PASSERINE POLLINATION OF *ERYTHRINA MEGISTOPHYLLA* DIELS (FABACEAE)[1]

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ABSTRACT

Floral morphology and behavior, nectar composition and observational data suggest that *Erythrina megistophylla* is adapted to passerine bird pollination. It has short, open-mouthed, backwardly directed flowers on horizontal racemes. The primary visitors are members of the Coerebidae (honeycreepers), passerine birds which perch on the inflorescence rachis while probing the flowers. The nectar has a low sugar concentration (6–9% W/V), is hexose dominant, and contains a high concentration of amino acids.

Pollination of Old World *Erythrina* species by perching birds (Passeriformes) has been known for some time (Ali, 1932; Docters van Leeuwen, 1932; Porsch, 1924; Singh, 1929), although similar pollination of species of this genus in the New World has gone largely unnoticed, probably due to the vast majority of hummingbird-pollinated species. Fifty-two of the 64 New World species of *Erythrina* are adapted to hummingbird pollination (as presented by Toledo, 1974). This estimate is based on descriptions and illustrations provided in Krukoff & Barneby's (1974) treatment of the genus. This leaves 12 species which show adaptations to "perching" or passerine birds.

Observations have been made on visitations to some of these species by several authors (Leck, 1974; Raven, 1974; Skutch, 1954; Snow & Snow, 1971; Steiner, unpubl.; Timken, 1970). Cruden & Toledo (1977) and in this symposium Feinsinger et al., Morton, and Toledo & Hernández have considered the syndrome for New World species of *Erythrina* in detail. Their studies have helped demonstrate that in the New World a "perching bird" syndrome based on floral morphology and nectar composition definitely exists. The nectar of *Erythrina breviflora* A. DC. studied by Cruden & Toledo (1977) differed from that of a typical hummingbird *Erythrina* (*E. coralloides* A. DC.) on the basis of sugar concentration, ratio of the sugars (glucose and fructose/sucrose), and on the concentration of amino acids. The analysis done by Irene Baker showed that *E. breviflora* had hexose-dominated nectar that was less concentrated and contained a greater proportion of amino acids than the sucrose rich nectar of the hummingbird adapted *E. coralloides*.

Since *Erythrina breviflora* is considered by Krukoff & Barneby (1974) to be phylogenetically primitive, the perching bird syndrome is most probably a primitive condition that has been retained by some New World species. Perhaps the most important adaptive change that has occurred facilitating hummingbird pollination among *Erythrina* species has been the morphological switch from

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short, open-mouthed corollas directed inwardly to long closed corollas directed outwardly. The more primitive short corollas are borne in horizontal racemes whereas the more specialized long corollas are borne in vertical racemes. Clearly, one permits perched probing for nectar while the latter makes hovering in mid-air necessary. These morphological changes reduced the number of birds that could successfully obtain nectar and therefore cut down on unspecialized opportunistic feeders that may have been less efficient pollinators than hummingbirds.

In addition to the obvious morphological changes, there has been a change in nectar composition associated with the transition from perching-bird- to hummingbird-pollinated *Erythrina* species. The nectar of perching-bird-pollinated *Erythrina* species may have less concentrated, hexose-dominated nectar with significantly more amino acids (Cruden & Toledo, 1977; Baker & Baker, 1980; Baker & Baker, this symposium). Thus, visitation and nectar data were collected for *Erythrina megistophylla*, a species morphologically similar to *Erythrina breviflora*, in order to provide further evidence for the existence of a passerine bird pollination syndrome in the New World.

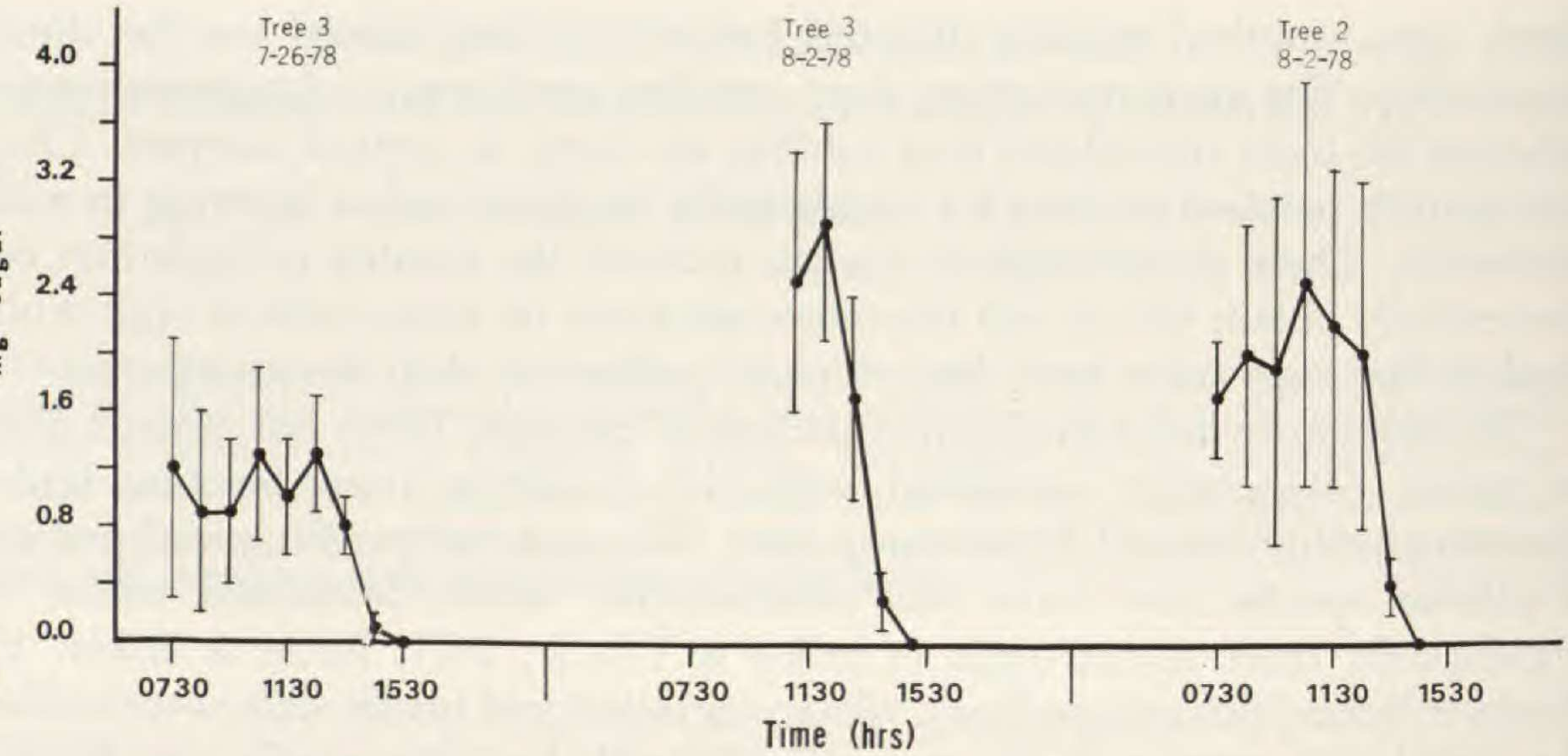
Study Site and Methods

This study was carried out at the Río Palenque Science Center located 65 km south of the equator, between Santo Domingo and Quevedo in the Pacific lowlands of central Ecuador (see Dodson & Gentry, 1978, for further details). Field observations and measurements were made on *Erythrina megistophylla* during two periods between 20 July 1978 and 2 Aug. 1978. *Erythrina megistophylla* is an understory tree of up to 4 m and is a fairly common component of disturbed and mature portions of the wet forest (sensu Holdridge) at the Science Center (Dodson & Gentry, 1978). In addition to its characteristic floral morphology, it is distinguished by the presence of a single-seeded, baseball-sized fruit and very large (ca. 30 cm) leaflets.

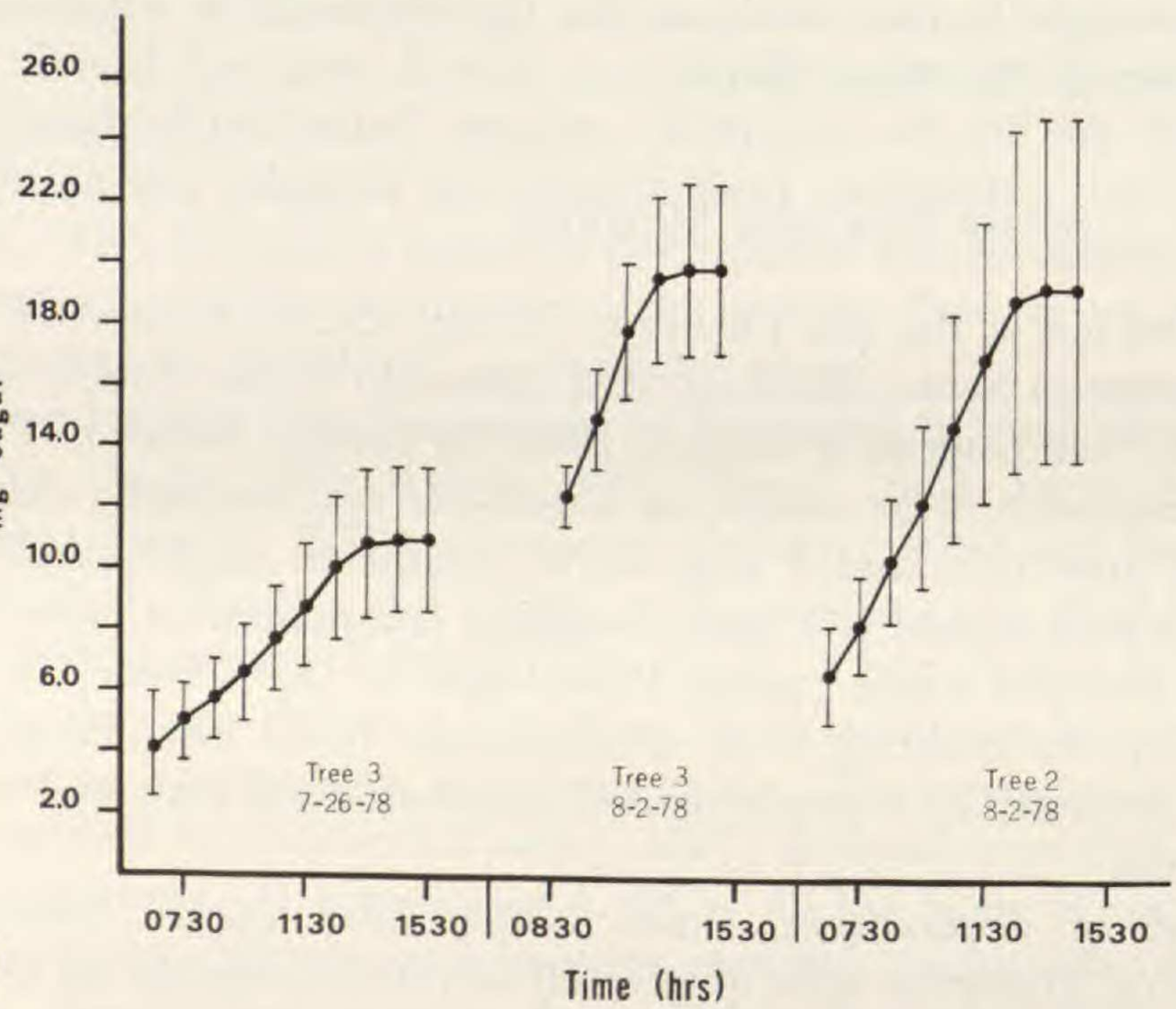
During each period of observation, floral visitors and nectar secretion patterns were recorded for *Erythrina* individuals. Observations totaling 60 hours from 0600 to 1700 EST were made on 4 trees at the Science Center. Three of these were located in forest edge habitats while the fourth was in the forest.

Two different trees on two different days (one week apart) were utilized for continuous nectar sampling (see Figs. 1–3). The same inflorescences on each tree were sampled both times. Data from tree 3 are an average of 10 flowers from two inflorescences, while only 5 flowers from a single inflorescence were measured for tree 2. Continuous nectar sampling consisted of hourly samples beginning at 0630 EST and ending when nectar secretion ceased (which was usually between 1350 and 1550) (Fig. 1). Five individual flowers were numbered on each inflorescence enabling the pattern of secretion for each flower to be followed. Nectar was easily removed repeatedly without injury to the flowers. Except when taking measurements, inflorescences were covered with nylon mesh bags, beginning prior to anthesis, to eliminate nectar removal by visitors during the sampling period.

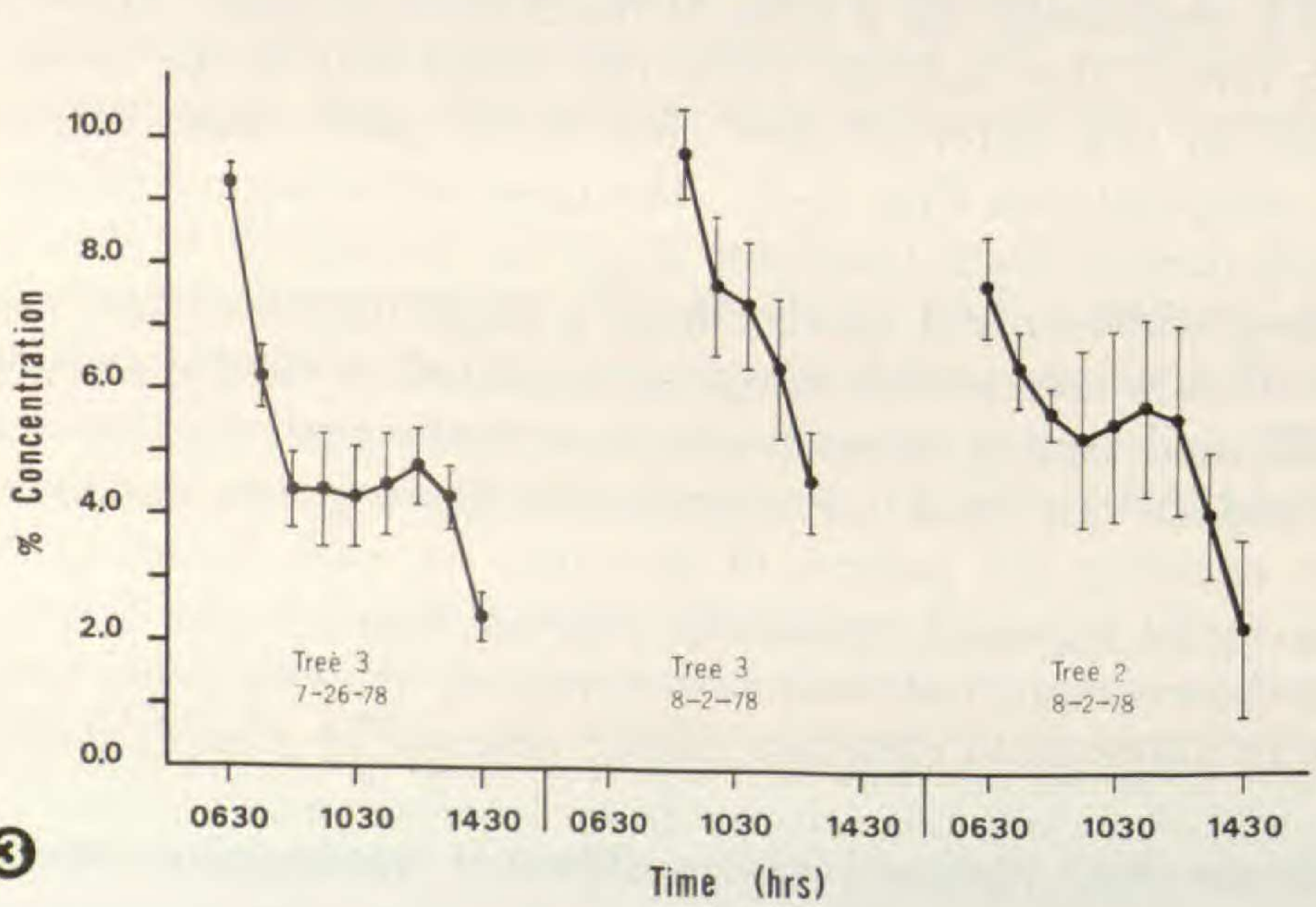
Volume measurements were obtained using calibrated micropipets. Nectar


mg Sugar
4.0
3.2
2.4
1.6
0.8
0.0
Tree 3
7-26-78
Tree 3
8-2-78
Tree 2
8-2-78
0730 1130 1530 0730 1130 1530 0730 1130 1530
Time (hrs)

1


mg sugar
26.0
22.0
18.0
14.0
10.0
6.0
2.0
Tree 3
7-26-78
Tree 3
8-2-78
Tree 2
8-2-78
0730 1130 1530 0830 1530 0730 1130 1530
Time (hrs)

2


% Concentration
10.0
8.0
6.0
4.0
2.0
0.0
Tree 3
7-26-78
Tree 3
8-2-78
Tree 2
8-2-78
0630 1030 1430 0630 1030 1430 0630 1030 1430
Time (hrs)

3

concentration was measured for each sample. This was done by using a pocket refractometer that allowed correction of readings to a standard temperature of 23°C. The refractometer measurements which are weight/total weight percentages were converted to weight/volume percentages so that nectar production could easily be expressed as mg equivalents of sugar (volume × concentration × density of sugar). Nectar analysis was done by Irene Baker (see Baker & Baker, 1976 for methodology).

In order to determine whether continuous nectar removal affected total nectar production and concentration, inflorescences were bagged as before and flowers sampled once at the end of the day. Both volume and concentration of nectar were measured.

Results

Floral Behavior

Erythrina megistophylla had an average of 9.4 inflorescences per tree (S.D. = 2.1, n = 5) during the study period. An inflorescence produced an average of 5.2 ± 1.4 (n = 18) new flowers per day. Based on this and the number of pedicel scars and buds present on sampled inflorescences, an inflorescence might produce flowers from at least 40 to more than 70 days. Since flowering times of the inflorescences are not synchronized, a single tree could potentially flower for several months. Although no information is available on the duration of flowering for this species at Río Palenque, like *E. breviflora* of Mexico (Cruden & Toledo, 1977), it probably flowers for several months.

Fruit set on individuals examined appeared rather low considering the large number of flowers produced. The average number of mature fruits produced was about one per inflorescence; however, this may be an underestimate since some inflorescences had many flower buds (therefore potential fruit) at the time of this study. It is not possible from fruit crop estimates to know how many flowers were actually pollinated since due to the size of mature fruits, it is likely that space and energetic constraints limit total fruit production. Figure 5 shows a clump of ca. seven very young fruits close together. It is doubtful that all of these fruits could mature along such a short portion of the rachis.

Nectar Secretion

The flowers of *Erythrina megistophylla* opened, with nectar present, between 0515 and 0615 EST and lasted for a single day. They were abscised daily whether visited or not. Figure 1 compares the rate of nectar secretion while Fig. 2 presents the average cumulative nectar production of a flower for two different trees. Tree 2 was sampled on two different days. It is apparent from these graphs that nectar production variability between flowers was very high. Clearly, for the

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Figures 1–3. Characteristics of nectar from flowers of *Erythrina megistophylla*.—1. Average rate of sugar production of an individual flower.—2. Average cumulative sugar production of an individual flower.—3. Average nectar concentration (W/V) of an individual flower.

same tree there is a daily component to this variability. Samples from tree 2 and tree 3 on 2 Aug. 1978 were much more similar than comparisons for tree 3 when sampled on different dates. The higher rate and overall production on 2 Aug. 1978 as compared to 26 July 1978 may be explained by a difference in weather conditions. On 2 Aug., it was clear and hot, while on 26 July it was overcast and warm. Both solar radiation and temperature have been shown to influence nectar production (Shuel, 1955; Beutler et al., 1957). The nectar present at anthesis was removed at 0630, thus subsequent hourly measurements represent the amount of nectar secreted during the previous hour.

Figure 3 illustrates how average nectar concentration of a single flower changed during the secretion period. It is evident when comparing this Fig. 3 with Fig. 1 that variability in sugar secretion results primarily from changes in the volume secreted, rather than in the sugar percentage. Tree 3 (2 Aug. 1978) had a slightly different curve since sampling was initiated later in the morning.

Although Raw (1953) found that nectar removal for flowers of *Rubus* species stimulated nectar production, data presented in Tables 1 and 2 provide no evidence that nectar removal stimulates nectar production in *Erythrina megistophylla*. Values indicated by *b* in Table 1 represent averages of the total nectar produced (summed hourly samples) over the secretion period. The other values are averages for flowers in which nectar was removed only at the end of the secretion period.

An inflorescence from tree 3 on 21 July 1978 produced an average of 12.6 ± 2.6 mg sugar per flower for a single end of day sample. On 26 July 1978 and 2 Aug. 1978 it was sampled hourly and produced total averages of 11.5 ± 2.8 and 19.8 ± 2.8 mg sugar, respectively. Thus the daily variability in total nectar secreted prevents one from making any definite conclusions about the effects of nectar removal. A similar situation occurred for tree 2 where variation between totals for end of day nectar sampling was greater than variation between hourly and end of day sampling.

Table 2 presents the average nectar concentration of a flower (weight/volume of solution) for single and multiple samples. These data suggest that the slight differences found in Table 1 are a reflection of changes in concentration of the nectar secreted.

NECTAR ANALYSIS

The nectar of *Erythrina megistophylla* is similar in composition to that of *E. breviflora* (Baker, I., pers. comm.). It is clearly hexose dominant (sucrose/glucose + fructose of less than 0.015) with a sugar concentration of less than 10% (see Table 2) and contains a high concentration of amino acids (ca. 3.9 mg/ml). It also contains a large number (20) of different amino acids, as do *E. breviflora* and *E. fusca* Loureiro, with 18 and 17, respectively (Cruden & Toledo, 1977). Hummingbird *Erythrina* species (*E. coralloides* and *E. herbacea* L.), in contrast, have been found to contain fewer and less concentrated amino acids with greater proportions of sucrose (sucrose/glucose + fructose of 0.47 and 0.668, respectively; Cruden & Toledo, 1977; Baker & Baker, this symposium).

TABLE 1. Average total nectar production (mg sugar) of a flower of *Erythrina megistophylla.*

Tree	21 July 1978	26 July 1978	2 Aug. 1978
1	15.4 ± 1.8[a]	22.8 ± 1.1	—
2	23.3 ± 2.3	28.5 ± 0.5	19.2 ± 5.6[b]
3	12.6 ± 2.6	11.5 ± 2.8[b]	19.8 ± 2.8[b]
5	32.9 ± 5.9	—	—
7	—	36.8 ± 2.5	—

[a] Standard deviation.
[b] Average of total nectar removed (summed from hourly samples).

FLORAL VISITORS

A list of the bird visitors to *Erythrina megistophylla* is presented in Table 3. Since many of these visitors were seen at only one or two of the study trees, an importance value was calculated based on the number of foraging visits and proportion of study trees visited. This gives a better estimate of the importance of any particular visitor at the Río Palenque site as a whole.

A comparison of importance values indicates that the male green honeycreeper was the most important visitor to *Erythrina megistophylla* during the study period (see Fig. 5). It was the only species that regularly visited all of the study trees throughout the observation period. It remains unknown, however, whether or not the male green honeycreeper is a regular visitor over the entire period of flowering and since birds were not marked, it is difficult to accurately assess their degree of individual constancy.

While the bananaquit also had a high importance value, it was not seen regularly at all trees throughout the study. It was seen at three of the study trees, but only on 1 Aug. and 2 Aug. On one occasion a bananaquit was seen flying from *Erythrina megistophylla* to a *Heliconia* species. Snow & Snow (1971) observed bananaquits in Trinidad at 50 different flowering species, indicating they are able to exploit a wide range of flowers for nectar. This suggests that shifts in the pollinator community may take place during the flowering period of the tree. Since it flowers for several months, it is likely that at various times some *Erythrina* visitors may be drawn away by more productive resources.

TABLE 2. Average nectar sugar concentration (% W/V) of a flower of *Erythrina megistophylla.*

Tree	21 July 1978	26 July 1978	2 Aug. 1978
1	6.7 ± 0.4[a]	8.2 ± 0.8	—
2	7.7 ± 0.5	8.3 ± 0.2	6.5 ± 0.3[b]
3	6.3 ± 0.8	6.5 ± 0.3[b]	8.9 ± 0.6[b]
5	8.7 ± 0.4	—	—
7	—	10.1 ± 0.3	—

[a] Standard deviation.
[b] Average concentration (summed from hourly samples).

TABLE 3. Visitation frequency, number of trees visited, and importance of the bird visitors to *Erythrina megistophylla*.

Family and Scientific Name	Common Name	Total Foraging Visits (1)	Proportion of Study Trees Visited (2)	Importance (1 × 2)
Coerebidae	Honeycreepers			
Chlorophanes spiza	Green honeycreeper	58	1.0	58.0
Coerba flaveola	Bananaquit	28	0.75	21.0
Dacnis lineata—male	Black-faced dacnis	2	0.25	0.5
—female		18	0.25	4.5
Thraupidae	Tanagers			
Ramphocelus icteronotus—male	Yellow-rumped tanager	10	0.75	7.5
—female		8	0.75	6.0
Mitrospingus cassinii	Dusky-faced tanager	2	0.50	1.0
Euphonia saturata	Orange-crowned euphonia	5	0.25	1.25
Trochidilidae	Hummingbirds			
Amazila tzactl	Rufous-tailed hummingbird	5	0.25	1.25
Thalurania colombica—male	Crowned woodnymph	41	0.25	10.25
Unidentified individuals	————	23	0.75	17.50
Unidentified	————	2	0.50	1.0

FIGURES 4–5. Birds visiting flowers of *Erythrina megistophylla*.—4. Bananaquit.—5. Male green honeycreeper.

Figures 4 and 5, respectively, show a bananaquit and a male green honeycreeper visiting the flowers of *Erythrina megistophylla.*

Other visitors with fairly high importance values include the male crowned woodnymph, male and female yellow-rumped tanagers and the female black-faced dacnis. Both the crowned woodnymph and the black-faced dacnis, despite being frequent visitors, were each seen at only one of the four study trees. This would suggest that they are probably less effective pollen dispersers than honeycreepers and bananaquits.

The large number of foraging visits by the male crowned woodnymph occurred at a single *Erythrina* individual located in the forest. Many of these visits were in conjunction with territorial defense against other birds including bananaquits, orange-crowned euphonias, and some unidentified hummingbirds. After chasing an intruder away, the crowned woodnymph would visit a few flowers and then return to its perch.

The unidentified hummingbird category had the third highest visitor importance value (Table 3). It is unfortunately impossible to know how many different species this represents. Seventy-four percent of these visits were to the tree visited by the crowned woodnymph. This suggests that frequent hummingbird visitation may occur in some situations; however, additional observations are needed to determine the extent of such visitations.

The primary interest of the orange-crowned euphonias was the fruit of *Lysianthus synanthera* (Schlecht.) Bitt. (Solanaceae), which was within 1–2 m of the *Erythrina* tree. Their visits to *Erythrina* occurred along with fruit eating at *Lysianthus* and may have been purely opportunistic as they did not regularly visit *Erythrina* flowers. It became obvious that these birds were more interested in fruit than nectar, since numerous return visits were made to *Lysianthus* without corresponding visits to *E. megistophylla.* During one visit, a *Euphonia* was quite destructive to flowers by removing stamens as it probed them. This provides additional evidence that euphonias are not important pollinators of *Erythrina megistophylla.*

Figure 6 presents daily visitation patterns of the six most important visitors to *Erythrina megistophylla.* The male green honeycreeper was the most regular visitor throughout the day. All birds, except the crowned woodnymph and the male yellow-rumped tanager visited most frequently between 0800 and 1000 EST. These two birds had visitation peaks at 1330 and 1400 EST, respectively. The earliest visit made by any bird was between 0630 and 0700 EST, while no visits were recorded later than 1430 EST. This pattern corresponds nicely with the nectar secretion pattern. No nectar was secreted in any flowers after 1430 EST (see Fig. 1).

Since two of the *Erythrina* individuals observed were within 50 m of each other, they could be watched simultaneously in order to follow movements of individuals. Of the birds that frequented these two trees, both the green honeycreeper and the yellow-rumped tanagers flew between them regularly. These birds, therefore, are actively searching for *Erythrina* flowers and thus are potentially effective cross-pollinators.

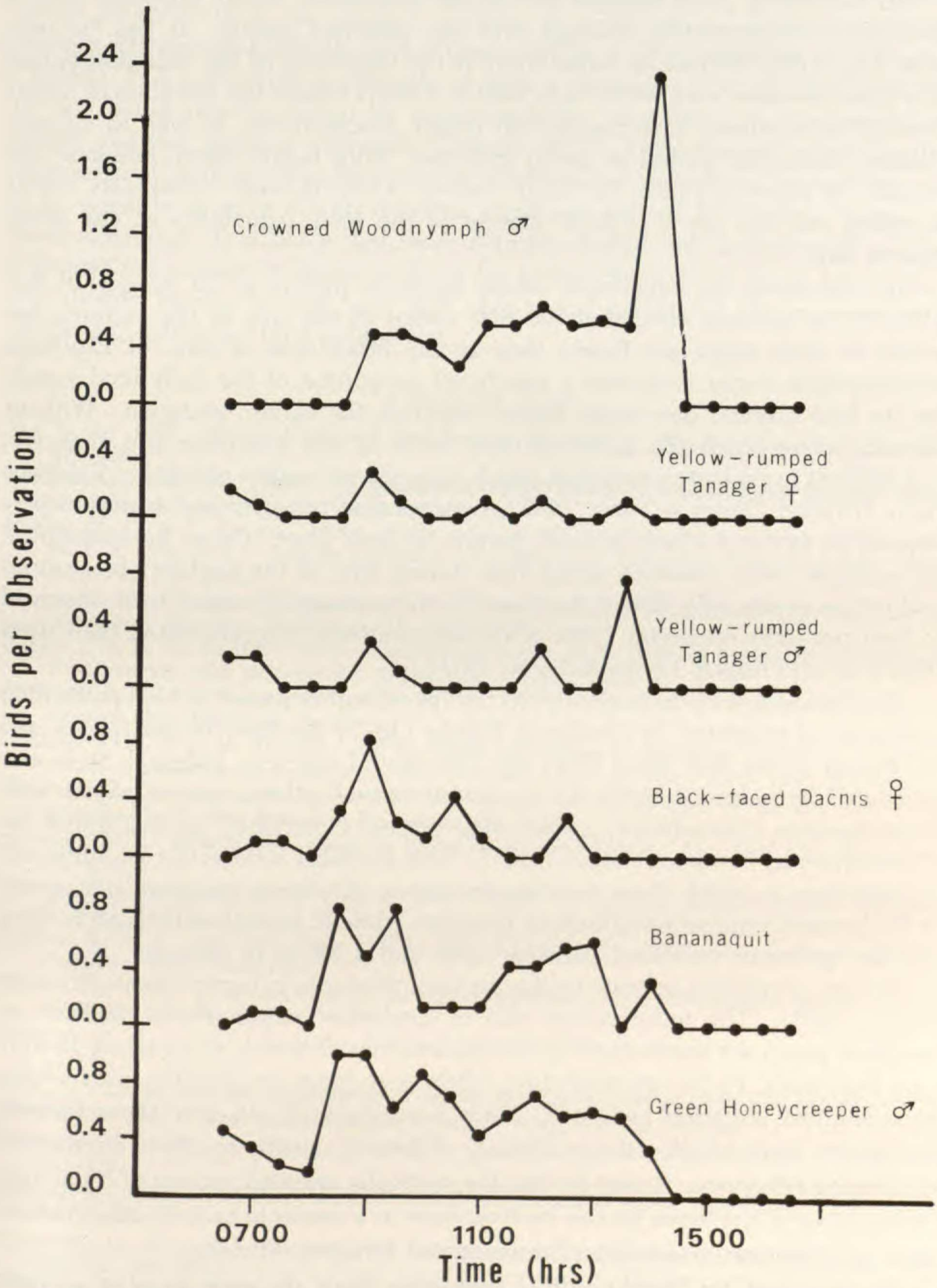

FIGURE 6. Daily visitation patterns of the six most important bird visitors to flowers of *Erythrina megistophylla*.

DISCUSSION

An interesting point brought out by the continuous nectar sampling data is that nectar concentration changes over the secretion period. It can be seen from Fig. 3 that there is an initial drop at the beginning of the secretion period to a fairly constant level which lasts until 1–2 hours before the cessation of nectar flow. It is important to recognize that nectar concentration, as well as volume, changes during the period of nectar secretion. Both factors, then, influence the amount of sugar available to floral visitors. Only through continuous nectar sampling can one get a realistic picture of the food availability at any given time of day.

By examining the cumulative nectar secretion pattern of an average flower (Fig. 2), it becomes clear that the first visitor to the tree in the morning has access to more sugar per flower than at any other time of day. If *Erythrina megistophylla* nectar comprises a significant proportion of the daily food supply for its bird visitors, one might expect selection for earlier visitation. Without knowing more about the habits of these birds at this particular site, however, it is difficult to evaluate constraints which may prevent earlier visitation. Evidence from Trinidad (Snow & Snow, 1971) suggests that tanagers and honeycreepers depend on nectar for only a small portion of their diets. Green honeycreepers, for example, were observed eating fruit during 63% of the feeding observations and fed on nectar only 22% of the time. Even bananaquits, which were observed to feed primarily on nectar (76% of the observations), supplemented their diets with fruit and insects (Snow & Snow, 1971).

Erythrina megistophylla clearly fits the "perching" or passerine bird pollination syndrome as presented by Cruden & Toledo (1977) for New World species and by Faegri & van der Pijl (1979) for Old World species. Although it is also pollinated by passerine birds, the main visitors to *Erythrina megistophylla* were honeycreepers (Coerebidae) rather than orioles (Icteridae) as was found for *E. breviflora* by Cruden & Toledo (1977). This probably reflects the very different communities in which these two species occur. *Erythrina megistophylla* grows in the lowland tropical wet forests of Ecuador, while *E. breviflora* is found in drier oak and pine-oak woodland between 1,200 and 2,300 m in Mexico.

Flower orientation appears to play an important role in bird-pollinated flowers (Stiles, 1978). The inflorescence axis of *Erythrina megistophylla* provides an excellent perch for birds visiting the backwardly directed, short-tubed flowers (see Figs. 4–5). Its flower orientation, while convenient for perching birds, makes hummingbird visitation awkward. Since hummingbirds do visit these flowers, it is hard to know whether the positioning of flowers actually results in a reduction of foraging efficiency. It may be that the vertically oriented raceme of hummingbird-pollinated *Erythrina* species evolved more as a means to exclude other visitors than as a response to maximize hummingbird foraging efficiency.

As suggested by Toledo (1977), passerine birds do seem to play a larger role in the pollination of New World plant species than previously suspected. Passerine flower visitors that may be legitimate pollinators have been reported by Alvarez del Toro (1963), Johow (1898), Leck (1974), Raven (1974), Schemske

(1975), Toledo (1975), and Cruden & Toledo (1977), in addition to Feinsinger et al., Morton, and Toledo & Hernández, all this symposium. In many instances where passerine birds are common visitors, it is difficult to evaluate their pollination efficacy (Baker et al., 1971; Toledo, 1977). *Ceiba pentandra* (L.) Gaertn. (Toledo, 1977) provides an example of such a situation. It is adapted primarily to bats but is heavily visited by passerine birds, in addition to hummingbirds, insects and four types of mammals (Toledo, 1977). Only through more detailed experimental analyses of pollen transfer effectiveness and stigma receptivity will it be possible to unravel the selective pressures exerted by various visitors in these situations. It is likely that more detailed studies will undoubtedly ascribe a greater importance to passerine birds for pollen dispersal in plants which they are already known to visit and will also reveal additional plants specifically adapted to passerine bird pollination.

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