely, if all three criteria are not met, alternative explanations might readily explain the use of a dietary item (Table 2).
TABLE 2. Importance criteria met (X) and alternative explanation for a dietary item’s use.

<table>
<thead>
<tr>
<th>Consistency</th>
<th>Ubiquity</th>
<th>Nutrition</th>
<th>Alternative explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>X</td>
<td></td>
<td>Dietary component is a ‘junk food’ (cf. Nelson et al. 2000), i.e., of little nutritional value</td>
</tr>
<tr>
<td></td>
<td>X</td>
<td>X</td>
<td>Dietary component is used sporadically/randomly, i.e., the component is neither a staple nor a keystone resource</td>
</tr>
<tr>
<td>X</td>
<td></td>
<td>X</td>
<td>A small percentage of the population uses the component, i.e., equivalent dietary alternatives likely exist</td>
</tr>
</tbody>
</table>

Important dietary items are not necessarily limiting resources, but have the greatest likelihood of being limiting among all the components in a species’ diet. Thus, in lieu of knowing which resources are in fact limiting a population, important dietary items may be the best surrogate for this information.

Whether figs are a limiting factor for this population of bats is difficult to ascertain. The importance criteria (Table 2) are clearly met by at least two types of fig trees, *F. x* and *F. variegata*, which are used consistently throughout the year, ubiquitously throughout the population, and likely supply a macronutrient (Ca) of known importance to flying foxes. Selection of these plant species from all the plant species available is clearly occurring when one considers the hundreds of plant species available in the study area (e.g., 745 species, Fernando et al. 1998), most of which are presumed unused (e.g., by their omission from the fecal analysis and hunter interviews). On the other hand, *F. variegata* is fairly prevalent in portions of the study area, where it is the twenty-first most common tree species based on relative density and the second most common *Ficus* spp.
(Dalmacio and Fernando, no date). The group of F. x hemi-epiphytic species is much less prevalent, tying for the lowest relative densities of all plant species recorded in the study area (Dalmacio and Fernando, no date). Hemi-epiphytic Ficus spp. exist at notoriously low densities in tropical forests, being dependent on mature trees for establishment (Leighton and Leighton 1983) which themselves are rare (e.g., less than half of Dalmacio and Fernando’s sample plots contained mature trees, i.e., trees over 75 cm dab), and within the canopies of which safe establishment sites are scarce (Laman 1996). Thus, if either is a limiting resource, F. x is more likely to be than F. variegata based on the relative density of each.

Still, both may be limiting and both may complement the other in providing these bats with important nutrients on a more consistent basis than if either were not available. It is notable, for example, that in addition to being used by A. jubatus to a fairly high degree throughout the year, the four collection periods with the highest incidence of F. variegata use (April, May, and July 1999, and April 2000) were during late pregnancy/lactation periods. Conversely, the highest use of F.x by A. jubatus occurred in August 1999, one of the absolute lowest months of F. variegata abundance.

Management of hunting

“In the last-named island of Gatigan, there are bats as large as eagles. As it was late we killed one of them, which resembled chicken in taste.”

- Antonio Pigafetta ca. 1525, First Voyage Around the World. On board Captain Magellan’s ship through the Philippines
Hunting is the other major reason besides habitat destruction for declines of megachiropteran populations, particularly large species (Mickelburgh et al. 1992), and dietary studies do not typically provide information useful for addressing this kind of problem. Hunting of large flying foxes in the Philippines and in the study area is particularly prevalent, although the roost itself is reasonably free from hunting. A consequence of hunting bats during nighttime foraging is that hunters generally cannot distinguish between *A. jubatus* and *P. vampyrus* until after they have been shot and caught. Thus, education/regulation campaigns against hunting the more endangered *A. jubatus* cannot be based on visual recognition and avoidance by bat hunters of this species, as they are, for example, with black and grizzly bears (*Ursus americanus* and *U. arctos horribilis*, respectively) in the United States.

The manner in which hunters often hunt bats is based on the plants their prey visits, and this may result in dietary studies holding some potential for suggesting means of addressing hunting. Bat hunters appear generally knowledgeable regarding plant identities, and in particular trees used by bats. Hunters typically select a bat food tree with available resources to wait near, and interviews suggest favorite hunting trees include *Ficus* spp., such as papaya and balete (subgenus Urostigma), tangisang bayawak (*F. variegata*), and others.

This study demonstrates that there is differential use of certain *Ficus* spp. by both bat species, so it should be possible to reduce hunting of *A. jubatus*, for example, by conducting education/regulation campaigns against hunting at their preferred food trees. Payapa would be the obvious first candidate for such a campaign. Hunters commonly describe this tree as a favorite of particularly *A. jubatus* (which the fecal analysis
corroborates well with). In fact, despite the presence of hunters, their fires, and even
gunshots, the many visiting *A. jubatus* to a payapa tree will apparently remain feeding (B.
Salenga, pers. comm.). A further refinement of an education/regulation campaign based
on reducing or eliminating hunting at payapa trees could include reducing or eliminating
hunting during the lactation period (roughly May-August), when mothers may be
particularly prevalent at these and other feeding trees.

METHODOLOGICAL CONSIDERATIONS

**Fecal Analysis**

*Advantages to day roost fecal analysis.* The prospect for generating useful data is
an important aspect of the desirability of a research method, and dietary analysis of
colonial roosting megabats based on day roost fecal matter has several important
advantages. In this study it is notable that the droppings of both bat species contained
high percentages of small seeds, rather than being seedless, as would be expected from
the remains of large-seeded or uningested small-seeded fruit meals (see next section).
Recognizing that fecal analysis does not provide information on the entire diet of a
species, and that little can be said for the absence of a potential dietary item in feces, this
study supports the view that fecal analysis can be a useful method for detecting at least
some commonly ingested small seeds. In addition, an important and underutilized aspect
to day roost fecal analysis is that the relative use of some dietary items can be quantified,
using frequency of occurrence measures.

Dietary analysis of colonial roosting megabats using fecal matter has several other
advantages. For example, collecting day roost fecal samples requires no capturing or
handling of wildlife and is thus a non-invasive research method, which is important given the threatened status of many large flying fox species. Secondly, day roost fecal analysis is relatively inexpensive. Equipment requirements for basic research are minimal, with most of the effort being a matter of labor. This is advantageous since almost all large, colonial roosting megachiroptera reside in poor countries where labor is relatively inexpensive. Third, day roost fecal analysis provides information on night-foraging bats whose habits are otherwise difficult to observe. Other dietary studies of megabats have used ejecta pellets for analysis rather than fecal matter (e.g., Banack 1998). However, these studies have been limited to bat species which forage at least part of the time during the day (only a couple such species exist), when the plants visited can be observed for later investigation of ejecta pellets.

Fecal investigation at day roosts can also provide an abundant and predictable data source for many megachiropteran species, depending primarily on their roosting habits. The data source is obviously most abundant for colonial species, and a significant proportion of megachiropterans are colonial. About one-quarter of the Pteropodidae genera (eleven out of 42) contain colonial roosting species (four genera in trees, seven in caves; Marshall 1983), including the largest genus in the family, _Pteropus_. About half of the _Pteropus_ species (26 of more than 50) are known to roost colonially (Pierson and Rainey 1992: 50). Additionally, colonial species often maintain colony sites over long periods of time (see reviews by Pierson and Rainey 1992: 4 and Mickleburgh et al. 1992: 2, and citations therein), providing for a predictable data source in which the temporal distribution of feeding patterns can be examined.
Bias and error in day roost fecal samples. Determining dietary composition from fecal samples collected under day roosts is subject to several sources of potential bias. To begin with, only small seeds are represented in megabat fecal matter, due to bat anatomy. Richards (1987: 88) observed that the anterior lumen of the esophagus of *Pteropus conspicillatus* is less than 5 mm, and the largest seeds ingested by that species are 3.7 mm long x 3.2 mm wide (but see Bollen and Elsacker 2002). *A. jubatus* and *P. vampyrus* may be able to ingest slightly larger seeds given their larger size, although the largest seeds found in the droppings examined in this study were only 3.2 mm in length. While nothing is known about average seed sizes in Subic Bay, Ng (1978) found that most (75%) tree species in Malaysia (a similar forest region to the study area), had seeds greater than 1 cm long, so this is an important bias to recognize.

Fecal analysis will not necessarily detect all small-seeded bat fruits, either. Frugivorous bats process fruits typically by “juicing them”, ejecting pellets of pulp and seed after pressing fruits between tongue and palate and ingesting the resulting liquid (Ratcliffe 1931). While some seeds may be adapted to be accidentally swallowed during this process (for instance, many *Ficus* seeds are covered in a slippery gelatinous coat, have narrowed ends, and are elliptoid, all of which make them tend to “slip” under compression forces; pers. obs.), Boon and Corlett (1989: 254), in a study of the megachiropteran *Cynopterus brachyotis*, found that seeds of fruits with drier and firmer texture may not be ingested despite being smaller than seeds from fruits with moister pulp. Other small-seeded fruits, like *F. aurantiaca* from this study, are fairly large (e.g., 8 cm in diameter), with thick fleshy walls, and cannot be taken whole into the bat’s mouth. Seeds from such fruits may be small enough to be ingested, but may be underrepresented.
in droppings because, due to fruit morphology, bats must tear pieces of pericarp from the fruit, rather than take the entire fruit into the mouth.

Fecal collections at day roosts are also biased towards recording only the last meal of the evening (Thomas 1988), because food passage rates in megachiropterans are high, typically between 10-100 minutes (Wolton et al. 1982, Utzurrum 1984: 53, Tedman and Hall 1985), with larger species tending to have slightly slower passage rates (Wolton et al. 1982). Dietary components utilized earlier in the evening are therefore not detected. Nightly foraging patterns of megachiropterans can include several distinct sites and vegetation communities (Palmer and Woinarski 1999: 831), and the high-use of *Ficus* spp. found in this study cannot be extrapolated to indicate use throughout the night. Nor are gut passage times necessarily the same for all seeds, thereby possibly biasing what is found at the roost. Utzurrum (1984: 55) mentioned gut passage times notably differed depending on the fig species ingested (but see Richardson et al. 1987).

A further consequence of short food passage times in megachiropterans is that there may be bats that leave no droppings at day roosts, if their last meal was voided before returning. If this is characteristic, day roost fecal analysis would neglect the dietary habits of this group of individuals and may overstate dietary habits of the colony in any generalizations derived from the analysis. The percentage of individuals leaving a dropping at the roost upon arriving from a night of foraging is unknown. However, limited evidence for *A. jubatus* (n = 14) suggests that the number of bat individuals in a roost tree and the number of droppings on collection plastic beneath are closely correlated (1:1 correlation; unpub. data). If this is generally the case, then most or all bats
at a roost have a chance of having a dropping sampled through day roost fecal sampling methods.

A converse problem is that day roost fecal samples may over represent foods obtained within the roost area. Okon (1974: 36), for example, found evidence that the megachiropteran *Eidolon helvum* fed on fruits in or near roost trees during the day. I observed no daytime feeding by either bat species. Furthermore, ejecta pellets were rarely found on collection plastic at the roost (2 *F. variegata* pellets total), suggesting feeding at the roost was not common. Nonetheless, day roost fecal samples may be biased towards food items found relatively near the roosting area.

Quantifying population-wide dietary choices using frequency of occurrence measures using day roost fecal matter assumes that fecal matter is collected randomly, and, each dropping represents a meal from a distinct bat individual. Roost trees from which I collected bat droppings were not randomly chosen in the strict sense, because I had to choose trees that a) I could clearly identify bat species in, b) contained one or the other bat species exclusively on a consistent basis, and c) had relatively open subcanopy space. I have no reason to believe that this roost tree selection criteria had any bearing on the independence of my fecal samples, therefore I have treated them as random and representative of the whole population.

I also selected trees that appeared, based on size, to have adult bats in them (i.e., avoiding young-of-the-year), and the sex of these adults could not be determined in most cases. Age and/or sex-specific dietary differences within the same megachiropteran species are known to occur (e.g., Bradbury 1981). Thus if dietary preferences differ by
sex in either of these species, and if collections happened to be predominantly of one sex or the other, this could bias the findings.

Males and females of *A. jubatus* and *P. vampyrus* appear similar when their wings are wrapped around their bodies. Males were often easy to distinguish when displaying, and females could be distinguished immediately after the birthing period (April-May), when young could be seen at their sides. During these times, limited examination of the potential of sex-biased sampling could be made, and all collections made during this time were from trees of bats in which both male and female bats were identified.

I also made collections over several months from under the same roost trees, and only switched collection areas when the bats moved, which happened on a few occasions. All droppings I collected were from four separate roosting trees per bat species (a total of 8 trees). Because I never observed bats from the same tree leaving to forage at the same time, but rather they left one-by-one over a period of half an hour or more, I took this as an indication that they did not forage together as a tree-associated group, and that their droppings were effectively independent samples of the population's dietary choices. It is unknown, however, how many bats were sampled (i.e., how many, if any, droppings between different collection periods came from bats that had been sampled previously). While some roost fidelity appeared evident, bats also moved between roosting locations. There were always many more bats in roost collection trees than droppings collected from them, and often many more droppings on the collection plastic than were collected. This reduced the chance of collecting droppings from the same bat individuals over different collection periods. To assess these assumptions, one could compare the
droppings from different roost collection trees to test if significant differences exist in dietary components between these.

Other sources of error are associated with the assumption that each dropping represents the meal of a distinct, single bat. Given the short food passage rates of megachiropterans, I assumed that each bat voided their last meal once, so that each dropping represented the food choice of one individual. Observation of bats at the roost appeared to support this assumption. However, fecal material dropped on collection plastic may result in a multiple, rather than a singular deposit (e.g., from splattered material, or, discontinuous deposition). To address this, splatters were minimized in this study by not collecting fecal matter immediately adjacent (within 5 cm) to a collected dropping having the same appearance. Shilton et al. (1999) found that Old World fruit bats could have extended gut retention times (e.g., over 12 hours, see also Okon 1974: 36) and A. jubatus was at times observed in this study to defecate after 3 hours at the roost following night foraging. However, this was rare, and droppings defecated after an extended period, which have a characteristically dark color (Shilton et al. 1999, see also Okon 1974: 36), were rarely encountered on collection plastic sheets.

Some weaknesses of fecal analysis at day roosts are discussed further in Table 3.
Table 3. Possible sources of error in day roost bat fecal analysis and their potential impact.

<table>
<thead>
<tr>
<th>Source of Error in Day Roost Fecal Analysis</th>
<th>Assessment of Impact</th>
</tr>
</thead>
<tbody>
<tr>
<td>only small-seeded fruits represented</td>
<td>method nonetheless potentially excellent for identifying the use of some small-seeded fruits; mitigated by supplementary information</td>
</tr>
<tr>
<td>only last meal of the night sampled</td>
<td>method nonetheless identifies and provides numerical information for at least part of the diet; mitigated by supplementary information</td>
</tr>
<tr>
<td>short-seasoned fruits missed</td>
<td>method nonetheless potentially excellent for identifying the use of some fruits; mitigated by frequent collections made over more than one year, and by supplementary information</td>
</tr>
<tr>
<td>multiple deposits from a single individual</td>
<td>can be minimized by collection methods; at worst decreases sample size but probably does not consistently skew relative percentages of dietary items</td>
</tr>
<tr>
<td>species origin of fecal material uncertain</td>
<td>collection under trees containing only one or the other bat species on a consistent basis; collection soon after deposition can minimize mistakes</td>
</tr>
</tbody>
</table>

**Bat hunter interviews**

"Finally, it is very difficult not to defer to an apparently honest man who has been in the wilderness, when you and your whole gang of pale authorities have not."

- Peter Matthiessen 1961: 24, *The Cloud Forest*

Bat hunting is widespread in most places where large megachiropterans are found, and a primary reason for the group’s decline (Mickelburgh et al. 1992). Thus, bat hunters are a valuable resource for dietary and other information from which conservation strategies might be shaped. I am aware of only one other dietary study of
megachiropterans that utilizes information from bat hunters (Wiles et al. 1997). Part of the explanation for this underutilized resource might be a hesitancy in researchers to use secondary information, preferring whenever possible to use primary information. I found that bat hunter information complemented modes of primary information gathering (i.e., fecal analysis and personal observation) by providing information otherwise unobtainable and which often corroborated other lines of evidence.

Given that dietary studies of megachiropterans typically involve a year or less of field research, it stands to reason that bat hunters who have lived and hunted bats in an area all of their lives may possess information that transient researchers overlook. If you compare the number of dietary items identified through fecal analysis and personal observation (12) with the number provided by bat hunters (13) in this study, bat hunters contributed more than all other sources of information (Table 1; one dietary item personally observed, *Erythrina fusca*, was observed as a result of hunter information) as well as 7 items or over a third (37%) of the total not detected through primary modes of information. Bat hunter information also yielded a total of at least 31 “suspected” dietary items not detected through other means (Appendix A). I discovered only three dietary items through alternate means that were not mentioned by bat hunters during interviews. This may be indicative of the infrequent use of these items: I observed *P. vampyrus* visiting flowers of *Bombax ceiba* and *Pterocymbium tinctoria* on only one occasion each, and results from the fecal analysis suggest that use of *F. aurantiaca* may likewise be infrequent.

Nonetheless, caution must be taken in deriving information from bat hunters given its secondary nature. Features found critical to the successful gathering of
information from hunters included a commitment to community entry (e.g., multiple visits, befriending of and later escort by a community leader, non-immediate pursuit of research objectives, use of native language, and demonstration that curiosity is the motivation) and the methodical execution of interviews. I found the use of photographs very useful during interviews, particularly since this effort depended on distinguishing between different bat species. I also found that conducting interviews in the field improved hunters' recall, as they confronted bat plants and the environment in which they hunted, rather than conducting interviews in homes or villages.

Results are not based on the percentage of hunters who mentioned each dietary item, because interviews are not equally reliable nor hunters equally knowledgeable. The number of interviewees naming a plant species has been used elsewhere to indicate the relative use of that plant by megachiropterans (Wiles et al. 1997). Instead, the process undertaken here was intended foremost to identify key informants with reliable knowledge, get a sense of the range of knowledge and the most common responses given by hunters, generate a list of 'suspected' bat plants for potential further investigation, and uncover interesting anecdotes and other pieces of natural history.

Bat hunters often had a wealth of natural history information exceeding that which seemed required simply to hunt successfully. But the depth and clarity of information was uneven. Particularly difficult was determining whether hunters had stored or organized knowledge about dietary information for each bat species separately. Determining this began with discerning whether the hunter had different names for the different bat species, could readily distinguished between them, and applied these terms when shown photographs. Many hunters considered all large bats to be essentially the

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same, applying the same name to them regardless of morphotype, while others had different names for different morphotypes, but did not differentiate their diets. Of those hunters who distinguished between morphotypes, it was notable that the morphotypes distinguished and the diagnostic characteristics distinguishing them were the same as recognized by field biologists (e.g., pelage patterns).

I then explored whether hunters believed these different types of bats had the same or differing diets. An important clue to the depth and clarity of a hunter’s information involved whether he stated the diets of both major color morphotypes of P. vampyrus – typically designated by different names (e.g., francis and negro) – had the same diet. Only the key informant did this. The key informant was characteristically precise about making comparisons between the dietary habits of A. jubatus and P. vampyrus, detailing even favored or rarely used food items of each species, and giving information which corroborated well with information derived from fecal analysis and personal observations. Nonetheless, though I have rated the quality of the data from the key informant “high”, and “reasonably certain”, any of the information from hunters could be incorrect or misrecorded, since it is necessarily secondary in nature.

While there are obvious advantages to deriving dietary information from bat hunters – readily available, potentially extensive and accurate data – it has its own limitations. For example, interviewees are undoubtedly more familiar with bat plants found in the places they live or frequent (e.g. Wiles et al. 1997). This represents a form of biased “sampling” of bat plants by hunters. For instance, none of the hunters from Tala (elevation 600 m), mentioned bolong-eta (Diospyros pilosanthera), although hunters from Pastolan (200 m) did; D. pilosanthera is predominantly a lowland species and found
in greater abundance at lower altitudes (E. Breganza, pers. comm., pers. obs., Dalmacio and Fernando, no date). Hunters did not mention any mangrove plants as being used by the bats, and while this could be a result of perhaps these plants not being used, it could also be a reflection of the difficulty of hunting in this semi-aquatic environment. Conversely, the frequency with which hunters mentioned fig trees as being used by the bats could reflect a relative preference for these trees by bats, or, it could be a reflection of the year-round availability of figs, and “big bang” fruiting of these trees, resulting in there always being bats at some fig trees and with many bats gathering at one time in them, making these trees especially profitable to hunt in.

Finally, there is an issue of finding the correct scientific names for the local names of plants identified by hunters as being used by bats. Lexicon guides have some use, but local names vary greatly over short distances, and a single local name sometimes refers to several different species, or different local names may refer to the same plant species. For instance, payapa was identified by several bat hunters as being an important dietary item especially of *A. jubatus*, but it became evident in the field that this referred to several different plant species in the subgenus Urostigma, genus *Ficus*. To address this issue, I found it necessary to go into the field with hunters and ask them to show me examples of the trees referred to by various local names, and identify these by botanical means rather than by the use of lexicons.
Chapter 3: Conclusions

“When I knew nothing of plants, I experienced a forest only as a tangle of forms, shapes, and colors without meaning or depth, beautiful when taken as a whole but ultimately incomprehensible and exotic. Now the components of the mosaic had names, the names implied relationships, and the relationships resonated with significance.”

- Wade Davis 1996, One River

Dietary research results in a set of ecological information that is referenced to vegetative data. Since the major cause of endangerment in megachiropteran populations appears to be the result of habitat destruction, and because megachiropterans are generally limited by foraging habitat, vegetatively referenced data is of direct relevance to conservation efforts for many Old World flying fox populations. I found foraging research had utility for wildlife conservation efforts through elucidating the effects of anthropogenic disturbance on wildlife (i.e., logging), providing a tool for discerning habitat use and prioritizing habitats of importance, providing a basis for selecting plant species for use in forest restoration efforts, and providing information useful for hunting regulations and education by discouraging hunting of bats at food trees favored by those species at greater extinction risk.

Large, Old World flying foxes are an endangered group of species (Mildenstein 2002). Because of this, their importance to forest maintenance and renewal, and their potential function as “umbrella” species, they are particularly worthy of conservation attention. They may also serve as “flagship” species, as they did in my study area of
southwestern Luzon, where their conspicuousness, size, and interesting habits and appearance made them popular with locals and visitors from further afield.

Dietary analysis of colonial roosting megabats using fecal matter has several advantages. The most important of these include: important small-seeded dietary items can often be detected, capturing or handling of threatened wildlife is not required, the research methods can be relatively inexpensive to conduct, the procedure does not require prior knowledge of feeding trees, fecal matter is plentiful and readily collectable, dietary choices over time can be recorded when roosts are stable and, finally, use of dietary items can be quantified using frequency of occurrence measures. Accessing the knowledge of local people, in this case bat hunters, can significantly expand the amount and kind of dietary knowledge available. With care, this information can be assembled and sorted for quality. Corroborations between different lines of evidence are an important tool for bolstering or questioning information.

This research provides the first dietary investigation of the endangered *A. jubatus*, and contributes to information about the dietary habits of *P. vampyrus*. It also provides the first information contrasting the diets of these two co-roosting species in the Philippines. General conclusions to be derived from this work about the dietary habits and conservation of these two species are that:

1) *Acerodon jubatus* appears to be a forest obligate, foraging principally or entirely from plant species found in lowland natural forests. The survival of this species is tied directly to the condition and extent of these forests.

2) *Ficus subcordata* as well as unidentified *Ficus* spp. in the subgenus Urostigma are used heavily by *A. jubatus* throughout the year, with a lesser but still notable use of *F. variegata*. A consequence of the reliance of *A. jubatus* on hemi-epiphytic figs is a dependence upon mature, lowland forests, in which these plants are primarily found. Commercial logging removes the germination substrate for these...
plants (large diameter trees) and is probably incompatible with the maintenance of $A. \text{jubatus}$ populations.

3) *Acerodon jubatus*’ diet is much more restrictive than that of $P. \text{vampyrus}$, containing primarily fruit and leaves but not apparently floral resources, whereas $P. \text{vampyrus}$ uses fruit, flowers, and perhaps to a lesser extent leaves. $P. \text{vampyrus}$ uses both natural forests and agroforests, and in natural forests, a wider variety of fruit than does $A. \text{jubatus}$.

4) Despite its use of agroforests, $P. \text{vampyrus}$ remains partially dependent upon natural forests for foraging, where it uses a wide variety of species, including notably $F. \text{variegata}$, and (to a lesser extent) other $Ficus$ spp. in the subgenus Urostigma. Lowland forests remain a critically important habitat for the survival of this species. In the study area, for instance, forests below 175 m contain an abundance of the heavily used $Parkia$ roxburghii.

5) Plant species found in riverine environments are used to a particularly high degree by both bat species, and riverine areas deserve special attention for protection and restoration efforts.

6) Coastal forests such as at the Subic Bay Forest Reserve may be a particularly critical habitat for large bats such as $A. \text{jubatus}$ and $P. \text{vampyrus}$, since these species use and probably depend on ocean water to obtain sufficient amounts of the essential nutrient sodium.

7) Reforestation efforts should be pursued further within the study area, and plant species of particular importance to threatened wildlife, such as the plant species documented here for two threatened species of bats, could be preferentially selected for planting. Such ‘Targeted Forest Restoration’ provides high-quality habitat for the species which need it most, and in the shortest possible period of time.

8) Hunting is another major cause for the decline of large flying foxes, and both $A. \text{jubatus}$ and $P. \text{vampyrus}$ are heavily hunted in the study area. An education/regulation campaign against hunting at papaya trees ($F. \text{subcordata}$ and other $Ficus$ spp. in the subgenus Urostigma), and against hunting bats during the lactation period (May-August) may help reduce hunting pressure on the more endangered $A. \text{jubatus}$, and on reproductively active females of both species.

Sites like the Subic Bay Forest Reserve are an important sanctuary for the Philippines’ beleaguered terrestrial biodiversity, but they are not enough. While the Philippines is extremely species-rich, and its endemic terrestrial biodiversity is strongly...
associated to its forests, it is at the same time one of the most heavily deforested countries in the world. Obviously, this set of circumstances will not persist indefinitely. Any hope of sustaining biodiversity in the Philippines will require carefully designed forest restoration. To a large degree, given the potential of dietary information to improve the biodiversity conservation value of forest restoration efforts, I undertook the study detailed in the preceding chapter. I hope that I have made the case that such restoration efforts are indeed much needed, particularly for countries such as the Philippines, and that the results of dietary studies are an important part of designing forest restoration efforts in the tropics.

At present, we are in the dark with regards to the dietary habits – and more to the point, the limiting resources – of threatened species in tropical forest fragments. One consequence of this is that we are in the dark with regards to forest restoration efforts. An objective of this study was not to find a way out of this darkness, but to find a direction to begin moving. An analogy would be to those spelunkers who get lost in caves without flashlights or candles, but with a lighter. Unfortunately, the lighter has no fluid left, so, they must strike the flint to see, piecing together the way to go by brief flashes of light. This is perhaps the most we can hope for from any wildlife investigation, which will never completely reveal a species’ habits. But it is certainly preferable to simply making guesses, or worse, standing still and doing nothing because it is too dark to see the way forward.
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APPENDIX A: ‘Suspected’ Bat Plants

All bat plants listed are derived from bat hunter interviews (see also Table 1). Local names are Tagalog unless noted as Aetan. Translations of local names into scientific names follow Salvosa (1963), PROSEA (1995), Hensleigh and Holaway (1988), and Whitford (1911). Botanical authorities can be found in Fernando et al. (1998), Salvosa (1963), and Pancho (1983) for *Ficus* spp.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Local name</th>
<th>Bat</th>
<th>Resource</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardiaceae</td>
<td><em>Anacardium occidentale</em> L.</td>
<td>kasoy</td>
<td>Pv</td>
<td>Flower and fruit</td>
</tr>
<tr>
<td></td>
<td><em>Dracontomelon dao</em> (Blanco) Merr. &amp; Rolfe</td>
<td>dao</td>
<td>large bats*</td>
<td>Fruit</td>
</tr>
<tr>
<td></td>
<td><em>D. edule</em> (Blanco) Skeels</td>
<td>lamio</td>
<td>large bats</td>
<td>?</td>
</tr>
<tr>
<td></td>
<td><em>Koordersiodendron pinnatum</em> (Blanco) Merr.</td>
<td>amugis</td>
<td>large bats</td>
<td>Fruit</td>
</tr>
<tr>
<td></td>
<td><em>Mangifera altissima</em> Blanco</td>
<td>pahutan</td>
<td>Pv</td>
<td>Fruit</td>
</tr>
<tr>
<td></td>
<td><em>M. indica</em> L.</td>
<td>mangga</td>
<td>Pv</td>
<td>Fruit</td>
</tr>
<tr>
<td></td>
<td><em>Spondias purpurea</em> L.</td>
<td>sineguelas</td>
<td>large bats</td>
<td>?</td>
</tr>
<tr>
<td>Annonaceae</td>
<td><em>Cananga odorata</em> (Lamk.) Hook. f. &amp; Thoms.</td>
<td>ilang-ilang</td>
<td>Pv</td>
<td>Flower</td>
</tr>
<tr>
<td>Bombacaceae</td>
<td><em>Ceiba petandra</em> (L.) Gaertn.</td>
<td>kapok, boboy</td>
<td>Pv, Pl</td>
<td>Flower</td>
</tr>
<tr>
<td>Caesalpinoideae</td>
<td><em>Cassia javanica</em> L.</td>
<td>cañafistula</td>
<td>large bats</td>
<td>?</td>
</tr>
<tr>
<td>Combretaceae</td>
<td><em>Terminalia catappa</em> L.</td>
<td>talisai</td>
<td>Pv</td>
<td>Fruit</td>
</tr>
<tr>
<td>Datiscaeeae</td>
<td><em>Octomeles sumatranus</em> Miq.</td>
<td>malasapsap, binuang, masapsap</td>
<td>Pv</td>
<td>Flower</td>
</tr>
<tr>
<td>Dilleniaceae</td>
<td><em>Dillenia philippinensis</em> Rolfe</td>
<td>katmon</td>
<td>large bats</td>
<td>?</td>
</tr>
<tr>
<td>Ebenaceae</td>
<td><em>Diospyros philippensis</em> (Desr.) Gurke</td>
<td>kamagong, mabolo</td>
<td>large bats</td>
<td>Fruit</td>
</tr>
<tr>
<td></td>
<td><em>D. pilosanthera</em> Blanco</td>
<td>bolong-eta</td>
<td>large bats</td>
<td>?</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td><em>Antidesma bunius</em> (L.) Spreng.</td>
<td>bugnai</td>
<td>Pv, Pl</td>
<td>Fruit</td>
</tr>
<tr>
<td>Flacouriaceae</td>
<td><em>Flacourtia rukam</em> Zoll &amp; Mor.</td>
<td>bitongol, cherry</td>
<td>large bats</td>
<td>?</td>
</tr>
<tr>
<td></td>
<td><em>Muntingia calabura</em> L.</td>
<td>aratiles, datiles</td>
<td>Pl</td>
<td>Fruit</td>
</tr>
<tr>
<td>Meliaceae</td>
<td><em>Aglaia harmsiana</em> Perk.</td>
<td>malatumbaga</td>
<td>Pv, Pl</td>
<td>Fruit</td>
</tr>
<tr>
<td></td>
<td><em>Lansium domesticum</em> Corr.</td>
<td>lansones</td>
<td>large bats</td>
<td>Fruit</td>
</tr>
<tr>
<td></td>
<td><em>Sandoricum koetjape</em> (Burm. f.) Merr.</td>
<td>santol</td>
<td>large bats</td>
<td>Fruit</td>
</tr>
<tr>
<td></td>
<td><em>Toona calantas</em> Merr. &amp; Rolfe</td>
<td>kalantas</td>
<td>large bats</td>
<td>?</td>
</tr>
<tr>
<td></td>
<td>Common Name</td>
<td>Tagalog Names</td>
<td>Part(s)</td>
<td>Description</td>
</tr>
<tr>
<td>---------------------------</td>
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<tr>
<td><strong>Moraceae</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><em>Artocarpus ovatus</em></td>
<td>anubing (large bats)</td>
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<tr>
<td><em>Artocarpus ovatus</em></td>
<td>himbabao, babayan</td>
<td><em>Pv, Pl</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Broussonetia luzonica</em></td>
<td>tibig</td>
<td><em>large bats</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Ficus nota</em></td>
<td>payapa (large bats)</td>
<td><em>Aj, Pv</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Ficus subcordata</em></td>
<td>payapa (large bats)</td>
<td><em>Aj, Pv</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Ficus variegata</em></td>
<td>tangisang bayawak</td>
<td><em>Aj, Pv</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Ficus spp.</em></td>
<td>bayate (large bats)</td>
<td><em>Pv</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Ficus spp.</em></td>
<td>amungan (Aetan)</td>
<td><em>large bats</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Ficus spp.</em></td>
<td>aymit (Aetan)</td>
<td><em>large bats</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Ficus spp.</em></td>
<td>muro-muro (Aetan)</td>
<td><em>large bats</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><strong>Musaceae</strong></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><em>Musa spp.</em></td>
<td>saging, pusa na saging</td>
<td><em>Pl</em></td>
<td>Flower</td>
<td></td>
</tr>
<tr>
<td><strong>Mimosaceae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Parkia roxburghii</em></td>
<td>kupang</td>
<td><em>Pv</em></td>
<td>Flower</td>
<td></td>
</tr>
<tr>
<td><strong>Myrtaceae</strong></td>
<td></td>
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</tr>
<tr>
<td><em>Psidium guajava</em></td>
<td>bayabas</td>
<td><em>Pv, Pl</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Syzgium bordenii</em></td>
<td>apalang</td>
<td><em>large bats</em></td>
<td>?</td>
<td></td>
</tr>
<tr>
<td><em>S. curtiflorum</em></td>
<td>lipoteng gubat, egot</td>
<td><em>large bats</em></td>
<td>?</td>
<td></td>
</tr>
<tr>
<td><em>S. xanthophyllum</em></td>
<td>malatumbay</td>
<td><em>Pv, Pl</em></td>
<td>?</td>
<td></td>
</tr>
<tr>
<td><em>Syzgium spp.</em></td>
<td>malaruhat</td>
<td><em>Pv</em></td>
<td>Flower</td>
<td></td>
</tr>
<tr>
<td><em>Syzgium spp.</em></td>
<td>makopa(g) gubat</td>
<td><em>large bats</em></td>
<td>?</td>
<td></td>
</tr>
<tr>
<td><em>Tristania decorticata</em></td>
<td>malabaya</td>
<td><em>Aj</em></td>
<td>Fruit</td>
<td></td>
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<tr>
<td><strong>Palmae</strong></td>
<td></td>
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<tr>
<td><em>Cocos nucifera</em></td>
<td>niog</td>
<td><em>large bats</em></td>
<td>Flower</td>
<td></td>
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<tr>
<td><strong>Papilionoideae</strong></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td><em>Erythrina fusca</em></td>
<td>ani-i</td>
<td><em>Pv</em></td>
<td>Flower</td>
<td></td>
</tr>
<tr>
<td><em>E. orientalis</em></td>
<td>dap-dap</td>
<td><em>large bats</em></td>
<td>Flower</td>
<td></td>
</tr>
<tr>
<td><strong>Rubiaceae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nauclea orientalis</em></td>
<td>bankal</td>
<td><em>large bats</em></td>
<td>Fruit</td>
<td></td>
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<tr>
<td><strong>Sapindaceae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Euphoria didyma</em></td>
<td>alupag</td>
<td><em>Pv</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Chrysophyllum cainito</em></td>
<td>kaimito</td>
<td><em>Pv</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Palaquium lanceolatum</em></td>
<td>palakpalak</td>
<td><em>large bats</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><strong>Sapotaceae</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><em>Chrysophyllum cainito</em></td>
<td>kaimito</td>
<td><em>Pv</em></td>
<td>Fruit</td>
<td></td>
</tr>
<tr>
<td><em>Palaquium lanceolatum</em></td>
<td>palakpalak</td>
<td><em>large bats</em></td>
<td>Fruit</td>
<td></td>
</tr>
</tbody>
</table>

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*“Large bats” refers to any of the large species found in the study area (*A. jubatus, P. vampyrus*, or *P. leucopterus*); the hunter did not specify beyond this.

*Exotic species
### APPENDIX B: Bat Plant Notes

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Note</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardiaceae</td>
<td><em>Anacardium occidentale</em></td>
<td>= kasoy (Tag.); cashew (English). Non-native and widely cultivated for seeds in the Philippines since at least the 1850's; a colonizer of open areas (Hensleigh and Holaway 1988)</td>
</tr>
<tr>
<td></td>
<td><em>Dracontomelon dao</em></td>
<td>= dao (Tag.). Found from 0-500 m elevation (PROSEA 1995), rarely to 1000 m (Hou 1978); height to 45 or even 55 m (PROSEA 1995); “...usually associated with amuguis [Koordersiodendron pinnatum], occupying a position in flats along streams, though found on moist slopes.” (Whitford 1911: 50). Intolerant of shade (Whitford 1911), grassland planting possible (Friday, Drilling, and Garrity 1999). Wood is moderately hard and used for light construction work and bancas (Whitford 1911), in demand for veneer, paneling, furniture, quality cabinet work, flooring, etc.; fruit, flower, and leaves eaten by humans; bark of possible medicinal value (Hou 1978).</td>
</tr>
<tr>
<td></td>
<td><em>D. edule</em></td>
<td>= lamio (Tag.). A large tree up to 37 m high; common on raised alluvial flats and on swampy ground (Hou 1978); Intolerant of shade; grassland planting possible (Friday et al. 1999). Fruits March, July, Sept. (Hou 1978).</td>
</tr>
<tr>
<td></td>
<td><em>Koordersiodendron pinnatum</em></td>
<td>= amugis (Tag.). Height to 50 m, a lowland tree rarely up to 460 m in the Philippines (Hou 1978, PROSEA 1995). Requires mesic soils and is found especially near streams in the lauan-apitong forest type (Whitford 1911). Intolerant of shade; grassland planting possible (Friday et al. 1999). Wood has good grain and fine texture; suitable for flooring, house construction, furniture, cabinet making; the gum is used in local medicine (Hou 1978); Wood is strong and durable; “This wood ranks among the first for general house construction.” (Whitford 1911: 50). Specific gravity is .67-.85 air dry, over 1 when green (Hou 1978). Fruits Feb – Dec. (Hou 1978).</td>
</tr>
<tr>
<td></td>
<td><em>Mangifera altissima</em></td>
<td>= pahutan (Tag.). Height to 30 m, a lowland tree rarely up to 400 m (Hou 1978). Usually found in the river bottoms (Whitford 1911: 52). Up to 20 m, in wet, evergreen forests in low and medium altitudes; fruit is 5-8 cm x 4-6 cm, green or slightly yellow when ripe (PROSEA 1995). Fruits April – Dec (Hou 1978).</td>
</tr>
<tr>
<td>Family</td>
<td>Genus</td>
<td>Common Name (Tag.)</td>
</tr>
<tr>
<td>--------------</td>
<td>------------------------</td>
<td>--------------------</td>
</tr>
<tr>
<td>M. indica</td>
<td>= mangga (Tag.)</td>
<td>Non-native and widely cultivated for fruit in the Philippines (PROSEA 1995, Hensleigh and Holaway 1988), generally below 500 m, with escaped or naturalized trees up to 1700 m (Hou 1978).</td>
</tr>
<tr>
<td></td>
<td>Spondias purpurea</td>
<td>= singuelas (Tag.)</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>Cananga odorata</td>
<td>= ilang-ilang (Tag.)</td>
</tr>
<tr>
<td>Bombacaceae</td>
<td>Bombax ceiba</td>
<td>= malabulak (Tag.), Salmalia malabarica, Bombax malabaricum. Large tree up to 40 m; found in lowlands often near streams (Jensen 1999). Flowers are 8-10 cm long, red (Jensen 1999). Wood is light (Whitford 1911); bark used for rope, wood for canoes, etc., young flowers as a vegetable, flowers, pods, roots, and gum in medicine (Jensen 1999). The seed is wind dispersed; found on forest edges (pers. obs.). Flowers in February/March in the study area.</td>
</tr>
<tr>
<td></td>
<td>Ceiba petandra</td>
<td>= kapok, boboy (Tag.)</td>
</tr>
<tr>
<td>Caesalpiniaceae</td>
<td>Cassia javanica</td>
<td>A small to medium-sized native tree found typically in molave type forest (Whitford 1911). Cassia fistula is apparently similar, but is a non-native, grows up to 1, 200 m elevation, ornamental, yellow flowers, pod fruit, wood with various construction and medicinal uses (Jensen 1999).</td>
</tr>
<tr>
<td>Combretaceae</td>
<td>Terminalia catappa</td>
<td>= talisay; Has two forms, one found on beaches and the other on river bottoms, the river-bottom form referred to both as Talasai and lumanog or lanipao (Whitford 1911); to 25 (~40) m (PROSEA 1995). Intolerant of shade; grassland planting possible (Friday et al. 1999); grows on denuded lands up to 300 m (Jensen 1999). Has construction and medicinal uses (Jensen 1999). Widmann (1996) identified the fruit being used by P. vampyrus.</td>
</tr>
<tr>
<td>Datiscaceae</td>
<td>Octomeles sumatrana</td>
<td>= malasapsap; A large tree growing best along streams. A light wood used for rafts and matches (Whitford 1911).</td>
</tr>
<tr>
<td>Dilleniaceae</td>
<td>Dillenia philippensis</td>
<td>= katmon; Height to 17 m (PROSEA 1995). Found along streams or on moist slopes and ridges; white flowers; wood used for furniture and construction (Whitford 1911).</td>
</tr>
<tr>
<td>Family</td>
<td>Species</td>
<td>Description</td>
</tr>
<tr>
<td>---------------------</td>
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<td>-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Ebenaceae</td>
<td><em>Diospyros philippensis</em></td>
<td>= kamagong; Height to 25-32 m, found on coastal hills and deeper soils of the Dipterocarp forests. Wood is hard and used for fine furniture, handles, etc. It is widely cultivated and its fruits, called mabolo, eaten (Whitford 1911). One hunter interviewed listed “Mabolo gubat” as a bat tree, probably a reflection of the fact that <em>D. philippensis</em> is cultivated as well as found wild in the forests. Widmann (1996) identified the fruit being used by <em>P. vampyrus</em>.</td>
</tr>
<tr>
<td></td>
<td><em>D. pilosanthera</em></td>
<td>= bolong-eta; A medium to large-sized tree often prominent in the understory of Dipterocarp forest types. Wood is very hard and used for same purposes as <em>D. philippensis</em> (Whitford 1911).</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td><em>Antidesma bunius</em></td>
<td>= bignai; A small tree found in the open grasslands; makes edible fruits (Whitford 1911).</td>
</tr>
<tr>
<td>Flacourtiaceae</td>
<td><em>Flacourtia rukam</em></td>
<td>= bitongol, cherry; Small tree 5-15 (~20) m; primary or secondary forest, often along rivers, up to 2100 m; cultivated for edible fruits, also medicinal and material uses; flowers June-Aug, fruits Sept-Nov (Sleumer 1954).</td>
</tr>
<tr>
<td></td>
<td><em>Muntingia calabura</em></td>
<td>= aratiles, datiles; Small tree up to 12 m; non-native, sometimes cultivated; a naturalized pioneer species; bears white flowers continuously; fruit a red berry with thousands of tiny seeds (Jensen 1999).</td>
</tr>
<tr>
<td>Meliaceae</td>
<td><em>Aglata harmsiana</em></td>
<td>Whitford (1911) states “Malatumbaga” is a Bataan name for the species given, and PROSEA (1995) lists it as a general Filipino name, and also give the following synonyms: <em>A. elliptica, A. oxyptetala, A. havilandii,</em> and <em>A. longipetiolata</em>. The tree can reach up to 20 (~40) m, and is found in primary and secondary evergreen forest, swamp forest, along rivers or roads and in periodically inundated locations, up to 2000 m (PROSEA 1995). Has various material and medical uses (PROSEA 1995). Note that Whitford (1911) says malatumbaga is a Zamboanga name for a close relative of Nauclea spp. called also Kalamansanai.</td>
</tr>
<tr>
<td></td>
<td><em>Lansium domesticum</em></td>
<td>= lansones; Tree up to 30 m, up to 800 m altitude, growing in shaded and humid conditions (Jensen 1999). Apparently native to the Philippines (Jensen 1999) and also cultivated. A wild variety (<em>L. dubium</em>) is known as lansones-bundok (Salvosa 1963).</td>
</tr>
<tr>
<td><strong>Sandoricum koetjape</strong></td>
<td>= santol; Medium-sized tree up to 20 m (Whitford 1911), from 0-800 m elevation (Friday et al. 1999); crown dense and compact; used for light construction (e.g. house building), carving, sacred images, furniture, edible fruit (also cultivated). (Whitford 1911: 46). Dry season tolerant; prefers evenly distributed rainfall (Friday et al. 1999). Widmann (1996) identified the fruit being used by <em>P. vampyrus</em>.</td>
<td></td>
</tr>
<tr>
<td><strong>Toona calantas</strong></td>
<td>medium-sized = kalantas; tree to 25 m (up to 40-50 m, Whitford 1911), low and medium altitudes in primary forest (PROSEA 1995); Crown wide spreading and open (Whitford 1911); typically occurs in flood plains in wetter forests, and along small streams in drier ones, not tolerant of shade (Whitford 1911); durable light-weight wood used for fine furniture etc. (Whitford 1911); closely allied with <em>T. ciliata</em> and <em>T. sureni</em> (PROSEA 1995). <em>T. ciliata</em> is a tree found principally along rivers up to 1500 m, <em>T. sureni</em> on riparian slopes to 1700 (~2100) m (PROSEA 1995).</td>
<td></td>
</tr>
<tr>
<td><strong>Moraceae</strong></td>
<td><em>Artocarpus ovatus</em> = anubing; Medium-sized tree to 30 m, lowland forest and shrubby vegetation to 750 m (PROSEA 1995); in drier forest types it is found in more mesic soils, wood is durable and hard (Whitford 1911).</td>
<td></td>
</tr>
<tr>
<td><strong>Moraceae</strong></td>
<td><em>Broussenieta luzonicus</em> = himbabao, babayan; syn. <em>Allaeanthus luzonicus, Morus luzonica</em>. Up to 15 m tall, found up to 1000m; in brush, secondary forests, and forest edges; light and durable wood which along with other parts of the plant has various uses (Hensleigh and Holaway 1988). “In thickets, secondary and lower edges of the forest, at low and medium altitudes, up to 1,000 m.” (Guzman et al. 1986). Described as a favorite of <em>P. vampyrus</em> by key informant. Widmann (1996) identified the fruit of a <em>Broussenieta</em> (species unknown) being used by <em>P. vampyrus</em>.</td>
<td></td>
</tr>
</tbody>
</table>
**Ficus aurantiaca**

*F. aurantiacea* is probably limited to growing on canopy trees of generally large diameter (S. Stier, pers. obs., see also Lambert and Marshall 1991: 801). All of the specimens of this climber at the National Herbarium in Manila (n=6) are recorded to have been on Dipterocarp hosts, large-sized commercial trees, and the only trees I ever saw them on in the study area were *Shorea contorta* (Dipterocarpaceae, also see Williams 1921). Corner (1938) records its habitat as forest up to 1700 m, Williams (1921) up to 2000 ft. Of *Ficus* spp. in the Synoecia section (including *F. aurantiaca*), Corner (1938: 87) says, “Concerning the biology of the fruits, one may remark that all animals seem to scorn these delightful objects...Malays always answer that neither birds, squirrels, monkeys nor bats will eat the fruits. Indeed, they commonly call the species of Synoecia ‘Tangisong Burong’ with such other plants as have bright inedible fruits over which the birds shed tears of disappointment.” Corner (1938) hypothesized that this variety was adapted especially to the monsoonal forests of the Malayan region.

<p>| <strong>F. crassiramea</strong> | A hemi-epiphytic strangler. |
| <strong>F. nota</strong> | = tibig; Hunters noted that use of <em>F. nota</em> (tibig) was rare, because only very tall individuals were used, and tall <em>F. nota</em> plants were very rare. “In forests and thickets usually near the river, 50 to 500 m. Endemic,” (Merrill 1906: 44). |
| <strong>F. pseudopalma</strong> | Up to 25 ft.; common in cut-over lowland forest (Williams 1921). |
| <strong>F. religiosa</strong> | Non-native to the Philippines; an ornamental tree in the Subic Bay Freeport. |
| <strong>F. subcordata</strong> | = payapa; syn. <em>Ficus calophylloides</em> (Elmer 1911, Williams 1921); Salvosa (1963) identifies payapa as <em>F. drupacea</em>. A hemi-epiphytic strangler that can assume a free-standing tree shape, making its identification difficult (see Williams 1921). |
| <strong>F. variegata</strong> | = tangisang bayawak; a pioneer tree common along watercourses (Spencer et al. 1996) |
| <strong>Ficus spp.</strong> | Balete refers to a large group of <em>Ficus</em> spp. in the subgenus Urostigma, generally characterized as being hemi-epiphytic. Amugan (Aetan; a large-fruited balete species), aymit (Aetan; a small-fruited balete species), and muro-muro (Aetan; a balete species) were also specified by interviewees. |
| <strong>Musaceae</strong> | <strong>Musa spp.</strong> | Fernando et al. (1998) lists <em>Musa errans</em> var. butuan as being present at Subic. |</p>
<table>
<thead>
<tr>
<th>Mimosaceae</th>
<th>Parkia roxburghii</th>
</tr>
</thead>
<tbody>
<tr>
<td>= kupang; A large tree reaching 35-40 m, crown wide spreading and open; a lowland tree common below 175 m (Whitford 1906). “Cupang is preeminently a tree of the rather open and second-growth forests where the dry season is pronounced, and is very scarce or entirely absent in those parts where a pronounced dry season is wanting.” It is also found in the open places within Dipterocarp forests (Whitford 1911: 40). Wood is light and used for paper and light construction, and other uses (Jensen 1999). Requires some shade when young (Jensen 1999) and a common species on forest edges and in forest gaps in the study area (pers. obs.); a nitrogen fixer (Jensen 1999).</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Myrtaceae</th>
<th>Psidium guajava</th>
</tr>
</thead>
<tbody>
<tr>
<td>= bayabas; height to 10 m, from sea level to 1600 m altitude (Jensen 1999). Introduced, cultivated, escaped, edible fruit and good firewood. (Whitford 1911: 88).</td>
<td></td>
</tr>
</tbody>
</table>

| Syzygium bordenii          | Apalang = Syzygium bordenii (PROSEA 1995); Interviewee said a synonym for Apalang was “tui”, defined by Salvosa (1963) as Dolicichandrone spathacea (Bignonaceae). S. bordenii is up to 25 m, flowers white (PROSEA 1995); Whitford (1911) calls the species the most abundant conspecific of the genera in the Philippines. |

| Syzygium spp.              | Malatampui = Syzygium xanthophyllum (PROSEA 1995), but interviewee instead listed “malatumbay”, so this needs clarification; S. xanthophyllum is in forests at low altitudes and not common, medium-sized tree to 20 m (PROSEA 1995). |

<p>| Syzygium spp.              | Malaruhat = Cleistocalyx operculatus (Salvosa 1963); = Eugenia bordenii (Whitford 1911), who says it is the most abundant Eugenia spp. PROSEA (1995) defines Eugenia bordenii as malaruhat-puti. PROSEA (1995) defines malaruhat as a general name for several Syzygium spp.: S. gratum (Laguna) (primary forest to 600 m), S. intumescens (Tag) (primary forest to medium altitude), S. nervosum (general) (forest up to 1500 m, usually at the edge of swamps and near streams), S. simile (Tag) (forest at low and medium altitudes). |</p>
<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Scientific Name</th>
<th>Natural Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Syzygium</td>
<td><em>Syzygium spp.</em></td>
<td>Makopa = <em>S. samarangense</em>, a non-native (Salvosa 1963). <em>S. samarangense</em> is cultivated for its fruit (PROSEA 1995). Makopag gubat is almost certainly a congeneric growing wild in the forests. It is of note that <em>S. samarangense</em> extends to 1200 m, requires moist soils and is often planted for that reason along streams (Jensen 1999). Fernando et al. (1998) lists <em>S. aqueum</em>, another non-native very closely allied with <em>S. samarangense</em>, as being present in the study area.</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Tristania decorticata</em></td>
<td>malabayabas; “...tree growing on dry coastal hills, and in the tanguile-oak type, where it sometimes occurs gregarious over small areas on very dry ridges or tops of low mountains.” (Whitford 1911: 88); PROSEA (1995) defines malabayabas as <em>Eugenia arcuatinaris</em>, and the synonym as <em>Cleistocalyx arcuatinaris</em>. Intolerant of shade; grassland planting possible (Friday et al. 1999).</td>
<td></td>
</tr>
<tr>
<td>Palmae</td>
<td><em>Cocos nucifera</em></td>
<td>niog; Distributed along coasts on beaches naturally but widely cultivated in the uplands up to about 600 m (1500 m; Jensen 1999), in climates with rainfall evenly distributed through year (Friday et al. 1999). Used for a variety of economic purposes (Jensen 1999). Widmann (1996) identified the flower being used by <em>P. vampyrus</em>. Sun-loving.</td>
<td></td>
</tr>
<tr>
<td>Papilionaceae</td>
<td><em>Erythrina fusca</em></td>
<td>ani-i, <em>Erythrina ovalifolia</em>. The tree was brought to the study area by the Batangas people as a coffee shade tree, but now seeds itself. Use of <em>Erythrina</em> spp. may have been due to use of leaves, which has been reported in other megachiropterans and new world bats (see Kunz and Diaz 1995: 114, and citations therein, Tan et al. 1998). [See Tan et al. 1998 for more discussion on the protein content of <em>Erythrina</em> spp.]. Sun-loving.</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>E. orientalis</em></td>
<td>dap-dap; Medium-sized tree with soft wood, growing along the seashore; cultivated as a shade tree for agricultural crops (Whitford 1911). Sun-loving.</td>
<td></td>
</tr>
<tr>
<td>Rubiaceae</td>
<td><em>Nauclea orientalis</em></td>
<td>bankal; intolerant of shade, found near streams, grasslands, secondary forest, resists well effects of fire; many uses (Whitford 1911). Used as a reforestation species (Guzman et al. 1986). Flowers from April to June, with fruits September to February (Guzman et al. 1986); has fruit in September in study area (pers. obs.). = bangkal; could be closely related to or synonymous with <em>Anatocephalus chinensis</em> (kaatoan bangkal).</td>
<td></td>
</tr>
<tr>
<td>Family</td>
<td>Species</td>
<td>Common Name</td>
<td>Description</td>
</tr>
<tr>
<td>-----------------</td>
<td>--------------------------</td>
<td>-------------------</td>
<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Sapindaceae</td>
<td><em>Euphoria didyma</em></td>
<td>Alupag</td>
<td>Whitford (1911) identifies alupag as <em>Euphoria cinerea</em>, a medium-sized tree up to 25 m; crown broad spreading and semi open. Found in molave and drier Dipterocarp forests. Intolerant of shade; used for house construction, tool handles, carabao yokes, ship parts. (Whitford 1911: 53).</td>
</tr>
<tr>
<td>Sapotaceae</td>
<td><em>Chrysophyllum cainito</em></td>
<td>Kaimito</td>
<td>Introduced, cultivated, up to 15 m tall (Hensleigh and Holaway 1988).</td>
</tr>
<tr>
<td>Sterculiaceae</td>
<td><em>Pterocymbium tinctorium</em></td>
<td>Taluto</td>
<td>Up to 40 (~50) m tall, most common on alluvial flats up to 1000 m (PROSEA 1995); common of forest edges (S.Stier, pers. obs.). At Subic the flowers are green. Widmann (1996) recorded use of its flowers by <em>P. vampyrus</em> in Leyte, Philippines. Soft wood used for rafts, matches, etc. (Whitford 1911).</td>
</tr>
</tbody>
</table>

---

| ?               | ?                        | Lusen             |                                                                 |
| ?               | ?                        | Bilulcao          |                                                                 |
| ?               | ?                        | Manipnip          |                                                                 |
| ?               | ?                        | Chico-bundok      |                                                                 |
| ?               | ?                        | Tomango           |                                                                 |
| ?               | ?                        | Malapusa          |                                                                 |

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APPENDIX C: Relationship of forest cover to bat population sizes*

Population Size vs. Forest Cover

Coefficients:
\( b[0] = -610.393 \)
\( b[1] = 65.077 \)

\( r^2 = 0.806 \)

*Each data point based on pooled data from 2 nights of observations.