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PLANT–HUMMINGBIRD INTERACTIONS: EFFECTS OF ISLAND SIZE AND DEGREE OF SPECIALIZATION ON POLLINATION

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SUMMARY

(1) Dispersal of pollen by hummingbirds in two plant species, *Mandevilla hirsuta* (Apocynaceae) and *Justicia secunda* (Acanthaceae), was investigated on Trinidad, a large continental island, and Tobago, a smaller island with fewer species of hummingbirds.

(2) Frequencies of hummingbird visits to flowers of each species (and, in *Justicia*, to flowers at different densities) on each island were quantified over a 13-month period.

(3) During February 1978, pollen dispersal on each island was monitored with fluorescent powders, and fruit-set of *Mandevilla* was recorded.

(4) In *Justicia*, which has a relatively open corolla accessible to many hummingbirds, frequencies of bird visits were similar on both islands. Patterns of total pollen dispersal, relating to labelled pollen deposited on any flower part, were also similar on both islands. Patterns of pollen deposition on reproductive parts were affected by feeding behaviour of the hummingbirds.

(5) On Trinidad, *Justicia* pollen was dispersed less far from flowers defended by territorial hummingbirds than from undefended flowers.

(6) *Mandevilla*, which has a long corolla accessible to only a few hummingbird species, received consistent visits from two hummingbirds 'constant' to that species at one Trinidad site.

(7) On Tobago, where these 'constant' hummingbird species were absent, visits to *Mandevilla* were sporadic and were made only by species that fed on many plant species, and were not 'constant' on *Mandevilla*.

(8) Accordingly, pollen dispersal of *Mandevilla* on Trinidad was extensive, with dye from marked flowers reaching most other flowers in the population on a given day, whereas on Tobago dye was dispersed only very short distances.

(9) Fruit-set in *Mandevilla* on Tobago was significantly lower than on Trinidad.

(10) These results support the prediction that a generalized plant such as *Justicia* would be affected less by an island-induced reduction in pollinator-diversity than would a specialized plant such as *Mandevilla*.

INTRODUCTION

Variation in the availability of plants or pollinators sets limits on the evolution of specificity in pollination systems (Baker & Hurd 1968; Stebbins 1970). Highly specialized plant–pollinator relationships are especially susceptible to perturbation of any sort, because any factor affecting the relative availability of either the plant or its pollinator necessarily affects both populations (Janzen 1974; Cruden *et al.* 1976). In a sense an island is a perturbation relative to a mainland, since many species occurring on a mainland are absent from islands, even from those which are nearby. For this reason, islands make ideal systems for studying the effects of decreased availability of pollinators on plant populations. Despite the great amount of attention paid in recent years to island ecology and biogeography on the one hand, and to pollen dispersal in plants on the other hand (Levin & Kerster 1974), so far the only published island–mainland comparisons of pollination systems known to us have dealt primarily with plant breeding systems: Hagerup (1951), Linsley, Rick & Stevens (1966) and Rick (1966) showed that plant species on islands tended to be more readily self-fertile, and to have more generalized pollination mechanisms, than their mainland counterparts. These authors suggested that this trend was a consequence of decreased availability of pollinators on islands. As yet there is no quantitative evidence that pollen flow and resulting seed-set in animal-pollinated island plants are substantially reduced.

Within a particular pollination guild, or set of plants relying on a common set of animal pollinators, one would expect that island living would have very different consequences, in terms of pollen flow, for highly specialized plants (which depend on a few specific pollinator species) as opposed to generalized plants that can be pollinated by any one of many visitors. In this paper we present results on the pollination biology of two hummingbird-pollinated plant species on Trinidad, a large mainland-like island, and Tobago, a much smaller, more isolated island. One plant species, *Mandevilla hirsuta*, produces long, tubular, relatively specialized flowers which only long-beaked hummingbird species can probe and pollinate, whilst the second species, *Justicia secunda*, has shorter, more open flowers which a wide variety of hummingbirds can visit and pollinate.

THE EXPERIMENTAL SYSTEM

Islands

Trinidad, a continental island 4520 km^2 in area, is about 15 km from the Venezuelan coast. Because of its proximity to continental South America, it possesses a nearly full complement of nearby mainland birds and vegetation (Beard 1946; ffrench 1973). Two study sites (one hilly and one lowland) were selected in areas representative of the most extensive associations of second-growth vegetation available to hummingbirds and bird-visited plants in northern Trinidad. The hilly site ('Simla') was in the Arima Valley in Trinidad's Northern Range (10°42′N, 61°18′W), at an altitude of 160–230 m. The lowland site ('Waller') was in an extensive zone of lowland, savanna-like, second-growth vegetation on the Caroni Plain (10°36′N, 61°14′W), *c.* 8 km from the Simla site.

Tobago, 42 km north-east of Trinidad and 295 km^2 in area, supports a sub-set of Trinidad's hummingbirds, bird-visited plants and habitats. The study site was located in the only extensive association of second-growth vegetation, which closely resembles the Arima Valley vegetation on Trinidad, at 11°14′N and 60°42′W, and at 155–230 m altitude.

Trinidad was treated as 'mainland' in this study because of its large size and habitat diversity relative to Tobago, and the ease with which birds migrate between Trinidad and the continent (ffrench 1973). A similar approach, treating a large island as 'mainland' relative to a smaller one, was used by Diamond (1970 a,b) and Terborgh & Faaborg (1973).

Plants

Trinidad and Tobago have in common several species of plants which are adapted for pollination by hummingbirds. These fall into one of two classes as defined by Feinsinger

& Colwell (1978). There are plants with specialized flowers, which secrete copious nectar and exclude all but a few hummingbird species by means of a long enclosed corolla; these species are called 'rich' because of the reward they offer. Other species have generalized flowers which secrete considerably less nectar and exclude few if any hummingbird species; these species are called 'moderate' (Feinsinger & Colwell 1978). For this study we chose one typical species from each category, both of which are relatively widespread on both islands (Fig. 1).

*Justicia secunda** Vahl (Acanthaceae), a herb with generalized 'moderate' flowers, produces tiny ($<0{\cdot}5$ mm long) wind-dispersed seeds, and colonizes disturbed sites characterized by intermittent shading and moist soils. Its flowering peak is November–February, but at both the Simla and Tobago sites (*Justicia* does not occur at the Waller site) there is never a month when no plants are in flower. Clumps containing more than seventy open flowers often support feeding territories of hummingbirds.

With one exception (see p. 751), features of the flower structure of *Justicia* do not differ between Trinidad and Tobago. Anthesis of the rose-red zygomorphic flowers occurs at dawn, when the lower lip drops open from a hinge point about 1·1–1·8 cm from the nectary. Flowers fall off during the afternoon of the same day. Hummingbirds can easily insert their heads to the hinge if necessary; hence, although the entire flower is 2·8–3·5 cm long, the effective corolla length is only about 1·4 cm (Fig. 1(a)). Anthers and stigma are separate from each other and positioned dorsally in the hood, and often contact the crown of a shorter-billed hummingbird or the forehead of a longer-billed one.

Mandevilla hirsuta (A. Rich) K. Schum. (Apocynaceae) is a vine which climbs over second-growth shrubs at all three study sites. It has specialized 'rich' flowers. Within a population, flowering is spread evenly throughout the year; there is no true peak. The vines are almost never clumped, and no vine produces more than five or six flowers per day; hence, flower density is insufficient to attract territorial hummingbirds.

Mandevilla has wind-dispersed seeds which may take at least a year to reach maturity. Inflorescences produce an average of one flower every 2 days although occasionally flowers are produced on successive days, or only at 3- or 4-day intervals. Bud scars show that individual inflorescences may produce as many as 102 flowers over their lifetime. Seeds are carried within follicles. Follicle-set is easily discernible, as even dehisced follicles stay attached to the inflorescence. The yellow-and-red actinomorphic flowers open at dawn, secrete nectar during the afternoon and close at dusk; they wither

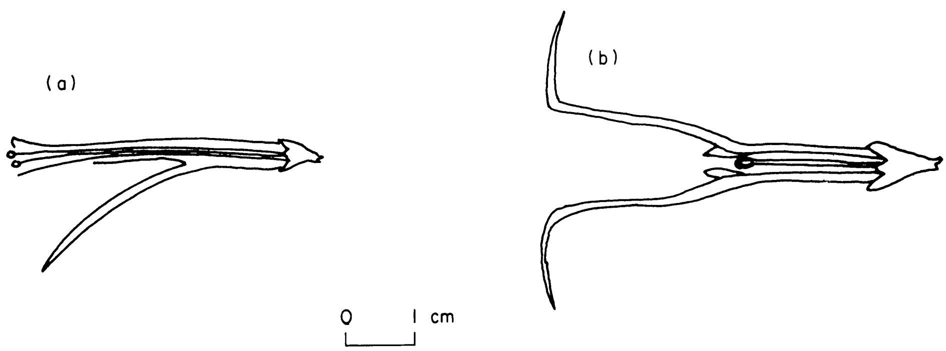

FIG. 1. Cross-sections of open flowers of (a) *Justicia secunda* and (b) *Mandevilla hirsuta*.

* Plants are referred to hereafter by their generic name, for convenience.

overnight. Anthers are appressed against one another and form a tight ring at the top of the corolla, beyond which a visitor's body cannot penetrate; the effective corolla length is 4·1 cm (Fig. 1(b)). The stigma is directly under the anthers and apparently in contact with their bases. Four flowers from which pollinators were excluded by bagging failed to set follicles, which suggests that flowers are not self-fertilizing.

Birds

Of the thirteen species of hummingbirds encountered on the study plots, nine visited either *Justicia*, or *Mandevilla*, or both. These nine species belong to two subfamilies within the family Trochilidae: the Phaethorninae and the Trochilinae. The Phaethorninae, called 'hermit hummingbirds', are typically dull-plumaged, have long curved bills, and travel widely in search of food. Such long-distance travel, which often follows precise routes, is usually called 'traplining'. Traplining by hermit hummingbirds often follows routes which include flowers secreting copious nectar, the 'rich' flowers mentioned above (Stiles 1975; Feinsinger & Colwell 1978). Three of the nine species considered here are hermits: *Glaucis hirsuta*, *Phaethornis guy* and *P. longuemareus*. The first two species are consistent 'trapliners', feeding primarily on the scattered 'rich' flowers of species such as *Mandevilla hirsuta*, whereas the considerably smaller *Phaethornis longuemareus* often forages among 'moderate' less nectar-rich flowers of species such as *Justicia secunda* as well as among 'rich' flowers when the latter are available.

The other subfamily, Trochilinae, includes hummingbird species with a variety of appearances and behaviours. Most species have bright plumage in either the male or in both sexes. Typically, the Trochilinae have straight bills. Their foraging can include the traplining of 'rich' flowers in a similar way to the Phaethorninae; traplining of dispersed, 'moderate', less nectar-rich flowers; movement within territories around dense clumps of flowers; or simply unpatterned movement between 'moderate' flowers of many plant species (Stiles 1975; Feinsinger & Colwell 1978). Six of the nine species to be considered here are in the Trochilinae. *Heliomaster longirostris* is strictly a trapliner of 'rich' flowers which secrete copious nectar; *Anthracothorax nigricollis* also feeds on some 'rich' flowers, occasionally in a regular pattern, but intersperses these visits with visits to many 'moderate' flowers; *Chrysolampis mosquitus*, *Chlorestes notatus*, *Amazilia chionopectus* and *A. tobaci* often act as generalists, feeding on 'moderate' flowers of many species; and *Amazilia tobaci* (and sometimes also *Chrysolampis*) sets up territories in especially dense patches of flowers.

FIELD PROCEDURES

Transects

Transects were established in areas that represented the largest associations of second-growth vegetation available to hummingbirds and bird-visited plants in northern Trinidad and Tobago. The most detailed comparisons were carried out between the hilly Simla site on Trinidad and the Tobago site. When choosing the two areas, we took care to select sites that were comparable in altitude, terrain, climate and other physical features. At Simla (Trinidad) and on Tobago the transects were 20 m wide and in segments whose total length added up to 1000 m; the lowland Waller site, on Trinidad, consisted of transects 20 m wide and 300 m long. This last site allowed comparisons to be made of plant–bird interactions in lowland savanna-like vegetation (Waller) with a hilly area (Simla).

Within these transects, plant–hummingbird interactions were studied for 13 months.

Nectar secretion

In both *Mandevilla* and *Justicia* nectar production was measured in February 1978, when both species were in full flower on both islands. Plants whose nectar production was to be compared were growing in similar physical situations on both islands. Flowers to be measured were covered by muslin bags, impenetrable to all insects and birds, the night before they were to open.

Nectar was extracted with fine glass tubes of known diameter. The volume of nectar could therefore be determined by measuring the length of the tube it occupied. Concentration of sugar in freshly collected nectar was determined with a refractometer which indicated percentage sucrose as g of solute per 100 g of nectar solution. This is often called the concentration on a 'weight per total weight' basis.

Flower visitors

Observation of frequencies of visits to flowers of each plant species on each island were made for every month when flowers occurred on our study plots (except at the lowland site on Trinidad), from February 1977 to February 1978. In some months two or more observations of a particular plant species were made. During months when some *Justicia* flowers were sufficiently clumped to support *Amazilia tobaci* or (on Tobago) *Chrysolampis mosquitus* territories, data were collected separately for these clumps. Observation periods lasted for the first 6 daylight hours, except when two or more bird species consistently visited the observed flowers, in which case the observation period was lengthened to 12 h in case there were temporal differences in visitors. The proportion of all visits which occurred in the afternoon on 12-h observation days was used to correct the results from 6-h observation days, in order to obtain comparable values for visits per flower per day. Observation procedures followed those used previously (Feinsinger 1976): each bird visiting the observed flowers was identified to species, sex if possible, and individual if marked, and the number of flowers probed was recorded. Foraging patterns of birds before and after the quantified visit were noted qualitatively, to provide estimates of fidelity.

Birds were also caught in mist-nets in order to mark them and measure them. The nets were set up in the vicinity of flowering plants. The shape and length of the bill of hummingbirds can be critical in determining which species of bird can feed on flowers of given length and shape (Linhart 1973; Stiles 1975; Feinsinger & Colwell 1978); results of these measurements are presented in Table 1. The effectiveness of the various species of bird as pollen-dispersers was also checked by collecting the pollen load from captured birds using clear plastic tape, and checking its identity.

Pollen dispersal studies

Pollen dispersal was investigated in both species during February 1978.

Pollen movement was traced with 'Day-Glo' fluorescent powders, following the methods used by Linhart (1973) with dyes and Stockhouse (1976). A single grain of the fluorescent powder is visible under long-wave ultraviolet light, yet it is small enough to adhere to a single pollen grain. The powder is insoluble, so humidity changes or even light rains do not affect its dispersal or visibility appreciably.

A different colour of powder was used for each plant species and (on Trinidad) for the separate clumps of *Justicia*; colours were changed on successive days to minimize the chance of contamination. In both species pollen was marked at dawn (05.15–06.00 hours), before hummingbirds had begun to forage and as soon after anthesis as possible. We used cotton-tipped swabs, dipping the tip into the powder and marking anthers only, as carefully as possible. Three to eight flowers were marked at the centre of a designated area, all within 1 m of each other. In late afternoon (16.00–18.00 hours) all open flowers were collected at pre-selected distances from the marking location (see below for sample sizes). Each flower collected was taken back to the laboratory, kept upright in a separate hole in a piece of styrofoam contained within a box, to ensure that flowers did not contaminate one another. Flowers were examined under long-wave ultraviolet light in the laboratory, and presence or absence of fluorescent powder was recorded for each. When powder was present, its location (corolla, anthers, stigma) was noted. Given that powder and pollen disperse in identical fashion, these results permitted us to differentiate between three types of pollen dispersal:—

(i) *Total* pollen dispersal: flowers with dye on any flower part.

(ii) *Potentially-effective* pollen dispersal: flowers with dye on anther or stigma or both; we believed that pollen deposited on the anthers of another flower might still be picked up and ultimately deposited on a stigma.

(iii) *Truly-effective dispersal*: flowers with dye on the stigma or stigma and anthers. This was recorded in *Justicia*, where the stigma is separated from the anthers, but not in *Mandevilla*, where the stigma is placed below the anthers and is in contact with them.

Anthers were marked with powder on successive days, as follows:— Trinidad, hilly site: *Justicia*, high density of flowers, 3 days; *Justicia*, low density of flowers, 4 days; *Mandevilla*, 5 days. Tobago: *Justicia*, low density of flowers, 4 days; *Mandevilla*, 3 days. Results are presented as the total of all observations.

Justicia. Dispersal was studied in a high-density and a low-density flower array in the hilly site on Trinidad, and in a relatively low-density flower array on Tobago (at the time of this study, high-density arrays on Tobago had been cut during land-clearing operations). The high-density clump on Trinidad contained > 100 open flowers within 30 m^2, and was defended by a territorial *Amazilia tobaci*. Precisely-equivalent low-density arrays could not be found on the two islands. On Trinidad, the low-density area where most of the dispersal of marked pollen took place consisted of a roadside strip 20 m long and 2 m wide, with about thirty open flowers dispersed evenly throughout the 40-m^2 area. On Tobago, a similar roadside strip was found, but it supported a clump of *Justicia* with thirty open flowers per day and several scattered flowers, giving a total density of about fifty flowers per 40 m^2. Beyond each transect, on both Trinidad and Tobago, there were flowers along the roadside for at least 100 m in either direction, at densities of *c*. ten flowers per 100 m^2. Neither site was defended by a territorial hummingbird. The total numbers of flowers collected per sampling distance and used to construct Fig. 2 varied from 17 to 67 (mean = 45) at distances within 30 m of the centre of origin, and from 39 to 111 (mean = 85) beyond that point.

Mandevilla. On each island a 1-ha area was studied, containing approximately twenty flowering vines which produced a total of fifteen to thirty flowers daily. The numbers of flowers collected per sampling distance and used to construct Fig. 3 varied from 9 to 23 (mean = 14).

In *Mandevilla* the overall effectiveness of pollinators could be measured by expressing the number of follicles attached per inflorescence as a proportion of the number of flowers produced on the inflorescence; flowers which had not produced a follicle fell off the day after anthesis, leaving a pedicel scar. To determine if follicles ever aborted after being set (Willson & Rathcke 1974), fourteen newly-set follicles on four different inflorescences were marked in early February and re-examined on March 1. No such measures of seed-set were possible in *Justicia*.

RESULTS

Nectar secretion

In *Justicia* there is a striking contrast in nectar secretion between the Trinidad and Tobago populations. Flowers on Trinidad secreted a daily average of 10·4 μl of nectar each ($n = 40$, $s^2 = 17{\cdot}3$), whereas flowers on Tobago secreted 27·3 μl each ($n = 30$, $s^2 = 58{\cdot}6$; $t = 11{\cdot}8$, $P < 0{\cdot}001$). Sugar concentration in freshly-secreted nectar was also lower on Trinidad than on Tobago (20·6% sucrose-equivalence by weight per total weight, $n = 5$; and 23·4%, $n = 10$, respectively), but the difference was not significant ($t = 2{\cdot}11$, $0{\cdot}10 > P > 0{\cdot}05$).

Mandevilla flowers on Trinidad produced a daily average of 90·1 μl nectar each ($n = 11$; range 22·9–145·7 μl, $s^2 = 1480$); on Tobago, flowers secreted 38·8 μl each. Sugar concentration averaged 31·0% on Trinidad and 40·7% on Tobago.

Flower visitors

In both *Justicia* and *Mandevilla*, hummingbirds were the primary visitors to flowers. The only other birds seen to visit these species were the nectar-feeding Bananaquits (*Coereba flaveola luteola* (Cab.)), which pierce the corolla at the base to reach the nectar; bananaquits visited *Justicia* on Trinidad and Tobago and *Mandevilla* on Tobago, but were never observed to contact the reproductive parts of the flowers. Occasionally, wasps, bees and hesperiid butterflies also visited *Justicia*, but these never contacted the reproductive parts of the flowers. Certain hesperiid butterflies with long proboscides also visited *Mandevilla*; when feeding on *Mandevilla*, they carefully probed through the anthers and into the corolla. They may have carried pollen between flowers, but in very small quantities.

The nine species of hummingbirds which visited *Justicia*, *Mandevilla*, or both are listed in Table 1, which also summarizes their bill morphology and potential pollination-effectiveness with respect to *Justicia* and *Mandevilla*. All hermit hummingbirds, as well as *Heliomaster longirostris*, visited *Mandevilla* flowers in 'traplining' fashion; *Anthracothorax nigricollis* also acted in 'traplining' fashion when visiting *Mandevilla*, although more often it visited less nectar-rich 'moderate' flowers. At Simla, *Heliomaster longirostris* specialized on flowers of *Mandevilla* and one other plant species. The other four species of hummingbird, however, tended to visit flowers of more than one plant species during a given foraging bout, except that *Phaethornis longuemareus* often visited several *Mandevilla* vines or *Justicia* patches in sequence. The four 'generalist' species listed in Table 1 were unable to feed at *Mandevilla* because of their short bills; they, as well as *Phaethornis longuemareus* and *Glaucis hirsuta*, visited flowers of *Justicia* only. *Amazilia tobaci*, and sometimes also *Chrysolampis*, set up feeding territories at dense patches of *Justicia*; individuals of both these species displayed broader diets (in terms of flower species visited) on Tobago than on Trinidad (L. A. Swarm & P. Feinsinger, unpublished).

Table 2 summarizes the records of frequency of visits by individual bird species to the plants concerned. *Justicia* at any one site was visited frequently by three species, of which one was always *Amazilia tobaci*. There was a contrast between Trinidad, where many

TABLE 1. Characteristics of the hummingbird species feeding at *Justicia secunda* and *Mandevilla hirsuta* flowers on Trinidad and Tobago; the designations 'trapliner' and 'non-trapliner' (defined on p. 748) apply to these plant species only, and *Phaethornis longuemareus* at least acts more like a trapliner at *Mandevilla*, more like a generalist at *Justicia*

	Place and abundance							
	Trinidad		Tobago					
	Simla (hilly)	Waller (lowland)		†Bill length (mm)	Bill shape	‡Fidelity to *Mandevilla*	‡Fidelity to *Justicia*	Frequency of pollination of *Justicia*§
Trapliners:								
Phaethorninae (hermits)								
Glaucis hirsuta Lawrence	C*	R*	C	32–39	Curved	Low	Low	High
Phaethornis guy Lesson	R	–	–	42–44	Curved	Low	–	–
Phaethornis longuemareus Lesson	C	C	–	26–29	Curved	Moderate	Moderate	High
Trochilinae								
Anthracothorax nigricollis Vieillot	F*	F	F	27–30	Slightly curved	Low	–	–
Heliomaster longirostris Audebert & Vieillot	F	–	–	38	Straight	High	–	–
Non-trapliners:								
Trochilinae								
Amazilia chionopectus Gould	F	F	–	22–26	Straight	–	Low	Moderate
Amazilia tobaci Lesson	C	R	C	21–25	Straight	–	Low	Low
Chlorestes notatus C. Reichenbach	F	R	–	20–22	Straight	–	Low	Moderate
Chrysolampis mosquitus L.	R	C	C	18–23	Straight	–	Low	Low

* C = common most or all of the year; F = frequent, or noted consistently most or all of the year; R = rare or noted occasionally; – = not noted.

† Samples of at least ten mist-netted individuals, except *Heliomaster* ($n = 1$); length measured is total culmen length from base at skull to tip.

‡ Qualitative judgement of fidelity, based on observations at plants and on pollen loads from netted birds.

§ Qualitative judgement: high = contact every time a flower was probed; moderate = contact on majority of flower probes; low = contact on half of flower probes, or fewer.

TABLE 2. Frequency of visits (%) of individual species of hummingbirds to flowers of *Justicia secunda* and *Mandevilla hirsuta*, based on 13 months' results; the values in parentheses are the number of observation-days, out of the total number of observations, when the particular bird species was observed to feed at flowers

	Justicia			*Mandevilla*		
Place	Trinidad, hilly		Tobago	Trinidad		Tobago
Flower density or site	High	Low	Low	Lowland	Hilly	
Days observed	6	19	14	5	12	9
Trapliners:						
Phaethorninae (hermits)						
Glaucis hirsuta	0·1% (1)	1·9% (2)	16·8% (6)	–	–	29·0% (4)
Phaethornis guy	–	–	–	–	1·6% (1)	–
Phaethornis longuemareus	28·4% (4)	15·4% (8)	–	80·0% (2)	80·0% (6)	–
Trochilinae						
Anthracothorax nigricollis	–	–	–	20·0% (1)	2·4% (1)	71·0% (2)
Heliomaster longirostris	–	–	–	–	16·0% (5)	–
Non-trapliners:						
Trochilinae						
Amazilia chionopectus	–	24·1% (1)	–	–	–	–
Amazilia tobaci	46·8% (6)	48·9% (17)	50·0% (9)	–	–	–
Chlorestes notatus	24·7% (3)	7·2% (4)	–	–	–	–
Chrysolampis mosquitus	–	4·5% (3)	33·2% (3)	–	–	–

other visits were made by consistent pollinators which rarely missed the reproductive parts (*Amazilia chionopectus*, *Chlorestes notatus*, *Phaethornis longuemareus*, *Glaucis hirsuta*), and Tobago, where most visits were made by *Chrysolampis* and *Amazilia tobaci*. These Tobago birds often missed the reproductive parts when probing flowers.

Mandevilla at any one site was visited primarily by one or two species of hummingbird, whose identity varied from site to site. With one exception, on any one day the flowers observed were visited by a single species only. At the hilly site on Trinidad, where *Mandevilla* received the highest frequency of effective visits, the highly specific *Heliomaster longirostris* visited the vines on five of twelve observation days, the less specific *Phaethornis longuemareus* on six of twelve observation days, and on only one day did observed flowers receive no visits at all. At the lowland site on Trinidad, where *Heliomaster longirostris* did not occur, *Phaethornis longuemareus* made occasional visits to *Mandevilla* flowers, but only in the midst of its more frequent visits to flowers of other abundant plant species. On Tobago, visits to *Mandevilla* flowers were primarily by *Anthracothorax nigricollis* and *Glaucis hirsuta*, neither of which was particularly faithful to *Mandevilla* (see Table 1).

Table 3 is a summary of the frequency of visits by all hummingbird species to *Justicia* and *Mandevilla*. Differences between sites and between flower densities are usually not statistically significant, because of large day-to-day variation, but may nevertheless be

TABLE 3. Total frequency of visits by all hummingbird species to flowers of *Justicia secunda* and *Mandevilla hirsuta*, based on 13 months' results; the Mann–Whitney *U*-test is of the null hypothesis that there are no differences in number of visits per flower per day between study sites shown in adjacent columns

	Justicia			*Mandevilla*		
Place	Trinidad, hilly		Tobago	Trinidad		Tobago
Flower density or site	High	Low	Low	Lowland	Hilly	
Days observed	6	19	14	5	12	9
Days with visits by hummingbirds*	6	18	12	3	11	5
Visits per flower per day:						
Mean, all days	8·20	5·09	3·23	1·73	7·82	3·56
Range	1·8–20·5	0–13·3	0–8·6	0–4·0	0–24·0	0–11·0
S.E. of mean,	3·57	1·00	0·68	0·93	2·25	1·57
Mann–Whitney *U*-test	$P > 0{\cdot}05$	$P > 0{\cdot}05$		$P > 0{\cdot}05$	$P > 0{\cdot}05$	

* On some days the flowers observed received no visits from hummingbirds.

biologically significant. The observed *Justicia* flowers were visited by birds on almost every day. At the hilly site on Trinidad, flowers at high density were visited more often than flowers at low density. At the hilly site on Trinidad *Mandevilla* flowers were visited very consistently but at the lowland site and on Tobago, flowers were visited much more sporadically. On some days they were not visited at all, and on other days they were visited only by hesperiid butterflies.

Pollen dispersal

Figure 2 gives the results of the marked-pollen dispersal studies on *Justicia*. A distinction is made between *total* dispersal and *potentially-effective* pollen dispersal. On Trinidad, pollen was dispersed to greater distances from flowers growing at low density than from flowers growing at high density. Patterns of pollen dispersal on Tobago were similar to those obtained at the Trinidad high-density population. Patterns of *truly-effective* dispersal are presented in Table 4. These results show that over the 30-m distance

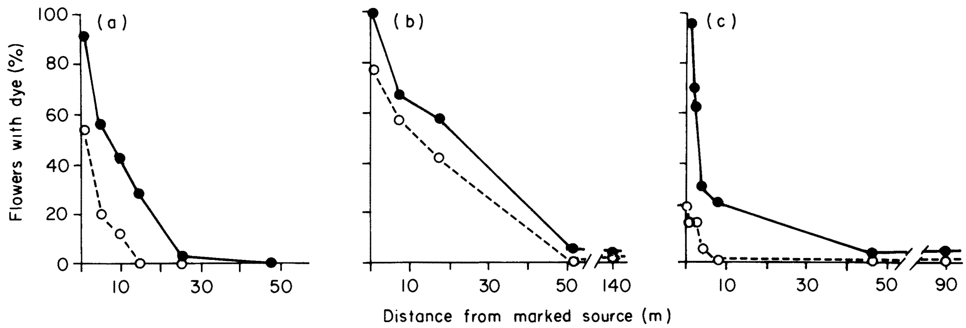

FIG. 2. Pollen dispersal from *Justicia secunda*: proportion of flowers carrying dye at the end of the day, at various distances from those marked at dawn. Filled circles = total dispersal (dye on any flower part); unfilled circles = potentially-effective dispersal (dye on anthers or stigma). (a) Trinidad, hilly site with high flower density; (b) Trinidad, hilly site with low flower density; (c) Tobago, low flower density.

where most dispersal occurred there were significant differences between *Justicia* populations. On Trinidad, the site with high density of flowers was defended by a territorial *Amazilia tobaci* which prevented *Phaethornis longuemareus* and *Chlorestes notatus* from feeding there regularly. These two species come into contact with the reproductive parts of *Justicia* repeatedly during their visits and are consistent pollinators. In the low-density area, there was freer access to flowers by a greater diversity of bird species, and hence a much greater truly-effective dispersal.

A substantially greater between-island contrast occurred in *Mandevilla* (Fig. 3). Total dispersal on Trinidad greatly exceeded that on Tobago; on one of the five days of the Trinidad study all flowers in the 1-ha study area had labelled pollen. Potentially-effective dispersal occurred consistently on Trinidad (21% of the flowers within the 1-ha area carried labelled pollen), but only once on Tobago (1%). A comparison of Figs 2 and 3 shows that total pollen dispersal on Trinidad was much higher for *Mandevilla* than for *Justicia* at any distance up to 30 m.

TABLE 4. 'Truly-effective' pollen dispersal of *Justicia secunda* at various distances from a marked source (i.e. where pollen was marked with dye early in the morning) at each of the three sites; n = total number of flowers examined, S = number of flowers (proportion given as %, in parentheses) carrying dye on the stigmas at the end of the day; for results from 0–2 m and 3–10 m, differences in proportions between sites are tested for statistical significance by a G-test, using Chi-square tables (Sokal & Rohlf 1969), against the null hypothesis that there are no differences between sites; results for 11–30 m are insufficient for such a test

	Distance from origin					
	0–2 m		3–10 m		11–30 m	
	n	S	n	S	n	S
Trinidad, hilly site:						
High density of flowers	36	4 (11%)	127	5 (4%)	65	0 (0%)
Low density of flowers	17	11 (65%)	64	22 (34%)	50	1 (2%)
Tobago:						
Low density of flowers	132	3 (2%)	89	0 (0%)	33	0 (0%)
G-value	42·2		53·1			
Statistical significance	$P < 0{\cdot}001$		$P < 0{\cdot}001$			

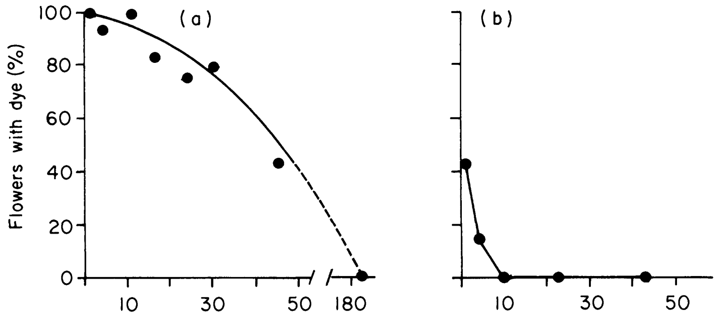

FIG. 3. Pollen dispersal from *Mandevilla hirsuta*; proportion of flowers bearing dye on any interior part at the end of the day, at various distances from flowers marked at dawn. (a) Hilly site, Trinidad; (b) Tobago.

TABLE 5. Follicle-set in inflorescences of *Mandevilla hirsuta*; only mature inflorescences no longer producing flowers were counted; the null hypothesis tested by Chi-square is that there are no differences between sites

	Trinidad				Tobago
	Lowland		Hilly		
Number of plants investigated	10		22		16
Number of follicles produced/total number of flowers produced	27/666		74/1340		32/1229
Chi-square		2·01, N.S.		13·8, $P < 0.001$	
Number of inflorescences with one or more follicles/total number of inflorescences	23/47		49/61		30/73
Chi-square		11·8, $P < 0.002$		21·1, $P < 0.001$	

The Trinidad/Tobago contrast in pollen dispersal of *Mandevilla* is reflected in the data for follicle-set (Table 5), which was highest at the hilly site on Trinidad, intermediate at the lowland site, and lowest on Tobago. Once set, follicles did not abort; of the fourteen newly-formed follicles marked at the hilly site in early February, all had developed into nearly mature follicles by 1 March.

DISCUSSION

'Generalist' and 'specialist' are terms most often applied to foraging animals (MacArthur 1972; Pianka 1978). In the context of pollination, generalist and specialist plants can also be distinguished. Among hummingbird-pollinated plants in Trinidad, *Justicia* can be considered a generalist. As shown in Tables 1 and 2, six of the thirteen hummingbird species seen on the study sites visited *Justicia*; of the thirteen plant species commonly pollinated by hummingbirds at our study sites, only two were visited by a greater variety of hummingbirds. Furthermore, *Justicia* flowers were visited by up to three species daily on Tobago, and up to five species daily on Trinidad (P. Feinsinger, unpublished). By contrast, *Mandevilla* is a specialist: Tables 1 and 2 show that, of the hummingbirds recorded, only one provided the great majority (over 70%) of visits to *Mandevilla* at any one site. Of the thirteen common bird-pollinated plant species studied, two at most were visited in a more exclusive fashion than was *Mandevilla*. Furthermore, on any one day *Mandevilla* was rarely seen to be visited by more than one hummingbird species, either on Trinidad or Tobago (P. Feinsinger, unpublished).

A generalist plant such as *Justicia* relies on pollinators that also visit many other plant species, and the opportunistic birds that visit *Justicia* flowers as one of many food choices rarely travel far in search of *Justicia* alone. As a result, pollen dispersal shows the pattern illustrated in Fig. 2, where the curves have either a normal distribution, or a 'leptokurtic' distribution characterized by a very high peak of dispersal near the source, a rapid reduction in dispersal within a few metres, and a small amount of pollen dispersed over long distances. Such leptokurtic patterns are typical of pollen-dispersal curves (Levin & Kerster 1974). In contrast, a specialist plant such as *Mandevilla*, when growing in a continental site, will have reliable pollination despite the sparse distribution of its flowers. At the hilly site on Trinidad *Mandevilla* has one pollinator (*Heliomaster longirostris*) which rarely visits any other plant species, and another pollinator (*Phaethornis longuemareus*) which is fairly constant. As a result, both bird species travel widely in search of *Mandevilla*, and produce a highly unusual pattern of pollen dispersal (Fig. 3(a)). This pattern resembles a platykurtic distribution: it shows relatively high frequency of pollen at middle distances. Similar patterns can be found in some species of *Heliconia*, also visited by hummingbirds (Linhart 1973). Such results are likely to be obtained whenever specialist plants are pollinated by obligate pollinators. If such pollen dispersal is a reflection of gene flow, then these results will necessitate modifications in our estimates of genetically-effective population sizes (often called 'neighbourhoods') of plants. These estimates are usually based on assumptions that gene flow follows a predominantly leptokurtic pattern (Levin & Kerster 1974).

Perturbations which disrupt normal plant–pollinator interactions can be expected to have more severe effects upon very specialized interrelationships than upon generalized ones. For example, specialized animal foragers are more susceptible to environmental variation (cf. MacArthur 1972). Plants which depend upon specific insects for pollination have greatly reduced seed-set if their pollinators are in low abundance, and such reduction can affect their geographic distribution (Janzen 1974; Cruden *et al.* 1976). In this context, *Mandevilla* is more susceptible to site-to-site differences than is *Justicia*. At the lowland site on Trinidad, the most constant pollinator of *Mandevilla* (*Heliomaster longirostris*) is absent, and its other chief pollinator has consistent access to alternative nectar sources where the somewhat shorter corollas must be easier for this bird to penetrate (see Table 1). Furthermore, *Mandevilla* flowers are visited much less frequently at this site (Tables 2 and 3). These are factors which contribute to considerably lower follicle-set here than at the hilly site (Table 5). On Tobago, both *Heliomaster longirostris* and *Phaethornis longuemareus* are absent, and *Mandevilla* receives only sporadic attention from *Glaucis hirsuta* and *Anthracothorax nigricollis*, both of which mainly visit other plants. *Heliomaster longirostris*, which is rare on Trinidad (where it feeds predominantly on *Mandevilla* during most of the year), may be absent from Tobago simply because the island does not hold a large enough number of the sparsely-dispersed *Mandevilla* flowers to support a viable population. Because of the large variation in frequency of visits to flowers at any one site, the between-island difference is not statistically significant (Table 3). Nevertheless, it is certainly biologically significant; not only are there many days on Tobago when no birds at all visit *Mandevilla* (Table 3), but also the pollination-effectiveness of the visits by *Glaucis hirsuta* and *Anthracothorax nigricollis* on Tobago is much lower than of those by Trinidad birds (Tables 1 and 2), resulting in ineffective pollen dispersal (Fig. 3) and significantly lower follicle-set (Table 5).

Biogeographic differences in number and frequency of pollinators (summarized in Tables 1–3) have a somewhat lower impact on *Justicia*. Its corolla is readily penetrable by most hummingbirds, as the list of visitors (Tables 1 and 2) shows, and by some insects. Even isolated islands in the Neotropics usually support at least one short-billed hummingbird species (Feinsinger & Colwell 1978), and a 'generalist' plant such as *Justicia* can expect visitors nearly anywhere. Total pollen dispersal in Trinidad (Fig. 2) is not very different from that in Tobago. Nevertheless, *Justicia* on Tobago illustrates two phenomena.

Firstly, the relatively open corolla does not specify precisely the direction of approach and entry of the flower by a hummingbird's bill and head, in contrast to *Mandevilla*. On Trinidad, four species (*Glaucis hirsuta*, *Phaethornis longuemareus*, *Chlorestes notatus* and *Amazilia chionopectus*) normally enter the corolla head-on, frequently contacting the reproductive parts. This is particularly true in areas with a low density of flowers. On Tobago however, except for *Glaucis hirsuta*, these bird species are absent. *Amazilia tobaci* and especially the short-billed *Chrysolampis mosquitus*, which make most of the visits on Tobago, often enter the corolla at an angle from the side and fail to contact the reproductive parts; pollen which had been picked up during a chance effective visit may be deposited on the corolla. The result is a substantial between-island contrast in potentially-effective pollen dispersal (Fig. 2), and an equally dramatic difference in pollen deposition on stigmas (Table 4).

Secondly, there are reduced opportunities for hummingbirds on Tobago to migrate between communities because of the small size of the island and a smaller number of suitable habitats. Therefore, the adjustment between numbers of birds and nectar supplies is less precise than on Trinidad, where birds engage in extensive patch-to-patch migration (Feinsinger 1979; P. Feinsinger, L. A. Swarm & J. A. Wolfe, unpublished). At certain times of the year, flowers are abundant relative to birds, and competition among plants for constant pollinators is intense; at other times flowers are very scarce, and birds are forced to forage among comparatively unrewarding flowers adapted for insect pollination. Not only populations but even individual birds on Tobago have broader diets than do members of the same species on Trinidad (L. A. Swarm & P. Feinsinger, unpublished). Therefore, pollinators are rarely constant to plants, particularly during times of flower abundance. The higher nectar rewards offered by *Justicia* flowers on Tobago relative to those on Trinidad may be the evolutionary result (Heinrich & Raven 1972; Heinrich 1975). Despite the higher rewards, plants of *Justicia* on Tobago receive less reliable pollination from their opportunistic visitors than do plants on Trinidad (Tables 2 and 3; Fig. 2), apparently because of the preponderance of the short-billed *Amazilia tobaci* and *Chrysolampis mosquitus*. Total pollen dispersal on Tobago resembles pollen dispersal in the area of high flower density on Trinidad (Fig. 2). This may result from similarities in the overall flower densities, even though *Justicia* on Tobago was not clumped sufficiently to support a territorial hummingbird; on Trinidad, the high-density area defended by a territorial *Amazilia tobaci* had a daily nectar yield of 1040 μl (i.e. 100 flowers $\times$ 10·4 μl) and the low-density area a yield of 312 μl per day (i.e. thirty flowers $\times$ 10·4 μl), whereas the Tobago site yielded about 1365 μl per day (fifty flowers $\times$ 27·3 μl).

Justicia illustrates two additional points relevant to pollination biology. Firstly, on Trinidad, pollen is dispersed to much greater distances from scattered flowers than from clumped flowers (Fig. 2). This result, which agrees with findings for other hummingbird-pollinated species (Linhart 1973) and insect-pollinated species (Levin & Kerster 1974), is apparently due to territorial *Amazilia tobaci*, which restricts visits by intruders and forages primarily among the defended flowers. Secondly, the notable contrast between total and truly-effective pollen dispersal (Fig. 2, Table 4) suggests that tabulations of flight distances or even descriptions of the dispersal of labelled pollen do not necessarily indicate the potential for cross-fertilization: the precise location of where the dye (or labelled pollen) landed must be noted. Furthermore, the high frequency (in our study) with which labelled pollen landed on the anthers, not the stigma, of a distant flower suggests the possibility of pollen 'leap-frogging' onto several flowers in succession, so that even those pollinators which made short flights could conceivably transfer quantities of pollen considerably longer distances over a period of time.

The results on pollen dispersal in both plant species suggest the following conclusion: there is an 'island effect' on the genetically-effective population (or 'neighbourhood') size in the plants studied. In both *Mandevilla* and *Justicia*, pollen disperses to greater distances on Trinidad than it does on Tobago; consequently, gene flow can be expected to be greater on Trinidad. Seeds of both species are wind-dispersed; although qualitatively stronger winds were noted on Tobago than at the Trinidad sites, it is doubtful whether there is a significant island-to-island contrast in seed-dispersal distances. Therefore, inter-island differences in neighbourhood sizes in both plant species will be determined primarily by differences in gene flow via pollen. These neighbourhoods will be smaller on Tobago than on Trinidad. This is particularly true for *Mandevilla*, which must have a strikingly large neighbourhood on Trinidad, but vanishingly small neighbourhoods on Tobago (definitions and examples are given in Falconer (1960) and Levin & Kerster (1974)). The evolutionary consequences of these contrasts have yet to be examined, but it is to be expected that when neighbourhood sizes are very small, as they are in *Mandevilla* on Tobago, then inbreeding and genetic drift will become important.

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