ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

VOLUME 68 1981 NUMBER 4

NECTARIVORY AND POTENTIAL POLLINATION BY A NEOTROPICAL MARSUPIAL[1]

KIM E. STEINER[2]

ABSTRACT

The neotropical marsupial, *Caluromys derbianus*, the red woolly opossum, is a regular visitor and potential pollinator of *Mabea occidentalis* (Euphorbiaceae), an understory rainforest tree on Barro Colorado Island, Panama. *Caluromys* also visits and may pollinate nocturnal nectar-producing flowers of other plants. Nectar is an important food source for the red woolly opossum during seasonal lows in fruit abundance. Pollination by nonflying mammals may commonly occur in tropical forests in light of recent information on tropical tree distribution.

The importance of nonflying mammals including rodents, marsupials and primates as pollinators has become more widely accepted recently in light of an increasing number of more critical observations (Rourke & Wiens, 1977; Wiens & Rourke, 1978; Carpenter, 1978; Sussman & Raven, 1978; Lumer, 1980; Janson et al. 1981; Wiens et al., 1979; Hopper, 1980). With the exception of Lumer (1980) and Janson et al. (1981), these studies have focused on Old World systems, geographically limited to the Cape Region of South Africa, Madagascar, and Australia.

Australian marsupials have undergone extensive diversification as a result of radiation into a wide range of ecological niches that are filled by placental mammals elsewhere. This diversification includes forms such as the honey possum, *Tarsipes*, that regularly visit flowers (Hopper, 1980).

In the New World, marsupial radiation has been constrained by competition from placental mammals and has been confined to only two families, the Didelphidae and the Caenolestidae. Since little ecological information is available on

---

[1] This study was supported by an Earl C. Anthony graduate fellowship from the University of California, Davis. Drs. Grady L. Webster, Robbin Thorp and Delbert Wiens made helpful comments on the manuscript. Dr. Herbert G. Baker, James Ackerman, Wendy O'Neil and two anonymous reviewers provided valuable suggestions on an earlier draft. I thank the Smithsonian Tropical Research Institute for the use of their facilities, William Glanz for the use of unpublished information and Robert Fischer for providing the weight data for *Caluromys derbianus*.

[2] Botany Department, University of California, Davis, California 95616.

ANN. MISSOURI BOT. GARD. 68: 505–513. 1981.
0026-6493/81/0505–0513/$01.05/0

the feeding habits of all but the common opossum, *Didelphis,* it is not surprising that floral visitation and pollination have been considered nonexistent for New World marsupials (L. G. Marshall, in Sussman & Raven, 1978). Although *Didelphis virginiana* has been reported visiting the flowers of *Ceiba pentandra* in Mexico (Toledo, 1977) and *D. marsupialis* in Panama (W. Glanz, pers. comm.), these reports, based on very limited observations in conjunction with other studies, provide little insight into the importance of flower visitation for these opossum species.

Caluromys derbianus, the red woolly opossum, is a relatively small (ca. 307 g), nocturnally active New World marsupial. It has a reddish and cream-colored body (180–290 mm) with a long (270–490 mm) prehensile tail. It is one of three species of woolly opossum and ranges from southern Mexico to Colombia and Ecuador (Walker, 1975). The other two species, *C. lanatus* and *C. philander,* are restricted to South America (Walker, 1975).

No information regarding the importance of various food types is available from field observations and even feeding experiments with captive *C. derbianus* are rare. *Caluromys,* according to Hunsaker (1977), is basically frugivorous, while Walker (1975) reports that a captive individual of *C. derbianus* ate bananas, young mice, and insects, including cockroaches. W. Glanz (pers. comm.) performed feeding experiments with fruits from the native environment (Barro Colorado Island, Panama) on a single animal and found that it preferred soft fruits such as *Ficus insipida* (Moraceae), *Eugenia nesiotica* (Myrtaceae), and *Spondias mombin* (Anacardiaceae) over hard-skinned fruit such as *Ficus yoponensis* and *Lacmellia panamensis* (Apocynaceae). The opossum also showed a definite pouncing behavior when faced with grasshoppers, cicadas, and katydids, all of which it ate.

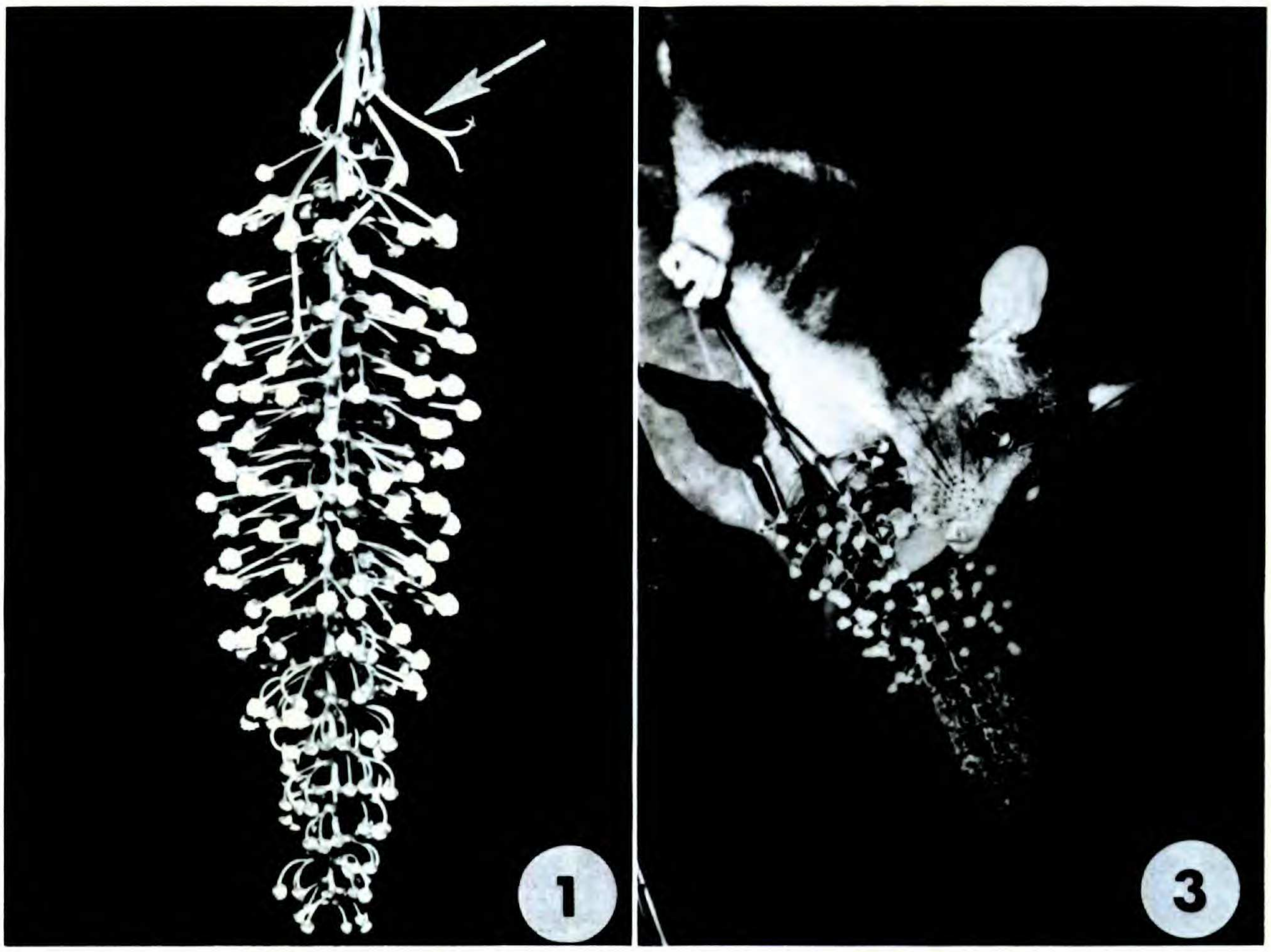
Nectar feeding by *C. derbianus* became apparent during a study of the reproductive biology of *Mabea occidentalis* (Euphorbiaceae) (Steiner, unpubl.). Observations at other nocturnally blooming flowers (*Ochroma pyramidale, Trichanthera gigantea,* and *Kigelia pinnata*), normally regarded as "bat flowers," reinforced the impression that *C. derbianus* commonly visits flowers for nectar.

As a result of initial observations, it was hypothesized that *Caluromys* acts as a pollinator of *M. occidentalis* and possibly other plants as well. To critically test this hypothesis, one should exclude all visitors except *C. derbianus* from the flowers and measure the resultant seed set. This was tried, but found to be unfeasible for *M. occidentalis* due to the difficulty of excluding bats and moths without excluding *Caluromys.*

Although selective exclusion experiments are unfeasible for *M. occidentalis,* I feel that the pollinating capability of *C. derbianus* can be assessed by addressing the following questions: 1. Is *Caluromys* a regular visitor? 2. Does *Caluromys* effectively transfer pollen from anthers to stigmas? 3. Is visitation synchronized with anthesis? 4. Does *Caluromys* visit the flowers nondestructively? 5. Is there interplant movement of *Caluromys*?

STUDY SITE AND METHODS

This study was carried out over an 84-day period between 27 November 1979 and 19 February 1980 on Barro Colorado Island, located in Gatun Lake, a part



FIGURES 1, 3.—1. *Mabea occidentalis* at anthesis showing beads of nectar (× ca. ½). Arrow points to a pistillate flower.—3. *Caluromys derbianus* visiting an inflorescence of *Mabea occidentalis* (× ca. ¼).

of the Panama Canal (see Croat, 1978 for additional information on BCI). A total of 88.6 hours on 45 different nights was spent in observation. Observation time per night was quite variable, but averaged 1.9 hours (s.d. = 1.4).

During each period of observation, I recorded: (1) the time spent per inflorescence, (2) the number of inflorescences visited per tree, (3) the manner in which flowers were manipulated, and (4) the extent of interplant movement by the red woolly opossum. Observations were made using a headlamp equiped with a red plastic filter. Photographs were made with a 200 mm telephoto lens and a Vivitar 283 electronic flash. Live trapping of *Caluromys* was tried, but was unsuccessful.

Nectar volume and concentration were measured with calibrated micropipets and an Atago hand refractometer corrected to 23°C respectively. Glandular bracts on each inflorescence were marked and then bagged with nylon mosquito netting. The eight marked glandular bracts from five inflorescences on five different trees were sampled every hour from 1800 to 0500 EST or until nectar production ceased.

Mabea occidentalis, an understory tree of 4 to 6 m in height, flowers in Panama mainly in the dry season during the months of December through April (Croat, 1978). It ranges from Mexico to northern South America (Webster & Burch, 1968) and is particularly common on Barro Colorado Island.

Mabea occidentalis is monoecious with staminate and pistillate flowers clustered in paniculate inflorescences that hang down from the tips of branches in the open areas between foliage layers. Each inflorescence is composed of about 200 staminate flowers and about 5 pistillate flowers. The staminate flowers are clustered in groups of three, subtended by a biglandular bract and borne on peduncles that are spirally arranged around a central axis (Fig. 1). Pistillate flowers are solitary and located at the basal nodes of the inflorescence. Although they usually hang down among the staminate flowers, little self-pollination occurs, since *M. occidentalis* is basically self-incompatible (Steiner, unpubl.).

RESULTS

FLORAL CHARACTERISTICS

The staminate flower clusters present pollen concomitantly with nectar secretion by the subtending biglandular bracts. An inflorescence secretes nectar for 2 or 3 nights with usually one-half to one-third of the staminate flowers reaching anthesis per night. Nectar secretion usually begins between 1630 and 1700 EST and can continue until 0700 the next day; however, at least 79% of the nectar is secreted before 2400. Nectar flow rate peaks for an average *Mabea* inflorescence between 1900 and 2200 and steadily declines thereafter. Nectar concentration starts at about 14% and eventually drops to about 9.5% g sucrose equivalents per 100 g of solution (Fig. 2). Each inflorescence produces a mean of 149 mg (s.d. = ±50 mg) sugar per night. The number of inflorescences secreting nectar per night for a given individual is quite variable, but is usually less than 20, except for unusually large trees.

VISITATION BEHAVIOR

The following observations were made to answer the questions posed in the introduction regarding the pollinating capability of the red woolly opossum: 1. *Caluromys derbianus* was a regular visitor to *Mabea occidentalis*. It was sighted on 30 of 45 observation nights. On 24 of the 30 nights, *Caluromys* was seen feeding at inflorescences, but because of intervening foliage, it was usually impossible to count the total number of inflorescences visited within a given tree. On one occasion, however, the opossum visited 27 inflorescences within a single tree. Although I never saw more than one individual at a tree, I twice saw two individuals in the same clump of trees.

2. The primarily arboreal red woolly opossum is very agile. Its strongly prehensile tail greatly enhances its manipulative capabilities as it often hangs down and holds inflorescences with its forepaws. This ability is necessary for successful foraging on *Mabea*, since the inflorescences hang down away from the foliage at the tips of small branches. Figure 3 shows *C. derbianus* removing nectar from a *Mabea* inflorescence; it does this by lapping up the nectar droplets that cling to the biglandular bracts. This process lasts an average of 13.5 seconds (s.d. = 5.4, $n = 41$) and results in complete removal of the nectar. While actively foraging within a tree, *Caluromys* visits a mean of 1.6 inflorescences per minute (s.d. = 0.5, observation periods, $n = 8$, of ≥ 7 minutes). As the red woolly opossum removes nectar, its snout contacts the staminate flowers (Fig. 3) and becomes covered with pollen. Although not apparent in black and white photographs such

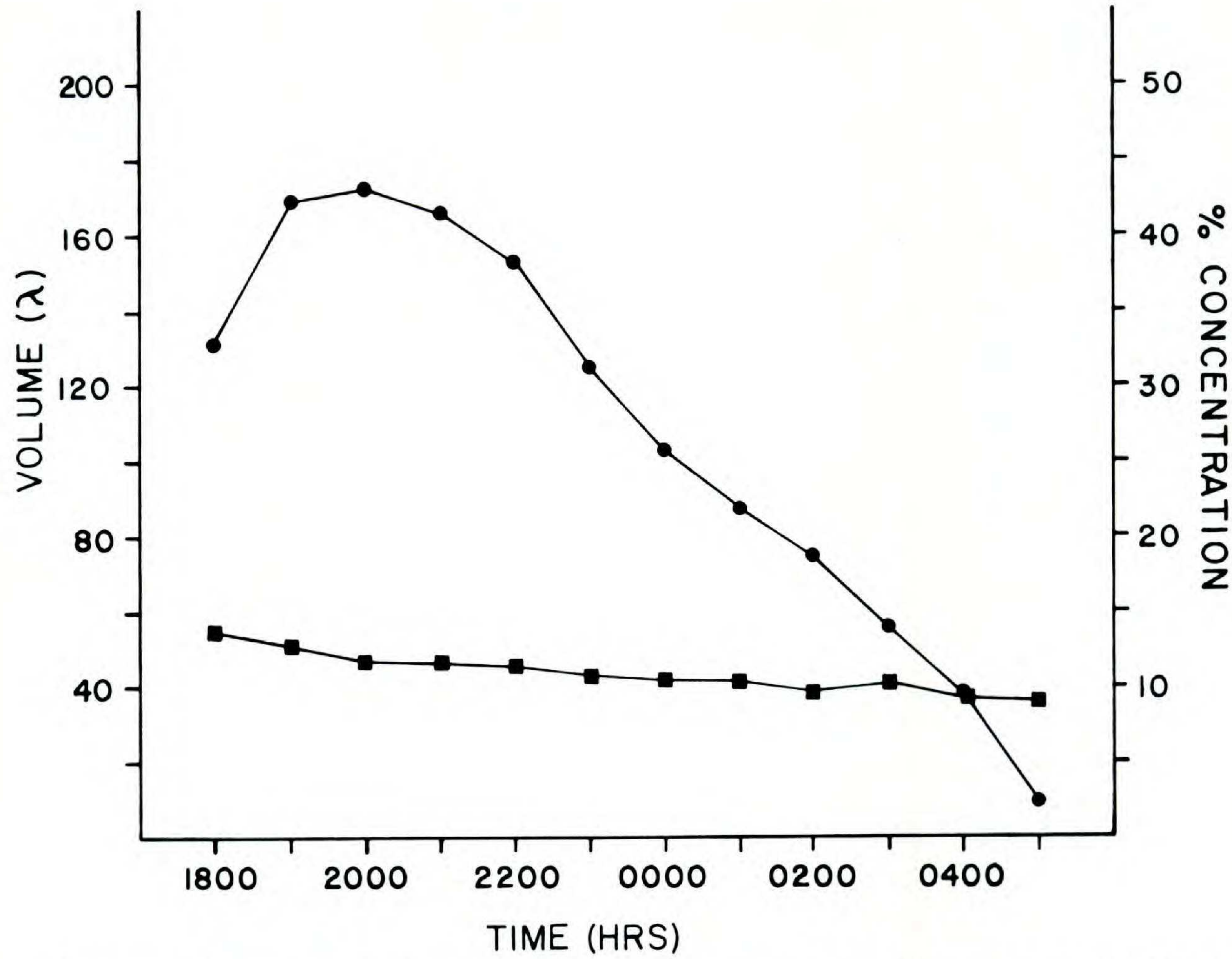


FIGURE 2. Mean nectar volume (λ) (solid dots) and concentration [(g sucrose equivalents per 100 g solution) %] (solid squares) vs. time. The means are based on the average nectar production of a single glandular bract × the average number of glandular bracts secreting nectar per inflorescence per night.

as Fig. 3, the presence of bright yellow pollen on the snout can be readily detected in color photographs. The pistillate flowers usually contact the opossum's snout as well (although not shown in Fig. 3), since they hang down among the staminate flowers. Although live traps were set out so that pollen loads could be collected and analyzed, no *Caluromys* were captured. Behavioral observations strongly suggest that effective pollen transfer occurs, but this cannot be conclusively shown without using marked pollen or some type of powdered dye.

3. Visitation by *C. derbianus* is well synchronized with anthesis. All observations of the opossum were between 1900 and 2400 EST, the period of maximum nectar secretion (Fig. 2), pollen presentation and stigma receptivity (Steiner, unpubl.).

4. I observed *Caluromys* visits to 215 inflorescences with no sign of damage to the flowers. Floral parts were not eaten nor were any broken off in handling. *Caluromys derbianus* visits *M. occidentalis* flowers primarily for nectar; however, it cannot help but ingest pollen at the same time. Additional pollen consumption was observed during grooming periods.

5. *Mabea occidentalis* generally occurs in discrete stands in the young (ca. 70 yr old) forest on BCI (DeSteven, in press; Steiner, unpubl.). Most of the red woolly opossum observations were made at one such stand. Although the trees

were closely spaced [mean nearest neighbor distance (trunk to trunk) = 2.45 ± 1.02 m, n = 12], it was often difficult to follow movement from one tree to another due to the presence of other vegetation. The canopies of most of these trees were overlapping and thus provided easy access for the arboreal woolly opossum. During the study period, 53 interplant movements were recorded. On January 9, *Caluromys* was followed for an hour, while it visited seven trees. Foliage obstructed my view, so that I could not count every inflorescence visited, but I did see at least one inflorescence visit in each tree. The foraging loop lasted one hour, however about 18% of this time was spent grooming, while the opossum remained stationary.

On BCI, *C. derbianus* was seen visiting flowers of two other species. This opossum fed at *Ochroma pyramidale* flowers on two of seven nights of which observations of one or more hours were made. The longest visit was on February 12 when *Caluromys* was present for an hour. During that time, it made a total of seven visits to three different flowers on two adjacent trees. Actual foraging time was only about 5 minutes, while the rest of the time was spent sitting and grooming. Two *Caluromys* individuals were present in these same trees for over 30 minutes on January 12 (M. Tuttle & L. Taft, pers. comm.).

Although I saw *Caluromys* on *Ochroma* only twice during the observation period, *Didelphis marsupialis* individuals were present the entire time on five of seven nights. On these nights, as many as three individuals were seen foraging within a single canopy. Although movement between overlapping canopies occurred, movement to more distant trees was uncommon.

Didelphis, although well suited to foraging on *Ochroma* with its sturdy flowers and branches, lacks the small size and agility which would permit it to exploit *M. occidentalis* as a nectar source. *Didelphis* was seen several times on the ground in the vicinity of *Mabea* and caught in traps on the sturdier branches around *Mabea* inflorescences, but it was never seen visiting the flowers.

Caluromys was seen twice visiting a heavily (ca. 100 flowers) flowering individual of *Trichanthera gigantea* (Acanthaceae) during a 5 day period from February 28 to March 3. The red tubular flowers of *Trichanthera* are clustered on leafless stalks that project up and out from the foliage. Both visits by *Caluromys* were brief. The longest visit lasted 9 minutes during which 8 flowers were visited. Heavy visitation by *Glossophaga soricina*, a small nectar-feeding bat and primary pollinator (Steiner, unpubl.), probably kept nectar levels too low for profitable foraging by *Caluromys* during these observations.

DISCUSSION

Since *Caluromys* appears to be capable of pollinating *Mabea occidentalis*, it is important to ask whether *M. occidentalis* shows adaptations which suggest coevolution between it and the opossum. The answer is no. The inflorescences of *Mabea*, although visited by noctuid and pyralid moths, cerambycid beetles, and *Trigona* bees, in addition to *C. derbianus*, are most clearly adapted to pollination by bats (Steiner, unpubl.). Nocturnal anthesis, exposed position outside the foliage, drab coloration, strong musty nocturnally produced odor, and production of relatively large amounts of pollen and nectar all characterize the inflorescences of *M. occidentalis* (Steiner, unpubl.), as well as the chiropterophilous syndrome as presented by Faegri & van der Pijl (1979). Bats were commonly observed visiting *Mabea* inflorescences on BCI (Steiner, unpubl.).

Although *C. derbianus* appears capable of pollinating *M. occidentalis*, its importance as a pollinator is not clear. Observations (Steiner, unpubl.) suggest that *C. derbianus* may vary in importance as a pollinator over the flowering period of *M. occidentalis* depending on the corresponding bat visitation rate. However, only controlled selective exclusion experiments can resolve this question satisfactorily.

The importance of nectar in the diet of neotropical mammals may fluctuate seasonally. Animal-dispersed fruits are scarce at the end of the wet season and beginning of the dry season (November–February) on Barro Colorado Island (Smythe, 1970). It is at this time that most bat-pollinated species flower (cf. Croat, 1978), as they do in Costa Rica (Heithaus et al., 1975). It is not surprising, therefore, that bats and other animals exploit nectar during this period. In Costa Rica (Heithaus et al., 1975) and to a lesser extent on BCI (Bonaccorso, 1979), bats such as *Artibeus jamaicensis* and *A. lituratus* that are normally frugivorous during most of the year become common flower visitors during this season.

Is nectar an important energy source for *Caluromys*? One can calculate the energy requirement of a marsupial using the equation $\mathrm{SMR} = 48.6 \times \mathrm{W}^{.75}$ kcal/day derived by Dawson & Hulbert (1970), where SMR is standard metabolic rate and W is the weight of the animal. Substituting in the average weight of *C. derbianus* [307 ± 72 g, n = 20 (based on specimen labels from Panamanian collections of *C. derbianus* in the National Museum, Washington, D.C.)], gives a SMR = 20.0 kcal/day. If one assumes an activity/feeding rate of 2 SMR, the daily energy requirement becomes 40.0 kcal. Since the sugar in nectar yields about 3.8 kcal/g, the red woolly opossum would require about 10.5 g of sugar/day. If its assimilation efficiency is 95% [Howell (1979) found a 96–99% assimilation efficiency for bats], then *C. derbianus* would have to ingest 11.1 g of sugar.

Mabea occidentalis produces an average of 149 mg sugar per inflorescence per day. To satisfy its daily requirement, therefore, *C. derbianus* would have to consume all of the nectar produced by 74 inflorescences. *Caluromys* concentrates its visits during the peak period of nectar secretion (i.e., 1900–2400 EST). Seventy-nine per cent of the total nectar produced is secreted before 2400 EST; therefore, if *C. derbianus* limits its visits to this time interval, it must visit 94 inflorescences.

Although no woolly opossums were marked, the visitation patterns observed at the main study site suggest that most visits were by a single individual. An individual *C. derbianus* was observed to either stay in the clump of flowering trees for several hours with inactive periods interspersed between foraging bouts or to make 2–3 foraging loops during an evening, but leave the clump after each loop for a variable amount of time. Unfortunately I was unable to follow the opossum once it left the study area. If to get all of the nectar produced by an inflorescence by 2400 EST a woolly opossum makes 3 visits to a given inflorescence, it would need to make 281 inflorescence visits in an evening.

While actively foraging, *C. derbianus* was found to visit 1.6 inflorescences per minute, therefore visits to 281 inflorescences would require about 176 minutes (2 hr 56 minutes) of foraging time, a little over half the time available between 1900 and 2400 EST.

It is not likely that 94 inflorescences were secreting nectar in the study area; however, if *C. derbianus* traplines between different clumps, which is suggested by its periodic departures, it could conceivably visit this many inflorescences. Even if *C. derbianus* visited only half this number of inflorescences, it would still be consuming a significant portion of its daily requirement. Since *C. derbianus* is omnivorous, there is no reason to assume that all of its calories must come from nectar. A diet consisting entirely of nectar would probably be nutritionally inadequate as it is for some rodents (D. Wiens, pers. comm.); however, ingestion of pollen along with nectar may help alleviate this problem as it does for some bats (Howell, 1974).

The following additional observations suggest that nectar is an important food source for *C. derbianus*. W. Glanz (pers. comm.) has seen red woolly opossums along with kinkajous (*Potus flavus*) in flowering trees of *Ceiba pentandra*. Steiner (pers. obs.) has seen *Caluromys* visiting a *Kigelia pinnata* (an Old World bat-pollinated tree) individual, while R. Zell (pers. comm.) observed *C. derbinaus* at a nectar feeder in Gamboa (former Panama Canal Zone). P. Charles-Dominique (pers. comm.) has observed another *Caluromys* species, *C. philander*, visiting large flowering trees of *Inga thibandiana*, *I. ingoides*, and *Hymenaea courbaril* in French Guiana.

Mabea occidentalis, *Ochroma pyramidale* (=*O. lagopus*) (Vogel, 1954), and *Trichanthera gigantea* (Vogel, 1969) have quite different floral morphologies, yet all three possess characteristics which adapt them to pollination by bats. On Barro Colorado Island, all of these species are indeed visited by bats (Steiner, unpubl.).

Flowers that utilize bats as pollen vectors usually provide relatively large amounts of food in the form of nectar. Associated with these flowers is a musty or fermented odor that acts as an important attractant. Since this odor signals a rich food supply, one would expect other nocturnal mammals to locate and utilize such food sources. It is, therefore, surprising that more nonflying mammals have not been reported visiting bat pollinated flowers in the New World tropics.

Until recently, tropical lowland forest trees have been considered to be uniformly dispersed and present as adults in low densities. Since most tropical trees are self-incompatible (Bawa, 1974), reproductive success is dependent on outcrossing. In such a system, long-distance pollinators (e.g., large bees, sphingid moths, bats, and hummingbirds) must play a disproportionately greater role in pollination than less mobile animals. However, since the foraging ranges of these less mobile animals are so poorly known, such a generalization must be made with caution. If all bat-pollinated trees are highly dispersed, it is unlikely that effective pollen transfer between conspecifics by a nonflying mammal such as *C. derbianus* would occur.

The classical notion of tropical forest tree distribution has been challenged by Hubbell (1979) as a result of work done at a tropical dry forest site in Costa Rica. He found that most trees were clumped rather than highly dispersed. In his study area, approximately 20% of the individuals of *Hymenaea courbaril*, a bat-pollinated tree, had touching canopies (S. P. Hubbell, pers. comm.). In a mass-flowering individual of this same species in French Guiana, P. Charles-Dominique (pers. comm.) saw 6–8 individuals of a related woolly opossum, *C. philander*, visiting flowers. The fact that many neotropical trees such as *M. occidentalis* (Steiner, unpubl.), *Ochroma pyramidale* (pers. obs.), and *Hymenaea courbaril* (Hubbell, 1979) are clumped suggests that opportunistic nectar feeding by *Caluromys* or other nonflying mammals may often result in effective pollination in neotropical forests.

LITERATURE CITED

BAWA, K. S. 1974. Breeding systems of tree species in a lowland tropical community. Evolution 28:85–92.

BONACCORSO, F. J. 1979. Foraging and reproductive ecology in a Panamanian bat community. Bull. Florida State Mus., Biol. Sci. 24:359–408.

CARPENTER, F. L. 1978. Hooks for mammal pollination? Oecologia 35:123–132.

CROAT, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, 943 pp.

DAWSON, T. J. & A. J. HULBERT. 1970. Standard metabolism, body temperature, and surface areas of Australian marsupials. Amer. J. Physiol. 218:1233–1238.

DESTEVEN, D. 1981. Predispersal seed predation in a tropical shrub (*Mabea occidentalis*, Euphorbiaceae). Biotropica 13:146–150.

FAEGRI, K. & L. VAN DER PIJL. 1979. The Principles of Pollination Ecology. Ed. 3. Pergamon Press, New York, 291 pp.

HEITHAUS, E. R., T. H. FLEMING & P. A. OPLER. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology 56:841–854.

HOPPER, S. D. 1980. Bird and mammal pollen vectors in *Banksia* communities at Cheyne Beach, Western Australia. Austral. J. Bot. 28:61–75.

HOWELL, D. J. 1974. Bats and pollen: physiological aspects of the syndrome of chiropterophily. Comp. Biochem. Physiol. 48A:263–276.

———. 1979. Flock foraging in nectar-eating bats: advantages to the bats and to the host plants. Amer. Naturalist 114:23–49.

HUBBELL, S. P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. Science 203:1299–1309.

HUNSAKER, D. (editor). 1977. The Biology of Marsupials. Academic Press, New York, 537 pp.

JANSON, C. H., J. W. TERBORGH & L. H. EMMONS. 1981. Non-flying mammals as pollinating agents in the Amazon forest. Reproductive Botany, suppl. to Biotropica 13:1–6.

LUMER, C. 1980. Rodent pollination of *Blakea* (Melastomataceae) in a Costa Rican cloud forest. Brittonia 32:512–517.

ROURKE, J. P. & D. WIENS. 1977. Convergent floral evolution in South African and Australian Proteaceae and its possible bearing on pollination by nonflying mammals. Ann. Missouri Bot. Gard. 64:1–17.

SMYTHE, N. 1970. Relationship between fruiting season and seed dispersal methods in a neotropical forest. Amer. Naturalist 104:25–35.

SUSSMAN, R. W. & P. H. RAVEN. 1978. Pollination by lemurs and marsupials: An archaic coevolutionary system. Science 200:731–736.

TOLEDO, V. M. 1977. Pollination of some rain forest plants by non-hovering birds in Veracruz, Mexico. Biotropica 9:262–267.

VOGEL, S. 1954. Blütenbiologische Typen als Elemente der Sippengliederung. Bot. Stud. 1:1–338.

———. 1969. Chiropterophilie in der neotropischen Flora. Flora Abt. B, 158:185–222.

WALKER, E. P. 1975. Mammals of the World. Ed. 3, revision by J. L. Paradiso. 2 vols. Johns Hopkins Press, Baltimore, 1500 pp.

WEBSTER, G. L. & D. BURCH. 1968. Euphorbiaceae. *In* R. E. Woodson, Jr. & R. W. Schery, Flora of Panama. Ann. Missouri Bot. Gard. 54:211–350.

WIENS, D. & J. P. ROURKE. 1978. Rodent pollination in southern African *Protea* spp. Nature 276: 71–73.

———, M. RENFREE & R. O. WOOLLER. 1979. Pollen loads of honey possums (*Tarsipes spenserae*) and nonflying mammal pollination in Southwestern Australia. Ann. Missouri Bot. Gard. 66:830–838.