

ASPECTS OF THE POLLINATION BIOLOGY OF THREE *ERYTHRINA* SPECIES ON TRINIDAD AND TOBAGO¹

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ABSTRACT

Trinidad and Tobago support populations of three *Erythrina* species: *E. pallida*, *E. fusca*, and *E. poeppigiana*. We obtained data on visit frequencies of potential avian pollinators over two flowering seasons, as well as supplementary data on pollen loads, nectar secretion and availability, breeding systems, and extrafloral nectaries. These data show that *E. pallida* is pollinated exclusively by long-billed hummingbird species, whereas passerine birds are apparently more important than hummingbirds as pollen vectors of the large trees *E. poeppigiana* and *E. fusca*. Characteristics of flowers and nectar in the three species correlate with these contrasting modes of pollination. Inflorescences of all three species are protected from herbivores through extrafloral nectaries, which attract belligerent ants.

Trinidad and Tobago, politically in the West Indies but geographically and biologically an extension of South America, support populations of three *Erythrina* species. During a 14-month investigation of the ecology of nectar-feeding birds and bird-pollinated plants on these islands, we quantified frequencies of bird visits to flowers of each species and obtained supplemental data relevant to pollination biology. Below we present the results and attempt to integrate them into a comparative picture of the floral biology of these three species.

Tobago is smaller and biologically less diverse than Trinidad. Only 295 km² in area, Tobago is 42 km northeast of Trinidad, which is 4,540 km² in area and only 12 km from the South American mainland. Our Trinidad study sites (described below) supported 21 species of plants adapted for bird pollination, whereas on Tobago we found only 16 species (see also Beard, 1944, 1946). Trinidad contains 16 species of hummingbirds in total, Tobago only 6. The diversity of other bird species is also reduced on Tobago. Most of Tobago's biota, in fact, also occurs on Trinidad, so that we considered Trinidad as a "mainland" relative to Tobago.

Both islands hold the same assortment of *Erythrina* species. One is a recent import. *Erythrina poeppigiana* (Walpers) O. F. Cook was introduced from the lower slopes of the Venezuelan Andes in the 19th century (H. D. Adams, pers. comm.; B. A. Krukoff, pers. comm.). Planted as cacao shade on both islands, *E. poep-*

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pigiana now reproduces naturally and has become the most common large tree in disturbed habitats. A mature individual, usually aphyllous at flowering, may hold up to 15,000 orange red flowers (illustrated in Krukoff & Barneby, 1974) at one time; flowers apparently last one day only. During the flowering peak of this species (see below), extensive areas on both islands, as seen from the air, seem entirely orange red; indeed, the boundary between orange red and green regions at that time of year demarcates the extent of past human disturbance.

Erythrina fusca Louriero, apparently native to both islands (B. A. Krukoff, pers. comm.), has also been replanted extensively for cacao shade. Natural reproduction occurs in wet soils such as those in lowland swamps or along streams, in contrast to *E. poeppigiana*, which grows on well-drained soils. Yellow orange flowers of *E. fusca* (illustrated in Krukoff & Barneby, 1974) last two days; if fertilization does not occur, flowers fall off during the second day. A single tree, usually aphyllous when flowering, may hold several thousand flowers. The flag of a flower must spring back to expose anthers and stigma. Apparently this action may occur spontaneously on the second day of flower maturity, but often pressure from foraging birds springs open a flower.

Erythrina pallida Britton & Rose is also native to both islands (B. A. Krukoff, pers. comm.; Krukoff & Barneby, 1974), where it is a small second-growth tree occasionally replanted as an ornamental or a "living fencepost." The pale rose-pink flowers last two days after anthesis; unfertilized flowers fall off late in the second day. Anthers and stigma are contained within the tubular flag, which must be penetrated at the distal end to obtain nectar. There are rarely more than a few dozen open flowers on a tree at any one time; trees we saw were always aphyllous at flowering. In short, the three *Erythrina* species exhibit two distinctive biologies. The two large, abundant tree species produce many conspicuous flowers, whereas the shrubby, uncommon *E. pallida* produces small numbers of less conspicuous flowers. The implications of this contrast to pollination biology are explored below.

METHODS

STUDY SITES AND VISIT SCHEDULES

During January, 1977, we set up 1,000 m of 20-m-wide transects in successional vegetation on each island, Trinidad and Tobago. The vegetation studied varied little within or between islands; both sites were at around 200 m elevation and faced similar climatic regimens. Floras at both sites, which had a dry season lasting from late December through early June, were also similar. Each site contained trees of all three *Erythrina* species; locations of trees were mapped. From February 1977 through 1 March 1978 we spent the first half of each month on Trinidad, the second half on Tobago. Below we term each two-week session a "time block."

FLOWER CENSUSES

On the first day of each time block, we counted the number of flowers on each bird-visited plant along the transects.

OBSERVATIONS

Each time block we spent the first six daylight hours (if few or no birds appeared) or the full 12-hour day observing and quantifying bird visits to a representative tree of each *Erythrina* species in flower. If some trees of *E. poeppigiana* or *E. fusca* possessed so many flowers that visit patterns differed from patterns at less fecund trees, we observed a representative low-density tree and a representative high-density tree. The subjectively determined cut-off point was ca. 300 flowers (*E. fusca*) or ca. 3,000 flowers (*E. poeppigiana*). For each bird visit to an observed tree, the following data were recorded: number of flowers visited, cumulative time spent probing flowers, direction of ingress and egress, aggressive interactions, and (qualitatively) frequency of contact with reproductive organs of flowers. From the number of open flowers on each tree observed, we calculated the mean frequency of probes per flower per day. To convert morning-only values to full-day values, for a given *Erythrina* species on each island we first determined the ratio of morning flower-probes to total flower-probes counted on those days having 12-hour observations; we then used this ratio to adjust 6-hour data to 12-hour estimates. We repeated this method on data for three distinct bird groups (see below): hummingbirds, bananaquits (*Coereba flaveola*), and all other bird visitors. Although data for hummingbirds should be accurate, we found it impossible to time flower-probes of passerine birds, which often foraged in large flocks, and also found it difficult to count accurately the number of flower-probes by passerines. Therefore, our data for birds other than hummingbirds are underestimates, if anything, of visit frequencies; this conservative bias should be consistent.

It has been suggested that *Erythrina fusca* is bat-pollinated (Helvesen, cited in Raven, 1977). Therefore, during January and February, 1978, we spent two evenings, one on each island, watching for possible bat visitors to dense arrays of flowering *E. fusca*.

CONTROLLED POLLINATIONS

During February, 1978, we performed controlled pollinations on flowers of *Erythrina fusca* and *E. pallida* (there were no *E. poeppigiana* trees with accessible flowers). Pollinations occurred in early morning on days with no significant rain or wind. We handled anthers with forceps, which were cleansed with 95% ethanol between pollinations. Inflorescences were kept bagged before and after pollinations with three layers of cheesecloth (solid bags, for example Kraft bags or special "pollination bags," could not be used because temperature and humidity tended to rise inside them, causing all flowers to drop off). When necessary, cheesecloth bags were supported with sticks so as not to touch the flowers inside. Bags were so tightly closed that not even ants could enter (see below); on those occasions where by chance bags had opened at all, their flowers were not included in the data.

Only newly opened flowers in bagged inflorescences were used for pollen sources. Selfing was carried out with fresh pollen from the same flower: anthers were clipped off and one or more rubbed against the stigma until visible clumps

of pollen adhered. On Tobago, for *Erythrina pallida* we also used pollen from other flowers on the same tree; there was no differential effect. Cross-pollination was effected with freshly dehiscent anthers from a bagged flower on another tree. Distances between trees used for cross-pollination varied from 20 m to 1 km. Because so few *E. fusca* flowers were within working distance of the ground, we did not perform cross-pollinations; instead, to determine if any self-compatibility existed, we performed only self-pollinations. We could obtain *E. pallida* data on both islands, but *E. fusca* data on Tobago only.

NECTAR AVAILABILITY

During each time block of January and February, 1978, we sampled nectar availability (standing crop) throughout the day in trees of *Erythrina poeppigiana* and *E. fusca* accessible to foraging birds (except that we could locate no reachable *E. poeppigiana* on Trinidad during January, 1978). Every two hours, from dawn through dusk, we clipped entire branches from the canopy with a pole pruner. Branches were carefully lowered to the ground so that nectar did not spill from the flowers. Each sample contained ten flowers, for each of which we determined nectar volume (with calibrated microcapillary tubes) and sugar concentration in g sucrose equivalents/100 g solution (with a temperature-compensated American Optical hand refractometer). Nectar samples were spotted on filter paper, dried, and sent to I. Baker and H. G. Baker at the University of California, Berkeley, for chemical analysis.

NECTAR SECRETION

On 24 February 1978 we investigated nectar secretion in the few accessible *Erythrina fusca* and *E. pallida* flowers on Tobago. Because flowers last two days, on the evening of the 22nd we had bagged with cheesecloth several flowers due to open on the 23rd; these were kept bagged through the 23rd, and on the evening of that day additional flowers due to open on the 24th were also bagged. On the 24th, the volume and sugar concentration of accumulated nectar in each flower were measured every two hours beginning at dawn.

EXTRAFLORAL NECTARIES

Careful examination of *Erythrina* flowers revealed protuberances on the ventral lip of each calyx. Protuberances were especially marked in buds (see illustrations in Krukoff & Barneby, 1974). The presence of ants at these protuberances suggested that they might be extrafloral nectaries (Bentley, 1977); therefore, we made observations on behavior of ants at these "bumps," and on "bumps" on inflorescences that had been bagged for other studies described above.

RESULTS

FLOWERING PHENOLOGIES

Trinidad study plots contained 7 *Erythrina pallida*, 30 *E. poeppigiana*, and 5 *E. fusca* trees. Tobago plots contained 6 *E. pallida*, 15 *E. poeppigiana*, and

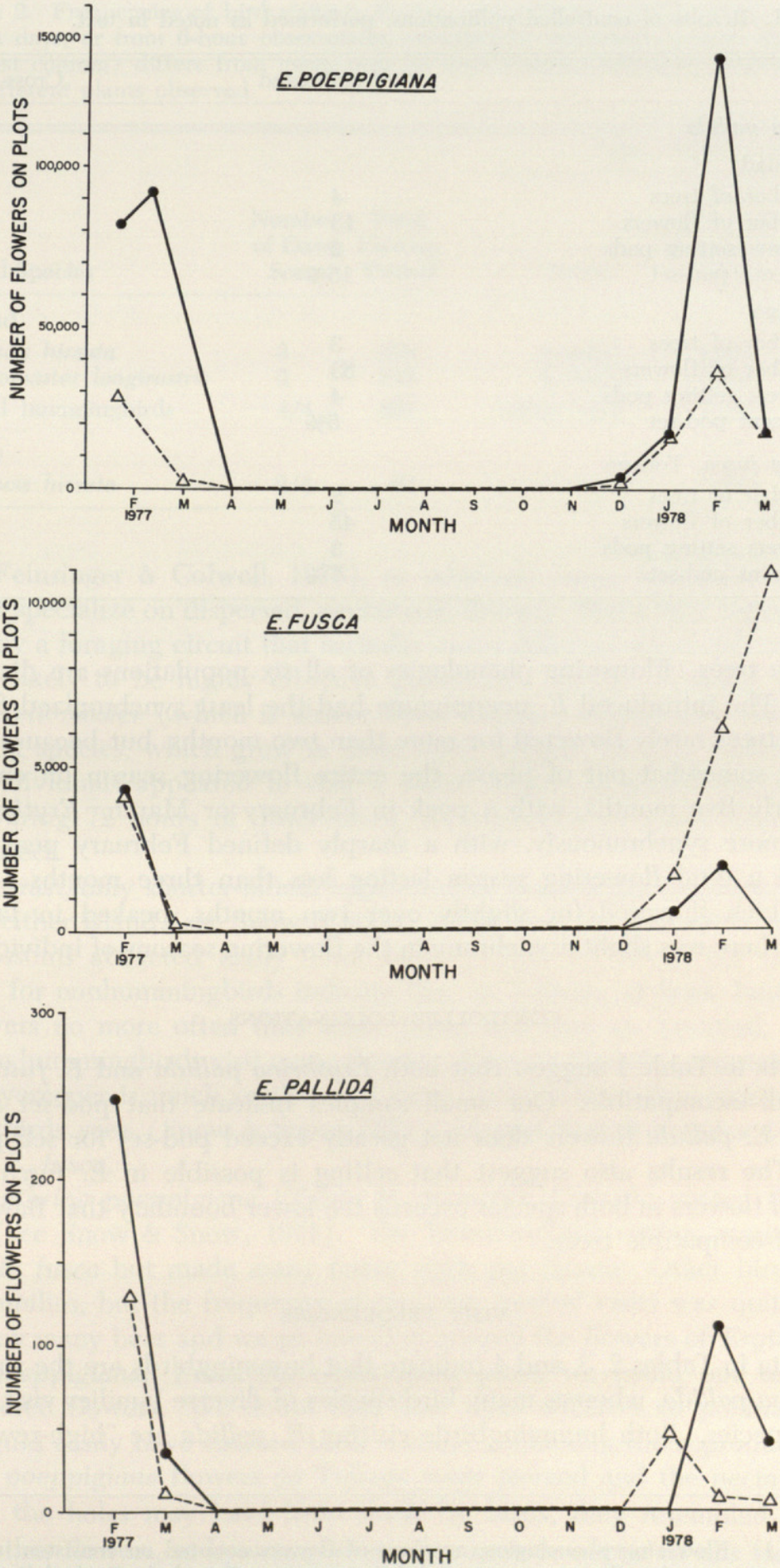


TABLE 1. Results of controlled pollinations, performed as noted in text.

	Self-pollinated	Cross-pollinated
A. <i>Erythrina pallida</i>		
1. Trinidad		
Number of trees	4	4
Number of flowers	13	9
Flowers setting pods	2	1
Per cent pod-set	15%	11%
2. Tobago		
Number of trees	3	3
Number of flowers	83	33
Flowers setting pods	4	7
Per cent pod-set	5%	21%
B. <i>Erythrina fusca</i> , Tobago		
Number of trees	2	
Number of flowers	45	
Flowers setting pods	3	
Per cent pod-set	7%	

12 *E. fusca* trees. Flowering phenologies of all six populations are diagrammed in Fig. 1. The introduced *E. poeppigiana* had the least synchronized flowering; individual trees rarely flowered for more than two months, but because different trees were somewhat out of phase, the entire flowering season on each island lasted nearly five months, with a peak in February or March. *Erythrina fusca* flowered more synchronously, with a sharply defined February peak on each island and a total flowering season lasting less than three months. *Erythrina pallida*, which flowered for slightly over two months, peaked in January or February; there was slight asynchrony in the flowering seasons of individual trees.

CONTROLLED POLLINATIONS

The data in Table 1 suggest that both *Erythrina pallida* and *E. fusca* are not entirely self-incompatible. Our small samples indicate that pod-set for cross-pollinated *E. pallida* flowers does not greatly exceed pod-set for self-pollinated flowers. The results also suggest that selfing is possible in *E. fusca*. Pod-set from selfed flowers in both species exceeds the lower boundary that Bawa (1974) set for self-compatible trees.

VISIT FREQUENCIES

The data in Tables 2, 3, and 4 indicate that hummingbirds are the sole visitors to *Erythrina pallida*, whereas many bird species of diverse families visit the other two tree species. Both hummingbirds visiting *E. pallida* are "high-reward trap-

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FIGURE 1. Flowering phenologies; numbers of flowers counted on consistent study plots, presented as two-month rolling averages. Solid line, circles: Trinidad. Dashed line, triangles: Tobago.

TABLE 2. Frequencies of bird visits to flowers of *Erythrina pallida*. Data from 12-hour observation days, or from 6-hour observations corrected as described in text. Mean over all flowers (last column) differs from mean over all days because different numbers of flowers were on different plants observed.

Island, Bird Species	Number of Days Seen	Total Flowers Visited	Visits / Flower / Day		
			Range	Mean Over All Observation Days	Mean Over All Flowers Observed
A. Trinidad					
<i>Glaucis hirsuta</i>	3	378	0-6.028	2.254	3.140
<i>Heliomaster longirostris</i>	3	313	0-2.813	1.332	1.704
Total hummingbirds	4/4	691	1.000-7.028	3.587	4.844
B. Tobago					
<i>Glaucis hirsuta</i>	2/4	67	0-13.000	4.620	4.360

liners” (Feinsinger & Colwell, 1978), or relatively large, long-billed hummingbirds that specialize on dispersed, nectar-rich flowers. Since they repeat throughout the day a foraging circuit that includes many different plant individuals, such birds are likely to be highly effective pollinators. In the Trinidad study area, we saw *Helimaster* (which is absent from Tobago) consistently visit only one other plant species, which grew in more open habitats than *E. pallida*. *Glaucis hirsuta* individuals appeared to visit a wider variety of plants during foraging bouts. During 72 hours of observation, we observed no other flower visitors, bird or insect.

In contrast, only shorter-billed, opportunistic hummingbirds visited *Erythrina fusca* on either island (see Snow & Snow, 1972), and the accessible nectar in *E. fusca* blossoms attracted many other birds (Table 3). Even the conservative estimates for nonhummingbirds indicate that on Tobago, at least, hummingbirds visit flowers no more often than other birds, and that on Trinidad, also, birds other than hummingbirds visit many flowers. Data on *Coereba*, separated because this honeycreeper is much smaller and more nectarivorous than most other non-hummingbirds seen (Snow & Snow, 1971), suggest that it is not a conspicuous visitor to *E. fusca*.

At *Erythrina poeppigiana* (Table 4), however, *Coereba* visited flowers frequently (see Snow & Snow, 1971). The hummingbird visitors were similar to those at *E. fusca* but made many fewer visits per flower. Other birds spanned several families, but the frequency of any one species’ visits was quite low.

We saw many bees and wasps hovering around the flowers of *Erythrina fusca* and *E. poeppigiana*. From our observation posts, we could not tell whether these entered flowers. We doubt that they were effective in pollination, since insects could easily have entered keels without contacting the reproductive parts. Many *E. poeppigiana* flowers on Tobago were pierced and the nectar removed. Although the holes may have been made by birds, they resembled holes bees chew in other flowers, so hymenopterans may remove nectar in this fashion without approaching the reproductive parts.

TABLE 3. Frequencies of bird visits to flowers of *Erythrina fusca*. Note that frequencies for birds other than hummingbirds are most likely underestimates (see text); visits by non-hummingbirds to high-density Tobago tree, February, 1977, were not counted at all because birds (especially *Thraupis episcopus*) were constantly in the tree in large numbers. See Table 2 for additional information.

Island, Bird Species	Number of Days Seen	Total Flowers Visited	Visits / Flower / Day		
			Range	Mean Over All Observation Days	Mean Over All Flowers Observed
A. Trinidad, low-density trees					
Hummingbirds:					
<i>Chrysolampis mosquitus</i>	2/2	190	0.345–0.587	0.466	0.544
Bananaquit:					
<i>Coereba flaveola</i>	1/2	9	0–0.047	0.024	0.039
Other birds (all Thraupidae):					
<i>Tachyphonus rufus</i>	2	23	0.023–0.168	0.096	0.049
<i>Thraupis episcopus</i>	1	12	0–0.143	0.072	0.025
<i>Thraupis palmarum</i>	1	17	0–0.043	0.022	0.035
Total other birds	2/2	52	0.066–0.311	0.188	0.109
B. Trinidad, high-density trees					
Hummingbirds:					
<i>Chrysolampis mosquitus</i>	2	6,635	1.015–1.169	1.092	1.088
<i>Anthracothonax nigricollis</i>	2	2,081	0.175–0.482	0.328	0.337
<i>Amazilia chionopectus</i>	2	223	0.014–0.056	0.035	0.036
<i>Amazilia tobaci</i>	2	440	0.052–0.091	0.072	0.073
<i>Chlorestes notatus</i>	2	242	0.006–0.082	0.044	0.042
Total hummingbirds	2/2	9,621	1.492–1.650	1.571	1.575
Bananaquit:					
<i>Coereba flaveola</i>	2/2	554	0.004–0.165	0.084	0.089
Other birds:					
Thraupidae:					
<i>Thraupis episcopus</i>	2	137	0.020–0.022	0.021	0.021
<i>Thraupis palmarum</i>	2	135	0.007–0.035	0.021	0.022
<i>Tachyphonus rufus</i>	2	418	0.025–0.109	0.067	0.065
<i>Ramphocelus carbo</i>	2	42	0.004–0.009	0.006	0.007
Icteridae:					
<i>Icterus nigrogularis</i>	1	5	0–0.002	0.001	0.001
<i>Psarocolius decumanus</i>	1	2	0–0.001	—	—
Fringillidae:					
<i>Saltator coerulescens</i>	1	14	0–0.004	0.002	0.002
Mixed passerines	1	88	0–0.026	0.013	0.014
Total passerines	2	841	0.122–0.142	0.132	0.131
C. Tobago, low-density trees					
Hummingbirds:					
<i>Chrysolampis mosquitus</i>	2	11	0–0.485	0.176	0.201
<i>Anthracothonax nigricollis</i>	2	19	0–0.791	0.213	0.219
Total hummingbirds	3/4	30	0–1.009	0.389	0.420

TABLE 3. *Continued.*

Island, Bird Species	Number of Days Seen	Total Flowers Visited	Visits / Flower / Day		
			Range	Mean Over All Observation Days	Mean Over All Flowers Observed
C. Tabago, low-density trees (<i>Continued</i>)					
Bananaquit:					
<i>Coereba flaveola</i>	2/4	44	0-0.511	0.132	0.159
Other birds:					
<i>Thraupis episcopus</i> (Thraupidae)	2	98	0-1.710	0.491	0.582
<i>Mimus gilvus</i> (Mimidae)	2	5	0-0.099	0.025	0.030
<i>Melanerpes rubricapillus</i> (Picidae)	1	5	0-0.045	0.021	0.023
Total other birds	2/2	108	0-1.847	0.537	0.635
D. Tobago, high-density trees					
Hummingbirds:					
<i>Chrysolampis mosquitus</i>	3	2,027	0.008-1.779	0.638	0.665
<i>Anthracothonax nigricollis</i>	2	346	0-0.354	0.121	0.113
<i>Amazilia tobaci</i>	1	6	0-0.006	0.002	0.002
Total hummingbirds	3/3	2,379	0.008-1.794	0.761	0.781
Bananaquit:					
<i>Coereba flaveola</i>	3/3	93	0.031-0.043	0.036	0.036
Other birds:					
Thraupidae:					
<i>Thraupis episcopus</i>	2	902	0.197-0.769	0.483	0.488
<i>Tachyphonus rufus</i>	2	7	0.002-0.013	0.008	0.007
Mimidae:					
<i>Mimus gilvus</i>	2	27	0.014-0.030	0.022	0.022
Icteridae:					
<i>Psarocolius decumanus</i>	1	16	0-0.015	0.008	0.008
Picidae:					
<i>Melanerpes rubricapillus</i>	1	2	0-0.002	0.001	0.001
Total other birds	2/2	954	0.240-0.802	0.521	0.526

Evening observations on *Erythrina fusca* trees provided no evidence for bat pollination. Although many bats, including potential flower-visitors, foraged on abundant mosquitoes in the swampy *E. fusca* habitat on both islands, we observed none to approach the flowers and heard no activity in the trees. The absence of claw marks or bite marks from fallen *E. fusca* flowers also indicated a lack of bat activity.

BEHAVIOR OF FLOWER VISITORS

Flower visitors do not necessarily transfer pollen (see Faegri & van der Pijl, 1971); thus values in Tables 2, 3, and 4 need not indicate the relative importance

of different birds in *Erythrina* pollination. Only on *E. pallida* did every visitor observed, *Glaucis hirsuta* or *Helioaster longirostris*, consistently contact flower parts with its forehead or the base of its bill. Therefore, the values in Table 2 may well indicate the frequency of pollen deposition on *E. pallida* stigmas.

Hummingbirds were much less consistent at *Erythrina fusca* flowers. *Chrysolampis mosquitus*, the most frequent visitor, invariably probed beneath the enclosed anthers when visiting closed flowers (flowers whose flag had not sprung open). Only at occasional sprung flowers did foraging *Chrysolampis* brush against the reproductive parts. *Anthracothorax nigricollis* also brushed against anthers of sprung flowers on occasion, but most often missed the upthrust anthers entirely. At least *Anthracothorax* often moved between different *E. fusca* trees during foraging bouts, so that any pollen picked up might have been transferred, but often *Chrysolampis* remained in a single tree for long periods of time or flew from *E. fusca* to other plant species, so that any pollen picked up at one tree would rarely have been transferred to other *E. fusca*. Other birds, however, circulated among *E. fusca* trees in flocks. We often saw *Thraupis episcopus*, relatively large and strong foragers, spring open flowers, whereupon the released anthers struck them in the face or on the underside. We estimate that *T. episcopus* sprung about 10% of the closed flowers visited, and often brushed against the reproductive parts of open flowers with their undersides. *Tachyphonus rufus* appeared to spring closed flowers at a higher rate, ca. 25% of the time. Most other birds also fed in such ways that they sometimes sprung flowers or brushed against reproductive parts of open flowers. Small *Coereba flaveola* were rarely observed to spring a closed flower, but their heads or undersides often brushed against already sprung flowers in the act of feeding.

Since flags on *Erythrina poeppigiana* flowers evidently opened spontaneously when anthers matured, reproductive parts were always exposed, and birds feeding from the keel often brushed against the anthers or stigma with their undersides. Foraging hummingbirds such as *Chlorestes notatus* often appeared to touch the anthers. Large birds such as the Thraupidae often brushed against the anthers of one flower while feeding on another. Apparently, the most consistent pollinator was the bananaquit, *Coereba flaveola*, which nearly always contacted the reproductive parts either on its belly, chin, or (by perching behind a flower and tucking its head under) on its forehead or crown. Such unlikely visitors as woodpeckers, mockingbirds, and "seed-eating" grassquits often contacted reproductive parts, moved from tree to tree, and may have effected outcrossing. Parrots, which actually ate or dislodged flowers, were not likely to be especially effective pollen vectors.

POLLEN LOADS

Pollen loads collected from netted birds during the 1978 *Erythrina* flowering season confirm the observation data. Table 5 shows that *Glaucis hirsuta* on both islands carried many *E. pallida* pollen grains (unfortunately, no *Helioaster* was netted during this period). Only three shorter-billed hummingbirds of ten examined carried any *Erythrina* pollen; on two this was clearly *E. poeppigiana* pollen. Four of eight *Coereba* carried *Erythrina* pollen; on one bird this was

TABLE 4. Frequencies of birds visits to flowers of *Erythrina poeppigiana*. Note that frequencies for birds other than hummingbirds are most likely underestimates (see text).

Island, Bird Species	Number of Days Seen	Total Flowers Visited	Visits / Flower / Day		
			Range	Mean Over All Observation Days	Mean Over All Flowers Observed
A. Trinidad, low-density trees					
Hummingbirds:					
<i>Chlorestes notatus</i>	2	224	0-1.130	0.208	0.102
<i>Amazilia tobaci</i>	3	149	0-0.673	0.113	0.067
<i>Amazilia chionopectus</i>	1	529	0-2.437	0.406	0.237
<i>Anthracothorax nigricollis</i>	3	124	0-0.396	0.209	0.067
<i>Florisuga mellivora</i>	1	2	0-0.009	0.002	0.001
Total hummingbirds	4/6	1,028	0-3.515	0.938	0.474
Bananaquit:					
<i>Coereba flaveola</i>	6/6	787	0.014-2.820	0.900	0.378
Other birds:					
Thraupidae:					
<i>Thraupis episcopus</i>	3	63	0-2.038	0.361	0.038
<i>Thraupis palmarum</i>	3	158	0-2.783	0.484	0.103
<i>Tachyphonus rufus</i>	2	36	0-0.161	0.040	0.017
<i>Ramphocelus carbo</i>	3	76	0-1.029	0.192	0.046
Icteridae:					
<i>Icterus nigrogularis</i>	1	39	0-0.180	0.030	0.018
<i>Psarocolius decumanus</i>	2	28	0-0.192	0.052	0.014
Picidae:					
<i>Piculus rubiginosus</i>	1	12	0-0.261	0.044	0.008
Total other birds	4/6	412	0-4.073	1.202	0.242
B. Trinidad, high-density trees					
Hummingbirds:					
<i>Chlorestes notatus</i>	4	2,444	0.001-0.314	0.109	0.076
<i>Amazilia chionopectus</i>	2	1,086	0-0.131	0.049	0.034
<i>Amazilia tobaci</i>	4	395	0.001-0.051	0.020	0.012
<i>Anthracothorax nigricollis</i>	4	532	0.001-0.080	0.022	0.017
<i>Florisuga mellivora</i>	2	23	0.001-0.002	0.001	0.001
Total hummingbirds	4/4	4,480	0.004-0.551	0.201	0.140
Bananaquit:					
<i>Coereba flaveola</i>	4/4	1,949	0.027-0.151	0.071	0.061
Other birds:					
Thraupidae:					
<i>Thraupis episcopus</i>	4	162	0.003-0.011	0.007	0.005
<i>Thraupis palmarum</i>	3	291	0-0.035	0.011	0.009
<i>Tachyphonus rufus</i>	4	89	0.001-0.010	0.004	0.003
<i>Ramphocelus carbo</i>	3	95	0-0.011	0.004	0.003
<i>Tangara mexicana</i>	1	8	—	—	—
Unidentified tanagers	2	174	0-0.027	0.008	0.005
Coerebidae					
(other than Bananaquit):					
<i>Dacnis cayana</i>	2	24	0-0.004	0.001	0.001
Icteridae:					
<i>Icterus nigrogularis</i>	2	21	0-0.001	—	—
<i>Psarocolius decumanus</i>	2	70	0-0.010	0.003	0.002
<i>Cacicus cela</i>	1	4	—	—	—
<i>Scaphidura oryzivora</i>	1	3	—	—	—

TABLE 4. *Continued.*

Island, Bird Species	Number of Days Seen	Total Flowers Visited	Visits / Flower / Day		
			Range	Mean Over All Observation Days	Mean Over All Flowers Observed
B. Trinidad, high-density trees (Continued)					
Vireonidae:					
<i>Cyclarhis gujanensis</i>	1	57	0-0.018	0.004	0.002
Fringillidae:					
<i>Saltator coerulescens</i>	1	4	—	—	—
Picidae:					
<i>Piculus rubiginosis</i>	1	12	0-0.001	—	—
Total other birds	4/4	1,014	0.011-0.095	0.043	0.032
C. Tobago, low-density trees					
Hummingbirds:					
<i>Chrysolampis mosquitos</i>	3	56	0-10.00	2.011	0.026
<i>Amazilia tobaci</i>	2	12	0-0.010	0.003	0.006
<i>Anthracothonax nigricollis</i>	1	32	0-0.033	0.007	0.015
Total hummingbirds	3/5	100	0-10.00	2.021	0.047
Bananaquit:					
<i>Coereba flaveola</i>	4/5	156	0-3.000	0.617	0.022
Other birds:					
Thraupidae:					
<i>Thraupis episcopus</i>	1	1	0-0.017	0.003	—
<i>Tachyphonus rufus</i>	3	24	0-0.183	0.041	0.008
Fringillidae:					
<i>Tiaris bicolor</i>	1	104	0-0.108	0.022	0.034
Mimidae:					
<i>Mimus gilvus</i>	1	1	0-0.001	—	—
Total passerines	3/5	130	0-0.200	0.066	0.042
D. Tobago, high-density trees					
Hummingbirds:					
<i>Chrysolampis mosquitos</i>	4	1,567	0.001-0.221	0.082	0.048
<i>Anthracothonax nigricollis</i>	2	277	0-0.020	0.010	0.008
<i>Amazilia tobaci</i>	2	42	0-0.043	0.012	0.002
<i>Florisuga mellivora</i>	1	766	0-1.154	0.288	0.023
Total hummingbirds	4/4	2,652	0.001-1.438	0.393	0.082
Bananaquit:					
<i>Coereba flaveola</i>	4/4	3,265	0.003-1.768	0.674	0.099
Other birds:					
Thraupidae:					
<i>Thraupis episcopus</i>	4	729	0.003-0.519	0.137	0.022
<i>Tachyphonus rufus</i>	4	166	0.001-0.025	0.009	0.005
Fringillidae:					
<i>Tiaris bicolor</i>	1	8	0-0.001	—	—
Mimidae:					
<i>Mimus gilvus</i>	4	151	0.001-0.023	0.011	0.007
Icteridae:					
<i>Psarocolius decumanus</i>	2	59	0-0.058	0.015	0.002
Picidae:					
<i>Melanerpes rubricapillus</i>	3	189	0-0.244	0.062	0.006
<i>Veniliornis kirkii</i>	1	15	0-0.022	0.006	0.001
Psittacidae:					
<i>Amazona amazonica</i>	2	383	0-0.218	0.059	0.011
Total other birds	4/4	1,700	0.026-1.101	0.298	0.051

TABLE 5. Pollen loads on birds mist-netted January and February, 1978. Number of pollen grains picked up by Scotch transparent tape (see text). If more than one bird of a given species was devoid of grains, the number of blank birds is given in parentheses.

Island, bird species	Number of Grains of			Either <i>E. fusca</i> or <i>E. poeppigiana</i>
	<i>E. pallida</i>	<i>E. poeppigiana</i>	<i>E. fusca</i>	
Trinidad:				
Hummingbirds:				
<i>Glaucis hirsuta</i>	135			
<i>Glaucis hirsuta</i>	1			
<i>Glaucis hirsuta</i>	33			
<i>Amazilia tobaco</i> (3)		— ^a		
<i>Chlorestes notatus</i>		— ^a		
Tobago:				
Hummingbirds:				
<i>Glaucis hirsuta</i>	763			
<i>Glaucis hirsuta</i>	990			
<i>Glaucis hirsuta</i>	330			
<i>Glaucis hirsuta</i>	8			
<i>Glaucis hirsuta</i> (2)		— ^a		
<i>Amazilia tobaci</i>		28		
<i>Amazilia tobaci</i>		12		
<i>Amazilia tobaci</i> (3)		— ^a		
<i>Chrysolampis mosquitus</i>				5
Bananaquits:				
<i>Coereba flaveola</i>				2
<i>Coereba flaveola</i>				1
<i>Coereba flaveola</i>				1
<i>Coereba flaveola</i>			2100	
<i>Coereba flaveola</i> (4)		— ^a		
Thraupidae:				
<i>Thraupis episcopus</i>				3
<i>Thraupis episcopus</i>				3
<i>Thraupis episcopus</i>			1	3
<i>Thraupis episcopus</i>				1
<i>Thraupis episcopus</i>			2	
<i>Thraupis episcopus</i>			2	
<i>Thraupis episcopus</i>		— ^a		
<i>Tachyphonus rufus</i>		3		1
<i>Tachyphonus rufus</i>		— ^a		

^a Devoid of pollen grains.

identified as *E. fusca*. Of the fourteen larger tanagers examined, half carried either *E. fusca* or *E. poeppigiana* pollen. Observed loads were often small; birds may have originally carried larger loads that were lost during their frantic activity in the mist nets.

NECTAR SECRETION

Figure 2 shows that *Erythrina fusca* flowers secrete nectar during the day only (again arguing against bat pollination). Most secretion is on the first day.

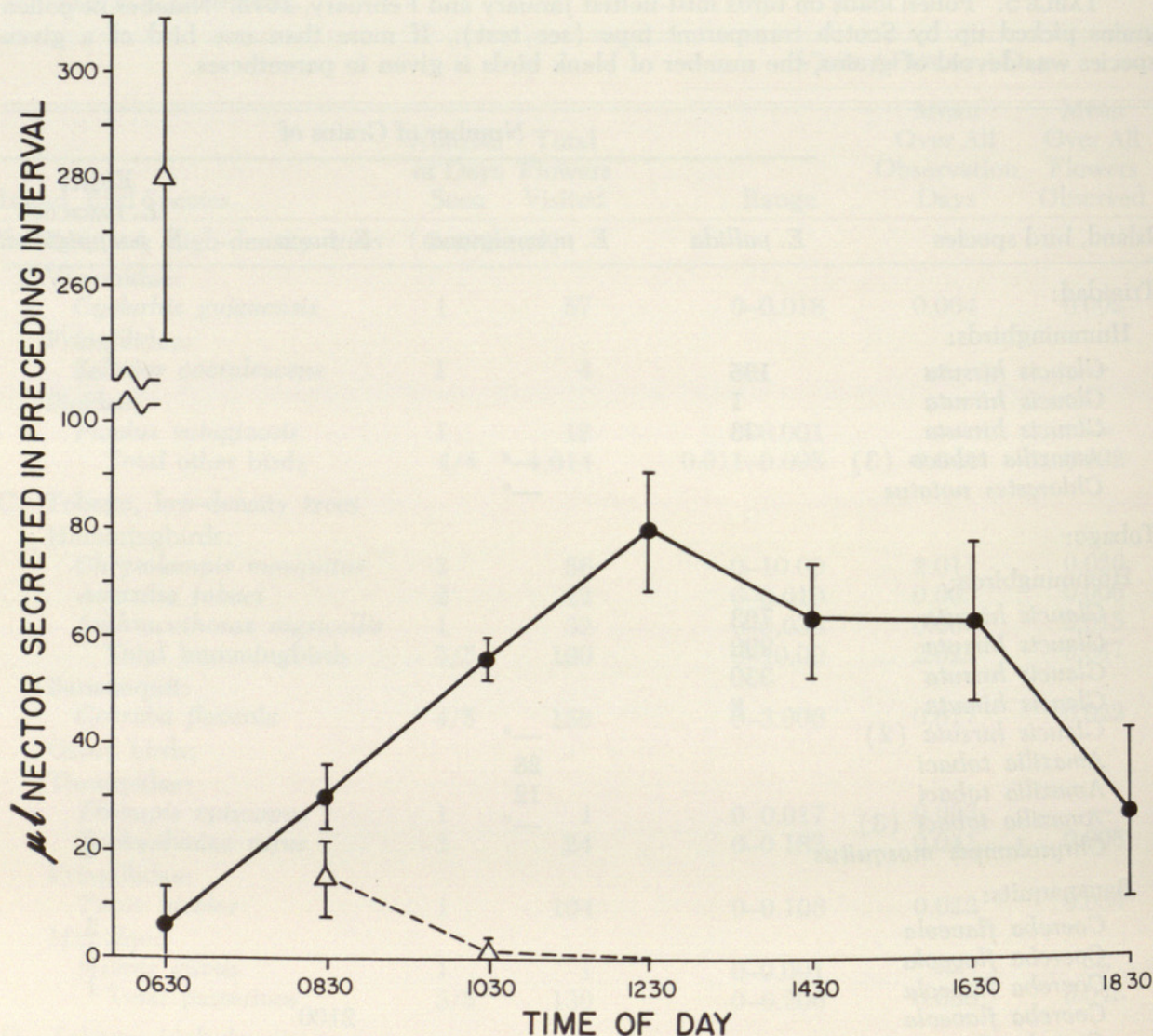


FIGURE 2. Nectar secretion in *Erythrina fusca* flowers. Solid line, circles: First-day flowers ($n = 5$). Dashed line, triangles: Second-day flowers ($n = 5$); so dawn value for second-day flowers is cumulative nectar from their first day of secretion. Mean $\pm$ one standard deviation.

The seven *E. pallida* flowers investigated secreted an average of $23.0 \mu\text{l}$ of nectar ($s = 10.8 \mu\text{l}$), with a sugar concentration of 29% in terms of g sucrose equivalence/100 g solution; day-old flowers secreted only trace amounts.

Erythrina fusca nectar analyzed by I. Baker and H. G. Baker (pers. comm.) had a higher concentration of monosaccharides than disaccharides: the ratio of sucrose to glucose + fructose was 0.038. The sucrose:glucose + fructose ratio for *E. poeppigiana* nectar was even lower (0.029). Both nectar samples contained many amino acids (see Baker & Baker, 1975); a complete list of tests performed is available from the authors or from I. Baker.

NECTAR AVAILABILITY

Copious secretion rates coupled with relatively infrequent bird visits left much nectar in flowers of *Erythrina fusca* and *E. poeppigiana* (Table 6). Even late in the day most flowers held large nectar volumes, up to $371 \mu\text{l}$ (concentration

TABLE 6. Nectar availability (standing crop) in flowers of *Erythrina* species exposed to foraging birds. Samples of 10 flowers.

A. Trinidad						
1. January 16, 1978. <i>Erythrina fusca</i> only.						
Time	Mean vol., μ l	s	Number with $\leq 10 \mu$ l			
0615	135.0	88.4	0			
0815	125.2	23.8	0			
1015	117.1	66.8	2			
1215	126.2	75.3	2			
1415	108.7	86.5	3			
1615	124.3	109.0	1			
1745	124.5	55.6	0			
Mean sugar concentration: 18.0% (s = 1.3%)						
2. February 3, 1978						
Time	Mean vol., μ l	s	Number with $\leq 10 \mu$ l	Mean vol., μ l	s	Number with $\leq 10 \mu$ l
<i>Erythrina fusca</i>				<i>Erythrina poeppigiana</i>		
0615	109.9	70.2	0	21.9	27.3	5
0815	108.8	60.3	1	50.0	33.3	1
1015	138.4	109.3	1	14.2	27.5	7
1215	109.4	69.1	1	19.5	16.5	4
1415	120.6	84.3	0	80.8	60.8	1
1615	75.7	83.3	2	49.6	37.2	0
1715	95.5	75.7	3	32.7	31.4	4
Mean sugar concentration: 19.7% (s = 4.2%)				17.6% (s = 1.5%)		

16.5 g sucrose equivalence/100 g solution) in *E. fusca* and up to 254.7 μ l (16.5 g sucrose equivalence/100 g solution) in *E. poeppigiana*. In February, many *E. poeppigiana* flowers on both islands held less than 10 μ l. Observed bird visits were less frequent in February than in January, however. Possibly the hillside soils upon which *E. poeppigiana* trees grew were so dry that nectar secretion was inhibited. It is also possible that insect visits had increased by this time; we noted that many flowers on the Tobago trees had been pierced as described above.

EXTRAFLORAL NECTARIES

For at least *Erythrina fusca* and *E. pallida*, we demonstrated protuberances on the calyces to function as extrafloral nectaries when we bagged inflorescences for controlled pollination studies. Figure 3 shows the results: the protuberances of both species, protected from foraging ants, secreted conspicuous, glistening droplets of nectar. Exposed nectaries on both species attracted many ants (e.g., Fig. 3d). We collected numerous *Cephalotes atratus* from Tobago *E. fusca*, and *Ectotomma tuberculatum*, *Monacis valida*, and *Camponotis* sp. from Tobago *E. pallida* nectaries. On Trinidad, we also noted *Ectotomma ruidum* and Was-

TABLE 6. Continued.

B. Tobago

1. January 23, 1978

Time	Mean vol., μ l	s	Number with $\leq 10 \mu$ l	Mean vol., μ l	s	Number with $\leq 10 \mu$ l
<i>Erythrina fusca</i>				<i>Erythrina poeppigiana</i>		
0625	169.1	118.6	0	139.0	40.4	0
0815	166.8	81.8	0	116.5	49.9	0
1015	154.1	77.6	0	123.6	58.1	0
1215	172.3	96.0	0	109.2	85.4	0
1430	251.9	20.4	0	141.0	81.1	1
1615	198.2	63.7	0	120.2	85.3	1
1720	194.3	122.7	2	129.1	103.3	2

Mean sugar concentration: 16.8% (s = 1.0%) 16.8% (s = 0.7%)

2. February 24, 1978

Time	Mean vol., μ l	s	Number with $\leq 10 \mu$ l	Mean vol., μ l	s	Number with $\leq 10 \mu$ l
<i>Erythrina fusca</i>				<i>Erythrina poeppigiana</i>		
0615	17.3	41.7	9	4.1	6.2	8
0815	70.9	83.6	3	31.0	18.1	2
1015	89.7	78.4	0	31.5	32.1	4
1215	62.5	33.6	1	9.7	13.4	7
1415	100.1	59.0	1	6.5	12.6	7
1615	116.5	81.6	1	5.6	11.4	8
1745	105.8	72.0	1	19.2	20.9	4

Mean sugar concentration: 13.4% (s = 2.9%) 15.5% (s = 2.7%)

mannia auropunctata at *E. fusca* nectaries and on *E. poeppigiana* as well (see Feinsinger & Swarm, 1978). All species acted aggressively towards human manipulation of flowers, moving quickly towards the source of disturbance with mandibles open (*Cephalotes*, *Ectotomma*, *Camponotis*) or stinging (*Wasmannia*). Bentley (1977) cites the genus *Ectotomma* as a common "pugnacious bodyguard" associated with extrafloral nectaries on tropical plants. To our knowledge the only other description of extrafloral nectaries on *Erythrina* is by Mattei (1925; cited in Bentley, 1977).

The function of extrafloral nectaries and their attendant ants was graphically illustrated on two Tobago *Erythrina fusca* trees. On Tree A, which grew in typical *E. fusca* habitat near a stream, extrafloral nectaries on bagged inflorescences secreted abundant nectar (e.g., Fig. 3a), and unbagged inflorescences on the tree were full of roving, aggressive ants. There was no visible predation on this tree's flowers. Tree B grew on a dry hillside some 20 m from the stream and was investigated on the same days as Tree A. Inflorescences bagged for controlled pollinations secreted no visible extrafloral nectar. This contrast between the two trees' nectaries was observed for three consecutive days. We saw



FIGURE 3. Extrafloral nectaries on calyces.—a. *Erythrina fusca* buds protected from ants for 12 hours.—b. *E. pallida* buds protected from ants for 12 hours.—c. *E. pallida* flowers protected from ants for 12 hours.—d. Unidentified ant foraging at nectary on *E. pallida* bud.

no ants on Tree B. Several inflorescences on Tree B were rendered into pulpy masses by an unidentified lepidopteran larva (Fig. 4a). Many flowers in other inflorescences had been attacked by flies of a previously undescribed species in the genus *Euxesta* (family Otitidae), whose larvae bore through the flower and doubtlessly reduce its reproductive potential (Fig. 4b). During the same period (late February, 1978) we repeatedly observed *Euxesta*, of a species similar to that of *E. fusca*, active around inflorescences of Tobago *E. pallida*. These flies often landed on *E. pallida* buds and flowers, but invariably fled as attendant ants moved towards them. Other species of *Euxesta* are important parasites of inflorescences of *Costus* (Zingiberaceae) in Panama (D. Schemske, pers. comm.).

DISCUSSION

MODES OF POLLINATION

Erythrina pallida.—The floral biology of *E. pallida* is a straight-forward case of hummingbird pollination. Data on flower visitors (Table 3) and pollen loads (Table 5) demonstrate that long-billed hummingbirds functioned as effective pollinators at our study sites. Nectar flow rates were low relative to the other two *Erythrina* species, as Cruden & Toledo (1977) discovered for hummingbird-pollinated *Erythrina* species in Mexico; yet nectar secretion and sugar concentration were sufficiently high to support large hummingbirds rather than the

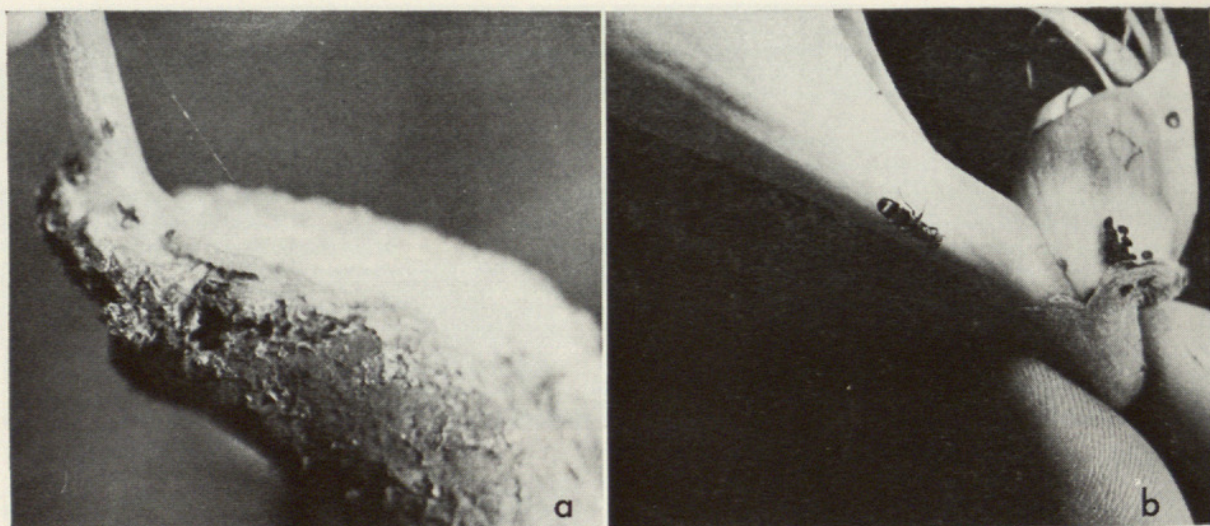


FIGURE 4. Damage to an *Erythrina fusca* tree whose extrafloral nectaries did not secrete nectar (see text).—a. Entire inflorescence rendered into pulpy mass by unidentified lepidopteran larvae.—b. Larval exit hole (round orifice), larval feces (black masses), and adult of fly *Euxesta* sp. on individual flower.

smaller, shorter-billed species (see Bolten & Feinsinger, 1978; Feinsinger & Colwell, 1978). Apparently, *E. pallida* flowers have thus evolved to utilize long-billed hummingbirds as pollen vectors such that hummingbirds are the only means by which outbreeding may be effected (see Raven, 1974, 1977). Anthers and stigma are in close proximity, however. Data from controlled pollination studies (Table 1) suggest that in the absence of hummingbirds fertilization might still occur through autogamy. Pods set per flower appeared to be quite high, at least 10% on Trinidad.

Erythrina fusca.—*E. fusca* contrasts with *E. pallida* in nearly every facet of floral biology. The easily obtained, copious nectar is typical of many *Erythrina* species pollinated by passerine birds (see Raven, 1974, 1977; Cruden & Toledo, 1977). Although bat flowers also secrete copious nectar (Heinrich & Raven, 1972), the diurnal nectar secretion pattern and lack of observed bat visits suggest that bats are not important in the floral biology of Trinidad and Tobago *E. fusca*, although they may act as pollinators of Colombian populations (Helvesen, cited in Raven, 1977). The pollen loads we obtained from mist-netted birds are not conclusive, but it is evident that passerine birds are capable of carrying *E. fusca* pollen and acting as outbreeding agents. Tanagers appear to be especially important in springing flowers and transferring pollen. Only on occasion do hummingbirds (which frequently visit flowers but rarely contact reproductive parts) or bananaquits (which rarely visit flowers although during visits they frequently contact reproductive parts on sprung flowers) assume importance in pollen transfer. The low sucrose:glucose + fructose ratio typifies passerine-pollinated plants throughout the tropics (Cruden & Toledo, 1977; Baker & Baker, 1980). The copious nectar left in flowers at the end of the day suggests that not all flowers receive bird visits; our sparse data on controlled pollinations, coupled with the observation that anthers and stigma are adjacent to one another, suggest that autogamy is possible. Qualitative observations on fruiting trees indicate that only a small fraction of flowers (fewer than 1%) results in mature pods.

Erythrina poeppigiana.—Like *E. fusca*, *E. poeppigiana* appears to be adapted for pollination by passerine birds. Nectar availability (and doubtless secretion rates), while lower than in *E. fusca* (Table 6), far exceed secretion rates in *E. pallida* or most other hummingbird-pollinated plants with which we are familiar. Again, the low disaccharide:monosaccharide ratio suggests passerine pollination (Baker & Baker, 1980). Data on pollen loads corroborate our observations that passerine birds (particularly *Coereba flaveola*), as well as occasional hummingbirds, can act as pollen vectors. Patterns on Trinidad and Tobago may not be representative of floral biology in native Venezuelan populations of *E. poeppigiana*; however, *Coereba flaveola* is apparently abundant throughout *E. poeppigiana*'s natural range (Krukoff & Barneby, 1974; Schauensee & Phelps, 1978). Although we could not obtain data on breeding systems in this species, the spread of feral trees on both islands argues that fertilization often occurs, whether by allogamy or autogamy. Nevertheless, pod-set is apparently quite low; most trees produced large seed crops, but the number of pods set appeared to be less than 1% of the total number of flowers each tree produced over its flowering season.

ISLAND EFFECTS ON FLORAL BIOLOGY

In another comparison of bird pollination on Trinidad and Tobago, Linhart & Feinsinger (in press) showed that life on a small island (Tobago) affected a plant species specialized for pollination by long-billed hummingbirds much more than a plant species with open flowers acceptable to a variety of birds. The contrast between the three *Erythrina* species is similar. *Erythrina pallida* was visited by two hummingbirds on Trinidad, one of which was a virtual specialist on the plant. Every observed plant was visited by one or both species. On Tobago, *E. pallida* received no visits whatsoever on two of four observation days. Its sole visitor on Tobago, the hummingbird *Glaucis hirsuta*, visited many other plant species during its foraging bouts, so that pollen may have been lost between successive visits to different *E. pallida* individuals. Therefore, it is likely that outbreeding was much more consistent among Trinidad than Tobago plants.

Although hummingbird visit frequencies to *Erythrina fusca* flowers were also higher on Trinidad than on Tobago, the reverse was true for other birds (Table 3), particularly *Thraupis episcopus*. These tanagers are much more dense on Tobago than Trinidad, so that the increase in visit frequencies (and possibly increased outbreeding) among Tobago *E. fusca* is an interesting consequence of "density compensation" in this island bird population (cf. Diamond, 1970; MacArthur et al., 1972). An important pollinator of *E. poeppigiana*, *Coereba flaveola*, is also much more frequent on Tobago than Trinidad, and its visits to large *E. poeppigiana* trees are consequently more frequent on Tobago. Our circumstantial evidence suggests that, in contrast to *E. pallida*, neither of the large-flowered, generalized *Erythrina* tree species suffered a considerable decrease in outbreeding in the transition from mainlandlike Trinidad to the small island Tobago.

CONCLUSIONS

Flowering in all three *Erythrina* species occurs at a time when most individuals have shed their leaves and photosynthesis is unlikely. The profligate use of

flowers and nectar in the two large tree species, at least, must constitute a considerable energy drain; we noted that only exceptionally large, healthy trees produced large flower crops. Copious nectar secretion may be necessary to attract passerine pollinators (cf. Cruden & Toledo, 1977); whether dense flower crops are another adaptation for attracting passerines, or whether passerines are especially adaptive for bird-pollinated plants with dense flower crops because flocking passerines respond to increased flower density more linearly than aggressive, territorial hummingbirds (cf. Feinsinger, 1978), is open to speculation. In either case, a smaller, dispersed plant species not capable of producing large flower crops, such as *E. pallida*, would be unlikely to benefit from visits by opportunistic passerines. Specialized, flower-specific hummingbirds are doubtless most effective in dispersing pollen among conspecifics, indicated by relatively frequent pod-set, although on a small island such as Tobago there is a danger of even hummingbirds becoming inconstant. In light of the energy all three species invest in reproduction, it is significant that inflorescences are protected by means of extrafloral nectaries, which function to attract pugnacious ants. Floral nectar, which must be left available to potential pollinators, can also attract ants when removed from the flower (Feinsinger & Swarm, 1978), but the waxy inner surface of flowers appears to deter ants from floral nectar. Thus functions of the two spatially proximate nectaries are kept separate. Finally, water stress may affect secretion by either type of nectary. Lack of nectar in extrafloral nectaries may increase predation on flowers, as shown for *E. fusca*, whereas low nectar secretion by floral nectaries may discourage birds from visiting trees, as proposed for *E. poeppigiana*. Thus water stress could exert selective pressure on flowering phenologies and habitat preferences of all three species.

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