

## Restricted Pollination on Oceanic Islands: Pollination of *Ceiba pentandra* by Flying Foxes in Samoa<sup>1</sup>

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### ABSTRACT

The very low diversity of animal pollinators on remote oceanic islands can act as a potent biotic filter to potential plant immigrants. To assess the relative difficulties faced by colonizing plant species, we studied the pollination ecology of kapok, *Ceiba pentandra* (Bombacaceae), a widespread aboriginal introduction to Pacific islands. The Samoan form of this tree is self-fertile, but requires pollination for fruit set. In continental areas *C. pentandra* attracts a diverse assemblage of pollinators, but in Samoa it is pollinated only by *Pteropus tonganus* (Megachiroptera: Pteropodidae)—an example of a plant exclusively dependent on one bat species for pollination. The pollination system is dystrophic, however, since foraging flying foxes may destroy up to 50 percent of *C. pentandra* flowers and developing fruits. Though resource defense is regarded as rare in nectarivorous bats, *P. tonganus* vigorously defends small feeding territories on the rich, but readily depleted, *C. pentandra* nectar resource. This intraspecific conflict probably shapes patterns of pollen transfer within and among trees, and enhances cross-pollination. Our study highlights the importance of conserving pollinators in remote oceanic islands with depauperate pollinator faunas.

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### AUTU

Ua ese lava le fa'atupulagaina o le vavae (*Ceiba pentandra*) i Samoa i lo le tulaga e masani ai le vavae i isi itu o le lalolagi, ae maise Aferika ma Amerika saute. E pau lava le manu e feavea'i ai le polini (pollen) mai le tasi fuala'au i se isi fuala'au, o le pe'a (*Pteropus tonganus*) lava lea. E leai lava ni manuiti po'o isi manu lele e feavea'i ai le polini. O lona uiga la, o le pe'a o se manu taua tele i le olaga o le vao matua ma e tatau lava ona faasao ia manu mo taeao.

THE COLONIZATION OF OCEANIC ISLANDS by plants has been a topic of interest since Darwin's time (Darwin, 1876). Such early workers as Wallace (1881), Henslow (1910), and Ridley (1930) examined mechanisms of long distance dispersal, while more recent attention has been directed to the consequences of different plant breeding systems for island colonization (Baker & Cox 1984; Cox 1985, 1989). The reproductive ecology of plant immigrants to oceanic islands subsequent to establishment remains little studied, but it appears that the

pattern of pollination syndromes in oceanic islands differs significantly from that of continental areas. For example, New Zealand, which has few potential pollinators in its fauna compared to continental areas, has a flora characterized by plants which are adapted to generalized pollinators (Lloyd 1985).

In general, plants requiring specific, specialized pollinators cannot easily colonize oceanic islands prior to the establishment of their pollinators. Similarly, pollinators with a narrow range of host plants will encounter difficulties as colonists. On oceanic islands, the difficulties imposed on potential plant colonists by depauperate pollinator faunas increase with increasing distance from continental source faunas.

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The reproductive ecology of very recent plant immigrants to isolated oceanic islands is of particular interest, since they are unlikely to have achieved significant *in situ* evolutionary adjustment to their pollination problems. The ideal species for study would be one whose pollination ecology is well-known in continental areas, where it is visited by a large number of different pollinators. Comparison of such a species in its continental headquarters and in an island outpost could yield insights both into the ecological problems plant immigrants face and into the nature of pollination systems in oceanic islands. The study of such a species could also provide a rough indication of the diversity of the island's pollinator pool.

*Ceiba pentandra* (L.) Gaertn. (Bombacaceae) is an example of a pantropical plant whose pollination ecology has been well studied in continental areas, but remains uninvestigated on isolated islands. In West Africa (Baker & Harris 1959), India (van der Pijl 1935), Brazil (Carvalho 1960), and Peru (Janson *et al.* 1981), a diverse assemblage of vertebrates and invertebrates visits its flowers. Van der Pijl (1956) suggested that the pagoda-like architecture of *C. pentandra* (Halle *et al.* 1978) and the absence of leaves during flowering are specific adaptations to chiropterophily, although others have argued that the phenotype was well established before nectar feeding bats had evolved (Baker 1973, Heithaus 1982).

In the Old World tropics, flying foxes (Megachiroptera: Pteropodidae) have been reported as frequent visitors to flowering *C. pentandra* trees. However, van der Pijl (1956) suggested that *Pteropus* spp. do not effect pollination because their visits result "nearly always in the destruction of flowers and young fruits." Although he regarded *C. pentandra* as primarily chiropterophilous, he believed fruit and seed set on oceanic islands to result from the introduction of self-fertile forms. Observations of flying fox visits to *C. pentandra* flowers have been reported, however, from Rarotonga, Mangaia, and Niue (Wodzicki & Felten 1975, 1980), Fiji (H. Baker and I. Baker, pers. comm.), Truk (I. Ain, pers. comm.), and Samoa (Cox 1983).

In Samoa, *C. pentandra* is an aboriginal introduction called *vavae*, the Samoan term for indigenous cotton. Although not deliberately cultivated, it is quite common near villages and in mixed agricultural forests, where the fruits provide kapok fiber for mattresses and pillows, and the bark is used for the treatment of asthma (Cox *et al.* 1989, Cox 1990). In order to clarify the relationship between flying foxes and reproduction of *C. pentandra*

in Samoa, we monitored flowering, nectar production, and fruit set for a group of trees, and analyzed visitation patterns of all potential pollinators.

## METHODS

The study was performed near Falealupotai, Savai'i, Western Samoa (14°S, 170°W). Flowers at anthesis on one *C. pentandra* tree were marked on 19 July 1988 and hand pollinated by pollen from the same flower (self,  $N = 15$ ), other flowers on the same tree (geitonogamous,  $N = 20$ ), and flowers on another tree (cross,  $N = 20$ ). For each treatment, the number of flowers abscised 22 hr after pollination was noted. On 8 August fruit production on these flowers was checked.

On 26 June five flower clusters on one tree (with no flowers yet opened) were bagged with large cotton fabric bags. Five control clusters were selected, marked, but left unbagged. The bagged clusters and the controls were checked for fruit production on 8 August.

Nectar samples were taken on 5–6 July from flowers on three branches detached from a single tree and kept in a bucket filled with water. The broken branches were recut underwater to eliminate vascular embolisms. Nectar samples from 12 flowers were taken, using calibrated 20 microliter capillaries, at intervals of approximately 1 hr, starting from anthesis (1930) and continuing to 0700 in the morning. At each interval ( $N = 12$ ) the time and the volume of nectar (to 1 microliter) for each flower was recorded. To test for temporal changes in sugar composition, samples of nectar (pooled from several flowers) were periodically spotted on chromatography paper and dried for subsequent analysis. Nectar volume was measured in two additional flowers prior to floral anthesis (1800) after removing portions of the petals.

On 30 June, two 12 × 2 m mist nets were set overnight among the flowering *C. pentandra* trees to catch potential vertebrate pollinators. A wattled honeyeater (*Foulebaio carunculata*) and a white necked flying fox (*Pteropus tonganus*) were caught in the nets. The facial area of each organism was dabbed with transparent adhesive tape and a few feathers or hairs were removed for SEM examination for pollen.

Nocturnal observations of floral visitors were made with night vision devices and supplemental infrared illumination (Farnsworth & Cox 1989). On five nights during the flowering period (30 June, 5 July, 20 July, 26 July and 4 August 1988)

observations were made beginning in early evening and continuing throughout the night until dawn.

The following flying fox activity data were recorded with a BASIC program on a laptop computer: arrival time at a tree; foraging duration; crawling and fighting time; resting time; movements within and between trees; and, departure time.

Only one flying fox was monitored in detail at one time, but the same animal may have been recorded more than once if it departed the area and later returned, because individuals were not identified. On 30 June and 5 July the total number of flying fox visits each hour per tree was also recorded.

## RESULTS

**FLOWER AND FRUIT CHARACTERISTICS.**—In Western Samoa, *C. pentandra* trees have few spines and bear fruit every year. Baker (1965) suggested that these characteristics were artificially selected in Africa. The Samoan fruits, however, open at maturity, while those of the cultivated forms in Africa and SE Asia remain closed. Flowering occurs in Samoa during June to August, a relatively dry period when the trees are largely leafless. The flowers terminate short lateral shoots produced by the horizontal branches. Shortened internodes in the region of flowering cause the flowers to be borne in clusters or fascicles. Only a few (2–3) flowers in each cluster open at the same time, but multiple clusters are present on one branch. The flowers are white, single-styled and bear five anthers. Herkogamy (spatial separation of male and female reproductive organs within a flower) is promoted by the bending of the style at an angle of 40–70 degrees approximately 2 cm above the ovary. This results in the stigma projecting outward, away from the anthers. There is overlap between fruiting and flowering; in mid-season a single tree may bear both receptive flowers and immature fruits. The fruits are elongate, pendant capsules, which mature before the trees start producing new leaves (Baker & Harris 1959).

On the cut branches, floral anthesis began at 1820, but few flowers were opened by 1900. We observed a similar pattern of anthesis of flowers on the trees, but did not attempt to monitor timing of anthesis in the uppermost branches at night. Anther dehiscence occurred between 1930–2000. Prior to dehiscence, the stigmas infrequently contacted the anthers. However, in a few flowers with precocious anther dehiscence, some pollen was deposited on the stigma. Flowers remained open until mid-morning, closed during mid-day and the corolla, stigma,

and stamens abscised in the late afternoon or early evening.

The two flowers which were sampled prior to floral anthesis (at 1809) yielded initial nectar volumes of 6  $\mu$ l. The mean initial nectar volume in the other flowers at anthesis was 110  $\mu$ l. Subsequent monitoring of nectar production revealed production was high for several hours, then declined before 2330, with almost no production after 0130 (Fig. 1). Considerable variation was observed among flowers both in the volume and duration of nectar production. Analysis of pooled nectar samples by paper chromatography–fluorometry indicated fluctuations, but no discernible temporal pattern in the ratio of sucrose to fructose and glucose (I. Baker, pers. comm.) The ratio was similar to that previously reported for Neotropical *C. pentandra* (Baker 1983). The colorless nectar tasted strongly of almonds.

The abscission rates for flowers after experimental pollination treatments differ. All of the cross-pollinated flowers, but only 80 percent of the geitonogamously pollinated and 65 percent of the self-pollinated flowers had abscised after 22 hr ( $\chi^2 = 8.3$ ,  $P < 0.05$ ,  $df = 2$ ). Fruit production also differed among treatments. None of the self-pollinated flowers produced fruits, while 10 percent of the geitonogamously pollinated flowers and 15 percent of the cross-pollinated flowers developed fruits. The flowers and developing fruits in this experiment were not protected from consumption and damage by flying foxes, but were all located on the lowest branches of the tree where the activity of flying foxes was very low.

None of the bagged flower clusters produced fruits, while a mean of 0.6 fruits per fascicle (SE = 0.4) were produced in the controls. The control fruiting clusters were not protected from flying fox damage (as were the treatments); hence, the control data represent net fruit production.

**FLORAL VISITORS.**—The flying fox *Pteropus tonganus* was the only pollinator observed at *C. pentandra* trees during the flowering period. Large numbers of *P. tonganus* visited *C. pentandra* trees every night. For example, on 30 June–1 July (still very early in the flowering season), there were over 258 *P. tonganus* visits to a single *C. pentandra* tree between 1830 and 0630 (Fig. 2). The other flying fox species present in Samoa, *P. samoensis*, which forages primarily in the daytime (Cox 1983, 1984), was never observed in *C. pentandra* trees during this study, nor during more than 22 hours of nocturnal observations made at other *C. pentandra* trees in both Western and American Samoa.

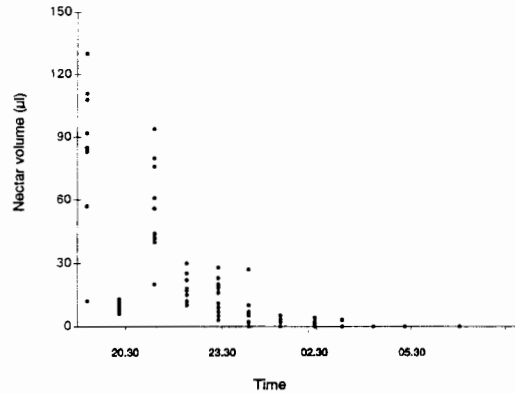


FIGURE 1. The standing crop of nectar ( $\mu\text{l}$ ) from flowers of *Ceiba pentandra* at different times during the night. Samples taken 5–6 July 1988.

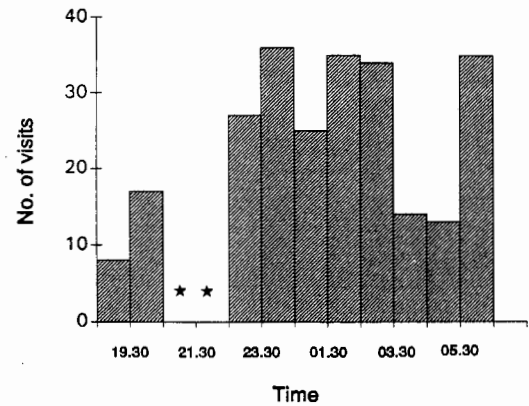


FIGURE 2. No. of visits by *P. tonganus* at one small *Ceiba pentandra* tree. Observations made 30 June–1 July 1988. \* = observations interrupted.

During this study, small numbers (1–9) of wattled honeyeaters (*Foulebaio carunculata*) came into the *C. pentandra* trees between 1640 and 1830 in the afternoon and were observed to probe the unopened flowers, presumably seeking nectar. They left the tree by 1830, about 30 min prior to anthesis. On 30 June, one *F. carunculata* caught in a mist net at 0626 failed to reveal any *C. pentandra* pollen. At 1655 on 5 July, 2 hr prior to flower opening, seven Samoan starlings (*Aplonis artifusca*), which are known to pollinate *Freycinetia reineckeii* (Pandanaeae) (Cox 1984), were seen in a *C. pentandra* tree, but ignored the closed flowers. No other birds were observed at *C. pentandra* trees during any of the observation periods. No other animals (e.g., flying insects, lizards, introduced rodents) were seen to approach *C. pentandra* flowers at any time.

Although *C. pentandra* flowers did not open until 1850–1900, and no foraging activity at flowers was observed prior to 1900, flying fox visits began at about 1830. Early in the season, prior to fruit production, the flying foxes spent the first half hour in the tree locating and defending foraging areas. They generally landed in the top of the tree, crawled down the trunk and along the horizontal branches until they found an unoccupied area. There they would hang, periodically crawling to test nearby flower clusters or defending the area by chasing, boxing, and squawking at any other flying foxes that came within about a 1.5–2.0 m radius. Aggressive encounters usually ended with one animal flying away or moving to another part of the tree. Once fruit production began (by 20 July), however, animals spent the half hour prior to floral anthesis primarily feeding on young fruits.

The flying foxes clearly preferred nectar to fruits, however, and throughout the season began foraging on nectar as soon as it was available. There was a significant increase in the proportion of time devoted to crawling and interference as soon as flowers opened (i.e., at 1900, Mann-Whitney *U*-test,  $P < 0.05$ ) (Fig. 3). The flying foxes maintained high levels of foraging activity throughout the nightly period of nectar production. Nectar production ceased by 0230 and flying fox foraging activity was generally very low after 0300 (Fig. 3). Reduced visitation between 0330 and 0530 was followed by another activity pulse just before dawn (Fig. 2). The animals observed between 0330 and 0530 were smaller and are presumed to have been juveniles.

In-flight reconnaissance by *P. tonganus* at a monitored *C. pentandra* tree changed markedly between 30 June, when relatively few flowers were available, and 5 July, when more flowers were open. Between 1800 and 1900 on 30 June, 17 flying foxes flew by to investigate the tree, and only three landed. On 5 July, the situation was reversed: 5 flew by, while 13 landed.

The mean duration of *P. tonganus* visits to *C. pentandra* trees (during the first 3 hr of activity) showed a small change during the study period, but the variance in time spent per visit differed. On 30 June, the mean duration of a visit was only 3.3 min per tree while the longest stay by any one animal was 8 min. By 5 July the mean duration had increased to 8.3 min, with two animals staying longer than 14 min. After 5 July the variance in visit duration showed a declining trend. Given the brief average duration and large number of foraging bouts,

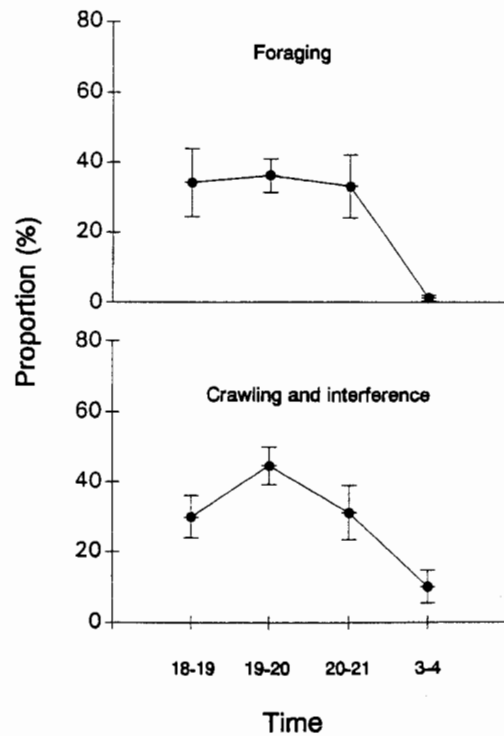


FIGURE 3. The proportion of time (%) devoted by *Pteropus tonganus* to foraging (before 1900 on immature fruits, after 1900 on flowers), and crawling and interference, in *Ceiba pentandra* trees at four different time intervals during the night. Observations made after mature fruits were available, *i.e.*, 20 July, 26 July and 4 August 1988. Mean  $\pm$ SE given,  $N = 7, 15, 5$  and  $10$ , respectively.

most flowers were likely visited by more than one bat during the night.

The time flying foxes spent engaged in three activities—foraging, crawling and interference, and resting—was monitored on four nights during the flowering season. Although the proportion of time spent foraging remained relatively constant, there was a significant increase in the proportion of time spent in crawling and interference (ANOVA  $F_3, 29 = 4.38, P < 0.01$ , arcsine-transformed data) (Fig. 4) during the study period (resting represents the residual time and decreased correspondingly as crawling time increased). Since crawling occurs both while searching for open flowers and fighting with other flying foxes, an increase in crawling time suggests greater effort expended on resource acquisition and defense.

Data collected on 45 departures revealed that in 17 cases (38%) flying foxes flew to a nearby *C. pentandra* tree and continued foraging, in 6 cases

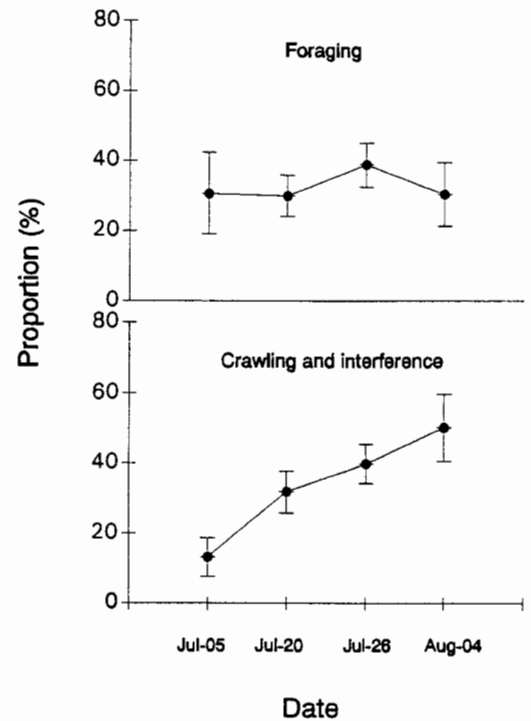


FIGURE 4. The proportion of time (%) devoted by *Pteropus tonganus* to foraging and crawling and interference in *Ceiba pentandra* trees at four different times during the flowering season 1988. Observations made during the time period 1800–2100. Mean  $\pm$ SE given,  $N = 6, 8, 13, 5$ , respectively.

(7%) they left and then returned to a different position on the same tree, and in the remainder of the cases (55%) they disappeared from view. Although the destinations of 55 percent of the departing animals were unknown, it is certainly possible they visited other *C. pentandra* trees which were patchily distributed throughout the village. *C. pentandra* was not the only food available to *P. tonganus* at this time, however. On 1 July, for example, a noisy aggregation of *P. tonganus* fed all night on the fruits of a large asi (*Syzygium inophylloides*) tree, within about 5 km of our study site.

In the process of foraging, *P. tonganus* causes considerable damage to both flowers and fruits of *C. pentandra*. *P. tonganus* destroys immature fruits by consuming them, and both flying foxes and honeyeaters knock flowers and fruits from the branches while moving about. The number of flowers and immature fruits falling to the ground as a

result of flying fox activity was estimated on 20 July to be on the average of 2.5/hr/tree between 1900 and 2200.

## DISCUSSION

**FLORAL ECOLOGY.**—*C. pentandra* in Samoa appears to be completely dependent on *P. tonganus* for successful reproduction. Although trees were found to be self-compatible, no fruits or seeds were set in the absence of pollinators. Furthermore, flying foxes were the only floral visitors whose pattern of visitation offered them the opportunity to act as pollinating agents.

Although bats are known to be important pollinators of many rain forest plants in both the Old and New World tropics (Start & Marshall 1976; Heithaus 1982; Marshall 1983, 1985; Dobart & Peikert-Holle 1985; Fleming 1988; Wiles & Fujita, in press; Pierson & Rainey, in press), very few "species-specific systems" have been investigated (Heithaus 1982). *Melonycteris woodfordi* may be the only pollinator of *Heliconia solomonensis* in the Solomon Islands (Kress 1985), and close associations have been documented between *Macroglossus minimus* and various mangrove (*Sonneratia*) species and between *Macroglossus sobrinus* and *Musa* (Start & Marshall 1976). There are also a number of plants that appear to be dependent entirely on bats for pollination (e.g., *Durio*, *Parkia* and *Musa*) (Start & Marshall 1976), but they are generally visited by a number of species. Although Gould (1978) suggests that in Malaysia *Oroxylum* is pollinated by one bat species, *Eonycteris spelaea*, organisms other than bats may also be involved in pollination.

The paucity of floral visitors to *C. pentandra* in Samoa contrasts greatly with the floral ecology of this species in continental areas. In Africa, Baker and Harris (1959) observed frequent visits to *C. pentandra* flowers by three species of bats, *Epomoporus gambianus*, *Nanonycteris veldkampii* and *Eidolon helvum*. In addition they noted visits to its flowers by bees, hawkmoths, and several species of smaller moths. At one site in Costa Rica *C. pentandra* was visited by all seven identified nectarivorous bat species, and was the most frequently visited resource for four (Heithaus *et al.* 1975). In other areas such as Indonesia, Mexico, and South America, *C. pentandra* flowers are also visited by birds, primates, and other nonvolant mammals (Toledo 1977, Janson *et al.* 1981), wasps and bees (Toxopeus 1950, Jaeger 1954, Janson *et al.* 1981).

Although wind pollination has been suggested as a possible alternative mode of pollination in *C.*

*pentandra* (Faegri & van der Pijl 1979), oil secretions in the anther, which cause pollen grains to adhere to each other, render anemophily unlikely (Baker & Harris 1959). Nevertheless, *C. pentandra* may not be primarily chiropterophilous throughout its range, since it has been successfully introduced to Tahiti, Hawaii, the Marquesas, and other oceanic islands devoid of flying foxes (Smith 1981, Cuzent 1983). Trees in Tahiti, Hawaii, and small atolls in the Marshall Islands set fruit. More information is needed on the pollination ecology and possible apomixis of *C. pentandra* in these areas.

The dependence of *C. pentandra* on *P. tonganus* in Samoa is not reciprocal. *P. tonganus*, like many primate, appears to be a generalist (Fleming 1982, Marshall 1985), and is known to feed on a wide variety of native and cultivated fruits and flowers both in Samoa (Cox 1983, Cox *et al.*, in press a) and elsewhere in its range (Wodzicki & Felten 1975, 1980). It does appear, however, that during its relatively restricted (*ca* 2 month) flowering period, *C. pentandra* is a favored and extremely important food resource for *P. tonganus*. Wodzicki and Felten (1980) suggest that the birth season for *P. tonganus* in the Cook Islands is synchronized with the flowering of *C. pentandra*, and Samoan hunters have told us that *P. tonganus* are fattest when *C. pentandra* is flowering.

Why are *C. pentandra* trees pollinated by only a single species in Samoa, while in other parts of the world they attract a diverse range of floral visitors? The paucity of potential pollinators in Samoa provides the probable answer. There are only 9 nectarivorous bird species (Watling 1982) and 11 native bee species in Samoa (Cockereil 1924; Perkins & Cheeseman 1928; Bryan 1930). Thus many different species of Samoan plants depend on only a few species for pollination. We have suggested elsewhere (Cox *et al.* 1991) that a very limited suite of pollinators and seed dispersers maintains much of the Samoan forest ecosystem, and have hypothesized that flying foxes, which are both pollinators and seed dispersers for major forest trees, likely play a role as keystone species (*sensu* Paine 1966, 1980) in many isolated island ecosystems of the Old World tropics.

The reliance of *C. pentandra* on *P. tonganus* in Samoa carries a cost. *P. tonganus* (and to a lesser extent *F. carunculata*) caused significant destruction of flowers and immature fruits while foraging. A conservative estimate based on the rate of fruit drop during flying fox foraging indicates that a moderately-sized *C. pentandra* tree may suffer a loss of 400–500 immature fruits during one season—up

to 50 percent of all initiated fruits. Thus a dystrophic pollination system maintains *C. pentandra* in Samoa in that significant damage to reproductive structures accompanies pollination. There are indications that dystrophic pollination occurs elsewhere in the species' range, but varies with the composition of the pollinator assemblage. As noted earlier, flying foxes in southeast Asia have been observed to damage large numbers of immature *C. pentandra* fruits and are viewed as pests in commercial kapok plantations (van der Pijl 1956). In West Africa, Baker and Harris (1959) noted that another large flying fox, *E. belvum*, bit unopened flowers in addition to lapping nectar from open ones, but mentioned no damage from two smaller pteropodid bats. Though data on flower or fruit damage by *C. pentandra* pollinators in the Neotropics are lacking, it seems probable that the smaller body mass (and, for some, hovering foraging mode) of flower visiting microchiropteran bats would lead to less damage. However, primates and other nonvolant mammal pollinators could well be quite destructive. In the Neotropics, at least some diurnal birds consume the flowers (Janson *et al.* 1981).

**FLYING FOX BEHAVIOR.**—Fleming (1982) predicts that for bats "group foraging should maximize individual foraging efficiency when resources occur in rich, but ephemeral, widely spaced patches." *C. pentandra* is just such a resource—it is patchily distributed and produces abundant flowers in a relatively short flowering season. Thus it is not surprising that it attracts aggregations of *P. tonganus*. It should be noted, however, that even though animals may rely on each other to locate patchy resources, and as many as 10–15 bats may be feeding in the same tree at one time, there does not appear to be any cohesiveness to the group. At dusk large numbers of *P. tonganus* can be observed flying in a single stream away from a day roost, presumably toward a foraging area, but the agonistic behavior of individuals in the vicinity of a feeding tree suggests that each bat acts opportunistically. Our data offer no evidence for simultaneous arrivals and departures, nor for any cooperation within a group.

Research on foraging behavior of nectarivorous and frugivorous bats, which has focused primarily on the Neotropics, suggests that feeding resources are not defended (Fleming 1982, 1988). In fact, cooperative behavior, with members of a group taking turns at a floral resource, has been documented for the phyllostomid *Leptonycteris sanborni* in Arizona (Howell 1979). However, Lemke (1985) observed individuals of *Glossophaga soricina* de-

fending *Agave* inflorescences for several hours until nectar volumes declined. Marshall (1983) also suggested that feeding territories were unnecessary among phytophagous bats. However, we observed individual *P. tonganus* at *C. pentandra* vigorously, if briefly, defending 1.5–2.0 m areas, and frequently chasing away intruders. Vocalizations of squabbling foragers are sufficiently frequent, distinctive and loud, that listeners (humans and probably other foraging bats) can locate feeding trees at night over several hundred meters. Similar behavior has been observed for other pteropodid species in Malaysia (Gould 1978) and Africa (Baker and Harris 1957) and Micronesia (Wiles & Conry 1990). In studies of three species of *Pteropus* in Australia, McWilliam (1985–1986) reports both agonistic encounters and repeated occupation (over several weeks) of a single foraging site by radiotracked individuals, suggesting longer term resource defense. It seems likely that resource defense will prove to be common at least among larger pteropodids feeding on patchy resources. Particularly on isolated islands which lack large, native, nocturnal predators, vocalizations and threat displays on exposed perches carry little risk, other than attracting additional competitors. Such inadvertent recruitment of competitors likely does occur. Bat hunters in several Pacific island cultures can readily attract flying foxes by imitating their vocalizations.

Activity patterns of *P. tonganus* within and among trees suggest these flying foxes are effective pollinating agents. Several behavioral characteristics (*i.e.*, the frequency of agonistic interactions, the short average duration of individual visits, and the tendency for individuals to change position within a tree or fly to other trees) likely promote greater productive success for many of their food plants by enhancing geitonogamous and cross pollination. The behavior of *P. tonganus* is clearly advantageous for *C. pentandra*, which showed seed set only when flowers were geitonogamously or cross-pollinated. Since obligate outcrossing is common for tropical forest trees (Bawa 1974, Heithaus *et al.* 1975), the foraging patterns of flying foxes may be critical for the survival of a number of plant species on remote oceanic islands.

## CONCLUSION

The highly restricted pollination system for *C. pentandra* in Samoa arises from generalist traits of both the plant and its pollinator. Although in Samoa, *C. pentandra* appears to depend entirely on the flying fox, *P. tonganus*, for reproduction, in continental areas this tree is a virtual sticky trap for pollinators.

*P. tonganus* is also a generalist, and its success, as with many *Pteropus* species on isolated islands, may stem in part from its dietary breadth, since it must contend with seasonal variation in flowering and fruiting of a limited flora on a small land area and periodic massive alterations in forest structure and biomass by typhoons. The presence of an eclectic forager, such as *P. tonganus*, in a remote island setting, greatly enhances the chances that a colonizing plant species, especially a relatively versatile one like *C. pentandra*, will find a suitable pollinating agent.

Our study suggests that flying foxes are critical pollinators for forest plants on isolated oceanic islands where the pollinator fauna is depauperate. Many flying fox taxa have extremely limited distributions (Rainey & Pierson, in press) and are declining from overhunting and habitat destruction (Brautigam & Elmquist 1990, Pierson & Rainey,

in press, Wiles 1987). The loss of flying foxes would have serious consequences for the long term viability of isolated island ecosystems (Cox *et al.*, in press b).

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