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Reproductive Biology of the Monoecious Understory Palm *Prestoea schultzeana* in Amazonian Ecuador[1]

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ABSTRACT

Prestoea schultzeana is a monoecious, protandrous palm in the forest understory of Amazonian Ecuador. We studied its leaf production, population density, sexual expression, phenology, pollination, and the specificity of the floral visitors. On average, 1.4 leaves and 0.9 inflorescences are produced per individual per year. The number of staminate flowers per inflorescence is relatively constant compared with the number of pistillate flowers which varies greatly. Flowering occurs in staminate and pistillate phases of approximately 19 and 0–7 days duration, respectively. Flowers open in the morning, and staminate flowers abscise in the afternoon of the same day whereas pistillate flowers last for two days. Flowers are whitish-yellow with a sweet odor and produce nectar. They were visited by Coleoptera (Chrysomelidae, Curculionidae, Nitidulidae, Ptiliidae, Staphylinidae), Hemiptera, Diptera (Drosophilidae, Syrphidae, Ceratopogonidae), Lepidoptera (Nymphalidae), and Hymenoptera (Formicidae, Halictidae). All examined individuals of the syrphid fly *Copestylum* sp. visiting pistillate flowers carried 100–500 grains of *P. schultzeana* pollen. Pollen occurred on all body parts, but especially on the legs, and this makes *Copestylum* sp. the most important pollinator. Most floral visitors were also frequent on the flowers of co-occurring plant species; notably the palm *Hyospathe elegans* shared most visitor species with *P. schultzeana.*

RESUMEN

Prestoea schultzeana es una palma monoica, protandra del sotobosque de la Amazonia ecuatoriana. Estudiamos su densidad de población, producción de ojas, expresión sexual, fenología, polinización, y la especificidad de sus visitantes florales. Cada individuo produce un promedio de 1.4 ojas y 0.9 inflorescencias por año. El número de flores estaminadas por inflorescencia es relativamente constante en comparación con el número de flores pistiladas, que es muy variable. La floración tiene una fase estaminada y una pistilada con una duración aproximada de 19 y 0–7 días, respectivamente. Las flores abren en la mañana, y las estaminadas caen en la tarde del mismo día; las pistiladas, en cambio, permanecen en antesis durante dos días. Las flores son blanco-amarillentas, con olor dulce, y producen nectar. Fueron visitadas por coleópteros (Chrysomelidae, Curculionidae, Nitidulidae, Ptiliidae, Staphylinidae), hemópteros, dípteros (Drosophilidae, Syrphidae, Ceratopogonidae), lepidópteros (Nymphalidae) e himenópteros (Formicidae, Harlictidae). Todos los individuos estudiados del Syrphidae *Copestylum* sp. que visitaban flores pistiladas llevavan 100–500 granos de polen de *P. schultzeana.* Había polen en todas las partes del cuerpo, especialmente en las patas. *Copestylum* sp. es el polinizador principal. La mayoría de los visitantes florales también eran comunes en las flores de otras especies de plantas cercanas, especialmente la palma *Hyospathe elegans* que compartía la mayor parte de los visitantes con *P. schultzeana.*

Key words: breeding system; Ecuador; leaf production; myiophily; palms; pollination; pollinator specificity; Prestoea schultzeana; *rainforest understory; reproduction.*

THE NEOTROPICAL GENUS *PRESTOEA* consists of ten species of small to medium-sized palms (Henderson & Galeano 1996). One species, *Prestoea acuminata* (Willd.) H. E. Moore (synonymous with *P. trichoclada* (Burret) Balslev and Henderson) produces palm hearts of economic importance in Ecuador (Balslev & Henderson 1987, Borgtoft Pedersen & Balslev 1992, Bonilla & Feil 1995). *Prestoea schultzeana* (Burret) H. E. Moore is a caespitose palm in the forest understory of Amazonian Ecuador, Colombia, and Peru. The leaves of *P. schultzeana* are used for thatch and fish traps (G. Tápuy, forest ranger at Jatun Sacha, pers. comm.).

While the demography and population dynamics of *Prestoea* recently have received attention (Bannister 1970, Harryson 1988, Bonilla & Feil 1995, Knudsen 1995), the reproductive biology of *Prestoea* is poorly known despite its economic importance and widespread occurrence. In Costa Rica and Colombia *Prestoea decurrens* (H. Wendl. *ex* Burret) H. E. Moore is pollinated mostly by bees (Bullock 1981, Ervik & Bernal 1996), and Bannister (1970) reported that *P. acuminata* (Willd.)

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H. E. Moore (as *Euterpe globosa* Gaertn.) in Puerto Rico was pollinated by "honeybees and small flies".

The purpose of the present study was 1) to estimate the population density and production of leaves and inflorescences of *P. schultzeana,* 2) to study its sexual expression, phenology, fruit predation, and pollination, and 3) to examine the degree of specialization of the flower visitors and pollinators.

STUDY SITE

The study was conducted in both primary and secondary tropical pre-montane *terra firme* forest at the reserve Jatun Sacha (01°04'S, 77°37'W, at an elevation of 450 m) in the Napo Province, Ecuador. Additionally, five flowering individuals were investigated at a location 7 km west of the reserve. The terrain is mostly steeply dissected hills crossed by many small streams. The soil consists usually of red clay Oxisol (Dystropept) (D. Neill, pers. comm.). Annual precipitation is about 4100 mm, with a peak from April to July and a drier period from December to February (A. Suárez, pers. comm.).

The palm population was studied during seven periods lasting from one to ten days from 19 October 1992 to 14 March 1993, and during five periods of one to 22 days duration between 18 February and 12 December 1994.

METHODS

Along a 1 km part of "Trail 1" starting at the biological station in the reserve, all reproductively mature individuals within a distance of 2.5 m from the centreline were tagged. Reproductively mature individuals were defined as being at least as tall as the smallest flowering or fruiting individual found, *i.e.,* more than 0.5 m high. The floral phenology, number of inflorescences, stem length, and number and growth of leaves (by marking the spear leaf) were recorded for nine months from March to November 1994. On caespitose individuals only the leaves of the oldest stem were counted.

The total number of flowers was counted on four inflorescences (from four randomly selected individuals) and flowers were inspected for scent emission, presence of rewards, and eggs and larvae of flower visitors. Indicator test tape used by diabetes patients to detect sugar in urine and sensitive to sugar concentrations as low as 0.1 percent, was used to test for the presence of nectar. Flowers were also immersed in a solution of neutral red in water. Neutral red stains lipids and terpenoids in pollen grains, pollen kitt, and scent-producing tissues as well as other glands (Vogel 1990). The temperature of an inflorescence was measured before and after splitting of the peduncular bract by inserting a digital thermometer with a 2 mm diameter probe into the centre of the inflorescence.

Insects visiting the staminate and pistillate inflorescences were observed for seven and eight hours, respectively. In order to investigate pollen transport by insects, three different methods were used: 1) living insect visitors were observed directly in the field with a 10× magnifying glass, 2) insects arriving at pistillate flowers were collected in cyanide killing jars and later examined under a stereomicroscope, and 3) insects arriving at pistillate inflorescences were collected, stored individually in vials with 70 percent ethanol, and ultra-sound-treated for ten minutes to remove any pollen grains. The alcohol was then centrifuged for five minutes at 2000 rpm and the pollen loads examined.

In order to investigate how restricted the floral visitors were to *P. schultzeana* inflorescences, insects were collected on several other species in the habitat, including *Aphandra natalia* (Balslev & Henderson) Barfod, *Astrocaryum urostachys* Burret, *Geonoma macrostachys* Mart., *Hyospathe elegans* Mart., *Mauritia flexuosa* L.f., *Phytelephas macrocarpa* Ruíz and Pav. (Arecaceae), *Asplundia* sp., *Carludovica palmata* Ruiz and Pav. (Cyclanthaceae), *Anthurium acrobates* Sodiro, *A. triphyllum* Bogn., and *Spathiphyllum cannaefolium* (Dryander) Schott (Araceae).

Voucher specimens of plants are deposited in the following herbaria: AAU, BG, QCA, QCNE. Insects are deposited in the entomological collection of the Zoological Museum, University of Aarhus, and in the collections of the respective specialists' institutions (see acknowledgments). Ceratopogonidae were deposited in the Canadian National Collection.

RESULTS

POPULATION DENSITY, LEAF PRODUCTION, AND FLOWERING PHENOLOGY.—In total, 28 potentially reproductive individuals were found along the transect covering an area of 5000 m^2. This corresponds to a density of 56 individuals per hectare. Most individuals of *P. schultzeana* were growing in low-lying humid areas close to streams. The average number of leaves per individual was 6.8 ± 2.0 (SD, $N = 26$). No correlation between leaf number per



FIGURE 1. (a) Inflorescence and infructescence of *Prestoea schultzeana.* (b) Staminate flowers visited by Alticinae beetles.

plant and stem length was found (Spearman correlation coefficient -0.21, $P < 0.32$, $N = 24$).

On average the palms produced 1.1 ± 0.28 leaves per individual per nine months (SD, $N = 21$). If the production of leaves is constant through the year this corresponds to an annual leaf production of 1.4 leaves per individual.

During the study period, 23 of the 28 individuals flowered and one specimen died. Flowering individuals were found throughout the period of observation, but the flowering peaked from December to June. On average, each flowering individual produced 0.7 ± 0.47 inflorescences per 9 months (SD, $N = 23$). The development of an inflorescence inside the peduncular bract took eight months, flowering lasted for about 30 days (see section on anthesis), and the development of the infructescence to maturity took 4–5 months. A mature infructescence may persist for several months before all fruits are dropped or dispersed.

FRUIT PREDATION.—A weevil (Baridinae, Madarini, Genus 1, sp. 2) was frequently observed to eat unripe fruits by penetrating the mesocarp and seed coat with its snout. Madarini beetles are likely to be common seed predators of *Prestoea.* A related species of Madarini was observed to bore holes in unripe fruits of *P. decurrens* in Colombia (Ervik & Bernal 1996). Bannister (1970) reported that a weevil infested the seeds of *P. globosa* in Puerto Rico apparently without affecting the germination percentages, but whether the predator in question was a Madarini is unknown.

INFLORESCENCES.—Inflorescences had 5-12 rachillae ($x = 7.4$, $N = 38$) which were 27–59 cm long ($x = 41$, $N = 26$) (Fig. 1) and enclosed in bud by a single, slender peduncular bract. Flowers were imperfect and grouped in sympodial units consisting of two lateral staminate flowers and one central pistillate flower (triads). Pistillate flowers, however, might be absent resulting in staminate dyads. Such dyads mostly occurred at the distal end of the rachilla. Thus, the inflorescences had at least twice as many staminate as pistillate flowers, and sometimes pistillate flowers were entirely absent (Table 1). The development of staminate flowers may be sup-

TABLE 1. *Floral expression of four randomly selected inflorescences of* Prestoea schultzeana.

Inflorescence number	Number of staminate flowers/ inflorescence	Number of pistillate flowers/ inflorescence	Ratio of staminate to pistillate flowers
1	3410	551	5.7
2	1781	93	19.2
3	5065	2	2533
4	4184	1993	2.1
Mean	3610	660	5.5

pressed at the distal end of the rachillae resulting in solitary staminate flowers.

ANTHESIS.—*Prestoea schultzeana* was protandrous. The staminate phase lasted about 19 days, with daily pulses of up to several hundred flowers per inflorescence. This phase was followed by a period of 4–8 d without open flowers whereupon the 0–7-day-long pistillate phase started. Flowers were whitish-yellow with a sweetish odor. Staining with neutral red solution indicated that the scent-producing tissues were located on the stamens of staminate flowers and scattered on all parts of pistillate flowers. This treatment also revealed the presence of pollen kitt. Both staminate and pistillate flowers produced nectar in septal nectaries.

When the peduncular bract opened all flowers were closed and neither scent nor insects were present. This lasted for more than a day until the next morning (0600 to 0800 h) when the first staminate flowers opened and started to emit scent (Fig. 2). Individual staminate flowers only lasted for a few hours and abscised in the afternoon of the same day. The staminate phase was often interrupted by one or a few days when no flowers opened and no insects were present. Pistillate flowers also opened in the morning (Fig. 2). Individual pistillate flowers lasted for one or two days after which their stigmas turned brown. No rise in temperature of the inflorescence was registered before or during anthesis.

FLOWER VISITORS.—Table 2 gives the insect visitors to *P. schultzeana* and Figure 2 their abundance during the day. Although their frequency varied considerably between observation periods, small flies belonging to Ceratopogonidae (Fig. 3, g–h) and Drosophilidae (Fig. 3, c–d) were the most numerous visitors to both staminate and pistillate flowers. As many as 200 ceratopogonids were present simultaneously on an inflorescence during the staminate phase. Typically, they clung to the thecae, apparently eating pollen. Occasionally, we observed pollen on their antennae, abdomen, and legs. The *Atrichopogon* sp. 1 (Ceratopogonidae) and up to a hundred individuals of *Drosophila* flies foraged on staminate-phase inflorescences simultaneously. The most conspicuous visitor was the syrphid fly *Copestylum* sp. 1 (Fig. 3, a–b). It arrived at about 0700 h, and typically 4–8 individuals were present at any time on inflorescences in the staminate phase. At each flower, they usually first searched for nectar and then pollen or sometimes only for pollen. During foraging their bodies touched the anthers. Each individual visited several rachillae and a visit to an inflorescence thus usually lasted several minutes.

In general, flies were more numerous at pistil-

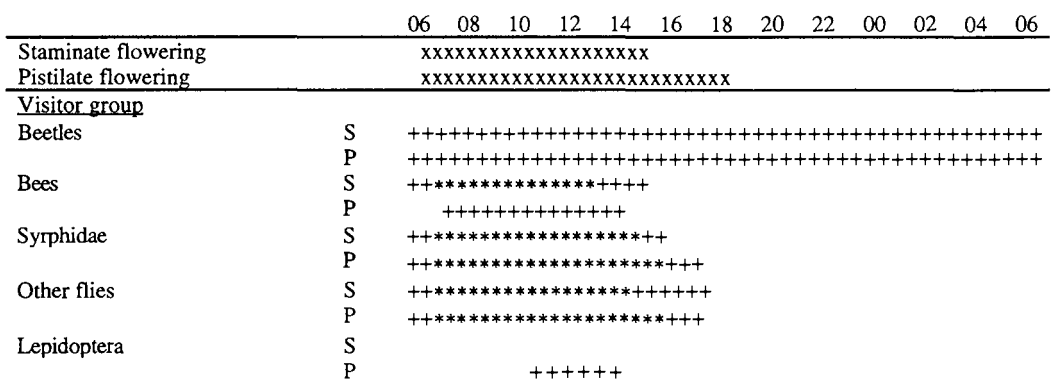


FIGURE 2. Time of day, anthesis of flowers, and activity level of floral visitors of *Prestoea schultzeana.*

TABLE 2. *Insects observed on inflorescences of* Prestoea schultzeana[a]. *Relative abundances are indicated as follows: very common (**), common (*), and rare (+). Insect taxa observed elsewhere are indicated with a number and an "s" or a "p" refering to plant species and its phase (s = staminate, p = pistillate):* Aphandra natalia *(1),* Astrocaryum urostachys *(2),* Geonoma macrostachys *(3),* Hyospathe elegans *(4),* Mauritia flexuosa *(5),* Phytelephas macrocarpa *(6),* Asplundia *sp. (7),* Carludovica palmata *(8),* Anthurium acrobates *(9),* A. triphyllum *(10), and* Spathiphyllum cannaefolium *(11).*

ORDER/Family Subfamily, tribe	Visitor	Staminate phase	Pistillate phase	Observed elsewhere
COLEOPTERA				
Chrysomelidae				
Alticinae	*Brasilaphthona* sp. (or near)	+	+	4s,9p
	Chorodecta sp. (or near)	+		
	Luprea sp. 1	+		
	Luprea sp. 2	+		
	Tetragonotes sp.	+		3p,5s/p
Galerucinae	*Monolepta* sp.	+		5s
	Undet. sp. 1	*	*	
Curculionidae				
Baridinae, Centrinini	C., Genus 3, sp. 1		+	
	C., G. 4, sp. 1	+		
	C., G. 5, sp. 2	+		
Cholinae	*Cholus brominus* Pascoe	+	+	
	C. ellipsifer Kirsch	*	*	3p,4s
	C. oberthuri Pascoe	+	+	
	Homalinotus cristatus (Kirsch)	+		6p
Erirhininae, Derelomini	*Phyllotrox* sp. 16	+		
	P. sp. 29	*		
	P. sp. 30	+	+	
Nitidulidae				
"Mystropinae"	*Mystrops obesus* sp. n.	+	+	
Ptiliidae	P. sp. 1	+		3p,4s
Staphylinidae				
Aleocharinae	*Hoplomicra* ? sp. 1	+		
HEMIPTERA	*Auchenorrhyncha* sp.	+	+	
DIPTERA				
Drosophilidae	*Drosophila* sp. 1	*	**	4s
	D. (*Sophophora*) sp. 2	+	+	
Syrphidae				
Melanostomatini	*Rhysops* sp.	+	+	
Volucellini	*Copestylum* sp.	*	*	4s
Ceratopogonidae				
Forcipomyiinae	*Atrichopogon* sp. 2	*	**	4s,9s,10s,11s/p
LEPIDOPTERA				
Nymphalidae, Ithomiinae	*Oleria agarista agarista* (Felder and Felder)		+	
	O. gunilla lota (Hewitson)	+	+	4s
	Ithomia salapia salapia (Hewitson)		+	
HYMENOPTERA				
Formicidae	F. spp.	+	+	4s
Halictidae	*Megalopta* sp. 1	+	+	4s

[a] Species and genera lacking names are given numbers corresponding with those in the collections of the specialists to permit comparisons with other publications of the specialists or the authors.

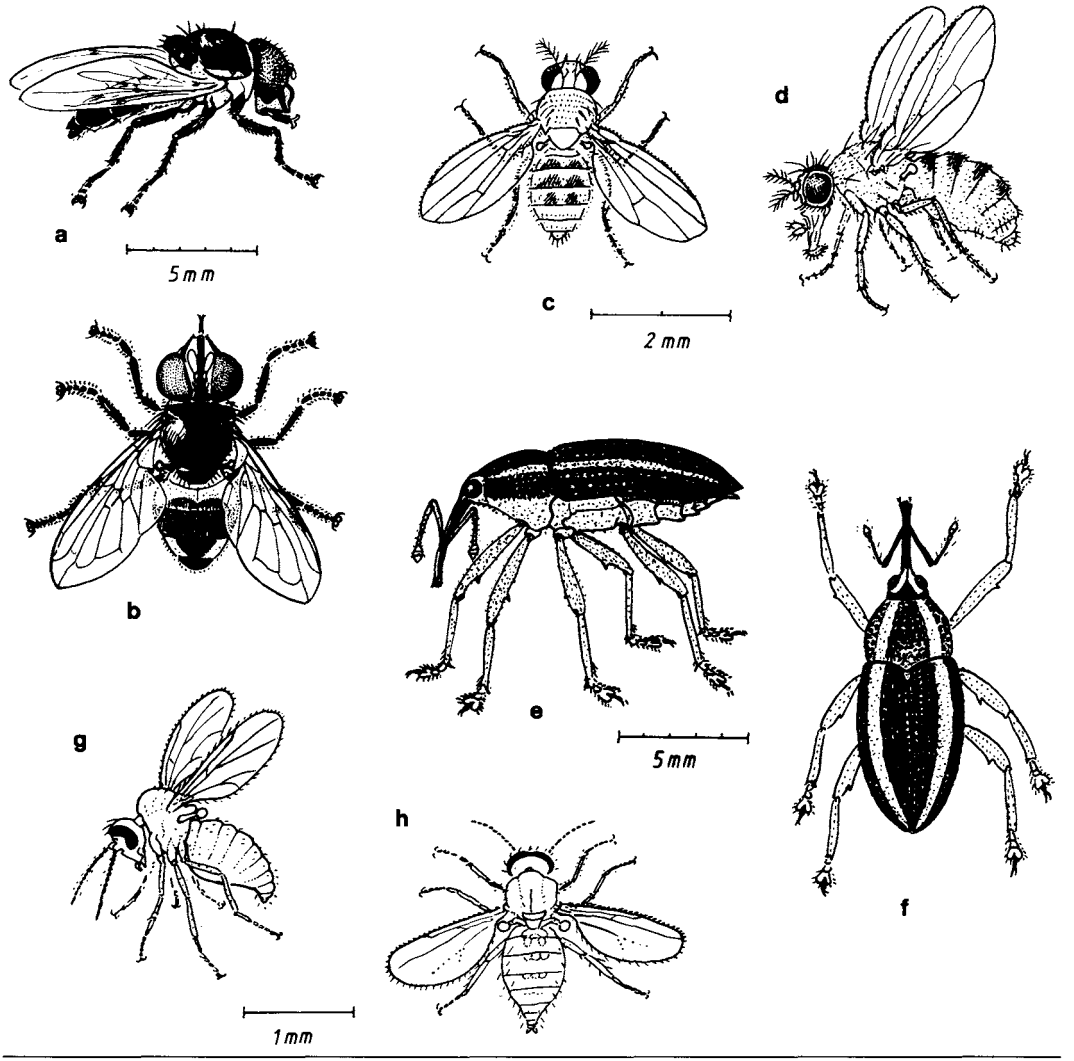


FIGURE 3. Insect visitors to *Prestoea schultzeana*. (a–b) *Copestylum* sp. (c–d) *Drosophila* sp. (e–f) *Cholus ellipsifer*. (g–h) *Atrichopogon*.

late flowers than at staminate flowers. Up to a few hundred individuals of *Drosophila* and of *Atrichopogon* sp. 1 arrived to forage for nectar. Thirty alcohol-collected individuals of *Drosophila* and 35 ceratopogonids from a pistillate-phase inflorescence had a surface load of approximately 100 pollen grains in total. Half of these grains belonged to *Prestoea*, and the rest were from at least three other plant species. Usually, 6–12 individuals of *Copestylum* sp. 1 were searching for nectar during the pistillate phase at any one time. Most often they touched the stigmas with their legs when licking nectar and with the rest of the body when walking along the rachillae. Eight dry and ten alcohol-collected specimens of this species carried about 100–500 pollen grains each. The pollen belonged exclusively to *P. schultzeana* and occurred on all parts of the flies' bodies, with the highest concentration on the legs.

Twenty species of beetles regularly visited the inflorescences. Ten of these were weevils. The most conspicuous was the black and yellow weevil, *Cholus ellipsifer* (Fig. 3, e–f). Usually fewer than eight individuals were sitting along the rachillae for hours, often copulating and sometimes taking up nectar. *Cholus ellipsifer* also visited *Hyospathe elegans* and *Geonoma macrostachys*. Two other species of *Cholus* behaved in the same manner, but were less

frequent. Three species of *Phyllotrox* and three species of Centrinini frequently foraged for nectar. A 20 mm long grey weevil, *Homalinotus cristatus* was occasionally observed to forage for nectar on staminate flowers, but was never found on pistillate flowers. In addition to the weevils, several species of chrysomelid beetles also foraged for both nectar and pollen, and in the field, we observed pollen on several individuals belonging to five species of Alticinae. Also species of ptiliid and nitidulid beetles came regularly, whereas a species of staphylinid beetle occurred occasionally. Compared with the other visitors, all these beetles were inactive.

The only bees observed were a few individuals of a light-brown *Megalopta* species (Halictidae) that collected pollen. Three species of butterflies (Ithomiidae) frequently foraged for nectar on pistillate flowers. One of these species, *Oleria gunilla,* also visited the inflorescences of *Hyospathe elegans.*

Other animals visited the inflorescences occasionally. A few wasps hovered along the rachillae, probably hunting floral visitors, and occasionally touching the flowers. Several species of ants foraged for nectar, and at least one species hunted small flies. Once, a 20 mm long dark-coloured frog spent more than an hour hunting small flies in an inflorescence.

DISCUSSION

Population density, leaf production, and flowering phenology.—Our results agree with those of Harryson (1988) who studied the demography of *P. schultzeana* at Añangu, 150 km north-east along the Río Napo River. The dispersion of *P. schultzeana* at both localities was clumped, with the highest densities in moist places. Potentially reproductive individuals had the same number of leaves (6.8) in the two populations. However, at Añangu, the percentage of flowering individuals, comparable in size to those studied in Jatun Sacha, was only 40–50 percent. This is about half as many as the 80 percent reproductive individuals found in the present study.

By far the highest number of inflorescences was found from March to June, which is a relatively wet period at Jatun Sacha. In December 1994, few inflorescence buds (inflorescences developing in the bract) were seen, indicating that flowering hardly was as intense in March 1995 as it was in March 1994. Thus, flowering apparently is synchronized among individuals but not restricted to a specific period of the year.

Flowering and breeding system.—The flowering sequence of *P. schultzeana* generally follows the same pattern as that described for *P. decurrens* (Bullock 1981, Ervik & Bernal 1996), but differs slightly from that of *P. globosa,* which has a short overlap between the staminate and pistillate phases (Bannister 1970, as *Euterpe globosa*).

Geitonogamy is absent or very rare in *P. schultzeana* because there is no overlap between the staminate and the pistillate phases of one inflorescence and because inflorescences in different phases are usually not present on the same individual.

Specificity of insects.—The majority of the frequent visitors to *P. schultzeana* also visited other plant species. In particular, the palm *Hyospathe elegans* had a fauna very similar to that of *P. schultzeana.* This clearly shows that few or none of the common visitors of *P. schultzeana* are species specific. This finding was expected because *P. schultzeana* does not offer breeding opportunities (*e.g.,* protection or fleshy tissues), which are often associated with specialized pollinators (Faegri & van der Pijl 1979).

Prestoea schultzeana at the two study localities attracted the same four species of Alticinae. These were different from those visiting *Mauritia flexuosa* growing midway between the two localities (Ervik & Feil, pers. obs.). Thus, species of Alticinae show at least some specificity. The *Brasilaphthona,* however, frequently mated and fed on nectar on a nearby *Spathiphyllum cannaefolium.*

The syrphid fly *Copestylum* also visits other plant species (Table 2), but the purity of the pollen loads suggests a high flower constancy. Such constancy in foraging bouts has previously been observed in polytropic syrphids (Grant 1949, van der Goot & van der Grabandt 1970, Leereveld 1982).

Pollination.—*Prestoea schultzeana* is not adapted to wind pollination because the pollen has pollen kitt and the flowers lack large stigmatic surfaces suitable for receiving airborne pollen. Also, the beetle visitors of *P. schultzeana* are probably unimportant for pollen-transfer owing to their sedentary behavior. Still, they visit both staminate and pistillate flowers regularly, and may occasionally act as pollinators.

Butterflies, such as ithomiines, are particularly attracted to white flowers and they are well known for their mutual relationship with the flowers of certain Boraginaceae and Compositae from which they obtain both nectar and pyrrolizidine alkaloids (secreted into the nectar) which they need for de-

fense and pheromones (Pliske *et al.* 1976, DeVries 1987). They forage for nectar and thus are attracted to both staminate and pistillate flowers and may be potential pollinators. However, ithomiines were relatively rare on *P. schultzeana,* and their role in pollination is therefore minor.

The role of wasps in pollination is insignificant because they only occasionally touch the flowers. Ants, on the other hand, frequently touch the flowers but can only transfer insignificant quantities of pollen between individuals.

The halictid bees are strong flyers and capable of transporting large amounts of pollen grains. One *Megalopta* species forages on both staminate and pistillate flowers of *P. schultzeana,* but was rare at the study sites. Halictid bees may, however, be more important for *P. schultzeana* elsewhere.

The certapogonid and drosophilid flies are small and relatively sedentary. For these reasons, they often are poor pollinators in other palm species in which they were found to carry little or no pollen when visiting pistillate flowers (Borchsenius 1993, Ervik 1993, Bernal & Ervik 1996). The finding of some pollen in a mixed collection of ceratopogonids and drosophilids from pistillate flowers does, however, demonstrate that at least one of the groups may participate in the pollination of *P. schultzeana.*

The syrphid fly *Copestylum* sp. is a capable flyer and frequently visited both staminate and pistillate flowers. When foraging it often touched stamens and stigmas with both legs and other parts of its body. Morever, it carried large quantities of pollen grains. We conclude that *Copestylum* is the major pollinator of *P. schultzeana* at least at our study sites. Species of *Copestylum* have previously been reported to pollinate other forest understory palms such as *Aiphanes erinacea* in Ecuador (Borchsenius 1993) and *Asterogyne martiana* in Costa Rica (Schmid 1970), and in Ecuador *Copestylum* species also visit the inflorescences of *P. decurrens* (Borchsenius 1993) and *Geonoma macrostachys* (Olesen & Balslev 1990).

This is the first record of fly pollination in the genus *Prestoea.* Both Bullock (1981) and Ervik and Bernal (1996) concluded that *P. decurrens* was pollinated primarily by bees, while Bannister (1970) considered "honeybees and small flies" to be the pollinators of *P. globosa.* Our results support Hendersons' (1986) statement that fly- and bee-pollinated palms have similar syndromes. Several differences between *P. schultzeana* and *P. decurrens* may, however, represent adaptations to syrphid flies and halictid bees, respectively. The number of rachillae per inflorescence is usually six to seven times higher in *P. decurrens* than in *P. schultzeana,* and the number of flowers about ten times higher. The flowers are also smaller in *P. decurrens.* These features correspond well with halictid bees being smaller and more numerous visitors than the syrphid flies. Additionally, the flowers of *P. decurrens* are apparently scentless whereas those of *P. schultzeana* have a strong scent, and the anthesis starts about three hours later in the morning in *P. decurrens* compared to *P. schultzeana.* Despite the different pollinators in *P. schultzeana* and *P. decurrens* the visiting faunas of these two species are similar, and include several shared genera, particularly of beetles. Such a similarity in fauna is likely to facilitate switches between the two syndromes.

Fly pollination, beetle pollination, and bee pollination are considered the major pollination syndromes in the palms, and myiophily is especially common in understory palms (Henderson 1986). Also at La Selva, fly pollination was exclusively found in the understory and for only five of the 151 plant species studied (Kress & Beach 1994). The fact that the bee-pollinated *P. decurrens* flowers in the sub-canopy and the fly-pollinated *P. schultzeana* in the understory is in concordance with this view.

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