On the Status, Reproductive Biology and Management of Fruit Bats of Yap

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Abstract—Traditional exploitation of fruit bats of Yap is limited, however commercial exploitation greatly reduced populations until they were protected indefinitely. There will be continued need to manage this resource. This paper is based on field work conducted while Yap's bats were intensively hunted. Data from field work is augmented with information from literature on other *Pteropus* to provide an overall picture of the life history of fruit bats for use by Micronesian resource managers.

The original data collected on Yap bats suggests that the populations of fruit bats on Yap islands and Ulithi atoll form two subspecies of *Pteropus mariannus*. In contrast to reports of seasonal breeding among other *Pteropus* over the past 51 years, *Pteropus mariannus yapensis,* reproduced throughout the time of this study. The reproductive ecology of Yap's bats and the importance of suitable habitat is also discussed.

Introduction

Yap State, one of the Federated States of Micronesia, in the Western Caroline Islands (9° 32′ N. 138° 8′ E.) consists of a group of high islands with a land area of 100.8 km, and 15 outer islands and atolls totaling about 19.2 km (Nicholson, 1969). The state's only indigenous mammals are fruit bats (*Pteropus*) found mainly on the four high islands of Yap and islets of Ulithi Atoll. Ecologically, fruit bats are believed to play an important part in pollination and seed distribution as summarized in Marshall (1985).

On Yap, fruit bats have legendary significance and are also a source of food. Traditional food taboos, however, restricted their use to certain groups in Yap's traditional social structure (Falanruw, 1982). Thus hunting pressure for local consumption is limited. However, on the nearby Marianas Islands, especially Guam and Saipan, fruit bats are much sought after as a specialty of the Chamorro cuisine. There, habitat change and overhunting have exhausted populations to the extent that Guam's fruit bats *Pteropus mariannus* and *P. tokudae* are listed as endangered species, the latter probably being extinct (Wiles and Payne, 1986). Demand for fruit bats remains high, however, and frozen bats command a high price on the Marianas' market. In response to this demand, large numbers of fruit bats have been exported from Yap to Guam and Saipan, (Wiles & Payne, 1986) causing a population decline on Yap. This paper reports research relevant to the management of the fruit bats of Yap.

Methods

Between June 1979 and June 1981, data were collected on 88 specimens of fruit bats from Yap and 10 from Ulithi. Examinations of specimens were of necessity opportunistic, and limited to a portion of hunters' kills with a bias toward mature females. Data collected included body weight to the nearest 0.1 g; forearm length to the nearest 1.0 mm; pelage color and condition of teeth. Reproductive data on females included width and length of mammae to the nearest 1.0 mm, lactation tested by expressing milk from engorged mammae, condition of the reproductive tract and location of uterine scars, and length and width of uterine horns and any enlargements to the nearest 1.0 mm. Cervices were examined and compared with human gynecological charts to determine whether they appeared primiparous or multiparous. Embryos in advanced stages of development were removed with the placenta, amniotic membrane, and fluid, and weighted to the nearest 0.1 g. The forearm length of 10 near-term fetuses was measured to the nearest 1.05 mm and notes taken on their development. Length and width of testes were measured to the nearest 1.0 mm and the visibility of seminiferous tubules noted. Representative specimens were preserved for scientific study with permission of Yap officials, and voucher specimens have been deposited at the American Museum of Natural History, New York.

Biweekly field trips were made throughout Yap, except for Rumung Island, to observe fruit bat activity and habitat. Records of food plants are based on observed feeding activity, chewed debris found under roosts and forage areas, and food material found on fur and in the buccal cavity or digestive tract of specimens. Lists of tree species common in fruit bat habitat were compiled and fruiting and flowering times noted. Records of the National Oceanographic and Atmospheric Administration weather station on Yap and the local farmer's market were analyzed to augment phenological observations.

Results and Discussion

TAXONOMY: The fruit bats of Yap belong to the genus *Pteropus* (Megachiroptera: Pteropodidae) which includes about 60 species (Honacki *et al.*, 1982). Species and subspecies reported from Micronesia include: *P. insularis* from Truk; *P. mariannus* from the southern Marianas; *P. molossinus* from Pohnpei and the Mortlocks; *P. mariannus paganensis* from Pagan and Alamagan; *P. pelewensis* from Belau; *P. pselaphon* from the Volcano and Bonin Islands; *P. tokudae* from Guam; *P. ualans* from Kosrae; *P. mariannus ulthiensis* from Ulithi; and *P. yapensis* from Yap (Koopman, personal communication). Anderson (1912) described a "mariannus group" of *Pteropus* which includes fruit bats from Guam, Yap, Palau, and Kosrae included in Table 1.

On Yap, fruit bats are called "maga'lau". Ulithians referred to them as "pochoy" originally, and more commonly today, gechel lemayural, literally meaning "the rat of the air". Scientists have referred the fruit bats of Yap state to a variety of taxa as listed below. For example, Corbet and Hill (1980) list them as separate species, while Honacki *et al.* (1982) list them as subspecies of *P. mariannus*. Data from this study are consistent with their designation as subspecies as given below:

Pteropus mariannus yapensis

Pteropus keraudreni, 1883, Tetens and Kubary, J. Mus. Godeffroy, 1.pt.ii, p. 50 (Yap).

Pteropus keraudreni var a, 1878, Dobson, Cat. Chir. B.M. p. 65 (Yap, Mackenzie).

Pteropus insularis, 1897, Trouessart, Cat. Mamm. i. p. 83 (Yap, Mackenzie).

Table 1. Forearm length of Micronesian members of the "Mariannus Group" of *Pteropus*.

Species[1] and locality	Number, age, and sex of specimens	Range of forearm length (average)	Reference
		mm	
P. mariannus, Guam	2 adult	134–136.5	Anderson, 1912
	8 adult males	135–154 (146.7)	Perez, 1973
	10 adult females	134–145 (141.4)	
P. marianus paganensis,[1] Pagan	3 adult males and 1 adult female	140–149	Yamashina, 1932
P. marianus ulthiensis,[1] Ulithi	3 adult males and 11 adult females	141–145	Yamashina, 1932
P. mariannus ulithiensis, Ulithi	4 adult males and	136–140 (137.8)	This study
	3 adult females	131–135 (133.7)	
P. yapensis, Yap	1 adult male	(130)	Anderson, 1912
P. mariannus yapensis, Yap	32 adult males and	117–138 (129.2)	This study
	44 adult females	115–138 (127.8)	
P. pelewensis, Palau	1 adult male and 3 juveniles	113.5–128	Anderson, 1912
	4 adult males and	110–122 (114.5)	Perez, 1968
	2 adult females and	115–125 (120)	
	1 young male	97	
P. ualanus, Kosrae	3 adult	130.5–133.5	Anderson, 1912

[1] Species names including misspellings of Yamashina (1932) are those used by the authors. Honacki et al. (1982) lists all as subspecies of *P. mariannus*.

Pteropus mariannus, 1899, Matschie, Megachir. p. 27 (Yap, Mackenzie).

Pteropus yapensis, 1908, K. Anderson, Ann. and Mag. N.H. (8) ii. p. 365 (Yap, Mackenzie).

Pteropus marianus yapensis, 1932, Yamashina, Trans. Nat. Hist. Soc., Formosa 22 (121): 241 (Yap).

Pteropus marianus ulithiensis

Pteropus marianus ulithiensis, 1932, Yamashina, Trans. Nat. Hist. Soc., Formosa 22 (121): 241 (Ulithi).

The mis-spellings of Yamashina above are hereby corrected to coincide with the proper spelling of the species "*P. mariannus*" and of the atoll "Ulithi".

Taxonomic studies of the *P. mariannus* group of fruit bats have been limited. Characters used to distinguish between members of the group include size of teeth, body size as measured by forearm length, and color of pelage. The difference in the length of teeth given for subspecies of *P. mariannus* in the literature is quite small (0.3 mm or 0.1% to 0.7% of the length of P3 teeth, and 1.2 or 2.0% to 4.0% of the length of P4 teeth). This small difference was beyond the precision of methods tried for measuring teeth of fruit bats in this study. Body size represented by forearm length extracted from Anderson (1912), Yamashina (1932), Perez (1968, 1973), and this study, are given in Table 1.

In general, the specimens of fruit bats from Yap were smaller than those from Ulithi, which were smaller that those from Guam. There is however, considerable overlap in size (Table 1).

COLOR OF PELAGE: Anderson (1912) states that the color pattern among the "mariannus group" of *Pteropus* is remarkably constant. The subspecies named by Yamashina (1932) however, are based largely on color variations. Traditionally, Yapese recognized up to seven "kinds" of bats on Yap alone. Distinctions were based largely on size, and coloration which appear to be related to social organization and habits of large males, females, and subadult animals. Fruit bats examined in this study exhibited a greater range of coloration than that described by Anderson or Yamashina. Thus pelage coloration is not a good means of distinguishing between fruit bats of Yap, Ulithi and Guam.

The most common color phase of Yap bats were animals with yellow buff mantles, mostly brown-black pelage on backs, and bellies flecked with silver hairs. The size, sex, and reproductive condition of bats exhibiting different color phases was compared but there was no definitive correlation. Large males often had especially golden mantles, however this coloration was also exhibited by a juvenile with milk teeth still present, an average size adult female, two subadult and two pregnant females. The golden hue of the mantle may be correlated with secretory activity of glands in the neck area (Nelson, 1964a). A group of 10 bats with especially whitish mantles and a greater abundance of white and silvery hairs on head, belly and back, included an immature male, two subadult females, three females in their first pregnancy, and three females in at least the second pregnancy. The most distinct color variation were bats with brown mantles, similar to the coloration described for *P. tokudae* (Tate, 1934). Only 6 of the 112 Yap specimens exhibited this phase, including two juvenile males, two subadult females and two females in a late stage of their first pregnancy. Ten specimens of *P. m. ulithiensis* included two adult males and one adult female with especially golden mantles. The rest exhibited the general coloration of Yap bats.

Given possibilities of genetic exchange between islands due to extensive flights (Wheeler, 1979; Wiles, 1982; Koopman and Cockrum, 1967; Ratcliffe, 1932; Nelson, 1964b; Daniel, 1975), transport by people (Hill, 1979), and overlap of size and coloration, more detailed studies of the genetic relationship of the *mariannus* group of *Pteropus* are in order.

DEVELOPMENT OF YOUNG: Literature estimates of gestation periods for *Pteropus* range from approximately 140 to 192 days (Anderson, 1912; Neuweiler, 1968; Marshall, 1947; Nelson, 1964b; Racey, 1973). A series of the nine largest fetuses and three smallest juvenile specimens of *P. mariannus yapensis* seen in this study indicate that forearm length is between 45 and 66 mm at birth. Milk teeth are erupted at least in the upper jaw at birth and pelage is present on head, neck and back, but is not fully developed on the belly. The lighter longer-haired mantle is distinct and the young are fully pigmented. After birth, by the time a forearm length of 80 mm is reached, adult canines begin to replace milk teeth and are fully emerged in a specimen with a forearm length of 95 mm.

The length of time that young bats are dependent on their mothers apparently varies. *P. giganteus* carry their young for the first few weeks (Neuweiler, 1968). Young *Pteropus* of other species are weaned between 10 and 27 weeks (Jones, 1980; Pook, 1978; Nelson, 1964b). *P. giganteus* and *P. poliocephalus* fly at 3 months (Marshall, 1947; Nelson, 1964b; Neuweiler, 1968), and young may remain associated with their mother for about 4 months to a year (Neuweiler, 1968; Pook, 1978; Jones, 1980).

MATURATION: Condition of the uterine tract, mammae, cervix, and teeth were used to define development classes of female *P. m. yapensis*. Immature females have very small mammae similar to those of males. The uteri of eight specimens measured 1.5 to 2.5 × 2 mm in width and length. Specimens categorized as subadult had uterine horns which were thickened throughout their length to at least 2 mm, no enlargements over 4.5 mm or uterine scars, and had uterine horns similar in length (within 2 mm). The mammae of subadult females ranged from 2 × 3 to 9 × 9 mm. Teeth of these animals were not worn. Adult specimens had uterine horns at least 4 mm wide, and/or uterine enlargements over 4.5 mm, and uterine horns unequal in length. Many were lactating and some had uterine scars.

Primiparous females with near-term fetuses had mammae 7 × 11 to 10 × 13 mm, the latter belonging to a female that had just delivered her first young. The mammae of multiparous females were often quite large, ranging from 7 × 10 to 12 × 18 mm. Young fruit bats have an instinct to bite and hold onto mammae. The period of lactation often overlaps with the next pregnancy and mammae appear to remain large after the first young is born. Thus the size and condition of mammae are roughly indicative of the development classes: immature, subadult or early first pregnancy, and advanced pregnancy or multiparous individuals. This correlation may be useful in the collection of data on animals that cannot be dissected.

Estimates of the time required for various species of *Pteropus* to reach sexual maturity range from 1½ to 2 years (Nelson, 1964a, 1964b; Asdell, 1964). The shortest forearm length at which a specimen of *P. m. yapensis* was pregnant was 115 mm. The range of forearm length of 9 primiparous specimens was 115 to 138 mm. Body weight appears to be a factor in sexual maturation. The lowest body weight (minus weight of embryo, amniotic fluids and placenta) of a pregnant female was 291 g for an individual with a forearm length of 122 mm. Females with longer forearms but weighing less were immature. A single immature female of *P. m. ulithiensis* had a forearm length of 122 mm and a single primiparous specimen a forearm length of 135 mm. Two specimens that had born at least one previous young had forearms 131 and 135 mm long.

Two female *P. m. yapensis* raised in captivity from 3 about weeks of age to 6½ months and 21 months, attained forearm lengths of 108 and 122 mm, and weights of 203.0 and 297.7 g respectively. The younger animal was immature, and although the older female had attained adult size, she had mammae characteristic of immature females.

Among males, the smallest testes and epididymis with visible seminiferous tubules were at least 14 mm wide. The shortest forearm length of a male fruit bat with testes at least this width was 116 mm, and the average of 14 such animals was 129 mm. Their average weight was 362 g. Two male fruit bats from Yap raised in captivity to ages of 1.5 and 3 years after separation from their mother, attained forearm lengths of 120 mm and 125 mm, and weights of 269 gm and 400 g respectively.

The lifespan of wild *Pteropus* is not known. A captive *P. giganteus* lived 17 years and 2 months (Koopman and Cockrum 1967), and a pet *P. mariannus* was kept 9 years before an accidental death.

REPRODUCTION: Both sides of the bicornate uterine tract are functional in *P. mariannus yapensis,* however a greater number of advanced pregnancies were noted in the left

Table 2. Reproductive state of *P. m. yapensis* examined June 1979–June 1981.

Description	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Bats examined	2	10	9	6	8	12	0	21	6	3	4	7	88
Males	2	2	2	1	5	4	0	8	0	2	1	4	31
Immature (or with testes <14 mm)	2	1	1	0	2	1	0	3	0	2	0	2	14
Mature (testes 14 mm or more)	0	1	1	1	3	3	0	5	0	0	1	2	17
Females	0	8	7	5	3	8	0	13	6	1	3	3	57
Juvenile	0	2	2	0	0	0	0	1	2	0	1	1	9
Subadult	0	2	0	2	0	0	0	0	0	0	0	0	4
Adult													
Not pregnant	0				1	4*	0						5
Pregnant													
Embryo <10 mm	0	1, 1*			1°, 1*	2*	0	4*			1°		11
Embryo >10 mm	0			1*			0	1°, 1*			1°	1°+, 1	6
Fetus near term		1°	1°, 1, 1	2*				1°	2°, 1*				10
Post-partum		1	1, 1*′					3*		1*			7
Post-partum, newly pregnant or both						2*		2*	1*				5

* lactating
° first pregnancy
\+ twins
′ had just given birth

horn. Uterine scars were found in horns opposite sites of successful implantation in 7 of 30 pregnant females with a higher incidence of scars in the right uterine horn.

One female bore twins of unequal size. Measured in the amniotic sac, the fetus in the right uterine horn was 22 × 33 mm and that in the left horn 25 × 37 mm. A literature search resulted in only 3 reports of twinning in other species of *Pteropus* (Asdell, 1964; Ratcliffe, 1932; Cheke and Dahl, 1981), in contrast to many reports of only single births.

Marshall (1953) stated that while both ovaries of *P. giganteus* are functional, only a single ovum is released each breeding season; however a progestational reaction occurs only in the horn adjacent to the ovary that contains the ruptured follicle so that the opposite horn retains its oestrous appearance. The case of twinning in *P.m. yapensis* would seem to have resulted from incomplete hormonal inhibition of a second pregnancy and closely spaced ovulation between the two sides of the reproductive tract, or from retarded development of the twin in the right horn. The low incidence of twinning in *Pteropus* may be due to physiological selection in the form of abortion of embryos in one side of the reproductive tract in this large flying mammal.

Breeding Pattern—Reproductive data on 57 female *P. m. yapensis* show most young in advanced stages of development and most postpartum uteri in February to April and August to October. The only nonpregnant adult females were found in May and June (Table 2). Three adult female *P. m. ulithiensis* shot in April included one female with an embryo over 10 mm, one in postpartum condition, and one that had borne at least one young but was not pregnant. Perez (1973) reported unborn *P. mariannus* in Guam in March and September.

The number of females lactating and also newly pregnant (Table 2), and observed copulation of males with females carrying unweaned young, suggest that one pregnancy follows another in fairly rapid succession in *P. m. yapensis*. Most mature females apparently become pregnant at least once a year, and possibly twice, as only one of the 44 mature females was neither lactating, in postpartum condition nor pregnant. During this study, *P. m. yapensis* reproduced throughout the year with perhaps a higher incidence of births during February to March and August to October. This data diverges from the breeding patterns reported for other *Pteropus* over the last 51 years.

Baker and Baker (1936) concluded on the basis of their fieldwork and the literature of the time, that most Pteropodidae have sharply defined breeding seasons with species north of latitude 4° N bearing young in March or April and species south of 4° N bearing young in September and October. Most recent reports suggest that species at higher latitudes tend to bear earlier in spring, and those at lower latitudes bear later in fall, with the exceptions of one Australian and three Indian Ocean species (Marshall, 1947; Moghe, 1951; Brosset, 1962; Neuweiler, 1968; Ratcliffe, 1932; Nelson, 1964a, 1964b; Cheke and Dahl, 1981). Despite the variations, all except Moghe (1951), who includes records of bats at the London Zoo, report or presume a single breeding period and birth per year. A number of authors, including Baker and Baker (1936) however, report some "acyclic" breeding of *Pteropus*. Such reports and the data on *P. m. yapensis* suggest that reproduction in the genus is not governed by a strict endogenous annual cycle.

REPRODUCTIVE ECOLOGY: If breeding of at least some *Pteropus* is not governed by an endogenous annual cycle, what are the factors which have resulted in reports of a defined breeding season for so many years? The work of Nelson (1964a, 1964b, 1965) and

Neuweiler (1968) point to the important influence of environmental and social factors in the timing of reproduction in *Pteropus*.

In Australia, Nelson described social organization and group mating behavior in two species of *Pteropus* aggregated in "summer camps" when environmental factors apparently contributed to aggregation. Bats then dispersed to other areas with seasonal changes in food sources and young were born during that time (Nelson 1965). In an undisturbed colony of *Pteropus giganteus* established in an area in India rich in food sources throughout the year, it appears that the reproductive cadence was determined more by the length of gestation, nursing and resulting intraspecific group dynamics in a small area (Neuweiler, 1968).

Yap lies near the intertropical convergence zone and experiences a variable rainfall pattern and wide range of phenological phenomena. An analysis of tree crop records showed considerable variation from year to year even for single season species. Fruit bats eat fruit or blossoms of species flowering annually, biannually, irregularly, and almost continuously. Given so many environmental variables and the frequent disruption of colonies by hunters during this study, it appears that there was neither an environmental nor a social metronome governing reproduction of Yap fruit bats during this study so that reproduction was determined largely by length of gestation and opportunistic copulation.

Habitat—Suitable habitat must be an important factor in fruit bat productivity. Carpenter (1975) reports that a flying *P. poliocephalus* consumes 20 times as much energy as a hanging individual. Energy requirements of pregnant females and females with attached young must be higher. A near-term fetus of *P. m. yapensis* weighted 13% of its mother's body weight and juveniles with milk teeth averaged 20% of the average weight of adult females. The presence of body fat appeared to be an important factor in females pregnant for the first time. It appears that the shorter the distance that fruit bats must fly to reach food, the higher the caloric and nutrient value of this food, and the less disturbance there is to roosts, the greater will be the reproductive rate and number of pregnancies carried full-term.

Yap appears to offer ideal habitat for fruit bats in the close proximity of roosting and feeding areas. Most of Yap's vegetation has been altered by man. Agroforests cover about 27% of the island and are generally adjacent to coastal mangroves which make up 12% of the vegetation. Forest, most of it secondary, makes up about 28% of the vegetation and *Pandanus* savanna occurs inland over about 22% of Yap (Falanruw *et al.*, 1987).

In the course of this study, 21 roosting sites were located. Fruit bat activity involved daytime roosting in mangroves (often in *Sonneratia alba* trees) and forest, sunset to just post sunset flights to forage in agroforest or *Pandanus* savanna; and pre-sunrise to sunrise flights back to roosts. Hunters reported increased roosting in mangroves and decreased feeding in *Pandanus* savanna with increased hunting pressure. In 1965, when populations were very high, large numbers of bats fed on ripe fruit of *Pandanus tectorius* in savanna areas (personal observation).

Agroforests provide high energy food and are major feeding grounds for fruit bats. Species eaten by fruit bats include the fruit of at least *Artocarpus altilis* (Park.) Fosb., *A. heterophyllus* Lam., *Citrus* spp., *Eugenia* spp., *Musa* spp., *Carica papaya* L., *Cocos nucifera* L., *Annona muricata* L., *Mangifera indica* L., *Inocarpus fagifer* (Park.) Fosb., *Terminalia catappa* L., and *Ceiba pentandra* (L.) Gaertn. In less anthropocentric forests, *Ficus prolixa* Forst f. and other species of *Ficus* are important food sources with at least some trees in fruit most of the time. Ripe fruits of *Semecarpus venenosus* Volk., *Calophyllum inophyllum* L., and *Campnosperma brevipetiolata* Volk., are eaten as well as blossoms of *Parinari* spp., *Freycinetia* spp., *Calophyllum inophyllum* L. and *Glochidion* sp. Mangrove species eaten include the flowers of *Lumnitzera littorea* (Jack) Voigt, and flowers, fruit and leaves of *Sonneratia alba*. J.E. Sm. It appears that Yap's bats eat a wide variety of plant parts when preferred foods are not available.

USE AND MANAGEMENT: Patterns of vegetation and populations of people and fruit bats were correlated on Yap. People aggregated in coastal areas where there was access to marine resources, and planted fruit trees. Bats ate and helped to spread some fruit trees, and fed at the outskirts of agroforests. Prior to contact with the outside world, the islands of Yap are believed to have had a very dense population (Mahoney, 1958; Underwood, 1969). The society was highly organized and stratified. Access to resources was proscribed and fruit bats were the food of less powerful groups living more inland with limited or no access to fishing grounds (Falanruw, 1982). The numbers in these groups were probably higher when resources were at a premium.

As was the case with fishing and gardening, harvesting of fruit bats was traditionally subject to considerable ritual and organization. This included a special house where men isolated themselves prior to hunting, and a shaman to perform appropriate ritual. Fruit bat harvesting in at least one village on Yap about 30 years ago, involved seasonal netting of bats in the hundreds from trees near the perimeter of their flight paths. The per capita fruit bat resource on Yap must have built up as the population of Yap declined from 7,464 in 1902 (Thilenius, 1917) to 2,478 in 1946 (Useem, 1946).

Limitation of the use of fruit bats to a portion of an island's population occurs elsewhere in the Pacific. On Tonga, hunting of fruit bats is the prerogative of chiefs. Hill (1979) reports that fruit bat flesh was appreciated by the "chiefs of old" in Rarotonga. A god of the fruit bat and permanent platforms as high as 150 feet in trees were reported from Niue (Loeb, 1926).

In the Marianas, the demand for fruit bats is high. They are boiled whole, generally with coconut cream, and their fruity–musky smell contributes to a unique taste which commands a high price. Any cultural limitations on the exploitation of this resource have long been forgotten. Linsley (1934), Bryan (1939) and Nicholson (1945) have commented on the popularity of fruit bats on Guam.

Since the 1940's, populations of fruit bats have declined markedly in the Marianas, probably due in part to the decline of agroforests, as Guam became more commercialized, combined with continued hunting pressure. The killing of Guam's fruit bats was made illegal in 1973, and they have subsequently been listed as endangered species by the U.S. Fish and Wildlife Service in 1984. Numerous reports on the decline and trade in fruit bats of Guam are summarized in Wiles and Payne (1986).

Fruit bats from Yap were initially brought to Guam as gifts. Later as the trade became commercialized, traditional patterns of exploitation were ignored. Associated with the rise of the trade was the extension of Yap's road system giving greater access to flightlines. The public nature of roads as opposed to traditional paths allowed a disproportionate number of non-Yapese to enter the trade. The number of rifles and shotguns on Yap increased, most likely in correlation with the trade in fruit bats as there is little else except the Micro-

Table 3. Known exports of fruit bats from Yap 1974–1981.

Year	Imported/exported	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1974														Few[1]
1975														About 1,000[1]
1976														About 3,300[1]
1977	No data													
1978	Number imported to Guam[1]							379	455	130	30	118[3]	225[3]	About 4,400[1]
	Pounds exported from Yap[2]	288	405	124	65	244	314	136	83	149	98	53	155	2,114
1979	Number imported to Guam	199[3]	239[3]	227[3]	180	250	464	100	80	0	485	207	530	2,961
	Pounds exported from Yap[2]	105	15	57	18	59	26	44	243	57	9	117	191	941
1980	Number imported to Guam	495	0	350[4]	148[4]	2,256[4]	364[4]	1,623	1,000	1,052				7,288
	Pounds exported from Yap[2]	65	32		174	350	120	30	305	421	898	145	463	3,003
1981	Pounds exported from Yap[2]	858	400	548	219	408		90[5]		51[5]				2,574

[1] Guam Division of Aquatic and Wildlife Resources Annual Reports 1978–79, 1980–81.

[2] Via air freight; compiled from Air Micronesia freight records.

[3] Estimate based on number of bats requested for importation that month and the percentage of requested bats imported during the rest of the fiscal year; Guam Division of Aquatic & Wildlife Resources.

[4] Estimate based on number of bats requested for that month and the percentage of requested bats imported during rest of sample period; Guam Division of Aquatic & Wildlife Resources.

[5] Refused entry into Guam.

nesian pigeon to hunt. The ratio of the number of fruit bats exported to the number of registered guns peaked in 1975 and 1976, and then declined (Falanruw, 1981). By 1979, fruit bats were becoming harding to harvest and some hunters quit the trade. Increased prices encouraged others and fruit bats began to be shot mainly in their roosts. The high rate of exports continued into 1981 when shipments included many juveniles and females in their first pregnancy.

Partial records of the numbers of fruit bats imported into Guam from Yap are available from Guam Department of Agriculture records for the years 1974 to 1980 (Table 3). These are estimates based largely on requests for import permits on which numbers are often inflated (Wiles and Payne, 1986). Additional data on bats exported via air freight from Yap to Guam and Saipan during the period January 2, 1978 to December 30, 1981 is presented (Table 3). This data was recorded in pounds rather than numbers of animals. An estimate of the minimal number of bats involved might be obtained by dividing the shipment weights by 0.76 lb, the average weight of adult *P. m. yapensis* measured in this study. The actual number of bats exported was higher however, as shipments included small bats weighing as little as 0.13 lb. Considerable numbers of fruit bats were also carried to Guam and Saipan in uninspected luggage. Other bats were killed by shotgun scatter and not recovered.

Fruit bats became Yap's highest priced export commodity from 1975 to 1981. While not officially recorded, fruit bats were a major export when compared with exports reported in the Trust Territory of the Pacific Islands Annual Reports to the United Nations (1975–1979), and the Yap State Government Statistical Yearbook for 1980.

After a number of years of non-enforcement of a three-month hunting season, the killing of fruit bats was prohibited by law by the First Legislature of the State of Yap in September 1981. A law prohibiting the possession of firearms in Yap State was passed at the same session. In recognition of Yap's law, Guam custom's officials do not allow the entry of Yap fruit bats into Guam.

Populations of *Pteropus* appear to be declining in many areas (Cheke and Dahl, 1981; Wheeler, 1979; Wiles and Payne, 1986), and there is particular concern for insular species as they are especially vulnerable to depletion. The reasons generally given for declines are habitat destruction combined with overhunting. Suitable roosting sites may also be a limiting factor (Racey, 1979).

On Yap, the decline of the fruit bat population was largely due to unsustainable harvest. Construction of the new airport removed a large foraging area and the impact of associated siltation and other damage to mangroves remains to be seen. However, much suitable habitat remains and, even with some poaching with air guns for local consumption, the limitation of exports has resulted in an increase in fruit bats on mainland Yap to an estimated population of 2,500 to 5,000 in 1984 (Engbring, 1985).

In the long run, survival of viable populations of fruit bats will be related to harvesting and to vegetation patterns produced or allowed by people. A 1987 change in the political status of the Federated States of Micronesia will result in an initial inflow of development funds which are expected to then decrease over a 15-year period beginning in 1987. As a result, local objectives stress economic development and increasing self-reliance (Yap State Government, 1982). In addition to their ecological value, fruit bats are valuable as a local food resource and tourist attraction (Wiles and Payne, 1986). There will be a continuing need to manage fruit bats wisely, especially for the years when aid funds decrease. The fate of *Pteropus mariannus yapensis* will be indicative of Yap State's ability to manage its natural resources on a sustainable basis.

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