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Habitat selection of endangered and endemic large flying-foxes in Subic Bay, Philippines

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Abstract

Large flying-foxes in insular Southeast Asia are the most threatened of the Old World fruit bats due to high levels of deforestation and hunting and effectively little local conservation commitment. The forest at Subic Bay, Philippines, supports a rare, large colony of vulnerable Philippine giant fruit bats (*Pteropus vampyrus lanensis*) and endangered and endemic golden-crowned flying-foxes (*Acerodon jubatus*). These large flying-foxes are optimal for conservation focus, because in addition to being keystone, flagship, and umbrella species, the bats are important to Subic Bay's economy and its indigenous cultures. Habitat selection information streamlines management's efforts to protect and conserve these popular but threatened animals. We used radio telemetry to describe the bats' nighttime use of habitat on two ecological scales: vegetation and microhabitat. The fruit bats used the entire 14,000 ha study area, including all of Subic Bay Watershed Reserve, as well as neighboring forests just outside the protected area boundaries. Their recorded foraging locations ranged between 0.4 and 12 km from the roost. We compared the bats' use to the availability of vegetative habitat types, riparian areas, and bat trees. The fruit bats' locations showed a preference for undisturbed forest types and selection against disturbed and agricultural areas. Bat locations also showed selection for particular fruiting/flowering bat trees. The bats showed strong preference for riparian areas; locations were in riparian areas over four times more than expected. From these results we recommend that management focus flying-fox conservation efforts on undisturbed forest and riparian areas.
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1. Introduction

Although flying-foxes (Old World fruit bats, Pteropodidae) have experienced nearly two decades of international conservation attention, populations are still declining (Mickleburgh et al., 1992; Kunz and Pierson, 1994; Tidemann et al., 1999). Large flying-foxes (genera

with max. forearm length >110 mm) in particular are of concern, because they tend to forage over wide ranges, roost conspicuously in colonies, and are heavily hunted (Mickleburgh et al., 1992; Pierson and Rainey, 1992; Kunz and Pierson, 1994). Most large flying-fox research has taken place in Australia (see citations in Pierson and Rainey, 1992). In Southeast Asia, where half (83/166) the world's flying-fox species are found, flying-foxes remain virtually unstudied (Mildenstein, 2002). This is a region with widespread fruit bat hunting, the world's highest amount of natural habitat loss, and where there is, effectively, no formal bat conservation commitment from governments (Mickleburgh et al., 1992; Whitmore, 1997).

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A daunting three quarters (20/27) of Southeast Asia's endemic large flying-foxes are threatened and endangered (Mildenstein, 2002).

Habitat use is an effective place to start conservation ecological research in Southeast Asia, because it provides protected area offices with information conducive to local management style. These offices often focus on their jurisdictions as geographical phenomena and have protected area management plans that are delineated by zones on maps. Areas of special interest such as endangered species' habitats can be easily addressed, understood, and incorporated into management plans and monitoring routines.

Unfortunately, there is little known about the habitat use of large flying-foxes. Most studies either infer habitat use from where bats were observed and/or caught (Heideman and Heaney, 1989; Widmann, 1996) or focus on habitat at roost sites and the surrounding vegetation (Eby, 1991; Palmer and Woinarski, 1999; Brooke et al., 2000; Vardon et al., 2001). In some cases, foraging habitat use on a local scale has been inferred from observations (Widmann, 1996; Brooke et al., 2000; Palmer et al., 2000).

Radio tracking, radio telemetry has proved useful in habitat use studies of smaller flying-foxes (Marimuthu et al., 1998; Winkelmann et al., 2000; Reiter and Curio, 2001). However, large flying-foxes are difficult to capture and difficult to track, since they fly above the canopy and travel long distances in mountainous terrain (Walton and Trowbridge, 1983; Mudar and Allen, 1986; Brooke, 2001). Radio telemetry has rarely been used on large flying-foxes in Southeast Asia.

At Subic Bay, Philippines, the protected area management office has been developing a conservation strategy for their roost of threatened and endangered large fruit bats, *Pteropus vampyrus lanensis* and *Acerodon jubatus*. This colony is particularly important, because it is one of only a few large colonies remaining of the Philippine endemic, *A. jubatus*. The fruit bats are not only important to Subic Bay ecologically, as pollinators and seed dispersers (Cox et al., 1991) and as an umbrella species for the whole protected area, but they are popular with the local community, who value them economically for eco-tourism, culturally as traditional food for indigenous Aetas, and as a flagship species for environmental awareness and conservation (Mildenstein, 2002). Since no ecological studies with any direct implications for conservation management exist on *A. jubatus* or *P. vampyrus lanensis*, the local government did not know how to protect their endangered bats beyond merely protecting where the bats roosted.

We assisted the protected area management's conservation efforts with habitat use information derived from radio telemetry. We focused our research specifically on the bats' use of the protected area within and near the boundaries of the national protected area, Subic Forest

Watershed Reserve, where the bats roost and are formally protected from hunting. Our objectives were to describe the bats' use of habitat on two ecological scales: vegetation type and microhabitat. We aimed to provide management with a map of areas within Subic Bay used by fruit bats and describe patterns of usage in terms of general vegetative types and microhabitat features, from which a habitat suitability model may be inferred.

2. Study area

The study area is a lowland monsoon dipterocarp forest in and around the Subic Bay Freeport Zone, Southwestern Luzon Island, Philippines (14° 47′ N, 120° 17′ E) (Fig. 1). The Subic Bay Freeport Zone is the former site of the largest overseas US Naval Base, which occupied the area from 1898 until 1991. The roads and buildings comprising the base are surrounded by a 10,000 ha forest relict, which once served as a buffer zone, storage area, and training grounds for the Navy. This area is
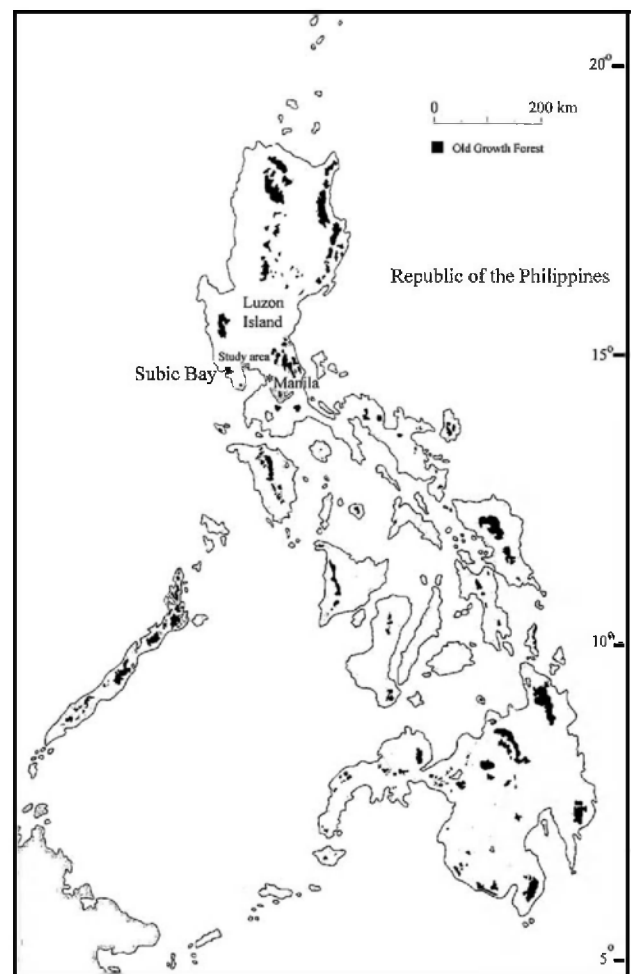

Fig. 1. Map of the Philippines with primary forests and Subic Bay. Remaining old growth forests in 1992 are shown in black (from Wildlife Conservation Society of the Philippines 1997).
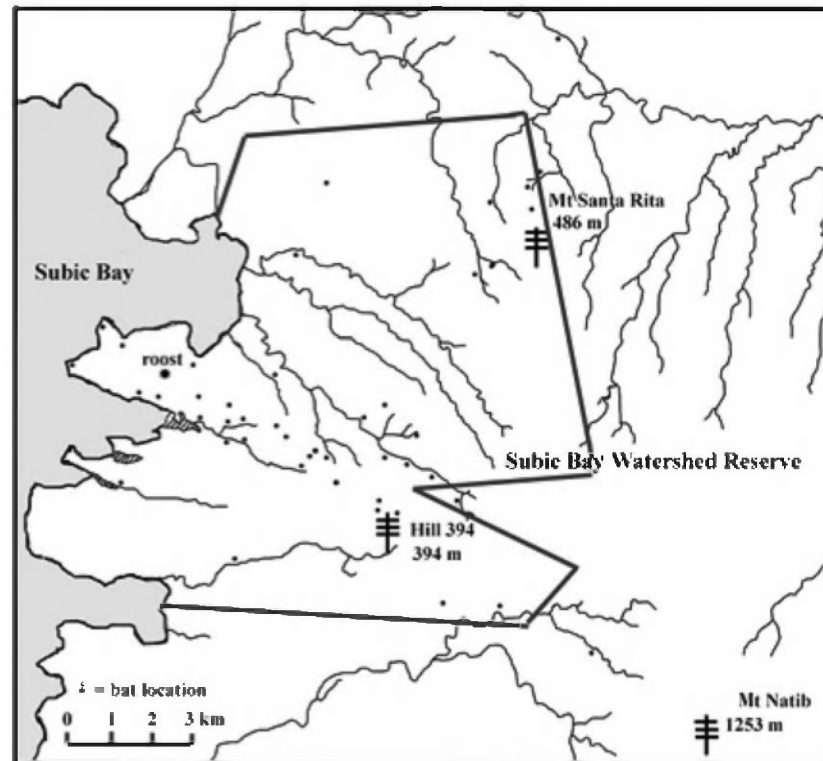
Fig. 2. Map of the study area with flying-fox roost site, telemetry receiver locations and flying-fox locations. Subic Bay protected area boundary is shown in black.

now a national protected area of the Philippine government called Subic Forest Watershed Reserve. It lies between Subic Bay and the Bataan mountains and ranges in elevation between sea level and 394 m and is adjacent to the larger protected area, Bataan Natural Park, which rises to 1253 m. The topography is interrupted by several steep volcanic plugs (the highest of these being 486 m high), which create very hilly terrain.

The climate of Subic Bay is affected by southeastern monsoons causing pronounced wet and dry seasons. Annual rainfall is reported as 3582 mm, based on a 41-year average by PAGASA Weather Station (Dalmacio and Fernando, 2000), with 95% of the rainfall between May and October. An average of five typhoons pass through Subic every three years. Average daily temperature is 26-27 °C.

The study area (Fig. 2) has 10 rivers flowing through it and consists of undisturbed old growth dipterocarp forest, mangrove forest, strand (beach) forest, selectively logged dipterocarp forest, and disturbed/secondary forest next to US Navy installations (e.g., roads, bunkers, and buildings). There is also some residential use of the study area both by the indigenous, forest dwelling, Aeta tribe and by prominent members of the Subic Bay community (e.g., investors, politicians, and government officials) in the neighborhoods created by the Navy to house officers and sailors with families. These residential areas are surrounded by natural forest but have also led

to the introduction of ornamental trees and agricultural varieties. The largest agricultural developments in the forest are a mango orchard (c. 100 ha), an ironwood tree plantation (c. 20 ha), and about 30 ha of mixed fruit orchards surrounding the Aeta village.

3. Methods

We conducted the radio telemetry study from January 2000 to May 2001, with the majority of the radio telemetry locations recorded between May and October, 2000.

3.1. Mist netting and capture procedures

To capture the fruit bats, we used three mist-netting sites: one located within the bat roost itself and the other two adjacent to, but outside of, the roost. Using tree climbers and/or slingshots, we hung ropes over upper canopy tree branches, about 30 to 35 m high in two trees about 10 to 15 m apart at each mist-netting site (Mildenstein, 2002). We used these ropes to raise the mist nets (four black nylon 6 m × 3 m mist nets sewn together to form a large, 6 m × 12 m mist net wall) up into the canopy with the top edge at a height of about 28 to 33 m. We raised the mist nets in the early morning, 2 to 5 am, as the bats were returning to the roost. Once the

nets were raised we monitored them continuously. As soon as a fruit bat was captured, we immediately lowered the mist nets and removed the bat to prevent injury.

We identified the species, sex, and age category (pups, juvenile, and adult) and measured the weight and forearm length of all captured bats (Mildenstein, 2002). To each bat over 300 g we attached a 12 g radio-transmitting collar (Holohil Inc., Ontario, Canada) with a position indicator mechanism that varied the rate of the signal pulse depending on the orientation of the fruit bat. Vertical transmitters on hanging bats produced a slow, one-pulse-per-second signal; horizontal transmitters (i.e. when the bat was flying) emitted a two-pulse-per-second signal. Cotton collars were substituted for the manufacturer's stainless steel wire collars to ensure that the collars would be likely to fall off after the one-year lifespan of the transmitter battery (all collars fell off between 5 and 8 months from being attached). The total time of bat handling from mist net capture to release was about 25 min.

3.2. Radio tracking/telemetry

Two days after collaring the bats, we began tracking them at night. With aluminum 3-element yagi antennas, we recorded bat locations remotely using triangulation of signal bearings. Two receiver teams on the tops of two of the highest peaks in the area (primarily: Hill 394, (394 m); Mt. Santa Rita, (487 m); or Mt. Natib, (1253 m); see Fig. 2) simultaneously sampled the bats' signal bearings at 10-min intervals regularly throughout the night, from around 6:00 pm until 6:30 am. The systematic sampling led to the reading of the signal bearing and location of any individual bat about once every two hours.

In addition to recording the signal bearings, receiver teams recorded whether the bats were hanging or flying, and both the general direction of as well as the observed strength of the received signal. This served as a check to be compared to the resulting triangulated locations of the bats. Of all the triangulated locations, we selected a subset to use in our habitat analysis based on the following criteria: bats in hanging position; bearings with an acute angle between them equal to or greater than 30°; consistency between observer notes on general direction and signal strength compared to the resulting triangulated location.

We tested error on 16 transmitters in known locations using the same methods and radio reception sites used to triangulate the foraging bat locations. Those being tested were "blind" to the test (they did not know they were being tested), thereby providing a more direct evaluation of the telemetry error than if the tests were known (Mills and Knowlton, 1989). We recorded error as the distance (m) between actual locations of transmitters and locations derived from triangulation of two signal bearings.

3.3. Habitat selection analysis: use vs. availability

We studied the bats' use of habitat on two different scales: broad-scale vegetative habitat types and two microhabitat features (i.e. riparian areas and tree species). We determined selection of habitat by comparing the bats' use to the availability of habitat types and microhabitat features. For all analyses, bat use was based on triangulated bat locations, which we visited in the field using global positioning system units (Garmin 12XL) and topographical maps of the area (Maps 7072 I and 7072 II, DENR, National Mapping and Resource Information Agency, Makati City, Philippines).

Many habitat use studies define habitat availability as the proportion of each habitat type within the home range of the study species (White and Garrott, 2000). For our study, however, it was necessary to define the availability of habitats as the proportions of each habitat type in the study area. Home range sizes of the study species are not known, but similarly-sized fruit bats fly an average of 20 km and a maximum of 50 km away from their roosts during nighttime foraging forays (e.g., McWilliam, 1985–1986; Eby, 1991; Spencer et al., 1991). This distance covers the Subic Bay protected area and much of neighboring provinces as well. With the limitations of our radio telemetry sampling equipment, topography, and access, it was impossible to sample the entire potential home range of the bats. In order to ensure that we were truly comparing use to availability, we limited our study area to the area in and around Subic Forest Watershed Reserve in which we had continuous radio coverage from both the receiver locations, thus eliminating the confounding effects of radio shadows (Fig. 2).

For the broad scale vegetative habitat analysis, we defined three types of undisturbed "natural" forest and two grades of disturbed forest. Undisturbed forest types included: (1) lowland dipterocarp forest, (2) mangrove forest, and (3) strand (or beach) forest. Disturbed forest included: (4) natural forest moderately disturbed by naval installations (e.g., roads, buildings, trails etc.) and by local residents for forest product extraction and/or low level agricultural use, (5) heavily disturbed forest areas, from here forth referred to as inhabited (e.g., residential areas with introduced ornamental and agricultural trees, heavily planted agricultural areas, and/or grassland with a few remaining natural forest trees remaining, esp. along waterways). Because we only assessed fixed locations of hanging bats, vegetative habitat types like large bodies of water, grassland devoid of trees, and residential areas with few trees and many buildings were omitted from the study area. We measured habitat available to the collared bats as the proportion of the entire study area comprised of each general habitat type (Neu et al., 1974). Using grids of 300 m × 300 m (a dimension close to our telemetry error; see below), we assigned a vegetative habitat type to each

grid based on the results of a floral inventory conducted by Dalmacio and Fernando (2000), our knowledge of the study area, and vegetative cover information on maps (Maps 7072 I and 7072 II, DENR, National Mapping and Resource Information Agency, Makati City, Philippines). We pooled all locations across individuals to determine the proportion of the locations in a particular habitat type.

The microhabitat analysis focused on riparian areas and known bat trees (e.g., tree species known to be used as a food source for bats). Availability of riparian areas included the proportion of the study area within 150 m of rivers and streams, and the bats' use of riparian areas is the proportion of the bat locations within this zone.

Bat use of trees focused on 11 tree species that were both known to be used by bats (either fruits and/or flowers eaten) based on bat hunter interviews, personal observations, and fecal analysis (Fujita, 1991; Stier and Mildenstein, 2005), and that would have been available for the bats' use during the season when we recorded their locations (based on phenological descriptions in DeGuzman et al., 1986 and by local foresters). These tree species were: *Mangifer altissma* (Anacardiaceae); *Terminalia catappa* (Combretaceae); *Calophyllum inophyllum* (Guttiferae); *Sandoricum koetjape* (Meliaceae); *Parkia roxburghia* (Mimosaceae); *Artocarpus blancoi, Ficus variegata, Ficus* sp. (Urostigma subgenus) (Moraceae); *Szygium cumini, Szygium simile* (Myrtaceae); *Nauclea orientalis* (Rubiaceae) (Table 1). Availability of bat trees in the study area was based on a systematic sample of 79, 20 m × 20 m plots throughout the forest (Dalmacio and Fernando, 2000). We determined the bat use of these tree species from 20 m × 20 m plots centered on the fixed hanging bat locations. Within the plots, we recorded which of the bat tree species were present with a size of at least 15 cm dbh.

For the broad scale habitat type analysis, we tested for statistical significance using a chi-square goodness of fit test, lumping beach and mangrove types to meet categorical sample size requirements (Dixon and Massey, 1969); beach and mangrove forests represented the smallest proportion of the study area and occur naturally in small amounts and often near to one another. For significance testing of riparian habitat selection, we used chi-square with Yate's correction. We evaluated the difference between the bats' use of all the bat trees and the availability of these trees in the forest with the Mantel-Haenzel chi-square approximation (Agresti, 1984).

Due to our low sample sizes of bat locations across individuals (mean # locations/animal ≡ 4.7, min. ≡ 1, max. ≡ 21), we pooled observations across animals for habitat selection analysis (White and Garrott, 2000). Pooling in this way leads to a loss of among animal variability (Neu et al., 1974) and decreases one's ability to assume independence of observations and availability of all habitats to all individuals (Thomas and Taylor, 1990). However, we only considered locations of hanging, not flying, bats for analysis, so successive locations of the same individual represent different locations the bats chose to land for at least 10 min, as opposed to flying locations on the way to hanging locations. Also, we recorded individuals' locations on a rotation usually leaving at least an hour between locations of the same bat, and no two successive locations were in the same area. Finally, although flying-foxes are known to often forage in large groups, none of our locations were grouped close together in space and time.

Table 1
Identification, use, and availability of tree species used by flying-foxes in Subic Bay, Philippines

Tree species	Local name	How identified[a]	Observed use[b]	Expected use[c]
Parkia roxburghii	Kupang	Fecal, obs., hunters	14	7.6
Sandoricum koetjape	Santol	Hunters, Widmann (1996)	9	4.7
Ficus variegata	Tangisang bayawak	Fecal, obs., hunters,	11	7.6
Szygium cumini	Malaruhat	Hunters	4	1.2
Nauclea orientalis	Bankal	Obs., hunters	2	0.1
Szygium simile	Panglongboien	Hunters	2	0.6
Terminalia catappa	Talisay	Hunters, Widmann (1996), Fujita (1991)	2	0.6
Artocarpus blancoi	Antipolo	Hunters	4	1.8
Ficus sp. Urostigma subgenus	Balete	Fecal, obs., hunters, Utzurrum (1984)	3	1.2
Callophyllum inophyllum	Bitaog	Widmann (1996)	2	0.6
Mangifera altissima	Pahutan	Hunters	5	5.9

[a] Bat tree identification: fecal ≡ fecal study (Stier, 2003; Stier and Mildenstein, 2005) obs. ≡ observed (Stier, 2003; Stier and Mildenstein, 2005) hunters ≡ bat hunter interviews (Stier, 2003; Stier and Mildenstein, 2005) literature as cited.

[b] Observed use ≡ # bat location plots in which species was present.

[c] Expected use ≡ # bat location plots in which species was expected based on proportion of plots where species was present in floral inventory (Dalmacio and Fernando, 2000).

4. Results

4.1. Mist netting and capturing

We spent 26 nights setting mist nets to capture fruit bats. Of the estimated roosting population of 26,333 flying-foxes at the Subic Bay colony (Mildenstein, T.L., Stier, S.C., Cariño, A.B. in litt.), we caught and affixed radio collars to a total of 13 bats, seven of which were of the endemic and endangered species, *A. jubatus*, (5 adult females, all lactating mothers; 1 adult male; and 1 juvenile female), and six were *P. vampyrus lanensis* (5 adult females, all lactating mothers; and 1 juvenile female), (see Mildenstein, 2002).

4.2. Radio tracking

From the collaring of the first bat in April, we spent 44 nights in the field recording bat locations. Many of these nights we stayed at the roost recording departure and arrival times and the directions of departure/arrival of the bats (unpublished data). On 23 nights, we tracked the bats from high locations by coordinated simultaneous triangulation.

Our radio tracking efforts resulted in 88 triangulated fixed locations of collared fruit bats during their nighttime feeding forays. Of the total 88 triangulated locations, we selected 47 hanging locations to use in the habitat analysis based on the quality control criteria listed above. These locations are from 10 animals (*A. jubatus*: 1 adult male, 4 lactating adult females, 36 locations; P. vampyrus: 4 lactating adult females and 1 juvenile female, 11 locations; Combined mean # locations/animal $= 4.7$, min. $= 1$, max. $= 21$). In general, the fruit bat fixed locations are spread over a 14,000-ha area (140 km^2) and are found in and around the protected area at Subic Bay. Average distance of the locations from the roost was 5.0 km ($n = 47$, SE $= 0.49$ km, min. $= 0.44$ km, max. $= 12.6$ km).

4.3. Habitat selection analysis: use vs. availability

The 47 locations in the various habitat types were distributed in undisturbed dipterocarp forest (32), disturbed forest (10), beach forest (3), and mangrove forest (2). No bats were located in the forests in the inhabited areas. The observed use of natural forest types (undisturbed lowland, beach, and mangrove forest) was nearly double that of the expected use based on availability. The use of disturbed forest and inhabited areas was less than expected (Fig. 3; $\chi^2 = 39.99$, $df = 3$, $p < 0.0001$), with the undisturbed lowland forest, and mangrove/beach forests contributing the most to the chi-square value. The preference of undisturbed forest types over disturbed habitats holds true for each species individually as well (Fig. 3), although in both cases the unpooled data were too few for statistical analysis.
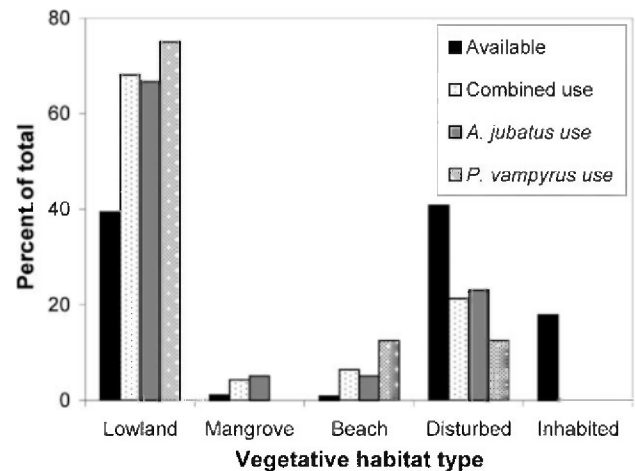

Fig. 3. Availability and bat use of vegetative habitat type for each species and both species combined. Y-axis is percentage of total plots represented by the habitat type for availability and percentage of total bat location fixes represented by the habitat type for use.
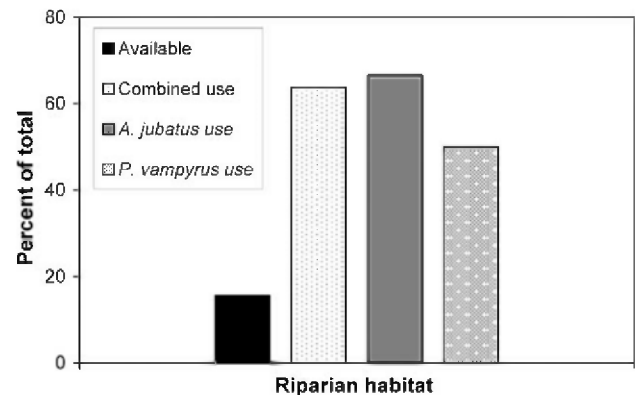

Fig. 4. Availability and bat use of riparian areas for each species and both species combined. Y-axis is percentage of total plots represented by the habitat type for availability and percentage of total bat location fixes represented by the habitat type for use.

Thirty of the 47 fixed locations were in riparian areas. Use of riparian locations was over four times what is expected based on riparian availability (Fig. 4; $\chi^2 = 21.57$, $df = 1$, $p < 0.0001$). Again, this preferential use of riparian areas by each species was also evident in the unpooled data.

Bat tree analysis is based on 46 plots; one plot was not visited in the field for security reasons. A large percentage of the plots (39/46 $= 85\%$) had bat trees in them that would have been fruiting, flowering, and otherwise available during the time when we recorded the location (Table 1), and we found bat use of plots with these tree species significantly different when compared to availability ($\chi^2 = 13.32$, $df = 1$, $p = 0.0003$).

4.4. Effect of telemetry error

The average error in location estimation was 238 m (SE $= 17.6$, $n = 16$). The average distance from a transmit-

ting collar to the receiver location was 11.9 km (SE = 2.2, $n = 16$). The tested transmitters were, in most cases, further from the receivers than were our recorded foraging locations of the flying-foxes. It is, therefore, likely that the estimated error of 238 m represents a larger error than what we experienced on the foraging data.

We assume that our estimated average error of 238 m does not confound our assessment of the vegetative habitat types and availability of bat trees in the bat locations. Whitford (1906) noted that natural forest vegetation in this region changes gradually with large-scale altitudinal gradients; the exceptions are beach vegetation and riparian areas, both of which tend to occur in narrow strips. These gradients and the topography of the area suggest that natural vegetative change in Subic Bay tends to occur at a much larger scale than the possible error in bat locations. Of the 47 bat locations, five had different habitat types within 238 m, and therefore could have led to misidentification of the habitat type used. The likelihood of misidentification of any of the locations' habitat types, however, is not great. All five of the locations are predominately surrounded by the same habitat, with a different habitat type representing only a small proportion of the surrounding area.

Since riparian locations are defined as those within 150 m of a river, it is also conceivable that error of 238 m led to an inaccurate count of locations in riparian areas. As an extreme example, consider an estimated bat location that falls on the edge of our designated 150 m riparian zone. An error of 238 m could mean that the actual location of the bat is as much as 388 m from the river. To test for this possible error, we expanded the availability of riparian habitat to include the largest possible error, while keeping the bats' actual use of riparian areas the same; bat use is still twice what would be expected ($\chi^2 = 8.36$, $df = 1$, $p = 0.0038$).

5. Discussion

This study addressed habitat use of flying-foxes in a mixed landscape of natural, disturbed, and agriculturally altered forest. With less than 10% of the country's original lowland forest cover remaining (Kummer, 1991), effective flying-fox conservation management requires information on how they select habitat in these landscapes. Some studies on related species have shown flying-foxes use orchards (e.g. Loebel and Sanewski, 1987), native as well as cultivated trees (Pierson and Rainey, 1992), and/or natural forests for roosting and tracking their food sources seasonally (e.g. Eby, 1991; Spencer et al., 1991; Vardon et al., 2001). Our data suggest that in Subic Bay, Philippines, P. vampyrus and A. jubatus use both disturbed and non-disturbed areas but are selecting disproportionately for natural forest areas (lowland dipterocarp, beach, and mangrove).

The data are limited for comparison of the two species. P. vampyrus is distributed throughout SE Asia and known in other areas to use agriculture and disturbed forest (Heideman and Heaney, 1992b; Rickart, 1993; Widmann, 1996). A. jubatus, on the other hand, is a Philippine endemic, that according to interviews with local hunters and anecdotal observations, tends to be in or adjacent to undisturbed natural forest (Heideman and Heaney, 1992a; Stier, 2003; Mildenstein and Stier, personal observations). While our data indicate both are preferentially selecting undisturbed forest and riparian areas, we tended to find P. vampyrus using the Subic Bay forest in a transient fashion en route to and from the roost (i.e. roughly at 6:30–8:00 pm on their way out to forage and 5:00–6:30 am on their way back). Only 1 of our 28 locations for adult bats between 8:00 pm and 5:00 am was from P. vampyrus. Because Subic Bay is a rare large tract of old growth lowland forest surrounded by a mixed matrix of agriculture, grassland, brush, and disturbed upland forest, with some scattered patches of natural forest, it is likely that P. vampyrus leaving the Subic Bay forest are foraging in areas much more disturbed than Subic Bay forest. It is curious why they would do this, especially since agricultural fruits offer less, nutritionally, than natural forest fruits (Nelson et al, 2000).

Others have remarked on this apparent habitat use difference between endemics and non-endemic fruit bats. In American Samoa, the local endemic, Pteropus samoensis, is characterized as being in large tracts of native, inaccessible forest, while Pteropus tonganus is capable of using both disturbed and undisturbed forest (Pierson and Rainey, 1992; Brooke, 2001). This same pattern appears to exist with the endemic Pteropus livingstonii and the non-endemic Pteropus seychellensis in Comoros (Cheke and Dahl, 1981).

On a microhabitat scale, we found that, of the 11 bat tree species likely fruiting and flowering during the time we were tracking bats, all but pahutan (M. altissma) were more frequently in bat locations than in the forest in general (Table 1). As a possible explanation for the unexpectedly low use of pahutan, we have heard from a bat hunter that pahutan is eaten by P. vampyrus but not by A. jubatus. Since only a quarter of our bat locations came from P. vampyrus, it is likely that our pooled locations underestimate the use of areas with pahutan by P. vampyrus.

Selection of some bat tree species may be underrepresented by our use vs. availability comparison. For example, tangisang bayawak (F. variegata) seeds are prominent in the fecal analysis of both species of fruit bats (Stier and Mildenstein, 2005). Our finding that it is 50% more frequent in bat plots than in the forest in general, is made more noteworthy by the fact that tangisang bayawak, like many other ficus, is dioecious (only females produce the figs that bats eat (Corner, 1933)) and it fruits year round non-synchronously with

con-specifics. Therefore, only a fraction of the *F. variegata* trees would have been fruiting at any point when a bat chose a location to hang, yet this fig species is still 50% more prevalent in bat locations than throughout the forest.

Perhaps the most dramatic bat habitat preference shown by our research is that of riparian areas. This has been noted in Australian large flying-fox species with speculation that bats use riparian areas for navigational purposes (Palmer and Woinarski, 1999; Eby personal communication) and for feeding (McWilliam, 1985–1986; Palmer et al., 2000). Many of the fruit trees used by bats in the Philippines are found most commonly along rivers. *M. altissma* (pahutan; Whitford, 1906), *Dracontomelon edule* (lamio; Flora Malaysiana, 1978), *F. variegata* (tang-isang bayawak; Whitford, 1906; Corner, 1933; Weiblen et al., 1995), *N. orientalis* (bankal; Chudnoff, 1984), and strangler figs (*Ficus* spp., subgenus Urostigma) (balete; Williams, 1921) have all been observed to be most common along watercourses. Figs in general tend to be more common in riparian areas than uplands (e.g. Gautier-Hion and Michaloud, 1989).

Finally, we acknowledge the limitations of our data. Our inferences are based only on a few individuals in a large population (Aebischer et al., 1993), and we could not link habitat selection to habitat quality leaving open important questions about ultimate factors of habitat selection and links to population dynamics (Garshelis, 2000; Morrison, 2001). However, for endangered and unstudied species in logistically challenging remote locations, a general habitat selection study provides initial insights into use of a highly disturbed landscape.

6. Management implications

Flying-foxes (Fam. *Pteropodidae*, Old World fruit bats) are important pollinators and seed dispersers in tropical forests and have been justly called "keystones" or strong ecological interactors, especially in Pacific Island ecosystems where there are few, or often no, alternate species to fill these roles (Cox et al., 1991). Over half (54%) of the 173 species in the *Pteropodidae* family are currently on the International Union for Conservation of Nature and Natural Resources (IUCN) list of threatened and endangered species (IUCN, 2000), and many others are thought to belong there but have not been listed due to insufficient data (Mickleburgh et al., 1992). Large fruit bats and fruit bats endemic to insular Southeast Asia, in particular, face serious threats from deforestation and hunting and should be considered conservation priorities.

Several international conservation organizations recognize the endangerment of Southeast Asian large flying-foxes and are promoting conservation through educational and research projects (e.g., Bat Conservation International, Wildlife Conservation Society, World Wildlife Fund, Lubee Foundation, etc.). Fruit bat conservation efforts are most lacking on a national and local scale. It is commonly asserted that this is due to disinterest, lack of environmental education and awareness, and/or ineffective government and natural resource management (Mickleburgh et al., 1992). But, in cases where there is a willing and able management body intact, there is still an absence of effective fruit bat conservation because of the lack of biological background information useful for conservation management. Such was the case where we worked in Subic Bay, Philippines. Managers knew little about how to protect the bats beyond the roost site, because no ecological studies with direct implications to conservation management had been done on *A. jubatus* or *P. vampyrus lanensis*. Our research provided the local conservation efforts with ecological information beyond the roost site and added to the small body of literature available on Southeast Asian fruit bats.

The Subic Bay large flying-foxes need more than Subic Bay's wildlife managers to protect them. Since they are wide-ranging animals, it will take cooperation between managers of neighboring protected areas and hundreds of landowners to promote their conservation throughout their home range. In addition to roosting in the Subic Bay protected area, the bats forage throughout the forest. As a group they tend to select natural, undisturbed forest over areas with agriculture and other human disturbances. For effective conservation of the bats, management should begin with curbing development in and along the forested area and monitoring access by people to enforce hunting restrictions and limit forest degradation.

Riparian areas in particular are important to the bats and are also the most threatened by human development. Rivers and river valleys are heavily impacted by upstream development, damming for water reserves, and factory effluents throughout SE Asia (Dudgeon, 1999). In Subic Bay, the mouth of every river is developed, and development projects are planned in riparian areas. Protected river corridors should be considered for the Subic Bay protected area management plan as an important step toward wildlife conservation.

Finally, it is important for managers to consider potential differences in habitat use between the two species. Unlike the widely distributed *Pteropus vampyrus*, *A. jubatus* is endemic to the Philippines, endangered, and evidence is mounting that they are natural forest obligates. With so little forest left in the Philippines, natural forest endemics, like *A. jubatus* should be a priority for conservation management.

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