Floral Ecology of Coastal Scrub in Southeast Jamaica

Mary Percival

Department of Botany, University College, Cardiff, Wales, United Kingdom

ABSTRACT

Species flowering during the dry season (late December to early April) form three main pollinator groups, namely, butterfly, solitary bee, and hummingbird flowers. The animal vectors present match these three flower syndromes. The daily and seasonal rhythms of flower opening and pollination activity are synchronized. Butterflies and solitary bees, active chiefly in the morning, visit flowers blooming only half a day. The number of seeds per fruit and the pollen-carrying capacity of the pollen vector are correlated. Butterflies, carrying few pollen grains, chiefly pollinate flowers with one to four seeds. Solitary bees, carrying many grains, chiefly pollinate flowers with many seeds per flower. These close links between the flowers and their visitors result in a high degree of successful pollination and a high percentage fruit set. A group of species, attracting no visitors, was characterized by a very narrow 'pollination gap,' making self-pollination almost inevitable. Heavy fruiting indicated self-fertility. Heterocorollary in *Cordia sebestena,* a double keel in *Stylosanthes hamata,* and several examples of andromonoecy are recorded for the first time. The presence of the adventive honeybee, *Apis mellifera,* in the association appeared detrimental to the native pollinators when forage was scarce. The whole scrub association appears balanced with a distinctive pattern of floral ecology. This circumstance, in terms of pollinators, is designated a Butterfly-Solitary bee-Hummingbird association.

STUDIES IN PLANT ECOLOGY seldom include any consideration of the floral ecology. Yet this facet of the life cycle can scarcely be ignored if an assessment of the plant association as a whole is to be reached. Indeed, without the floral data, errors in interpretation of the ecological factors involved may be made. In *Salvia,* isolation between two species was assigned to edaphic and topographical features, when it was really due to differences in floral morphology and insect vectors (Grant and Grant 1964). Although patterns of floral ecology are tacitly acknowledged to exist with, for example, ornithophily and psychophily dominating the pattern in the tropics, and melittophily dominating that of the temperate regions, most workers have limited their investigations to the floral ecology of individual or closely related species. Hagerup (1932) is an exception, broadly describing the floral ecology of the desert at Timbuctu. Grant and Grant (1965) have made an intensive study of floral form and pollination in a single family, the Polemoniaceae, and have shown that adaptive radiation has occurred to embrace most of the major groups of pollinating animals. Grant also suggested that in any one locality a mixture of flower types would be present to 'satisfy' the pollinators occurring there. Linsley, Rick, and Stephens (1966) have studied the insect-flower relationships of a portion of the flora on the Galapagos Islands, but do not include any floral data beyond the animal food available. Baker and Hurd (1968) indicate lines of approach which may be profitable in pollination studies, but these chiefly relate to the evolutionary aspect of the intimate relations between flower and pollinator.

The present study is firstly an attempt to elucidate the floral ecology of a community as a whole and to show that it is a biotic factor equal in importance to the classical habitat factors. Secondly, to reveal the general pattern of floral syndromes and animal vectors, and to attempt to discover other intrinsic characteristics of the association as well. Thirdly, to describe the association simply, either in terms of the biological types of flowers or of the pollinating animals.

DESCRIPTION OF SITE AND CLIMATE

The area studied was some 10 hectares of coastal scrub at Morant Point, Jamaica (76° 11.5′W, 17° 55′N), from which the trees had been removed for fuel at the beginning of the nineteenth century. It is an elevated reef of quaternary age with slabs and pitted rocks and coral, partially covered by thin soil with deeper pockets. It is mostly covered by shrubs from 0.5 to 2.0 m tall. Several acres of herbaceous vegetation cover the damp alluvial mud spreading out from the mangrove swamp which borders the site on the north and west. This area merges into an extensive thicket of logwood, *Haematoxylum campechianum,* which is extending its boundaries with many small shrubs, 0.6–1.0 m tall, possibly grazed to this form as mules and cattle have access to the land. There is a fringe of trees on the southern side, composed of species listed as major components of the Southern Coastal scrub woodland by Asprey and Robbins (1953).

According to the seasonal rainfall map of Jamaica (Asprey and Robbins 1953), the Morant Point site has an average yearly rainfall of over 60 inches and lies in the area of "Slight Dry Season," i.e., each year it has 2–3 months each with less than 4 ins of rain. The dry season occurs from January to March. In the Caribbean area, a monthly rainfall of less than 4 ins is considered to produce drought conditions on soils of normal porosity since evaporation will exceed precipitation. This situation was true of the site, where the foliage of many shrubs was severely wilted during February and March and even the alluvium near the mangrove swamp became very dry. The chief rains fall in April and October and bring on the main flushes of plant growth and of pollinator activity (Turner, pers. comm.).

COMPOSITION OF THE FLORA AND NOTES ON FLOWER FORM

The plant register, table 1, shows over a hundred species flowering during the dry season. Major components, and also those of special floral biological interest, are described below under family headings. Some are illustrated in figs. 1 and 2.

ACANTHACEAE. *Blechum pyramidatum* and *Ruellia tuberosa* both have short-lived flowers, the corollas falling by noon. *Blechum* has a slightly zygomorphic lilac corolla (8 mm wide, 12 mm deep) with stigma and anthers level at its mouth. *Ruellia* has a violet funnel-shaped corolla (40 mm wide, 32 mm deep). The stigma has one long and one very short lobe and is curved down into the corolla tube towards the two superposed pairs of anthers. Some flowers have abortive ovaries, so the species is andromonoecious (fig. 2, G and H). *Thunbergia fragrans,* naturalised here, has a white flat-topped zygomorphic corolla (34 mm wide 22 mm deep) with a narrow orifice and wider belly housing the introrse anthers. The stigma has two flat lobes and occupies the top centre of the corolla mouth. The flower is not scented by day.

AIZOACEAE. The succulent *Sesuvium portulacastrum* carpets an extensive zone of damp ground edging the mangrove swamp. The pink, star-like flowers (12–19 mm wide, 4 mm deep) are open in the morning and have a brush of spreading stamens which move inwards to form a compact mass on being visited by an insect.

APOCYNACEAE. *Rhabdadenia biflora* and *Urechites lutea* both have handsome, deep, funnel-shaped flowers. The former is white, slightly fragrant in daytime (55 mm wide, 46 mm deep), the latter bright yellow (54 mm wide, 32 mm deep) and scentless. *Tabernaemontana laurifolia* has jasmine-like yellow-green flowers (33 mm wide, 20 mm deep), faintly almond scented. In all three the corollas are choked above the tube by the anthers which form a tight cone over the stigma.

AVICENNIACEAE. *Avicennia germinans* (fig. 1 G). The white scented flowers have corolla lobes (12 mm across), which reflex from the short tube (3 mm). The exserted anthers stand in two pairs at the back of the flower, the stigmas being a little below them. The stigmas begin to diverge as the anthers dehisce but remain fresh and juicy after the stamens blacken.

BORAGINACEAE. Represented by the climbers *Tournefortia polichros* and *T. volubilis,* and the weed *Heliotropium angiospermum.* The *Tournefortia* spp. have inconspicuous green-yellow to dull-orange, star-shaped flowers in branched cymes and appear to be autogamous. *Heliotropium* has tiny white flowers in scorpioid cymes.

EHRETIACEAE (Hutchinson 1959) was the family proposed to receive the three genera of which the site representatives were the shrubby *Cordia brownei* and *C. globosa* var. *humilis,* and the trees *C. gerascanthus, C. sebestena, Ehretia tinifolia,* and *Bourreria venosa. Ehretia tinifolia* has paniculate cymes of fragrant white flowers (4 mm wide, 1.5 mm deep). *Bourreria venosa* has loose cymes of very fragrant, white, flat-topped, medium-tubed flowers (14 mm wide, 7 mm deep) with stigmas and anthers all exserted 2 mm from the corolla tube. No indication of heterostyly was found in these two species. *Cordia brownei* and *C. globosa* var. *humilis* have slightly fragrant, white, shallow-cup-shaped flowers. The latter species shows several grades of heterostyly and slight "heterocorollary," the short-styled flowers having shorter corollas (table 2). The anthers tend to be clasped together either over or below the stigmas, depending on the type of flower. In both types of flower in *C. brownei* the anthers protrude 0.7 mm from the petal cup. In the long-styled flower the branched stigmas are exserted 1 mm from the cup; in the short-styled, they extend halfway up the cup. The slightly fragrant, white corolla of *C. gerascanthus,* with its flared top and tubed base, turns brown and persists to act as a parachute to the single seed fruit (fig. 1 E). Heterostyly was not observed. Both anthers and stigmas are exserted from the corolla tube, the latter raised about 4 mm above

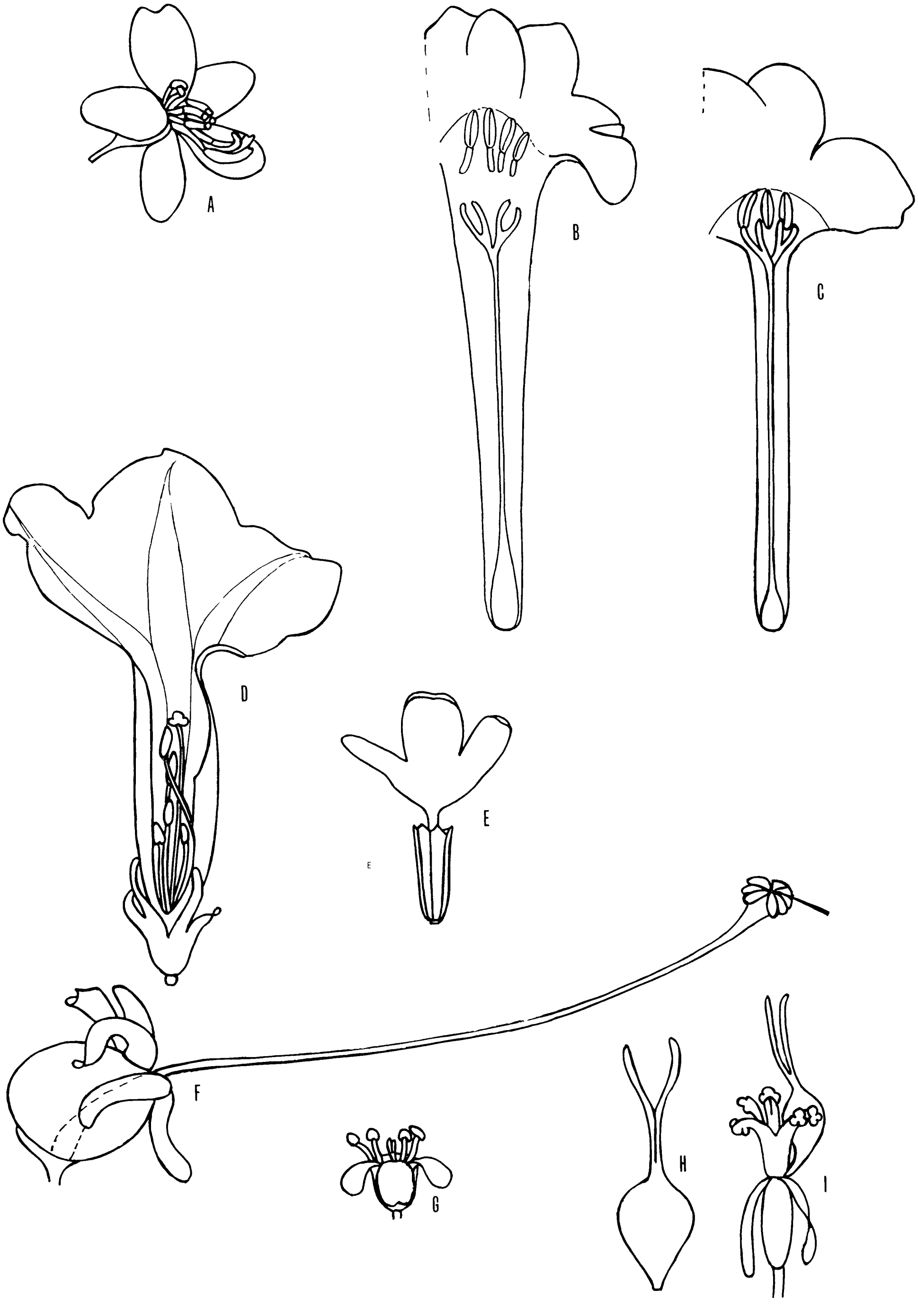

FIGURE 1. Flower forms and heterocorollary (flower length shown in parentheses, except as indicated). A *Cassia ligustrina,* open, 4 fodder and 2 vibratable anthers (22 mm across open corolla); B *Cordia sebestena,* long corolla (48 mm); C *Cordia sebestena,* short corolla (40 mm); D *Ipomoea acuminata,* deep funnel, irregular stamens (65 mm); E *Cordia gerascanthus,* medium funnel, persistent corolla (20 mm); F *Helicteres jamaicensis,* gynophore, ring of anthers and exserted stigma (73 mm); G *Avicennia germinans,* shallow cup (5 mm); H *Guazuma ulmifolia,* petal with terminal forked process (7 mm); I *Guazuma ulmifolia*, open, ring of stamens, anthers bent downwards (7 mm).

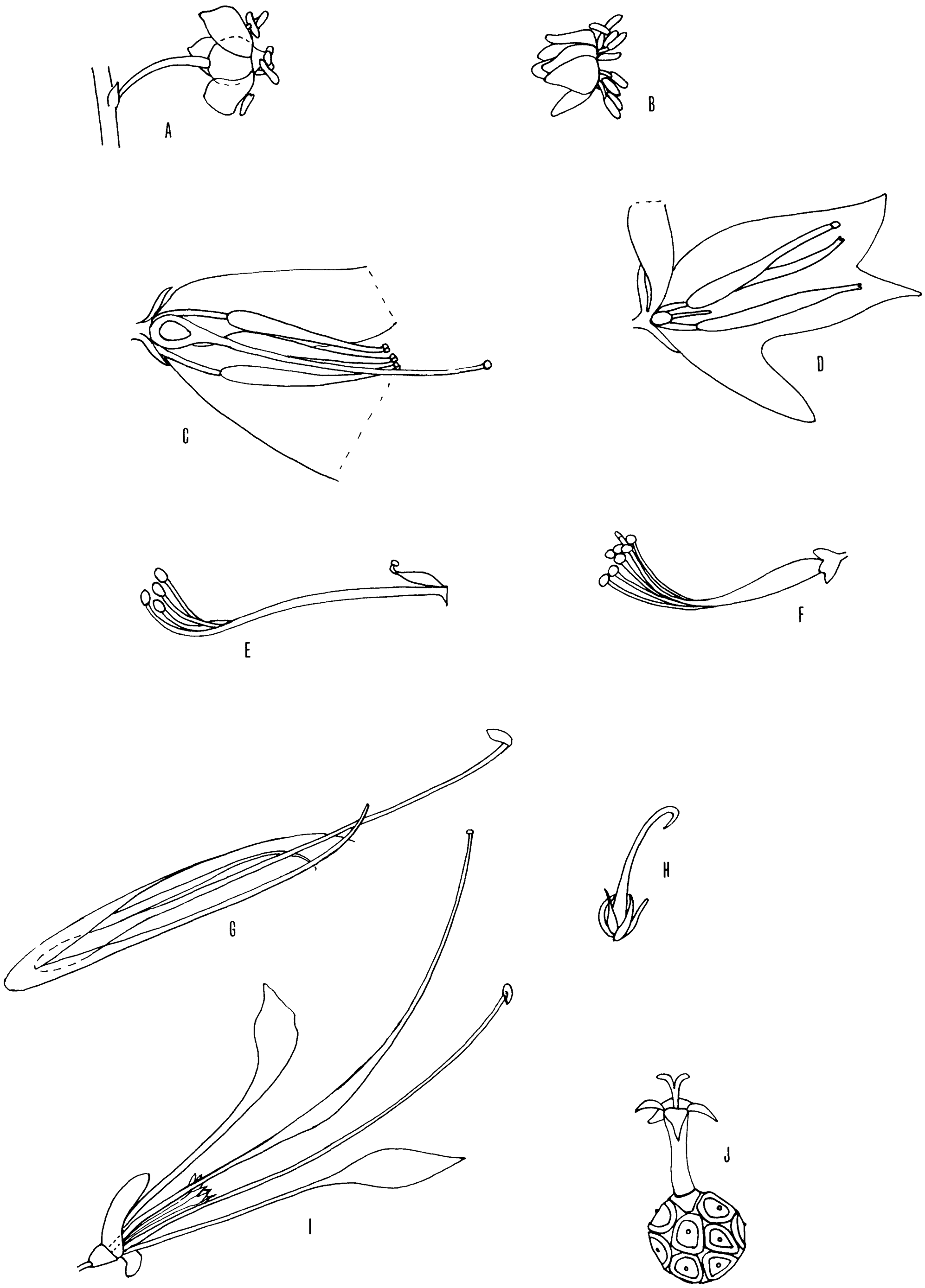

FIGURE 2. Floral morphology and heterostyly (total length of structures drawn shown in parentheses). A *Bursera simaruba*, female flower? (5 mm); B *B. simaruba*, male flower (3.5 mm); C *Solanum torvum*, hermaphrodite flower (13 mm); D *S. torvum*, male flower (15 mm); E *Abrus precatorius*, male flower (14 mm); F *A. precatorius*, hermaphrodite flower (14 mm); G *Ruellia tuberosa*, ovary of hermaphrodite flower (30 mm); H *R. tuberosa*, ovary of male flower? (8.5 mm); I *Bauhinia divaricata*, hermaphrodite flower (41 mm); J *Morinda royoc*, long-styled flower (15 mm).

TABLE 1. *Flower data.*

Species	Status[a]	Plant form at site	Flower form	Length of flower life (days)
Abrus precatorius L.	I	Climbing shrub	pea	1+
Achyranthes indica (L.) Mill.	I	Erect herb	open	1
Alternanthera ficoidea (L.) Roem. & Schult.	I	Prostrate herb	small, in heads	1
Alysicarpus vaginalis (L.) DC.	I	Creeping herb	pea	1
Ammannia coccinea Rottb.	I	Erect herb	shallow cup	?
Annona glabra L.	I	Coppiced tree	medium cup	?
Argythamnia candicans Sw.	I	Straggling shrub	shallow cup ♀	1
Asclepias curassavica L.	I	Erect herb	medium cup	1+
Avicennia germinans (L.) L.	I	Tree	medium cup	1+
Bauhinia divaricata L.	I	Shrub & tree	deep funnel	1
Blechum pyramidatum (Lam.) Urb.	I	Erect herb	labiate	.5
Borreria laevis (Lam.) Griseb.	I	Scrambling herb	open	.5
Bourreria succulenta Jacq.	I	Shrub	flat topped, medium tubed	1
Broughtonia sanguinea (Sw.) R. Br.	E	Epiphyte	vertical faced, long tubed	1+
Bucida buceras L.	I	Tree	flowering missed	?
Bunchosia media (Ait.) DC.	I	Shrub	open	1
Bursera simaruba (L.) Sarg.	I	Tree	open	1
Byrsonima coriacea (Sw.) DC.	I	Tree	open	1+
Capparis ferruginea L.	I	Tree	medium cup	1
Capparis flexuosa (L.) L.	I	Tree	medium cup	.5
Capraria biflora L.	I	Shrub	medium cup	.5
Cassia chamaecrista L.	I	Low shrub	pea	.5
Cassia ligustrina L.	I	Shrub	pea	.5
Cassia sp.	I	Under shrub	pea	.5
Cassia occidentalis L.	I	Under shrub	pea	.5
Chloris barbata SW.	I	Herb	open	.5
Cissampelos pareira L.	I	Climbing shrub	open	1
Cissus sicyoides L.	I	Climber	shallow cup	?
Citrus aurantifolia (Christm.) Swingle	C	Tree	flat topped, medium tubed	1+
Commelina elegans Kunth	I	Herb	open	.5
Comocladia pinnatifolia L.	I	Shrub	open	1
Conocarpus erectus L.	I	Tree	minute, in heads	1
Corchorus siliquosus L.	I	Shrubby herb	flowering missed	?
Cordia brownei (Freisen) I. M. Johnston	I	Shrub	medium cup	1
Cordia gerascanthus L.	I	Tree	deep funnel	1+
Cordia globosa (Jacq.) Kunth var. ***humilis*** (Jacq.) I. M. Johnston	I	Shrub	medium cup	1+
Cordia sebestena L.	I	Shrub & tree	deep funnel	1+
Crotalaria verrucosa L.	I	Sub-shrub	pea	1+
Croton discolor Willd.	I	Shrub	shallow cup	1+
Dalbergia brownei (Jacq.) Urb.	I	Shrub	pea	1+
Desmodium canum (J. F. Gmel.) Schinz & Thell. var. *angustifolium* (Griseb.) León & Alain	I	Herb	pea	.5
Desmodium triflorum (L.) DC.	I	Creeping herb	pea	.5
Ehretia tinifolia L.	I	Tree	open	1+
Emilia sonchifolia (L.) DC.	I	Annual herb	composite	1+
Eupatorium odoratum L.	I	Straggling shrub	composite	1+
Euphorbia heterophylla L.	I	Erect herb	cyathium	1
Euphorbia hirta L.	I	Prostrate herb	cyathium	1
Euphorbia hyssopifolia L.	I	Erect herb	cyathium	1
Evolvulus nummularius (L.) L.	I	Creeping herb	open	.5
Ficus aurea Nutt.	I	Tree	closed flask, flowering missed	?
Guazuma ulmifolia Lam.	I	Tree	open	1+
Haematoxylum campechianum L.	N	Tree	flowering missed	?
Helicteres jamaicensis Jacq.	I	Shrub	medium cup	?
Heliotropium angiospermum Murr.	I	Herb	flat topped, short tubed	1
Hyptis pectinata (L.) Poit.	I	Herb	labiate	.5

Animal food present in flower: Pollen	Nectar	Sugar in nectar (%)	Depth of nectary (mm): 0–2	3–8	8+	Pollen consistency	Pollination gap (mm)	Position of stigmas relative to anthers	Seeds per fruit	Fruit set	Classes of native visitors	Honeybee visits
x[d]	x					tacky	1.5	above	4	good		
x						tacky	.25	below	1	good		
x	x	19		x		tacky	.25	below	1	none found[c]	2	x
x						tacky	none		5 – 7	not observed		
									100's	abundant		
									many	good		
x	x	25♂ 29♀		x		tacky	.25 – 2	various	3	good	1	
x	x	44		x		pollinia	.5	level	many	few	2	
x	x	25		x		tacky	1	below	4	not observed		x
x	x	17			x	tacky	5 – 18	beyond[b]	3 – 9	fair	4	x
x	x	20			x	tacky	none		8	good	3	
x	x	16	x			tacky	1	level	2	abundant	4	x
x	x	15		x		tacky	1.25	level	2	one	1	
x	x	9			x	pollinia	1	below	many	fair	1	
x						tacky	none		3	good	1	
x	x	19	x			tacky	1 or $\propto$	above	1	abundant	2	x
x						tacky	1	above	3	not observed	1	
x	x	21	x			tacky	1.5	above	few	not observed		x
x	x					tacky	8.	beyond	15	one pod seen		
x						tacky	0.5 – 2.	beyond	many	abundant	1	x
x						dry	.25	beyond	5 – 12	not observed		
x						dry	.5	below	50	good		
x						dry	1	below	80	abundant	2	
x						dry	2.5	beyond	50	abundant	2	
x						dry	2	below	1	good		
							$\propto$		1	none found		
x	x		x						1	abundant	1	
x	x			x		tacky	3.3	level	18 – 20	abundant		x
x						tacky	1.1	beyond	5	not observed		
x						tacky	.2	above ⚥	1	good		
x	x		x			tacky	1	below	1	not observed	1	
									many	abundant		
x	x	20		x		tacky	.5 – 1.5	above or below	1	none found	2	
x	x	13		x		tacky	3 – 6	above	1	abundant	4	x
x	x	23		x		tacky	1 – 2	below or above	1	abundant	6	x
x	x	13			x	tacky	4 – 13	below	1	few	4	
x	x	50			x	tacky	none		11	good	2	
x	x	16	x			tacky	$\propto$		3	good		
x	x	38		x		tacky	.5	beyond	3	not observed		
x						tacky	none		2 – 7	good		
x						tacky	.25	beyond	5	good		
x	x	17	x			tacky	2.5	level	4	one	3	x
x	x			x		tacky	1	above	1	good		
x	x	23		x		tacky	3.5	above	1	good	5	
x	x		x			tacky	1	various	3	abundant	1	
x	x		x			tacky	2.5	various	3	good		
x	x		x			tacky	1.5	various	3	abundant		
x						tacky	1.5	below	4 ?	none found	2	x
									many	abundant		
x						tacky	.75	above	many	good	2	
x	x						1.5	beyond	1 (–3)	good	several	x
x	x					tacky	2.5	beyond	many	4 seen		
x	x		x			tacky	.15	below	2	few		
x	x		x			tacky	.4	beyond	4	abundant		

TABLE 1. (continued)

Species	Status[a]	Plant form at site	Flower form	Length of flower life (days)
Indigofera tinctoria L.	I	Sub-shrub	pea	.5
Ipomoea acuminata (Vahl) Roem. & Schult.	I	Climber	deep funnel	.5
Ipomoea tiliacea (Willd.) Choisy	I	Climber	deep funnel	1
Ipomoea triloba L.	I	Scrambler	deep funnel	.5
Jacquinia arborea Vahl	I	Shrub	medium cup	1+
Lantana camara L.	I	Shrub	flat topped, long tubed	1+
Lantana involucrata L.	I	Shrub	flat topped, medium tubed	1+
Lasiacis divaricata (L.) Hitchc.	I	Herb	open	.5
Leucaena leucocephala (Lam.) De Wit	I	Shrub	pea, flowering missed	?
Lippia nodiflora (L.) Michx.	I	Herb	flat topped, short tubed	1+
Malpighia glabra L.	I	Shrub	open	1
Malvastrum corchorifolium (Desr.) Britton	I	Herb	flowering missed	
Melochia nodiflora Sw.	I	Under shrub	flat topped, short tubed	1
Melothria guadalupensis (Spreng.) Cogn.	I	Climber	shallow cup, flowering missed	?
Merremia umbellata (L.) Hallier f.	I	Climber	deep funnel	1+
Mikania micrantha Kunth	I	Climbing shrub	composite	1
Mimosa pudica L.	I	Herb	small, in heads	.5
Momordica charantia L.	I	Climber	shallow funnel	?
Morinda royoc L.	I	Climbing shrub	flat topped, long tubed	1+
Passiflora suberosa L.	I	Climber	shallow cup	1
Philoxerus vermicularis (L.) Beauv.	I	Prostrate herb	small, in heads	1
Physalis angulata L.	I	Sub-shrub	shallow funnel	1
Piscidia piscipula (L.) Sarg.	I	Tree	pea	1+
Portulaca oleracea L.	I	Prostrate herb	shallow cup	.5
Priva lappulacea (L.) Pers.	I	Herb	labiate	.5
Rhabdadenia biflora (Jacq.) Müll. Arg.	I	Climber	deep funnel	1+
Rhynchosia minima (L.) DC.	I	Twining herb	pea	1
Rivina humilis L.	I	Erect herb	open	1
Ruellia tuberosa L.	I	Herb	deep funnel	.5
Sarcostemma clausum (Jacq.) Roem. & Schult.	I	Climber	medium cup	1+
Sesuvium portulacastrum (L.) L.	I	Trailing herb	shallow funnel	.5
Sida acuta Burm. f.	I	Herb	open	.5
Sida spinosa L.	I	Herb	open	.5
Solanum bahamense L.	I	Shrub	open	1+
Solanum erianthum D. Don.	I	Shrub	open	1+
Solanum havanense Jacq.	I	Shrub	open	1
Solanum torvum Sw.	I	Shrub	open	1+
Spilanthes urens Jacq.	I	Trailing herb	composite	1+
Stachytarpheta jamaicensis (L.) Vahl	I	Herb	vertical faced, long tubed	.5
Stylosanthes hamata (L.) Taub.	I	Procumbent herb	pea	.5
Tabernaemontana laurifolia L.	I	Shrub	flat topped, long tubed	1+
Teramnus labialis (L.f.) Spreng.	I	Prostrate herb	pea	1
Thunbergia fragrans Roxb.	N	Herbaceous vine	vertical faced, long tubed	1+
Tournefortia poliochros Spreng.	I	Climber	flat topped, short tubed	1
Tournefortia volubilis L.	I	Climber	flat topped, short tubed	1+
Tragia volubilis L.	I	Twining shrub	open	1
Tribulus cistoides L.	I	Procumbent herb	shallow cup	.5
Trichostigma octandrum (L.) H. Walt.	I	Shrubby climber	open	1
Triumfetta lappula L.	I	Herb	vertical faced, tubed, flowering missed	?
Triumfetta semitriloba Jacq.	I	Herb	vertical faced, tubed, flowering missed	?
Turnera ulmifolia L.	I	Shrub	deep funnel	.5
Urechites lutea (L.) Britton	I	Climber	deep funnel	1
Vernonia cinerea (L.) Less.	I	Herb	composite	1+
Waltheria indica L.	I	Under shrub	shallow cup	1

[a] I = indigenous, E = endemic, N = naturalized, C = cultivated.

[b] Stigma protruding beyond anthers in horizontal flowers.

Animal food present in flower: Pollen	Nectar	Sugar in nectar (%)	Depth of nectary (mm): 0–2	3–8	8+	Pollen consistency	Pollination gap (mm)	Position of stigmas relative to anthers	Seeds per fruit	Fruit set	Classes of native visitors	Honeybee visits
x	x			x		tacky	.2	beyond	7	abundant	1	
x	x	25			x	tacky	none		4	few	3	
x	x	49			x	tacky	none		4	abundant	1	
x	x				x	tacky	none		2 – 4	not observed		
x	x	22		x		tacky	2	below	3	abundant	1	
x	x	22			x	tacky	.5	below	1	fair	1	
x	x	20		x		tacky	.3	below	1	abundant	3	x
x						dry	1	various	1	good		
									24	good		
x	x		x			tacky	.35	below	1 – 2	some	1	
x						tacky	.5	above	3	good	1	
									11 – 12	some		
x	x		x			tacky	.6	above	5	some	2	
						tacky			many	not observed		
x	x				x	tacky	2.5	above	4	abundant[c]	2	
x	x	23	x			tacky	.5	above	1	good	2	x
x						tacky	.5	below to above	3 – 4	good	1	
						tacky			6 – 8	one	1	
x	x	22			x	tacky	1.5 – 3	below & above	1	abundant	6	x
x	x	27		x		tacky	1.25	above	many	some		
x							.25	below	1	some	1	
x	x	10	x			tacky	none		60	some	1	
x	x	22			x	tacky	none		1 – 6	good	6	x
x						tacky	none		many	abundant		
x	x			x		tacky	1.25	above	4	some		
x	x	40			x	tacky	none		many	some	1	
x						tacky	none		2	abundant		
x						tacky	none		1	good		
x	x	20			x	tacky	5.4	above	10	some		
x	x			x		pollinia	.5		many	none found		x
x	x	21		x		tacky	1	above	many	not observed	1	
x						tacky	none		7 – 12	some		
x						tacky	none		5	some		
x						dry	1	beyond	19	some		
x						dry	1.6	beyond	208	good	1	
x						dry	2.4	beyond	many	few	1	
x						dry	2.8	beyond ⚥	237	abundant	1	
x	x		x			tacky	.4	above	1	some	4	x
x	x	27			x	tacky	1.5	above	1 – 2	abundant	2	x
x						tacky	none		2	some	1	
x	x?					tacky	none		60	good		
x						tacky	none		7 – 9	good		
x	x	5			x	tacky	9	beyond	2 – 4	good	2	
x						tacky	none		2 – 4	fair		
x						tacky	none		2 – 4	abundant		
x						tacky	2	various	3	some		
x	x	13	x			tacky	none		25	not observed		x
x						tacky	1	level	1	good		
						tacky	1.4	beyond	2 – 4	abundant		
						tacky	.5	beyond	3 – 6	abundant		
x	x	15			x	tacky	4	various	many	good	2	
x	x	30			x	tacky	none		many	few	3	
x	x		x			tacky	.25	above	1	some	1	
x	x	22		x		tacky	.5	above	1	some	3	

[c] Species was in fruit but no good seeds were found

[d] x = present

TABLE 2. *Heterostyly and heterocorollary in* Cordia globosa.

Flower type	Style + stigmas (mm)	Stamens	Anther level	Length of corolla (mm)
1	long (7)	Short	top of cup	7
2	long (7)	long	protrude from cup	7
3	medium (5.5)	short	top of cup	5
4	medium (5)	3 short, 2 long		7
5	short (3.8)	short	top of cup	5.5

the former. *Cordia sebestena* exhibits an unusual condition, heterocollary (fig. 1, B and C). In all flowers the style and stigmas are of one length, average 27 mm; so too are the epipetalous anthers which protrude 3 mm from the corolla tube. But there are two lengths of corolla tube, averaging 39 mm and 32 mm, respectively, which make the flower appear heterostylous. In an extreme case, tube length 25 mm, the stigmas reached the mouth of the tube and were only 1 mm below the anthers. The significance of these different grades of heterostyly in the cordias was not investigated.

COMPOSITAE. Represented by the weeds *Emilia sonchifolia* and *Vernonia cinerea,* the climbing *Mikania micrantha* and *Eupatorium odoratum,* and the trailing herb *Spilanthes urens* (which occurs in extensive pure stands). *Mikania* and *Eupatorium* have paniculate capitula of small, heavily scented florets. All the above species have narrow tube florets (0.3 to 0.75 mm wide) and from 2 mm (*Mikania* and *Spilanthes*) to 5 to 8 mm long (*Vernonia* and *Emilia*).

CONVOLVULACEAE. *Ipomoea acuminata, I. tiliacea, I. triloba,* and *Merremia umbellata* are climbers with the trumpet-shaped corollas characteristic of the family. *I. acuminata* (fig. 1 D) has stamens of varying length, so that pollen is presented over a length of 16 mm within the corolla tube. The base of the stigma is level with the tip of the longest anther. *Evolvulus nummularius* is a procumbent herb with white flowers (9 mm wide, 2 mm deep). All flowers are ephemeral excepting *Merremia* which has a yellow corolla of greater substance which lasts overnight.

EUPHORBIACEAE. *Euphorbia heterophylla, E. hirta,* and *E. hyssopifolia* have tiny cyathea, the two former with green glands, the last with white gland appendages. *Argythamnia candicans* bears axillary spikelike racemes of unisexual flowers, the upper male, the lower female. In both, a nectary occurs opposite the base of each sepal. *Tragia volubilis* has racemes of male flowers. The solitary female flower is almost sessile at the time of pollination and only 2 mm from the nearest anther. The long stalk, which it subsequently develops, is more in the nature of a dispersal mechanism, than for cross-pollination. Only unisexual bushes of *Croton discolor* were found at the site. Both the male and female flowers have a nectary at the base of each sepal, flattish, rounded, and orange colored in the male, round and green in the female. Nectar collects in the curve of each sepal.

The following Leguminosae, with nineteen species, are a major component of the site flora.

PAPILIONACEAE. *Alysicarpus vaginalis, Desmodium canum, D. triflorum, Indigofera tinctoria, Rhynchosia minima, Stylosanthes hamata,* and *Teramnus labialis* all have very small flowers (width of standard 4–5 mm, length of keel 4–7 mm). *Alysicarpus* has monadelphous stamens, the rest diadelphous, with *D. triflorum* having both kinds. *Stylosanthes hamata* is remarkable in possessing two keels which diverge slightly. Each is formed from a single boat-shaped petal. One houses five anthers; the other, the remaining five and the stigma. Both anthers and stigma become released from the keels without the flower being tripped and self-pollination takes place. The flowers of the two *Desmodium* spp. appear, on occasion, to spring spontaneously. In *Teramnus labialis,* a creeping form, the wings are flattened parallel with the ground, forming a horizontal landing platform 5 mm wide. The keel is of two small white petals, widely separated. *Abrus precatorius, Piscidia piscipula,* and *Crotalaria verrucosa* are medium-sized pea flowers, the last of very stout construction, requiring heavy pressure to trip it. *Abrus precatorius* has crowded racemes of fragrant, pale pink, nectarless flowers. Both hermaphrodite and male flowers occur in the same raceme (fig. 2, E and F). The inflorescence axis secretes large drops of nectar (22 percent sugar) which attracts large red ants. *Dalbergia brownei* has strongly fragrant white flowers in clusters (width standard 6 mm, length of keel 6 mm). The stamen filaments are monadelphous, the tube being wrapped around the pod, but open above to allow the insect tongue to probe the nectar.

MIMOSACEAE. *Leucaena leucocephala* and *Mimosa pudica* have small flowers, massed into heads, with long exserted styles and stamens. The latter inflorescence lasts only half a day.

CAESALPINACEAE. *Haematoxylum campechianum* has subregular yellow flowers in racemes. They secrete abundant nectar which is the source of Logwood honey. *Cassia chamaecrista, C. ligustrina, C. occidentalis,* and *Cassia* sp. have yellow, vertical-faced flowers, lacking a keel. Short, forwardly directed fodder anthers occupy the centre of the flower, flanked by two large curved vibratable anthers on short filaments (fig. 1 A). All have porose dehiscence and live half a day. *Bauhinia divaricata,* present both as a shrub and tree, has racemes containing roughly 40 percent hermaphrodite and 60 percent male flowers (fig. 2 I). The broad filaments of the sterile stamens form a 13-mm tube protecting the strong nectar (45 percent sugar). The style and single fertile stamen are long exserted (30–40 mm) from the very fragrant white petals and staminal tube, which change to pink on the second day.

MALPIGHIACEAE. *Bunchosia media, Malpighia glabra, Byrsonima coriacea* all have clawed petals, slightly uneven in size, inserted below the ovary, with the anthers and stigmas approximately level in the centre of the flower.

PORTULACACEAE. *Portulaca oleracea* is a prostrate succulent herb on muddy ground near the mangroves, with pale- or bright-yellow flowers which open briefly in the early morning. The stigmas are level to 1 mm above the anthers, and in 60 percent of the flowers are already curved into a tight group in the centre by 8:30 a.m. The old flower parts remain as a gelatinous cone on top of the young fruit.

RUBIACEAE. *Borreria laevis* has crowded inflorescences of small flowers (4 mm wide, 1.5 mm deep). The petals are white and hairy above, pink below. The four violet anthers are exserted level with the stigmas. In *Morinda royoc* the flower ovaries are fused into a globose head. The white, waxy petalled flowers (8 mm wide and 7 mm deep) are heterostylous (fig. 2 J) and short-styled with stigmas included in the tube.

SCROPHULARIACEAE. *Capraria biflora* bears subregular white flowers, remarkable for the line of long, very thin hairs which project towards the centre of the flower from each petal. These are seen only in the opening flower, and are not visible in the older ones. The anthers dehisce downwards facing the bottom of the corolla tube. The style curves, bringing the club-shaped stigma down and out of the flower and placing it just at the point of the join between the two lower petals.

SOLANACEAE. *Solanum bahamense, S. erianthum, S. havanense,* and *S. torvum* all show the typical facies of a central anther cone protruding at right angles from the flat petals. *S. bahamense* and *S. torvum* appear to be andromonoecious. The stigma protrudes from the anther cone in the hermaphrodite flowers of *S. bahamense.* The male flowers of *S. torvum* have a tiny, short-styled ovary (fig. 2, C and D). *Physalis angulata* has funnel-shaped, nectariferous white flowers, 10 mm wide, 9 mm deep.

STERCULIACEAE. In *Guazuma ulmifolia* (fig. 1, H and I) the stamen filaments and alternating staminodes are fused to form a bell around the superior, single-styled ovary. From the edge of the bell five pairs of trilobed anthers bend outwards so that they face the base of the flower, and the pollen is shed downwards. Each pair of anthers is enclosed in a hooded petal, which bears a long, bifid appendage terminally. There is a space between the bases of the petals which would allow a visitor to enter. The mechanism of pollination was not discovered. *Melochia nodiflora* has dense clusters of regular flowers (5mm wide) with the united filaments of the stamens forming a false corolla tube, 3 mm deep centrally, the six stigmatic branches narrowly overtopping the anthers (0.75 mm). The petals are white with pink veins and shortly clawed so that five gaps are present between their bases through which the visitor can probe the nectar. *Waltheria indica* resembles *Melochia* in all essentials, but is yellow with a tangy fragrance. *Helicteres jamaicensis* (fig. 1 F) is remarkable for the long gynophore, with the anthers forming a flat ring at the tip from which the stigma protrudes at right angles. The cup-shaped calyx is lined at the base with nectar tissue, the entrance to the chamber being partly barred by flanges on the petals.

TURNERACEAE. *Turnera ulmifolia* has yellow, funnel-shaped flowers. A degree of heterostyly was present. In the flowers of one bush the stigmas overtopped the anthers by 4 mm; in another, the anthers overlapped the stigmas in height giving the chance of self-pollination as the petals twist around them in closing.

VERBENACEAE. *Stachytarpheta jamaicensis* is a major component of the meadow. The tough, erect, spicate inflorescence produces 2–6 flowers per day. The violet corolla has a vertical face and curved limb (11 mm wide, 11 mm deep), dropping by midday. The anthers are immersed 1 mm in the tube and have huge dumbell-shaped pollen grains, easily dislodged onto the stigma which is almost level with them. *Priva lappulacea* has slightly irregular pink corollas (5 mm wide, 4 mm deep), falling by midmorning. *Lippia nodiflora* has a flat-topped inflorescence of minute white flowers (3 mm wide, 2 mm deep) which change to pink on ageing. Two claw-like anthers are situated in the mouth of the tube, with the second pair below and the stigma still lower. *Lantana camara* and *L. involucrata* have close heads of orange and pink flowers respectively. The corollas are minimal in breadth, functioning as tongue guides as in *Buddleja variabilis* (Percival 1965). The flowers of *L. involucrata* have a strong fragrance which is distinct from the aroma of the foliage.

ANALYSIS OF FLORAL DATA

All floral features usually assessed in the building of a pollination syndrome were examined, particularly the relationship of the stigmas and anthers. As these data have not been collected before and may possibly be of use in other disciplines, they are given in their entirety. The data are incomplete but the trends they show are pronounced.

SEX DISTRIBUTION. MONOECIOUS: *Argythamnia candicans, Euphorbia heterophylla, E. hirta, E. hyssopifolia, Melothria guadalupensis, Mormordica charantia, Tragia volubilis.* ANDROMONOECIOUS: *Abrus precatorius, Bauhinia divaricata, Commelina elegans, Ruellia tuberosa, Solanum bahamense, Solanum torvum, Tournefortia poliochros.* ANDRODIOECIOUS: *Bursera simaruba.* DIOECIOUS: *Cissampelos pareira, Croton discolor.* Apart from these exceptions, the majority of the species have hermaphrodite flowers. In all the andromonoecious species, the male flowers contain small ovaries with short styles. *Tournefortia poliochros* was judged to be in this class, as some flowers with normal anthers had blackened pinpoint stigmas and sometimes blackened ovaries. The flower sexes in *Bursera simaruba* are also in doubt, for the anthers in the hermaphrodite flowers are only half the size of those in the male, and do not seem to contain much pollen (fig. 2, A and B). So these may be female flowers, in which case the species is dioecious. Plants of *Comocladia pinnatifolia* bearing solely male inflorescences were found, while other plants appeared to have hermaphrodite flowers or female flowers with staminodes, at the base of the inflorescences, and male flowers terminating the branches. Fawcett and Rendle (1926) state that the flowers are polygamous but do not give their distribution. More observations are needed on this species.

FLOWER FORM

Fourteen different types of flower form, named and numbered in table 3, were distinguished. Categories 1, 2, 4, 6, and 9 (44 species) are shallow and actinomorphic. The rest, 61 species, are more specialized, that is, deeper and/or zygomorphic. Categories 2, 3, 6, 7, 8, and 12 (37 species), were favored by butterflies, categories 1, 10, and 11 (36 species) by solitary bees and categories 5 and 8 (16 species) were favored by hummingbirds. These categories amount to 85 percent of the species analysed. Categories 7 and 12 conform to the psychophilous syndrome of Faegri and Van der Pijl (1966), Vogel (1954), and Grant and Grant (1965). Categories 2, 3, and 6 were medium-sized, relatively shallow, nectar flowers which would be considered unspecialized bee flowers in temperate regions. Here, they were constantly visited and pollinated by butterflies, a criterion of a genuine insect-flower partnership permitting one to account them butterfly flowers. In this we appear to have a parallel case to that of the north-temperate *Bombi* and their flowers, where the typical syndrome pertains only in a portion of the range of flowers they visit. Categories 5 and 8 are composed of typical hummingbird flowers being delicate textured, scentless, long-tubed, and mostly presenting vertical faces to the hovering visitor. Their conformation is also suitable for certain long-tongued butterflies. Categories 10 and 11 worked by the solitary bees typify highly evolved melittophilous

TABLE 3. *Analysis of flower form.*

Flower type	Number of species
1. Open	23
2. Cup, shallow (0–2 mm)	9
3. Cup, medium (3–8 mm)	11
4. Funnel, shallow (0–2 mm)	3
5. Funnel, deep (8+ mm)	11
6. Flat-topped, short tube (0–2 mm)	5
7. Flat-topped, medium-long tube (3 — 8+ mm)	6
8. Vertical faced, long tube (8+ mm)	5
9. Small in rounded heads	4
10. Labiate	3
11. Pea[a]	16
12. Composite	5
13. *Cyathium*	3
14. Fig	1

[a] Includes keel-less Caesalpinaceous species.

syndromes. They include species of *Cassia* with their two enlarged, porose, vibratable anthers, which are an essential part of the *Xylocopa* bee-flower syndrome. The open flowers (type 1) varied in conformation and size, the majority being pollen flowers. Therefore, apart from the butterfly syndrome which is more widely drawn than anticipated, the floral types and pollinating animals match.

The disposition of the essential organs is a facet of flower form closely related to the pollination mechanism. The minimal "pollination gap," defined as the shortest distance between anthers and stigmas, was measured and the data are given in table 1. It was found to be very narrow (0–1 mm) in 63 percent of the species measured, and only exceeds 2.75 mm in 9 percent. In the androdioecious *Bursera simaruba* and the dioecious *Cissampelos pareira* and *Croton discolor,* the gap was assessed at infinity.

The relative position of anthers and stigmas is detailed in table 1. Nineteen species which have a pollination gap of between 0.25 and 2.25 mm have the stigma positioned below the anthers, in a favorable position for self-pollination, although this circumstance may be invalidated by the implied self-sterility in the heterostylous *Cordia brownei, C. globosa,* and *Morinda royoc.* In *Broughtonia sanguinea* too, pollination would be dependent on the brushing of the pollinia, of which there are four per anther, against the stigma by wind. This may well occur for pollinia were seen dangling from the anthers in several flowers in a manner similar to those of *Ophrys apifera* which is wind-pollinated.

THE PROVISION, SITING AND QUALITIES OF THE ANIMAL FOOD

Among 95 species, 62 percent produced nectar and pollen, the rest pollen only (table 1). This finding leads, as one would expect, to a preponderance of nectar-seeking visitors at the site. This expectation was realised for the birds (3 species), butterflies (16 species), wasps (3 species), ants (5 species), and flies (2 species), all of which work only for nectar, outnumbered in species and number of individuals the solitary bees (6 species), syrphid flies (3 species), and beetles (2 species), which work for both nectar and pollen.

Nectaries, sited at the base of the corolla tubes, were placed in three groups according to the tube length (table 4). An almost equal number of species occurred in each group. The data show that butterflies and hummingbirds exploited the deepest flowers with their long tongues (10+ mm) from which the shorter-tongued visitors, apart from the invasive ants and thrips, are excluded. Competition

TABLE 4. *Number of plant species visited by different classes of animals as a function of corolla length.*

	Length of corolla tube (mm)		
Number of plant species studied	0–2 19	3–8 20	8+ 18
Hummingbirds	—	3	7
Butterflies	7	3	6
Solitary bees	3	—	—
Wasps	2	6	1
Flies	3	3	1
Beetles	1	2	1
Ants	7	11	10
Thrips	2	5	5
Honeybee	6	8	3

by the honeybee, tongue 6 mm, is reduced in the long corolla flowers.

Nectar samples were available from 39 species and show a range in sugar content, determined as cane sugar by a Bellingham and Stanley pocket refractometer, from 13 to 50 percent (table 1). Von Frisch demonstrated (1965) that, other things being equal, the concentration of sugar conditions honeybees visiting flowers. Whether this conclusion is true for other groups of pollinators is not yet established. Table 5 shows that there is a tendency for the classes of visitors generally regarded as efficient pollinators to visit the flowers with the more

TABLE 5. *Number of plant species visited by different classes of animals as a function of sugar concentration in nectar.*

	Concentration of sugar in nectar			
Number of plant species studied	0–10% 3	11–20% 15	21–30% 16	Over 30% 5
Hummingbird[a]	—	3	6	—
Butterflies[a]	—	6	6	1
Solitary bees[a]	—	2	3	1
Wasps[a]	—	2	5	1
Flies	—	2	3	—
Beetles[a]	—	2	1	1
Ants	3	11	10	1
Thrips	1	4	5	1
Honeybee[a]	—	8	7	—

[a] Long-tongued visitor.

concentrated nectar. The exotic honeybee exploits the middle ranges, being debarred from the high sugar nectars by the long corolla tubes.

The consistency of the pollen is a vital factor in pollen transference. Tacky pollen requires an animal vector; so do pollinia. Tacky pollen is tractable for packing into pollen baskets and adheres well to beaks, feathers, and body hairs. Of 97 species at the site 86 percent have tacky pollen, 3 percent possess pollinia, and 10 percent have dry pollen (table 1). There is, therefore, a strong dependence on mobile pollinators, and this is increased to almost 100 percent since the dry pollen species, with the exception of the two wind-pollinated grasses *Chloris* and *Lasiacis,* are adapted to the mode of pollen collection employed by certain solitary bees, e.g., *Xylocopa,* which vibrate the porose anthers to dislodge the dry pollen (refer to floral form in *Solanum* spp. and *Cassia* spp.).

With the exception of *Solanum bahamense,* species in which self-pollination is assumed have tacky pollen (see section on fruit set in absence of visitors). Since tacky pollen requires an animal vector this appears to be a relict character and suggests the loss of the pollinator.

FLOWER LIFE AND PHENOLOGY

A feature of the flower life is its short duration (table 1). Only 35 percent of the flowers last more than a day, i.e., the petals remain intact overnight. Whether the overnight retention of the petals is significant in the effective life of the flower is doubtful, as 90 percent present all their pollen on the morning of opening, and the stigmas looked moist and glistening, and held pollen on the morning of opening. Of the flowers which received animal visits, 70 percent last all day and 30 percent last half a day, the former receiving the majority of visits by all classes of the dry season animals (table 6). Butterflies and solitary bees were the chief visitors to the half-day flowers, and we may note that both these have a short morning period of foraging (see under phenology of pollinators).

TABLE 6. *Distribution of animal visitor effort with reference to flower persistence.*

	Percentage of visits	
	All-day flowers	Half-day flowers
Coereba sp. (Aves)	100	0
Hummingbirds	75	25
Butterflies	59	41
Solitary bees	59	41
Wasps	100	0
Flies	85.7	14.3
Beetles	50	50
Ants	87.5	12.5
Thrips	83	17
Honeybee	75	25

The phenology of flowering during the dry season is detailed in table 7. The daily rhythm of blooming (fig. 3) shows that there is a big burst of blooming between 7 and 9 a.m. which is sustained until 11 a.m. when the fall, due to the closing or shedding of the corolla of the short-lived flowers, begins. While no great stress may be placed on the presence/absence data (it was not possible to cover the whole area on any one visit and flowers may have been missed), they are probably substantially correct. The tendency is for the trees and shrubs to produce a flush of flowers after the occasional rains which occur during the dry period. There was a severe drought in early March, and many of the shrubs were in permanent wilt and the ground flora desiccated, except where protected by the canopy of trees. Recovery is rapid, for by April 3 an inch of grass had appeared on the bare ground and the shrubs had new foliage and flower buds.

THE ANIMAL VISITORS

The major classes of pollinating visitors are butterflies, solitary bees, and hummingbirds (table 7). The butterflies predominate both in number of species and individuals. Only a few specimens of the solitary bees were seen, and the birds appeared chiefly when certain trees were in flower. The only group for which biological data are available is that of the butterflies (table 11). All are native and chiefly meadow and scrubland types. Breeding is continuous, with peaks after rain in May and November.

Some of the favorite adult and larval food plants of the butterflies, such as *Croton* and *Stachytarpheta,* are present in quantity at the site. Turner (pers. comm.) has recently discovered that *Avicennia germinans* is the larval food of one of two species of *Junonia* which occur here.

PHENOLOGY OF VISITORS (table 7)

Towards the end of December the wet season flush of visitors was beginning to diminish. This decline was progressive until the beginning of April, when recovery began. Throughout February and March all visitors, except the ants, were few in number and sporadic in appearance. The ants heavily invaded the nectar flowers as the duration of the drought increased. There are indications of phenological links between the butterflies and solitary bees and the flowering of certain species.

The birds did not appear regularly in the association until the trees, *Cordia* and *Piscidia,* came into flower, although 15 Vervain hummingbirds, *Mellisuga,* came in to exploit a flush of *Merremia* flowers on January 20.

DAILY RHYTHM OF ANIMAL VISITS (fig. 3)

The arrival of the visitors is coincident with the early morning blooming, but they mostly disappear while many flowers are still open. This disappearance may be because the supply of food is exhausted, but, in the case of the butterflies, it is compatible with their normal daily rhythm which is: 7.30-8.30 a.m. sunning wings; 7.45 a.m.-2.30 p.m. feeding; 2.30-4 p.m. settling. A few begin feeding earlier and a few feed later. Feeding time during the current dry season was shorter, virtually ceasing by noon.

The solitary bees, too, were seen to forage for pollen only early in the day. This practice links with the half-day blooming of *Cassia* spp., *Mimosa* and *Sesuvium.*

ANIMAL-FLOWER RELATIONSHIPS

SPECTRA OF NATIVE VISITORS

The species visited by each animal are listed in table 7, and it will be seen that many are exploited by more than one potential pollinator. There are eight classes of native visitors (table 8) if we exclude the quits (*Coereba* spp.) which severely damage the flowers and are not considered to be effective pollinators. The number of classes visiting each species, summarised from table 7, is listed in table 1. For example, *Cordia globosa* attracts six classes of visitor, namely hummingbirds, butterflies, wasps, ants, flies, and thrips and also the exotic honeybee, and therefore has a wide spectrum of potential pollinators. If the spectrum is checked against the flower form (table 1), it is seen that all the species attracting from three to six classes of visitors have highly evolved flowers with medium to deeply situated nectar. Species which attracted only one or two classes of visitor are predominantly open or shallow-flowered, there being 26 percent of open and 54 percent of shallow flowers in this group, respectively.

These results were not anticipated. The usual trend is for the more specialized types of flower to have a narrower pollinator spectrum. These reversals may be due to the shortage of forage here in the dry season. Table 8 shows that the majority of species have a narrow spectrum of visitors (1-2 classes) and that there is but a low percentage of long-tongued animals amongst them.

COMPETITION BETWEEN SPECIES AND CLASSES OF VISITORS (table 7)

All classes of visitors compete for nectar; the solitary bees compete for pollen as well.

COMPETITION BETWEEN SPECIES

BIRDS. The quits (*Coereba* spp.) compete with the hummingbirds for *Piscidia piscipula* and the two tree species of *Cordia*, and the hummingbirds between themselves for the former and *Morinda royoc.* The quits damage the flowers, piercing and slitting them to steal the nectar.

BUTTERFLIES. The main competition between the butterflies is for *Stachytarpheta jamaicensis* and *Spilanthes urens,* 11 species foraging on the former and seven species foraging on the latter. There are large areas of both these species on the site, and when both are in flower, competition may not be severe. In the dry season the number of individuals working them diminishes as the crops go out of flower.

SOLITARY BEES compete for pollen, the black *Anthophorid* and *Euglossa* for *Cassia*, and the two *Centris* species for *Bunchosia media.*

ANTS. Brown and black ants, although visiting 35 species, only overlap on four: *Conocarpus erectus, Cordia globosa, Indigofera tinctoria*, and *Urechites lutea.* They are present in large numbers, up to 30 per flower, in the bottom of the trumpets of *Urechites.* They completely remove the nectar without pollinating, thereby effecting a disservice, as none is left for the hummingbirds which are able to pollinate. The ants pollinate both types of *Morinda royoc* flowers. Here, too, they empty the flowers of nectar and are in serious competition with *Papilio polydamas* and the Vervain hummingbird, *Mellisuga humilis.*

The strongest interclass competition is between the hummingbirds and butterflies which work seven species in common. Butterflies compete with wasps for six species, with flies for five, and with solitary bees for four. There is a greater population density of butterflies, and so other groups have a greater pressure on them.

HONEYBEE FORAGING

Honeybee colonies may be maintained in Jamaica only if protected from ants. This situation makes the presence of the bees at this site puzzling for no hives were said to be in the area and the location of the colony was unknown. The honeybees visited 21 species, the majority for nectar (table 9). They were seen only on the male tree of *Bursera simaruba* and so were ineffective pollinators. Transference of pollinia by the bees was not observed in the asclepiad vine, *Sarcostemma clausum.* This species did not set any fruit. *Bauhinia divaricata* has long exserted anthers and stigma which the bees did not touch when taking nectar. The rest of the species visited were all of suitable proportions for pollina-

TABLE 7. *Phenology of plants and animal visitors and efficacy of pollinators.*

Animal visitor	Plant species	Daiy period of visits 0700[a]	0800	0900	1000	1100	1200	1300	Daily period of blooming
AVES									
Coerebidae									
Coereba flaveola	*Cordia gerascanthus*		v			v			All day
	Cordia sebestena		v						,, ,,
	Piscidia piscipula			v	v	v		v	,, ,,
Trochilidae									
Mellisuga humilis	*Cordia gerascanthus*		v						,, ,,
	Cordia globosa							v	8am onwards
	Merremia umbellata						v	v	All day
	Morinda royoc		v						8am onwards
	Piscidia piscipula			v					All day
	Stachytarpheta jamaicensis				v				6:30am-1pm
Trochilus polytmus	*Cordia sebestena*		v			v		v	All day
	Ipomoea acuminata		v						8am-1pm
	Morinda royoc			v				v	8am onwards
	Piscidia piscipula				v	v			All day
	Turnera ulmifolia		v						7am-noon
	Urechites lutea			v					All day
LEPIDOPTERA									
Agraulis vanillae	*Blechum pyramidatum*			v					7am-12:30pm
	Spilanthes urens		v			v			8am onwards
	Stachytarpheta jamaicensis		v	v	v	v			6:30am-1pm
Anartia jatrophae	*Melochia nodiflora*			v					8am onwards
	Spilanthes urens					v			8am onwards
	Stachytarpheta jamaicensis						v		6:30am-1pm
Ascia josephina	*Morinda royoc*		v						8am onwards
	Stachytarpheta jamaicensis		v		v				6:30am-1pm
Danaus eresimus	*Stachytarpheta jamaicensis*			v					6:30am-1pm
Danaus gilippus	*Asclepias curassavica*						v		All day
	Spilanthes urens			v					8am onwards
	Stachytarpheta jamaicensis				v	v	v		6:30am-1pm
Eurema nise and *E. lisa*	*Borreria laevis*				v				7am-1pm
	Spilanthus urens					v			8am onwards
	Vernonia cinerea					v			10am onwards
Hylephila phyleus	*Eupatorium odoratum*			v					9am onwards
Junonia spp.	*Borreria laevis*			v	v				7am-1pm
	Cordia globosa				v				8am onwards
	Melochia nodiflora			v					8am onwards
	Spilanthus urens			v					8am onwards
	Stachytarpheta jamaicensis		v	v	v	v			6:30am-1pm
Leptotes cassius	*Borreria laevis*				v				7am-1pm
	Piscidia piscipula				v				All day
	Spilanthes urens			v		v			8am onwards
Papilio polydamas	*Bauhinia divaricata*		v						All day
	Blechum pyramidatum					v			7am-12:30pm
	Cordia gerascanthus		v						All day
	Lantana camara					v			9am onwards
	Morinda royoc		v	v	v	v			8am onwards
	Spilanthes urens		v						8am onwards
	Stachytarpheta jamaicensis	v	v	v	v	v	v		6:30am-1pm
Phoebis sennae	*Cordia sebestena*				v				All day
	Merremia umbellata					v	v		All day
	Stachytarpheta jamaicensis			v	v				6:30am-1pm
Polygonus leo	*Blechum pyramidatum*		v						7am-12:30pm
	Cordia globosa			v	v				8am onwards
	Stachytarpheta jamaicensis				v				6:30am-1pm
	Waltheria indica				v				8am onwards
Strymon columella	*Evolvulus nummularius*				v				9am-2pm
	Spilanthes urens			v		v			8am onwards
Urbanus proteus	*Cordia gerascanthus*		v			v			All day
	Spilanthes urens		v						8am onwards
	Stachytarpheta jamaicensis		v	v	v	v	v		6:30am-1pm

v = visit   F = flush of flowers   x = flower present

Weekly periods of visits							Weekly periods of blooming							Efficacy of pollinator (% of stigmas pollinated)
24 XII 68	17-20 I 69	28 and 31 I 69	21-24 II 69	3 III 69	16-19 III 69	3-8 IV 69	24 XII 68	17-20 I 69	28 and 31 I 69	21-24 II 69	3 III 69	16-19 III 69	3-8 IV 69	
				x						F	x			nil, thieving
				x				x	x		F	x	x	nil, thieving
					x	x					x	F	x	nil, thieving
				x						F	x			
						x		F	x	x	x	F	F	100
	x							F		x				high
				x	x	x		x		F	x	x	F	
					x						x	F	x	
				x			x	F	x	x	x	x	x	
				x		x		x	x		F	x	x	100
			x							F	x	x	x	
						x		x		F	x	x	F	100
						x					x	F	x	
					x						x	x	x	
						x		x		x	x	x	F	100
					x					x	x	F	x	
					x		x	F	x	x	x	x	x	
	x		x		x		x	F	x	x	x	x	x	
x							F	x		x	x			
			x				x	F	x	x	x	x	x	
	x		x				x	F	x	x	x	x	x	
				x				x		F	x	x	F	
			x				x	F	x	x	x	x	x	
	x						x	F	x	x	x	x	x	
				x				x		x			x	
	x						x	F	x	x	x	x	x	80
	x		x				x	F	x	x	x	x	x	
						x	x	F	x	x	x	x	x	
			x				x	F	x	x	x	x	x	
			x					F	x	x	x		x	
				x				F		x	x	x		
	x	x					x	F	x	x	x	x	x	63
					x			F	x	x	x	F	F	80
x							F	x		x	x			100
	x						x	F	x	x	x	x	x	100
	x	x	x				x	F	x	x	x	x	x	94
				x			x	F	x	x	x	x	x	
					x						x	F	x	
			x			x	x	F	x	x	x	x	x	
				x					x		x	x	F	
					x					x	x	F	x	
				x						F	x			
			x							x	x	x	x	
					x	x		x		F	x	x	F	86
					x		x	F	x	x	x	x	x	
x	x	x	x	x	x		x	F	x	x	x	x	x	93
	x							x	x		F	x	x	100
			x					F		x				60
	x	x	x				x	F	x	x	x	x	x	100
				x						x	x	F	x	nil
	x				x			F	x	x	x	F	F	66
			x				x	F	x	x	x	x	x	
	x									x		x		
				x						F	x	x	x	
x			x				x	F	x	x	x	x	x	
				x						x	x			
					x		x	F	x	x	x	x	x	
x	x	x	x	x	x		x	F	x	x	x	x	x	90

TABLE 7. (continued).

Animal visitor	Plant species	Daily period of visits 0700[a]	0800	0900	1000	1100	1200	1300	Daily period of blooming
HYMENOPTERA									
Apidae									
Anthophorinae									
Anthophorid (black)	*Brysonima coriacea*					v			All day
	Cassia sp.			v					8am-12:30pm
	Cassia occidentalis			v					8am-11am
	Piscidia piscipula			v	v				All day
Exomalopsis sp.	*Borreria laevis*			v					7am-1pm
	Mimosa pudica		v						8am-noon
	Sesuvium portulacastrum			v					8:45am-noon
	Spilanthes urens			v					8am onwards
Euglossa ? cordata	*Cassia* sp.		v						8am-12:30pm
	Cassia occidentalis		v						8am-11am
	Solanum erianthum					v			All day
	Solanum havanense		v			v			8am onwards
Apinae									
Centris dirrhoda	*Bunchosia media*			v					All day
	Morinda royoc				v				8am onwards
Centris sp.	*Bunchosia media*			v					All day
	Crotalaria verrucosa			v					All day
Xylocopinae									
Xylocopa sp.	*Bursera simaruba*					v			All day
Scoliidae									
Dielis dorsata	*Cordia gerascanthus*			v	v				All day
	Cordia globosa			v	v		v		8am onwards
	Eupatorium odoratum				v				9am onwards
	Ipomoea tiliacea		v		v				8am onwards
	Lantana involucrata					v			8:30am onwards
	Mikania micrantha				v				10am onwards
	Morinda royoc			v	v				8am onwards
	Spilanthus urens			v	v				8am onwards
Sphecidae									
Microbembex monadonta	*Cordia globosa*						v		8am onwards
	Eupatorium odoratum					v			9am onwards
	Waltheria indica					v			8am onwards
Wasp (unidentified)	*Waltheria indica*					v			8am onwards
Formicidae									
Brown ants (including	*Capraria biflora*			v					8am onwards
Brachymyrmex sp.,	*Conocarpus erectus*			v					All day
Tapinoma melanocephalum)	*Cordia globosa*		v						8am onwards
	Euphorbia hyssopifolia		v						9am onwards
	Indigofera tinctoria			v					8am onwards
	Piscidia piscipula				v				All day
	Thunbergia fragrans			v					All day
	Urechites lutea		v		v				All day
Black ants (including	*Alternanthera ficoidea*				v				8:30am onwards
Monomorium carbonarium	*Argythamnia candicans*				v				9am onwards
ebeninum, *Paratrechina*	*Bauhinia divaricata*				v				All day
longicornis, *Solenopsis* sp.)	*Blechum pyramidatum*	v							7am-12:30pm
	Borreria laevis	v	v	v	v				7am-1pm
	Bourreria succulenta		v	v	v	v			8am onwards
	Broughtonia sanguinea		v			v			All day
	Bursera simaruba, male tree				v		v		All day
	Capraria biflora				v				8am-1pm
	Cissus sicyoides				v				All day
	Conocarpus erectus			v					All day
	Cordia brownei				v		v		8am onwards
	Cordia globosa		v	v	v	v	v		8am onwards
	Cordia sebestena			v					All day
	Crotalaria verrucosa			v					All day
	Ehretia tinifolia				v				All day
	Eupatorium odoratum					v			9am onwards
	Guazuma ulmifolia			v					8am onwards
	Indigofera tinctoria				v				8am onwards
	Ipomoea acuminata				v				8am-1pm
	Jacquinia arborea		v						9am onwards
	Lantana involucrata			v					8:30am onwards

v = visit F = flush of flowers x = flower present

Weekly periods of visits							Weekly periods of blooming							Efficacy of pollinator (% of stigmas pollinated)
24 XII 68	17-20 I 69	28 and 31 I 69	21-24 II 69	3 III 69	16-19 III 69	3-8 IV 69	24 XII 68	17-20 I 69	28 and 31 I 69	21-24 II 69	3 III 69	16-19 III 69	3-8 IV 69	
						x							F	
				x							F	x	x	100
				x						F	x			100
				x	x						x	F	x	
						x	x	F	x	x	x	x	x	
						x		x		x	x		x	100
						x						x	x	100
						x	x	F	x	x	x	x	x	
			x								F	x	x	
			x							x	x			69
						x				x		x	x	
						x		x				x	x	100
								x	x	x				100
	x		x					x		F	x	x	F	100
	x							x	x	x				100
	x							F	x	x	x	x		
						x						F	F	
			x	x						F	x			41
		x			x	x		F	x	x	x	F	F	100
			x					F		x	x	x		100
			x		x					x	x			
			x							x	x	x		
			x							x	x			100
	x							x		F	x	x	F	
	x	x					x	F	x	x	x	x	x	85
						x		F	x	x	x	F	F	
	x							F		x	x	x		
			x							x		x		
			x							x		x		100
			x					x		F	F	x	x	
						x							x	100
					x			F	x	x	x	F	F	100
					x			x		x		x	x	
					x						x	x		
				x							x	F	x	
			x					F	x	x	x	x	x	
				x	x			x	x	x	x	x	F	
		x						F	x	x	x	x		
						x		x	x	x	x	x	x	
						x			x		x	x	F	
					x					x	x	F	x	
			x		x	x	x	F	x	x	x	x	x	100
						x							x	100
					x							x	x	
						x						F	F	
			x					x		F	F	x	x	100
			x							x				
						x							x	100
			x	x						x	x	x	x	100
			x		x	x		F	x	x	x	F	F	90
	x							x	x		F	x	x	
					x			F	x	x	x	x		
						x							x	
	x							F		x	x	x		
					x					x	x	x	x	
				x							x	x		
			x							x	x	x	x	100
					x							x	x	
					x					x	x	x		

TABLE 7. (continued).

Animal visitor	Plant species	0700[a]	0800	0900	1000	1100	1200	1300	Daily period of blooming
				Daily period of visits					
	Malpighia glabra		v						8am onwards
	Melochia nodiflora					v			8am onwards
	Mikania micrantha						v		10am onwards
	Morinda royoc		v	v	v				8am onwards
	Philoxerus vermicularis		v			v			8:30am onwards
	Physalis angulata			v	v				9am onwards
	Turnera ulmifolia			v	v				7am-noon
	Urechites lutea		v	v	v	v			All day
	Waltheria indica			v					8am onwards
Exotic species									
Apidae									
Apis mellifera	*Alternanthera ficoidea*					v			8am onwards
	Avicennia germinans			v	v				9am onwards
	Bauhinia divaricata		v						All day
	Borreria laevis		v	v	v				7am-1pm
	Bursera simaruba					v			All day
	Capparis ferruginea							v	All day
	Capraria biflora		v	v	v				8am-1pm
	Citrus aurantifolia						v		All day
	Cordia gerascanthus		v	v		v	v		All day
	Cordia globosa				v				8am onwards
	Ehretia tinifolia							v	All day
	Evolvulus nummularius				v	v			9am-2pm
	Lantana involucrata					v			8:30am onwards
	Mikania micrantha				v				10am onwards
	Morinda royoc		v	v	v	v			8am onwards
	Piscidia piscipula			v	v	v		v	All day
	Sarcostemma clausum						v		All day
	Spilanthes urens				v	v			8am onwards
	Stachytarpheta jamaicensis		v						6:30am-1pm
	Tribulus cistoides		v	v					8am-12:30pm
DIPTERA									
Culex sp.	*Morinda royoc*				v				8am onwards
Eristalis vinatorum (and other syrphids)	*Bauhinia divaricata*		v						All day
	Borreria laevis			v	v				7am-1pm
	Cordia globosa					v			8am onwards
	Mikania micrantha					v			10am onwards
	Spilanthes urens					v			8am onwards
Fly (unidentified)	*Cordia globosa*			v					8am onwards
HETEROPTERA									
Oncopeltus pictus	*Asclepias curassavica*					v			All day
	Blechum pyramidatum			v					7am-12:30pm
	Ehretia tinifolia							v	All day
	Eupatorium odoratum				v				9am onwards
COLEOPTERA									
Green beetle (unidentified)	*Euphorbia heterophylla*				v				9am onwards
Beetle (unidentified)	*Cassia* sp.			v	v				8am-12:30pm
	Cassia occidentalis		v						8am-11am
THYSANOPTERA									
Thripidae	*Alternanthera ficoidea*				v	v			8:30am onwards
	Cordia brownei			v					8am onwards
	Cordia globosa		v				v		8am onwards
	Ehretia tinifolia				v				All day
	Eupatorium odoratum			v					9am onwards
	Evolvulus nummularius					v	v		9am-2pm
	Guazuma ulmifolia			v					8am onwards
	Ipomoea acuminata			v	v				8am-1pm
	Lantana involucrata				v	v			8:30am onwards
	Lippia nodiflora					v			8:30am onwards
	Momordica charantia, male					v			8am onwards
	Piscidia piscipula			v	v				All day
	Rhabdadenia biflora			v					All day
	Solanum torvum					v			All day
	Stylosanthes hamata				v				8am-12:30pm
	Thunbergia fragrans				v		v		All day
	Urechites lutea					v			All day

v=visit F=flush of flowers x=flower present

Weekly periods of visits 24 XII 68	17-20 I 69	28 and 31 I 69	21-24 II 69	3 III 69	16-19 III 69	3-8 IV 69	Weekly periods of blooming 24 XII 68	17-20 I 69	28 and 31 I 69	21-24 II 69	3 III 69	16-19 III 69	3-8 IV 69	Efficacy of pollinator (% of stigmas pollinated)
					x							x		
				x			F	x		x	x			
			x							x	x			
	x		x	x	x	x		x		F	x	x	F	100
					x	x		F				x	x	
				x		x					x		x	
					x	x					x	x	x	100
				x	x	x		x		x	x	x	F	
x							x			x		x		54
	x		x					F	x	x	x	x		100
						x							F	
				x					x		x	x	F	
	x	x	x	x			x	F	x	x	x	x	x	100
						x						F	F	
						x							x	
	x			x				x		F	F	x	x	100
		x								x	x			
				x						F	x			41
	x							F	x	x	x	F	F	100
						x							x	
			x	x						F	x	x	x	100
			x							x	x	x		90
			x							x	x			100
			x		x	x		x		F	x	x	F	100
				x	x	x					x	F	x	
			x							x				
	x		x				x	F	x	x	x	x	x	62
	x						x	F	x	x	x	x	x	100
	x	x						x	F	x	x	x		100
	x							x		F	x	x	F	
				x					x		x	x	F	
	x						x	F	x	x	x	x	x	75
				x		x		x	x	x	x	x	x	
			x							x	x			
	x						x	x	x	x	x	x	x	21
					x			F	x	x	x	F	F	
				x				x		x			x	
					x					x	x	F	x	100
						x							x	
				x				F		x	x	x		100
		x							x					
				x							F	x	x	
			x							x	x			
		x			x			F	x	x	x	x		
						x				F	x	x	x	
	x					x		F	x	x	x	F	F	
						x							x	
					x			F		x	x	x		
			x	x						F	x	x	x	
				x						x	x	x	x	
			x							x	x	x	x	
			x							x	x	x		100
			x					F		x		x	x	100
			x							x	x			
				x	x						x	F	x	
						x							x	
			x							F	x			
			x					x	F	x	x	x	x	33
			x					F	x	x	x	x	x	
			x					x		x	x	x	F	

TABLE 8. *Spectra of native visitors to plant species.*

Number of classes of visiting animal	6	5	4	3	2	1
Number of plant species visited	3	1	5	7	15	24
	Percentage of plant species visited					
Coereba spp. (Aves)	33		40			
Hummingbirds[a]	100		40	21	20	
Butterflies[a]	100	100	100		30	8
Solitary Bees[a]	66		40		26	25
Wasps	66	100	40	21	7	4
Flies[a]			60	14		
Beetles[a]		100		21	26	4
Ants	100	100	60	100	53	41
Thrips	66	100		57	33	21

[a] Long-tongued visitor.

TABLE 9. *Honeybee foraging.*

Species	Insect food available in flower			Honeybee foraging		
	Pollen	nectar	% sugar in nectar	Pollen	nectar	Pollination efficacy
Alternanthera ficoidea	+	+	19		+	100
Avicennia germinans	+	+	25		+	
Bauhinia divaricata	+	+	17		+	0
Borreria laevis	+	+	16	+	+	100
Bursera simaruba (male tree)	+	+	19	?	+	0
Capparis ferruginea	+	+	21		+	+[c]
Capraria biflora	+			+		100
Citrus aurantifolia	+	+		+		+
Cordia gerascanthus	+	+	24		+	
C. globosa v *humilis*	+	+	19-23	+	+	100
Ehretia tinifolia	+	+	17		+	
Evolvulus nummularius	+			+		100
Haematoxylum campechianum[a]	+	+			+	+
Lantana involucrata	+	+	20		+	90
Mikania micrantha	+	+	23		+	100
Morinda royoc	+	+	22		+	100
Piscidium piscipula	+	+	22	+	+	+
Sarcostemma clausum	+[b]	+			+	0
Spilanthes urens	+	+		+	+	50
Stachytarpheta jamaicensis	+	+	27		+	100
Tribulus cistoides	+			+		100

[a] Source of logwood honey.
[b] Pollinia.
[c] + = Flowers were successful pollinated but no actual percentage counts were taken.

tion by the bees, and pollinating efficiency was high. *Capraria biflora*, a pollen flower ignored by the solitary bees, owed its heavy crop of fruit to the honeybees collecting pollen in large quantities in the early morning.

In the dry-season period of shortage the adventive honeybee is a serious competitor with the native animals for nectar (table 10). Its relatively short tongue, 6 mm, usually deters it from foraging the deep, narrow-tubed flowers, but at another site it was seen to enter the broad-mouthed trumpets of *Ipomoea tiliaceae* and effectively remove nectar. It forages in a wider range of weather conditions. For example, it worked *Cordia globosa* when the sky was overcast and a strong on-shore breeze was blowing. The native pollinators were inactive under these conditions. At another site where observations began at sunrise, the bees began foraging on the same species as those present at the Morant Point site up to two hours before the butterflies and an hour before the solitary bees. It is probable that they do the same at Morant Point, and if so, the practice will further increase the pressure on the native visitors by lessening the supply of food available.

TABLE 10. *Honeybee in competition with native animals.*

	Quits	Hummingbirds	Butterflies	Solitary bees	Wasps	Flies	Beetles	Ants	Thrips
Number of species worked in common with honeybee	2	5	5	5	5	6	1	10	6

EFFICACY OF POLLINATORS (table 7)

It is evident from the table that the flying visitors were highly efficient pollinators. Ants, in their passage up and down the corolla tubes, moved the pollen onto the stigma in both long- and short-styled flowers of *Morinda royoc, Cordia brownei,* and *C. globosa.* It is unlikely that they carry pollen from one plant to another or even between adjacent flowers, for their bodies are usually completely free of grains.

Thrips shelter in the deeper corolla tubes. They were plentiful in *Lantana involucrata* where they might be seen arranged with their abdomens inside the mouth of the corolla and with their heads facing outwards. They were credited with the pollination here, and in *Lippia nodiflora.*

FRUIT SET

Details of fruit set (table 1) show that heavy fruiting was a feature of 61 percent of the dry-season flowering species. The fruiting of six species was missed, and seven had just begun to flower so these had to be excluded. Of the remaining species only four failed to set seed: *Alternanthera ficoidea, Cis-*

sampelos pareira, Cordia brownei, and *Evolvulus nummularius.* The *Cissampelos* vines bore female flowers only. The absence of fruit in *Alternanthera* and *Evolvulus* is unexplained as both were pollinated by their visitors. *C. brownei* is heterostylous and was only visited by ants and thrips, so there was probably no carriage of pollen between plants which may be necessary for seed set.

FRUIT SET IN ABSENCE OF VISITORS (table 1)

No pollinators were observed on 39 species which set seed. Floral data were available for 33.

Excluding *Cassia ligustrina,* which was pollinated by an unseen visitor, 10 species have stigmas and anthers in contact or coming into contact following movement, as in *Sida* spp. and *Rivina humilis.* These are self-pollinated. In the next group of six species, pollination gap 0.15-0.5 mm, self-pollination is almost inevitable, the more so because in two species the stigma lies below the level of the anthers. The next group of four species, pollination gap 0.6-1.0 mm, comprises *Solanum bahamense* with pendent flowers where dew could bridge the 1 mm gap between anther pore and stigma; *Lasiacis divaricata,* a wind-pollinated grass; and *Emilia sonchifolia* and *Trichostigma octandrum* which have extensive stigmatic surfaces and need but one pollen grain to satisfy the single ovule. The next group of seven species, pollination gap 1.1-2.0 mm, contains one grass and two in which the stigma is variously positioned. These three too may be selfed, bringing the total to 23 species, i.e., 72 percent of the group.

Of the remaining five species with a pollination gap greater than 2 mm, *Helicteres jamaicensis,* pollination gap 2.5 mm, and *Capparis flexuosa,* pollination gap 8 mm, are nocturnal flowers and were probably moth-pollinated. *Ruellia tuberosa,* pollination gap 5.4 mm, a butterfly type, flowered sparsely, and the visitor may have been missed. *Croton discolor* is dioecious. On a raised beach at Galina Point it was visited by a *Centris, Junonia evarete,* and the honeybee. These insects were present at Morant Point, and it is assumed that they were responsible for the pollination.

The mechanism of pollen transport in *Abrus precatorius,* pollination gap 1.5 mm, *Passiflora suberosa,* 1.25 mm, *Priva lappulacea,* 1.25 mm, *Triumfetta lappula,* 1.4 mm, and *Euphorbia hirta,* 2.5 mm, was not solved.

Excluding the exceptions detailed above, it would appear that fruit set in the absence of visitors is here consequent on a narrow pollination gap permitting self-pollination and self-fertility.

NUMBER OF SEEDS PER FRUIT AND CLASSES OF VISITORS

An assumption has been made that the minimal number of pollen grains required to fertilize the ovules is equal to the number of seeds in the fruits. Figure 4, block A shows the pattern of seed number per fruit in the dry-season flora. The majority of the species belong to the 1-4 seed per fruit category and potentially require to receive only 1-4 pollen grains per flower at pollination. The succeeding blocks (fig. 4) show the classes of visitors to the 3-seed categories delimited in block A. All groups, except the beetles, forage chiefly on the 1-4 seed class. Flies, ants, and thrips carry very little pollen on their bodies and transfer very little. Butterflies also, in effecting 'tongue-tip' pollination, normally transfer very few grains. Hummingbirds, solitary bees, wasps, and beetles usually transfer many grains on beak, body and legs. So there would be over-pollination of the 1-4 seed species when these classes were in action. This would also be the case with the honeybee as pollinator.

If we compare the two major native pollinating classes of the butterflies (block B) and the solitary bees (block C), there appears to be a link between the transferring powers of the visitors and the number of pollen grains required per flower. (The wasp, fly, and beetle data are too scanty to be stressed.)

REVIEW AND DISCUSSION OF RESULTS

The flower form is highly evolved in the majority of species, with features preventing promiscuous pollination and associated with long-tongued animal pollinators. There are three main groups, namely, butterfly, solitary bee, and hummingbird flowers, and it is precisely these animals which are present as the dominant groups of pollinators at the site. This situation is indicative of integration between the flowers and pollinators.

The length of flower life is positively linked with the visitors. The majority of flowers which last all day received most visits by all classes of animals.

The daily period of activity and the flower life is also synchronised in two major pollinating groups, both the butterflies and solitary bees having a short period which matches the half-day life of their favorite flowers.

The high percentage of nectar-producing species points to a dependence on nectar-seeking animals as pollinators, and this requirement is satisfied by the preponderance of these types, namely, butterflies,

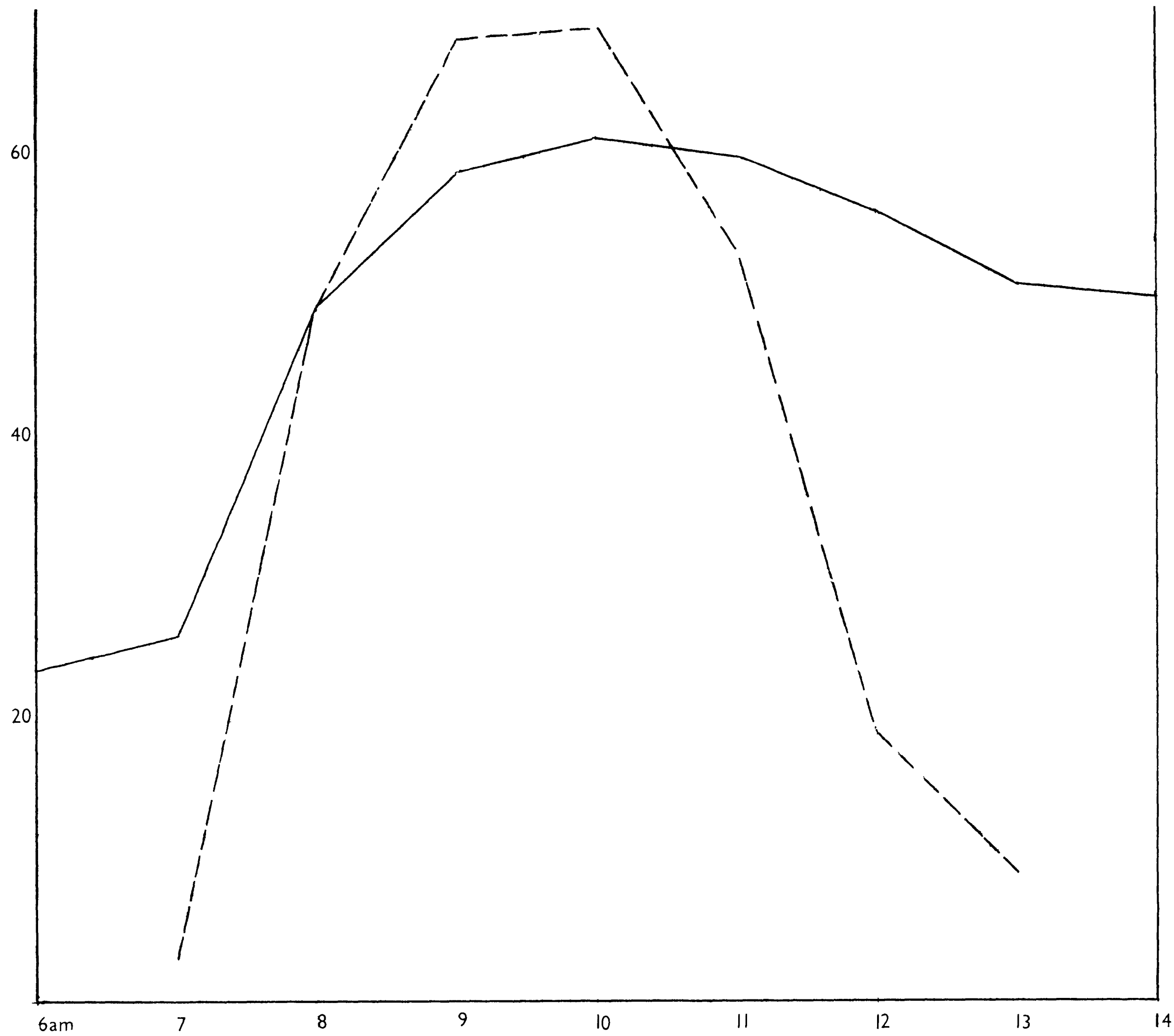

FIGURE 3. Daily rhythm of blooming and visiting by animals. Vertical axis represents number of items; the solid line indicates the number of species of plants blooming; the interrupted line represents the number of animal visits to plants in bloom; the horizontal axis represents time from 0600 to 1400 hrs.

hummingbirds, solitary bees, and wasps. The more concentrated nectars attracted the more specialized pollinators, namely, the hummingbirds and butterflies. The comparatively deep siting of the nectar indicates a link with long-tongued animals, and these were present. Also, the expected stratification of visitors, depending on the depth at which the nectar was available, was realised.

The tacky consistency of the pollen of most species pointed to dependence on animal visitors. In most cases active collection of the pollen was not involved as pollen-collecting animals were few; rather, there was simply the dislodgement from the anther and passive transfer by the animal vector. The physical quality of the pollen was also a factor in its collection, the tacky pollen being suitable, i.e., capable of being packed, by *Exomalopsis* and *Centris* bees, and the powdery pollen being suitable for the vibratory technique employed by the anthophorids.

The dependence of the major pollinators, the butterflies, on the flora is seen by their diminution in numbers as their flowers go out of bloom. This situation is not entirely due to migration away from the site, but because butterfly breeding rises and falls with the flowering of the species with which they are associated. There is also a change in species content of the butterfly population, those persisting through the dry season being drought resistant, and this condition links with the January to March dry period at the site.

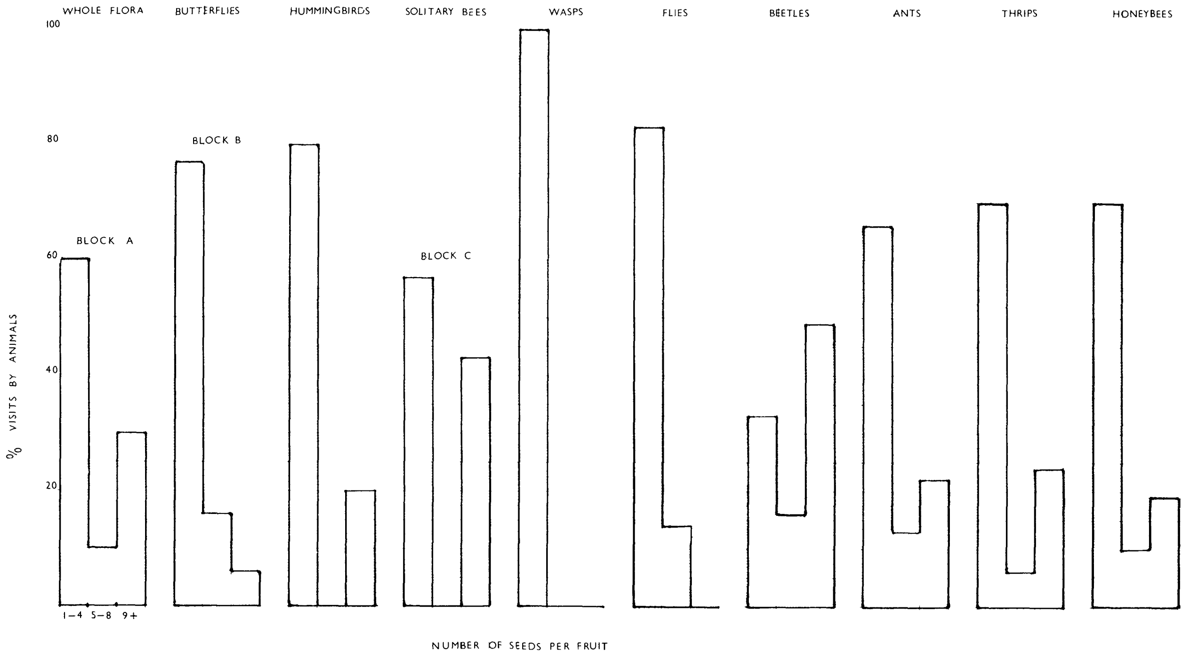

FIGURE 4. Number of seeds per fruit and class of visitors. Each histogram triplet represents the percentage of total visits by each class of visitor to each of three classes of flower: left, those setting 1–4 seeds per fruit; middle, those setting between 5 and 8; and right, those setting 9 or more seeds per fruit.

Another significant feature of the floral ecology is the very narrow "pollination gap." This permitted self-pollination and seed set in species which received no visitors during the dry season.

Grant (1965: 165) would regard this autogamy as "an adaption to a sparse climate of pollinators," which undoubtedly pertains here in the dry season, but whether this is still the case during the April and November flush seasons is not known.

The number of self-pollinated species (20) is greater than those visited by the birds (10), the solitary bees (14), and the wasps (9), and equals those visited by butterflies. This finding tends to confirm Grant's observations elsewhere that self-pollinated species coexist in larger numbers in the area compared with those possessing any single method of pollination.

Yet another feature is the division of the plants into two major groups: those with a very small number of seeds per fruit (59 percent) and those with many seeds per fruit (30 percent). This division appears to be linked with the pollen-carrying powers of their visitors, the sparse transference of butterflies matching the low pollen requirement of the former group, and the greater capacity of the solitary bees, matching the latter. This facet of the butterfly and solitary bee flower's relationship has hitherto not been demonstrated.

Competition between classes of animal was severe, and was indicated by the wide spectra of visitors to some species normally associated with one type of pollinator. Competition was not considered to be due to imbalance between pollinators and flowers because there is no disparity between the types of pollinator and the types of flowers at this site. Rather, it was judged to be due to the severe drought, unalleviated by the expected intermittent, dry-season rains, which brought about a curtailment of flowering and caused the crowding of the animals onto the only fodder available. There is interspecific competition also in the butterflies and birds. The butterflies often have especially intimate associations with their flowers involving both larval and imago stages.

CONCLUSION

One may conclude from the evidence presented above that the pattern of floral ecology which has developed at this site over the past century and a half is that of an integrated association with a well-defined physiogamy. This pattern is designated in terms of pollinators, a Butterfly, Solitary bee, Hummingbird association. It appears balanced at the present time and is a local adjustment between pollinators and flower species already present in the is-

TABLE 11. *Butterfly habitats and food.*

Species	Status	Habitat	Favorite food plants of adult	Larval food plants
Agraulis vanillae	native	strictly meadow and wayside	*Lantana camara*	*Passiflora suberosa*, *Passiflora* spp.
Anartia jatrophae	native	meadow, open grassland	*Ruellia tuberosa, Blechum pyramidatum, Heliotropium*	*Ruellia tuberosa, Blechum pyramidatum*
Ascia josephina	native	strictly woodland	Tree flowers	*Capparis ferruginea*
Danaus eresimus	native	open grassland	*Asclepias curassavica, Stachytarpheta jamaicensis*	unknown
Danaus gilippus	native	meadow and wayside	*Asclepias curassavica, Sarcostemma clausum*	*A. curassavica, S. clausum*
Eurema nise	native	prefers woodland, found edge woods and roads	Small flowers	*Mimosa pudica, Desmanthus virgatus*
Eurema lisa	native	meadow, wayside, open scrubland	Small flowers	*Mimosa pudica*
Hylephila phyleus	native	open grassland in wet areas		various grasses and *Cynodon dactylon*
Junonia sp. A	native	meadow, wayside	*Stachytarpheta jamaicensis*	*Ruellia tuberosa, Blechum pyramidatum, Stachytarpheta jamaicensis*
Junonia sp. B	native	woodland	*Eupatorium odoratum, Avicennia germinans*	*Avicennia germinans*
Leptotes cassius	native	meadow, scrub	*Bauhinia divaricata, Heliotropium angiospermum*	Leguminosae, *Phaseolus, Pithecellobium*
Papilio polydamas	native	meadow (oviposits in woodland)	*Stachytarpheta jamaicensis*	*Aristolochia* spp.
Phoebis sennae	native	meadow, wayside, scrub	*Lantana involucrata, Stachytarpheta jamaicensis*	*Cassia* spp.
Polygonus leo	native	chiefly woodland, wayside	*Cordia globosa*	*Piscidia piscipula*
Strymon columella	native	scrub, meadow	*Croton discolor*	unknown
Urbanus proteus	native	meadow	*Lantana involucrata, Stachytarpheta jamaicensis*	herbaceous Leguminosae

land. Change might be anticipated if the grazing animals were excluded.

One biotic factor, the honeybee, *Apis mellifera*, is exerting pressure on the native pollinators which can only be regarded as damaging to them during this dry season, although the pollination may be enhanced. In many cases, excepting *Capraria biflora*, its activities must lead to needless overpollination. In the interests of conservation of the natural environment, this poses the question of the advisability of introducing an invasive polytropic insect.

ACKNOWLEDGEMENTS

I am much indebted to Dr. Dennis Adams, Department of Botany, University of the West Indies, for identifying and naming the plants according to his Flora; to Dr. Tom Turner, Department of Zoology, University of the West Indies, for the butterfly data; and to Dr. Reece I. Sailer and his colleagues of the Entomology Research Division, U.S. Department of Agriculture, who identified the ants and thrips.

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