

COCKROACH POLLINATION AND BREEDING SYSTEM OF *UVARIA ELMERI* (ANNONACEAE) IN A LOWLAND MIXED-DIPTEROCARP FOREST IN SARAWAK¹

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Tropical forest plants are known to be pollinated by a diverse array of animals. Here we report on the pollination of a woody climber species, *Uvaria elmeri* (Annonaceae), by cockroaches in a lowland mixed-dipterocarp forest in Sarawak, Malaysia. To the best of our knowledge, this is the first report of pollination by cockroaches. The cauliflorous flowers in the understory are protogynous and bloomed for 50 h. An odor similar to decayed wood or a mushroom was secreted by flowers and was stronger during the male stage. Pollinators were cockroaches (Blattellidae) and drosophilid flies (Drosophilidae). Cockroaches, the main pollinators, visited flowers during both female and male stages at night, feeding on stigmatic exudate and pollen. Drosophilids, the secondary pollinators, mainly visited female-stage flowers during daytime, fed on stigmatic exudate, and laid eggs on stigmas. Neither autogamy nor self-compatibility was observed. Fruit production appeared to be pollen-limited. The fruit set, which was 2% of flowers in natural condition, was significantly lower than the 30% fruit set obtained by artificial cross-pollination. We discuss the traits of cockroaches as pollinators and the breeding system of *U. elmeri*.

Key words: Annonaceae; Blattodea; breeding system; dipterocarp forest; Drosophilidae; pollinator; Sarawak; *Uvaria elmeri*.

Pollination is accomplished by various insect taxa, which implies diverse interactions between plants and insects. To date, Hymenoptera, Coleoptera, Lepidoptera, and Diptera are reported as frequent insect pollinators. Thysanoptera also appear to be pollinators in some plant groups (Appanah and Chan, 1981). Cockroaches (Blattodea) would be the sixth order of insects recognized as pollinators (Proctor and Yeo, 1972).

Perry (1978) observed that cockroaches visited flowers of a neotropical canopy species, *Dendropanax arboreus* (Araliaceae). Roth and Willis (1960) collected cockroaches on flowers of various plants. Floral resources are used by some cockroach species though the majority are scavengers or detritus feeders (Proctor and Yeo, 1972). However, so far there has been no direct evidence to support the notion that cockroaches pollinate plants. Here we describe the first direct observation showing that cockroaches are major pollinators of understory cauliflorous flowers of *Uvaria elmeri* (Annonaceae) in a lowland mixed-dipterocarp forest.

The lowland mixed-dipterocarp forests in Borneo are noted for their plant species diversity, primarily in the understory (Ashton, 1988), where pollination syndromes

are often most diverse (Kato and Inoue, 1994; Kato, Inoue, and Nagamitsu, 1995; Kato, 1996). The Annonaceae are one of the predominant families in the understory of the forests. Annonaceous plants are pollinated mainly by beetles (Bernhardt and Thien, 1987). Most beetle-pollinated species have floral chambers, which facilitate pollination by beetles (Gottsberger, 1988). Some species in the genera *Lettowianthus*, *Malmea*, *Monocyclanthus*, and *Uvaria*, however, do not have chambers; the petals are open and spreading (van Heusden, 1992). The floral morphology observed in the latter four genera suggests the possibility of another pollination syndrome.

Here, we first describe the pollination biology, floral phenology, floral rewards, and flower visitors of *Uvaria elmeri*. Next, we evaluate the flower visitors as pollinators, based on attachment of pollen grains on their bodies, visitation frequency, and their apparent match with flowering phenology. Finally, we examine the breeding system and factors limiting seed production in this species.

MATERIALS AND METHODS

Uvaria elmeri Merr. (Annonaceae) is a woody climber with canopy foliage, whose cauliflorous flowers bloom in the understory. We found three genets of *U. elmeri* in an 8-ha study plot in Lambir Hills National Park, Sarawak, Malaysia (4°2'N, 113°50'E, 150 m altitude). In the study site, these plants grow at very low density on sloping clay soils near valley bottoms. At the forest floor in the plot, relative light intensity was 0.1–3%, air temperature was 23°–28°C, and relative humidity was 85–100% during the study period (Inoue and Hamid, 1994).

Two genets of *U. elmeri* in the plot bloomed in May and June 1994. One genet (Ug1) produced 108 flowers and the other (Ug2) produced five. The flowering phenology of 22 individual flowers of Ug1 was observed every 3 h from 0900 to 2100 from 25 to 31 May 1994.

The flower visitors were observed and collected from 2000 to 2400 from 24 May to 3 June 1994. Total observation time was 26 h, 18 h in female stage and 8 h in male stage. Flower visitors were collected with a hand net and killing bottles with potassium cyanide. Red light was

¹ Manuscript received 26 July 1995; revision accepted 13 August 1996.

The authors thank Messrs. H. S. Lee and A. A. Hamid for permission to conduct this research; Drs. P. J. A. Kessler, L. M. Roth, M. Toda, and S. Yamane for identification of the plant, cockroaches, drosophilid flies, and ants, respectively; Dr. H. Nagamasu and Mr. K. Momose for help in this research; and Drs. S. Appanah, K. S. Bawa, D. W. Roubik, and K. Yamaguchi for suggestions that improved this manuscript. This study was partly supported by the Japan Ministry of Education, Science and Culture for International Scientific Research Grant Number 04041067.

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used for night observation to minimize effects on the behavior of the insects on the flowers. A visit is defined as landing on or touching a flower. We estimated the mean frequency of visits per hour and calculated its variance, assuming a Poisson distribution. We documented the visitor's behavior on flowers: contact with anthers and stigmas, feeding (confirmed by gut contents), and oviposition (verified by the emergence of new adults from flowers incubated in plastic containers). The number of pollen grains on the bodies of the collected visitors was counted by examination of pinned specimens under a light microscope. The pollen grains of *U. elmeri* were distinguished by size and color of the grains compared with those collected from flowers. Pollen grains were rarely dislodged before counting due to their cohesion.

To clarify the breeding system of *U. elmeri*, we enclosed 30 flower buds of Ug1 and four of Ug2 in bags made of fine nylon mesh. The bagged flowers were treated in three ways: (1) 13 flowers were kept in bags but not pollinated; (2) 11 flowers were hand-pollinated with pollen of another flower on the same genet; (3) ten flowers were hand-pollinated with pollen of the other genet. We also marked 49 unmanipulated flowers as controls.

Fertilization and fruit and seed set of the bagged and the marked flowers were monitored. We recorded dates when the fruits under treated and natural conditions were aborted. The immature fallen fruits were collected within 2 d after falling. While still fresh, the fallen fruits were fixed in FAA (formaldehyde, acetic acid, and 70 % ethanol in the proportions 5:5:90 v/v/v). We examined the growth of pollen tubes in carpels of the fixed fruits with aniline-blue staining (Martin, 1959; Alexander, 1987). Mature fruits were collected in May 1995, 11 mo after flowering, and their dry mass and the number of seeds and carpels were measured.

RESULTS

Flowers—The 22 flowers whose phenology was observed bloomed for 50 ± 5 h (mean $\pm$ SD) (Fig. 1). Petals opened from midnight until morning. Flowers were protogynous. We defined the female stage as the period when stigmas secreted exudate, and the male stage as the period from the beginning of anther dehiscence to the fall of all stamens. Stigmas were wet just after petal anthesis, and the female stage lasted for 36 ± 7 h. A nonsexual stage (3 ± 5 h), when the stigma surface became dry before anther dehiscence, occurred in 32% of the observed flowers (Fig. 2). Stamens began to project and anthers started dehiscence between 1800 and 2100 on the 2nd d (Fig. 3). The projected stamens fell from flowers a few hours after the dehiscence until the morning on the 3rd d. The male stage continued for 11 ± 5 h. At the end of the male stage the petals fell, and afterward carpels remained alone in the center of the calyx.

Flowers had creamy-white or brown petals spreading horizontally to downward (Fig. 4) and secreted an odor like decayed wood or a mushroom. The odor was stronger during the male stage. No nectar was secreted, but stigmatic exudate was produced as a reward for flower visitors (Fig. 5). The exudate was 0.5–1.0 mm thick on stigmas, and their standing crop was constant throughout the female stage.

Flower visitors—We collected 79 individual insects on flowers of *U. elmeri*, including cockroaches, crickets, bugs, flies, ants, and stingless bees (Table 1). Only species of crickets, cockroaches, and drosophilid flies were found on both of the studied genets. Female-stage flowers were most frequently visited by drosophilid flies, fol-

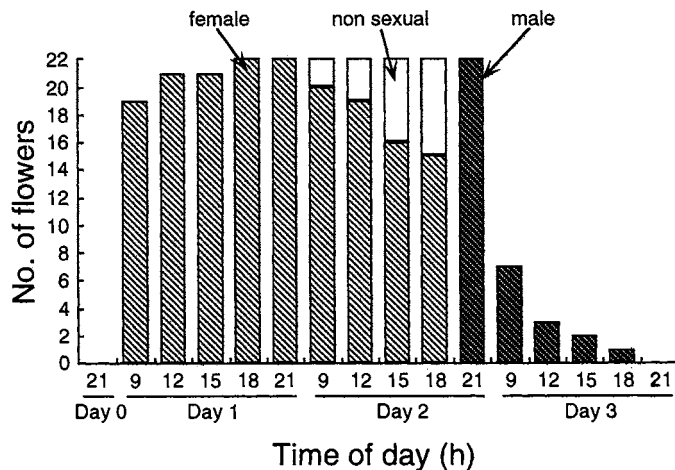


Fig. 1. Temporal changes in the number of flowers in female, non sexual, and male stages of *Uvaria elmeri*.

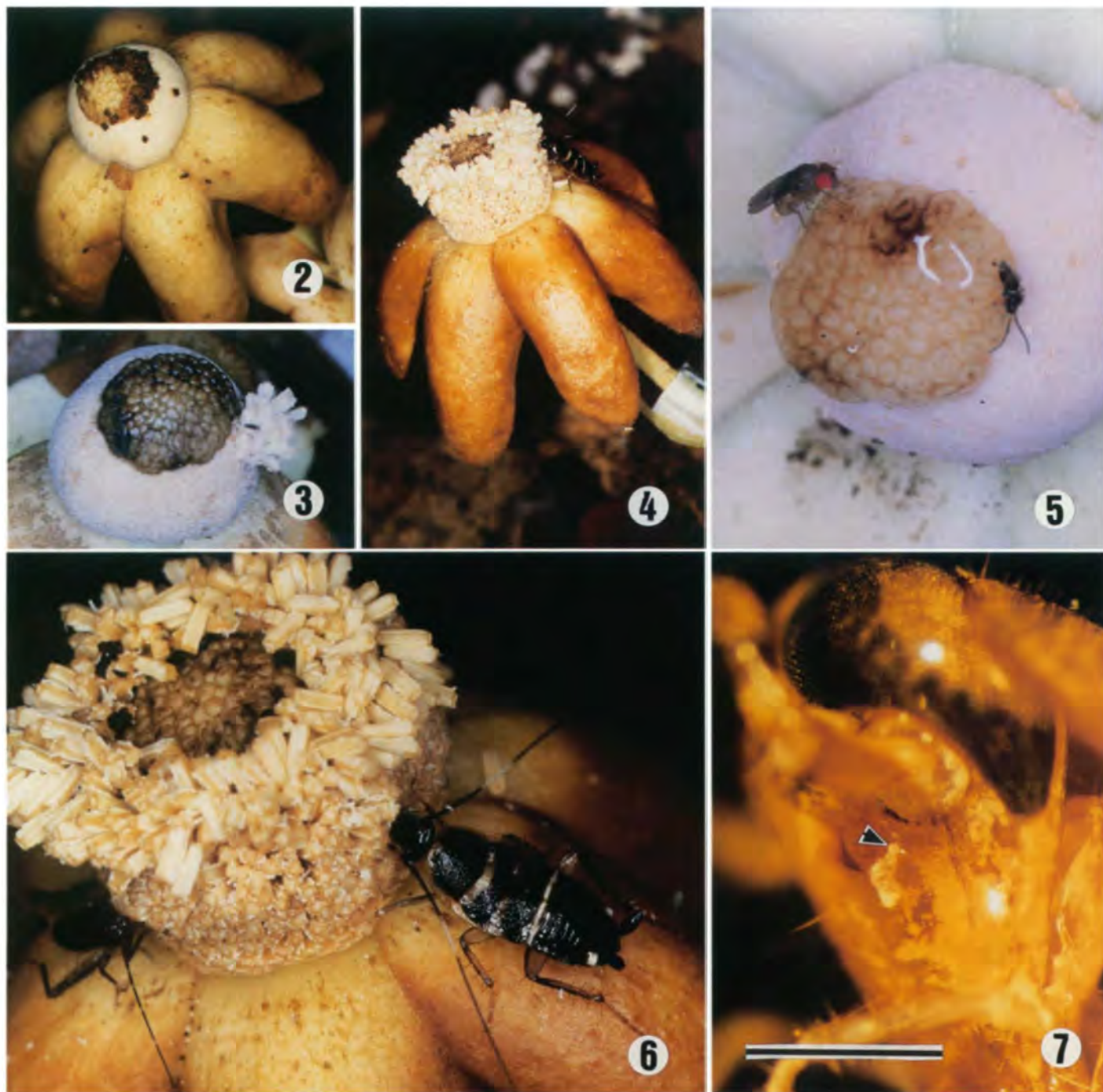
lowed by myrmicine ants, cockroaches, and phorid flies (Table 2). Male-stage flowers were most frequently visited by cockroaches, followed by crickets and drosophilids. The insect groups differed in the amount of diurnal activity (Fig. 11). Cockroaches were active at night, whereas drosophilids visited flowers during daytime.

Visitor feeding behavior on flowers is shown in Table 2. Adult cockroaches flew between flowers but nymphs walked. Cockroaches stayed on a flower for 5–15 min and touched both stigmas and anthers. They fed on both stigmatic exudate and pollen. Pollen was eaten with anther sacs, and >90% of the stamens were removed from a flower during the course of a visit (Fig. 6). Three of five sampled cockroach nymphs had guts filled with pollen grains of *U. elmeri*. Drosophilids fed only on stigmatic exudate and rarely touched the anthers. Drosophilids laid eggs on stigmas. Fly larvae grew on the stigmas and emerged 2 wk later, but they did not destroy the carpels. Ants made shelters at the base of flowers and foraged on stigmatic exudate during both day and night. Most stingless bees collected pollen from fallen stamens on the ground and rarely landed on male-stage flowers; they were never observed on female-stage flowers.

Pollen attachment was observed on cockroaches, drosophilids and stingless bees (Table 2). Three of the nine collected cockroaches carried 1–21 pollen grains on their heads (Fig. 7). One of the 27 drosophilids carried three pollen grains on one eye. Stingless bees carried many (>50) pollen grains, but most were packed in corbicular loads, which were transported as food and thus were unavailable for pollination.

Breeding systems and fruit maturation—In the bagged treatment, pollen grains that fell on stigmas germinated, but their pollen tubes were arrested at the top of the carpels. In the selfed treatment, pollen tubes reached ovules (Fig. 8). The pollen tubes near ovules lost their callose and swelled. We did not find any pollen tubes entering micropyles. In the crossed treatments, we observed pollen tubes penetrating ovules.

The periods of abortion were different among the bagged, selfed, and crossed treatments (Fig. 12; Kruskal-

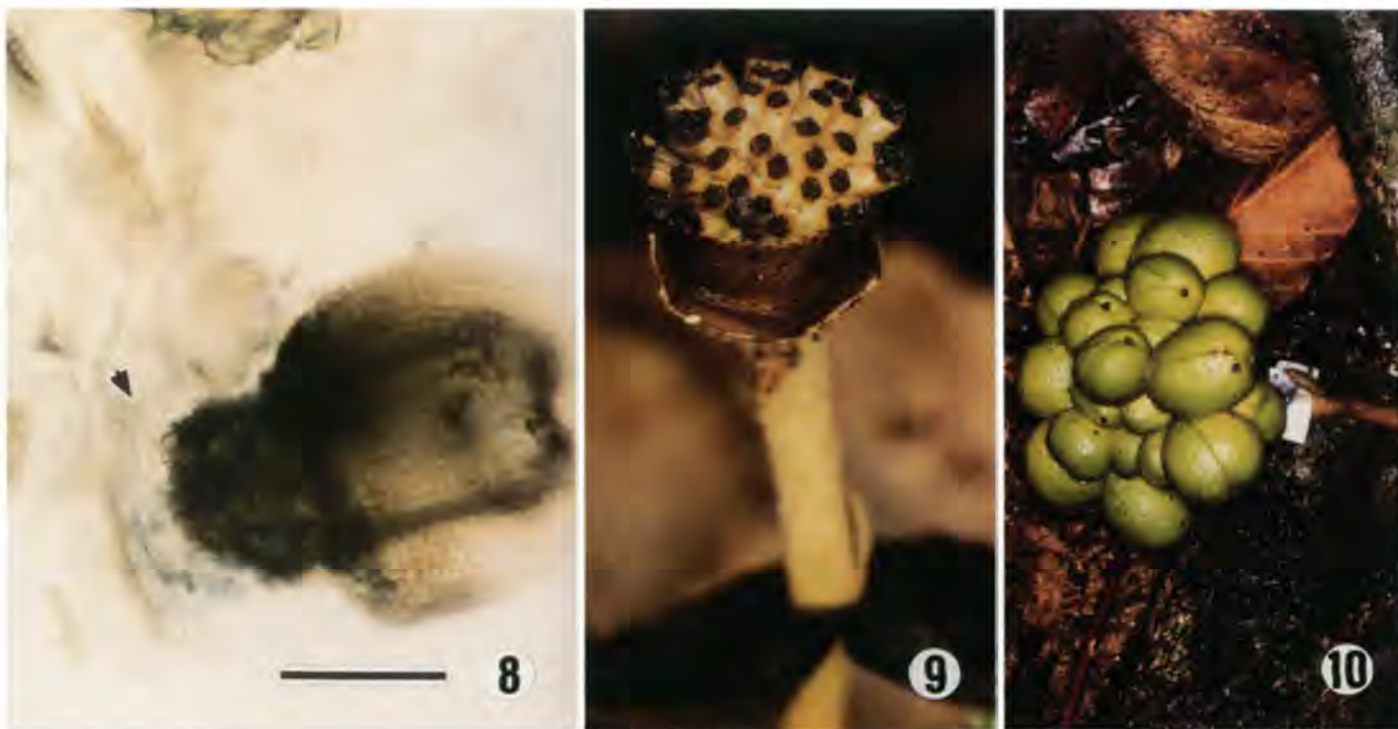


Figs. 2–10. Flowers, ovules, and fruits of *Uvaria elmeri* and their pollinators. 2. A flower in the nonsexual stage. 3. A flower at the beginning of the male stage with stamens projecting from torus. 4. A total view of a male-stage flower visited by a cockroach. 5. A drosophilid fly visiting a female-stage flower and feeding on stigmatic exudate. 6. A blattellid nymph and cricket visiting a male-stage flower and feeding on pollen. 7. Pollen grains on the bottom surface of the head of an adult blattellid cockroach visiting male stage flowers (bar = 1 mm). 8. Pollen tubes reaching ovules in the selfed treatment (bar = 0.1 mm). 9. An immature fruit. 10. A mature fruit.

Wallis *H* test: $P < 0.05$). All fruits in the bagged treatment aborted within 1 wk after flowering, but 73% of the fruits in the selfed and 40% of the fruits in the crossed treatments remained for >1 wk (Fig. 9).

Fruit set in the control flowers was 2% ($N = 49$), which was significantly lower than the 30% produced by

the outcrossing treatment ($N = 10$; Fisher's exact probability test: $P < 0.03$). Bagged and selfed flowers did not set mature fruits. Fruit maturation required 11 mo, and dry mass of a mature fruit was 102.9 ± 4.8 g (mean $\pm$ SD, $N = 2$; Fig. 10). The number of seeds per fruit in the crossed treatment (18.5) was significantly greater than



Figs. 2–10. Continued.

TABLE 1. Flower visitors to *Uvaria elmeri* and the number of individuals collected on each plant genet.

Order Family Species	No. of individuals collected	
	Genet 1	Genet 2
Orthoptera		
Gryllidae		
gen. spp. ^a	1	2
Blattodea		
Blattellidae		
<i>Hemithysocera</i> sp. nov.	1	0
gen. spp. ^a	7	1
Hemiptera		
Miridae	2	0
Diptera		
Asteiidae	2	0
Diopsidae	1	0
Drosophilidae		
<i>Drosophila (Drosophila) kohkoa</i>	9	1
<i>D. (D.)</i> sp. 1	2	0
<i>D. (D.)</i> sp. 2	1	0
<i>D. (Sophophora) mimetica</i>	2	0
<i>D. (S.)</i> sp. 1	8	1
<i>Liodrosophila dictenia</i>	1	0
<i>L. dimidiata</i>	2	0
<i>L.</i> sp. 1	1	0
<i>Scaptodrosophila</i> sp. 1	5	0
Phoridae	3	0
Hymenoptera		
Formicidae		
<i>Myrmecaria carinata</i>	24	0
Apidae		
<i>Trigona melanocephala</i>	2	0
Total	74	5

^a The genus is unknown, since the specimens are in nymph stage.

that in the natural condition (1.26) (Mann-Whitney *U* test: $P < 0.005$). A mature fruit had 28 ± 9.9 carpels ($N = 2$), while a flower had 65 ± 7.9 carpels ($N = 10$). A carpel of a mature fruit had 2.2 ± 0.9 seeds ($N = 10$), whereas a carpel of a flower had 16 ± 3.5 ovules ($N = 10$).

DISCUSSION

Cockroaches as pollinators—Our study shows that cockroaches and drosophilid flies were the most likely

TABLE 2. Frequency of insect visits to *U. elmeri* flowers, their feeding behavior, and the number of pollen grains on a body. Pollen grains were counted for all collected insect individuals shown in TABLE 1.

Order Family	No. visits/h to a flower in		Feeding on		Average no. of pollen grains on the body
	Female stage	Male stage	Stigma exudate	Pollen	
Orthoptera					
Gryllidae	0.1	0.5	+		0.0
Blattodea					
Blattellidae	0.4	1.5	+	+	3.9
Hemiptera					
Miridae	0.06	0.1			0.0
Diptera					
Asteiidae	0.1	0.0			0.0
Diopsidae	0.06	0.0			0.0
Drosophilidae	1.8	0.3	+		0.1
Phoridae	0.2	0.0			0.0
Hymenoptera					
Formicidae	1.5	0.1	+		0.0
Apidae	0.0	0.1		+	>50.0

^a Laying eggs on stigma surface.^b Carrying pollen as corbicular loads.

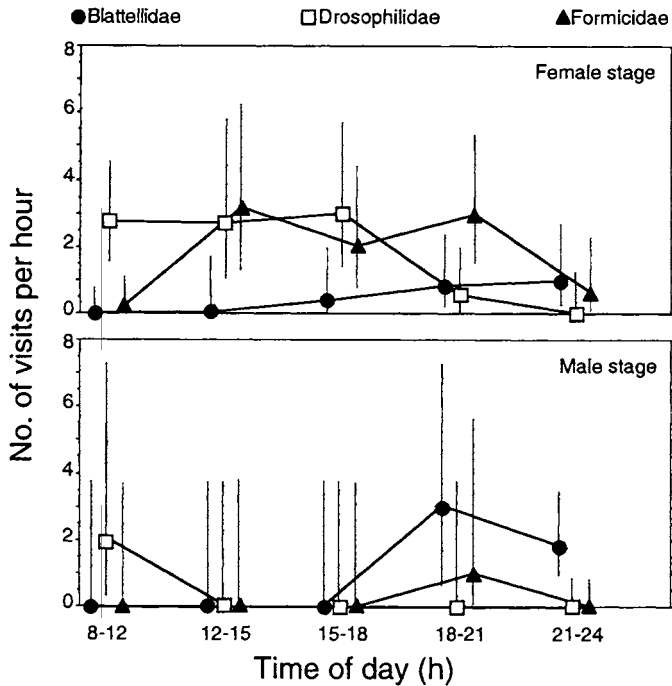


Fig. 11. Diurnal changes in the frequency of visits per hour (mean $\pm$ 95 % CI) to a female and a male stage flower of *Uvaria elmeri*.

pollinators of *Uvaria elmeri*. Among flower visitors, only cockroaches and drosophilids visited both male- and female-stage flowers, carrying conspecific pollen grains on their bodies when they visited female-stage flowers. Furthermore, cockroach pollination of *U. elmeri* is strongly implicated by: (1) correspondence of visitation time of cockroaches with nocturnal dehiscence of anthers; (2) presence of the same cockroach species on both plant genets and on flowers in both sexual stages, and (3) pollen grains of *U. elmeri* filling guts of the cockroaches, which demonstrated constant visits to these flowers during foraging. However, we still lack direct proof, that is, seed set in flowers visited only by cockroaches.

Cockroaches were estimated to be 8.9 times more effective than drosophilids as pollinators. We estimated the maximum possible number of pollen grains transferred to a female-stage flower per hour (p) by $p = vc$, where v is the number of visits to a female-stage flowers per hour, and c is the number of pollen grains on an individual visitor. Based on values in Table 2, the average p values are 1.6 for cockroaches and 0.18 for drosophilids.

The capacity for locomotion and site constancy are basic requirements for pollinators. A blattellid cockroach species in Costa Rica moved 600 m from their normal resting sites to find food (Schal, Gautier, and Bell, 1984). Constancy to feeding sites was observed in females of this species. They returned to the feeding site at 8–9 d intervals for egg production (Schal and Bell, 1982).

Most cockroach species are regarded as omnivorous scavengers and detritus feeders. In contrast, some cockroaches occasionally hunt insects and feed on living plants, particularly on flowers (Cooke, 1968; Gorton, 1980). In Costa Rican forests, pollen was one of the food items of male blaberid cockroaches, which mainly fed on leaf-litter and epiphytic materials (Schal and Bell, 1986).

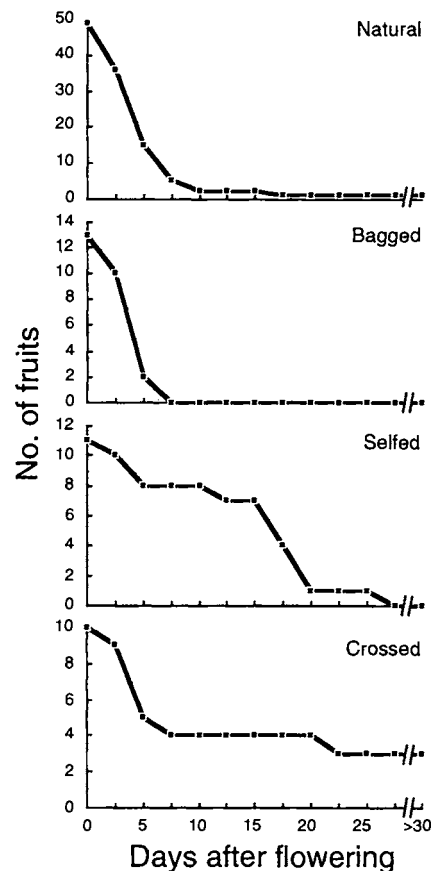


Fig. 12. Temporal changes in the number of fruits on plants of *Uvaria elmeri* in natural open condition, and in bagged, selfed, and crossed treatments.

A British cockroach species was recorded licking the nectar of flowers (Proctor and Yeo, 1972).

High-protein food like pollen facilitates growth and reproduction of cockroaches (Melampy and Maynard, 1937; Mullins, 1984). Nitrogen eaten during the nymph stage influences reproduction in adults because cockroaches convert excess nitrogen to urates, stored in urate cells in a fat body (Cohcran, 1985). Fecundity of blattellid cockroaches increases in response to increased food nutrients at feeding sites (Schal, Gautier, and Bell, 1984).

Non-beetle pollination in Annonaceae—The pollination syndrome in Annonaceae has been characterized by beetle pollination and floral chambers that are adapted to beetles (Gottsberger, 1989a; Kress and Beach, 1993). Gottsberger (1988) defined the floral chamber as a dark, chamber-like room formed by petals. Once pollinators visit flowers, they stay in the floral chambers until anther dehiscence, and come out when flowers fall on the ground (Gottsberger, 1989a). The flowers with floral chambers receive a limited number of pollinator visits because the chambers have limited space for pollinators to stay. When the number of pollen grains transported by a pollinator decreases, plants with floral chambers may suffer unsuccessful pollination.

In contrast, flowers with spreading petals provide no closed, chamber-like space. Such open flowers are found

in some genera including *Uvaria* (van Heusden, 1992). Flowers of *U. elmeri* provide only food, and cockroaches do not stay on the flowers to mate or rest. Thus, this type of flower seems to be adapted for pollinators visiting more frequently with lower pollination efficiency per visit.

Breeding system and fruit maturation—In many angiospermous plants, mechanisms to avoid inbreeding are absent, though self-incompatibility is common in the Magnoliidae (Bernhardt and Thien, 1987; Gottsberger, 1989b). Autogamy was also found in *Polyalthia littoralis* (Okada, 1990).

The lack of fruit set in bagged and selfed flowers of *U. elmeri* suggests neither autogamy nor self-compatibility. In the bagged flowers, pollen of the same flower was deposited on the stigmas after the end of the female stage since *U. elmeri* is completely protogynous. Inhibited growth of pollen tubes in the bagged treatment shows that stigmas had already lost pollen receptability after the female stage. *U. elmeri* may have late-acting self-incompatibility because pollen tubes reaching ovules did not enter micropyles in the selfed treatment (Seavey and Bawa, 1986; Gibbs and Bianchi, 1993).

The significant increase in fruit and seed set in the hand-outcrossed treatment, compared with those in the natural condition, suggests that seed production of *U. elmeri* was limited by pollination during the study period. The lower chance of outcrossing pollination under natural conditions may be due to both the low density of flowers and the low efficiency of the pollinators. Though selfing increases seed production of pollen-limited plants, *U. elmeri* has a self-incompatibility mechanism. These results suggest that lifetime seed production of this species may not be limited by pollination (Janzen et al., 1980), or that the self-incompatibility mechanism of this species allows cryptic self-fertility (Bertin and Sullivan, 1988). These points remain to be clarified in the future.

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