POLLINATORS OF TROPICAL DIOECIOUS ANGIOSPERMS[1]

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Dioecy is frequent in tropical forests. It has been suggested that small, unspecialized pollinators are among the factors responsible for gender separation in this habitat. The underlying assumption is that poor fliers and/or communal foragers frequently effect selfing which in turn, given sufficiently severe inbreeding depression, should favor the establishment of dioecy. At least 10% of the genera of the angiosperms includes dioecious species; in tropical flowering plants, however, pollinators are reliably known only in a few species. Whereas temperate dioecious species commonly are wind- or water-pollinated, anemophily is less important in tropical forests, but occurs in at least 30 dioecious genera. Our survey of tropical dioecious zoophilous species in 29 genera (in 21 families) for which detailed pollination information is available shows that these species have specialized flowers adapted to specific pollinators rather than generalized flowers suitable for diverse insects. Known pollinators include solitary and eusocial bees, beetles, moths, flies, wasps (including fig wasps), and rarely bats and birds, and cover a wide range in animal size and locomotive capabilities. Floral rewards comprise pollen, nectar, stylar mucilage, nutritious tissues, brood-places, and resins. About a third of the species offer no reward in the female morph, pollination by deceit apparently being common. Our data thus do not support the hypothesis that there is a broad correlation between a dioecious breeding system and unspecialized pollination, although such a correlation may be found in certain taxa. Specialized plant-pollinator relationships seem as critical in dioecious plants in tropical forests, where individuals often grow far apart, as they are in tropical plants with other breeding systems.

Seventeen years ago Bawa and Opler (1975) put forward the proposition that a correlation exists between dioecy and pollination by diverse small insects. To explain this correlation they suggested that the limited interplant movements of small pollinators would result in high levels of selfing in hermaphrodites, whereas such pollinators could be used effectively by dioecious species. A corollary hypothesis (Bawa, 1980a; Beach and Bawa, 1980; Bawa and Beach, 1981; Beach, 1981) was that opportunistic foragers respond dramatically to intrapopulational differences in floral resources such as might be expected in species developing dioecy, which would result in asymmetric pollen flow, with some plants acting as pollen donors (proto-males) and others as pollen receivers (proto-females). Finally, it was proposed (Beach, 1981) that most tropical dioecious species have generalized flowers suitable for allotropic visitors (i.e., animals not specialized for obtaining floral rewards) in sharp contrast to hermaphrodites that were said to typically have specialized morphologies. The postulated association between dioecy and pollination by small, generalist insects, hereafter referred to as the "Bawa Hypothesis," and its corollary hypotheses seem to have gone unscrutinized and have become widely accepted (Givnish, 1980, 1982; Lloyd, 1982; Ross, 1982; Sobrevila and Arroyo, 1982; Frankie et al., 1983; Baker and Cox, 1984; Charlesworth, 1984; Kay et al., 1984; Kubitzki and Kurz, 1984; Bawa et al., 1985; Fox, 1985; Kevan and Lack, 1985; Muenchow, 1987; Lovett Doust and Lovett Doust, 1988; Ibarra-Manríquez and Oyama, 1992).

Since the original publication of the Bawa Hypothesis more information has become available on the pollinators of tropical dioecious angiosperms. We here review these data in order to evaluate what role, if any, promiscuous pollinators may have played in the evolution of dioecy in tropical species. Specifically, we address the following questions: 1) Does the pollinator spectrum of tropical dioecious species differ from that of tropical plants with other breeding systems, and if so, is it skewed toward small insects? 2) Are single tropical dioecious species pollinated by (taxonomically) diverse insects? 3) What are the pollinators' flight ranges, behavior on the flower, and rewards?

A problem in previous analyses of correlations between dioecy and other traits, such as woodiness or fleshy fruits, has been the generally insufficient knowledge of the phylogenetic relationships among the plant taxa possessing these features (recent summary: Thomson and Brunet, 1990). Our analysis avoids this difficulty as plants and their pollinators usually are not phylogenetically linked. In any case, the sample (Table 1) does not consist of closely related groups, but includes taxonomically isolated Old and New World representatives from 21 families in 18 orders, thereby reducing the likelihood of phylogenetic bias (but see Armbruster, 1992).

MATERIALS AND METHODS

The names and numbers of tropical dioecious genera and families were taken from Yampolsky and Yampolsky (1922), Charlesworth (1985), Mabberley (1987), and recent taxonomic literature. Information on pollination in tropical dioecious species was compiled from published sources and our own observations. Tropical, dioecious angiosperms are here defined as species occurring in frost-free forests in the tropical belt at altitudes below 1,500 m, with individuals belonging to two classes, i.e., func-

tioning as males or females throughout their lives. This excludes gynodioecious and androdioecious species in which the hermaphrodites regularly have functional male and female parts, but includes morphologically gynodioecious or androdioecious species in which the hermaphrodites function either as a maternal or as a paternal parent, such as figs and *Decaspermum* (Galil, 1973; Kevan and Lack, 1985; Verkerke, 1987). There is, however, a morphological, physiological, and evolutionary continuum between hermaphroditism and dioecy (Lloyd, 1980; Ross, 1982), so that populations and species cannot always easily be placed into discrete classes. Synchronized dichogamy or heterodichogamy, sometimes misleadingly referred to as temporal dioecy (Cruden and Hermann-Parker, 1977), and sequential hermaphroditism, diphasy, or gender choice (for recent summaries: Poppendieck, 1987; Schlessman, 1988; Zimmerman, 1991) are outcrossing mechanisms differing fundamentally from dioecy in that all individuals function as male and female.

Our survey is restricted to detailed studies on species' modes of pollination. Studies qualified as "detailed" if they reported actual flower visits by identified animals, supported by such evidence as pollen load analyses or detailed observations on the animals' behavior on the flowers. Studies assigning pollinators to broad categories, such as "small diverse insects" (e.g., Bawa and Opler, 1975; Bawa, 1980a; Bawa et al., 1985), cannot test the hypothesis that dioecy is correlated with pollination by just such insects; further information is required on the taxonomy of the insects and their behavior on the flowers. First, it is necessary to show that members of such groups are pollinators rather than mere visitors. Second, the label "diverse" should only be attached after a taxonomic analysis.

Important dioecious taxa for which we were unable to find pollination reports satisfying these criteria are Amaranthaceae (*Iresine*), Amborellaceae (*Amborella trichopoda*), Anacardiaceae (*Astronium, Rhus, Spondias*), Annonaceae (*Ephedranthus, Stelechocarpus*), Aquifoliaceae (*Ilex*), Balanophoraceae, Bromeliaceae (*Catopsis*), Brunelliaceae (*Brunellia*), Burseraceae (*Bursera, Protium, Tetragastris, Trattinnickia*), Cucurbitaceae (hundreds of dioecious spp.), Crypteroniaceae (a few dioecious species), Dioscoreaceae (*Dioscorea, Tamus*), Euphorbiaceae (ca. 500 dioecious spp.), Flacourtiaceae (*Carpotroche, Xylosma*), Icacinaceae (*Ioedes, Phytocrene, Pyrenacantha*), Loranthaceae (*Struthanthus*), Memecylaceae (*Lijndenia*), Menispermaceae (ca. 500 dioecious spp.), Myrsinaceae (*Cybianthus, Stylogyne*), Nepenthaceae (*Nepenthes*), Nyctaginaceae (*Neea, Pisonia*), Passifloraceae (*Adenia*), Piperaceae (*Piper dioica, P. betel*), Polygonaceae (*Coccoloba, Triplaris*), Rutaceae (*Zanthoxylum*), Sapindaceae (*Allophylus, Matayba, Talisia*), Sapotaceae (*Pouteria stipitata*), Smilacaceae (ca. 200 dioecious spp.), Symplocaceae (*Symplocos*), Theophrastaceae (*Clavija*), Thymelaeaceae (*Daphnopsis*), Tiliaceae (*Vasivaea*), and Verbenaceae (*Aegiphila, Citharexylum*).

RESULTS

The plants—Table 1 summarizes pollination data for 29 genera (and some 50 species) representing 21 families, about half from the Old World, half from the New. This data set is as complete as we believe currently possible but does not reflect the numeric frequency nor the phylogenetic distribution of dioecy. Perhaps 10% percent of the ca. 13,500 angiosperm genera recognized today are dioecious, and dioecy is particularly common in woody plants (Darwin, 1877; Yampolsky and Yampolsky, 1922; Baker, 1959; Charlesworth, 1985). In terms of absolute species numbers, dioecy is a tropical lowland phenomenon, but the relative frequency of dioecy is highest in certain temperate floras where wind pollination is important, such as the Patagonian alpine flora (Arroyo and Squeo, 1990), the Cape flora of South Africa (Steiner, 1988), and island floras (New Zealand, Hawaii [Baker and Cox, 1984]).

Also in the tropics anemophily and dioecy are frequently correlated. At least 30 tropical dioecious genera, predominantly from midelevations, are anemophilous, including *Baccharis* (Asteraceae), *Bursera* (Burseraceae [Ruiz and Arroyo, 1978], but see below), *Hedyosmum* (Chloranthaceae [Todzia, 1988]), *Acalypha* (Croat, 1978), *Alchornea, Mallotus* (Lock and Hall, 1982), and several other euphorbiaceous genera, some Moraceae and Cecropiaceae (Croat, 1978; Ruiz and Arroyo, 1978; Bawa and Crisp, 1980), *Ateleia* (Leguminosae [Janzen, 1984]), *Pandanus* (Pandanaceae [Cox, 1990]), *Gynerium, Spinifex* (Poaceae), and Urtiaceae (*Myriocarpa, Pilea, Urera*). In addition, wind pollination plays a secondary role in a few entomophilous tropical dioecious taxa, for example, *Triplaris* (Polygonaceae [Bawa and Opler, 1975; Brandbyge, 1986]) and certain palms (*Chamaedorea, Orbignya, Mauritia* [Bawa and Crisp, 1980; Anderson, Overal, and Henderson, 1988; Ervik, in press]). Most tropical submerged plants also are dioecious (Cox, 1988). Thus, the correlation between abiotic pollination and dioecy, which is well established in temperate regions (Stebbins, 1951), seems to hold in the tropics, albeit less strongly.

The rewards—Rewards offered in the species surveyed (Table 1) include nectar (13 species), pollen (15), broodplaces (five), nutritious tissues (one), resin (two), and sugary mucilage (one). (Some flowers offer more than one kind of reward; *Guarea, Ocotea, Randia, Siparuna,* and *Solanum,* of which several species have been studied and found to offer the same rewards, were scored as one entry each.) Except for the Rubiacaeae and Caricaceae pollinated by sphingids, few dioecious plants provide nectar suitable for really long-tongued visitors, such as butterflies, Tabanidae and Nemestrinidae (flies), or euglossines. In 12 of 40 species (Table 1) no reward is offered in the female flowers, and in *Rafflesia* neither sex may offer a reward. Mistake pollination (Gilbert, 1975; Baker, 1976), in which pollinators visit the unrewarding morph of dioecious or monoecious species by mistake, thus seems to occur in about a third of the cases, and pollinators that are fooled include beetles, carrion flies, cecidomyiids, fig wasps, and sphingids, and bats and birds in *Freycinetia* (Table 1). Sometimes, however, it is difficult to decide to what degree a morph may be rewarding. For example, gall midges laying eggs in male flowers of *Siparuna* are rewarded because male flowers are suitable sites for larval development (Feil, 1992). The same gall midges trying to lay eggs in female flowers usually, but not always, go

TABLE 1. Pollinators of tropical dioecious angiosperms.

Taxon	Reward M: male, F: female	Pollinators	Reference
Actinidiaceae			
Actinidia deliciosa	Both sexes: pollen	Bees *Bombus* spp. (Apidae)	Corbet, Chapman, and Saville (1988)
Araliaceae			
Polyscias pancheri	Both sexes: pollen and little nectar	Bees: *Nomia sicheli* (Halictidae)	Schlessman, Lowry, and Lloyd (1990)
Arecaceae			
Aphandra natalia	M: pollen?, F: brood-place	Beetles: Curculionidae Baridinae	Ervik (in press)
Mauritia flexuosa	M: pollen, F: none	Beetles: Chrysomelidae, Alticinae, also wind?	Ervik (in press)
Orbignya phalerata (= *O. martiana*)[a]	M: pollen, brood-place, F: brood-place?	Beetles: *Mystrops mexicana* (Nitidulidae), also wind	Anderson, Overal, and Henderson (1988)
Phytelephas microcarpa	M: brood-place, F: none	Beetles: *Mystrops* sp. (Nitidulidae) and *Phyllotrox* spp. (Curculionidae)	Barfod, Henderson, and Balslev (1987)
Salacca edulis	M: pollen, nectar?, F: nectar, brood-place	Beetles: *Derelomus* sp. (Curculionidae)	Mogea (1978)
Boraginaceae			
Cordia inermis[a] *C. collococca, C. panamensis Cordia* sp.	Both sexes: nectar, also pollen?	Wasps, Anthophoridae, Halictidae, flies, and butterflies syrphid flies: *Chelosia,* butterflies: *Marpesia* and *Udranomia kikkiwai,* and bees: *Melipona*	Opler, Baker, and Frankie (1975) A. Dulmen, Diemen (personal communication)
Caricaceae			
Carica papaya	M: nectar, F: none	Sphingidae: esp. *Hyles*	Baker (1976)
Jacaratia dolichaula	M: nectar, F: none	Sphingidae	Bawa (1980b)
Clusiaceae			
Clusia insignis	Both sexes: resin	Bees: *Eulaema* (Euglossini)	V. Bittrich, Manaus (personal communication)
Clusia small-flowered sp.	Both sexes: resin	Bees: possibly *Trigona*	V. Bittrich, Manaus (personal communication)
Clusia nemerosa	Both sexes: resin	Bees: *Euglossa* (Euglossini)	Armbruster (1984)
Garcinia hombroniana	Both sexes: nectar, M: pollen	Bees: possibly *Trigona*	Richards (1990)
Dilleniaceae			
Saurauia veraguensis[a]	Both sexes: pollen	Medium-sized bees: esp. *Melipona*	Haber and Bawa (1984)
Ebenaceae			
Diospyros pentamera	M: pollen, F: none	Beetles	House (1989)
Euphorbiaceae			
Margaritaria nobilis	Both sexes: nectar, M: pollen	Wasps, 3–4 species	A. Dulmen, Diemen (personal communication)
Lauraceae			
Ocotea guianensis, O. opifera, O. sp.	Both sexes: nectar	Brown bees, 1 cm lg.	Kubitzki and Kurz (1984)
Malvaceae			
Hampea appendiculata	Both sexes: nectar, M: pollen	Nonsphingid moths?	Fryxell (1969)
Meliaceae			
Guarea bullata, G. guidonia, G. rhopalocarpa	Both sexes: nectar	Nonsphingid moths	Bullock, Beach, and Bawa (1983); Bawa et al. (1985)
Monimiaceae			
Siparuna 8 spp.[b]	M: brood-place, F: none	Flies: *Asynapta* (Cecidomyiidae)	Feil (1992)
Tambourissa cordifolia	M: pollen, F: stylar exudate	Flies: *Drosophila nasuta, Zaprionus vittiger* (Drosophilidae)	Lorence (1985)

TABLE 1. Continued.

Taxon	Reward M: male, F: female	Pollinators	Reference
T. peltata	M: pollen; F: sweet mucilage	Flies: Syrphidae	
Moraceae			
Ficus fistulosa[a]	M: brood-place, F: none	Wasp: *Ceratosolen hewitti*	Galil (1973)
F. asperifolia[a]	M: brood-place, F: none	Wasp: *Kradibia gestroi*	Verkerke (1987)
Myristicaceae			
Myristica fragrans	M: pollen, F: none	Beetles: *Formicomus braminus* (Anthicidae)	Armstrong and Drummond (1986)
M. insipida	M: pollen, F: none	Beetles: 8 spp. of Curculionidae, Nitidulidae, and Staphylinidae	Armstrong and Irvine (1989)
Myrtaceae			
Decaspermum parviflorum[a]	Both sexes: pollen	Bees: mostly *Apis dorsata, Nomia* spp.	Kevan and Lack (1985)
Pandanaceae			
Freycinetia reineckei[b]	M: bracts, F: none	Mainly the bat *Pteropus samoensis*; birds	Cox (1982, 1984)
Rafflesiaceae			
Rafflesia pricei	Both sexes: none	Carrion flies: *Lucilia papuensis* and *Chrysomya pinguis*	Beaman, Decker, and Beaman (1988)
R. kerrii	M: mucilage and pollen?, F: mucilage?	*L. porphyrina, C. villeneuvei, C. ruffacies,* and *Hypopygiopsis tumrasvini*	Bänziger (1991)
Rubiaceae			
Alibertia edulis	Both sexes: nectar	Sphingidae	Haber and Frankie (1989)
Randia lasiantha, R. spinosa	Both sexes: nectar	Sphingidae	Haber and Frankie (1989)
R. subcordata, R. dioica			Ruiz and Arroyo (1978)
Simaroubaceae			
Simarouba amara (= *S. glauca*)	Both sexes: nectar	Nonsphingid moths	Haber in Bawa and Crisp (1980)
Solanaceae			
Solanum spp.	Both sexes: pollen	Bees: mainly *Amegilla* (Anthophoridae), also *Nomia* (Halictidae)	Anderson and Symon (1987)

[a] Species morphologically androdioecious, gynodioecious, or heterostylous but functionally dioecious as described in the cited references.
[b] Leaky dioecy; see text for explanation.

TABLE 2. Pollinators of zoophilous dioecious angiosperms in tropical lowland forests.

Pollinator[a]	Percentage of species ($N = 40$)
Bees	22.5
Beetles	20.0
Sphingids	17.5
Small moths	7.5
Flies	12.5
Wasps	7.5
Bats	2.5
Diverse insects (wasps, bees, butterflies, flies)	10.0

[a] Pollinators of the species listed in Table 1. *Freycinetia reineckei* may be bird- in addition to bat-pollinated.

rewardless because females are much less suitable for oviposition.

In summary then, rewards in dioecious taxa are usually pollen or nectar, but in perhaps as many as one-third of the species no reward is offered by the female flowers.

The pollinators—Most of the zoophilous species in our sample are pollinated by insects (Table 2; the species of *Guarea, Ocotea,* and *Siparuna* were scored as one entry each), especially bees (nine species), beetles (eight), sphingids (seven), small moths (three), flies (five), and wasps (three). Only in the four species of *Cordia* are diverse insects implicated as legitimate pollinators, i.e., wasps, halictids and anthophorids, flies, and butterflies. There is at least one anthophorid bee that appears to be a specialist on *C. inermis* (Opler, Baker, and Frankie, 1975), but it is unclear if it is a particularly effective pollinator. *Freycinetia reineckei* (Pandanaceae) is the only known bat-, and perhaps bird-, pollinated dioecious species, although the epiphytic lily *Collospermum hastatum* (Liliaceae) on New Zealand also may be pollinated by bats (Daniel, 1976). Moth pollination is expected in several additional groups for which we lack data, e.g., Cucurbitaceae, Nyctaginaceae, Flacourtiaceae, Menispermaceae, and Dioscoreaceae. The latter are mainly pollinated by small nocturnal moths according to Cursey (1967), but some species almost certainly are fly-pollinated. Thrips have been implicated as pollinators in two dioecious taxa—*Mollinedia* (Monimiaceae) and *Compsoneura sprucei* (Myristicaceae) (Gottsberger, 1977; Bawa et al., 1985)—but it is unclear if they transfer pollen from males to females. In other species of *Mollinedia,* nitidulid beetles have been found visiting the flowers and thrips pollination seems unlikely (R. Schönfelder, Aarhus, personal communication).

The available data thus show that while most tropical dioecious species may be pollinated by bees, other pollinator classes, such as beetles and sphingids, are almost equally important. Very few, if any, tropical dioecious species are adapted for pollination by a broad spectrum of taxonomically diverse animals.

DISCUSSION

We first comment on the sources of bias in our data and then take up the questions raised in the introduction. Our data are subject to bias from two sources. First, pollination in trees with small inconspicuous flowers is ex-

tremely difficult to study, and there is a widespread tendency to assume rather than observe their mode of pollination. Such trees are therefore underrepresented in our sample. Secondly, since we have had to exclude most studies reporting pollination by "small diverse insects" because they did not meet the criteria specified beforehand (Materials and Methods) we may in fact have discarded some of the evidence in support of the Bawa Hypothesis. Thus we suspect that some large palms may indeed be pollinated by taxonomically diverse insects or even by wind as well as insects.

Turning to the first question posed in the introduction, does the pollinator spectrum of tropical dioecious species differ from that of tropical plants with other breeding systems, and if so, is it skewed toward small insects? Several pollinator spectra for tropical lowland hermaphrodite communities are available, for example, from an undisturbed evergreen wet forest in the Caribbean lowlands of Costa Rica (Kress and Beach, in press), from a secondary deciduous forest in Miranda State in Venezuela (Ruiz and Arroyo, 1978) and from a shrubland in the Venezuelan Guayana (Ramirez, 1989). In Costa Rica, 61 of 165 hermaphroditic species were pollinated by medium to large bees, 23 by small bees, 39 by hummingbirds, 13 by beetles, eight by moths, five by butterflies, three by flies, eight by bats, and five by "small diverse insects." Of 11 bisexual species of trees, shrubs, vines, and hemiparasites studied in Miranda, all were bee-pollinated (Anthophoridae, Apidae, Halictidae). In the Guayana shrub community, 39 of the 55 bisexual species were pollinated by bees, five by hummingbirds, four by butterflies, one by beetles, and six were anemophilous. Obvious phylogenetic and ecogeographic biases preclude a statistic comparison of these results with the data presented in Table 2. Nevertheless, the available data show that in tropical species, as in angiosperms in general, pollination by bees predominates. The pollinator spectrum of tropical dioecious plants seems to differ, however, from that of other tropical species in including fewer bat- and bird-pollinated species. Possible reasons for this are discussed below. Based on our sample, however, it is clear that single tropical dioecious species are not pollinated by (taxonomically) diverse insects; in 36 of 40 species a single insect genus or even species is the sole or major pollinator.

To address the question of whether the behavior of the observed pollinators of tropical dioecious plants is in agreement with the Bawa Hypothesis, i.e., if they provide low-quality pollination in terms of outcrossing, it is necessary to examine their locomotive capacity, foraging behavior, fidelity, and home ranges. Low-quality insect pollinators were defined by Bawa (1980a) as small, unspecialized foragers, typified by the highly social meliponine bees *Trigona* and *Melipona,* but comprising also other bees, beetles, flies, wasps, and butterflies. The same paper explored a supposed association between pollination by short-tongued bees and dioecy. Addressing the last point first, short-tongued bees include *Nomia, Halictus* (Halictidae), and *Andrena* (Andrenidae), but not *Trigona, Melipona,* and *Apis,* which are long-tongued relative to their size (Roubik, 1989; O'Toole and Raw, 1991). And whereas *Trigona, Melipona,* and *Apis,* are polylectic (because they are highly eusocial), some short-tongued halictids and andrenids are oligolectic. Tongue length

therefore does not predict a bee's pollinator qualities; of course, tongue lengths are irrelevant where the reward is pollen, perfume, oil, or resin.

The more advanced Hymenoptera, particularly honey bees, are capable of discriminating between floral morphs (Free, 1970; Kay, 1982; Kay et al., 1984; Seeley, 1985). Thus, in plantations of dioecious crops like *Actinidia deliciosa, Pimenta dioica, Piper betel, Nephelium lappaceum,* and *Diospyros kaki,* honey bees specialize on the more rewarding morph and do not visit the other. It is significant in this context that in Panama dioecious trees, including *Spondias mombin, Pouteria stipitata, Zanthoxylum* spp., and the partly or entirely anemophilous *Bursera simaruba* and *Coussapoa panamensis,* are among the most important pollen sources for honey bees (Roubik, 1989), but they are not honey bee-pollinated. Also meliponine bees, like honey bees, are not specific to any particular plant (Michener and Grimaldi, 1988; Roubik, 1989). The resulting lack of fit between them and most of the flowers they visit implies that meliponines frequently are predators on floral resources rather than pollinators (Janzen, 1975; Renner, 1983; Roubik, 1989). This is the case in *Carica, Solanum, Orbygnia, Mauritia,* some species of *Clusia,* and *Mollinedia* which are visited but not pollinated by *Trigona* (Baker, 1976; Anderson and Symon, 1987; Anderson, Overal, and Henderson, 1988; Ervik, in press; R. Schönfelder, personal communication for *Mollinedia*; S. Renner, personal observations on *Solanum*). All this supports Bawa's suggestion that social bees are likely to be poor pollinators of dioecious species. Contrary to the Bawa Hypothesis, however, the available data (Table 1) show that very few tropical dioecious species are actually pollinated by small social generalist bees. Bees that do pollinate tropical dioecious taxa include halictids, anthophorids, euglossines, and bumble bees, all with good locomotive capabilities and intermediate to high fidelity.

Turning now to insects other than bees that pollinate tropical dioecious plants, it appears that their locomotive capacity and fidelity are also high. They travel considerable distances between the sexes as has been shown for flies in *Tambourissa* (Lorence, 1985) and *Neolitsea* (House, 1989) and for beetles in *Myristica* (Armstrong and Drummond, 1986; Armstrong and Irvine, 1989). Thus, the small, 2–3-mm-long Curculionidae and Nitidulidae pollinating *M. inspida* are strong, rapid fliers, which easily covered the 7–19 m male-to-female distance at the study sites of Armstrong and Irvine (1989). On the male flowers the beetles oriented their ventral surface along the androecial column parallel to the anthers to feed on pollen grains (for 30 sec); on the females they stood astride the stigma, accurately positioned to efficiently transfer pollen (during 10–15-sec-long visits). Although the authors stress that these are generalist, pollen-foraging beetles, *Myristica* floral morphology is clearly euphilic (adapted to pollination by specific agents) rather than allophilic (available for pollination by any visitor). Drosophilids and strong-flying syrphids that pollinate *Tambourissa cordifolia* and *T. peltata* covered nearest neighbor distances at the study sites of 0.78 and 9.75 m, respectively (Lorence, 1985). These flies and also the beetles that pollinate *Myristica fragrans, Orbygnia phalerata, Phytelephas microcapa,* and *Salacca edulis* (Anthicidae, Nitidulidae, and Curculion-

idae; Mogea, 1978; Armstrong and Drummond, 1986; Barfod, Henderson, and Balslev, 1987; Anderson, Overal, and Henderson, 1988) are high-quality pollinators in terms of outcrossing per unit reward. Furthermore, beetles, carrion flies, cecidomyiids, and fig wasps looking for foral oviposition sites seem to rely mainly on a few innate cues, particularly scent (Pellmyr and Thien, 1986). They are therefore probably reliable pollinators as long as both sexual morphs produce the same cues. Clearly, the assumption of the Bawa Hypothesis that small pollinators in general provide little outcrossing is not supported by the available data.

Recognizing the inadequacy of the available data on pollination in tropical dioecious plants, we propose two more general arguments in favor of specialized rather than generalized pollinator relationships in this set of plants. First, in about one-third of the species, pollination is by deceit. This is indicative of the strength of the attraction exerted by certain floral cues; such cues likely are attractive to specific animals rather than to taxonomically diverse ones. And it is precisely in rewardless or almost rewardless morphs that the pollinator has to fit the flower closely to ensure that even during brief exploratory visits pollen is left on the stigma(s). Opportunists, such as honey bees and meliponines, learn to avoid poor resources, whereas instinct-guided pollinators will come to their flower even at a cost, i.e., going unrewarded part of the time. This would also explain why large territorial pollinators, such as birds and bats, pollinate few dioecious species. They quickly learn to avoid the less rewarding morphs. Hawkmoths, on the other hand, pollinate many dioecious species. Because they do not have home ranges, but instead explore numerous different flowers in their habitat (Haber and Frankie, 1989), they may not recognize and remember unrewarding morphs.

Second, the idea that a lack of specialized pollinators should have been responsible for the occurrence of dioecy in tropical taxa as implied by the Bawa Hypothesis seems unlikely. By contrast, the alternative hypothesis that reliable pollination is a necessary precondition for the evolution of dioecy, as suggested by Darwin (1877), appears supported by the available data, provided that most dioecious species have not acquired specialized pollinators after becoming dioecious. All initial stages of dioecy, whether gynodioecy, heterostyly, or heterodichogamy, increase outcrossing in self-fertile species, but only those protodioecious species with pollinators reliably visiting both sexes may have been able to evolve complete dioecy.

Floral visitors (vs. pollinators) play different roles at different times, ranging from predation to pollination, and more studies looking at spatiotemporal variation in the pollination of species apparently depending on poor pollinators are needed before the effects of such mutualistic-parasitic relationships can be assessed. It is among such species we expect to find evidence in support of the Bawa Hypothesis. Often prolonged observation and exclusion experiments will be necessary, however, to distinguish effective from incidental pollinators, particularly because pollinator effectiveness and efficiency may differ not only inter- but also intraspecifically (Delph and Lively, 1992). The search initiated by Darwin (1877) and picked up in the 1980s (Bawa and Beach, 1981; Willson, 1983; Wyatt, 1983; and others) for associations between particular pol-

linators and breeding systems, of which dioecy is but one, has so far been remarkably unsuccessful (Lloyd, 1980; Bullock, 1985; Arroyo and Squeo, 1990; Barrett and Eckert, 1990). It is time to concentrate on detailed studies of monophyletic groups.

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